Landscape and Paleoclimatic influences on the genetic population structure of four forest-dependent passerines in the Eastern Cape of South Africa

by

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Declaration

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This dissertation includes one original paper published in a peer-reviewed journal with me as lead author, and one articles submitted and under peer-review. The development and writing of these published and unpublished papers were the principal responsibility of myself.

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Abstract

Anthropogenic activity has placed increasing pressure on the restricted, fragmented forest biome of South Africa. Recent assessments of forest-dependent avifauna strongly indicate the vulnerability of this taxon to deforestation, and ongoing forest exploitation. Half of the forest-dependent bird species in South Africa have reportedly experienced range declines over the past quarter century, most notably within forests of the Eastern Cape province that are incorporated in the Maputaland-Pondoland-Albany Biodiversity Hotspot. These apparent declines have motivated a need to understand the population dynamics, and forest connectivity patterns of forest-dependent avifauna within the country, to better inform conservation efforts seeking to preserve the genetic integrity of these vulnerable bird species.

This study investigated the population genetic structures of four range-declining forest-dependent Oscine passerines across the Eastern Cape and southern KwaZulu-Natal provinces of South Africa: *Batis capensis* (range decline: 1.30%), *Cossypha dichroa* (range decline: 19.53%), *Phylloscopus ruficapilla* (range decline 20.69%), and *Pogonocichla stellata* (range decline 23.02%). These four bird species are small-bodied (<50g) insectivores, that preferentially inhabit the temperate Afromontane forests, and represent a globally important functional group vulnerable to forest fragmentation.

The landscape genetics study conducted on these four species revealed that reported range declines did not correspond closely to the genetic responses of these bird species to anthropogenic activity. *Batis capensis* showed substantial geneflow disruption, and declining effective populations, whereas *P. ruficapilla* and *P. stellata* populations appeared comparatively stable, although *P. stellata* did exhibit geneflow disruption. Only the South African endemic *C. dichroa* displayed simultaneous decline in distribution and effective population size, alongside geneflow disruptions, highlighting a vulnerability to forest loss and degradation. Landscape resistance modelling revealed the importance of both forest and coastal/mesic thicket for maintaining geneflow within these species.

A phylogeographic study investigated the regional species-climate relationships of *B. capensis*, *P. ruficapilla* and *P. stellata*. The effective populations of these species were found not to have been constrained during the last glacial maximum – a climate event speculated to have resulted in drastically restricted forest distributions across South Africa. Furthermore, lowland scarp forests were affirmed as climate refugia for *B. capensis* and *P. stellata*, while the Afromontane forests of the Amatole Mountains and central Transkei appear to have harboured regional source populations of *P. ruficapilla*.

Finally, comprehensive mist-netting of regional forests during sampling collection for the genetic studies afforded an opportunity to compare the effectiveness of point counts and mist-netting survey techniques at representing aspects of regional forest bird community structure. These comparisons found that point counts alone were sufficient to reliably assess these bird communities, with mist-netting contributing negligibly towards species detection. Combined survey efforts under-represented forest-edge foragers, woodland and grassland habitat generalists (collectively comprising ~63.6% total diversity), large birds, Palaearctic migrants, and carnivores (raptors), highlighting the potential shortcomings of these survey techniques in determining bird community composition.

Overall, this study provided novel insights into forest connectivity; and past forest dynamics of forest-dependent insectivorous passerines within previously poorly investigated forests of the southern Maputaland-Pondoland-Albany Biodiversity Hotspot, and provides recommendations for future field surveys of these forests.

Opsomming

Antropogeniese aktiwiteite plaas toenemende druk op die gefragmenteerde woudbioom van Suid-Afrika. Onlangse studies van voël spesies wat afhanklik is van die woudbioom, dui sterk op die negatiewe gevolge van ontbossing en die gevare daarvan op hierdie soort voëls. Verskeie waarnemings dui aan dat die getalle van meer as die helfte van die woudafhanklike voël spesies oor die afgelope kwart eeu gedaal het, veral in die woude in die Oos-Kaap Provinsie, en spesifiek in die Maputaland-Pondoland-Albany distrik. Hierdie afname is ŉ groot motiveerder vir rehabilitasie programme as deel van bewaringpogings binne woude om sodoende die bevolkingsgetalle van verskeie voël spesies te laat groei.

Hierdie studie fokus spesifiek op die bevolkingsgenetika van vier woudafhanklike voël spesies wat dalings in hulle getalle vertoon en wat voorkom in die Oos-Kaap- en suidelike dele van die KwaZulu-Natal Provinsies: *Batis Capensis* (streeksafname: 1.30%), *Cossypha dichroa* (streeksafname: 19.53%), *Phylloscopus ruficapilla* (streeksafname: 20.69%), en *Pogonocichla stellata* (streeksafname: 23.02%). Hierdie vier voëlspesies is klein insekvreters (<50 g) en is woonagtig in Afrobergagtige-woude. Al vier voëlspesies bekleë ŉ belangrike rol in woude wat bedreig word deur woudfragmentasie.

Die landskapsgenetika studie wat op die vier voëlspesies gedoen is, het bewys dat die afname van die spesies se gatelle nie in noue vervantskap saamwerk nie en dat dit ook nie ‘n genetiese reaksies op antropogene aktiwiteite is nie. *Batis capensis* het aansienlike geenvloei ontwrigting en afnemende populasies getoon, terwyl die bevolkings van *P. ruficapilla* en *P. stellata* relatief stabiel voorgekom het oor tyd, maar *P. stellata* het wel ontwrigting van geenvloei vertoon oor tyd. Slegs *C. dichroa* het ‘n gelyktydige afname in verspreidingsgebied asook ‘n groeiende bevolkingsgrootte getoon, en tesame met die ontwrigting van geenvloei beklemtoon dit die kwesbaarheid van die woudgebied. Modellering van landskapweerstand het die belangrikheid van beide woud en kus gebiede beklemtoon vir die voortbestaan van hierdie voëlspesies.

Hierdie filogeografiese studie het ook spesifiek gefokus op die verwantskap tussen die vier voëlspesies en plaaslike klimaatsveranderinge. Daar is gevind dat die effektiewe bevolkingsgroote van *B. capensis, C. dichroa*, *P. ruficapilla*, en *P. stellata* gedurende die laaste gletsermaksimum nie ingekrimp het nie – ŉ klimaatsgebeurtenis waar bespiegel word dat die verspreiding van woude in Suid-Afrika drasties vermeerder het. Verder het die studie bewys dat woudgebiede wat teen die escarpement voorkom in die Oos-Kaap- en Kwazulu Natal

Provinsies dien as kerngebied vir *B. capensis* en *P. stellata*, terwyl die Afrobergagtige woude van die Amatole berge en sentraal Transkei dien as plaaslike bronbevolkings vir *P. ruficapilla*.

Ten slotte is omvattende mistnet-werk in streekswoude gedoen tydens veldwerk, wat die geleentheid geskep het om die effektiwiteit van punt-tellings te vergelyk met plaaslike woudvoëlgemeenskapstrukture. Hierdie vergelyking het bevind dat net die punt-tellings voldoende is om voëlspesies te bestudeer met misnet-werk wat kan bydra tot die vastelling van die voël verskeidenheid in woude. Gekombineerde data insameling het aangetoon dat woudkruitvoerders, asook voëls wat in die bosveld- en grasveld kan voorkom (~63.6% totale diversiteit), groot voëls, palaearktiese migrante en roofvoëls nie algemeen verteenwoordig word in die opnames nie, wat die potensiële tekortkominge van hierdie opnametegnieke beklemtoon.

Oor die algemeen het hierdie studie nuwe insigte gelewer oor verbindinge tussen woude asook die dinamika van woude en die invloed hierop op woudafhanklike voëls in woude wat voorheen swak ondersoek is in die suidelike Maputoland-Pondoland-Albany distrikte. In die studie word daar dan aanbevelings gegee vir toekomstige veldopnames in hierdie gebiede.

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Chapter 2

Mulvaney, J. M., & Cherry, M. I. (2020). The effectiveness of point counts and mist-netting in surveying Afrotemperate forest bird community structure in South Africa. *Emu-Austral Ornithology*, 120(2), 103-113. DOI: 10.1080/01584197.2020.1726186

Chapter 3

Mulvaney, J. M., Matthee, C. A., and Cherry, M. I., (in review). Species-landscape interactions drive divergent population trajectories in four forest-dependent bird species following anthropogenic habitat transformation of fragmented Afrotemperate forests in South Africa. *Evolutionary Applications*

Chapter 4

The Chapter 4 manuscript has been written with the intention of submitting to *Journal of Biogeography*.

Conference presentations of the PhD work

Mulvaney, J. M., Matthee, C. A., and Cherry, M. I. (2019). Gene flow of three forest-dependent passerines in the Eastern Cape. Oral presentation at the 39th *Zoological Society of southern Africa National Congress*, Skukuza, South Africa.

Mulvaney, J. M., & Cherry, M. I. (2018). Bird species detection efficacy of point counts and mist-netting in Afrotemperate forests. Oral presentation at 4th Biodiversity Information Management Forum (BIMF)–Foundational Biodiversity Information Programme (FBIP) Forum, Cape St Francis, South Africa.

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Chapter 1: General introduction

1.1 The forest biome of South Africa: an overview

Indigenous forests in South Africa are evergreen tree-dominated communities with multi-strata vegetation structure, and which form a continuous, closed canopy of ≥75% cover (Mucina, 2018; Mucina & Geldenhuys, 2006; von Maltitz et al., 2003). The forest biome is the smallest of the terrestrial biomes in South Africa, with core forest habitats, where canopy height exceeds exceeding 6 m, collectively represents 0.36% (~5040 km^2) of national land surface area (Dayaram et al., 2019; Thompson, 2019). This is bolstered to 0.56% (~7100 km^2) when including lower canopy (2.5-6 m) secondary forest, and forest-adjacent/transitional thicket (Low & Rebelo, 1996; Mucina & Geldenhuys, 2006). Most indigenous forests are small habitat fragments <10 ha, with few tracts >250 ha, and form an archipelago of scattered islands amidst the broader grassland, savanna, Albany thicket, and fynbos biomes. These forest habitats are confined to mesic, or sheltered areas of the country which receive ≥725 mm annual summer rainfall (eastern South Africa), or ≥525 mm annual winter rainfall (southwest South Africa) (Mucina, 2018; von Maltitz et al., 2003).

Despite the limited extent of this biome, forests support disproportionately high biodiversity, boasting the highest plant species density among the South African biomes – 0.38 plant species/km^2 in forest, compared to 0.11 plant species/km^2 in fynbos (Berliner, 2009). In terms of faunal diversity, forests contain high invertebrate endemism (Berliner, 2009; van Aarde et al., 2014; Wassenaar & Dippenaar-Schoeman, 2006), 14% of terrestrial birds and mammals (Geldenhuys & Macdevette, 1989), and >20% frog species (Measey, 2011). Updated species inventories may yield taxonomic diversity within this biome than previously estimated. Twenty-four floristic forest ecotypes are recognised in South Africa (Mucina, 2018; von Maltitz et al., 2003) – shaped by regional climatic, topographic, and ecological gradients – and these ecotypes ultimately represent the southernmost extents of two globally important Afrotropical forest sub-biomes: Afromontane forests, and Indian Ocean coastal belt forests (Lawes et al., 2007a; Mucina & Geldenhuys, 2006; von Maltitz et al., 2003).

South African Afromontane forests are discontinuously present on south-facing aspects of mountain slopes of the eastern and southern escarpments, and are generally restricted to higher elevations (600-1800m) further north, but become established near sea-level along the south coast of the country (Mucina, 2018; Mucina & Geldenhuys, 2006; von Maltitz et al., 2003). Indian Ocean coastal belt forests predominately occur as part of the Tongaland-Pondoland-

Albany Forest Mosaic along the lowland regions of east coast, attenuating abruptly after 30°S, but extending towards the south coast (34°S) (Mucina et al., 2006; Mucina, 2018; von Maltitz et al., 2003).

1.2 Biogeography of South African forests

The South African forest biome is unique among Afrotropical forest ecosystems in being almost entirely within the subtropics, and is generally regarded as comprising the remnants of an ancient pan-African forest that existed during the Palaeocene and Eocene (~40 mya) until the late Miocene when steeper latitudinal climate gradients were established, alongside tectonic upheaval of the East African Rift Valley, which induced widespread aridification across the continent 10-8.4 mya (Bryja et al., 2017; Dupont et al., 2013; Linder, 2003, 2014; Maslin et al., 2014; Mittermeier et al., 2004; Pound et al., 2012). Afromontane forests, today comprising a disparate complex of temperate forest habitats isolated to the remote highland of Africa (White, 1981, 1983), have characteristic elements (*Afrocarpus* and *Podocarpus* conifers) which date to the Cretaceous (Migliore et al 2020a). Ancestral Afromontane forests are thought to have existed continuously in East Africa and South Africa prior to the late Miocene climate upheavals (Bryja et al., 2017; Dupont et al., 2013; Neumann & Bamford, 2015; Pound et al., 2012), along windward, sheltered mountain aspects which perennially sequester moisture form Indian Ocean trade winds (Fjeldså et al., 2012). In South Africa, these conditions were afforded by the escarpment mountains created by the breakup of Gondwanaland during the late Jurassic/early Cretaceous (Clark et al, 2011; Neumann & Bamford, 2015; Padayachee & Procheş, 2016), and in East Africa these conditions were provided by volcanic ridge development at the onset of the East African Rift Valley ~25 mya (Ring, 2014).

The Indian Ocean coastal belt forest sub-biome (also known as the Coastal Forests of East Africa, CFEA) (Moll & White, 1978; White, 1983) comprise the tropical Northern and Southern Zanzibar-Inhambane Coastal Forest Mosaics extending along the East African coast from southern Somalia to southern Mozambique (Burgess & Clarke, 2000; Burgess et al., 1998; Burgess et al., 2004; Mittermeier et al., 2004). The subtropical extension of the sub-biome comprises the Tongaland-Pondoland-Albany Forest Mosaic which extends to the south coast of South Africa (Mittermeier et al., 2004; Moll & White, 1978; Mucina et al., 2006; Mucina, 2018). This forest sub-biome is similarly considered a relic of Palaeocene/Eocene-late Miocene pan-African lowland forests, shaped initially by tectonic upheaval of the Oligocene which saw the repeated marine inundation of the east African coast from 44-23 mya (Burgess & Clarke, 2000; Linder, 2017; Perissinotto et al., 2013). Later, these forests were influenced by faulting associated with the progression East African Rift Valley of the late Miocene (Dupont et al., 2013; Linder, 2014, 2017; Maslin et al., 2014). South African Indian Ocean coastal belt forests are understood to be younger than Afromontane forests, with successive infiltrations of this sub-biome thought to have occurred during the late Pleistocene (Huntley et al., 2016; Lawes et al., 2007a).

The biodiversity patterns of forest sub-biomes have been shaped substantially by climate oscillations throughout the Pliocene, Pleistocene, and Holocene (Abiem et al., 2020; Bryja et al., 2017; Gehrke & Linder, 2014; Linder, 2014; Voelker et al., 2010; Wogan et al., 2014b). The climate relationships of these forest biomes are distinct, although both are understood to expand under mesic climate regimes, and contract to sheltered climate refugia under xeric conditions (Ivory et al., 2018; Linder, 2017; Mairal et al., 2017). These palaeoecological dynamics are inform both the disjunct distributions of many Afromontane forest species which typically do not disperse over lowlands habitats (Chala et al., 2017; Dupont et al., 2011; Ivory et al., 2019; Migliore et al., 2020b), and lowland forest species which seldom engage with open habitats (Azeria et al., 2007; Barratt et al., 2018; Burgess et al., 1998). Glacial-interglacial Milankovitch cycles were traditionally thought to drive these fluctuations in forest prevalence, with global glaciations enduring for 100 000 years inducing widespread aridity across Africa, with brief 20000-year interglacial periods affording climatic amelioration which saw the re-emergence of forest habitats (Jolly et al., 1998; Partridge, 1993; Partridge et al., 1999; Prentice et al., 2000). Recently, however, increasing evidence of regional hydroclimatic variability across the continent, which operated of glacial-interglacial cycles suggests palaeoecological forest dynamic were likely more complex (Ivory et al., 2012; Ivory et al., 2018; Lézine et al., 2019; Peterson & Ammann, 2013; Singarayer & Burrough, 2015).

The fragmentation of South African forests is thought to have arisen naturally through Palaeoclimatic climatic oscillations; colder glacial periods, and xeric climates are thought to have more adversely affected mid-elevation Afromontane forests, through displacement and contraction of forest habitats, and homogenisation of their diversity (Eeley et al., 1999; Lawes et al., 2007a). Sub-tropical Indian Ocean coastal belt forests in South Africa, however, are semi-continuous with the tropical Zanzibar-Inhambane Coastal Forest Mosaic that are perennially stabilised by the warm, humid maritime climates afforded by the tropical Somali and Mozambique ocean currents (Burgess et al., 2004; Mittermeier et al., 2004; Simon et al., 2015). So these forests exhibit greater species richness when expanding into the subtropical coastlines of South Africa (Eeley et al., 1999; Lawes et al., 2007a).

Lower-elevation Afromontane forests have integrated with inland Indian Ocean coastal belt forests forming a transitional array of forest ecotypes known as scarp forests. Scarp forests support species compositions of both forest sub-biomes, but are considered primarily to be a variant of Afromontane forests which increasingly blend into Indian Ocean coastal belt forests (Mucina, 2018; von Maltitz et al., 2003). Scarp forests occur along sheltered aspects of low-lying steep terrain, where Palaeoclimates have seemingly remained temperate, and humid during the late Pleistocene (Eeley et al., 1999), and so many scarp forests are thought to function as regional climatic refugia for both forest sub-biomes (Busschau et al., 2019; Lawes et al. 2007a; Moir et al., 2020a; Tolley et al., 2018). Additionally, notable minor climate refugia for each distinct forest sub-biome within South Africa include: the Indian Ocean coastal belt forests of the Maputaland lowlands (Huntley et al., 2016; Ribeiro et al., 2014; Stone & Ntetha, 2013), certain Afromontane forests of the Northern Drakensberg and Soutpansberg Mountains of Limpopo (Dalton et al., 2015; Herbert, 2016), Afromontane forests of KwaZulu-Natal midlands (da Silva & Tolley, 2017), Transkei Midlands (Barnes & Daniels, 2019), Amatole Mountains (Hughes et al., 2005; Kushata et al., 2020; Madisha et al., 2018), and the Outeniqua and Tsitsikamma Mountains of the southwestern Cape (Daniels et al., 2017; Kushata et al., 2020; McDonald & Daniels, 2012).

In the southeast Eastern Cape, Albany (subtropical) thicket comprises a variety habitats ranging from dense shrubland (arid thicket) to low contiguous forests of 2.5-6 m high canopies (mesic thicket) (Lloyd et al., 2002; Rutherford et al., 2006). Mesic thicket resembles adjacent Albany forest, an ecotype of IOCB forests (Mucina, 2018; von Maltitz et al., 2003). Albany thicket, including mesic thicket, persisted through Palaeoclimatic shifts (Potts et al., 2013), and may have offered additional refugia for select, more generalised forest-dependent taxa.

1.3 Forest-dependent birds of South Africa

Despite the limited extent, and disjunct configuration of the South African forest biome, an estimated 14% of national terrestrial bird species are recognised as forest-dependent species (Geldenhuys & Macdevette, 1989), which rely of forest ecosystems to ensure long-term population viability, and where the majority of individuals rely upon forests to meet ecological requirements. An inventory of fifty-seven forest-dependent birds has been compiled for South Africa (Cooper et al., 2017; Geldenhuys & Macdevette, 1989), of which nine species are endemic to the country (BirdLife International, 2021; Taylor & Peacock, 2018): brown scrub-robin *Erythropygia signata*, bush blackcap *Lioptilus nigricapillus*, Cape parrot *Poicephalus robustus*, chorister robin-chat *Cossypha dichroa*, forest buzzard *Buteo trizonatus*, forest canary

Crithagra scotops, Knysna turaco *Tauraco corythaix*, Knysna warbler *Bradypterus sylvaticus*, and Knysna woodpecker *Campethera notata*. An additional five species may be seen as near-endemics to South Africa (Hockey et al., 2005; Sinclair & Ryan, 2010): Cape batis *Batis capensis*, Barratt's warbler *Bradypterus barratti*, olive bush-shrike *Telophorus olivaceus*, olive thrush *Turdus olivaceus*, and Rudd's apalis *Apalis ruddi*

Most South African forest-dependent bird species have broader distributions in tropical Africa, and are thought to have evolved either in the Afromontane forest complexes of the Eastern Afromontane Biodiversity Hotspot (Abiem et al., 2020; Bowie et al., 2006; Burgess et al., 2007; Fjeldså et al., 2012; Fjeldså & Bowie, 2008; Fjeldsa & Lovett, 1997; Levinsky et al., 2013; Mittermeier et al., 2004; Voelker et al., 2010), or in the Northern/Southern Zanzibar-Inhambane Coastal Forest Mosaics of Eastern African Biodiversity Hotspot (Azeria et al., 2007; Burgess et al., 2004; Burgess & Clarke, 2000; Levinsky et al., 2013; Mittermeier et al., 2004)

Climatic and ecological gradients, together with geographic barriers have limited the southward expansion of many East African species into South Africa (Eiserhardt et al., 2013; Kaliba, 2014; Pinkert et al., 2020). It is speculated that the more varied temperate and subtropical palaeoclimates at the southern limits of the continent imposed repeated extinction filters on forest-dependent species which evolved in comparatively stable equatorial climates (Lawes et al., 2007a). The hypothesised colonisation pathways, proposed by Lawes et al. (2007), suggest that both Afromontane and Indian Ocean coastal belt forest bird species colonised South Africa during the late Pleistocene during climatic ameliorations when transient Afromontane-Indian Ocean coastal belt forest integrations expanded into the subtropical lowlands of KwaZulu-Natal (Castañeda et al., 2016; Finch & Hill, 2008; Mazus, 2000; Scott et al., 2012). Scarp forests across the lowlands of KwaZulu-Natal and the Eastern Cape served as regional refugia, with subsequent northwest expansions of forest birds into the northern Drakensburg and Soutpansberg Mountains, and southwest expansions to the south coast and Cape Peninsula (Lawes et al., 2007a) during climatic ameliorations.

1.4 Anthropogenic threats to South African forest-dependent birds

Recent historic and contemporary anthropogenic activity has impacted the forest ecology of South Africa significantly. Anthropogenic fire-management of forests is detectable 5 kya, and forest clearance increased noticeably following the arrival Iron Age farmer ~1.2 kya (Coetzer et al., 2020; Fitchett et al., 2016; Neumann et al., 2010; Neumann et al., 2008; Russell & Ward, 2016). Large-scale deforestation, and forest degradation commenced only during the Colonial period <350 years ago, particularly when commercial logging industries peaked from1860-1940 (King, 1938, 1941; Lawes et al., 2007b; McCracken, 2004; Mucina & Geldenhuys, 2006; Olivier et al., 2013). Commercial selective logging largely subsided after 1940 – except in two strictly managed forests in Knysna, Western Cape, and Stutterheim, Eastern Cape (Downs, 2005; Wilson et al., 2017). The long-term consequences of this exploitation have been forest loss and reduced forest structural complexity (Berliner, 2009; Lawes et al., 2004; Lawes et al., 2007b; Mangwale et al., 2017; Olivier et al., 2013). Subsistence harvesting of forest resources is ongoing, and in certain instances may be unsustainable, exacerbating forest degradation (Cocks & Wiersum, 2003; Lawes et al., 2004; Mangwale et al., 2017; Njwaxu & Shackleton, 2019; Shackleton & Shackleton, 2004).

Historic forest clearance was also driven by an increased need for agricultural land and human habitation (Cooper, 2015; Russell & Ward, 2016). Approximately 50% of indigenous forest is assumed have been removed or degraded (Berliner, 2009; Eeley et al., 2001; Macdonald, 1989), but the unknown extent of pre-colonial forests precludes exact estimates of national forest loss (Berliner, 2009). Estimated loss of Indian Ocean coastal belt, and adjacent scarp forests ranges between 60% (Berliner, 2009) to 82% (Olivier et al., 2013), with Afromontane forests remaining more intact, with 15-20% estimated to have been lost (Berliner, 2009; Lawes et al., 2004). Although Afrotemperate forest coverage is less diminished, the number of small forest patches (>0.5ha) has declined, decreasing spatial proximity between remnant forest fragments (Berliner, 2009; Kotze & Lawes, 2007; Lawes et al., 2004; Lawes et al., 2007b). The matrix transformation for plantation, agriculture, and human habitation has further disrupted forest community compositions, and interfered with forest connectivity dynamics (Bailey et al., 2016; Botzat et al., 2015; Eberle et al., 2017; Ehlers-Smith et al., 2017, 2018, 2020; Freeman et al., 2018; Reynolds et al., 2018; Zungu et al., 2020).

Globally, the impact of anthropogenic forest fragmentation on forest-dependent avifaunal assemblages generally manifests as declines in the diversity of forest specialist species, alongside increased homogenization of functional diversity (Bregman et al., 2014; Coster et al., 2015; Devictor et al., 2008; LaManna & Martin, 2017; Newbold et al., 2013, 2014; Robinson & Sherry, 2012; Wilson et al., 2016). Long-term consequences of selective logging and deforestation have included uniform species loss in tropical forests (Haddad et al., 2015; LaManna & Martin, 2017; Newbold et al., 2013), while in temperate forests, such activity generally results in the replacement of forest specialists with habitat generalists (Huhta &

Jokimäki, 2015; LaManna & Martin, 2017). Sensitivity to habitat fragmentation varies between avian feeding guilds (Bregman et al., 2014; Korfanta et al., 2012; Newbold et al., 2013; Olivier & van Aarde, 2017; Robinson & Sherry, 2012), with the most vulnerable forest specialist guilds being large-bodied frugivores (Berens et al., 2014; Bregman et al., 2014; Kirika, Farwig, & Böhning-Gaese, 2008), and small-bodied insectivores (Bregman et al., 2014; Cosgrove, 2017; Korfanta et al., 2012; Peter et al., 2015; Sekercioglu, 2012).

Population declines and species loss of forest-dependent birds raises conservation concerns as birds contribute to many fundamental aspects of forest regeneration, and maintenance of forest integrity (Barros et al., 2019; Devictor et al., 2008; Kirika et al., 2008; Mueller et al., 2014; Sekercioglu, 2012). Frugivores, and nectarivores facilitate genetic dispersal of forest plants within forests through seed distribution and pollination, respectively (Berens et al., 2014; Dixon, 2009; Lehouck et al., 2009). Frugivores may additionally play a major role in inter-forest seed dispersal (Holbrook et al., 2002; Lehouck et al., 2009; Lenz et al., 2015; Mokotjomela et al., 2016; Mueller et al., 2014), although this is not always the case (Mokotjomela et al., 2016; Wilson & Downs, 2012). Insectivores and carnivores (raptors), in turn, partially mitigate the impeding effects herbivorous insects and small mammals may have on plant regeneration (Maas et al., 2016; Rosin & Poulsen, 2016; Sekercioglu, 2012). Despite having persisted through palaeoclimatic shifts, and being naturally predisposed to forest fragmentation, South African forest-dependent birds have experienced population and range declines in the advent of anthropogenic landscape transformation (Coetzer et al., 2020; Cooper et al., 2017, 2020; Ehlers-Smith et al., 2018; Kalle et al., 2018; Maseko et al., 2017; Olivier et al., 2013; Olivier & van Aarde, 2017).

Cooper et al. (2017) provided evidence suggesting that from an inventory of fifty-seven forest-dependent species, twenty-eight species had experienced range declines across South Africa from 1992-2014, most notably in the Eastern Cape. Insectivores and raptors were shown to have experienced the largest range declines, followed by frugivores. Deforestation between 1990-2014 was limited, and this was not strongly associated with observed declines of any avian functional group. This suggests that historic deforestation may have been the driver of these declines, which may be manifestations of extinction debts – severe population disequilibria which manifest generations after environmental disturbance (Botzat et al., 2015; Brooks et al., 1999; Epps & Keyghobadi, 2015; Olivier et al., 2013; Samarasin et al., 2017). These could have resulted from past deforestation of Indian Ocean coastal belt forests and scarp forests, historic selective logging of forest timber, and clearance of small forest patches from the landscape; subsistence harvesting may have contributed towards these declines (Leaver et al., 2020a, 2020b; Leaver et al., 2019a, 2019b). Overall reduction of plantation cover during the study period explained some species loss, which was mitigated in areas where plantations increased (Cooper et al., 2017). Plantations have to a large extent replaced mesic grassland/savannah matrix habitats adjacent to forests, as well as transitional forest ecotones (Lawes et al., 2004; Malan, 2014; Mucina & Geldenhuys, 2006). This has been detrimental for grassland/savanna avifauna (Allan et al., 1997), and is suspected to have impact South African forest ecosystems negatively (Bremer & Farley, 2010; Terraube et al., 2016). At the local scale, plantations and farmlands altered forest community compositions in favour of habitat generalists, and dispersive species (Aben et al., 2012; Ehlers-Smith et al., 2018a, 2019b; Freeman et al., 2018; Neuschulz et al., 2013; Wethered & Lawes, 2003, 2005). Regional influences of landscape matrix transformations on forest birds dynamics in South Africa are largely unknown, and may reveal emergent patterns and processes not apparent at local scales (Boulinier et al., 2019; Olivier & Van Aarde, 2014; Ricklefs, 2015). Afforestation through carbon sequestration in degraded thickets and savanna has been recently documented in certain part of South Africa (Buitenwerf et al., 2012; Mangwale et al., 2017; Stickler & Shackleton, 2014). These newly emergent thicket/forest communities are unstructured, and likely contain floral compositions not yet conducive to forest birds (Cooper et al., 2017; Martinuzzi et al., 2009), although its establishment potentially may better facilitate dispersal of forest-dependent taxa (Ehlers-Smith et al., 2017, 2019a).

Birds are regarded as cost-effective, and reliable indicators of forest ecological health, and avifaunal assessments frequently serve to represent the population viability of more obscure taxa (Chowfin & Leslie, 2021; Gao et al., 2015; Gregory et al., 2003; Schulze et al., 2004; Sutherland et al.,2007). The state of decline of South African forest birds may vicariously signal the increasing precarity of sessile, or sedentary forest-dependent taxa, which may be even more adversely affected by anthropogenic landscape change and forest exploitations. Better understanding of regional forest bird population dynamics therefore may inform conservation efforts for wide array of forest-dependent species, as well as to help determine optimal strategies for mitigating the looming effects of anthropogenic climate change (Colyn et al., 2020; Erasmus et al., 2002; Los et al., 2019; Neate-Clegg et al.,2020).

1.5 Knowledge gaps and research motivation

This research project was motivated by the urgent need to better understand the population dynamics of South Africa’s forest-dependent bird species, made apparent by the reported range declines of nearly half of the national forest-dependent bird species (Cooper et al., 2017). It is hoped that the findings of this research will contribute towards informing conservation efforts focussed on preserving national forest resources. These forest-dependent birds inhabit a naturally fragmented habitat system, and it is unknown whether the behaviour of the spatially discrete populations comprising each bird species conforms better to Island Biogeography Theory (IBT, Wilson & MacArthur, 1967), or Metapopulation Theory (MPT, Levins, 1969). IBT proposes that population parameters of size, and internal complexity and diversity are proportional to, and dependent upon, the surface area and configuration of primary habitats, alongside the distance between fragments. IBT further regards the extralimital matrix habitats of the regional landscape as largely impermeable to interpopulation dispersal, especially of sessile and sedentary taxa (Diamond, 1975; Diamond et al., 1976; Hubbell, 1997; Kadmon & Allouche, 2007). According to this theory, individual forest populations would function predominately as insular units, and would need to be managed as such to preserve the intrinsic genetic complexity and adaptations to local environmental conditions, and to prevent the inadvertent spread of maladaptive alleles and disease, which could inadvertently undermine population viability through diminished local environmental adaptation (Edwards et al., 2016; Fenderson v2020; Richardson et al.,2016). Population interactions, and long-term viability would be dependent upon structural connectivity - the extent and configuration of primary forest habitats – and forest populations would be sensitive primarily to deforestation and forest degradation (Hubbell, 1997; Kadmon & Allouche, 2007). Conversely, MPT assumes spatially discrete populations to be functionally continuous, with functional connectivity operating independently from structural connectivity of primary habitats (Baguette et al., 2017; Hanski & Ovaskainen, 2003; Levins, 1969). This theory better accommodates scenarios where population size and diversity are disproportionate to the physical constraints of the environment (Ewers & Didham, 2006; Kramer et al., 2008; Lowe, et al., 2015).

Metapopulation connectivity can be maintained across forest fragments through high vagility, as seen in many large-bodied forest-dependent frugivores and carnivores (raptors) at the regional scale (Chibesa & Downs, 2017; Chibesa et al., 2017; Coetzer et al., 2020; Kalle et al., 2018; Lenz et al., 2015; McPherson et al., 2019); and many other forest-dependent bird species at the local scale (Neuschulz et al., 2013). Additionally, species may engage with elements of the landscape matrix to augment structural connectivity (Ehlers-Smith et al., 2017, 2019; Zungu et al., 2020), especially during dispersal (Keeley et al., 2017). Many South African forest-dependent birds are altitudinal/local migrants (Craig & Hulley, 2019; Ehlers-Smith et al., 2018; Johnson & Maclean, 1994; Oatley, 2017), and the reliance of these species on non-forest habitats during migrations has been anecdotally observed (Johnson & Maclean, 1994; Oatley, 2017), but remains to be adequately investigated. Transformation of landscape matrix habitats which facilitate dispersal of forest-dependent taxa may isolate the species populations to unsustainably small habitats (Alexander et al., 2019; Ehlers-Smith et al., 2019; Freeman et al., 2018; Zungu et al., 2020), and leave these population vulnerable to inbreeding, genetic drift, and local extinction (Cosset et al., 2019; Keyghobadi, 2007; Richardson et al., 2016).

In addition to preserving areas of high biodiversity, regional forest conservation should identify and prioritise the protection of forest palaeoclimatic refugia (Eeley et al., 2001; Pinkert et al., 2020). These are necessary for the long-term viability of multiple forest species, and likely support source populations that serve to colonise newly established forest habitats, and recolonise forests which declining populations, or those which experienced local extinctions. Although South African forests, especially Afromontane forests, are generally considered to be relicts of bygone pan-African forests (Lawes et al., 2007a; Mittermeier et al., 2004). These higher latitude forests were more adversely affected by palaeoclimatic oscillations than the forests of tropical Africa, but nonetheless harbour considerable endemism (Castañeda et al., 2016; Huntley et al., 2016; Levinsky et al., 2013; Mittermeier et al., 2004; Perera et al., 2018; Pinkert et al., 2020; Ribeiro et al., 2014). A large proportion of South African forests fall within the Maputaland-Pondoland-Albany Biodiversity Hotspot, a region which fosters high levels of endemicity (Mittermeier et al., 2004). The last glacial maximum (LGM, 21 kya) was previously assumed to have induced cold, xeric conditions across South Africa, severely diminishing regional forests and eradicating many forest-dependent species (Eeley et al., 1999; Lawes et al., 2007a; Partridge, 1993; Partridge et al., 1999; Potts et al., 2013). Some of these species are thought to have recolonised the region during forest expansions of the Holocene Interglacial (Eeley et al., 1999; Lawes, 1990; Lawes et al., 2007a; Miller et al., 2019, 2020). However, palaeoecological records, and refined palaeoclimate models increasingly suggest increased precipitation over South Africa during the LGM (Engelbrecht et al., 2019; Simon et al., 2015), challenging the long-standing perspectives regarding the refugial potential of South African forests.

To better understand the nature of forest connectivity among South African forest-dependent birds, we conducted multi-species landscape genetic and phylogeographic studies using microsatellites and mitochondrial control region DNA sequence data generated for selected forest-dependent Oscine passerines (see Section 1.7). Microsatellites are highly informative for assessing population structure (Bhargava & Fuentes, 2010; Putman & Carbone, 2014), and are popular genetic makers in forest fragmentation studies (Radespiel & Bruford, 2014). Mitochondrial control region is a particularly hypervariable non-genic sequence considered appropriate for assessing shallow population structure, recent evolutionary divergences anticipated for regional forest-dependent bird populations in response to palaeoclimatic shifts (Barker et al., 2012; Randi et al., 2001; Zink & Barrowclough, 2008).

Finally, the fieldwork component of this study for sample collection of genetic materials afforded comprehensive mist-netting of all forest sites included in this study (see Section 1.6). Total mist-netting efforts amounted to ~30 000 mist-net hours (1 net-hour = 12 m net open/hr), and detected 2029 individuals of 82 bird species. This afforded an unexpected opportunity to compare the effectiveness of mist-netting and point counts – which I conducted alongside mist-netting – at surveying different aspects of the bird community structures within these forests. Point count (Buckland, 2006; Ralph et al., 1995) and mist-netting (Karr, 1981) are two field surveys techniques that are frequently employed in avifaunal assessments of Afromontane and Indian Ocean Coastal forest bird community health (Dulle et al., 2016; Ehlers-Smith et al., 2017, 2018a, 2018b; Engelen et al., 2017; Freeman et al., 2018; Korfanta et al., 2012; Leaver et al., 2019a, 2019b, 2020; Mulwa et al., 2013; Newmark, 2009; Olivier et al., 2013; Olivier & Van Aarde, 2014; Romdal & Rahbek, 2009; Ulrich et al., 2018; Uwimbabazi et al., 2017; Van Rensburg et al., 2000), and so the identification of detection biases within these methods can inform future implementation of these field survey techniques to more accurately and reliably represent the bird communities within these two forest sub-biomes.

1.6 Study area

The study area extends across eleven forest sites, incorporating six forest floristic ecotypes (von Maltitz et al., 2003), and falls within the Maputaland-Pondoland-Albany Biodiversity Hotspot (Mittermeier et al., 2004) (Figure 1.1). The study area is centred across much of the Eastern Cape, which supports 46% of South African forests (Berliner, 2005), and which is province where observed forest-dependent bird range declines were most pronounced (Cooper et al., 2017). However, accessible forest sites present in southern KwaZulu-Natal have been included in this study to boost representation of forest ecotypes present in both provinces, but which are less accessible in the Eastern Cape. The general forest site characteristics are presented in Table 1.1.

Table 1.1 Attributes of forest sites included in this study, showing forest ecotype (von Maltitz et al., 2003), forest locality, approximate size (ha), and altitudinal range (m.a.sl.). Respective sub-biomes are included for each forest site: A = Afromontane, S = scarp, and I = IOCB

Forest	Forest ecotype	Locality	Size (ha)	Altitude (m a.s.l.)
Ngele	Eastern mistbelt (A)	30.526°S 29.679°E	755	1250 - 1550
Oribi Gorge	Pondoland scarp (S)	30.718°S 30.271°E	1917	120 - 680
Mbotyi	Pondoland scarp (S)	31.429°S 29.737°E	2380	35 - 335
Gomo	Transkei mistbelt (A)	31.014°S 29.348°E	1170	920 - 1460
Nqadu	Transkei mistbelt (A)	31.427°S 28.753°E	935	857 - 1185
Baziya	Transkei mistbelt (A)	31.576°S 28.396°E	1150	800 - 1550
Manubi	Transkei scarp (S)	32.453°S 28.599°E	760	150 - 230
Pirie	Amatole mistbelt (A)	32.726°S 27.282°E	3173	540-1300
Kubusi	Amatole mistbelt (A)	32.608°S 27.285°E	3370	920 - 1300
Fort Fordyce	Amatole mistbelt (A)	32.687°S 26.499°E	1730	630 - 1120
Alexandria	Albany forest (I)	33.720°S 26.389°E	12330	30 - 205
The Island	Albany forest (I)	33.989°S 25.355°E	480	150 - 225

Six forest sites – Ngele, Gomo, Nqadu, Baziya, the Kubusi (Pirie-Isidenge-Kubusi forest complex), and Fort Fordyce – three Afromontane forest ecotypes that are incorporated into the Southern Mistbelt Forest Group (Figure 1.1). Southern Mistbelt Forest Group occurs at mid-elevations from 850-1600m along the KwaZulu-Natal and Eastern Cape Midlands, and Amatole Mountains. These forests possess 15-20m high canopies, dense understoreys with a prominent fern-dominated herbaceous layer, and characteristically experience heavy summer mist (Mucina, 2018; Mucina & Geldenhuys, 2006; von Maltitz et al., 2003). Three forests – Oribi Gorge, Mbotyi, and Manubi – are part of the Scarp Forest Group (Figure 1.1) which occur at mid-low elevations (0-600 m, occasionally 800 m) 140 km inland from southern Mpumalanga to the coast in the Eastern Cape until the Kei River Mouth. These forests have 15-25 m tall canopies, dense understoreys, and sparse herbaceous cover (Mucina, 2018; Mucina & Geldenhuys, 2006; von Maltitz et al., 2003). The final two forests – Alexandria, and The Island – are part of the Southern Coastal Group (Figure 1.1), which are established along the coastal dune systems of the Eastern Cape, and sheltered southern coastlines of the Western

Cape. These are short, dense forests with 5-15 m high canopies, and generally impregnable understoreys, although understoreys may be minimal within seaward forests (Mucina, 2018; Mucina & Geldenhuys, 2006; von Maltitz et al., 2003). Remnant Alexandria forest tracts are protected within the Woody Cape section of Addo Elephant National Park (South African National Parks). The Island and Fort Fordyce forests are managed and protected by the Eastern Cape Parks and Tourism Agency (ECPTA). The remaining forests at state-managed, and fall under the jurisdiction of Department of Environment, Forestry and Fisheries (DEFF). Four forests are incorporated into the Important Bird Area (IBA) conservation programme (Marnewick et al., 2015): Ngele (Kwa-Zulu Mistbelt Forests); Kubusi and Fort Fordyce (Amatole-Katberg Mountain); Alexandria (Woody Cape Section: Addo Elephant National Park). Potential declaration of the Pondoland National Park (Kepe, 2014) may protect the Pondoland and Transkei scarp forests, including Mbotyi.

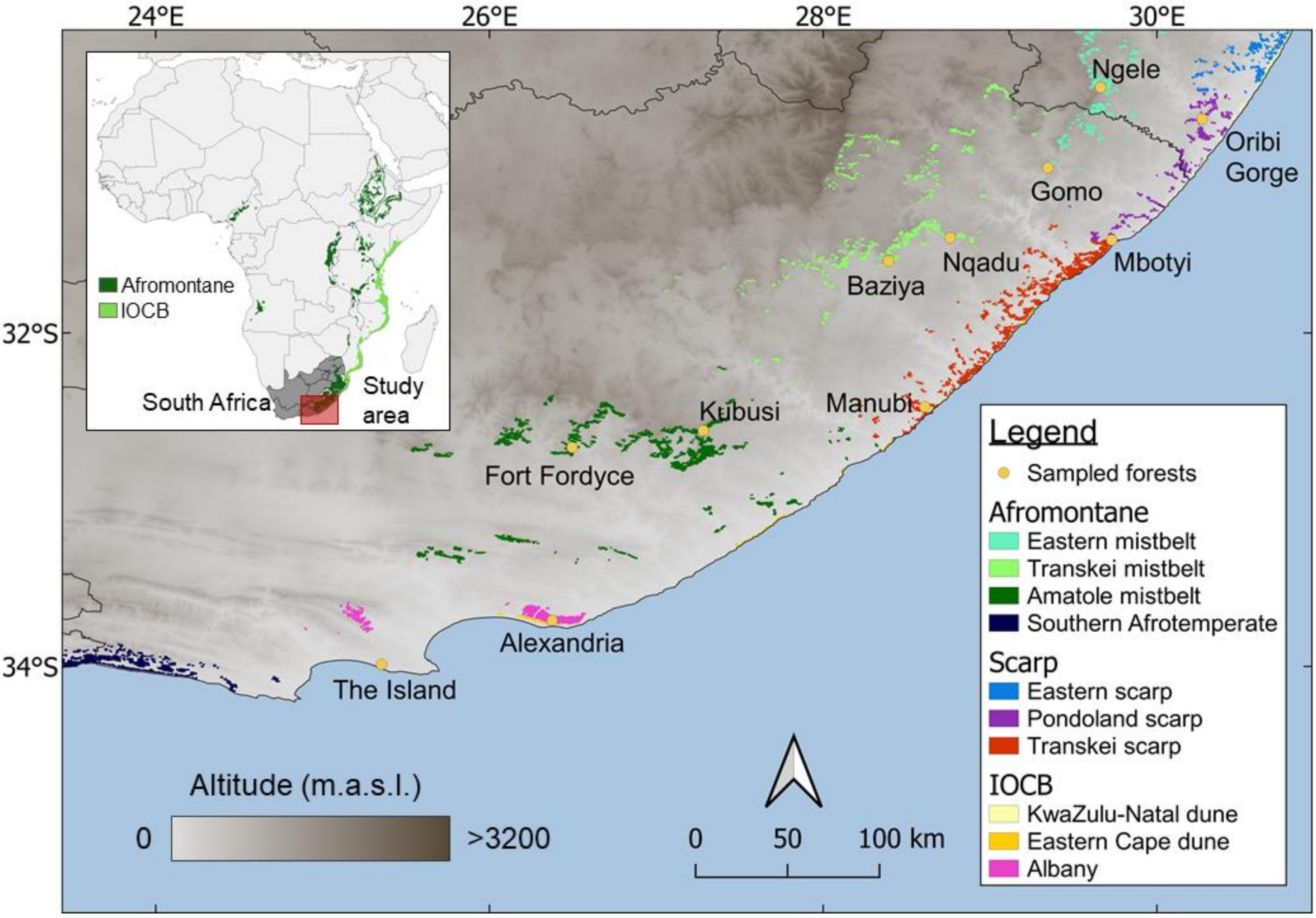


Figure 1.1 Map of study area showing forest sampling sites in the Eastern Cape and southern KwaZulu-Natal provinces of South Africa, with forest patches colour coded according to the respective forest ecotypes (von Maltitz et al., 2003; Mucina, 2018) of Afromontane, scarp, and Indian Ocean coastal belt (IOCB) forest sub-biomes.

1.7 Study species

The population genetic and phylogeographic components of this study included four focal Oscine passerine (songbird) species (Figure 1.2) which have declines in range (Cooper et al., 2017), to investigate forest connectivity patterns, and past species-climate relationships of forest-dependent avifauna.

1. Cape batis *Batis capensis* (Linnaeus, 1766). IUCN status: Least Concern, stable populations (BirdLife International, 2017a). South African range declines (1997-2014): 1.30%. South African endemic subspecies (Figure 1.3): *B. c. capensis* (Linnaeus, 1766), and *B. c. hollidayi* (Clancey, 1952).
2. Chorister robin-chat *Cossypha dichroa* (Gmelin, 1789). IUCN status: Least Concern, decreasing populations (BirdLife International, 2017b). South African range declines (1997-2014): 19.53%. South African endemic subspecies (Figure 1.3): *C. d. dichroa* (Gmelin, 1789), and *C. d. mimica* (Clancey, 1981).
3. Yellow-throated woodland-warbler *Phylloscopus ruficapilla* (Sundevall, 1850). IUCN status: Least Concern, decreasing populations (BirdLife International, 2016a). South African range declines (1997-2014): 20.69%. South African endemic subspecies (Figure 1.3): *P. r. ruficapilla* (Sundevall, 1850), and *P. r. voelkeri* (Roberts, 1941).
4. White-starred robin *Pogonocichla stellata* (Vieillot, 1818). IUCN status: Least Concern, decreasing populations (BirdLife International, 2016b). South African range declines (1997-2014): 23.02%. South African endemic subspecies (Figure 1.3): *P. s. stellata* (Vieillot, 1818), and *P. s. transvaalensis* (Roberts, 1912).

These four species share overlapping functional traits: small body mass (<50 g), insectivorous diet, high affinity for Afromontane forests, foraging in mid- and understorey strata of forest interiors (Hockey et al., 2005), co-occur within the eleven forest sites selected for this study (see Section 1.6). Additionally, these species are breeding residents to South Africa that do not migrate intra- or intercontinentally, instead remaining dependent on the year-round conditions within regional forests (Hockey et al., 2005). Genetic inferences from these species are therefore expected to specifically reflect responses to landscape and climate changes within the study area, and not be obfuscated by events which have occurred elsewhere in Africa, Europe, and Asia. However, these species reportedly do differ in the level of forest habitat specialisation, and intra-regional movement behaviour, and are therefore expected to demonstrate unique responses to environmental changes within the study area.

Breeding populations of *C. dichroa* (Oatley, 1997a) , *P. ruficapilla* (Berruti, 1997), and *P. stellata* (Oatley, 1997b) are largely confined to Afromontane (and scarp) forests, whereas breeding populations of *B. capensis* are additionally present within Albany thicket, and tall, dense fynbos pockets prevalent across the south and southwest Cape of South Africa (Johnson, 1997). Two species, *C. dichroa* and *P. stellata*, are thought to be altitudinal migrants within in KwaZulu-Natal, wintering in lowland forests, including certain Indian Ocean coastal belt forests (Johnson & Maclean, 1994; Oatley 1982a, 1997a, 1997b, 2017), however, only *P. stellata* is considered to be an altitudinal migrant in the Eastern Cape (Craig & Hulley, 2019). Neither *B. capensis*, nor *P. ruficapilla* are suspected to undergo substantial seasonal movements (Berruti, 1997; Craig & Hulley, 2019; Johnson, 1997). Although *C. dichroa* and *P. stellata* are potential non-breeding migrants to lowland forests and Indian Ocean coastal belt forests in KwaZulu-Natal, the coastal scarp and Indian Ocean coastal belt forests of the more temperate Eastern Cape province are assumed to support perennial breeding populations of both species, alongside *B. capensis* and *P. ruficapilla*. This is evidenced by: (i) by year-round presence of these birds within the low-elevation forests of this province (Berruti, 1997; Johnson, 1997; Oatley, 1997b, 1997a); (ii) hybridisation of *C. dichroa* between and *C. natalensis* within lowland scarp forests of southern KwaZulu-Natal and the Eastern Cape (Clancey, 1982; Davies et al., 2011); (iii) nest records of all four species within low-elevation forests present along the south coast of South Africa (Oatley, 2005a, 2005b; Smith, 2005; Vernon & Dean, 2005) – nest records are understandably scant within the poorly ornithologically surveyed forests of the Eastern Cape; and (iv) personal observations of brood-patches – a physiological indicator of actively nesting birds (Turner, 1997) – exhibited by captured focal species individuals within all visited forest sites during this study.

These four songbird species differ further in their overall occurrence, and evolutionary history, across Africa. Two species, *P. ruficapilla* and *P. stellata*, have distributions extending across multiple isolated Afromontane forest blocs from South Africa to East Africa, with *P. stellata* being more widespread (Figure 1.3), and are understood to have evolved within the lower-latitude forests of the latter region (Alström et al., 2018; Bowie et al., 2006; Fjeldså & Bowie, 2008). By contrast, *B. capensis* and *C. dichroa* are more confined to southern Africa (Figure 1.3), with *C. dichroa* recognised as a South African endemic species (BirdLife International, 2021; Taylor & Peacock, 2018). The biogeographic history of the latter two species is less clear, although it is suspected these species would have a more ancient presence within the higher latitude forests of southern Africa, given their confinement, or predominance, within the region.

Figure 1.2 The four focal Oscine passerines, *Batis capensis*, *Cossypha dichroa*, *Phylloscopus ruficapilla*, and *Pogonocichla stellata*, included within the population genetic and phylogeographic component of this study. Both male (♂) and female (♀) birds are shown for the sexually dimorphic B. capensis, and the immature (<1 year) form of *P. stellata* is shown alongside the adult form of this species.

Selection of these focal species over other forest-dependent birds similarly facing range declines in the Eastern Cape was a partly pragmatic decision, constrained by the requirements for sufficiently sampling forest-dependent bird species that are (i) relatively abundant and resident to all eleven forest sites, despite apparent contemporary range declines, and (ii) frequent the mid- and understoreys of forests, for relative ease and reliability of bird capture for genetic sampling. South African forest-dependent bird species typically have low populations densities, and forest bird communities are skewed towards the canopy (Koen, 1989; Koen & Crowe, 1987; Mulvaney & Cherry, 2020; Perrin et al., 2000; Symes et al., 2002; Williams, 2016). Selecting bird species that readily occur at lower forest strata minimizes the risk of inadequate sampling necessary for meaningful genetic inferences. It was therefore crucial that the focal bird species chosen met the above two criteria to ensure project feasibility. Additionally, microsatellites libraries are already available for each species: *B. capensis* (Wogan et al., 2016); *C. dichroa* (Wogan et al., 2014b); *P. ruficapilla* (Bensch et al., 1997; Callens et al., 2011); and *P. stellata* (Callens et al., 2011; Wogan et al., 2014b). Additionally, clear conception of which bird species to sampled from the outset of fieldwork was ethically motivated. Mist-netting of birds requires short storage and handling times per individuals (< 1hr), due to reduce the interference with breeding populations (Bates & Voelker, 2015; De Beer et al., 2001). Handling of target species, though only a few minutes, is considerably longer than standard procedure (Bates & Voelker, 2015; De Beer et al., 2001). The cumulative time spent on potentially mismanaged fieldwork could jeopardize the health/survivability of captured individuals. This concern is compounded by the fact that birds are best caught within a few hours of sunrise and sunset (De Beer et al., 2001; anecdotal observations), coinciding with times of day when birds crucially need to feed, return to roosts, and tend to nests. Targeting only a few species from the outset greatly reduces storage and handling times, safeguarding the well-being of captured birds.

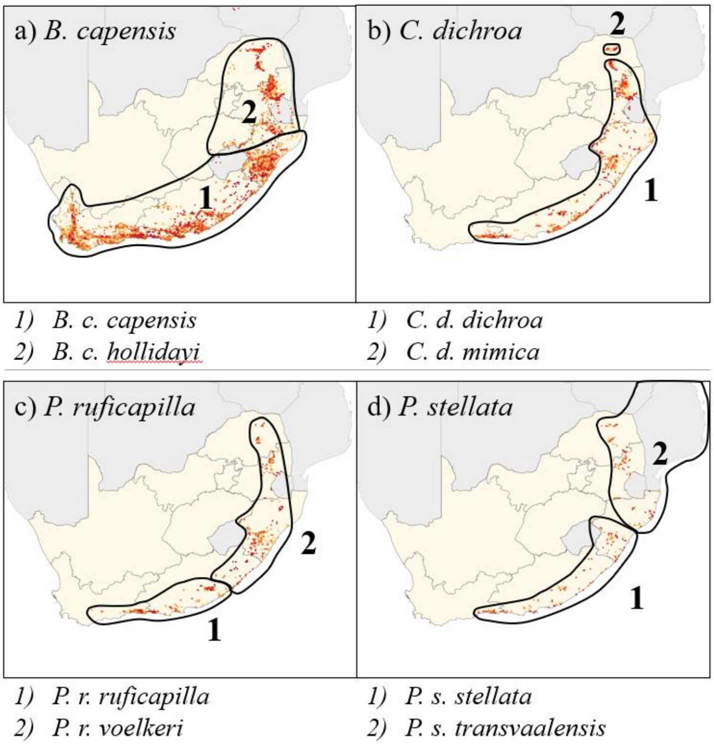


Figure 1.3 Distributions of the endemic subspecies of (a) *B. capensis*, (b) *C. dichroa*, (c) *P. ruficapilla*, and (d) *P. stellata* within South Africa (Hockey et al., 2005).

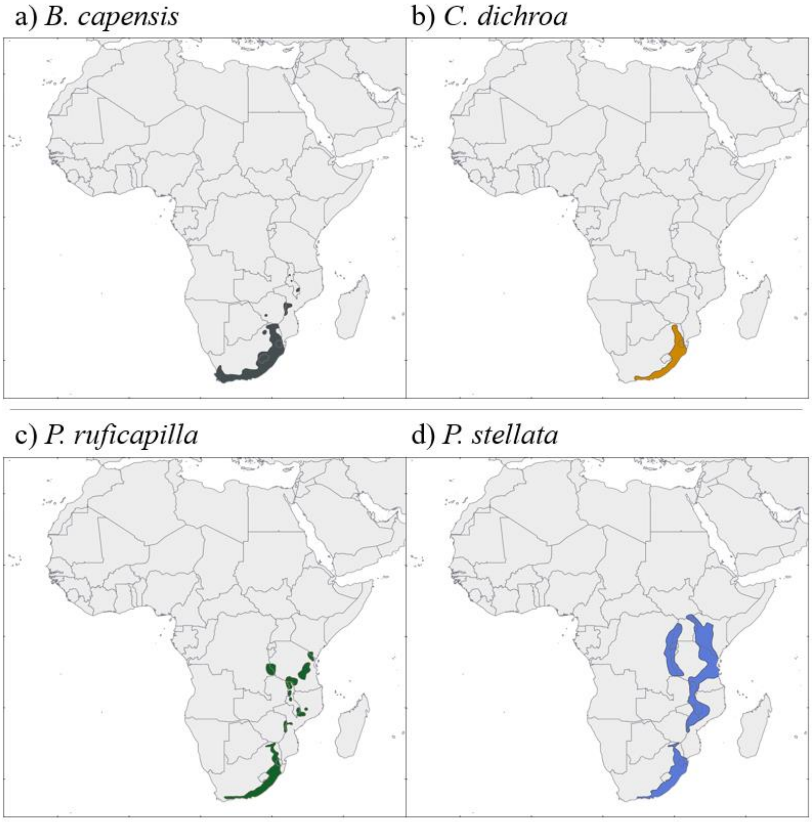


Figure 1.4 The global distributions of (a) *B. capensis*, (b) *C. dichroa*, (c) *P. ruficapilla*, and (d) *P. stellata* (BirdLife International, 2021).

1.8 Study aims, objectives and hypotheses

1.8.1 Chapter 2

The aims and objectives of Chapter 2 are to assess the effectiveness of point count and mist-netting ornithological field survey techniques at detecting bird diversity; and representing different aspects of bird community structures within forests of both sub-biomes across the Eastern Cape and southern KwaZulu-Natal provinces of South Africa. I hypothesise that point counts will outperform mist-netting at overall detection of forest bird diversity, given that South African forest bird communities are dominated by canopy species which mist-netting would be unable to detect. I further hypothesise mist-netting would be better able than point counts to detect species in the species-poor understories of these forests. Vegetation structure varies slightly between forests, with canopy heights ranging from 10-25 m, so mist-netting performance should improve in lower-canopy forests.

1.8.2 Chapter 3

The aims and objectives of Chapter 3 are to investigate the influence of the regional landscape on the population genetic structures of the four focal forest-dependent songbird species *B. capensis*, *C. dichroa P. ruficapilla*, and *P. stellata* across the forests of the Eastern Cape and southern KwaZulu-Natal provinces of South Africa. Given the differences in local movement dynamics, I suspected *B. capensis* and *P. ruficapilla*, as sedentary species, to have greatest population genetic substructuring, whereas *C. dichroa* and especially *P. stellata* would have the weakest population genetic substructuring. Given that study area is where the greatest level of ranges declines were observed for these species from 1997-2014, I expect to detect geneflow disruption and declines in effective population sizes within *C. dichroa*, *P. ruficapilla*, and *P. stellata*. By contrast, the populations of *B. capensis* are expected to have remained comparatively stable and intact, as this species showed the lowest extent of range decline from 1997-2014. I further hypothesise landscape features are utilised by these species to maintain functional connectivity between forests, and predict that landscape transformation of both forest and matrix landcover across the study area would have negatively impacted the population sizes and functional connectivity within the first three species.

1.8.3 Chapter 4

The aims and objectives of Chapter 4 are to investigate the phylogeographic structures, long-term demographic trends, past species-climate relationships, and forest climate refugia of *B. capensis*, *P. ruficapilla*, and *P. stellata* within the study area of the Eastern Cape and southern KwaZulu-Natal. Although the LGM has been associated with cold, xeric climates over South

Africa, I suspect that forest contractions during this time were not as severe as previously thought, given that wetter climates are now predicted over South Africa during this palaeoclimatic period. Therefore, I hypothesise that these three species would not show population bottlenecks during the LGM, and the occurrence of these three species within the study area would predate the LGM. This is further reinforced by the recognition of South African endemic subspecies of all three species, which suggests a well-establishment presence of these species within the country. I additionally hypothesise that lowland scarp forests are the climate refugia of all three species, as cold climates during global glaciations likely inhibited the establishment of mid-elevation Afromontane forests in the higher latitude regions for South Africa. I further hypothesise that the advent of the current Holocene interglacial, a period associated with forest expansion in South Africa, would have permitted population growth and distribution expansion of all three species within the study area, with mid-elevation Afromontane forests functioning as demographic sinks for these expanding populations. Lastly, I hypothesise that *B. capensis*, as a near-endemic species to South Africa, would show more divergent lineages that *P. ruficapilla* and *P. stellata*, which evolved in tropical east Africa, and that *B. capensis* would show higher genetic diversity, as the broader habitat generalisation of this species likely conferred greater resilience against palaeoclimate-induced forest loss.

Chapter 2: The effectiveness of point counts and mist-netting in surveying Afrotemperate forest bird community structure in South Africa

2.1 Abstract

Point counts and mist-netting are two frequently employed survey techniques used in assessing forest avian communities, although the reliability of these methods varies according to species composition and habitat. This study investigates how effectively these two methods can survey forest bird community structures within South African Afrotemperate forests. Seven forests within the Eastern Cape were surveyed from 140 duplicate point count and 63 mist-netting stations. Both methods were compared for assessing species richness, as determined from bird atlas data. Generalised linear mixed-effect modelling was used to determine functional traits which most impacted species detection, and to identify detection biases for both methods. Both methods compared consistently across the seven forests, which shared similar community structure. Point counts detected 79.2% of the total diversity versus 41.0% using mist-netting, and mixed-effects modelling corroborated that species detection is more effective using point counts. All functional traits tested (body size, primary foraging stratum, feeding guild, habitat specialisation, and dispersal behaviour) affected detection outcome. Point counts better represented all aspects forest bird community structure, including mid- and understorey birds which are presumed to be better detected by mist-netting. Use of mist-netting only slightly enhanced diversity assessments, and combined survey efforts under-represented forest-edge foragers, woodland and grassland habitat generalists (~63.6% total diversity), large birds, Palaearctic migrants, and carnivores.

2.2 Introduction

Birds are attractive ecological indicators for use in forest monitoring studies (Gao et al., 2015; Gregory et al., 2003), owing to their reliable and cost-effective field identification (Gardner et al., 2008), and the sensitivity of many species to habitat degradation (Sutherland et al., 2007). Point counts and mist-netting are two popular survey techniques used to infer local bird distribution, abundance, and diversity. Point counts involve timed, and typically distance-defined, bird observations at a series of stations (Buckland, 2006; Ralph et al., 1995). Mist-netting involves the catching and handling of birds by qualified persons using finely meshed nets (Karr, 1981). Both methods are relatively inexpensive and can be easily executed, following appropriate training. The limitations of each method are broadly known (Pagen et al., 2002; Wang & Finch, 2002): point count success is affected by observer skill, environmental conditions, and conspicuousness of the species present (Alldredge et al., 2007; Lynch, 1991; Pacifici et al., 2008); mist-netting is more labour-intensive, yet less efficient, than point counts, being more influenced by bird body size and flight paths – typically only detecting birds within <3 m above ground – and more adversely affected by weather (Dunn & Ralph, 2004; Remsen & Good, 1996). Although these limitations are broadly acknowledged prior to most field surveys, reliable ecological inferences require comprehensive understanding of the detection biases associated with each method.

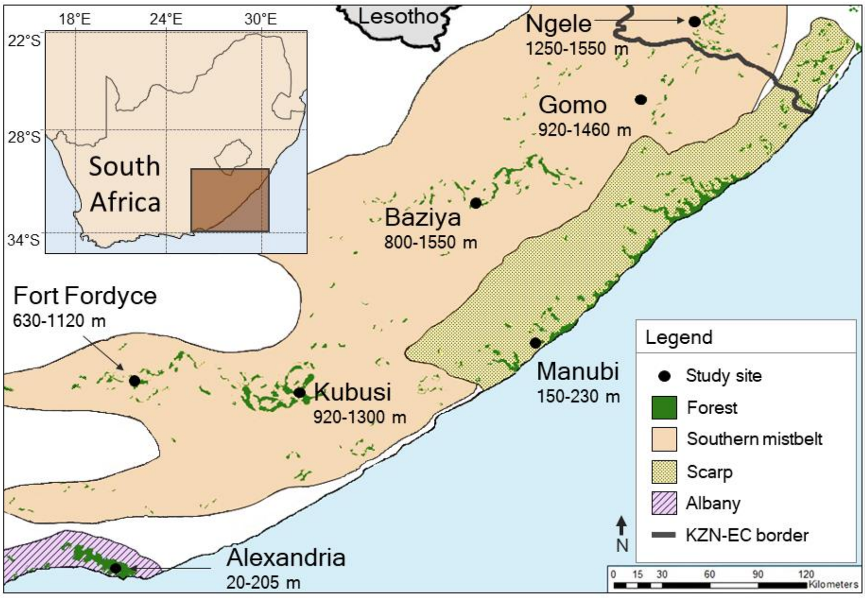
In select Neotropical and Indo-Malayan forest ecosystems, detection biases have been reasonably well determined (Blake & Loisille, 2001; Cavarzere et al., 2013; Derlindati & Caziani, 2005; Martin et al., 2010, 2017), but have limited general applicability as environmental conditions and bird community structures vary across regions and habitats (Martin et al., 2017). These studies largely focussed on continuous forest, yet monitoring schemes are often implemented in fragmented forests (Bregman et al., 2014; Keinath et al., 2017; Newbold et al., 2013, 2014). In Afrotropical forests, fragmentation studies typically consider the habitat specialisation of the observed species. These bird communities comprise both forest-dependent species that rely on forest ecosystems for at least some ecological functions (Geldenhuys & MacDevette, 1989), and habitat generalists that can survive and reproduce in surrounding non-forest landscapes. Forest-dependent birds can be further divided to forest specialists, which are largely restricted to the interiors of intact forests, and forest generalists which tolerate a broader range of forest conditions and quality, and occasionally woodlands (Bennun et al. 1996). Temperate forests support lower levels of forest specialists than in the tropics, and fewer sedentary species (Bregman et al., 2014; Salisbury et al., 2012). Both habitat specialisation and dispersal behaviour affect species susceptibility to fragmentation (LaManna & Martin, 2017; Newbold et al., 2014; Robinson & Sherry, 2012).

The naturally fragmented temperate evergreen (Afromontane) forests of South Africa occur along the southern and eastern escarpments, and south-east coast (Mucina, 2018; von Maltitz et al., 2003). These forests are related to the Afromontane forests of tropical east Africa (Mucina, 2018), and share similar avian phylogenetic compositions with these forests (Fjeldså & Bowie, 2008; Lawes et al., 2007a). Recent comparisons between the first and second Southern African Bird Atlas Projects (SABAP and SABAP2) suggest that 28 of the 57 forest-dependent bird species within the country have experienced range declines from 1992-2014 (Cooper et al., 2017). These declines are most apparent in the Eastern Cape, which contains 46% of South Africa’s forests (Berliner, 2005). Recent studies show forest bird communities in this province (Leaver 2019a, 2019b; Leaver & Cherry, 2020a), and elsewhere in South Africa (Ehlers-Smith et al., 2017; Freeman et al., 2018; Neuschulz et al., 2013; Olivier et al., 2013; Olivier & van Aarde, 2017) sensitive to habitat fragmentation and forest degradation. Preventing further bird declines requires increased monitoring within these forests, and continual assessments of the contemporary forest bird community structure, conducted using accurate and effective survey methodology. Thus, the aims of this study were to determine how reliably point counts and mist-netting assess bird diversity, and represent different aspects of bird community structure in Afrotemperate forests of the Eastern Cape. South African forests appear to be dominated by canopy species, and having species-poor understorey communities (Koen & Crowe, 1987; Olivier & Van Aarde, 2014; Symes et al., 2002), so species detection by mist-netting is expected to be less effective compared to point counts. Vegetation structure varies slightly between forests, with canopy heights ranging from 10-25 m, so mist-netting performance should improve in lower-canopy forests.

2.3 Methods

2.3.1 Study sites

Fieldwork was conducted in seven Afrotemperate forest sites, largely confined to the Eastern Cape of South Africa (Figure 2.1), within the Maputaland-Pondoland-Albany biodiversity hotspot (Mittermeier et al., 2004). Ngele is in southern Kwa-Zulu Natal, Gomo and Baziya are on the Transkei escarpment, and Kubusi and Fort Fordyce lie at eastern and western ends of the Amatole Mountains, respectively. These five forests are part of the southern mistbelt forest group: mid-altitude (850-1600 m) forests that occur discontinuously inland along the southern South African escarpment (Mucina, 2018; von Maltitz et al., 2003). Manubi lies on the Transkei coast and is a scarp forest: low- to mid-altitude (0-1300 m) forests, transitional between mistbelt and coastal forests (Lawes et al., 2007a; Mucina, 2018; von Maltitz et al., 2003). Finally, Alexandria is situated in Algoa Bay, and is part of the southern coastal forest group: low-altitude (0-500 m) evergreen forest along the southern South African coast (Mucina, 2018; von Maltitz et al., 2003). All forests experience a similar climate annual temperature range of 1-29 °C, and 600-1200 mm rainfall, peaking January-March. Southern mistbelt (15-25 m) and scarp forests (15-25 m) have similar canopy heights, although the understorey is more developed in mistbelt than scarp forests. Southern coastal forests have low canopies of 5-15 m, and dense undergrowth vegetation (von Maltitz et al., 2003).



Forest coordinates		
Ngele (755 ha)	30.517˚S	29.667˚E
Gomo (1170 ha)	31.000˚S	29.350˚E
Baziya (1150 ha)	31.567˚S	28.383˚E
Manubi (760 ha)	32.433˚S	28.600˚E
Kubusi (3370 ha)	32.600˚S	27.283˚E
Fort Fordyce (1730 ha)	32.683˚S	26.483˚E
Alexandria (12330 ha)	33.700˚S	26.350˚E

Figure 2.1 Map of the study region in the Eastern Cape, South Africa, showing the co-ordinates, altitude range (m.a.s.l.), size (ha), and forest groups (von Maltitz et al. 2003)

2.3.2 Data collection

Most forest sites were surveyed for two-week periods during September-December 2017, although Alexandria was surveyed in October 2018. Surveys were conducted during the breeding season when bird vocalisation is heightened, and when summer migrants are present. Survey intensity was standardised across forests. For point counts, 20 duplicate fixed radius 50 m observation stations were arranged along four linear transects, each comprising five observation stations spaced >150m apart. Stations along transects were visited within the first two hours of sunrise, and revisited on a new morning in reverse order. Visits lasted 10 min and all bird seen/heard within the station were recorded; unidentified birds were ignored. Mist-netting surveys in each forest were standardised to 3600 net-hours (1 net-hour = 12 m net open/hr), or a total of nine stations of 180 m transects of 2.5 m x 12/18 m length five-shelved, 16 mm mesh nets along forests tracts in forest-edge and interior. Two mist-netting stations were operated simultaneously for 2.5 days before relocating to new stations in another part of the forest. Nets were opened before sunrise to after sunset, closed during midday and inclement weather, and inspected every 30 minutes when open. Captured birds were identified, ringed, measured, and promptly released. Surveys were conducted when weather conditions were conducive to species detection, and safe for bird capture (calm and dry/lightly misty). Both survey methods were conducted in close proximity. Point count transects were spaced >500 m apart, and mist-netting stations were spaced >300 m apart where feasible. Survey stations were selected to maximise coverage throughout a given forest fragment. At each forest site, eight point count stations were at the forest-edge, and twelve were within the forest interior, while for mist-netting, four stations were at forest-edge and five were in the forest interior. Surveys were conducted by a single observer, JM.

2.3.4 Checklist construction

Species checklists for the contemporary bird communities of the seven forest sites were compiled using data from the second Southern African Bird Atlas Project (SABAP2, 2007-2018) (Brooks, 2018), which included observations made during this study. Quarter degree grid cells (QDGC) were centred over each forest, consolidating the species lists from the nine pentads (5'x5') therein. Recorded species were assessed in terms of their interaction with forests – such as foraging, breeding, or roosting – categorising any species with a non-negligible engagement with forest as forest-utilising (Harrison et al., 1997a, 1997b; Hockey et al., 2005). Migratory species were included, but nocturnal birds were excluded as these were not surveyed. The regional assemblage across the seven forest sites included 173 forest-utilising bird species (Appendix S2.1) of 54 families (Gill & Donsker, 2018). Compiled SABAP2 checklists were filtered for forest-utilising species to generate complete species inventories for each forest (Appendix S2.1). Non-forest-utilising species detected during surveys were removed from analysis, but have been included in Appendix S2.1.

2.3.5 Functional traits

A set of functional traits were determined for each forest-utilising species, sourced from local literature (see Appendix S2.1). Information on body mass (<50 g: small; 50-100 g: medium; >100 g: large), primary foraging stratum in/around forest (understorey; mid-storey; canopy; forest-edge; aerial), and feeding guild (carnivore; insectivore; frugivore/granivore; nectarivore) was derived from Hockey et al. (2005). Bird habitat specialisation (forest specialist; forest generalist; woodland habitat generalist; grassland habitat generalist) was determined from Bennun et al. (1996) and Harrison et al. (1997b, 1997a). Finally, dispersal behaviour of birds within the Eastern Cape (sedentary resident; dispersive resident; local migrant; Intra-African migrant; Palaearctic migrant) was sourced from Hockey et al. (2005), Harrison et al. (1997b, 1997a), Neuschulz et al. (2013), and Craig and Hulley (2019). Proportions of each functional traits across forests were compared using a series of χ^2 tests (Gibbons & Chakraborti, 2011).

2.3.6 Statistical analysis

Analyses were performed in R version 3.4.3 (R Core Team, 2020), largely following Martin et al. (2017). Proportions of total species detected per forest, and detection ratios between forest sites within functional groups, were compared for each method using χ^2 tests with Yates continuity correction. Kruskal-Wallis (Gibbons & Chakraborti, 2011) tests were used to determine if species richness found at each observation station varied significantly among forests for either point counts or mist-netting. Generalised linear mixed-effect (GLM) modelling was performed on survey data (Appendix S2.1) to determine the factors most affecting species detection when using combined survey methods in the seven forests. Forest-utilising species checklists for each forest were assumed to represent all species present. A logistic regression curve was fitted to determine factors influencing detection outcome, which were taken as separate Bernoulli trials (1 = detected and 0 = undetected), for each method. The global model factored survey method, and all functional traits (body size, primary foraging stratum, feeding guild, habitat specialisation, and dispersal behaviour) as fixed effects; and forest site as a mixed effect, due to similarities in community structure and consistent survey performance between forests. Sub-models progressively excluded each factor. Two null (intercept-only) models were included (1) with, and (2) without the random effects. Mixed-effects models were fitted using the 'glmer' function in lme4 R package (Bates et al., 2014), while models ignoring random effects were fitted with function 'glm' in the Stats R package (R Core Team, 2020). Model selection was conducted using Akaike's Information Criteria (AIC) (Burnham & Anderson, 2002) in the MuMIn R package (Bartoń, 2019); models with non-significant terms were omitted. Akaike weights (w_i) gave likelihood estimates to each candidate models being the best-supported model. Model fit was assessed using conditional R^2, which is insensitive to the number of variables factored (Nakagawa & Schielzeth, 2013). We performed additional GLM models separately for point count and mist-netting surveys. Post hoc analysis, using least-square mean difference with Tukey adjustment in the Lsmeans R package (Lenth, 2016), further distinguished the biases of each method within each functional trait group.

To illustrate how effectively species detection rewards survey effort through time, we drew species accumulation curves from 100 randomisations of complete point count and mist-netting datasets across the seven forests. We then plotted species extrapolations from the data to assess how accurately forest diversity could be approximated. We used the incidence based Chao2, and MMMeans non-parametric species estimators, which are considered appropriate for inferences on in tropical forest bird communities: MMMeans is considered more accurate, but is sensitive to variability in community structure (Herzog et al., 2002); Chao2 is less affected by sampling strategy, but is sensitive to sample size (Hortal et al., 2006). Curves were created using EstimateS version 9.1.0 (Colwell, 2013).

2.4 Results

Compiled checklists show the number of forest-utilising bird species at each forest: Manubi – 157; Kubusi – 150; Alexandria – 143; Ngele – 135; Gomo – 129; Fort Fordyce – 129; and Baziya – 121 (Appendix S2.1). Community structure was highly similar across forest sites for all functional groups (Figure S2.1; Appendix S2.2). All seven forests had high proportions of small and insectivorous species. Forest interiors – understorey, mid-storey, and canopy – hold mostly canopy-foraging species (71.4%), but comprise only 40.4% of total diversity – compared to 49.7% present at the forest-edge. Only 36.4% of forest-utilising species are forest-dependent, suggesting most avian diversity is from woodland and grassland habitat generalists foraging at the forest-edge. Lastly, 43.9% of species are sedentary forest residents, with the rest being more dispersive and migratory species. Total combined survey efforts detected 9017 individuals from 139 forest-utilising species. Point counts detected 7278 individuals detected from 137 species, while mist-netting detected 1739 individuals from 71 species. Appendix S2.3 (point counts) and Appendix S2.4 (mist-netting) break down species and individual totals observed at each forest.

Across the seven forests, higher species richness was recorded at point count observation stations compared to mist-netting (Figure 2.2). Point counts detected 59.87-75.56% of forest checklist totals ($\chi2$ test $p = 0.908$) (Appendix S2.3). Functional group representation from point counts varied among forests for carnivores, frugivores/granivores, grassland generalists, local migrants, and Palaearctic migrants. Mist-netting detected 20.83%-28.67% of forest checklists totals (χ^2 test $p =0 .936$) (Appendix S2.4). Functional group representation from mist-netting was less consistent compared to point counts, differing among forests for mid-storey, aerial and forest-edge foragers, carnivores, frugivores/granivores, nectarivores, grassland generalists, local migrants, and Intra-African migrants. Mist-netting detected no Palaearctic migrants, and only one aerial species, the white-throated swallow *Hirundo albigularis*, at Kubusi. All aspects of forest bird community structure were better represented by point counts than mist-netting.

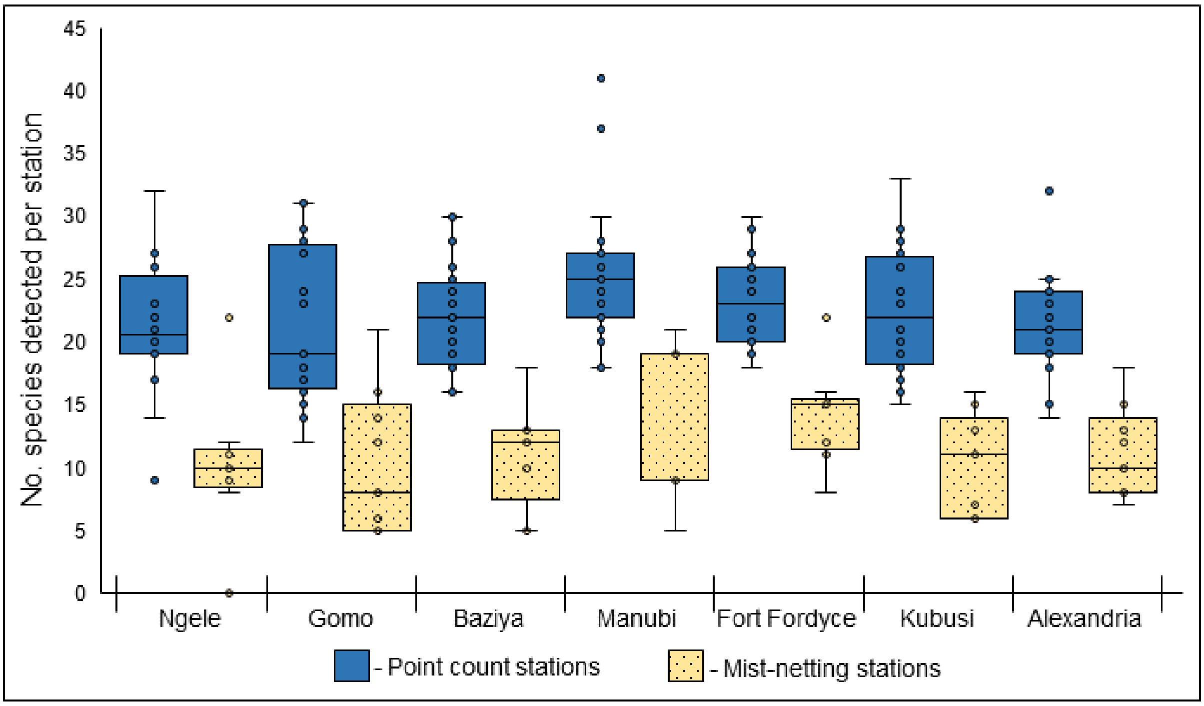


Figure 2.2 Boxplots showing species richness detected by point counts is consistently higher than mist-netting across the seven Afrotemperate forest sites. Kruskal-Wallis scores for average species richness per observation among forests were 2.46 for point counts (p =0.78), and 4.22 (p=0.65) for mist-netting, suggesting consistent survey performance across forests.

The global GLM model was the best supported model (Table 2.1), explaining detection outcomes within the seven forest sites to be affected by survey method and all functional traits factored. Table 2.2 shows point counts to be more effective at species detection than mist-netting. Combined survey methods significantly under-represent large birds, forest-edge foragers, and aerial feeders, both woodland and grassland generalists (most of which are forest-edge foragers), Palaearctic migrants, and carnivorous species. Factoring in feeding guild increased model explanatory power only slightly. Model selection of stand-alone point count and mist-netting surveys are shown in Appendix S2.5 and Appendix S2.6, respectively; post-hoc results of the best-supported model for each method are shown in Figure S2.2.

Point counts detected 79.2% of the regional forest-utilising species, compared to the 41.0% by mist-netting (Table 2.2). Only two species were detected solely by mist-netting: southern tchagra *Tchagra tchagra* (Gomo) and white-browed scrub-robin *Cercotrichas leucophrys* (Kubusi), both woodland generalists. Point counts required considerably less time, and effort than mist-netting. Observation time devoted to point counts was 6 hrs 40 min per forest (46 hrs 40 min total), and ~3600 hrs were invested into mist-netting (~26000 hrs total). The species accumulation curves displaying total survey effort showed point count effectiveness plateaued below 140 species (Figure 2.3), while mist-netting effort was less productive, but steadily accumulated species throughout the study period (Figure 2.2). Chao2 and MMMeans estimates from mist-netting were well below those from point counts. For both methods, MMMeans extrapolated greater diversity from brief surveys, but at higher intensity surveys Chao2 estimated more species. Another appropriate, abundance-based metric, ACE, produced similar results.

Table 2.1 AIC model selection of generalised linear mixed-effect logistic regression model representing factors affecting species detectability in Afrotemperate forests. Included are the AIC values, AIC difference (ΔAIC), conditional R2 ($C. R^2$), and Akaike weights (w_i) for each model

Model R code*	AIC	ΔAIC	*C.* R^2	w_i
~Method+Stratum+Size+Specialization+Dispersal+Diet+(1|Forest)	1803.39	0.00	0.53	0.98
~Method+Stratum+Size+Specialization+Dispersal+(1|Forest)	1811.97	8.58	0.52	0.014
~Method+Stratum+Size+Dispersal+(1|Forest)	1827.59	24.20	0.51	0.000
~Method+Stratum+Size+(1|Forest)	1855.56	52.17	0.49	0.000
~Method+Stratum+(1|Forest)	1904.37	100.98	0.46	0.000
~Method+(1|Forest)	2307.24	503.85	0.19	0.000
Null (~1)	2643.01	839.62	0.00	0.000
Null (~1+(1|Forest))	2645.01	841.62	0.00	0.000

*Mixed-effects models were fitted using ‘glmer’ function in the ‘lme4’ R package, and the final null model was fitted using the function ‘glm’ in the ‘Stats’ R package.

Table 2.2 Parameter estimates for the best-supported logistic regression model for determining factors affecting bird species detection by combined point count and mist-netting surveys in Afrotemperate forests. Shown are the percentage of total forest-utilising bird species detected per category (%T), coefficient estimate (Estimate), and standard error of the estimate (SE), Z-score values, and *p*-values. Results in bold are significant.

Factor	**Level**	**% Total**	**Estimate**	**SE**	**Z-score**	***p*-value**
Intercept	-	-	**-2.34**	**0.36**	**-6.53**	**<0.0001**
Method	**Point**	**79.20**	**2.49**	**0.14**	**18.33**	**<0.0001**
	Mist-netting	41.04	-	-	-	-
Body size	**Small**	**83.49**	**0.57**	**0.20**	**2.87**	**0.004**
	Medium	92.00	0.00	0.23	0.00	0.997
	Large	64.10	-	-	-	-
Primary foraging stratum	**Understorey**	**100.00**	**1.63**	**0.37**	**4.41**	**<0.0001**
	Mid-storey	**100.00**	**3.22**	**0.67**	**4.77**	**<0.0001**
	Canopy	**100.00**	**0.80**	**0.28**	**2.85**	**0.004**
	Forest-edge	**63.95**	**-0.69**	**0.26**	**-2.61**	**0.009**
	Aerial	82.35	-	-	-	-
Habitat specialization	Forest specialist	100.00	-0.16	0.20	-0.77	0.440
	Forest generalist	90.63	-	-	-	-
	Woodland generalist	**71.43**	**-0.72**	**0.18**	**-3.87**	**0.0001**
	Grassland generalist	**72.50**	**-0.89**	**0.22**	**-4.00**	**<0.0001**
Dispersal behaviour	**Sedentary resident**	**90.20**	**0.57**	**0.23**	**2.51**	**0.012**
	Dispersive resident	76.92	-0.01	0.23	-0.05	0.964
	Local migrant	100.00	0.33	0.30	1.12	0.262
	Intra-African migrant	90.91	-	-	-	-
	Palaearctic migrant	**20.00**	**-1.35**	**0.44**	**-3.09**	**0.002**
Feeding guild	Carnivore	69.57	-	-	-	-
	Insectivore	**81.55**	**0.60**	**0.25**	**2.40**	**0.016**
	Frugivore/Granivore	82.05	0.18	0.25	0.72	0.470
	Nectarivore	**87.50**	**1.05**	**0.37**	**2.85**	**0.004**

2.5 Discussion

Point count and mist-netting species detection performance was consistent across the seven surveyed Afrotemperate forests of the Eastern Cape, which shared highly similar bird community structure (Figure S2.1; Appendix S2.2). Both the GLM model (Table 2.2), and species accumulation curves (Figure 2.3) show that point counts outperform mist-netting at species detection. Mist-netting did not contribute significantly to an understanding of forest bird community structure (Table 2.2; Appendix S2.3 vs Appendix S2.4). Increased survey intensity using point counts better approximated estimated species diversity than did mist-netting (Figure 2.3). Point counts appear to suffice as a stand-alone method for surveying these Afrotemperate forests, reducing the need to undertake protracted mist-netting surveys. Although all functional traits factored contributed towards species detection, the primary foraging stratum contributed the most substantially. This holds for combined surveys (Table 2.2), point counts (Appendix S2.5; Appendix S2.8), and mist-netting (Appendix S2.6; Appendix S2.8). Forest interior foragers were reliably detected by point counts, but even combined surveys under-reported forest-edge and aerial species. Many forest-edge species are habitat generalists which have lower abundance in forests, even if common in adjacent non-forest habitats. The SABAP2 data used for checklist construction spanned 12 years, and included species which are less likely to be detected by the relatively brief sampling we conducted. Estimated species diversity (Figure 2.3) did not approximate total forest-utilizing bird diversity, suggesting some habitat generalists are not reliably present in forests. More extensive surveys should focus on elucidating species occupancy at forest-edge transition zones, as this could benefit an understanding of how natural forest fragments are integrated into the landscape (Kupfer et al., 2006; Terraube et al., 2016), and to help monitor the effects of habitat degradation. Fortunately, forest-dependent birds were reliably detected by combined survey efforts (Table 2.3), and by point counts alone (Appendix S2.5; Appendix S2.8).

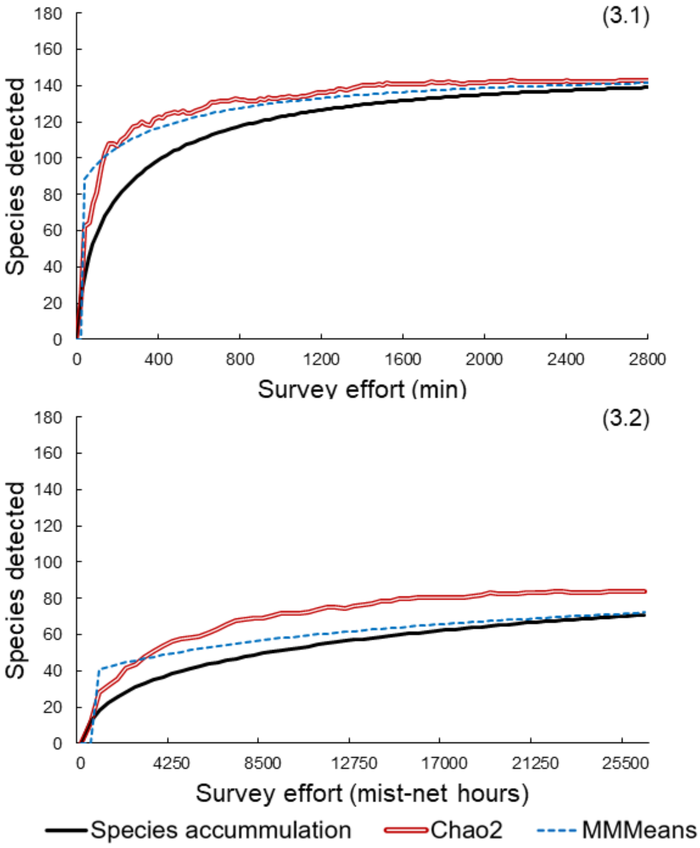


Figure 2.3 Species accumulation curves (100 randomized permutations) and species extrapolation curves (100 permutations of Chao2, and MMMeans estimations), respectively showing the number of species detected, and species presence estimated from (4.1) 2800 min of point count observations, and (4.2) 26000 mist-net hours, across seven Afrotemperate forests.

Point count performance was less affected by bird body mass than was mist-netting (see below), although large species were less likely to be detected than smaller ones (Figure S2.2). Species dispersal behaviour better explained detection outcomes by point counts (Appendix S2.3). Dispersive residents – such as raptors, parrots, and hornbills – may have infrequent occurrence, or large territories. For these birds, increasing the ‘grain’ (observation area/period) of the survey may improve detection; this approach is also appropriate for large species, including sedentary residents. Species’ active periods should also be considered to ensure these coincide with survey times. Palaearctic migrants were poorly detected by combined survey efforts (Table 2.3; Appendix S2.3; Appendix S2.4; Appendix S2.8). These are all habitat generalists reluctant to utilise forest interiors (Hockey et al., 2005), and so most may be rare/absent from forests. Future studies should pay closer attention to Palaearctic migrants, given the extent to which they interact with different ecosystems within the study area and elsewhere in Africa (Thorup et al., 2019). Feeding guilds did not affect detection by point counts (Appendix S2.5). The inconsistent representation of carnivores and frugivores/granivores in point counts among forests may be an artefact of their relatively short duration, or alternatively related to foraging stratum or dispersal behaviour. Although point counts should suffice for species detection in these forests, use of this method for bird abundance/occupancy inference has been criticised, particularly in forest habitats (Hayes & Monfils, 2015; Nichols et al., 2009; Pacifici et al., 2008). This is especially important as surveys may under-detect cryptic/reclusive species, where individuals are more difficult to detect.

GLM models better demonstrated the limitations of mist-netting for assessing functional diversity (Appendix S2.5; Appendix S2.8; Figure S2.2). Despite the notion that mist-netting removes observer bias occasioned by dense forest undergrowth (Dulle et al., 2016; Karr, 1981), point counts were found to outperform mist-netting at detecting forest understorey and mid-storey foragers (Tables S2.4 vs Appendix S2.5). Significantly lower representation of canopy foragers, which constitute 71.4% of forest interior species, reaffirms the impracticalities of using mist-netting to assess forest diversity where most species are present in the canopy (Cavarzere et al., 2013; Martin et al., 2017). Although canopy-level nets are a possibility (Derlindati & Caziani, 2005), a far more feasible alternative for passive monitoring is afforded by wildlife acoustics (Blumstein et al., 2011), which compares favourably to point counts in temperate forests (Klingbeil & Willig, 2015), and camera trapping (Trolliet et al., 2014). Mist-netting surveys in this study were deliberately non-specific and showed strong biases against medium and large species, frugivores/granivores, and carnivores; mist-netting is also unsuitable for assessing aerial feeders around forests (Appendix S2.4; Appendix S2.8; Figure S2.2). Mist-netting can be adjusted for better detection of different size classes, such as using larger/smaller mesh-size, or tailored to individual species (Bub, 1992), but without these adjustments, inferences relating to larger birds should be made with caution. The effects of setting up nets along forest tracks instead of in undergrowth proper is unknown; the latter case would require extensive clearing of vegetation to the detriment of the forests. It should be mentioned that mist-netting has applications beyond only species detection, and is an invaluable tool for performing demographic studies of age structures and movement through capture-recapture and satellite tracking, morphometric analysis, and sample collection for genetic, ectoparasite, and disease studies (Dunn & Ralph, 2004; Ralph & Dunn, 2004). Consequently, mist-netting is more appropriate for long-term assessments of bird populations

(Symes et al., 2002; Wilson et al., 2016), rather than brief assessments of bird communities, and can be used to create population indices of the species that are reliably detected by mist-nets: small birds, insectivores, and nectarivores, foraging in the understorey and mid-storey.

Species detection effectiveness by both survey methods was consistent among forests (Figure 2.2; Appendix S2.3; Appendix S2.4), despite Alexandria having a considerably lower canopy and greater understorey biomass than the other forests sites. The Afrotemperate forests in the Eastern Cape support similar bird community structures to tropical Afromontane forests in east Africa, although the latter forests hold a higher proportion of forest specialists (Chiawo, Kombe, & Craig, 2018; Engelen et al., 2017; Njuguna et al., 2014; Ulrich et al., 2016; Uwimbabazi et al., 2017; Werema, 2016). The results of this study are thus likely to be germane to surveying Afromontane forests across the continent, and possibly even to other well-wooded habitats, as Lee et al. (2015) reported similar survey effectiveness for point counts and mist-netting in fynbos. Further assessments are needed to assess how applicable point counts and mist-netting are for assessing nocturnal birds, which were not assessed in this study.

2.6 Conclusion

In summary, point counts are more effective than mist-netting for assessing the bird communities of Afrotemperate forests in the Eastern Cape, detecting 79.2% vs 41.0% of forest-utilising species. Although outperformed by point counts, mist-netting is still reliable for detecting mid- and understorey species. Combined survey efforts could reliably detect forest-dependent species, and birds which forage in the forest interior. Combined survey efforts, however, under-represented forest-edge species and habitat generalists – many of which may be rare in forests, although the extent of their interactions with forests is unknown – as well as medium-large birds, dispersive residents, and Palaearctic migrants. Not accounting for these survey biases could significantly misrepresent avian community structures within these forests, and misinform conservation efforts.

2.7 Chapter 2 appendices

Appendix S2.1 Forest-utilising bird species across the Eastern Cape of South Africa (Harrison et al., 1997a, 1997b; Hockey et al., 2005), showing habitat specialisation (FS = forest specialist; FG = forest generalist; W= woodland habitat generalist; O = Grassland/wetland habitat generalist), primary foraging stratum (Und = understorey; Mid = mid-strum; Can = canopy; Edg = forest edge; Mtx = matrix habitats), body mass (Sml = small <50g; Med = medium 50-100g; Lrg = large >100g), feeding guild (F/G = frugivore/granivore, Car = carnivore; Ins = insectivore; Nec = nectarivore), and dispersal behaviour (Sed = sedentary resident; Dis = dispersive resident; LM = local migrant; AM = Intra-African migrant; PM = Palaearctic migrant). * denotes unassessed nocturnal forest-utilising species. ** denotes non forest-utilising species recording during surveys of forest edge.

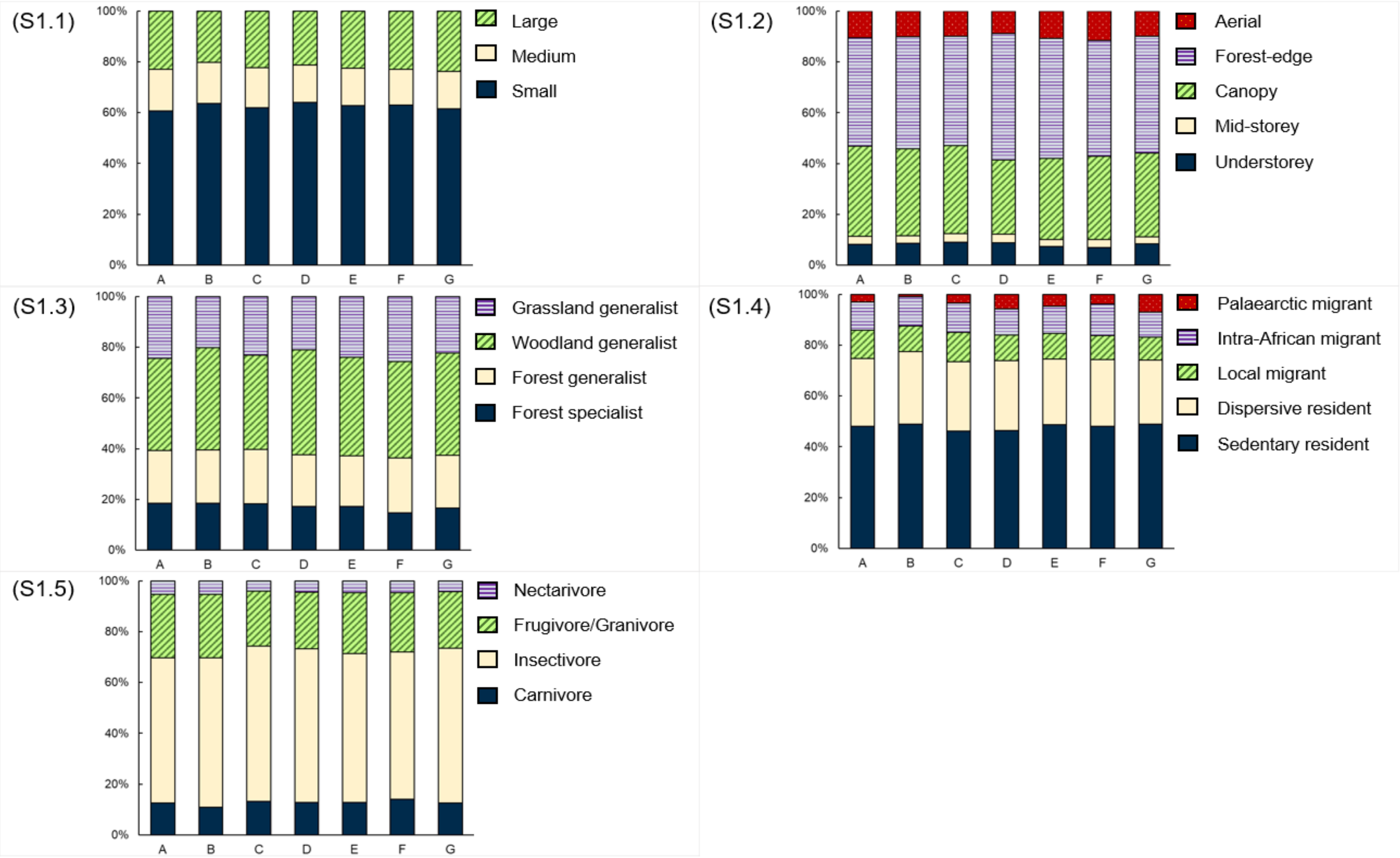
Species	**Habitat specialisation**	**Foraging stratum**	**Body mass**	**Feeding guild**	**Dispersal behaviour**
Apalis, Bar-throated *Apalis thoracica*	FG	Mid	Sml	Ins	Sed
Apalis, Yellow-breasted *Apalis flavida*	FG	Can	Sml	Ins	Sed
Barbet, Black-collared *Lybius torquatus*	W	Can	Med	F/G	Sed
Batis, Cape *Batis capensis*	FG	Mid	Sml	Ins	Dis
Batis, Chinspot *Batis molitor*	W	Edg	Sml	Ins	Sed
Bishop, Yellow *Euplectes capensis*	O	Edg	Sml	F/G	Sed
Blackcap, Bush *Lioptilus nigricapillus*	FS	Can	Sml	F/G	LM
Boubou, Southern *Laniarius ferrugineus*	FG	Und	Med	Ins	Sed
Brownbul, Terrestrial *Phyllastrephus terrestris*	FG	Und	Sml	Ins	Sed
Bulbul, Dark-capped *Pycnonotus tricolor*	W	Can	Sml	F/G	Sed
Bush-shrike, Grey-headed *Malaconotus blanchoti*	W	Edg	Med	Ins	Sed
Bush-shrike, Olive *Chlorophoneus olivaceus*	FS	Can	Sml	Ins	Sed
Bush-shrike, Orange-breasted *Telophorus sulfureopectus*	W	Edg	Sml	Ins	Sed
Buzzard, Forest *Buteo trizonatus*	FS	Edg	Lrg	Car	LM
Buzzard, Jackal *Buteo rufofuscus*	O	Edg	Lrg	Car	Dis
Buzzard, Steppe *Buteo buteo*	O	Edg	Lrg	Car	PM
Camaroptera, Green-backed *Camaroptera brachyura*	FG	Und	Sml	Ins	Sed
Canary, Brimstone *Serinus sulphuratus*	FG	Can	Sml	F/G	LM
Canary, Cape *Serinus canicollis*	O	Edg	Sml	F/G	LM
Canary, Forest *Crithagra scotops*	FS	Can	Sml	F/G	Sed
Canary, Yellow-fronted *Crithagra mozambicus*	W	Edg	Sml	F/G	Sed
Cisticola, Lazy *Cisticola aberrans*	W	Edg	Sml	Ins	Sed
Coucal, Burchell's *Centropus burchellii*	W	Edg	Lrg	Car	Sed

Crested-flycatcher, Blue-mantled *Trochocercus cyanomelas*	FS	Mid	Sml	Ins	Sed
Crow, Cape *Corvus capensis*	O	Edg	Lrg	Ins	Sed
Crow, Pied *Corvus albus*	W	Edg	Lrg	Car	Sed
Cuckoo, African Emerald *Chrysococcyx cupreus*	FS	Can	Sml	Ins	AM
Cuckoo, Black *Cuculus clamosus*	W	Can	Med	Ins	AM
Cuckoo, Diderick *Chrysococcyx caprius*	W	Can	Sml	Ins	AM
Cuckoo, Klaas's *Chrysococcys klaas*	W	Can	Sml	Ins	AM
Cuckoo, Red-chested *Cuculus solitarius*	W	Can	Med	Ins	AM
Cuckoo-shrike, Black *Campephaga flava*	W	Can	Sml	Ins	LM
Cuckoo-shrike, Grey *Coracina caesia*	FS	Can	Med	Ins	LM
Dove, Lemon *Aplopelia larvata*	FS	Und	Lrg	F/G	Sed
Dove, Red-eyed *Streptopelia semitorquata*	W	Can	Lrg	F/G	Dis
Dove, Tambourine *Turtur tympanistria*	FG	Und	Med	F/G	Sed
Drongo, Fork-tailed *Dicrurus adsimilis*	W	Can	Sml	Ins	Sed
Drongo, Square-tailed *Dicrurus ludwigii*	FS	Can	Sml	Ins	Sed
Duck, African Black *Anas sparsa*	O	Edg	Lrg	F/G	Sed
Eagle, African Crowned *Stephanoaetus coronatus*	FS	Can	Lrg	Car	Sed
Eagle, Long-crested *Lophaetus occipitalis*	FG	Edg	Lrg	Car	Sed
Falcon, Amur *Falco amurensis*	O	Edg	Lrg	Ins	PM
Falcon, Peregrine *Falco peregrinus*	O	Edg	Lrg	Car	Dis
Firefinch, African *Lagonosticta rubricata*	W	Edg	Sml	F/G	Dis
Fiscal, Southern Common *Lanius collaris*	O	Edg	Sml	Car	Sed
Flufftail, Buff-spotted *Sarothrura elegans*	FS	Und	Sml	Ins	Dis
Flufftail, Red-chested *Sarothrura rufa*	O	Edg	Sml	Ins	Sed
Flycatcher, African Dusky *Muscicapa adusta*	FG	Edg	Sml	Ins	LM
Flycatcher, Ashy *Muscicapa caerulescens*	FG	Can	Sml	Ins	Sed
Flycatcher, Southern Black *Melaenornis pammelaina*	W	Edg	Sml	Ins	LM
Flycatcher, Spotted *Muscicapa striata*	W	Edg	Sml	Ins	PM
Goshawk, African *Accipiter tachiro*	FG	Can	Lrg	Car	Sed
Grassbird, Cape *Sphenoeacus afer*	O	Edg	Sml	Ins	Sed
Greenbul, Sombre *Andropadus importunus*	FG	Can	Sml	F/G	Sed
Green-pigeon, African *Treron calvus*	W	Edg	Lrg	F/G	Dis
Ground-hornbill, Southern *Bucorvus leadbeateri*	W	Edg	Lrg	Car	Dis
Ground-thrush, Orange *Geokichla gurneyi*	FS	Und	Med	Ins	LM
Ground-thrush, Spotted *Geokichla guttata*	FS	Und	Med	Ins	LM
Guineafowl, Helmeted *Numida meleagris*	W	Edg	Lrg	Ins	Sed
Harrier-hawk, African *Polyboroides typus*	W	Edg	Lrg	Car	Sed
Hawk, African Cuckoo *Aviceda cuculoides*	W	Can	Lrg	Car	Dis
Heron, Green-backed *Butorides striata*	W	Edg	Lrg	Car	Dis
Honeybird, Brown-backed *Prodotiscus regulus*	W	Edg	Sml	Ins	Dis
Honey-buzzard, European *Pernis apivorus*	W	Edg	Lrg	Ins	PM
Honeyguide, Greater *Indicator indicator*	W	Edg	Sml	Ins	Dis
Honeyguide, Lesser *Indicator minor*	W	Edg	Sml	Ins	Dis
Honeyguide, Scaly-throated *Indicator variegatus*	FG	Can	Sml	Ins	Sed
Hoopoe, African *Upupa africana*	W	Edg	Med	Ins	Dis

Hornbill, Crowned *Tockus alboterminatus*	FG	Can	Lrg	Ins	Dis
Hornbill, Trumpeter *Bycanistes bucinator*	FS	Can	Lrg	F/G	Dis
House-martin, Common *Delichon urbicum*	O	Aer	Sml	Ins	PM
Ibis, Hadeda *Bostrychia hagedash*	W	Edg	Lrg	Ins	Dis
Indigobird, Dusky *Vidua funera*	W	Edg	Sml	F/G	Dis
Kestrel, Rock *Falco rupicolus*	O	Edg	Lrg	Ins	Dis
Kingfisher, Brown-hooded *Halcyon albiventris*	W	Edg	Med	Ins	Sed
Kingfisher, Giant *Megaceryle maxima*	O	Edg	Lrg	Car	Sed
Kingfisher, Half-collared *Alcedo semitorquata*	FG	Edg	Sml	Car	Sed
Kingfisher, Mangrove *Halcyon senegaloides*	FS	Mid	Med	Car	LM
Kite, Black *Milvus migrans*	W	Edg	Lrg	Ins	PM
Kite, Yellow-billed *Milvus aegyptius*	W	Edg	Lrg	Ins	AM
Longclaw, Yellow-throated *Macronyx croceus*	O	Edg	Sml	Ins	Dis
Mannikin, Bronze *Lonchura cucullatus*	W	Edg	Sml	F/G	Dis
Mannikin, Red-backed *Lonchura nigriceps*	FG	Edg	Sml	F/G	Dis
Martin, Banded *Riparia cincta*	O	Aer	Sml	Ins	AM
Martin, Brown-throated *Riparia paludicola*	O	Aer	Sml	Ins	Dis
Martin, Rock *Ptyonoprogne fuligula*	O	Aer	Sml	Ins	Dis
Mousebird, Red-faced *Urocolius indicus*	FG	Edg	Med	F/G	Dis
Mousebird, Speckled *Colius striatus*	W	Edg	Med	F/G	Sed
Neddicky *Cisticola fulvicapilla*	W	Edg	Sml	Ins	Sed
Olive-pigeon, African *Columba arquatrix*	FS	Can	Lrg	F/G	Dis
Oriole, Black-headed *Oriolus larvatus*	W	Can	Med	Ins	Dis
Palm-swift, African *Cyprius parvus*	W	Aer	Sml	Ins	Dis
Paradise-flycatcher, African *Terpsiphone viridis*	FG	Can	Sml	Ins	AM
Parrot, Cape *Poicephalus robustus*	FS	Can	Lrg	F/G	Dis
Petronia, Yellow-throated *Petronia superciliaris*	W	Edg	Sml	Ins	Sed
Pipit, Striped *Anthus lineiventris*	W	Edg	Sml	Ins	Dis
Prinia, Drakensberg *Prinia hypoxantha*	O	Edg	Sml	Ins	Sed
Prinia, Tawny-flanked *Prinia subflava*	O	Edg	Sml	Ins	Sed
Puffback, Black-backed *Dryoscopus cubla*	W	Can	Sml	Ins	Sed
Pygmy-kingfisher, African *Ispidina picta*	W	Edg	Sml	Ins	AM
Raven, White-necked *Corvus albicollis*	O	Edg	Lrg	Car	LM
Robin, White-starred *Pogonocichla stellata*	FS	Mid	Sml	Ins	LM
Robin-chat, Cape *Cossypha caffra*	W	Edg	Sml	Ins	Sed
Robin-chat, Chorister *Cossypha dichroa*	FS	Und	Sml	Ins	LM
Robin-chat, Red-capped *Cossypha natalensis*	FG	Und	Sml	Ins	LM
Roller, European *Coracias garrulus*	W	Edg	Lrg	Ins	PM
Saw-wing, Black *Psalidoprocne pristoptera*	FG	Aer	Sml	Ins	AM
Scrub-robin, Brown *Cercotrichas signata*	FS	Und	Sml	Ins	Sed
Scrub-robin, White-browed *Cercotrichas leucophrys*	W	Edg	Sml	Ins	Sed
Seedeater, Streaky-headed *Crithagra gularis*	W	Edg	Sml	F/G	Sed
Sparrowhawk, Black *Accipiter melanoleucus*	FG	Can	Lrg	Car	Sed
Sparrowhawk, Little *Accipiter minullus*	W	Can	Med	Car	Sed
Sparrowhawk, Rufous-chested *Accipiter rufiventris*	FS	Can	Lrg	Car	Sed
Spurfowl, Red-necked *Pternistis afer*	FG	Edg	Lrg	F/G	Sed

Starling, Black-bellied *Lamprotornis corruscus*	W	Can	Med	F/G	Dis
Starling, Cape Glossy *Lamprotornis nitens*	W	Edg	Med	F/G	Sed
Starling, Red-winged *Onychognathus morio*	O	Can	Lrg	F/G	Dis
Starling, Violet-backed *Cinnyricinclus leucogaster*	W	Edg	Sml	Ins	AM
Stonechat, African *Saxicola torquatus*	O	Edg	Sml	Ins	Dis
Sunbird, Amethyst *Chalcomitra amethystina*	W	Edg	Sml	Nec	Dis
Sunbird, Collared *Hedydipna collaris*	FG	Can	Sml	Nec	Sed
Sunbird, Greater double-collared *Cinnyris afer*	FG	Edg	Sml	Nec	Sed
Sunbird, Grey *Cyanomitra veroxii*	FG	Can	Sml	Nec	Dis
Sunbird, Malachite *Nectarinia famosa*	O	Edg	Sml	Nec	LM
Sunbird, Olive *Cyanomitra olivacea*	FS	Can	Sml	Nec	Sed
Sunbird, Southern Double-collared *Cinnyris chalybeus*	FG	Can	Sml	Nec	Sed
Sunbird, White-bellied *Cinnyris talatala*	W	Edg	Sml	Nec	Dis
Swallow, Barn *Hirundo rustica*	O	Aer	Sml	Ins	PM
Swallow, Greater Striped *Hirundo cucullata*	O	Aer	Sml	Ins	AM
Swallow, Lesser Striped *Hirundo abyssinica*	W	Aer	Sml	Ins	AM
Swallow, Pearl-breasted *Hirundo dimidiata*	W	Aer	Sml	Ins	AM
Swallow, White-throated *Hirundo albigularis*	O	Aer	Sml	Ins	AM
Swift, African Black *Apus barbatus*	O	Aer	Sml	Ins	Dis
Swift, Alpine *Tachymarptis melba*	O	Aer	Med	Ins	AM
Swift, Common *Apus apus*	O	Aer	Sml	Ins	PM
Swift, Horus *Apus horus*	O	Aer	Sml	Ins	AM
Swift, White-rumped *Apus caffer*	O	Aer	Sml	Ins	AM
Tchagra, Black-crowned *Tchagra senegalus*	W	Edg	Med	Ins	Sed
Tchagra, Southern *Tchagra tchagra*	W	Edg	Sml	Ins	Sed
Thrush, Olive *Turdus olivaceus*	FG	Und	Med	Ins	Dis
Tinkerbird, Red-fronted *Pogoniulus pusillus*	FG	Can	Sml	F/G	Sed
Tit, Southern Black *Melaniparus niger*	W	Can	Sml	Ins	Sed
Trogon, Narina *Apaloderma narina*	FG	Can	Med	Ins	Dis
Turaco, Knysna *Tauraco corythaix*	FS	Can	Lrg	F/G	Sed
Turtle-dove, Cape *Streptopelia capicola*	W	Edg	Lrg	F/G	Dis
Twinspot, Green *Mandingoa nitidula*	FS	Und	Sml	F/G	Sed
Wagtail, African Pied *Motacilla aguimp*	W	Edg	Sml	Ins	Sed
Wagtail, Cape *Motacilla capensis*	O	Edg	Sml	Ins	Sed
Wagtail, Mountain *Motacilla clara*	FS	Edg	Sml	Ins	Sed
Warbler, Barratt's *Bradypterus barratti*	FS	Und	Sml	Ins	LM
Warbler, Dark-capped Yellow *Iduna natalensis*	O	Edg	Sml	Ins	LM
Warbler, Knysna *Bradypterus sylvaticus*	FS	Und	Sml	Ins	Sed
Warbler, Marsh *Acrocephalus palustris*	W	Edg	Sml	Ins	PM
Warbler, Willow *Phylloscopus trochilus*	W	Edg	Sml	Ins	PM
Waxbill, Blue *Uraeginthus angolensis*	W	Edg	Sml	F/G	Dis
Waxbill, Common *Estrilda astrild*	O	Edg	Sml	F/G	Sed
Waxbill, Swee *Coccopygia melanotis*	FG	Edg	Sml	F/G	Dis
Weaver, Cape *Ploceus capensis*	O	Edg	Sml	F/G	Dis
Weaver, Dark-backed *Ploceus bicolor*	FS	Can	Sml	Ins	Sed
Weaver, Spectacled *Ploceus ocularis*	W	Edg	Sml	Ins	Sed

Weaver, Thick-billed *Amblyospiza albifrons*	FG	Can	Sml	F/G	Dis
Weaver, Village *Ploceus cucullatus*	W	Edg	Sml	Ins	Dis
Weaver, Yellow *Ploceus subaureus*	O	Edg	Sml	F/G	Dis
White-eye, Cape *Zosterops virens*	W	Can	Sml	Ins	Sed
Whydah, Pin-tailed *Vidua macroura*	W	Edg	Sml	F/G	Dis
Wood-hoopoe, Green *Phoeniculus purpureus*	W	Can	Med	Ins	Sed
Woodland-warbler, Yellow-throated *Phylloscopus ruficapilla*	FS	Can	Sml	Ins	Sed
Woodpecker, Golden-tailed *Campethera abingoni*	W	Can	Med	Ins	Sed
Woodpecker, Knysna *Campethera notata*	FS	Can	Med	Ins	Sed
Woodpecker, Olive *Dendropicos griseocephalus*	FS	Can	Sml	Ins	Sed
*Eagle-owl, Spotted *Bubo africanus*	W	Edg	Lrg	Car	Dis
*Eagle-owl, Verreaux's *Bubo lacteus*	W	Edg	Lrg	Car	Dis
*Night-heron, Black-crowned *Nycticorax nycticorax*	O	Edg	Lrg	Car	Dis
*Night-heron, White-backed *Gorsachius leuconotus*	W	Edg	Lrg	Car	Dis
*Nightjar, Fiery-necked *Caprimulgus pectoralis*	W	Edg	Med	Ins	Dis
*Nightjar, Swamp *Caprimulgus natalensis*	O	Edg	Med	Ins	Dis
*Owl, Barn *Tyto alba*	O	Edg	Lrg	Car	Sed
*Wood-owl, African *Strix woodfordii*	FG	Can	Lrg	Car	Sed
**Bishop, Yellow-crowned *Euplectes afer*	O	Mtx	Sml	F/G	Dis
**Bunting, Golden-breasted *Emberiza flaviventris*	W	Mtx	Sml	F/G	Dis
**Chat, Familiar *Cercomela familiaris*	O	Mtx	Sml	Ins	Sed
**Cisticola, Levaillant's *Cisticola tinniens*	O	Mtx	Sml	Ins	Sed
**Cisticola, Wailing *Cisticola lais*	O	Mtx	Sml	Ins	Sed
**Rock-thrush, Cape *Monticola rupstris*	O	Mtx	Med	Ins	ML
**Rush-warbler, Little *Bradypterus baboecala*	O	Mtx	Sml	Ins	Sed
**Sparrow, Southern Grey-headed *Passer diffusus*	W	Mtx	Sml	F/G	Sed
**Vulture, Cape *Gyps coprotheres*	O	Mtx	Lrg	Car	Dis
**Woodpecker, Cardinal *Dendropicos fuscescens*	W	Mtx	Sml	Ins	Sed
**Wryneck, Red-throated *Jynx ruficollis*	O	Mtx	Med	Ins	Sed



Appendix S2.2 Stacked bar-graphs showing the proportions of different aspects within each functional trait group present at each of the seven Afrotemperate forests surveyed: (S2.1.1) body size; (S1.2) primary foraging stratum; (S1.3) habitat specialisation; (S1.4) dispersal behaviour; and (S1.5) feeding guild. Forest: A – Ngele; B – Gomo; C – Baziya; D – Manubi; E – Kubusi; F – Fort Fordyce; G – Alexandria. Forest community structures were highly similar (no significant $\chi2$ results with $p>$ 0.05)

Appendix S2.3 Species-levels within each functional trait class across seven Afrotemperate forests in the Eastern Cape. Bracketed values are the number of species present, as estimated from SABAP2 data, and percentage values show the contributions by each trait-level towards the diversity within each functional trait class. Proportional differences within each functional trait class between forests were determined from χ2 tests

		Ngele	**Gomo**	**Baziya**	**Manubi**	**Kubusi**	**Fort Fordyce**	**Alexandria**	**χ2 value**	***p* of χ2**
Total Community		135	129	121	157	150	129	143	-	-
Body size	**Small (<50 g)**	(82) 60.7%	(82) 63.6%	(75) 62.0%	(100) 64.0%	(94) 62.7%	(81) 63.6%	(88) 61.5%	0.18	0.999
	Medium (50-100 g)	(22) 16.3%	(21) 16.2%	(19) 15.7%	(23) 14.7%	(22) 14.7%	(18) 14.0%	(21) 14.7%	0.42	0.999
	Large (>100 g)	(31) 23.0%	(26) 20.2%	(27) 22.3%	(34) 21.7%	(34) 22.7%	(30) 23.3%	(34) 23.8%	0.75	0.993
Foraging stratum	**Understorey**	(11) 8.2%	(11) 8.5%	(11) 9.1%	(14) 8.9%	(11) 7.3%	(9) 7.0%	(12) 8.4%	0.45	0.998
	Mid-storey	(4) 3.0%	(4) 3.1%	(4) 3.3%	(5) 3.2%	(4) 2.7%	(4) 3.1%	(4) 2.8%	0.10	1.000
	Canopy	(48) 35.6%	(44) 34.1%	(42) 34.7%	(46) 29.3%	(48) 32.0%	(42) 32.6%	(47) 32.9%	0.86	0.990
	Edge	(58) 42.5%	(57) 44.2%	(52) 43.0%	(78) 49.7%	(71) 47.3%	(59) 45.5%	(66) 46.1%	0.88	0.990
	Aerial	(14) 10.4%	(13) 10.1%	(12) 9.9%	(14) 8.9%	(16) 10.7%	(15) 11.6%	(14) 9.8%	0.42	0.999
Feeding guild	**Carnivore**	(17) 12.6%	(14) 10.9%	(16) 13.2%	(20) 12.7%	(19) 12.7%	(18) 14.0%	(18) 12.6%	0.43	0.999
	Insectivore	(77) 57.0%	(76) 58.9%	(74) 61.2%	(95) 60.5%	(88) 58.7%	(75) 58.1%	(87) 60.8%	0.20	0.999
	Frugivore/Granivore	(34) 25.2%	(32) 24.8%	(26) 21.5%	(35) 22.3%	(36) 24.0%	(30) 23.3%	(32) 22.4%	0.46	0.998
	Nectarivore	(7) 5.2%	(7) 5.4%	(5) 4.1%	(7) 4.5%	(7) 4.7%	(6) 4.6%	(6) 4.2%	0.31	0.999
Habitat specialization	**Forest specialist**	(25) 18.5%	(24) 18.6%	(22) 18.2%	(27) 17.2%	(26) 17.3%	(19) 14.7%	(24)16.8%	0.84	0.991
	Forest generalist	(28) 20.7%	(27) 20.9%	(26)21.5%	(32) 20.4%	(30) 20.0%	(28) 21.7%	(29) 20.8%	0.12	1.000
	Woodland generalist	(49) 36.3%	(52) 40.3%	(45) 37.2%	(65) 41.4%	(58) 38.7%	(49) 38.0%	(58) 40.6%	0.77	0.993
	Grassland generalist	(33) 24.4%	(26) 20.2%	(28) 23.1%	(33) 21.0%	(36) 24.0%	(33) 25.6%	(32) 22.4%	0.98	0.987
Dispersal behaviour	**Sedentary resident**	(65) 48.1%	(63) 48.8%	(56) 46.3%	(73) 46.5%	(73) 48.7%	(62) 48.1%	(70) 49.0%	0.26	0.999
	Dispersive resident	(36) 26.7%	(37) 28.7%	(33) 27.3%	(43) 27.4%	(39) 26%	(34) 26.4%	(36) 25.2%	0.48	0.998
	Local migrant	(15) 11.1%	(13) 10.1%	(14) 11.6%	(16) 10.2%	(15) 10.0%	(12) 9.3%	(13) 9.1%	0.58	0.997
	Intra-African migrant	(15) 11.1%	(15) 11.6%	(14) 11.6%	(16) 10.2%	(16) 10.7%	(16) 12.4%	(14) 9.8%	0.54	0.997
	Palaearctic migrant	(4) 3.0%	(1) 0.8%	(4) 3.3%	(9) 5.7%	(7) 4.7%	(5) 3.9%	(10) 7.0%	6.02	0.420

Values indicated by * denotes χ2 test p-value <0.05; Values indicated by ** denotes χ2 test p-value <0.01

Appendix S2.4 Bird species detected (Det.), and the proportion of total diversity within different functional trait class represented (%T) by point count surveys within seven Afrotemperate forests in the Eastern Cape. A series of χ2 tests were used to determine the proportional differences of the representation for each functional trait class by point count surveys between all seven forests.

		Ngele		Gomo		Baziya		Manubi		Kubusi		Fort Fordyce		Alexandria			
		Det.	% T	Det.	% T	Det.	% T	Det.	% T	Det.	% T	Det.	% T	Det.	% T	χ2 value	*p* of χ2
Of total community		102	75.56	83	64.34	78	64.46	94	59.87	98	65.33	84	65.12	92	63.89	2.11	0.908
Body size	**Small (<50 g)**	67	81.71	56	68.29	48	64.00	63	63.00	67	71.28	53	64.63	61	70.11	3.60	0.731
	Medium (50-100 g)	15	68.18	13	61.90	13	68.42	18	78.26	12	54.55	15	83.33	16	80.00	9.24	0.160
	Large (>100 g)	20	64.52	14	53.85	17	62.96	13	38.24	19	55.88	16	53.33	15	40.54	11.64	0.071
Foraging stratum	**Understorey**	11	100.00	9	81.82	9	81.82	13	92.86	9	81.82	9	100.00	10	83.33	4.99	0.545
	Mid-storey	4	100.00	4	100.00	4	100.00	5	100.00	4	100.00	4	100.00	4	100.00	0.00	1.000
	Canopy	40	83.33	39	88.64	35	83.33	43	93.48	41	85.42	34	80.95	41	91.11	1.46	0.962
	Edge	36	62.07	24	42.11	21	40.38	24	30.77	32	45.07	29	49.15	25	36.23	13.86	0.030
	Aerial	11	78.57	7	*53.84	9	75.00	9	64.29	12	75.00	8	*53.33	12	85.71	**13.86**	**0.030**
Feeding guild	**Carnivore**	12	70.59	8	57.14	9	56.25	6	**30.00	10	52.63	9	50.00	7	**36.84	**21.63**	**0.001**
	Insectivore	61	79.22	54	71.05	49	66.22	62	65.26	62	70.45	52	69.33	59	68.60	1.79	0.938
	Frugivore/Granivore	23	67.65	8	**25.00	16	61.54	20	57.14	21	58.33	18	60.00	21	63.64	**21.50**	**0.001**
	Nectarivore	6	85.71	5	71.43	4	80.00	6	85.71	5	71.43	5	83.33	5	83.33	2.92	0.818
Habitat specialization	**Forest specialist**	22	88.00	22	91.67	22	100.00	23	85.19	24	92.31	19	100.00	17	77.27	4.35	0.629
	Forest generalist	24	85.71	22	81.48	21	80.77	27	84.38	24	80.00	21	75.00	22	75.86	1.18	0.977
	Woodland generalist	30	61.22	29	55.77	22	48.89	36	55.38	30	51.72	26	53.06	22	36.07	0.53	0.991
	Grassland generalist	26	**78.78	10	38.46	13	46.43	8	24.24	20	55.56	18	54.55	10	31.25	**42.09**	**<0.001**
Dispersal behaviour	**Sedentary resident**	52	80.00	44	69.84	37	66.07	46	63.01	48	65.75	44	70.97	46	65.71	2.30	0.888
	Dispersive resident	22	61.11	19	51.35	17	51.52	26	60.47	22	56.41	17	50.00	25	69.44	1.08	0.983
	Local migrant	12	80.00	10	76.92	11	78.57	10	62.50	12	80.00	10	83.33	6	*46.15	**13.52**	**0.035**
	Intra-African migrant	14	93.33	9	*60.00	12	85.71	11	*68.75	15	93.75	12	*75.00	13	92.86	10.08	0.121
	Palaearctic migrant	2	50.00	1	**100.00	1	25.00	1	11.11	1	14.29	1	20.00	1	10.00	**193.51**	**<0.001**

Values indicated by * denotes χ2 test p-value <0.05; Values indicated by ** denotes χ2 test p-value <0.01

Appendix S2.5 Bird species detected (Det.), and the proportion of total diversity within different functional trait class represented (%T) by mist-netting surveys within seven Afrotemperate forests in the Eastern Cape. A series of χ2 tests were used to determine the proportional differences of the representation for each functional trait class by mist-netting surveys between all seven forests

		Ngele		Gomo		Baziya		Manubi		Kubusi		Fort Fordyce		Alexandria			
		Det.	% T	Det.	% T	Det.	% T	Det.	% T	Det.	% T	Det.	% T	Det.	% T	χ2 value	*p* of χ2
Det. observed community		31	22.96	31	24.03	28	23.14	39	24.84	43	28.67	27	20.93	30	20.83	1.81	0.936
Body size	**Small (<50 g)**	24	29.27	26	31.71	24	32.00	32	32.00	24	25.53	21	25.61	23	26.44	1.91	0.927
	Medium (50-100 g)	5	22.73	3	14.29	3	15.79	6	26.09	4	18.18	5	27.78	5	25.00	7.93	0.243
	Large (>100 g)	2	6.45	2	7.69	1	3.70	1	2.94	0	0.00	1	3.33	2	5.41	9.23	0.161
Foraging stratum	**Understorey**	7	63.64	6	54.55	7	63.64	12	85.71	7	63.64	6	66.67	8	66.67	8.09	0.232
	Mid-storey	3	75.00	4	100.00	4	100.00	4	80.00	4	100.00	3	75.00	2	*50.00	**25.26**	**<0.001**
	Canopy	12	25.00	13	29.55	10	23.81	18	39.13	20	41.67	15	35.71	15	33.33	8.57	0.199
	Edge	9	15.52	8	14.04	7	13.46	*5	6.41	10	14.08	*3	5.08	*3	4.35	**13.74**	**0.032**
	Aerial	0	0.00	0	0.00	0	0.00	0	0.00	**1	6.25	0	0.00	0	0.00	**37.50**	**<0.001**
Feeding guild	**Carnivore**	2	11.76	1	7.14	**0	0.00	1	5.00	**0	0.00	1	5.56	1	5.26	**20.30**	**0.002**
	Insectivore	22	28.57	21	27.63	19	25.68	28	29.47	30	34.09	20	26.67	21	24.42	2.12	0.908
	Frugivore/Granivore	5	14.71	6	18.75	7	26.92	5	14.29	10	27.78	3	10.00	5	15.15	**14.93**	**0.021**
	Nectarivore	**2	28.57	3	42.86	2	40.00	**5	71.43	3	42.86	3	50.00	3	50.00	**22.27**	**0.001**
Habitat specializati	**Forest specialist**	7	28.00	9	37.50	9	40.91	13	48.15	13	50.00	8	42.11	11	50.00	9.02	0.173
	Forest generalist	11	39.29	12	44.44	10	38.46	16	50.00	17	56.67	13	46.43	14	48.28	5.17	0.522
	Woodland generalist	8	16.33	9	17.31	6	13.33	10	15.38	10	17.24	6	12.24	5	8.20	4.48	0.599
	Grassland generalist	5	15.15	1	3.85	3	10.71	**0	0.00	3	8.33	**0	0.00	**0	0.00	**40.81**	**<0.001**
Dispersal behaviour	**Sedentary resident**	20	30.77	23	36.51	28	50.00	26	35.62	28	38.36	17	27.42	23	32.86	8.70	0.191
	Dispersive resident	4	11.11	5	13.51	4	12.12	6	13.95	7	17.95	4	11.76	4	11.11	2.68	0.847
	Local migrant	6	40.00	3	23.08	6	42.86	5	31.25	6	40.00	4	33.33	3	23.08	11.81	0.066
	Intra-African migrant	1	**6.67	0	0.00	0	0.00	2	**12.50	2	**12.50	2	**12.5	0	0.00	**37.17**	**<0.001**
	Palaearctic migrant	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0.00	1.000

Values indicated by * denotes χ2 test p-value <0.05; Values indicated by ** denotes χ2 test p-value <0.01

Appendix S2.6 AIC model selection of generalised linear mixed-effect logistic regression model representing factors affecting avian species detection in Afromontane forests by point counts. Included are the AIC values, AIC difference (ΔAIC), model fit (*Conditional* R^2), and Akaike weights (w_i) for each model. The global model is in bold

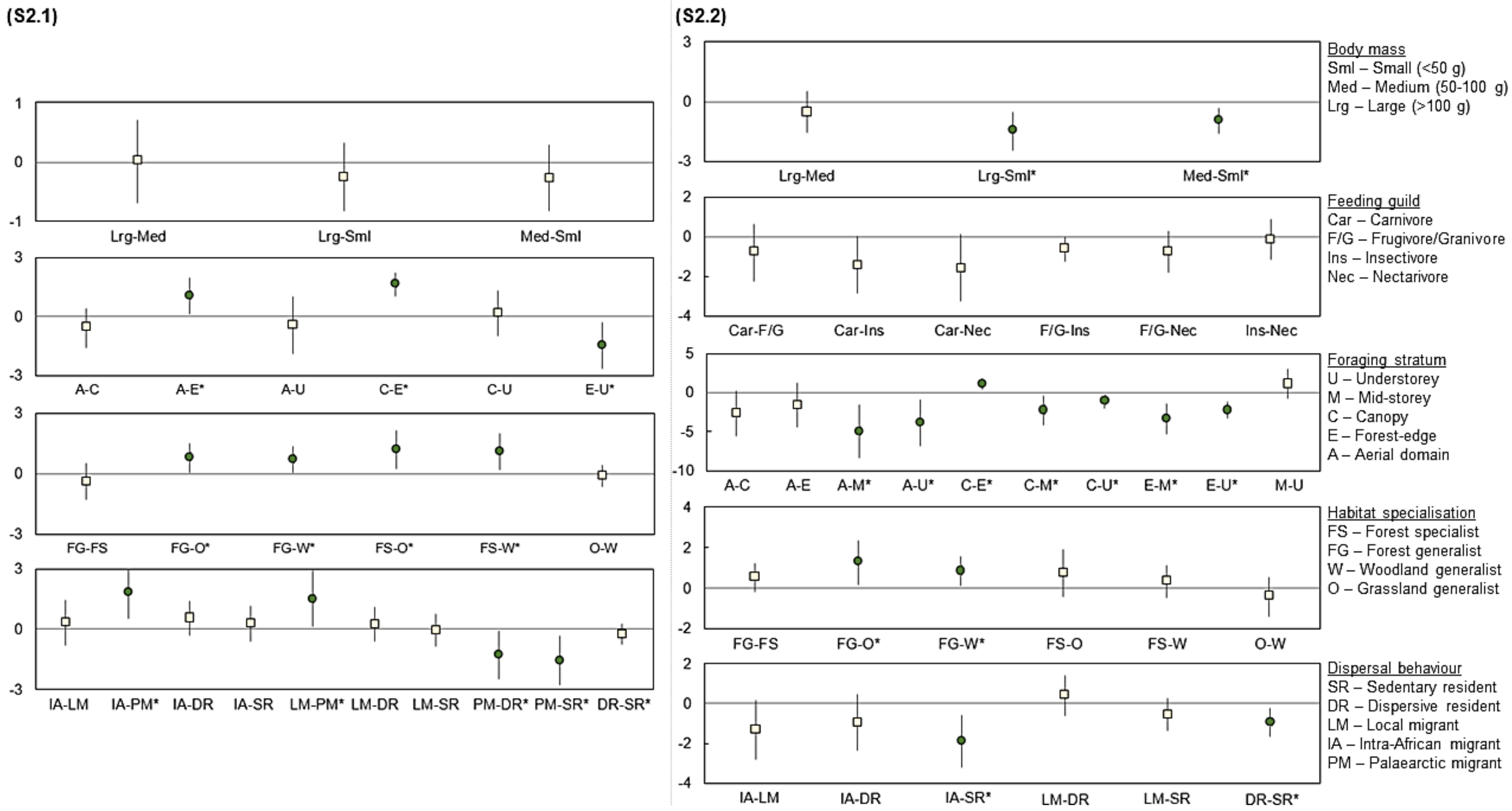
Model R code*	AIC	ΔAIC	*Cond.* R^2	w_i
~Stratum+Size+Specialization+Dispersal+(1|Forest)	1021.98	0.00	0.80	0.43
~Stratum+Specialization+Dispersal+(1|Forest)	1022.25	0.27	0.70	0.40
~Stratum+Size+Specialization+Dispersal+Diet+(1|Forest)	1024.60	2.62	0.78	0.04
~Stratum+Dispersal+(1|Forest)	1033.36	11.38	0.70	0.00
~Stratum+(1|Forest)	1048.16	26.18	0.84	0.00
Null (~1)	1256.19	234.21	0.00	0.00
Null (~1+(1|Forest))	1257.96	235.98	0.00	0.00

*Mixed-effects models were fitted using 'glmer' function in the 'lme4' R package, and the final null model was fitted using the function 'glm' in the 'Stats' R package.

Appendix S2.7 AIC model selection of generalised linear mixed-effect logistic regression model representing factors affecting species detection in Afromontane forests by mist-netting. Included are the AIC values, AIC difference (ΔAIC), model fit (*Conditional* R^2), and Akaike weights (w_i) for each model

Model	AIC	ΔAIC	*Cond.* R^2	w_i
~Stratum+Size+Specialization+Dispersal+Diet+(1|Forest)	736.50	0.00	0.83	0.66
~Stratum+Size+Dispersal+Diet+(1|Forest)	738.20	1.70	0.86	0.29
~Stratum+Size+Dispersal+(1|Forest)	744.28	7.78	0.83	0.01
~Stratum+Size+(1|Forest)	761.31	24.81	0.48	0.00
~Stratum+(1|Forest)	830.98	94.48	0.39	0.00
Null (~1)	1049.06	312.56	0.00	1.00
Null (~1+(1|Forest))	1051.06	314.56	0.00	1.00

*Mixed-effects models were fitted using 'glmer' function in the 'lme4' R package, and the final null model was fitted using the function 'glm' in the 'Stats' R package.



Appendix S2.8 Post hoc comparisons of effect sizes between sub-levels between factors of the best-supported GLM models explaining forest-utilising bird species detectability by point counts (S2.1) and mist-netting (S2.2) across the seven Afrotemperate forest sites: body mass, feeding guild, foraging stratum, habitat specialisation, and dispersal behaviour. Error bars indicate 95 % confidence intervals (CI). Green circles are significant comparisons (*=*p* <0.05), while light squares are non-significant. Comparisons not shown are non-significant, with CI exceeding the range of related comparisons.

Chapter 3: Species-landscape interactions drive divergent population trajectories in four forest-dependent bird species following anthropogenic habitat transformation of fragmented Afromontane forests in South Africa

3.1 Abstract

A landscape genetics study was undertaken to investigate mechanisms driving documented avian population declines in naturally fragmented Afromontane forests across the Eastern Cape and southern KwaZulu-Natal provinces of South Africa. Microsatellite data for four forest-dependent passerines were used to conduct *a priori* optimisation of landscape resistance surfaces (landcover, freshwater systems, and topography) using least cost pathway (LCP), and resistance distances (IBR). We detected pronounced declines in effective population sizes over the past two centuries for the endemic forest specialist *Cossypha dichroa* and near-endemic *Batis capensis,* alongside geneflow disruption in *B. capensis*, *C. dichroa*, and *Pogonocichla stellata*, highlighting vulnerability to increasing anthropogenic activity. Landscape resistance modelling showed both forest, and coastal/mesic thicket configuration to facilitate geneflow in *P. stellata*, *B. capensis*, and *C. dichroa*. Facultative dispersal of *P. stellata* through thicket likely aided species resilience against historic landscape transformation, whereas combined forest-thicket degradation adversely affected the forest generalist *B. capensis*. Forest connectivity in all four species is improved at lower elevations, along river valleys, and riparian corridors. Consistent outperformance of LCP over IBR landcover models for *P. stellata*, *B. capensis*, and *C. dichroa*, demonstrates the benefits of wildlife corridors for regional Afromontane forest bird conservation. In contrast, the fourth species, *Phylloscopus ruficapilla,* appears highly dispersive, least reliant upon landscape features to maintain connectivity, and consequently was least impacted by anthropogenic landscape transformation. Additionally, the study supports a pattern of adult philopatry in these species, finding geneflow to be more contingent upon natal dispersal than on adult mobility.

3.2 Introduction

The impacts of anthropogenic habitat fragmentation on biodiversity are characterized by different spatial and temporal responses among taxa (Epps & Keyghobadi, 2015; Lowe et al., 2015; Radespiel & Bruford, 2014), and are thus difficult to elucidate (Fahrig, 2017a, 2017b; Fahrig et al., 2019; Fletcher et al., 2018). Interpretations of species responses to distinct historic and contemporary anthropogenic environmental disturbances can be particularly difficult in species endemic to inherently fragmented habitats, where population complexity may arise naturally (Epps & Keyghobadi, 2015; Fenderson et al., 2020; Richardson et al., 2016; Samarasin et al., 2017). Factors obfuscating true species responses to anthropogenic habitat fragmentation, include temporally delayed population-level manifestation of environmental perturbations (Epps & Keyghobadi, 2015; Lowe et al., 2015; Samarasin et al., 2017); dissonant changes to both small-scale (local dispersal) and large-scale (long distance migration) species movements (Freckleton et al., 2005; Richardson et al., 2016); species-specific sensitivity to habitat degradation (Amos et al., 2012; Devictor et al., 2008; Dondina et al., 2017); and landscape configuration change (DeCamargo et al., 2018). Higher vagility in species typically improves functional connectivity across fragmented habitats (Amos et al., 2014; Callens et al., 2011; Canales-Delgadillo et al., 2012; Kalle et al., 2018), as does the ability of facultative dispersal through otherwise unsuitable intermediary habitats (Keeley et al., 2017). This latter trait is under-appreciated in landscape ecology, yet can be critical for understanding structural connectivity between fragmented primary habitat of vulnerable species (Driscoll et al., 2013; Kadmon & Allouche, 2007; Kupfer et al., 2006). As the loss of important matrix habitats can reduce landscape permeability to species dispersal, and exacerbate the effects of primary habitat loss, identifying and preserving matrix elements necessary for short-term species viability, even when infrequently utilized, is imperative in conserving species. Testing adaptation to both natural and anthropogenic fragmentation is best achieved by comparative research on multiple species which differ in their level of habitat specialisation and mobility.

The forest biome in South Africa represents ~0.5 % of the total land surface area, yet supports >14 % of local terrestrial bird and mammal diversity (Geldenhuys & Macdevette, 1989). This biome experienced Paleoclimatic fragmentation (Eeley et al., 1999; Lawes et al., 2007a), and is broadly partitioned into two sub-biomes: Afromontane forests along the eastern/southern escarpment and south coast, and Indian Ocean coastal belt (IOCB) forest confined to the east coastal plain (Mucina, 2018; von Maltitz et al., 2003), with an intermediate type, scarp forest, transitional between these sub-biomes. Over the last two centuries, deforestation has reduced the IOCB and Afromontane forest extent by >80% and ~15%, respectively (Berliner, 2009; Olivier et al., 2013). Commercial logging of natural forests largely ceased by 1940 (Adie et al., 2013; Lawes et al., 2007b), but ongoing illegal harvesting of forest products is widespread, and can impede ecological restoration (Leaver & Cherry, 2020a). Small forest patchwork clearance has reduced forest structural connectivity (Kotze & Lawes, 2007), alongside matrix conversion to plantation, agriculture, and urbanisation (Freeman et al., 2018; Russell & Ward, 2016). Forest community responses to anthropogenic processes have been reasonably well studied (Ehlers-Smith et al., 2020; Olivier & Van Aarde, 2014; Piñeiro et al., 2017; Wethered & Lawes, 2003; Zungu et al., 2020), but the effects upon genetic diversity and metapopulation structure of species is less known. Also undetermined are temporal changes in effective population sizes of forest dependent species, and this can illuminate the extent and causes of population declines over time (Callens et al., 2011; Habel et al., 2014; Khimoun et al., 2017; Woltmann et al., 2012).

From a broad conservation perspective, birds are viewed as relatively resilient to habitat fragmentation (DeCamargo et al., 2018). Forest-dependent birds, however, often have lower dispersal propensities, and are thus susceptible to fine-scale isolation following forest fragmentation (Callens et al., 2011; Habel et al., 2014; Khimoun et al., 2017; Woltmann et al., 2012). Approximately half of South African forest-dependent birds have undergone range contractions since 1992 (Cooper et al., 2017), but these do not necessarily entail population declines, particularly for nomadic frugivores (Downs et al., 2014; Kalle et al., 2018; Lenz et al., 2015). Range and population declines could indicate extinction debts resulting from delayed responses to historic and contemporary forest exploitation (Brooks et al., 1999; Leaver et al., 2020; Olivier et al., 2013), and landscape change (Bailey et al., 2016; Jewitt et al., 2015). Present-day forest remnants are ostensibly state protected, but nonetheless experience habitat degradation through largely unregulated informal harvesting (Leaver & Cherry, 2020a), which has led to changes both in habitat quality (Leaver & Cherry, 2020b), avian functional diversity (Leaver et al., 2019a), and community structure (Leaver et al., 2020; Leaver et al., 2019a).

In this study, we investigated the regional landscape influence on the genetic population structure of four geographically sympatric forest-dependent passerines across the region of South Africa where observed avian declines were most severe. Small-bodied (≤50 g) insectivores were selected as they represent a functional group especially sensitive to global forest fragmentation (Bregman et al., 2014; Sekercioglu et al., 2002). Each passerine included in this study is classified as ‘Least Concern’ [IUCN, 2020], but has undergone range declines (shown in parentheses), most notably in the Eastern Cape Province (Cooper et al 2017): chorister robin-chat, *Cossypha dichroa* (-19.5%); yellow-throated woodland-warbler, *Phylloscopus ruficapilla* (-20.7%); white-starred robin, *Pogonocichla stellata* (-23.0%); and Cape batis, *Batis capensis* (-1.3%). All four species show high affinity for mid- and understoreys of Afromontane and scarp forests, although *B. capensis* is additionally present in mesic and valley thicket (Harrison et al., 1997b; Hockey et al., 2005), and thus more readily engages with various habitat types in the matrix. Partial altitudinal migration is suspected in each species (Johnson & Maclean, 1994; Oatley, 2017), particularly *P. stellata* (Craig & Hulley, 2019; Oatley, 1982a), although adult philopatry (Habel et al., 2016; Oatley, 1982a) could mean that geneflow is mostly contingent upon natal dispersal of young birds (Garrard et al., 2012). The impact of anthropogenic landscape conversion on both individual movement and geneflow of these species is unknown.

Landscape genetic frameworks can be hugely informative (Cushman et al., 2012; Eberle et al., 2017; Khimoun et al., 2017): specifically, relationships between genetic distances and various landscape features can be modelled using resistance surfaces of spatially arranged cost values to geneflow (Manel & Holderegger, 2013; Manel et al., 2003; Waits et al., 2015). These frameworks consider varying degrees of landscape complexity and spatial scales to investigate ecological integration with the landscape. *A priori* algorithmic optimisation of resistance surfaces within unconstrained parameter space of each landscape variable circumvents two major drawbacks of previous parameterisation approaches, namely the subjectivity of conflicting expert opinion (Charney, 2012; Zeller et al., 2012), and limited applicability of niche-model derivations towards atypical landscape use (Balkenhol et al., 2015; Keeley et al., 2017; Vasudev et al., 2015; Zhan et al., 2017). Here we use resistance optimization methods created by Peterman et al. (2014), and Peterman (2018), both to infer the extent of facultative dispersal in each species, and to determine the relative influences of various landcover classes (both natural and anthropogenic) on geneflow. Freshwater systems and landscape topography were also tested, as both landscape features can influence altitudinal migrations (Oatley, 2017), and thus geneflow. We hypothesized that anthropogenic landscape transformation would negatively impact the population sizes and forest connectivity of *C. dichroa, P. ruficapilla,* and *P. stellata,* which have undergone the largest range contractions, and which are most at-risk to forest interior degradation. Second, we predicted that across species, landscape features influence forest connectivity more than geographic distance alone, and that each species would show varying responses to anthropogenic matrix transformation.

The present study provides genetic evidence for population declines in forest-dependent birds in South Africa, highlighting the risk of extinction debts from past forest exploitation, and encouraging implementation of legislation regulating informal forest-product harvesting to

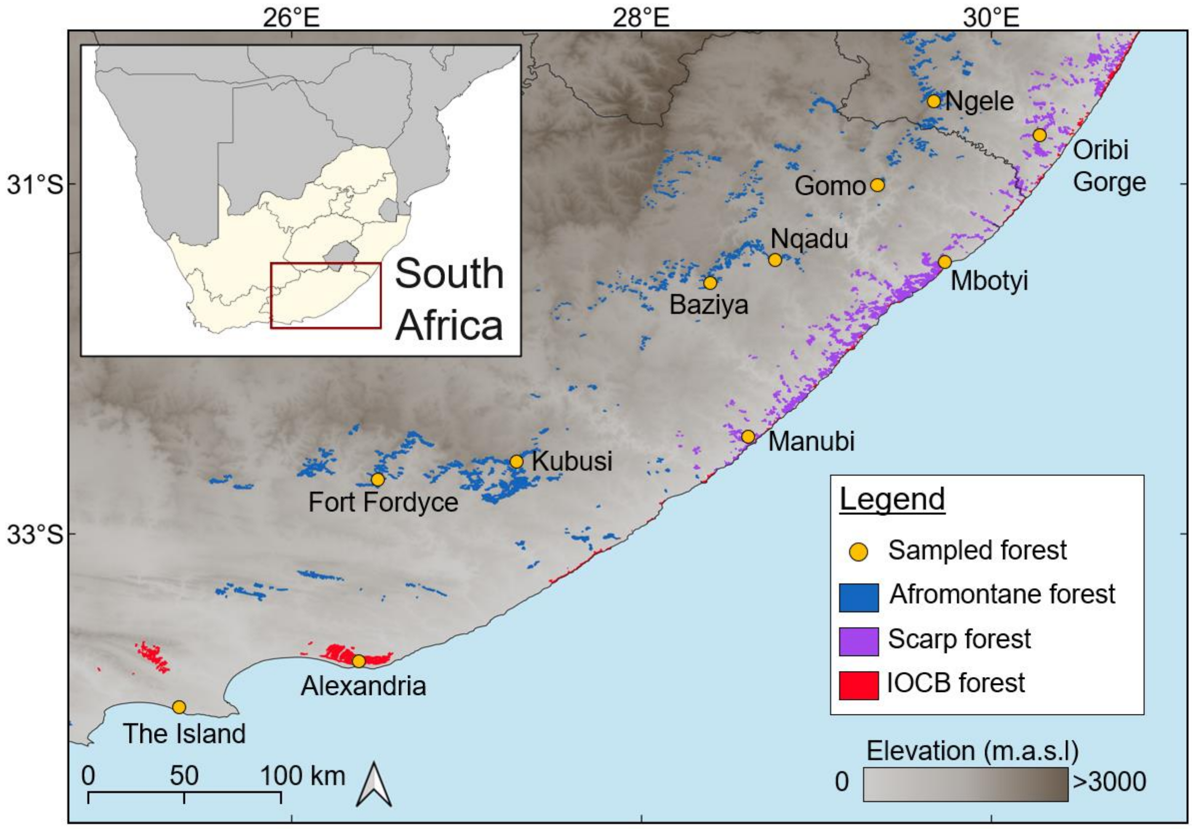


Figure 3.1 The distribution of Afromontane (blue), scarp (purple), and Indian Ocean coastal belt (IOCB) (red) forests across the Eastern Cape and southern KwaZulu-Natal Provinces of South African, shown alongside sampled forest locations.

preserve extant forest integrity (Leaver & Cherry, 2020b). Despite differences in forest specialisation, and the extent of observed range contractions, *B. capensis* and *C. dichroa* showed substantial population declines over the past century, and, alongside *P. stellata*, experienced strong geneflow disruption. Only *P. ruficapilla* appeared genetically resilient against present anthropogenic habitat changes. Finally, our results demonstrate the importance of coastal/mesic thicket vegetation in the matrix; and riparian corridors, to the genetic integrity of these forest-dependent passerines, which have low effective population sizes within an already precarious habitat.

3.3 Materials and Methods

3.3.1 Field sampling and laboratory procedures

From 2017-2018, standardized mist-netting (De Beer et al., 2001) was conducted over three-week periods in eleven forests sites – eight Afromontane, two scarp, and two IOCB – in the Eastern Cape and southern KwaZulu-Natal provinces of South Africa, falling within the

Maputo-Pondoland-Albany biodiversity hotspot (Mittermeier et al., 2004) (Figure 3.1). In total, 114 *B. capensis*, 94 *C. dichroa*, 92 *P. ruficapilla*, and 200 *P. stellata* were captured (Table 3.1). Birds were banded to prevent resampling, and released at the capture location after sampling of 20-50 µL of blood, collected from the brachial vein using sterile hypodermic needles, and heparinized tubes in conformity to South African legal requirements (see Acknowledgements). Collected blood samples were preserved in 500 µL 95% ethanol, and genomic DNA was extracted using a Nucleospin Tissue DNA extraction kit (Macherey-Nagel, Germany). Species- and genus-specific microsatellite libraries were available for each focal bird species, of which eight informative microsatellite loci were reliably amplified per species (see Appendix S3.1 for microsatellite locus authorship, screening, and amplification conditions). We randomized within-species sample prior to amplification to minimize false-positive discovery from downstream analyses (Meirmans, 2015). Microsatellite alleles were genotyped on an ABI377xl sequencer (CAF, Stellenbosch), against LIZ 500© internal size marker, and scored in GENEIOUS 7.1.4 (©Biomatters), using three positive control individuals per species for each marker to verify scoring accuracy.

3.3.2 Population genetic diversity and structure

Amplification errors (large allele drop-out, stuttering, and null alleles) were screened in MICROCHECKER 2.2.3 (Van Oosterhout et al., 2006) and FREENA (Kawashima et al., 2009). Forest-level deviations from expectations of Hardy-Weinberg equilibrium (HWE), and linkage disequilibrium (LD) within forests were assessed in GENEPOP 4.7 (Rousset, 2008); adjusting significance values using a Benjamini-Hochberg correction (Benjamini & Yekutieli, 2001) to control for false discovery rate. Forest-level species genetic diversity was estimated as rarefied allelic richness (*AR*), and private allelic richness (*PrAR*) in ADZE 1.0 (Szpiech et al., 2008); observed (H_o) and expected (H_e) heterozygosity; and inbreeding coefficient (F_{IS}), in GENETIX 4.05 (Belkhir et al., 2001). Additionally, we used POWSIM 4.1 (Ryman & Palm, 2006) to assess the power of each microsatellite dataset to detect population substructures at $F_{ST} = 0.05$ (effective population size, $N_e = 2000$; generations of genetic drift, $t = 210$), $F_{ST} = 0.01$ ($N_e = 2000$, $t = 40$), and $F_{ST} = 0.001$ ($N_e = 2000$, $t = 4$). An N_e of 2000, approaching the upper bounds of the estimated effective population size (see Table 3.5), was selected as larger N_e are considered more appropriate; the value of t was selected following recommendations by Ryman & Palm (2006) to test for the particular F_{ST}. Simulations were performed assuming two subpopulations ($N = 50$ and $N = 40$) over 1000 replicates, and statistical power was measured as the proportion of tests which were significant.

Population genetic substructures were investigated through spatial Bayesian clustering in TESS 2.3.1 (Chen et al., 2007a). The optimal number of genetic clusters per species (K) were tested and ranged from 2 – 12. Twenty independent runs of 5×10^5 Markov Chain Monte Carlo (MCMC) iterations and a burn-in period of 5×10^4 were performed per K, using the conditional autocorrelation (CAR) admixture model, with an default interaction parameter (ψ) of 0.6 (Chen et al., 2007b; Durand et al., 2009). Model fit was assessed using deviance information criterion (DIC), and 20% lowest DIC runs per K were retained to infer the most likely number of clusters. TESS results were visualized in the Pophelper R package (Francis, 2017). To further investigate population structure we also performed principal component analysis in the adegenet R package (Jombart & Ahmed, 2011) based on individual allele frequencies. Finally, to determine population differentiation we calculated global and pairwise F_{ST} among forests for each species in ARLEQUIN 3.5 (Excoffier & Lischer, 2010).

3.3.3 Demographic history

To infer dissonance between historic and contemporary geneflow, we compared pairwise F_{ST}, estimated in ARLEQUIN 3.5, to the dissimilarity in proportions of shared alleles, D_{PS}, calculated in MSA 4.0 (Dieringer & Schlötterer, 2003). The former metric better measures historic population differentiation, while the latter more accurately reflects contemporary population connectivity of the most recent generations. Large $D_{PS}/\mathrm{F_{ST}}$ ratios suggest recently restricted geneflow (Robin et al., 2015). Additionally, we estimated regional contemporary effective population sizes (CN_e) for each species in NEESTIMATOR 2.1 (Do et al., 2014), using the LD model, and assuming both random and monogamous mating to reflect general dispositions towards monogamy within focal species (Hockey et al., 2005). We observed results at 0.02 and 0.01 critical allele frequencies, and used a pairwise jackknife approach to assess confidence intervals; within-species samples were pooled to accommodate overlap/interbreeding among the most recent generations. We further inferred variation in focal species N_e over the most recent 100 generations using the VarEff R package (Nikolic & Chevalet, 2014). Default parameter conditions were kept across species, adjusting maximum distance between alleles ($DMAX$ = 18 – *P. stellata*; 17 – *C. dichroa;* 22 – *B. capensis;* 10 – *P. ruficapilla)*, number of past N_e changes ($JMAX$ = 3); and generations since the most recent common ancestor ($GBAR$ = 1000; reduced from the default $GBAR$ = 5000 given the low population differentiation observed for each species). Runs were performed under both single-step mutation model (SMM), and 10% single-step two-phase mutation (TPM), assuming a mutation rate of $\mu = 5x10^{-4}$ per generation (Brohede et al., 2002; Coetzer et al., 2020), with an acceptance ratio of 0.25.

3.3.4 Landscape resistance modelling

3.3.4.1 Landscape genetics framework

Landscape influences on species connectivity were assessed using the RESISTANCEGA 4.1 R package (Peterman, 2018), which integrates mixed-effects modelling and stochastic genetic algorithms mimicking natural selection (Scrucca, 2013) specifically to maximize the relationship between pairwise genetic distances of samples and resistance surfaces. Models were fitted using maximum-likelihood population effects (MLPE) parameterization (Clarke et al., 2002) in the LME4 R package (Bates et al., 2014) where fitness was assessed using corrected Akaike information criteria (AIC_c). Models with an AICc difference (ΔAIC_c) < 2 were considered equivalent (Burnham & Anderson, 2002). We modelled two ecological distances for each landscape surface: isolation-by-resistance (IBR) considers cumulative current-flow costs across all possible paths between two points, whereas least cost pathways (LCP) reflect costs of traversing the most efficient routes. The IBR models were drafted using commute-time resistance distances, an equivalent to circuit-theory models for determining flow resistance (McRae et al., 2013), in RESISTANCEGA 4.1. The LCP models in turn were made using the cost distance function in the gdistance R package (Van Etten, 2015). We used pairwise F_{ST} between forests (Appendix S3.6-S3.9) as the dependent variable for mixed-effects modelling, and scaled and centred LCP and IBR surfaces as predictor variables.

3.3.4.2 Landscape variables

We assessed the relative influence of three landscape variables on connectivity in each focal species (Figure 3.2): (i) landcover; (ii) freshwater systems; and (iii) topography. Landcover, and freshwater systems resistance surfaces were based on 20 m categorical landcover classes taken from the South African National Landcover (SANLC) 2018 (Thompson, 2019), while topographic surfaces were based on 7.5 arc-second (250 m) categorical map of mean elevation in metres above sea level (m.a.s.l), taken from the Global Multi-resolution Terrain Elevation Data 2010 (Danielson & Gesch, 2011). We up-scaled the spatial grain to grid size of 250 m x 250 m for all raster layers to expedite analyses without significant loss of landscape-genetic associations (McRae et al., 2008). For freshwater systems, we consolidated rivers, estuaries, lakes, dams, and herbaceous wetlands, and classified all up-scaled cells containing these variables into the freshwater system class, regardless of proportion of this class present within the cell. For landcover (see below), we classified cells according to the majority landcover class within each cell. We prepared resistance surfaces by creating a convex hull around forest sites using the ConvexHull plug-in for QGIS 3.10 (QGIS Development Team, 2018), and setting a 50 km buffer as the boundary for downstream analyses. The latter condition was included to accommodate total movement among available forest habitat throughout the study area.

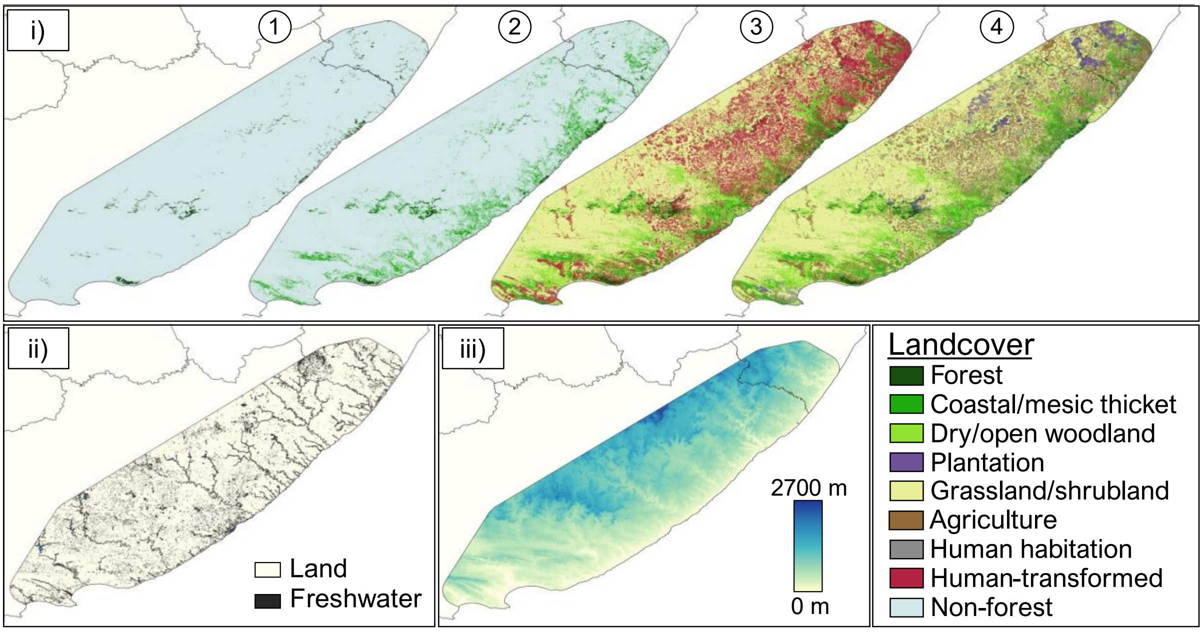


Figure 3.2 Landscape surfaces at a spatial resolution of 250 x 250 m cell size used to calculate LCP and IBR ecological distance modelling. (i) Four classifications of landcover surfaces: (1) forest configuration; (2) forest and coastal/mesic thicket configuration; (3) natural vegetation (forest, coastal/mesic thicket, dry/open woodland, and grassland), and combined human-transformed areas (plantation, agriculture, and human habitation); (4) all seven recognised landcover classes; (ii) categorical freshwater systems; (iii) continuous topographic surface (in metres above sea level).

3.3.4.5 Thematic resolution of landscape matrix

To infer matrix permeability across different landcover classes, we tested four alternative landcover surfaces under different classification schemes (Figure 3.2). The original 72 landcover classes were consolidated into seven categories: (a) forest; (b) coastal/mesic thicket (including valley thicket); (c) open woodland; (d) grassland/shrubland; (e) *Pinus*/*Eucalyptus* plantation; (f) agriculture; and (g) human habitation (urban, suburban, rural, industrial, transportation networks, and mining). From this, the four resistance surfaces were prepared as follows: (1) forest configuration; (2) forest and coastal/mesic thicket configuration; (3) natural vegetation (forest, coastal/mesic thicket, open woodland, grassland/shrubland) vs modified landcover (agriculture, plantation, human habitation); and (4) a comprehensive surface of all seven categories. For computational efficiency, resistances surfaces 1-4 were optimized three times per species, using least-cost distances based on pairwise F_{ST}. Additionally, to test whether a more contemporary geneflow metric better reflects recent landscape change, we optimized these four surfaces once using pairwise D_{PS} (Appendix S3.6-S3.9).

3.3.4.6 Resistance surface optimisations and landscape distance model comparisons

Univariate optimisation was conducted separately on the best-supported thematic landcover; freshwater systems; and topography resistance surfaces. Multivariate optimisation was subsequently conducted on a composites of the three resistance surfaces. Optimisations were repeated three times each for IBR and LCP ecological distance modelling regimes, separately for each species. Following Cushman et al. (2013), and Khimoun et al. (2017), we used causal modelling to compare species-specific IBR and LCP ecological distance models to isolation-by-distance (IBD), according to Spearman correlations between genetic- and landscape distances. We inferred whether landscape models correlated significantly with genetic distances using Mantel and partial Mantel tests in the ecodist R package (Goslee & Urban, 2015), with 10000 random permutations, using distance values for LCP and IBR models, and log-transformed Euclidean distances for IBD. Despite the high rates of type I error alleged for partial Mantel tests (Castellano & Balletto, 2002; Raufauste & Rousset, 2001), use of these tests in a causal model framework to reject the incorrect causal model, and to identify the most applicable models driving observed genetic patterns is considered appropriate (Cushman et al., 2013; Cushman & Landguth, 2010; Khimoun et al., 2017). Spatially constrained dispersal which is not impacted by the landscape should be best supported by the IBD model. Efficient dispersal dictated by landscape features would reveal LCP, whereas inefficient or haphazard dispersal following landscape features would show IBR.

3.4 Results

3.4.1 Microsatellite characteristics and genetic diversity

All individuals were successfully genotyped for all loci (Table 3.1). The eight informative microsatellite markers retained per species exhibited no large allele dropout, or stuttering, displayed null allele frequencies <5% across populations, and had limited deviations from expectations of LD and HWE (Appendix S3.2-3.5). At the forest level, loci were in HWE after Benjamini-Hochberg corrections, except for BMI-32 for *B. capensis* at The Island. Only 2/252 (0.79%) LD tests concerning different loci/population combinations in *P. stellata* remained significant after Bonferroni-Hochberg corrections, while linkage between loci of the other three species were non-significant. All loci were therefore assumed independent. Genetic diversity, in terms of standardized allelic richness and observed heterozygosity, was similar between *B. capensis* (AR = 10.625; H_o = 0.625), *P. stellata* (AR = 9.750; H_o = 0.646), and *C. dichroa* (AR = 8.00; H_o = 0.648), yet lowest in *P. ruficapilla* (AR = 3.375; H_o = 0.391) (Table 3.1). Private allelic diversity was highest in *C. dichroa* ($PrAR$ = 0.26), slightly lower in *B. capensis* ($PrAR$ = 0.20) and *P. stellata* ($PrAR$ = 0.19), and very low in *P. ruficapilla* ($PrAR$ = 0.04) (Table 3.1). Observed heterozygosity was slightly higher than expected in *C. dichroa* (H_o =0.648; H_e = 0.636) and *P. ruficapilla* (H_o =0.391; H_e = 0.381), slightly lower than expected in *P. stellata* (H_o =0.646; H_e = 0.651), and far lower than expected in *B. capensis* (H_o =0.625; H_e = 0.701) (Table 3.1). A relatively high inbreeding coefficient in *B. capensis* (F_{IS} = 0.151) indicates a greater genetic diversity deficit than observed in the other three species, for which F_{IS} estimates were close to zero (Table 3.1). Microsatellite performance assessments showed it was possible to detect genetic divergence as low as F_{ST} = 0.01 (t = 40) with 94.4% certainty in *B. capensis*, 92.4% in *C. dichroa*, and 91.1% in *P. stellata*, but only 55.7% certainty for *P. ruficapilla*, although F_{ST} = 0.02 (t = 80, n = 2000) could be detected with 84.7% certainty for this species. All four microsatellite datasets had low certainties (6.5-12.0%) to detect F_{ST} = 0.001 (t = 4).

3.4.2 Genetic population structure

Global genetic differentiation was significant for *C. dichroa* (F_{ST} = 0.036, $p < 0.001$) and *P. stellata* (F_{ST} = 0.016, $p < 0.001$), but not for *B. capensis* (F_{ST} = 0.013, p = 0.100) and *P. ruficapilla* (F_{ST} = 0.006, p = 0.261). Using 20% lowest DIC per K, best supported TESS results indicated a maximum of K ≤ 2, respectively, for each species. Progressing from north to south (Figure 3.1), a northeast-southwest geographic gradient in admixture proportions between two genetic clusters was discernible in *B. capensis* and *C. dichroa*, but was more pronounced in the latter (Figure 3.3). For *B. capensis*, individuals from Ngele to Kubusi align closer with cluster 1, and those from Fort Fordyce and The Island mostly with cluster 2. For *C. dichroa*, individuals from Ngele to Manubi represented one extreme of cluster 1, and could be partitioned from those from Kubusi to Alexandria. Kubusi is noteworthy for harbouring a residual subpopulation, evident for K ≥ 3 (Figure 3.3; Appendix S3.10), and the PCA graphs (Appendix S3.11) show a large genetic dissimilarity between *C. dichroa* individuals at Kubusi. Additionally, Oribi Gorge is readily differentiated from adjacent forests across multiple K values. All *P. ruficapilla* individuals uniformly aligned with cluster 1, and appear to belong to a single, undifferentiated population (Figure 3.3). Finally, *P. stellata* individuals from Alexandria and The Island were starkly differentiated from other forest subpopulations showing weak structuring (Figure 3.3).

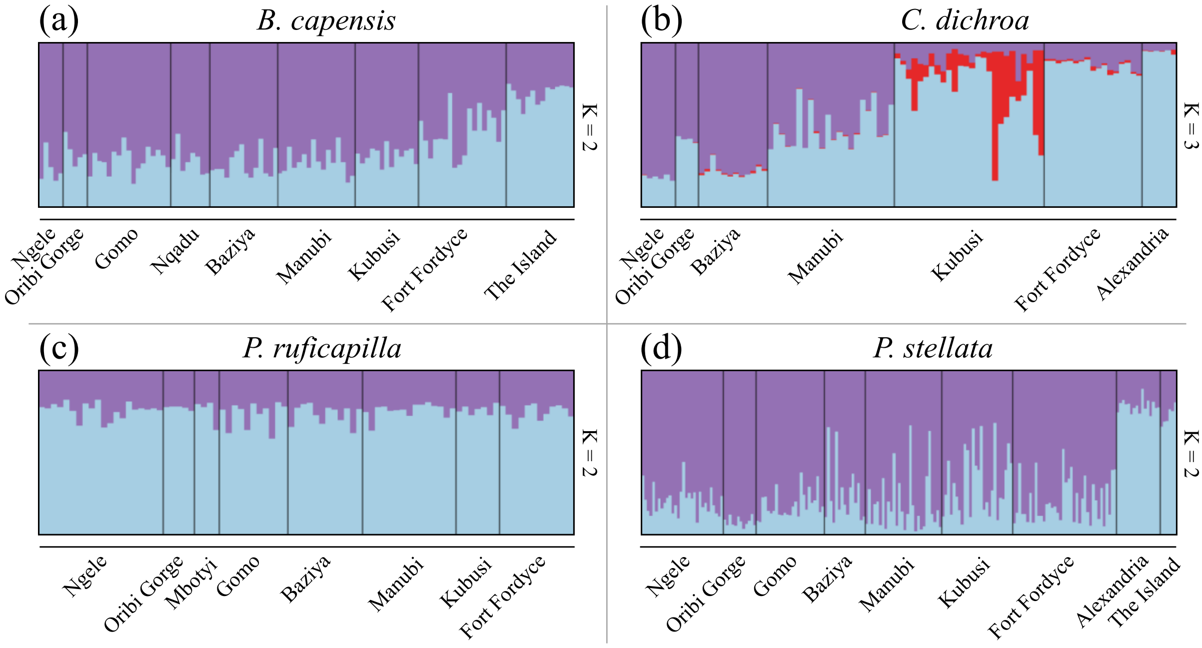


Figure 3.3 Best supported TESS Bayesian genetic clustering assignments for (a) *B. capensis*, (b) *C. dichroa*, (c) *P. ruficapilla*, and (d) *P. stellata*, grouped by sampled forests across the Eastern Cape and southern KwaZulu-Natal. Each line represents the admixture proportions within one individual, respectively derived from eight species-specific microsatellite loci. For *C. dichroa* K=3 is shown over K=2 to highlight genetic diversity restricted to Kubusi Forest.

Table 3.1 Sample sizes, estimates of genetic diversity and inbreeding coefficients within each forest (respective sub-biomes shown) for the four focal bird species.

	Forest	Sub-biome	*N*	*AR*	*PrAR*	H_o	H_e	F_{IS}
B. capensis	Ngele	Afromontane	6	4.750	0.475	0.771	0.775	0.005
	Oribi	Scarp	8	4.250	0.035	0.650	0.717	0.103
	Gomo	Afromontane	17	6.750	0.179	0.603	0.682	0.119
	Nqadu	Afromontane	8	5.625	0.243	0.607	0.806	0.260
	Baziya	Afromontane	14	6.500	0.253	0.580	0.688	0.161
	Manubi	Scarp	16	7.625	0.148	0.578	0.705	0.184
	Kubusi	Afromontane	13	6.375	0.109	0.635	0.708	0.165
	Fort Fordyce	Afromontane	18	7.125	0.252	0.597	0.712	0.107
	The Island	IOCB	14	5.625	0.070	0.607	0.720	0.162
	Total		**114**	**10.625**	**0.196**	**0.625**	**0.709**	**0.151**
C. dichroa	Ngele	Afromontane	6	4.000	0.228	0.688	0.653	-0.058
	Oribi	Scarp	5	3.125	0.157	0.500	0.536	0.077
	Baziya	Afromontane	12	5.000	0.225	0.635	0.636	0.001
	Manubi	Scarp	22	7.500	0.345	0.710	0.692	-0.027
	Kubusi	Afromontane	26	7.000	0.395	0.702	0.720	0.026
	Fort Fordyce	Afromontane	17	5.750	0.278	0.632	0.639	0.011
	Alexandria	IOCB	6	3.625	0.220	0.667	0.642	-0.042
	Total		**94**	**8.000**	**0.264**	**0.648**	**0.636**	**0.002**
P. ruficapilla	Ngele	Afromontane	20	1.429	0.104	0.425	0.361	-0.184
	Oribi	Scarp	6	2.250	0.005	0.325	0.364	0.119
	Mbotyi	Scarp	6	2.375	0.050	0.429	0.541	-0.135
	Gomo	Afromontane	11	2.250	0.046	0.386	0.343	0.001
	Baziya	Afromontane	14	2.500	0.032	0.417	0.415	-0.003
	Manubi	Scarp	15	2.875	0.100	0.367	0.401	0.087
	Kubusi	Afromontane	9	2.375	0.003	0.375	0.354	-0.063
	Fort Fordyce	Afromontane	11	0.286	0.002	0.403	0.390	-0.035
	Total		**92**	**3.375**	**0.043**	**0.391**	**0.381**	**-0.047**
P. stellata	Ngele	Afromontane	30	6.625	0.212	0.667	0.673	0.009
	Oribi	Scarp	13	4.875	0.122	0.625	0.683	0.088
	Gomo	Afromontane	26	6.125	0.188	0.705	0.679	-0.038
	Baziya	Afromontane	15	5.875	0.181	0.667	0.659	-0.012
	Manubi	Scarp	28	6.250	0.094	0.612	0.668	0.086
	Kubusi	Afromontane	26	6.250	0.176	0.606	0.652	0.072
	Fort Fordyce	Afromontane	39	5.875	0.058	0.622	0.648	0.042
	Alexandria	IOCB	17	4.750	0.070	0.656	0.605	-0.088
	The Island	IOCB	6	4.375	0.319	0.646	0.595	0.095
	Total		**200**	**9.750**	**0.185**	**0.646**	**0.651**	**0.022**

3.4.3 Demographic history

Pairwise F_{ST} (Appendix S3.6-S3.9) was highest in *C. dichroa*, and comparable between *B. capensis*, *P. ruficapilla*, and *P. stellata* (Figure 3.4). Pairwise D_{PS}/F_{ST} ratios were highest for *B. capensis*, *P. stellata*, and *C. dichroa*, and lowest for *P. ruficapilla* (Figure 3.4). Across the four passerines, regional CN_e estimates resulting from monogamy were likely more realistic, and over twice those assuming random mating (Table 3.2).

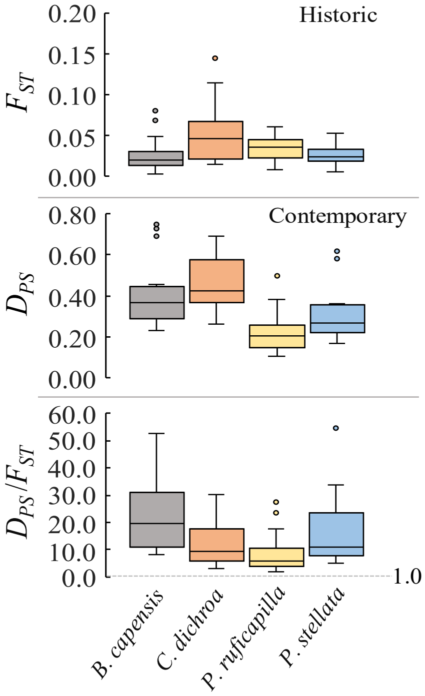


Figure 3.4 Comparison between historic (F_{ST}) and contemporary (D_{PS}) population connectivity metrics in the four forest-dependent passerines.

Disparities between CN_e at 1% and 2% critical allele frequencies were minimal in *B. capensis*, 18% in *P. stellata*, 33% in *C. dichroa*, and 150% for *P. ruficapilla*, reflecting lower rare allele frequencies in the latter three species (Do et al., 2014). Overall *CNe* appears lowest in *C. dichroa* and highest in *P. ruficapilla*, although both have larger 95% *CI* compared to *P. ruficapilla* and *P. stellata*. Fluctuations in N_e over the past 100 generations vary across the four passerines, consistent across single-step (Figure 3.5), and two-phase (Appendix S3.12) mutation models. Historically, *B. capensis* and *C. dichroa* had the largest N_e, but declined to levels comparable to *P. ruficapilla* and *P. stellata*, which both appear more temporally stable, but still in decline. Assuming a two-year generation time (Bird et al., 2020), or three years for

P. stellata (Oatley, 1982b), these events relate to the past three centuries, with most declines beginning <100 years (~20-60 generations) ago.

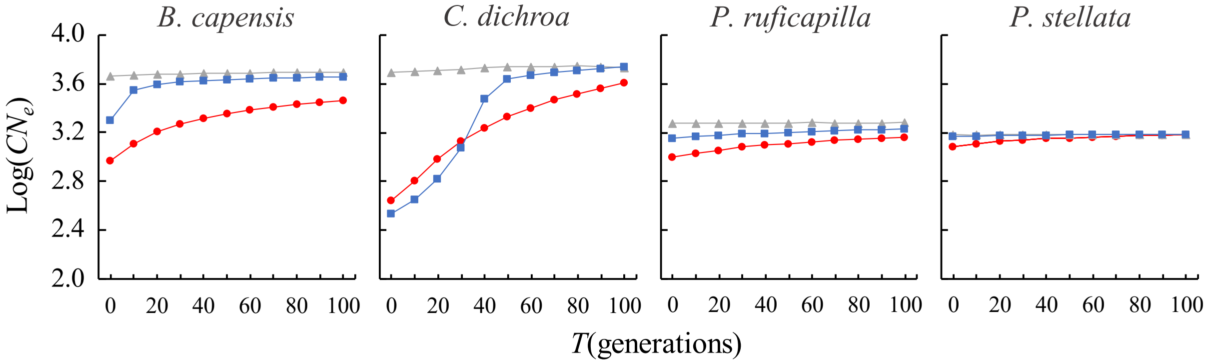


Figure 3.5 VarEff plots showing variaion in CN_e over the past 100 generations for *B. capensis*, *C. dichroa*, *P. ruficapilla*, and *P. stellata* among eleven forests across a region for the Eastern Cape and KwaZulu-Natal Provinces of South Africa, based respectively on eight microsatellites loci for each species, and assuming a single-step mutation model at a constant mutation rate of μ = 5x10-4 per generation.

Table 3.2 Estimated current effective populative sizes (CN_e) for *B. capensis*, *C. dichroa*, *P. ruficapilla*, and *P. stellata* across a region of the Eastern Cape and southern KwaZulu Natal, inferred from eight species-specific microsatellite loci. Estimated CN_e are for 1% and 2% critical allele frequencies, assuming both random mating and monogamy, with 95% confidence intervals (95% *CI*)

	B. capensis		*C. dichroa*		*P. ruficapilla*		*P. stellata*	
	0.02	0.01	0.02	0.01	0.02	0.01	0.02	0.01
CN_e Random	340.6	342.3	238.8	358.8	831.7	332.1	424.3	515.3
95% CI	162.5-5497.9	169.1-2982.8	98.9-∞	137.8 -∞	76.7-∞	71.5-∞	202.8-3902.9	240.1-11734.7
CN_e Monogamy	682.7	686.0	479.1	719.0	1664.9	665.7	850.1	1032.1
95% CI	326.5-10997.5	339.7-5967.0	199.3 -∞	277.0 -∞	154.9-∞	144.5 -∞	407.1-7807.2	481.6-23470.9

3.4.4 Landscape genetics

3.4.4.1 Landcover thematic resolution

Landcover thematic surface evaluation (Figure 3.6) revealed that forest and coastal/mesic thicket configuration best explained genetic differentiation within *P. stellata*, outperforming the geographic distance model by >17 AICc units. For *B. capensis* and *C. dichroa*, forest configuration, and forest and coastal/mesic thicket configuration were equivalent to the geographic distance model (<2 AICc units), whereas for *P. ruficapilla*, the geographic distance model marginally outperformed the forest configuration, the relatively best landcover model, by <4 AICc units. Results across species were similar for both pairwise F_{ST} and D_{PS} (Figure 3.6, Appendix S3.17), except for *C. dichroa*, for which the geographic distance model, and forest and coastal/mesic thicket configuration LCP model were equivalent, marginally outperformed the null model by <4 AICc units. Both connectivity metrics indicated that across species, detailed landcover configurations were inadequate to explain forest connectivity patterns, both according to pairwise F_{ST} and D_{PS}.

3.4.4.2 Landscape resistance surfaces

Univariate optimisations of best-supported landcover, freshwater systems, and topography landscape surfaces improved LCP and IBR model fit over geographic distance alone for *P. stellata* (Figure 3.6), especially for LCP modelling of forest and coastal/mesic thicket configuration, followed by the three IBR models. For *B. capensis*, only IBR modelling of topography strongly outperformed geographic distance alone by >8 AICc units, although LCP and IBR modelling of freshwater systems were comparable to geographic distance alone. Similarly, the geographic distance model performed best for *P. ruficapilla*, closely followed by both LCP and IBR models of landscape topography and freshwater systems models. Neither ecological, nor geographic distance modelling sufficiently explained population differentiation in *C. dichroa* according to pairwise F_{ST}, however, according to pairwise D_{PS}, forest and coastal/mesic thicket configuration and geographic distance were comparable, and adequately explanatory (Appendix S3.17). Across species, multivariate optimisations of composite landscape surfaces failed to explain connectivity patterns.

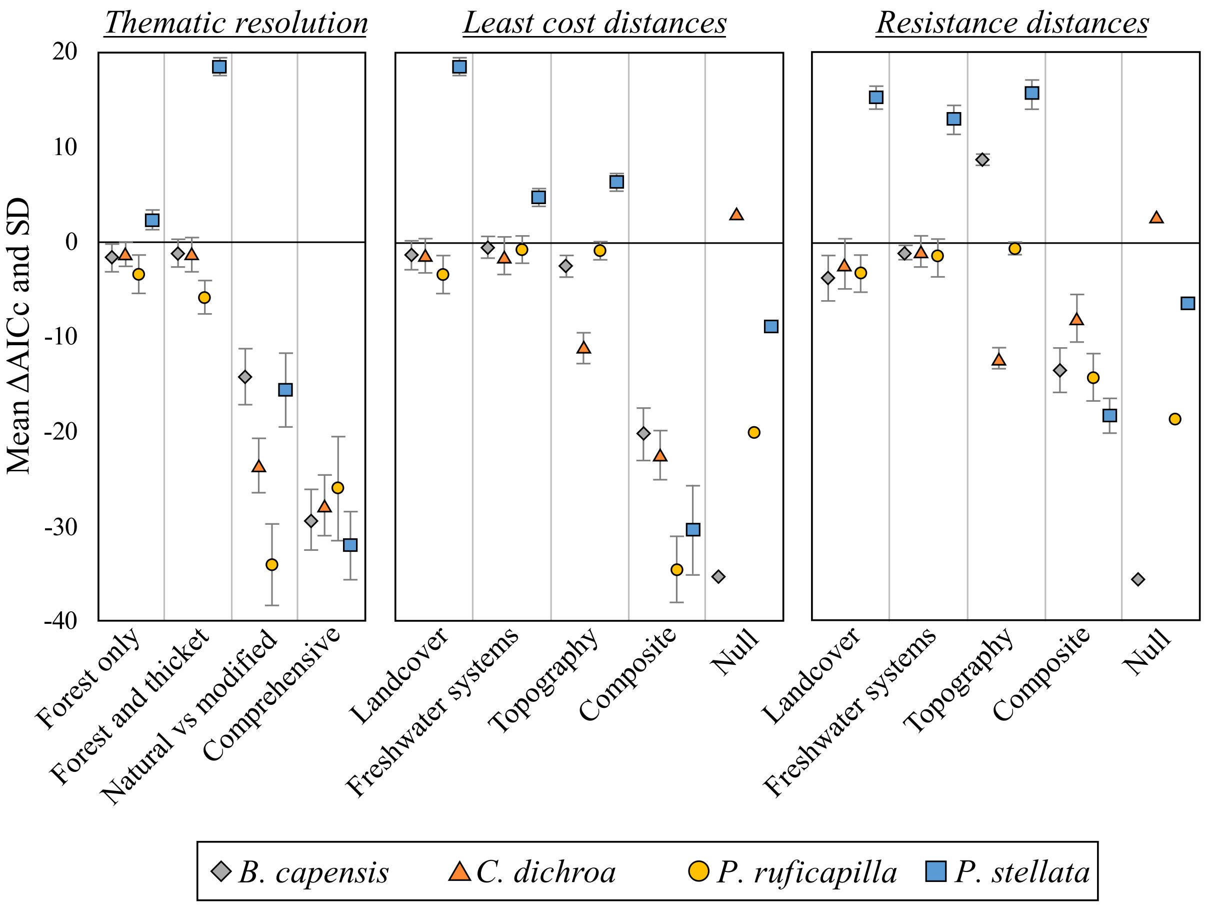


Figure 3.6 Relative performance of least cost pathway and resistance distance models based on landscape surfaces for the four focal bird species, inferred from F_{ST}. Univariate optimizations were independently conducted upon four landcover thematic surfaces, modelling least cost paths (left). Univariate optimizations were also conducted separately for best-supported landcover, freshwater systems, and topography, and multivariate optimisations integrated the three landscape layers into a composite surface. Both univariate and multivariate optimisations employed three replicates of least cost (middle), and resistance distance (right) modelling regimes. Positive ΔAICc values denote improved model performance over Euclidean distances (the geographic distance alone model, ΔAICc = 0).

3.4.4.3 Comparative performance of landscape models

Pairwise F_{ST} genetic distances correlated significantly with Euclidean distances (IBD) for *B. capensis* and *P. stellata* (Figure 3.7), although held true only for *P. stellata* when comparing pairwise D_{PS} genetic distances (Appendix S3.13, S3.16). For both passerines, however, ecological distances were more explanatory (Figure 3.7). Landscape topography is most pertinent to geneflow in *B. capensis*, with LCP and IBR models retaining significance after controlling for Euclidean distances (r(F_{ST}(IBR|IBD) = 0.850, p = 0.001; r(F_{ST}(LCP|IBD) = 0.855, p = 0.001), unlike the converse (r(F_{ST}(IBD|IBR) = 0.322, p = 0.126; r(F_{ST}(IBD|LCP) = -0.028, p = 0.501). For *B. capensis*, causal modelling did not support the LCP model over IBR for topography (r(F_{ST}(LCP|IBR) = 0.413, p = 0.085; r(F_{ST}(IBR|LCP) = 0.372, p = 0.081), and supported only the LCP model of forest and coastal/mesic thicket configuration over IBD for pairwise F_{ST} (r(F_{ST}(LCP|IBD) = 0.509, p = 0.006), but not pairwise D_{PS} (r(D_{PS} (LCP|IBD) = 0.207, p = 0.179) (Appendix S3.15-S3.16). For *P. stellata*, genetic distance correlated with all ecological models (Appendix S3.13), especially for the LCP model of forest and coastal/mesic thicket configuration. Both IBD-controlled LCP and IBR landcover models for this robin were significant (r(F_{ST}(LCP|IBD) = 0.772, p = 0.002; r(F_{ST}(IBR|IBD) = 0.562, p = 0.024), with causal modelling supporting the LCP model over IBR (r(F_{ST}(LCP|IBR) = 0.645, p = 0.001; r(F_{ST}(IBR|LCP) = -0.069, p = 0.493). Furthermore, this IBD-controlled landcover LCP model remained significant across genetic distance metrics (r(D_{PS} (LCP|IBD) = 0.353, p = 0.021). For *C. dichroa*, no landscape model was correlated to pairwise F_{ST} genetic distances. Pairwise D_{PS} genetic distances, however, did reveal significant IBD (Appendix S3.16), although this was better explained by LCP modelling of forest and coastal/mesic thicket configuration (r(D_{PS} (LCP|IBD) = 0. 445, p = 0.032; r(D_{PS} (IBD|LCP) = 0.132, p = 0.289), which also outperformed the respective IBR model (r(D_{PS} (LCP|IBR) = 0. 583, p = 0.003; r(D_{PS} (IBR|LCP) = -0.441, p = 0.0.913) – performed using pairwise D_{PS} only for *C. dichroa*. Neither genetic distance metrics yielded significant IBD models for *P. ruficapilla*, for which only the topography IBR model proved significant, even when controlling for IBD (r(F_{ST}(IBR|IBD) = 0.752, p = 0.003), and the respective LCP model (r(F_{ST}(IBR|LCP) = 0.639, p = 0.012). Additionally, the IBD-controlled IBR model of forest configuration was significant (r(F_{ST}(IBR|IBD) = 0.367, p = 0.038), but not when applied to pairwise D_{PS} (r(D_{PS} (LCP|IBD) = -0.090, p = 0.585). Interestingly, despite low AICc rankings of the LCP and IBR models of detailed landcover and composite surfaces, these resistance surfaces consistently yielded strong, significant correlations with genetic distances across the four passerines, both for pairwise F_{ST} and D_{PS} (Appendix S3.13, S3.16).

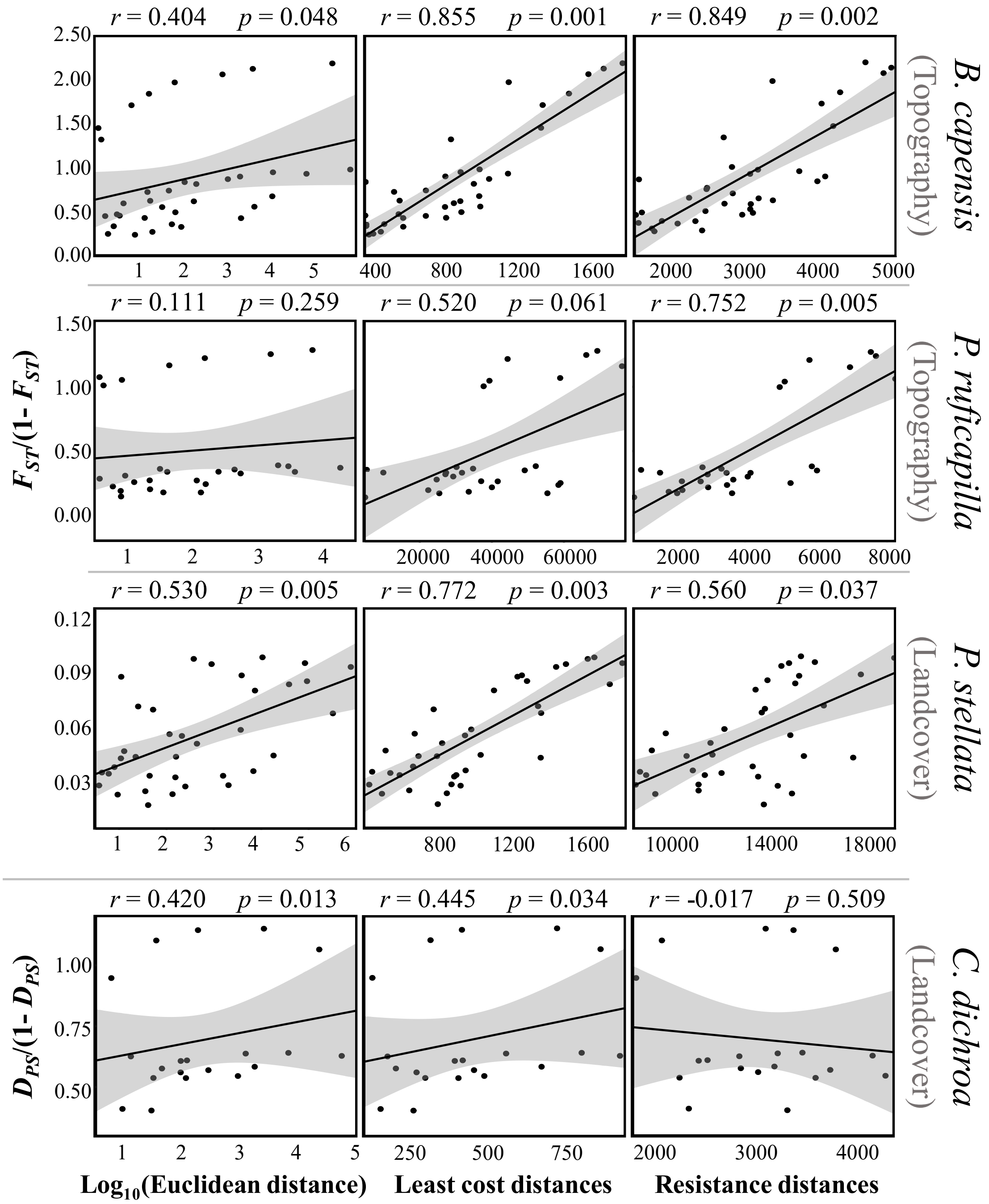


Figure 3.7 Mantel tests between genetic distances and Euclidean (left), least cost pathway (middle), and resistance (right) distances modelled from best performing landscape surfaces (in brackets) for the four focal passerines, and including the Spearman correlation coefficient (*r*) for each respective species model. Genetic distances were derived from pairwise F_{ST} for *B. capensis*, *P. ruficapilla,* and *P. stellata,* and from pairwise D_{PS} for *C. dichroa*.

3.5 Discussion

3.5.1 Disrupted landscape-genetic associations within focal passerines over the past two centuries

The four focal forest-dependent passerines studied adequately maintain functional connectivity among highly fragmented primary forest habitats throughout the study area of the Eastern Cape and southern KwaZulu-Natal (Figure 3.3). Geneflow disruptions are however notable in *B. capensis*, *P. stellata*, and *C. dichroa* (Figure 3.4). Two species, *B. capensis* and *C. dichroa*, show pronounced declines in effective population sizes (Figure 3.5), signifying vulnerability of these insectivores to increasing anthropogenic habitat changes. The endemic forest-specialist *C. dichroa* has experienced the most drastic population declines over the past two centuries, which have continued well after the widespread cessation of commercial selective logging and deforestation 80 years ago. Although deforestation has impacted Afromontane forests less than IOCB forests (Berliner, 2009; Cooper et al., 2020; Finch et al., 2013; Lawes, et al. 2007b), forest-dependent species within both sub-biomes may be susceptible to isolation through reduced structural connectivity from pervasive clearance of small forest patches (<1 ha) (Berliner, 2009; Kotze & Lawes, 2007; Lawes et al., 2004).

In addition to forest configuration, landscape resistance modelling highlighted the importance of coastal/mesic thicket for effective geneflow within *P. stellata* and *B. capensis* (Figure 3.6, 3.8, Appendices S3.13-S3.16). Both species show more acute geneflow disruption than *C. dichroa*, which may similarly benefit from coastal/mesic thicket (Appendix S3.16, Oatley, 1997a), but appears more sensitive to forest degradation. Surprisingly, *B. capensis* exhibited the most restricted geneflow, and highest signs of inbreeding (Table 3.1), despite showing the lowest range contraction (-1.3%), and broadest habitat tolerance, extending into coastal/mesic thicket. The Albany thicket biome has experienced minimal loss (-8.9%) between 1750-2014 (Skowno et al., 2019), and total thicket vegetation has steadily increased across the Eastern Cape since 1950 (Njwaxu & Shackleton, 2019; Skowno et al., 2019; Stickler & Shackleton, 2014). But 63% of Albany thicket is severely degraded (14.0-25.4% valley thicket, and 12.8% mesic thicket) (Lloyd et al., 2002), and the extent of coastal thicket degradation is unknown. The cumulative effect of both forest and thicket transformation has likely affected *B. capensis* more adversely than either *P. stellata* or *C. dichroa*, which probably use thicket only for facultative dispersal. Recuperation of the thicket biome augurs well for the recovery of *B. capensis*, as well as the improved viability of *P. stellata*, and *C. dichroa*. Improved landscape resistance modelling performance according to pairwise D_{PS} for *C. dichroa* (Appendix S3.16, S3.17) may reflect species recovery.

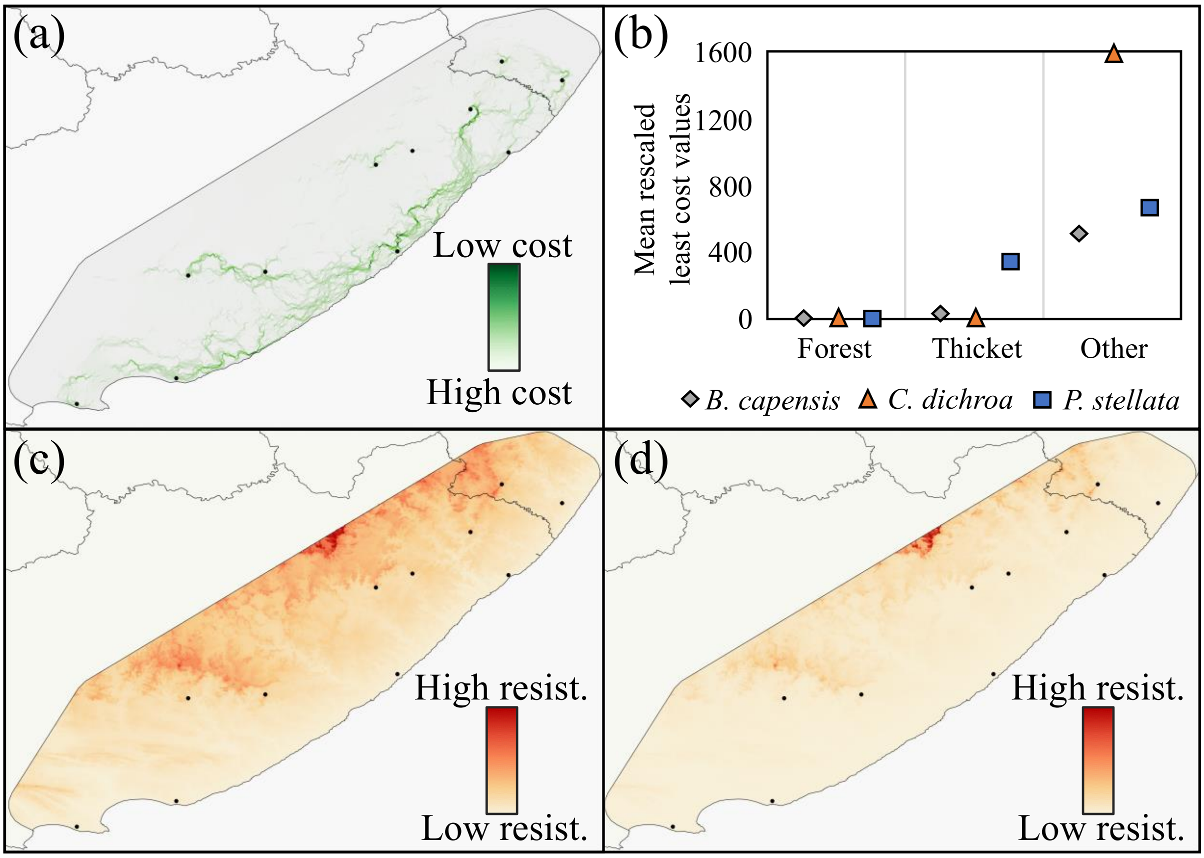


Figure 3.8 Most relevant optimised landscape surfaces impacting geneflow between sampled forests among the four focal bird species. (a) Current flow density representing least cost pathways through forest and coastal/mesic thicket landcover; (b) mean rescaled least cost values for forest, coastal/mesic thicket, and other landcover classes for *B. capensis*, *C. dichroa*, and *P. stellata*; (c) optimised topographic resistance surface for *B. capensis*, and (d) *P. ruficapilla*.

Dispersing *P. ruficapilla* appear not to discriminate landcover beyond forest configuration (Figure 3.6). This weak landcover association may be due to a type II error derived from low sample size (Winiarski et al., 2020), but the near panmixia within *P. ruficapilla* (Figures 3.3, 3.7), and equilibrium between historic and contemporary geneflow (Figure 3.4) supports high dispersal within this species, and tolerance towards anthropogenic landscape transformation. In east Africa, post-fragmentation sensitivity is evident for *P. ruficapilla* and *P. stellata* (Callens et al., 2011; Githiru & Lens, 2006; Sirén et al., 2018), yet the populations of both species in the Eastern Cape appear to have been largely resilient to historic forest exploitation. Afrotropical forest-dependent species can initially show positive, or neutral responses to fragmentation (Husemann et al., 2015; Lens et al., 2002), but continued forest degradation eventually undermines population viability (Habel et al., 2014; Korfanta et al., 2012; Lens & Van Dongen, 1999), and this is observable in both *P. ruficapilla* and *P. stellata* (Figure 3.5). The greater resilience of *P. ruficapilla* and *P. stellata* populations in South Africa to anthropogenic disturbance, compared to the corresponding Kenyan populations, may be due a greater adaptation of the former populations to long-term disturbances (see Betts et al., 2019). The higher latitude forests of South Africa were likely more adversely affected by Palaeoclimatic shifts (Eeley et al., 1999; Lawes et al., 2007a), resulting in more extensive forest contractions and extinction filters which may have decreased the sensitivity of South African populations of these species to contemporary habitat loss and degradation.

The impact of informal harvesting on the viability of these four passerine species was not addressed in this investigation, but it is arguably less important than historic forest exploitation. Sustainable informal harvesting that minimizes forest degradation is achievable (Leaver & Cherry, 2020b, 2020a; Leaver et al., 2019a), and all four species tolerate human proximity (Craig et al., 2020). The contemporary effective population sizes of all four species (Table 3.2) are likely underestimates resulting from pooled generations (Luikart, et al., 2010), and true numbers are likely to remain low. Given the heightened precarity of forest-dependent birds within South Africa (Coetzer et al., 2020; Colyn et al., 2020; Cooper et al., 2020), successful implementation of legislation sustainable utilisation of this restricted biome is strongly advised.

3.5.2 Forest history of focal passerines

The South African endemic *C. dichroa* displayed the highest population structuring (Figure 3.3), and the large genetic variability unique to Kubusi (Appendices S3.8-S3.9) affirms the climatic refugial importance of the eastern Amatole forest complex (Dalton et al., 2015; Kushata et al., 2020; Madisha et al., 2018). The higher population complexity of this forest specialist contrasts with that of the forest generalist *B. capensis*, which is near endemic to South Africa, and more genetically diverse than *C. dichroa* (Table 3.1). Higher historic availability of suitable habitat for *B. capensis* likely afforded larger populations that were more buffered against Paleoclimatic fluctuations, although both forest (Ivory et al., 2018; Lawes et al., 2007a) and thicket (Potts et al., 2013) biomes were susceptible to contractions during periodic aridity.

Consistently higher genetic diversity at Manubi (Table 3.1) corroborates the refugial significance of regional scarp forests (Grass et al., 2015; Lawes et al., 2007a; Moir et al., 2020a, 2020b), while the lower diversity at Oribi Gorge may reflect closer contact with subtropical IOCB forests (Mucina, 2018; Mucina et al., 2006), generally avoided by these four passerine species. Temperate conditions in the Eastern Cape permit coastal delineation of Afromontane and scarp forests, and limited IOCB forest present re-established only ~8 kya (Huntley et al., 2016; Lawes et al. 2007a). Young IOCB forest presence is reflected by *C. dichroa* and *P. stellata* exhibiting the combination of low allelic diversity, coupled to high population differentiation between the two sampled IOCB forests (Alexandria and The Island) and all other forests adjacent forests (Figure 3.3, Table 3.1, Appendix S3.3, S3.5) characteristic of recently colonised, peripheral populations (Eckert et al., 2008; Johannesson & André, 2006) within sampled IOCB (Albany) forests. *Batis capensis*, by contrast, which was already inhabiting adjacent mesic and valley thicket, shows more prolonged contact with these forests.

Although *P. ruficapilla* and *P. stellata* originated in East Africa (Alström et al., 2018; Bowie et al., 2006; Fjeldså & Bowie, 2008; Singh et al., 2008), both lacked the aforementioned features of peripheral populations. The low genetic diversity observed in *P. ruficapilla* suggests more recent, or perhaps constrained, colonisation of South Africa than does *P. stellata*, and the unexpectedly low regional complexity within *P. ruficapilla* contrasts with the strong population insularity observed in East Africa (Callens et al., 2011). This alludes to shifting dispersal behaviour of this species in these higher latitude forests (P. R. Martin & Tewksbury, 2008; Moore et al., 2008; Salisbury et al., 2012).

3.5.3 Resistance modelling insights into the landscape ecology

Metapopulation dynamics of these four passerine species do not appear wholly contingent upon observed adult mobility. Seasonal altitudinal migration between mid-altitude (800-1400 m) Afromontane and coastal scarp and IOCB forests in the Eastern Cape is most apparent in *P. stellata* (Craig & Hulley, 2019) which undergoes local migrations throughout its distribution (Burgess & Mlingwa, 2000; Dowsett, 1985; Oatley & Arnott, 1998). Anecdotally observed altitudinal migration of *C. dichroa* in KwaZulu Natal Province (Johnson & Maclean, 1994; Oatley et al., 2017; Oatley, 1966, 1969), does not appear to occur in the Eastern Cape (Craig & Hulley, 2019), nor is it supported by pronounced genetic population structuring (Figure 3.3), which is not influenced by topography (Figure 3.6, Appendix S3.13-S3.14). Additionally, isotopic analysis shows *C. dichroa* to be largely sedentary (Wolmarans, 2015). Minimal seasonal movements are reported for *B. capensis* and *P. ruficapilla* (Berruti, 1997; Craig & Hulley, 2019; Johnson & Maclean, 1994), although the apparent panmixia observed within *P. ruficapilla* strongly indicates underestimated regional dispersal ability of this species. *Ad hoc* South African bird recapture data (Oschadleus & Ranwashe, 2017) reports adult travel distances of 83 km in *P. stellata* (through coastal thicket), 50 km in *B. capensis* (across open savanna), 8.5 km in *C. dichroa*, and 3.4 km in *P. ruficapilla*. Additionally, *P. stellata* movements may exceed 120 km (Oatley, 1997b), and adults readily traverse unsuitable matrix conditions (Aben et al., 2012, 2014; Callens et al., 2011; Galbusera et al., 2004), while *B. capensis* can traverse several kilometres of coastal ocean (Dane & Bolton, 2017). Surprisingly, only the reportedly mobile *B. capensis*, and *P. stellata* exhibited significant long-term isolation-by-distance (Figure 3.7), though in both species this is better explained by ecological interactions with the landscape (Figure 3.6, 3.7; Appendix S3.13-S3.15).

The significant influence of regional topography on the population structure of *B. capensis*, *P. ruficapilla*, and *P. stellata* (Figure 3.6, 3.7, Appendix S3.13-S14) could indicate an elevation gradient to geneflow, potentially supporting altitudinal migration in *P. stellata*. For these three species, lower elevations appear more conducive to dispersal (Figure 8), with ravines, valleys, and gorges serving as conduits into interior Afromontane forests. Outperformance of IBR over LCP topography models respectively demonstrate inefficient navigation of landscape topography, or interference by other landscape features. Freshwater systems appear most crucial to the geneflow of *P. stellata*, and potentially *C. dichroa* (Figure 3.6; Appendix S3.13-S3.16). This landscape genetic association is similarly observed in a forest-associated pipistrelle (Moir et al., 2020b), yet may more immediately reflect coinciding thicket presence. Altitudinally- migrating *P. stellata* frequently navigate well-wooded riparian corridors (Oatley, 1982a, 2017), and this behaviour may be similarly present in the other three passerine species.

Strong adult site fidelity is observed in all four species (Callens et al., 2011; Habel et al., 2016; Oatley, 1982a; Oschadleus & Ranwashe, 2017), and attested to by recapture records (Oschadleus & Ranwashe, 2017). Additionally, philopatry is reported in migratory *P. stellata* (Dowsett, 1985) and *C. dichroa* (Oatley, 2017). Although stochastic adult movement may be underestimated, natal dispersal of immature birds is the most likely primary geneflow mechanism of these four passerine species. Natal dispersal is poorly documented in South Africa, but has been observed in *P. stellata* (Oatley, 1982a), with 2-3 month old individuals having been observed moving through plantations, woodland, and riparian thicket. Intuitively, young *P. stellata* should seek to minimize exposure, and attempt cost-efficient navigation of hospitable matrix vegetation, explaining the high performance of the LCP model of forest and coastal/mesic thicket configuration.

Regardless of dispersal mechanism, the higher population structuring (Figures 3.3, 3.7) observed in the larger bodied *C. dichroa* (48 g), and *P. stellata* (21 g), compared to *B. capensis* (12 g), and *P. ruficapilla* (8 g) (Hockey et al., 2005), corroborates the constraining effect of body mass to dispersal in terrestrial birds (Dawideit et al., 2009; Garrard et al., 2012). Demographic signatures (Figure 3.4, 3.5) show body mass alone is a poor predictor of species sensitivity to anthropogenic habitat transformation.

3.5.4 Considerations for regional Afromontane forest bird conservation

Stronger performance of the LCP models of forest and coastal/mesic thicket configuration over respective IBR models for *P. stellata* (Figure 3.7), as well as *B. capensis* and *C. dichroa* (Appendix S3.13-S3.16) demonstrate the potential utility of conservation corridors in the Eastern Cape and southern KwaZulu-Natal to preserve genetic integrity within regional Afromontane forest birds, and to promote resilience against anthropogenic climate change, as recommended by Colyn et al. (2020). The highest priority forests for conservation are the scarp forests present along the Wild Coast, as well the eastern Amatole Afromontane forests, and Afromontane (eastern mistbelt) forests in southern KwaZulu-Natal. These forests harbour the largest overall and unique genetic diversity (Table 3.1), and are therefore the most probable candidates as climatic refugia. Effective creation of these conservation corridors would incorporate forest and coastal/mesic thicket vegetation at lower elevations, particularly where these two landcover classes coincide with freshwater systems, to ensure the preservation of optimal dispersal pathways beneficial for the four focal species. The utility of coastal thicket for facilitating movement of forest-dependent taxa is already recognized, and many authorities regard coastal thicket as secondary forest (Ehlers-Smith et al., 2017, 2018, 2019; Olivier et al., 2013). Beyond forest and coastal/mesic thicket configuration, matrix landcover was not shown to significantly impact the geneflow of these four passerine species. Avian connectivity between IOCB forests in KwaZulu-Natal can remain high across anthropogenically-transformed areas, but least so for forest-dependent insectivores (Neuschulz et al., 2013). Matrix transformation, however, can diminish regional forest integrity (Ehlers-Smith et al., 2017, 2018, 2019, 2020; Freeman et al., 2018), and inhibit geneflow of sedentary, forest-dependent taxa (Aben et al., 2012, 2014; Callens et al., 2011; De Santis et al., 2018), including forest tree species (Botzat et al., 2015).

3.6 Conclusion

Our results show that reported forest-dependent bird range contractions in South Africa do not closely reflect species genetic responses to anthropogenic activity within the study area of the Eastern Cape and southern KwaZulu-Natal. The forest generalist *B. capensis* underwent the lowest range contraction (-1.3%), yet showed the most substantial geneflow restrictions, alongside pronounced declines in effective population size. More extensive range contractions observed in *P. ruficapilla* (-20.7%), and *P. stellata* (-23.0%) do not correspond to the comparatively stable effective population sizes observed, although geneflow restriction is evident in the latter species. Only the South African endemic forest specialist *C. dichroa* showed simultaneous decline in distribution (-19.5%) and effective population size, alongside geneflow disruption, and thus appears especially vulnerable to forest degradation.

In all four species, landscape resistance modelling demonstrated closer associations between population structure and landscape features than could be explained by geographic distance alone. Forest, and mesic/coastal thicket configuration is important to geneflow in *P. stellata*, *B. capensis*, and *C. dichroa*, with *B. capensis* seeming most averse to thicket degradation. Beyond coastal/mesic thicket, all four species, but particularly *P. ruficapilla*, do not facultatively disperse through matrix landcover. Finally, we propose that by conserving optimal dispersal routes through the two landcover classes, predominately within low-elevation regions and coinciding with prominent river systems, should effectively ameliorate geneflow disruption, and mitigate extinction debts culminating from historic forest exploitation.

3.7 Chapter 3 appendices

Appendix S3.1 Procedures for polymerase chain reaction (PCR) for amplifying the microsatellites used to genotype *Batis capensis*, *Cossypha dichroa*, *Phylloscopus ruficapilla*, and *Pogonocichla stellata*

Microsatellite sequences were amplified using polymerase chain reaction (PCR) in 10 µL reaction volumes containing approximately 50% (5 µL) KAPA2G Fast Multiplex Mix (© 2016 Kapa Biosystems) (1U *HotStart* DNA Polymerase; 1.5X KAPA2G Buffer A; 0.2 mM of each dNTP; 3.0 mM $MgCl_2$); 0.1-0.6 µM of each forward and reverse primer (adjusted from 0.2 µM); and 20-50ng/µL template DNA. For each species, combinations of 3-5 microsatellite primer pairs were simultaneously amplified in multiplex PCRs in an GeneAmp PCR System 2700 thermocycler (® Applied Biosystems, USA), under the following PCR conditions: initial denaturation at 95°C for 3 min, followed by 25-35 cycles of 95°C for 15 s, T_{anneal} for 30 s, and 72°C for 25 s, with a final extension of 72°C of 2 min.

Appendix S3.1.1 *B. capensis*

Microsatellite	Reference	No. cycles	T_{anneal} (°C)	Size (bp)
BMI-16	(Wogan et al., 2016)	25	60	334-358
BMI-17	(Wogan et al., 2016)	25	60	148-204
BMI-22	(Wogan et al., 2016)	25	60	247-287
BMI-44	(Wogan et al., 2016)	25	60	144-164
BMI-96	(Wogan et al., 2016)	25	60	195-300
BMI-41	(Wogan et al., 2016)	25	60	Monomorphic; 204
BMI-71	(Wogan et al., 2016)	25	60	136-192
BMI-98	(Wogan et al., 2016)	25	60	341-373
BMI-32	(Wogan et al., 2016)	35	60	304-332

Appendix S3.1.2 *C. dichroa*

Microsatellite	Reference	No. cycles	T_{anneal} (°C)	Size (bp)
CNA99	(Wogan et al., 2014a)	25	54	92-156
CNA130	(Wogan et al., 2014a)	25	54	164-192
CNA109	(Wogan et al., 2014a)	25	54	182-210
WBSW9	(McRae & Amos, 1999)	25	54	102-112
Gf06	(Petren, 1998)	25	59	Stuttering; null alleles
CNA180	(Wogan et al., 2014a)	25	59	107-139
CNA113	(Wogan et al., 2014a)	25	59	118-154
CACA3	(Wogan et al., 2014a)	25	59	338-358
CACA27	(Wogan et al., 2014a)	25	59	Stuttering; null alleles

Appendix S3.1.3 *P. ruficapilla*

Microsatellite	Reference	No. cycles	T_{anneal} (°C)	Size (bp)
Patmp2-43	(Otter et al., 1998)	30	55	119-121
Dpu-16	(Dawson et al., 1997)	30	55	116-128
MLSP4	(Ishibashi et al., 2000)	30	55	147-155
POCC8	(Bensch et al., 1997)	30	55	Null alleles; linked to POCC9
POCC1	(Bensch et al., 1997)	25	55	153-1533
POCC5	(Bensch et al., 1997)	25	55	Monomorphic; 100
POCC6	(Bensch et al., 1997)	25	55	94-98
POCC7	(Bensch et al., 1997)	25	55	209-215
POCC9	(Bensch et al., 1997)	25	55	251-257
Cu02*	(Gibbs et al., 1999)	35	57	151-169

*amplified with cyclic extension period of 45 s

Appendix S3.1.4 *P. stellata*

Microsatellite	Reference	No. cycles	T_{anneal} (°C)	Size (bp)
WBSW2*	(McRae & Amos, 1999)	25	55	121-123
Ltmr6*	(D. B. McDonald & Potts, 1994)	25	55	Monomorphic; 194
Mcyu4*	(Double et al., 1997)	25	55	129-137
Gf05*	(Petren, 1998)	25	55	Stuttering; null alleles
CNA142*	(Wogan et al., 2014a)	25	55	199-243
CNA162	(Wogan et al., 2014a)	35	59	228-276
CACA3	(Wogan et al., 2014a)	35	59	312-352
CACA27	(Wogan et al., 2014a)	35	59	330-368
Gf06	(Petren, 1998)	35	59	106-116
WBSW9	(McRae & Amos, 1999)	30	50	141-159

* reactions performed with 5% Dimethyl sulfoxide (DMSO)

Appendix S3.2 Microsatellite locus genetic diversity measures for *B. capensis*: *N* – number of individuals; *NA* – number of alleles; *AR* – allelic richness; *HO* – observed heterozygosity; *HE* – expected heterozygosity; *NULL* – null allele frequency; F_{IS} – inbreeding coefficient. *Significant deviations to Hardy–Weinberg equilibrium after Bonferroni-Hochberg ($p < 0.05$)

	Ngele	Oribi Gorge	Gomo	Nqadu	Baziya	Manubi	Kubusi	Fort Fordyce	The Island	Overall
	BMI-16									
N	6	8	17	14	8	16	13	18	16	116
NA	2	3	3	3	1	5	2	4	4	7
AR	1.94	2.58	1.55	1.85	1.00	2.33	1.83	1.86	2.16	1.90
Ho	0.40	0.40	0.12	0.07	0.00	0.25	0.23	0.18	0.27	0.21
He	0.32	0.54	0.16	0.31	0.00	0.33	0.31	0.29	0.42	0.30
NULL	0.00	0.09	0.00	0.00	0.05	0.03	0.04	0.02	0.11	0.07
F_{IS}	-0.14	0.36	0.00	0.00	0.78	0.27	0.29	0.63	0.84	0.50
	BMI-17									
N	6	8	17	14	8	16	13	18	16	116
NA	5	4	7	6	6	7	8	8	7	15
AR	3.97	3.33	4.63	4.43	4.57	4.23	4.99	4.58	4.76	4.39
Ho	0.80	0.60	0.82	0.71	0.88	0.54	0.85	0.78	0.79	0.75
He	0.68	0.66	0.79	0.78	0.80	0.68	0.81	0.78	0.80	0.75
NULL	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.04
F_{IS}	-0.07	0.20	-0.02	-0.03	0.12	0.46	0.00	0.04	0.06	0.10
	BMI-22									
N	6	8	17	14	8	16	13	18	16	116
NA	6	5	9	8	7	9	9	7	8	11
AR	4.64	4.00	4.79	5.07	5.04	5.25	5.10	4.87	5.24	4.89
Ho	1.00	0.80	0.88	0.86	0.88	0.81	0.92	0.83	0.79	0.86
He	0.78	0.72	0.78	0.81	0.82	0.83	0.80	0.81	0.84	0.80
NULL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00
F_{IS}	-0.18	0.00	-0.10	0.00	-0.02	0.06	-0.12	0.00	0.10	-0.02
	BMI-44									
N	6	8	17	14	8	16	13	18	16	116
NA	1	2	3	2	3	2	2	2	2	6
AR	1.00	1.99	2.21	1.72	2.54	1.76	1.91	1.92	1.97	1.89
Ho	0.00	0.60	0.41	0.14	0.38	0.25	0.31	0.33	0.43	0.32
He	0.00	0.42	0.41	0.24	0.48	0.22	0.36	0.35	0.41	0.32
NULL	0.00	0.00	0.00	0.09	0.11	0.00	0.04	0.01	0.00	0.05
F_{IS}	0.00	-0.33	-0.28	0.28	0.45	-0.11	0.17	0.06	0.01	0.03

Appendix S3.2 (continued)

	Ngele	Oribi Gorge	Gomo	Nqadu	Baziya	Manubi	Kubusi	Fort Fordyce	The Island	Overall
	BMI-96									
N	6	8	17	14	8	16	13	18	16	116
NA	7	6	11	12	11	17	12	14	9	22
AR	5.28	4.83	6.00	6.43	6.52	7.31	6.46	6.70	5.36	6.10
Ho	1.00	1.00	0.94	1.00	1.00	1.00	0.92	0.94	0.86	0.96
He	0.82	0.80	0.86	0.88	0.89	0.92	0.89	0.90	0.83	0.87
NULL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F_{IS}	-0.11	-0.14	-0.07	-0.06	-0.10	-0.06	0.00	-0.03	0.01	-0.05
	BMI-32									
N	6	8	17	14	8	16	13	18	16	116
NA	8	6	9	7	6	9	9	8	7	15
AR	5.61	4.62	5.15	4.70	4.56	5.64	5.39	5.53	5.06	5.14
Ho	0.80	0.80	0.71	0.79	0.62	0.88	0.77	0.83	0.86	0.78
He	0.86	0.80	0.81	0.79	0.82	0.86	0.85	0.85	0.81	0.83
NULL	0.00	0.00	0.03	0.12	0.00	0.00	0.05	0.02	0.00	0.04
F_{IS}	0.18	0.11	0.15	0.30	0.04	0.01	0.14	0.05	-0.02	0.09
	BMI-98									
N	6	8	17	14	8	16	13	18	16	116
NA	5	5	7	8	6	6	5	7	4	9
AR	4.18	4.16	4.29	4.73	3.87	4.45	4.12	4.66	3.78	4.25
Ho	0.80	0.80	0.59	0.79	0.50	0.81	0.92	0.72	0.79	0.75
He	0.78	0.76	0.76	0.73	0.73	0.74	0.76	0.80	0.74	0.76
NULL	0.00	0.00	0.08	0.15*	0.00	0.00	0.00	0.02	0.00	0.01
F_{IS}	0.09	0.06	0.25	0.38	-0.04	-0.07	-0.17	0.12	-0.02	0.06
	BMI-71									
N	6	8	17	14	8	16	13	18	16	116
NA	4	3	8	6	5	6	4	5	4	8
AR	3.25	2.35	3.98	3.62	3.09	3.65	2.77	3.60	3.32	3.29
Ho	0.60	0.33	0.41	0.59	0.57	0.59	0.45	0.52	0.59	0.52
He	0.64	0.46	0.73	0.76	0.75	0.79	0.66	0.76	0.70	0.69
NULL	0.02	0.02	0.09	0.03	0.03	0.34	0.03	0.03	0.04	0.05
F_{IS}	0.17	0.14	0.36	1.00*	0.15	0.78	0.18	0.12	0.22	0.47

Appendix S3.3 Microsatellite locus genetic diversity measures for *C. dichroa*: *N* – number of individuals; *NA* – number of alleles; *AR* – allelic richness; *HO* – observed heterozygosity; *HE* – expected heterozygosity; *NULL* – null allele frequency; F_{IS} – inbreeding coefficient. *Significant deviations to Hardy–Weinberg equilibrium after Bonferroni-Hochberg ($p < 0.05$)

	Ngele	Oribi Gorge	Baziya	Manubi	Kubusi	Fort Fordyce	Alexandria	Overall
	WBSW9							
N	6	5	12	22	26	17	6	94
NA	5	2	2	6	6	3	5	6
AR	3.36	1.70	1.30	2.71	3.47	1.89	3.77	2.60
Ho	0.83	0.25	0.08	0.41	0.58	0.24	0.83	0.46
He	0.61	0.22	0.08	0.48	0.67	0.29	0.75	0.44
NULL	0.00	0.00	0.00	0.02	0.05	0.05	0.00	0.05
F_{IS}	-0.28	0.00	0.00	0.17	0.22	0.24	-0.02	0.13
	CNA130							
N	6	5	12	22	26	17	6	95
NA	4	4	4	8	6	5	4	8
AR	3.36	3.38	3.38	4.41	3.72	3.60	3.04	3.56
Ho	1.00	1.00	0.59	0.86	0.73	0.88	0.83	0.84
He	0.68	0.69	0.73	0.79	0.73	0.71	0.62	0.71
NULL	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00
F_{IS}	-0.40	-0.33	0.24	-0.08	0.02	-0.21	-0.25	-0.07
	CNA109							
N	6	5	12	22	26	17	6	95
NA	3	4	5	6	6	4	4	8
AR	2.71	3.14	3.64	3.56	3.50	2.88	3.20	3.23
Ho	0.50	0.50	0.67	0.82	0.81	0.59	0.50	0.63
He	0.62	0.56	0.70	0.72	0.70	0.62	0.68	0.66
NULL	0.06	0.00	0.00	0.00	0.00	0.02	0.08	0.02
F_{IS}	0.29	0.05	0.10	-0.12	-0.13	0.08	0.35	0.01
	CNA99							
N	6	5	12	22	26	17	6	95
NA	6	6	9	12	13	7	4	17
AR	3.92	4.46	4.59	4.82	4.85	4.04	3.25	4.28
Ho	0.83	0.75	0.83	0.82	0.73	0.82	0.67	0.78
He	0.69	0.78	0.80	0.82	0.83	0.75	0.69	0.77
NULL	0.00	0.00	0.00	0.00	0.04	0.00	0.01	0.01
F_{IS}	-0.11	0.18	0.00	0.03	0.14	-0.06	0.1304	0.05

Appendix S3.3 (continued)

	Ngele	Oribi Gorge	Baziya	Manubi	Kubusi	Fort Fordyce	Alexandria	Overall
	CNA142							
N	6	5	12	22	26	17	6	95
NA	4	3	6	8	6	7	3	8
AR	3.23	2.36	4.14	4.22	3.95	4.45	2.77	3.59
Ho	0.67	0.50	0.75	0.91	0.77	0.76	0.67	0.72
He	0.65	0.41	0.79	0.75	0.76	0.81	0.61	0.68
NULL	0.00	0.00	0.03	0.00	0.00	0.01	0.00	0.03
F_{IS}	0.07	-0.09	0.10	-0.19	0.01	0.09	0.00	0.01
	CNA113							
N	6	5	12	22	26	17	6	95
NA	3	3	6	9	8	9	4	10
AR	2.74	2.32	3.41	4.34	4.50	4.72	2.95	3.57
Ho	0.67	0.25	0.83	0.82	0.81	0.88	0.83	0.73
He	0.61	0.41	0.61	0.79	0.81	0.82	0.58	0.66
NULL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F_{IS}	0.00	0.50	-0.33	-0.01	0.02	-0.05	-0.35	-0.04
	CACA3							
N	6	5	12	22	26	17	6	95
NA	3	1	4	4	5	4	2	6
AR	2.33	1.00	2.79	2.37	2.69	2.10	1.50	2.11
Ho	0.50	0.00	0.58	0.36	0.42	0.35	0.17	0.34
He	0.40	0.00	0.55	0.41	0.44	0.31	0.15	0.32
NULL	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00
F_{IS}	-0.15	0.00	-0.02	0.14	0.07	-0.12	0.00	0.0242
	CNA180							
N	6	5	12	22	26	17	6	95
NA	4	2	4	7	6	7	3	9
AR	2.79	1.72	2.98	3.31	3.52	3.48	2.79	2.94
Ho	0.50	0.25	0.75	0.68	0.81	0.53	0.83	0.62
He	0.51	0.22	0.62	0.66	0.70	0.65	0.61	0.57
NULL	0.00	0.00	0.00	0.03	0.02	0.05	0.00	0.02
F_{IS}	0.12	0.00	-0.16	-0.01	-0.14	0.21	-0.28	-0.04

Appendix S3.4 Microsatellite locus genetic diversity measures for *P. ruficapilla*: *N* – number of individuals; *NA* – number of alleles; *AR* – allelic richness; *HO* – observed heterozygosity; *HE* – expected heterozygosity; *NULL* – null allele frequency; F_{IS} – inbreeding coefficient. *Significant deviations to Hardy–Weinberg equilibrium after Bonferroni-Hochberg ($p < 0.05$)

	Ngele	Oribi Gorge	Mbotyi	Gomo	Baziya	Manubi	Kubusi	Fort Fordyce	Overall
	Pat-43								
N	20	6	6	11	14	15	9	11	92
NA	2	2	2	2	2	2	2	2	2
AR	1.99	2.00	1.99	2.00	1.87	1.99	1.77	1.98	1.95
Ho	0.60	0.60	0.43	0.45	0.25	0.47	0.25	0.45	0.44
He	0.45	0.42	0.50	0.50	0.33	0.46	0.22	0.43	0.41
NULL	0.00	0.00	0.00	0.03	0.07	0.00	0.00	0.00	0.00
F_{IS}	-0.30	-0.33	0.5714	0.14	0.28	0.03	-0.07	0.00	0.00
	MLSP4								
N	20	6	6	11	14	15	9	11	92
NA	5	2	4	2	3	4	4	3	7
AR	1.94	1.68	3.45	1.37	2.22	2.11	2.88	2.21	2.23
Ho	0.20	0.20	0.83	0.09	0.25	0.27	0.50	0.36	0.34
He	0.19	0.18	0.65	0.09	0.39	0.24	0.54	0.31	0.32
NULL	0.00	0.00	0.00	0.00	0.09	0.00	0.01	0.00	0.02
F_{IS}	-0.04	0.00	0.00	0.00	0.40	-0.07	0.07	-0.13	0.06
	Dpu-16								
N	20	6	6	11	14	15	9	11	92
NA	3	2	3	3	3	3	3	2	5
AR	1.98	1.68	2.19	1.78	2.45	1.82	1.96	1.63	1.94
Ho	0.30	0.20	0.33	0.18	0.50	0.20	0.25	0.18	0.27
He	0.26	0.18	0.29	0.17	0.40	0.18	0.23	0.17	0.24
NULL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F_{IS}	-0.12	0.00	0.00	-0.03	-0.20	-0.05	-0.03	-0.05	-0.10
	Cu02								
N	20	6	6	11	14	15	9	11	92
NA	4	2	2	2	3	3	2	2	10
AR	2.43	1.67	1.97	2.00	2.35	2.28	2.00	2.00	2.09
Ho	0.55	0.20	0.52	0.73	0.58	0.53	0.62	0.64	0.55
He	0.54	0.18	0.49	0.50	0.53	0.53	0.49	0.48	0.47
NULL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F_{IS}	0.00	0.00	0.57	-0.43	-0.05	0.02	-0.05	-0.27	-0.07

Appendix S3.4 (continued)

	Ngele	Oribi Gorge	Mbotyi	Gomo	Baziya	Manubi	Kubusi	Fort Fordyce	Overall
	POCC9								
N	20	6	6	11	14	15	9	11	92
NA	4	4	4	3	3	4	2	1	4
AR	2.21	3.04	3.42	2.31	2.13	2.38	1.48	1.00	2.25
Ho	0.30	0.43	0.67	0.45	0.33	0.39	0.12	0.00	0.34
He	0.27	0.58	0.65	0.37	0.29	0.46	0.12	0.00	0.34
NULL	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F_{IS}	-0.09	0.71	0.25	-0.19	-0.11	0.59	0.00	0.00	0.21
	POCC6								
N	20	6	6	11	14	15	9	11	92
NA	2	2	2	2	2	2	2	2	2
AR	1.76	1.99	1.96	1.89	1.87	1.95	1.78	1.90	1.89
Ho	0.20	0.60	0.17	0.36	0.25	0.33	0.25	0.27	0.30
He	0.26	0.42	0.49	0.30	0.33	0.42	0.22	0.35	0.35
NULL	0.06	0.00	0.22	0.00	0.07	0.07	0.00	0.07	0.04
F_{IS}	0.24	-0.33	0.57	-0.18	0.28	0.24	-0.07	0.27	0.17
	POCC7								
N	20	6	6	11	14	15	9	11	92
NA	4	4	4	4	4	5	4	4	3
AR	2.80	3.52	3.20	3.28	3.37	3.58	3.34	3.27	3.30
Ho	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
He	0.58	0.66	0.62	0.64	0.64	0.66	0.65	0.64	0.64
NULL	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F_{IS}	-0.58	0.27	-0.50	-0.13	-0.13	-0.13	-0.11	-0.13	-0.22
	POCC1								
N	20	6	6	11	14	15	9	11	92
NA	2	2	2	2	2	2	2	2	2
AR	1.94	1.66	1.97	1.77	1.99	1.87	1.98	1.95	1.89
Ho	0.45	0.20	0.33	0.27	0.58	0.33	0.50	0.36	0.38
He	0.35	0.18	0.44	0.24	0.41	0.28	0.38	0.40	0.34
NULL	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.03	0.00
F_{IS}	-0.27	0.00	0.00	-0.11	-0.38	-0.17	-0.23	0.13	-0.17

Appendix S3.5 Microsatellite locus genetic diversity measures for *P. stellata*: *N* – number of individuals; *NA* – number of alleles; *AR* – allelic richness; *HO* – observed heterozygosity; *HE* – expected heterozygosity; *NULL* – null allele frequency; F_{IS} – inbreeding coefficient. *Significant deviations to Hardy–Weinberg equilibrium after Bonferroni-Hochberg ($p < 0.05$)

	Ngele	Oribi Gorge	Gomo	Baziya	Manubi	Kubusi	Fort Fordyce	Alexandria	The Island	Overall
	WBSW2									
N	30	13	26	15	28	26	39	17	6	200
NA	2	2	2	2	2	2	2	2	2	2
AR	1.98	2.00	2.00	1.98	2.00	2.00	2.00	1.70	1.68	1.93
Ho	0.37	0.58	0.56	0.33	0.43	0.46	0.45	0.19	0.17	0.39
He	0.43	0.47	0.49	0.42	0.50	0.43	0.49	0.17	0.15	0.39
NULL	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
F_{IS}	0.17	-0.20	-0.12	0.24	0.16	-0.06	0.10	-0.07	0.00	0.05
	Mcu4									
N	30	13	26	15	28	26	39	17	6	200
NA	4	3	4	4	3	4	3	2	2	5
AR	2.75	2.81	2.85	2.65	2.61	2.48	2.56	2.00	1.65	2.48
Ho	0.53	0.43	0.48	0.53	0.54	0.33	0.42	0.62	0.17	0.45
He	0.55	0.64	0.59	0.55	0.54	0.46	0.52	0.49	0.15	0.50
NULL	0.00	0.09	0.05	0.00	0.00	0.05	0.04	0.00	0.00	0.04
F_{IS}	0.05	0.51	0.20	0.07	0.03	0.51	0.30	-0.24	0.00	0.18
	CNA142									
N	30	13	26	15	28	26	39	17	6	200
NA	10	7	7	8	10	11	9	9	5	12
AR	5.18	4.78	5.02	5.26	5.52	6.42	5.64	5.79	4.44	5.34
Ho	0.80	0.67	0.76	0.87	0.79	0.85	0.82	0.75	0.83	0.79
He	0.75	0.72	0.76	0.78	0.81	0.86	0.83	0.84	0.76	0.79
NULL	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.04	0.00	0.01
F_{IS}	-0.05	0.12	0.02	-0.07	0.04	0.04	0.03	0.14	0.00	0.03
	WBSW9									
N	30	13	26	15	28	26	39	17	6	200
NA	3	3	3	4	3	2	2	2	2	6
AR	2.17	2.37	2.19	2.56	2.07	1.98	1.95	2.00	1.99	2.14
Ho	0.47	0.33	0.48	0.47	0.25	0.42	0.37	0.56	0.50	0.43
He	0.50	0.43	0.41	0.38	0.33	0.41	0.33	0.45	0.38	0.40
NULL	0.02	0.05	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.02
F_{IS}	0.09	0.27	-0.14	-0.19	0.25	-0.01	-0.10	-0.22	-0.25	-0.01

Appendix S3.5 (continued)

	Ngele	Oribi Gorge	Gomo	Baziya	Manubi	Kubusi	Fort Fordyce	Alexandria	The Island	Overall
	CNA162									
N	30	13	26	15	28	26	39	17	6	200
NA	6	6	7	7	6	6	7	4	6	13
AR	4.99	4.87	4.80	4.96	4.75	4.28	4.74	2.84	4.86	4.57
Ho	0.73	0.75	0.84	0.73	0.61	0.69	0.66	0.62	1.00	0.74
He	0.80	0.80	0.78	0.78	0.78	0.72	0.78	0.58	0.78	0.76
NULL	0.02	0.01	0.00	0.00	0.09	0.01	0.07	0.00	0.00	0.03
F_{IS}	0.10	0.10	-0.05	0.10	0.24	0.06	0.17	-0.05	-0.20	0.09
	CACA3									
N	30	13	26	15	28	26	39	17	6	200
NA	7	5	7	5	6	7	5	4	4	10
AR	3.74	3.50	3.87	3.20	3.82	3.90	3.28	2.61	3.26	3.46
Ho	0.57	0.67	0.76	0.53	0.61	0.62	0.58	0.56	0.50	0.60
He	0.56	0.63	0.64	0.51	0.67	0.64	0.54	0.53	0.51	0.58
NULL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00
F_{IS}	0.01	-0.02	-0.17	-0.01	0.11	0.05	-0.07	-0.04	0.12	-0.01
	CACA27									
N	30	13	26	15	28	26	39	17	6	200
NA	14	8	12	10	12	11	12	9	10	20
AR	7.68	5.73	6.89	6.21	7.06	6.51	6.51	6.32	7.13	6.67
Ho	0.97	0.92	0.88	0.93	0.89	0.85	0.84	0.94	1.00	0.91
He	0.91	0.82	0.89	0.85	0.89	0.87	0.85	0.86	0.89	0.87
NULL	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F_{IS}	-0.05	-0.07	0.03	-0.06	0.01	0.04	0.03	-0.06	-0.03	-0.01
	Gf06									
N	30	13	26	15	28	26	39	17	6	200
NA	7	5	7	7	8	7	7	6	4	20
AR	4.84	3.96	4.61	5.34	4.39	4.39	4.69	4.72	3.88	4.54
Ho	0.90	0.75	0.88	0.93	0.79	0.73	0.89	1.00	1.00	0.87
He	0.79	0.73	0.76	0.81	0.73	0.73	0.78	0.77	0.74	0.76
NULL	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F_{IS}	-0.12	0.01	-0.13	-0.12	-0.06	0.02	-0.14	-0.26	-0.28	-0.11

Appendix S3.6 Pairwise F_{ST} and pairwise D_{PS} (below and above diagonal, respectively) values for *B. capensis* (global $F_{ST} = 0.013$, $p = 0.10$) based on eight microsatellite loci.

	Ngele	Oribi Gorge	Gomo	Nqadu	Baziya	Manubi	Kubusi	Fort Fordyce	The Island
Ngele	-	0.7	0.8	0.84127	0.78571	0.81122	0.82143	0.78571	0.82381
Oribi Gorge	0.08109	-	0.45714	0.41429	0.40536	0.39592	0.36224	0.33846	0.3381
Gomo	0.04497	0.02148	-	0.40635	0.38036	0.41531	0.40204	0.37143	0.41429
Nqadu	0.0693	0.03944	0.01285	-	0.33829	0.28685	0.31689	0.31746	0.33175
Baziya	0.01803	0.04918	0.016	0.00843	-	0.32781	0.27423	0.27747	0.2869
Manubi	0.0246	0.03712	0.01137	0.01464	0.01107	-	0.22959	0.27276	0.26429
Kubusi	0.0153	0.031	0.01856	0.0171	0.0111	0.0071	-	0.24137	0.23401
Fort Fordyce	0.0265	0.03101	0.0104	0.01606	0.00888	0.0257	0.00386	-	0.2652
The Island	0.0428	0.03091	0.02007	0.02022	0.02632	0.02419	0.0162	0.01997	-

Appendix S3.7 Pairwise F_{ST} and pairwise D_{PS} (below and above diagonal, respectively) values for *C. dichroa* (global $F_{ST} = 0.036$, $p < 0.001$) based on eight microsatellite loci.

	Ngele	Oribi Gorge	Baziya	Manubi	Kubusi	Fort Fordyce	Alexandria
Ngele	-	0.51429	0.67857	0.66667	0.69156	0.68254	0.63265
Oribi Gorge	0.08776	-	0.41071	0.37738	0.35844	0.43095	0.43469
Baziya	0.02252	0.11502	-	0.43452	0.33442	0.4246	0.44643
Manubi	0.03069	0.02047	0.01537	-	0.26353	0.37698	0.37585
Kubusi	0.03966	0.05405	0.06054	0.0158	-	0.26479	0.36132
Fort Fordyce	0.04254	0.07338	0.04485	0.0207	0.01884	-	0.39966
Alexandria	0.05904	0.14447	0.08728	0.05107	0.04691	0.0589	-

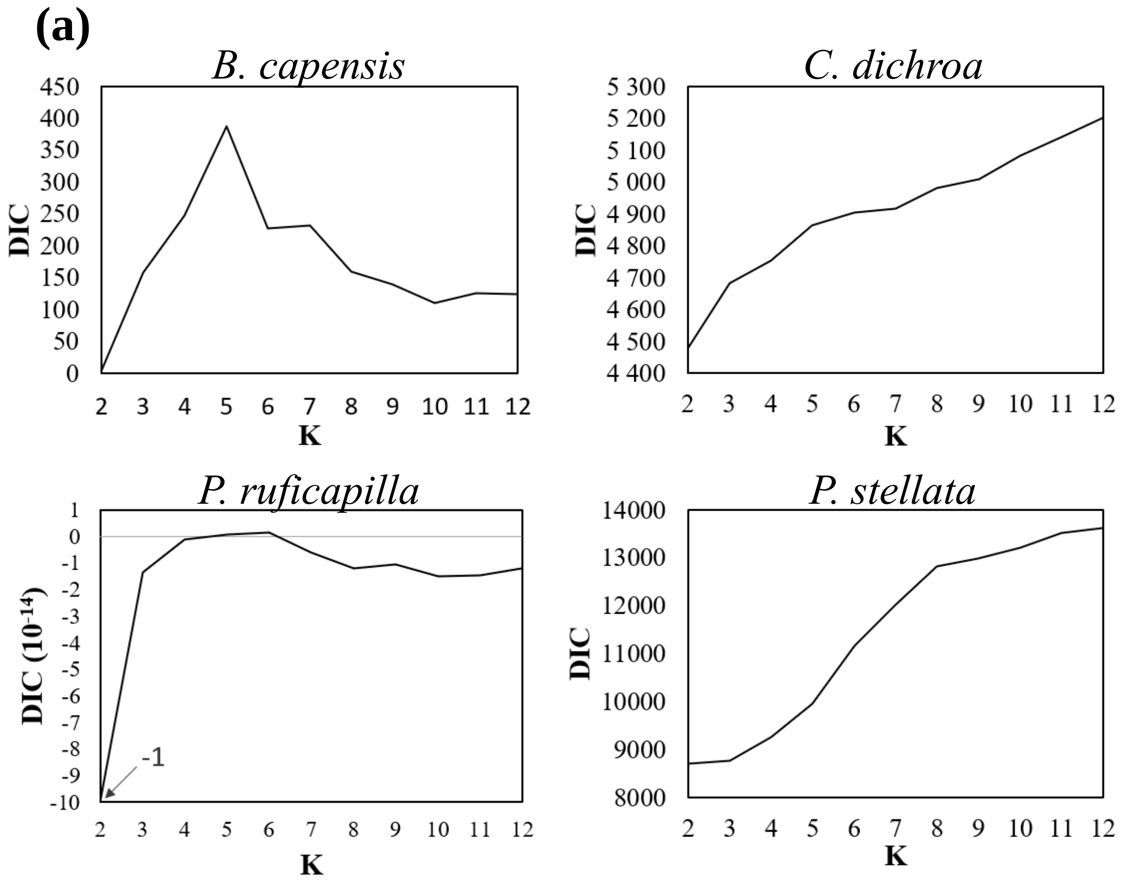
Appendix S3.8 Pairwise F_{ST} and pairwise D_{PS} (below and above diagonal, respectively) values for *P. ruficapilla* (global F_{ST} = 0.003, p = 0.261) based on eight microsatellite loci.

	Ngele	Oribi Gorge	Mbotyi	Gomo	Baziya	Manubi	Kubusi	Fort Fordyce
Ngele	-	0.5119	0.54286	0.53571	0.48052	0.5	0.52143	0.50794
Oribi Gorge	0.01864	-	0.12857	0.25	0.1342	0.17262	0.12381	0.19841
Mbotyi	0.038	0.00873	-	0.24643	0.15974	0.17738	0.10714	0.23968
Gomo	0.033	0.01409	0.02537	-	0.21429	0.2381	0.2	0.22222
Baziya	0.047	0.0362	0.0361	0.0493	-	0.14989	0.12857	0.19048
Manubi	0.0213	0.05115	0.06081	0.02	0.03162	-	0.15119	0.10516
Kubusi	0.045	0.04062	0.02495	0.03	0.01222	0.041	-	0.2119
Fort Fordyce	0.04469	0.05743	0.02274	0.03719	0.0342	0.055	0.03753	-

Appendix S3.9 Pairwise F_{ST} and pairwise D_{PS} (below and above diagonal, respectively) values for *P. stellata* (global $F_{ST} = 0.016$, $p < 0.001$) based on eight microsatellite loci.

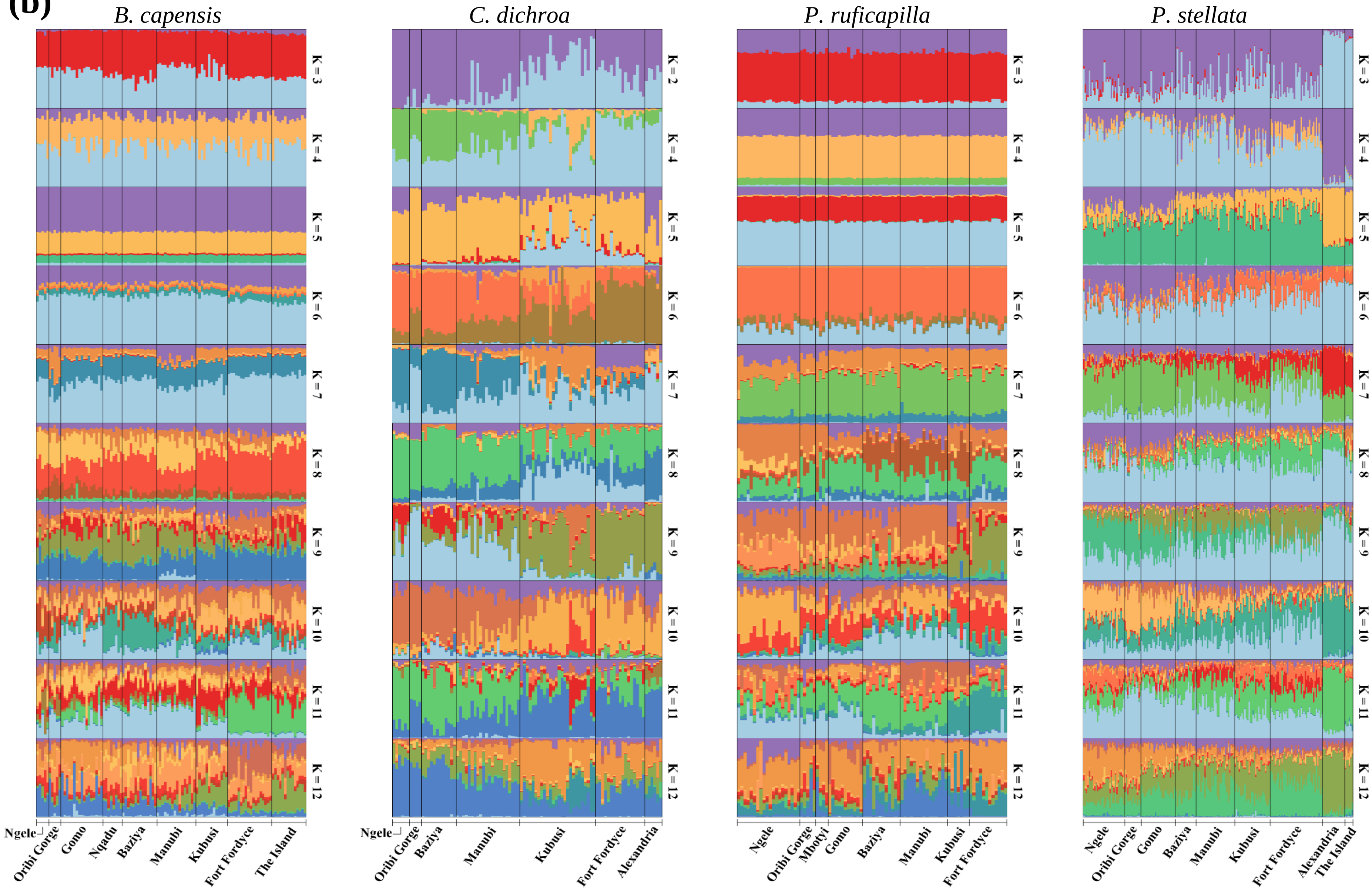
	Ngele	Oribi Gorge	Gomo	Baziya	Manubi	Kubusi	Fort Fordyce	Alexandria	The Island
Ngele	-	0.58242	0.6369	0.62946	0.62857	0.61905	0.62363	0.61765	0.60204
Oribi Gorge	0.0417	-	0.26923	0.23935	0.26374	0.26475	0.24176	0.31157	0.32575
Gomo	0.0207	0.0214	-	0.16815	0.21786	0.2209	0.24908	0.28501	0.31122
Baziya	0.0278	0.025	0.0274	-	0.17083	0.19444	0.25172	0.26602	0.32079
Manubi	0.01869	0.0307	0.0304	0.029	-	0.17566	0.18608	0.22381	0.28299
Kubusi	0.01139	0.02014	0.02399	0.0251	0.0085	-	0.20014	0.19997	0.29403
Fort Fordyce	0.01847	0.02557	0.02304	0.0226	0.00568	0.00832	-	0.22463	0.27355
Alexandria	0.03727	0.0394	0.04876	0.01517	0.04058	0.01878	0.0452	-	0.36375
The Island	0.0208	0.05298	0.03478	0.01128	0.03904	0.01235	0.03156	0.0241	-

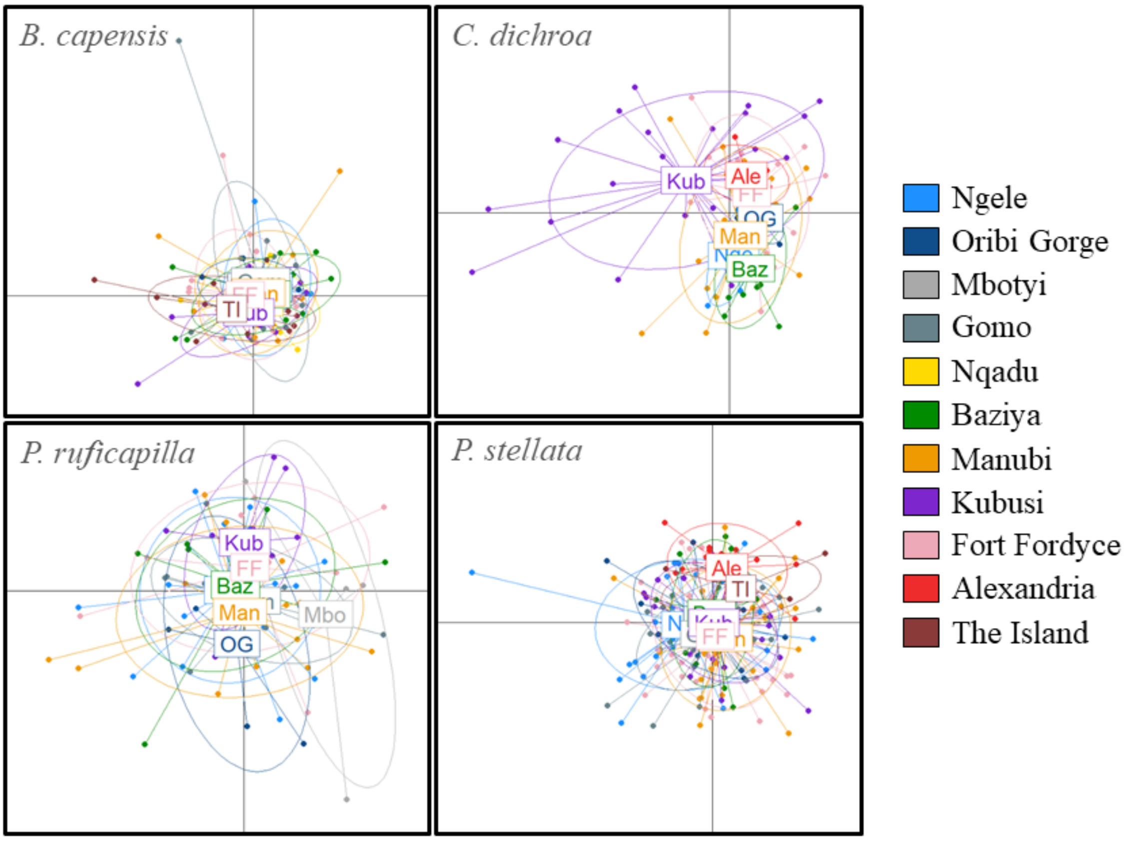
Appendix S3.10 Bayesian clustering analysis



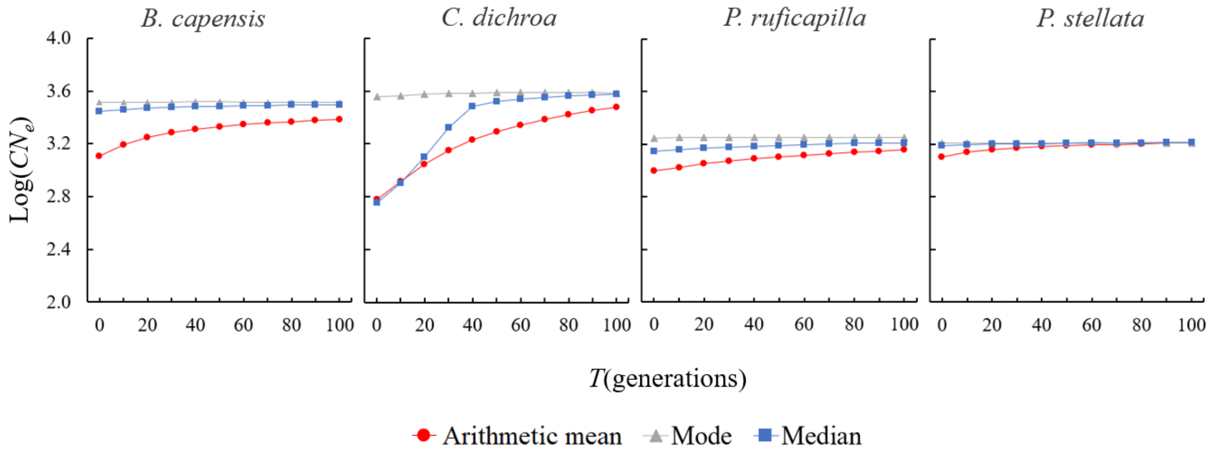
Appendix S3.10 TESS Bayesian clustering exploration of potential genetic clusters K≤12 in *B. capensis*, *C. dichroa*, *P. ruficapilla*, and *P. stellata*. (a) average DIC of lowest 10% DIC iteration per value of K. (b, next page) genetic clustering assignments for the four focal species, grouped by sampled forests across the Eastern Cape and southern KwaZulu-Natal. Each line represents the admixture proportions within one individual, respectively derived from eight species-specific microsatellite loci.

(b)


B. capensis
K = 3
K = 4
K = 5
K = 6
K = 7
K = 8
K = 9
K = 10
K = 11
K = 12
Ngele
Oribi Gorge
Gomo
Nqadu
Baziya
Manubi
Kubusi
Fort Fordyce
The Island
C. dichroa
K = 2
K = 4
K = 5
K = 6
K = 7
K = 8
K = 9
K = 10
K = 11
K = 12
Ngele
Oribi Gorge
Baziya
Manubi
Kubusi
Fort Fordyce
Alexandria
P. ruficapilla
K = 3
K = 4
K = 5
K = 6
K = 7
K = 8
K = 9
K = 10
K = 11
K = 12
Ngele
Oribi Gorge
Mbotyi
Gomo
Baziya
Manubi
Kubusi
Fort Fordyce
P. stellata
K = 3
K = 4
K = 5
K = 6
K = 7
K = 8
K = 9
K = 10
K = 11
K = 12
Ngele
Oribi Gorge
Gomo
Baziya
Manubi
Kubusi
Fort Fordyce
Alexandria
The Island



Appendix S3.11 Principal component analysis plots for *B. capensis*, *C. dichroa*, *P. ruficapilla*, and *P. stellata*, based on individual allele frequencies from eight species-specific microsatellite loci.



Appendix S3.12 VarEff plots showing variaion in CN_e over the past 100 generations for *B. capensis*, *C. dichroa*, *P. ruficapilla*, and *P. stellata* among eleven forests across a region for the Eastern Cape and KwaZulu-Natal Provinces of South Africa, based respectively on eight microsatellites loci for each species, and assuming a two-phase (10% single-step) mutation model at a constant mutation rate of $\mu = 5x10^{-4}$ per generation.

Appendix S3.13 Mantel tests showing Spearman's correlation between landscape and genetic distances (F_{ST}) for focal species populations in the Eastern Cape and southern KwaZulu-Natal. Least cost pathway (LCP) and isolation-by-resistance (IBR) models for each resistance surface, are compared alongside the log-transformed Euclidean distances between spatial points. Bold identifies significant correlations $p < 0.05$ (in parentheses)

	B. capensis		*C. dichroa*		*P. ruficapilla*		*P. stellata*	
Landscape surface	LCP	IBR	LCP	IBR	LCP	IBR	LCP	IBR
True forest	0.345 (0.122)	-	0.147 (0.250)	0.335 (0.068)	0.290 (0.141)	**0.367** **(0.036)**	**0.550** **(0.004)**	-
True forest and thicket	**0.509** **(0.009)**	0.129 (0.289)	0.268 (0.223)	0.227 (0.250)	0.335 (0.061)	-	**0.772** **(0.005)**	**0.560** **(0.037)**
Natural vegetation vs modified areas	**0.685** **(0.002)**	0.381 (0.127)	**0.694** **(0.036)**	-	**0.509** **(0.010)**	-	**0.731** **(0.007)**	-
Comprehensive landcover	**0.689** **(0.002)**	-	**0.669** **(0.043)**	-	**0.666** **(0.002)**	-	**0.721** **(0.011)**	-
Freshwater systems	0.372 (0.085)	0.306 (0.145)	0.314 (0.081)	0.358 (0.069)	0.308 (0.105)	0.373 (0.060)	**0.555** **(0.007)**	**0.589** **(0.006)**
Topography	**0.855** **(0.001)**	**0.849** **(0.002)**	0.371 (0.175)	0.395 (0.175)	0.520 (0.061)	**0.752** **(0.005)**	**0.698** **(0.014)**	**0.656** **(0.009)**
Composite	**0.559** **(0.007)**	**0.536** **(0.027)**	0.371 (0.181)	0.469 (0.138)	0.512 (0.083)	**0.764** **(0.005)**	**0.707** **(0.018)**	**0.808** **(0.006)**
Euclidean Distance	**0.404 (0.048)**		0.281 (0.109)		0.338 (0.061)		**0.530 (0.003)**	

Appendix S3.14 Partial Mantel tests comparing Spearman's correlations between landscape and genetic distances (F_{ST}) for focal species populations across a region of the Eastern Cape and southern KwaZulu-Natal. Least cost pathway (LCP) and isolation-by-resistance (IBR) ecological distances modelled for each resistance surface control for isolation-by-distance (IBD). Bold indicates significantly supported correlations ($p < 0.05$) (shown in parentheses)

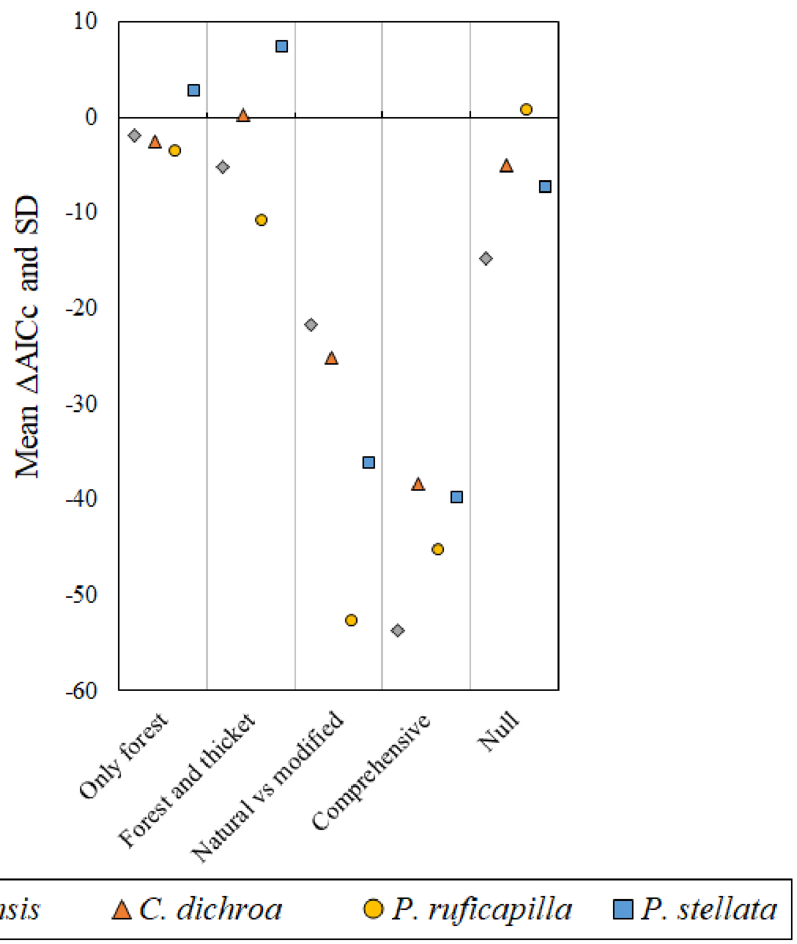
	B. capensis		*C. dichroa*		*P. ruficapilla*		*P. stellata*	
Landscape surface	LCP	IBR	LCP	IBR	LCP	IBR	LCP	IBR
True forest	0.345 (0.119)	-	0.147 (0.217)	0.335 (0.071)	0.290 (0.122)	**0.367** **(0.038)**	**0.550** **(0.007)**	-
True forest and thicket	**0.509** **(0.006)**	0.129 (0.300)	0.269 (0.229)	0.227 (0.278)	0.335 (0.070)	-	**0.772** **(0.002)**	**0.562** **(0.024)**
Natural vegetation vs modified areas	**0.689** **(0.001)**	0.381 (0.149)	**0.694** **(0.036)**	-	**0.509** **(0.002)**	-	**0.731** **(0.014)**	-
Comprehensive landcover	**0.727** **(0.001)**	-	**0.669** **(0.041)**	-	**0.666** **(0.005)**	-	**0.721** **(0.016)**	-
Freshwater systems	0.372 (0.082)	0.306 (0.145)	0.314 (0.072)	0.358 (0.073)	0.308 (0.121)	0.373 (0.063)	**0.555** **(0.006)**	**0.589** **(0.005)**
Topography	**0.855** **(0.001)**	**0.850** **(0.001)**	0.371 (0.175)	0.395 (0.165)	0.527 (0.070)	**0.752** **(0.003)**	**0.698** **(0.014)**	**0.657** **(0.015)**
Composite	**0.559** **(0.007)**	**0.512** **(0.026)**	0.371 (0.160)	0.469 (0.133)	0.512 (0.088)	**0.0764** **(0.001)**	**0.707** **(0.014)**	**0.808** **(0.004)**

Appendix S3.15 Causal modelling of pairwise F_{ST} distance models presented in Appendices 3.13 and 3.14

Species (best supported surface)	IBD|LCP	IBD|IBR	LCP|IBR	IBR|LCP
B. capensis (Topography)	-0.028 (0.500)	0.322 (0.126)	0.413 (0.085)	0.372 (0.081)
B. capensis (Freshwater systems)	0.270 (0.134)	**0.401 (0.005)**	**0.301 (0.014)**	-0.209 (0.903)
C. dichroa (Landcover)	0.190 (0.184)	0.241(0.109)	0.160 (0.254)	-0.064 (0.615)
P. ruficapilla (Freshwater systems)	0.161 (0.245)	-0.100 (0.708)	-0.342 (0.889)	0.323 (0.131)
P. ruficapilla (Topography)	0.083 (0.335)	0.135 (0.234)	0.090 (0.310)	**0.639 (0.012)**
P. stellata (Landcover)	-0.040 (0.667)	**0.433 (0.018)**	**0.645 (0.001)**	-0.069 (0.493)

Appendix S3.16 Mantel and partial Mantel tests (controlling for isolation-by-distance) comparing Spearman's correlations between landscape and genetic distances (D_{PS}) for focal species populations in the Eastern Cape and southern KwaZulu-Natal. Only least cost pathways (LCP) are modelled for each resistance surface, testing four alternative landcover thematic classification. Bold indicates significantly supported correlations of $p < 0.05$ (in parentheses)

	B. capensis		*C. dichroa*		*P. ruficapilla*		*P. stellata*	
Landscape surface	Mantel	P. Mantel	Mantel	P. Mantel	Mantel	P. Mantel	Mantel	P. Mantel
True forest	0.016 (0.372)	0.015 (0.392)	**0.422** **(0.029)**	**0.422** **(0.022)**	-0.090 (0.588)	-0.090 (0.585)	0.206 (0.189)	0.206 (0.194)
True forest and thicket	0.200 (0.190)	0.207 (0.199)	**0.445** **(0.034)**	**0.445** **(0.025)**	-0.200 (0.714)	-0.200 (0.703)	**0.353** **(0.041)**	**0.353** **(0.022)**
Natural vegetation vs modified areas	**0.449** **(0.039)**	**0.449** **(0.042)**	**0.665** **(0.026)**	**0.669** **(0.012)**	-0.184 (0.694)	-0.184 (0.701)	0.320 (0.189)	0.320 (0.163)
Comprehensive landcover	**0.613** **(0.031)**	**0.613** **(0.037)**	**0.823** **(0.001)**	**0.823** **(0.004)**	-0.232 (0.792)	-0.232 (0.793)	0.443 (0.052)	0.443 (0.051)
Euclidean Distance	0.073 (0.312)		**0.420 (0.013)**		-0.123 (0.670)		**0.349 (0.013)**	



Appendix S3.17 Relative performance of least cost pathway models based on landcover thematic surfaces for the four focal bird species, inferred from D_{PS}. Positive ΔAICc values denote improved model performance over Euclidean distances alone.

Appendix S3.18 *Batis capensis* microsatellite genotypes, with respective SAFring ring/band numbers, and forest localities for all individuals included in this study

Individual	**Forest**	**BMI 16**	**BMI 17**	**BMI 22**	**BMI 44**	**BMI 96**	**BMI 32**	**BMI 98**	**BMI 71**
AS14565	Ngele	334334	148148	251271	156156	250285	156188	349357	304324
AS14573	Ngele	334334	148188	255271	156156	230250	160160	353353	316316
AS14576	Ngele	334350	172180	247255	156156	235275	164184	357365	316324
AS14586	Ngele	334350	148176	255275	156156	235295	172192	357361	324328
AS14598	Ngele	334334	148172	271287	156156	225250	180184	361365	324324
AS14599	Ngele	334334	172176	255271	156156	225235	156172	357361	324328
AR89424	Oribi Gorge	342342	172180	263279	156160	225285	164184	361365	320320
AR89425	Oribi Gorge	334342	172176	251255	156156	225275	164180	361369	320320
Unbanded	Oribi Gorge	342342	176176	255263	160160	225235	156164	361361	320324
AS31232	Oribi Gorge	334334	172172	251255	156160	235285	172172	369369	320324
AS31246	Oribi Gorge	334334	172176	263263	156156	275285	164172	357361	316320
AS31254	Oribi Gorge	334342	172172	251263	156160	235250	164164	357369	316324
AS31260	Oribi Gorge	334334	176176	255255	156156	225275	136188	361365	312312
AS31264	Oribi Gorge	334338	148176	251271	156160	195215	164180	353357	320320
AR89404	Gomo	334334	176180	267271	156160	215235	136192	365365	324324
AR89405	Gomo	334334	168184	263275	156156	215225	136188	357365	320320
AR89406	Gomo	334334	172180	255275	156156	225230	184184	349361	316316
AR89411	Gomo	334334	172184	259275	156160	235285	184184	361373	308320
AR89412	Gomo	334334	176176	255271	156156	235280	136188	361361	324324
AS15605	Gomo	334334	172180	255275	156156	215225	172188	361361	312320
AS15609	Gomo	346346	172172	255255	156160	215220	188188	349365	304304
AS15610	Gomo	334334	172180	255279	156156	215220	188188	353365	312320
AS15612	Gomo	334334	180184	255271	156156	195230	188188	357361	320320
AS15621	Gomo	334342	164180	255271	144144	205285	188192	341357	328332
AS15622	Gomo	334334	148176	255271	156160	225225	168192	361365	320324
AS15633	Gomo	334334	168180	263271	156160	230280	172176	353353	316316
AS15634	Gomo	334334	172180	255283	156160	210225	180184	353365	320320
AS15635	Gomo	334334	148172	255279	156156	215230	176188	361361	320324
AS15725	Gomo	334334	176176	275275	156156	215225	164180	357365	320320
AS15726	Gomo	334334	172176	247275	156156	230265	172184	361361	320320
AS15769	Gomo	334334	172176	255271	156160	195225	188192	365365	316324
AR37685	Nqadu	334334	172180	251275	156156	210230	164164	357357	316316
AR89425	Nqadu	334334	176192	255279	156160	195230	160160	361361	320320
AR89436	Nqadu	334334	176180	251271	156156	225240	176184	353365	324324
AR89437	Nqadu	334334	180188	271279	160160	200260	176180	361361	316316
AR89438	Nqadu	334334	172176	251271	156156	205225	184184	365365	308308
AR89441	Nqadu	334334	176180	279283	156156	250255	136184	361365	312312
AR89442	Nqadu	334334	148172	255267	156164	215260	136180	349365	316316
AR89444	Nqadu	334334	148148	255255	156164	215230	164180	365369	324324
AR37668	Baziya	334334	168176	275275	156156	195230	188188	361373	316324

AR37666	Baziya	334334	172172	267271	156156	235270	180184	349357	320320
AS15638	Baziya	334334	148148	275275	156156	215240	172188	361361	316324
AS15639	Baziya	358358	176176	255271	156160	215290	176188	353361	316316
AS15644	Baziya	334334	148176	251271	156156	230235	188188	353365	312312
AS15647	Baziya	346346	172180	263275	156160	230275	176188	353361	316316
AS15664	Baziya	334334	168180	251255	160160	220240	172184	361369	308308
AS15666	Baziya	334358	148184	259271	156156	235245	180180	361361	320324
AS15667	Baziya	334334	176180	271275	156156	215235	176180	345361	324324
AS15674	Baziya	334334	148172	255267	156156	215220	176188	365369	324324
AS15707	Baziya	334334	148172	267279	156156	220225	180184	357365	320320
AS15716	Baziya	334334	176176	255271	156156	205230	180184	353361	324324
AS15717	Baziya	334334	176180	267275	156156	225235	136180	357361	316328
AS15721	Baziya	334334	172176	267275	156156	230240	160180	361361	320320
AR89458	Manubi	334354	148176	275275	156156	215240	172176	357361	316316
AR89463	Manubi	334334	176176	255255	156156	210215	180188	357361	324324
AR89468	Manubi	334334	176176	271283	156156	225250	184188	353357	308308
AR89473	Manubi	334334	172172	271279	156160	210240	172188	353361	324324
AR89474	Manubi	334346	184184	279283	156156	215245	176180	353365	320324
AR89475	Manubi	334334	180188	275279	156160	200230	160176	349369	312312
AR89476	Manubi	334342	188188	255275	156156	245275	180188	357365	316316
AR89482	Manubi	334334	176180	255279	156156	260275	160172	361365	320320
AR89492	Manubi	350350	172180	255279	156160	195205	172184	361361	312312
AR89493	Manubi	334334	180180	267271	156160	225240	172180	361361	316316
AR89494	Manubi	334334	168172	275275	156156	220250	164164	349361	320324
AR89528	Manubi	334342	148172	263271	156156	215280	180188	353357	312316
N05714	Manubi	334334	148180	247255	156156	230255	160192	361365	320320
N05715	Manubi	334334	176176	275279	156156	215230	188188	353361	316316
N05738	Manubi	334334	176176	251271	156156	240270	168180	361369	328328
N05751	Manubi	334334	176176	267279	156156	245285	164184	361361	324324
AS14423	Kubusi	338338	148148	255255	156160	215290	160160	353365	316316
AS14457	Kubusi	334338	172184	251255	156156	220240	156172	353357	316316
N05775	Kubusi	334334	172176	255271	156156	220260	176184	357361	316320
N05776	Kubusi	334338	148176	255275	156156	230230	164172	353365	316316
N05781	Kubusi	334334	176188	251271	156160	240255	164176	357365	316320
N05782	Kubusi	334334	180184	255283	156160	225255	168188	357361	316316
AS14446	Kubusi	334334	148180	255275	156156	230235	180188	353365	320320
N03555	Kubusi	334334	172180	271279	156160	215280	176184	353361	324324
N03564	Kubusi	334334	172176	267275	156156	225240	188188	361365	320320
N03566	Kubusi	334334	148172	255259	156156	210250	172184	357357	316316
N03586	Kubusi	334334	176176	247251	156156	230240	184188	361365	320320
N03589	Kubusi	334334	164172	251255	156156	230260	180188	357361	312312
N03593	Kubusi	334338	168172	251275	160160	215220	172172	349365	324324
AS14463	Fort Fordyce	346346	172176	267275	160160	220250	172184	361369	320320
AS14468	Fort Fordyce	334334	180180	255267	156156	250265	164180	357369	320320

AS14470	Fort Fordyce	334334	180204	255279	156156	205235	176184	361361	312312
AS14471	Fort Fordyce	334334	172180	263275	156156	215230	160188	349361	316316
AS14480	Fort Fordyce	334334	172180	255271	156160	230230	176180	353357	324324
AS14486	Fort Fordyce	334334	172172	279279	156156	210230	164176	353357	316316
AS14510	Fort Fordyce	334342	180180	255271	156160	220235	160160	357365	308320
AS14533	Fort Fordyce	334334	164176	275275	156160	220300	192192	361361	324324
AS14536	Fort Fordyce	334334	176180	255279	156156	215235	176184	341353	324324
AS14537	Fort Fordyce	334334	148176	267271	156156	245255	172180	365369	312316
AS14540	Fort Fordyce	334346	148172	271279	156156	220245	160188	357365	308324
AS15690	Fort Fordyce	334334	172180	255283	156156	245260	180188	361361	320320
AS15693	Fort Fordyce	346346	148176	271271	156156	235255	160164	353357	308320
AS15699	Fort Fordyce	334334	148176	255263	156156	210255	164176	357365	312312
N05822	Fort Fordyce	334334	172172	271275	156156	230235	160184	353353	320320
N05825	Fort Fordyce	334334	176192	255279	156160	195230	160160	361361	320320
N05826	Fort Fordyce	334334	172184	271279	156160	220225	172180	357365	324324
N05827	Fort Fordyce	334334	148172	255275	156160	220260	160188	353365	316316
AS31204	The Island	334342	148180	255259	156156	220225	160176	353361	308320
N07613	The Island	334334	148148	251263	156156	220220	180184	365365	320320
AR89562	The Island	334334	172176	247255	156156	220260	180188	365365	312324
AR89566	The Island	334334	180188	271271	156160	240260	164172	353361	308324
AR89569	The Island	334334	148168	255275	156156	200260	188188	353357	320320
AR89571	The Island	334334	172180	255259	156156	225230	184188	357365	320320
AR89587	The Island	334334	172172	275275	156160	220260	176180	357361	324324
AR89588	The Island	334334	164176	255275	156156	230230	160180	361361	320320
AR89596	The Island	334334	180180	271279	156160	250255	160164	353365	312312
AR89597	The Island	334334	172180	259263	156156	220225	180188	357365	320320
AR89598	The Island	346346	148172	247259	156160	215220	160188	353361	312320
N03548	The Island	342342	148168	255279	156160	225250	160164	357361	308308
N03550	The Island	334334	148176	275279	156160	220260	160184	353357	312312
N03552	The Island	350350	168180	275275	160160	230255	160160	361365	308308

Appendix S3.18 *Cossypha dichroa* microsatellite genotypes, with respective SAFring ring/band numbers, and forest localities for all individuals included in this study

Individual	**Forest**	**WBSW 9**	**CAN 130**	**CAN 109**	**CAN 99**	**CAN 142**	**CAN 113**	**CACA 3**	**CAN 180**
BF01265	Ngele	106106	172184	186186	100112	216216	134142	346358	119135
BF01266	Ngele	106110	172180	182194	100124	208224	134138	346346	111119
BF01268	Ngele	102106	172180	182194	100100	196216	134142	346346	119119
BF01269	Ngele	104106	172180	186194	100148	208216	142142	346358	123135
BF01272	Ngele	106110	172180	186186	132136	216216	134138	346346	119119
BF01273	Ngele	106108	176184	194194	100124	208224	134134	346354	119119
BF02112	Oribi Gorge	106106	172176	182182	100100	208212	142146	346346	119119
BF02114	Oribi Gorge	106110	172180	182202	132136	212212	134134	346346	119119
BF02116	Oribi Gorge	106106	172180	182182	100112	212220	134134	346346	119119
BF02117	Oribi Gorge	106106	180184	190194	104124	212212	134134	346346	111119
Unbanded	Oribi Gorge	106110	172184	182190	104112	212212	134134	346346	111119
BE77549	Baziya	106112	184184	186194	104116	208216	138142	346354	111119
BE77550	Baziya	106106	172180	182182	104156	216216	134142	346358	111135
BE77557	Baziya	106106	172180	182186	104144	200220	134142	346346	119119
BE77559	Baziya	106106	176180	182206	100148	216220	138142	346346	119135
BE77560	Baziya	106106	176180	194194	104132	200208	142146	354354	119119
BE77561	Baziya	106106	184184	194206	100104	216220	122142	346350	119135
BE77562	Baziya	106106	172172	194194	100100	216220	134142	346350	135139
BE77563	Baziya	106106	176180	194194	100104	208216	138142	346350	119119
BF01285	Baziya	106106	172172	182186	100100	208208	142142	346354	119135
BF01293	Baziya	106106	180184	194198	100148	204212	142142	346346	119135
BF01296	Baziya	106106	172176	186194	144148	212212	118142	346354	119135
BF01297	Baziya	106106	172172	194198	92112	200208	134142	346346	111135
BE77565	Manubi	106106	172172	194194	100100	216220	134134	346354	111119
BE77568	Manubi	106106	180188	182194	100112	212212	134142	346346	111119
BE77569	Manubi	104106	164176	182198	100104	212224	142142	346350	119135
BE77575	Manubi	106106	172192	182194	132148	208220	130142	346346	119119
BE77576	Manubi	106106	180184	182182	100100	196220	134138	346354	119119
BE77577	Manubi	106112	176188	182186	128144	212212	138146	346346	119119
BE77582	Manubi	106106	176180	182194	104136	208212	134142	346346	119135
BE77586	Manubi	106106	172180	186194	100124	204212	126130	346346	107107
BE77587	Manubi	106110	176180	182194	100136	212220	130134	350350	107127
BE77589	Manubi	106106	176180	182194	104136	208212	134142	346346	119135
BE77590	Manubi	106106	168176	202206	100112	208212	142146	346346	111135
BE77591	Manubi	106106	180184	182186	100104	212224	142142	346354	119139
BE77592	Manubi	106108	172192	194202	100148	200212	134142	346350	119135
BE77595	Manubi	106112	168172	182186	104148	208212	134134	342346	119135
BF01221	Manubi	106112	172172	194194	104140	216224	138150	350354	119135
BF01222	Manubi	106106	172188	182194	104140	204220	138142	346354	119119
BF01223	Manubi	106106	176180	182202	100100	212220	138146	346346	111111

BF01224	Manubi	112112	172180	186186	104104	208212	138142	346346	111119
BF01225	Manubi	102104	172176	182186	108132	200212	142146	346346	119135
BF01226	Manubi	104106	172184	182186	112136	208212	138142	346346	119131
BF01227	Manubi	102112	172172	182194	104136	208212	122134	346346	119135
BF01228	Manubi	106106	172180	182186	104116	212216	118146	346346	119119
BF01204	Kubusi	104108	172172	182186	100112	200212	130142	346346	119119
BF01205	Kubusi	106112	172172	182202	100132	212216	134142	346346	119119
BF01207	Kubusi	106106	180184	182186	100132	204212	134142	346346	119135
BF01208	Kubusi	106110	180188	182186	108128	204212	138142	350354	119135
BF01209	Kubusi	112112	172176	182182	124148	212216	122138	346354	119119
BF01210	Kubusi	106106	172180	198202	108116	200212	134142	346350	119135
BF01211	Kubusi	106106	172188	186202	092104	204212	138146	346346	111119
BF01212	Kubusi	106110	172180	182202	100100	212216	130142	346354	119135
BF01213	Kubusi	106106	172180	186186	100124	208212	142146	350358	119135
BF01214	Kubusi	102102	172172	182202	100104	200212	134146	346346	119123
BF01215	Kubusi	102112	172172	182186	104144	204204	130138	346346	119139
BF01216	Kubusi	106106	164172	186202	104144	200216	126134	346346	107107
BF01217	Kubusi	106106	176188	182210	104112	216216	130134	346346	107107
BF01218	Kubusi	106106	172184	182182	100100	200212	130138	346346	119135
BF01219	Kubusi	106106	172180	186202	100100	216220	146146	346346	111119
BF01220	Kubusi	102106	172176	186202	100100	200212	146146	346346	111119
BF01232	Kubusi	112112	176180	182186	100104	204216	134146	338346	119135
BF01236	Kubusi	102102	180180	182198	128152	204208	134138	354358	119139
BF01237	Kubusi	106112	172180	182202	128128	204212	142150	346358	135139
BF01238	Kubusi	106108	176184	182186	104152	200204	134134	346358	111135
BF01241	Kubusi	106112	176176	182186	144144	204204	134138	346346	111119
BF01242	Kubusi	102106	172176	182194	116140	200208	134146	346346	119135
BF01244	Kubusi	102106	172180	194202	100152	204204	146146	346346	111119
BF01245	Kubusi	104106	172184	186202	100100	212216	138142	346346	111119
BF01246	Kubusi	106108	176176	182182	144152	204204	134134	346358	111119
BF01247	Kubusi	104110	176184	182182	100152	204204	138150	346350	119139
BF01250	Fort Fordyce	106112	172176	186186	100104	216220	142146	346346	119139
BF01252	Fort Fordyce	106106	172176	186202	100124	204220	142146	346346	119119
BF01254	Fort Fordyce	106106	172176	202202	100104	200200	138146	346350	135139
BF01257	Fort Fordyce	106106	172180	186186	104112	200216	142142	346346	107107
BF01258	Fort Fordyce	106106	172176	182186	112112	200216	122154	346346	111119
BF01259	Fort Fordyce	106106	172180	186202	100124	204220	134146	346346	119119
BF01260	Fort Fordyce	112112	172184	182186	104112	212220	130142	346346	119119
BF01261	Fort Fordyce	106112	176188	186202	100144	200216	146150	346346	119119
BF01262	Fort Fordyce	102106	172172	186186	104144	208216	130134	346350	135139
BF01264	Fort Fordyce	106106	172180	186186	100104	220220	134142	346346	119135
BF01286	Fort Fordyce	106112	176180	182182	100144	212216	134142	346346	115119
BF01287	Fort Fordyce	106106	172180	182206	100112	212216	122134	346358	107127
BF01288	Fort Fordyce	106106	172184	182202	104140	212212	134134	346350	119119

BF01289	Fort Fordyce	106106	172188	182186	100112	212224	118146	346346	119119
BF01290	Fort Fordyce	106106	172176	182186	100100	200204	118134	346346	111135
BF01291	Fort Fordyce	106106	176180	186186	104148	220220	142146	346354	119119
BF01292	Fort Fordyce	106106	180180	182186	100100	220224	142154	346350	119135
BF02104	Alexandria	104112	176180	186186	112112	212216	142142	346346	119135
BF02105	Alexandria	108108	172176	182182	100100	216216	118142	338346	119135
BF02106	Alexandria	106110	172184	182182	112124	212220	142146	346346	119119
Unbanded	Alexandria	106112	172172	194198	108112	212216	134142	346346	111119
FC00186	Alexandria	108112	172176	182186	108112	216216	142146	346346	119135
FC11948	Alexandria	106112	172176	186194	100108	212220	142146	346346	111135

Appendix S3.20 *Phylloscopus ruficapilla* microsatellite genotypes, with respective SAFring ring/band numbers, and forest localities for all individuals included in this study

Individual	Forest	Pat 43	MLSP 4	Dpu 16	Cu 02	POCC 9	POCC 6	POCC 7	POCC 1
L22542	Ngele	119119	126126	153153	155155	209213	155155	096096	251251
N05831	Ngele	119121	122126	153153	153153	213213	155155	96980	251257
N05832	Ngele	119121	120126	151153	153155	211213	155155	096098	251251
N05836	Ngele	119121	126126	153153	153155	211213	155155	096098	251251
N05837	Ngele	119119	126126	153153	155155	213213	155155	096098	251257
N05841	Ngele	119121	126126	153153	155155	213215	155155	096098	251257
N05842	Ngele	119119	126126	147153	155155	213213	155155	096096	251257
N05846	Ngele	119121	126126	153153	153155	213213	153155	096098	251251
N05847	Ngele	119119	126126	147153	153153	213213	155155	096098	251251
N05848	Ngele	119121	126126	153153	153155	209213	153153	096098	251257
N05849	Ngele	119121	126126	147153	155155	213215	155155	096098	251257
N05850	Ngele	119119	126126	153153	153155	213213	153155	096098	251251
N05851	Ngele	119119	126126	153153	153155	213213	155155	096098	251257
N05852	Ngele	119121	126126	153153	153155	213213	155155	096098	251251
N05853	Ngele	119121	116126	153153	151153	213213	155155	098098	251257
N05854	Ngele	119121	126126	147153	153153	213213	155155	096098	251251
N05857	Ngele	119119	126126	153153	155169	213213	155155	096098	251251
N05858	Ngele	119121	126126	153153	155155	213213	153155	096098	251257
N05859	Ngele	119121	124126	153153	153155	213213	153155	096098	251251
N05862	Ngele	121121	126126	147153	153155	213213	155155	098098	251251
N07617	Oribi Gorge	119121	126126	153153	155155	215215	153155	096098	251251
N07619	Oribi Gorge	119119	126126	153153	155155	213213	153155	096096	251257
N07625	Oribi Gorge	119119	126126	153153	153155	213213	155155	098098	251251
N07626	Oribi Gorge	119121	126126	153153	153155	209213	155155	096098	251257
N07627	Oribi Gorge	119121	122126	149153	155155	209211	153155	096096	251251
N07642	Oribi Gorge	119121	126126	153153	155155	213213	155155	096098	251251
L64377	Mbotyi	121121	122128	153153	153153	209213	155155	096098	251251
L64378	Mbotyi	119119	126126	153153	153153	213213	155155	096098	251251
L64383	Mbotyi	121121	126128	153153	153155	211215	153153	096098	251257
L64385	Mbotyi	119121	122126	153153	153155	213213	153155	098098	251251
L64386	Mbotyi	121121	122128	153153	155155	211213	155155	096096	257257
Unbanded	Mbotyi	119121	126128	153153	153155	211215	153155	096096	251257
AR89409	Gomo	119119	126126	153153	155155	213213	155155	096096	251251
L64361	Gomo	119121	122126	153153	153155	213213	153155	096096	251251
L64370	Gomo	119121	126126	147153	153155	213213	155155	096096	251251
N05865	Gomo	119121	126126	153153	153155	209213	153155	096098	251251
N05867	Gomo	119121	126126	153155	153155	209213	153155	098098	251251
N05868	Gomo	119119	126126	153153	153155	209213	155155	096098	251257
N05869	Gomo	119121	126126	153153	153155	209213	153155	096098	251251
N05870	Gomo	119119	126126	153153	153153	213213	155155	096098	251257

N05871	Gomo	121121	126126	153153	153155	213213	155155	096098	251251
N05872	Gomo	121121	126126	153153	155155	213213	155155	096098	251251
N05873	Gomo	121121	126126	153153	153155	213215	155155	096096	251257
L64359	Baziya	119121	126126	149153	155155	213213	155155	098098	251251
N05874	Baziya	119119	126126	153153	153155	213213	155155	096098	251257
N05875	Baziya	119119	122128	149153	155155	213213	153155	096096	251251
N05877	Baziya	119121	122122	153153	153153	213213	153153	096098	251251
N05878	Baziya	119121	122126	153153	153155	209213	155155	096098	251257
N05879	Baziya	119119	126126	149153	155169	209213	153155	098098	251251
N05880	Baziya	121121	126126	147153	155155	211213	155155	096096	251257
N05894	Baziya	119119	126126	153153	153153	209213	155155	096098	251257
N05896	Baziya	119119	126126	153153	153155	213213	155155	098098	251251
N05897	Baziya	119119	126126	153153	153155	213213	153155	096098	251257
L64360	Baziya	119119	122126	149153	153155	213213	155155	096098	251257
L64389	Baziya	119119	126126	147153	153155	213213	155155	096098	251257
L64390	Baziya	119121	122128	147149	153155	209211	155155	096098	251257
Unbanded	Baziya	121121	126126	149153	155153	211213	153155	098098	251257
AR89481	Manubi	119121	126126	153153	153155	213213	155155	096098	251251
AR89501	Manubi	119119	126126	153153	153155	213213	155155	096098	251251
AR89502	Manubi	121121	126126	153153	155155	213213	153155	098098	251257
L64392	Manubi	119119	126126	153153	155155	213215	155155	094096	251257
L64394	Manubi	119119	126126	153153	153153	213213	155155	096096	251251
L64399	Manubi	119121	126126	153153	153155	213213	153153	096098	251257
N03515	Manubi	119121	126126	153153	153155	209209	153155	098098	251251
N03516	Manubi	121121	126126	153153	155169	213213	155155	096098	251251
N03521	Manubi	119119	126126	153153	155155	211213	153155	096098	251251
N03524	Manubi	119119	126126	153153	155155	215215	153155	096098	251251
N05708	Manubi	119121	122126	153153	153155	213213	153155	096098	251257
N05709	Manubi	119121	126128	153153	153155	213213	155155	096098	251251
N05716	Manubi	119121	116126	149153	153153	213215	155155	096096	251251
N05726	Manubi	119119	116126	147153	153155	215215	155155	096096	251257
N05758	Manubi	119121	126126	149153	153153	213213	153153	096096	251251
N05777	Kubusi	119119	126126	149153	153155	213213	155155	096098	251251
N05787	Kubusi	119119	124126	153153	153155	213213	153155	098098	251257
N05799	Kubusi	119119	126126	153153	153153	213213	155155	098098	251251
N03563	Kubusi	119121	126126	153153	155155	209213	155155	096098	251257
N03567	Kubusi	119119	122122	147153	153155	213213	155155	096096	251251
N03575	Kubusi	119119	122126	153153	155155	213213	153155	096098	251257
N03576	Kubusi	119119	126128	153153	153155	213213	155155	096098	251251
N03547	Kubusi	119121	122126	153153	153155	213213	155155	098098	251257
N03578	Kubusi	119121	126128	147153	155155	209213	155155	096098	251257
N05810	Fort Fordyce	119119	126126	147153	155155	213213	155155	096098	257257
N05815	Fort Fordyce	119119	126126	153153	153155	213213	155155	096096	251257
N05817	Fort Fordyce	119119	124126	153153	153155	213213	155155	096098	251251

N05828	Fort Fordyce	119121	126126	153153	153155	213213	155155	096098	251251
N05829	Fort Fordyce	119121	124126	153153	153153	213213	153155	098098	251251
N05882	Fort Fordyce	119119	126126	153153	153155	213213	153155	098098	251257
N05883	Fort Fordyce	119121	126126	153153	153155	213213	155155	096098	251251
N05884	Fort Fordyce	119121	126126	153153	153155	213213	153155	098098	251251
N05888	Fort Fordyce	121121	126126	153153	155155	213213	153153	096098	251257
N05891	Fort Fordyce	119121	124126	147153	155155	213213	155155	098098	251257
N05892	Fort Fordyce	119119	122126	153153	153155	213213	155155	096098	251251

Appendix S3.21 *Pogonocichla stellata* microsatellite genotypes, with respective SAFring ring/band numbers, and forest localities for all individuals included in this study

Individual	**Forest**	**WBSW 2**	**MCU 4**	**CAN 142**	**WBSW 9**	**CAN 162**	**CACA 3**	**CACA 27**	**GF0 6**
Y21931	Ngele	121121	133133	211223	106108	252256	328332	330354	145159
Y21932	Ngele	121121	131133	211213	106108	260264	328328	354364	147149
Y21934	Ngele	123123	131133	211211	108108	244260	312332	342344	147157
Y21935	Ngele	121123	129133	211211	106106	244248	328328	330346	147151
Y21936	Ngele	121121	131131	207211	106106	252252	328332	342350	145147
Y21937	Ngele	121123	131131	211215	106108	244248	328328	346362	157157
Y21938	Ngele	121121	131133	211211	106106	252252	328340	330350	157157
Y21939	Ngele	123123	131133	211223	108108	256264	332340	342356	147157
Y21940	Ngele	121121	133133	211211	106108	252260	312328	334362	151151
Y21941	Ngele	121123	133133	211227	108108	256256	328332	356356	147151
Y21942	Ngele	121121	133133	207219	106108	252260	328328	354358	149151
Y21943	Ngele	121123	129135	211227	106108	248264	328328	354356	147157
Y21944	Ngele	121123	131133	211243	106108	252260	328328	344350	151157
Y21945	Ngele	123123	133133	215223	108108	248248	328328	348354	147151
Y21947	Ngele	121121	131133	207211	106106	248260	324336	350358	143151
Y21948	Ngele	121121	131131	223223	106108	256256	336340	338350	145147
Y21949	Ngele	121121	131133	211215	106106	252252	328332	342348	145147
Y21950	Ngele	121121	131131	207211	106108	248252	328328	354356	145147
Y21953	Ngele	121121	131133	211215	106108	244248	328328	330346	145147
Y21954	Ngele	121123	131133	223223	108108	248264	328332	330354	145147
Y21955	Ngele	123123	133133	203211	106106	252252	328328	346358	151157
Y21956	Ngele	121121	131133	211223	106110	248260	328332	356362	151157
Y21957	Ngele	121123	133133	207211	108108	260264	312328	338358	149151
Y21959	Ngele	121121	133133	199211	106106	252264	328328	342356	151157
Y21960	Ngele	121123	129133	211243	106106	244260	328328	350354	149151
Y21961	Ngele	121123	133133	211235	106106	248252	320332	344352	147151
Y21963	Ngele	121123	131133	215235	106108	252264	328328	342346	147151
Y21964	Ngele	121121	129131	215227	106108	252256	328336	338342	149157
Y21965	Ngele	121123	131133	215227	106106	252252	328332	352358	145157
Y21968	Ngele	121121	133133	211243	106108	248256	328336	350356	145157
AR89419	Oribi Gorge	121121	131131	239243	108110	248256	328328	342346	157157
AR89420	Oribi Gorge	121123	129133	211215	106110	248252	332336	338346	145157
Y22049	Oribi Gorge	121123	131133	215223	106106	248252	332336	338352	147157
Y22050	Oribi Gorge	121123	129129	223231	106108	244260	328332	350350	151157
Y22051	Oribi Gorge	121123	131133	211211	106106	244256	328336	352358	151151
Y22052	Oribi Gorge	121123	129133	203211	106108	252256	328332	350352	147151
Y22053	Oribi Gorge	121121	131131	211223	106106	248248	328328	350354	147155
Y22054	Oribi Gorge	121123	131131	211215	106106	252256	328332	350356	145151
Y22056	Oribi Gorge	121123	133133	211211	106108	252252	328332	346352	147147
Y22057	Oribi Gorge	123123	131133	211211	106106	252260	332332	338352	147151

Y22058	Oribi Gorge	121123	131131	215239	108108	248260	328332	350356	147151
Y22059	Oribi Gorge	121121	129129	215223	106106	260264	312340	338354	147157
Y22060	Oribi Gorge	121121	133133	211211	106106	256256	328328	346350	145151
AR89402	Gomo	121123	133133	211239	106106	248256	332336	334354	147157
AR89403	Gomo	123123	131133	211211	106108	252256	328336	354356	147151
AR89407	Gomo	121123	131131	215231	106106	256260	328332	346350	145147
Y21969	Gomo	121123	131133	223231	106106	256260	328332	342346	145147
Y21970	Gomo	121121	131133	211215	106106	256260	328328	350352	149157
Y21971	Gomo	121123	133133	211223	106108	256260	328328	342350	151157
Y21972	Gomo	121123	131131	235239	106108	248260	328328	330338	147157
Y21973	Gomo	121121	131133	211235	106106	256260	328332	338360	151151
Y21974	Gomo	121123	133133	223239	106108	256260	328328	338342	151157
Y21975	Gomo	123123	131131	239239	106108	260260	328328	338342	157157
Y21976	Gomo	121123	129131	211235	106108	244252	328332	350352	147153
Y21977	Gomo	123123	129133	211211	106108	228252	328340	354356	157157
Y21978	Gomo	121121	131133	211215	106106	248260	328336	330342	147157
Y21979	Gomo	121123	133135	211215	106106	260264	312328	350360	153157
Y21980	Gomo	121121	133133	211215	106114	248264	328332	356356	147157
Y21981	Gomo	121121	129131	211211	106108	248252	328328	350352	151157
Y21982	Gomo	121123	133133	211235	108108	228260	328332	360360	145147
Y21984	Gomo	121121	131133	199211	106106	248260	324336	342352	145147
Y21986	Gomo	123123	131131	211235	106108	256260	328336	330350	145157
Y21987	Gomo	121123	131133	235235	106106	248248	312332	334350	145147
Y21988	Gomo	121123	133133	211215	106108	256256	328332	342350	147153
Y21989	Gomo	121123	129131	223231	106106	252256	336352	338348	147157
Y21990	Gomo	121123	133133	211223	106106	256256	328336	330346	141147
Y21991	Gomo	121123	131131	211211	106108	248264	328332	346362	151157
Y22028	Gomo	121121	131131	199215	106106	248252	328336	342342	147151
Y22029	Gomo	121123	129133	211215	106108	248256	328336	338346	141147
AR37663	Baziya	121123	131133	211211	106108	252256	328328	338354	151153
AR37667	Baziya	121121	131133	211235	106108	248256	328332	346360	141147
Y21992	Baziya	121123	131131	223231	106106	264268	328336	338346	145151
Y21993	Baziya	121123	131133	203211	106106	252264	328328	334342	151157
Y21994	Baziya	121121	133133	211235	106116	256256	328328	330350	147153
Y21995	Baziya	121121	131133	215243	106108	252264	328328	346354	151157
Y21998	Baziya	121121	131133	211223	106106	248264	332340	342350	147153
Y21999	Baziya	123123	133135	211215	106106	256256	320328	350354	147157
Y22022	Baziya	121121	133133	203239	106106	244260	328328	342350	151159
Y22023	Baziya	121121	131131	211211	106106	256256	328332	338346	151157
Y22024	Baziya	121121	133133	211235	106108	248256	332336	338350	147151
Y22025	Baziya	121123	131131	215223	106106	248256	328328	352354	145147
Y22026	Baziya	121121	129133	203215	106110	252252	328328	346366	147147
AR89429	Baziya	123123	133133	215235	106106	252264	328332	342342	157159
AR89443	Baziya	121123	131133	211215	106108	260264	328332	338342	145157

AR89450	Manubi	123123	131133	203215	106108	264264	332336	346350	147159
AR89453	Manubi	121123	133133	199215	106106	252252	336340	356356	147149
AR89461	Manubi	123123	129131	203215	106106	252260	328336	348350	147151
AR89462	Manubi	121121	129133	223235	106106	252256	332336	338354	151157
AR89483	Manubi	121123	131133	203211	106106	256256	328328	352360	151157
AR89487	Manubi	123123	133133	211211	106106	256264	328328	330350	147157
AR89490	Manubi	121123	133133	211231	112112	252252	328332	350350	147147
AR89503	Manubi	121123	131133	211215	106108	248260	328336	342348	147147
AR89527	Manubi	121121	133133	215239	106108	244256	328332	330338	147147
AR89529	Manubi	121123	133133	223227	106108	248256	328328	342356	147151
AR89531	Manubi	121121	131133	211215	106106	252252	320332	346346	147151
AR89535	Manubi	123123	133133	215215	106106	252252	332336	342358	151157
AR89536	Manubi	121123	131133	219223	106106	252256	332336	330342	151153
AR89538	Manubi	121121	131133	211211	106106	248260	328332	338358	145157
AR89546	Manubi	121123	133133	211215	106106	260264	328328	348358	147149
AR89548	Manubi	121121	131131	215227	108108	264264	328328	346348	147149
AR89549	Manubi	121121	133133	199223	106106	256264	320328	334346	141147
AS14401	Manubi	121123	131131	203203	106106	256256	328328	342350	157157
AS14402	Manubi	121123	129131	203211	106106	244260	328328	350354	147151
AS14403	Manubi	121123	133133	211239	106106	244260	312328	342358	145151
AS14404	Manubi	123123	133133	203211	106106	256260	328328	342356	147157
AS14405	Manubi	121123	131133	211235	106106	244256	328336	338354	151157
AS14406	Manubi	121121	131133	215223	106106	252252	336340	338360	147157
AS14407	Manubi	121121	131131	223235	106108	252256	332332	330356	151151
AS14408	Manubi	121123	131133	211223	106108	252252	328328	342348	147147
AS14409	Manubi	121121	129131	211215	106106	248256	336336	330342	147157
AS14411	Manubi	123123	131133	215215	106106	256256	328336	346350	151157
AS14412	Manubi	123123	131133	211211	106108	248256	332336	342350	147151
AS14413	Kubusi	121123	133135	211215	106106	244252	328332	342356	147151
AS14414	Kubusi	121123	133133	215215	106106	252252	328332	346348	151153
AS14415	Kubusi	121121	133133	211227	106106	252256	320348	342350	151157
AS14416	Kubusi	121121	133133	227239	106106	244252	328340	342354	145157
AS14417	Kubusi	121123	133133	207215	106108	248248	328332	346350	147147
AS14418	Kubusi	121121	131133	203215	106108	244248	328328	338346	147147
AS14419	Kubusi	121123	133133	211227	106108	252252	328332	342342	147147
AS14420	Kubusi	123123	133133	211227	106106	252256	328336	354354	147147
AS14421	Kubusi	121123	133133	207235	106108	256256	332332	342350	147157
AS14425	Kubusi	121121	133133	207223	106106	252256	328340	338338	151157
AS14430	Kubusi	121123	131131	211223	106108	244252	328328	338354	147151
AS14433	Kubusi	121121	133137	235235	106108	252256	328332	338358	147159
AS14441	Kubusi	121121	133133	203215	106106	252252	320332	338354	147157
AS14443	Kubusi	121123	133133	215243	106106	256260	332348	346362	145147
Y21917	Kubusi	121121	131133	207215	106106	256256	328328	346360	145147
Y21918	Kubusi	123123	133133	215223	106106	248252	332340	348358	145153

Y21901	Kubusi	121123	131131	203227	106108	252252	312328	338356	147147
Y21902	Kubusi	121123	133133	211243	106106	256260	328328	354358	147151
Y21903	Kubusi	121123	131131	231243	106106	252256	328328	334350	149151
Y21904	Kubusi	121121	133133	170235	106106	256260	320328	338362	147157
Y21905	Kubusi	121123	133133	211211	106108	248252	328332	342354	147157
Y21906	Kubusi	121123	131133	203207	106108	248256	328340	338354	157157
Y21907	Kubusi	121121	131131	211211	106108	244260	328328	350360	147157
Y21909	Kubusi	121121	133133	215223	108108	252256	328328	342354	151151
Y21910	Kubusi	121121	131131	207211	106108	256264	332332	346356	151153
Y21913	Kubusi	121121	133135	211235	108108	252252	328328	338338	147157
AF90440	Fort Fordyce	121123	133133	211211	106106	248252	328336	338358	145157
AP23682	Fort Fordyce	121123	133133	215215	106106	248252	328336	330334	153157
AS15684	Fort Fordyce	121123	133133	215215	106108	252256	328336	330346	141147
AS15685	Fort Fordyce	123123	129133	235239	106108	248264	328332	346362	151157
AS15686	Fort Fordyce	121123	131133	215215	106106	264268	328336	338346	145151
Unbanded	Fort Fordyce	123123	129131	203211	106108	256268	328332	330346	147157
Y21920	Fort Fordyce	121123	129133	215239	106106	252256	328328	342342	157157
Y21921	Fort Fordyce	121121	129129	207235	106108	252268	328328	342366	151157
Y21922	Fort Fordyce	121123	131133	203211	106106	252260	328328	338354	149151
Y21923	Fort Fordyce	121121	131131	203215	106108	256256	328332	330342	147151
Y21924	Fort Fordyce	121123	133133	215215	106106	248252	328332	334342	153157
Y21925	Fort Fordyce	121123	131133	215215	106106	244244	328336	330330	147151
Y21926	Fort Fordyce	121123	133133	211215	106106	252260	332336	338358	147153
Y21927	Fort Fordyce	121121	131133	211215	106106	248248	328332	346356	149151
Y21928	Fort Fordyce	121123	133133	207211	106106	248248	328328	342342	147157
Y21929	Fort Fordyce	121121	133133	203211	106106	248248	328328	338338	147157
Y21930	Fort Fordyce	121121	133133	207211	106106	248256	328336	342342	151157
Y22000	Fort Fordyce	121123	129133	207211	108108	252256	328328	338354	147157
Y22001	Fort Fordyce	123123	131133	227235	106108	260264	328328	334342	151157
Y22002	Fort Fordyce	121123	131131	223235	106108	256256	328328	330350	147153
Y22003	Fort Fordyce	121121	133133	203235	106106	252252	328328	338342	153157
Y22004	Fort Fordyce	121121	133133	203211	106106	256256	328332	338356	147157
Y22005	Fort Fordyce	121121	131131	203231	106108	248260	320328	346360	147151
Y22006	Fort Fordyce	123123	129129	211215	106106	256260	328328	338358	145147
Y22007	Fort Fordyce	121123	133133	211235	106108	256260	328328	330342	147147
Y22008	Fort Fordyce	121123	131133	211227	106108	252252	328328	342354	151157
Y22009	Fort Fordyce	123123	131133	203235	106106	252252	336336	350360	145145
Y22010	Fort Fordyce	121121	131133	207235	106106	252252	328328	338342	151157
Y22011	Fort Fordyce	123123	133133	227235	106106	248256	328336	338356	145147
Y22012	Fort Fordyce	123123	131133	207211	106108	248264	328336	338342	147157
Y22013	Fort Fordyce	121123	131131	223235	106106	256260	320336	338356	147157
Y22014	Fort Fordyce	121121	131133	211215	106106	252252	328328	338338	151157
Y22015	Fort Fordyce	121123	133133	203239	106106	248268	328328	338342	149151
Y22016	Fort Fordyce	121121	131133	211227	106108	248252	320328	358360	147151

Y22017	Fort Fordyce	123123	133133	211215	106106	248252	328336	346358	151157
Y22018	Fort Fordyce	121121	133133	211215	106108	248248	328332	338366	145147
Y22019	Fort Fordyce	123123	133133	207235	106106	244260	312332	342350	147157
Y22020	Fort Fordyce	121121	131131	207211	106108	248252	328332	330362	151151
Y22021	Fort Fordyce	121123	133133	207207	106108	252256	328332	342366	147151
Y22031	Alexandria	121123	133133	207215	106108	256256	328328	330346	145157
Y22032	Alexandria	121121	131131	223235	108108	256256	328332	342350	147151
Y22033	Alexandria	121121	131133	199219	106106	252256	328332	330350	141147
Y22034	Alexandria	121121	133133	211223	106108	252256	328332	330350	141151
Y22035	Alexandria	121121	133133	235235	106108	252264	328328	350362	147151
Y22037	Alexandria	121121	131133	211211	106106	252256	328332	338350	147151
Y22038	Alexandria	121121	131131	215215	106106	252256	320320	352356	147151
Y22039	Alexandria	121121	131133	207235	106108	252252	328328	342350	147151
Y22040	Alexandria	121123	131133	211215	106108	252256	332336	338342	147151
Y22041	Alexandria	121123	133133	215215	106108	256256	328332	342360	145149
Y22042	Alexandria	121121	131133	223235	106106	252256	328332	338360	145147
Y22043	Alexandria	121121	131133	199203	106108	252256	328328	330338	147157
Y22044	Alexandria	121121	131133	207235	106108	256256	328332	350350	145151
Y22045	Alexandria	121123	131133	215235	106106	248252	332336	346356	141157
Y22046	Alexandria	121121	131133	207235	106106	248256	328328	346362	145147
Y22047	Alexandria	121121	131133	203215	106108	252256	328332	330356	147151
Y22048	Alexandria	121121	131133	223231	106108	252252	328328	338342	141151
AR89556	The Island	121121	133133	211211	106108	256264	328340	352360	147157
AR89558	The Island	121121	131133	203215	106108	256260	328328	330366	147157
AR89590	The Island	121123	133133	211235	106108	248252	328328	342350	141145
AR89592	The Island	121121	133133	211223	106106	248276	328332	352356	141145
AR89595	The Island	121121	133133	223235	106106	248256	328328	348368	147157
AR89600	The Island	121121	133133	215235	106106	252256	320340	354356	145147

Chapter 4: Phylogeographic history of three forest-dependent passerines within Afromontane forests of the Eastern Cape, South Africa shows their resilience as a forest refuge during the late Pleistocene

4.1 Abstract

Aim: Pleistocene climate shifts are a known driver of biodiversity patterns within Afromontane forest sky islands across Africa. These forests are thought to serve as climate refugia for Afrotropical forest biota, and are of high conservation significance. Palaeoclimatic shifts are believed to have homogenised diversity within southern African subtropical forests, yet endemic complexity is also evident. We will investigate the hypothesis that Afromontane forest patches acted as refugia for bird species and that connectivity among habitat patches was significantly influenced by paleoclimatic events.

Location: Maputaland-Pondoland-Albany Hotspot situated in the Eastern Cape and southern KwaZulu-Natal provinces of South Africa.

Taxa: Three species of Oscine passerines *Batis capensis*, *Phylloscopus ruficapilla*, and *Pogonocichla stellata*

Methods: We conducted a multi-locus phylogeographic study using complete mitochondrial control region sequences, and microsatellite genotypes (eight species-specific loci). Geographic population structure, past changes in effective population size, and regional source-sink demographic dynamics were determined. We then contextualised our genetic findings using palaeodistribution modelling of each species.

Results: High genetic diversity within species, and coalescent modelling of mitochondrial lineages suggest that the presence of the three species predate the last glacial maximum (21 kya), previously considered as a climatic extinction filter of South African forest biota. Source-sink demographic modelling, alongside species palaeodistribution predictions, show that low-elevation scarp forests, situated between Afromontane and coastal forests, were prominent glacial refugia for *B. capensis* and *P. stellata*, while southern mid-elevation Afromontane forests served as stronger refugia for *P. ruficapilla*. Palaeodistribution modelling revealed regional persistence of suitable forest habitats since at least the last interglacial period (120 kya), which alongside demographic expansion prior to the Holocene, is indicative of regional forest expansions under warm, mesic climates.

Main Conclusions: Scarp forests, as well as certain Afromontane forests within the southern Maputaland-Pondoland-Albany Hotspot acted as prominent climate refugia for subtropical African forest biota.

4.2 Introduction

The climate refugia hypothesis posits that many terrestrial habitats have isolated strongholds which persisted through the climatic oscillations of the Plio-Pleistocene (Bennett & Provan, 2008; Gavin et al., 2014; Migliore et al., 2018; Vanzolini & Williams, 1981). These strongholds acted as hotspots for vicariant diversification, and are centres from which species populations would subsequently expand under favourable conditions (Brown et al., 2020; Garzón-Orduña et al., 2014; Smith et al., 2014). This hypothesis is exemplified by the exceptionally high endemism within Afromontane forests (Burgess et al., 2007; Demos et al., 2014; Fjeldsa & Lovett, 1997; Mairal et al., 2017; Roy, 1997; Roy et al., 2001; Voelker et al., 2010), an sub-biome of archipelagic Afrotropical forest ecosystems associated with the highlands of Africa (White, 1981, 1983). The remote sky islands comprising this sub-biome share distinct species assemblages, despite exclusively Afromontane species rarely dispersing across lowland regions (Fjeldså et al., 2010; Gehrke & Linder, 2014; Matthee et al., 2004; Wondimu et al., 2014). Palaeoecological records reveal Afromontane forests to have been periodically widespread, integrating into lowland forests in the early-mid Pleistocene (Dupont et al., 2011; Ivory et al., 2019; Kadu et al., 2011; Migliore et al., 2020b). Glacial-interglacial cycles were previously thought to have driven forest extent through the continental aridification relegating forests to refugia during glacial periods, (Castañeda et al., 2016; Cowling et al., 2008; Dupont et al., 2011), although regional hydroclimates likely operate asynchronously, often independent from global temperature fluctuations (Ivory et al., 2012, 2018; Lézine et al., 2019; Singarayer & Burrough, 2015), complicating the perception of past Afromontane forest dynamics (Ivory et al., 2018; Peterson & Ammann, 2013).

Considerable attention has been devoted towards understanding climate refugia in the Eastern Afromontane Biodiversity Hotspot (EA Hotspot) of East Africa (Chala et al., 2017; Fjeldså & Bowie, 2008; Huntley et al., 2018; Mairal et al., 2017; Mizerovská et al., 2019; Voelker et al., 2010). This forest archipelago, however, extends southwards into the Maputaland-Pondoland-Albany Biodiversity Hotspot (MPA Hotspot), which stretches from southern Mozambique to the Eastern Cape of South Africa (Mittermeier et al., 2004). Afromontane forest presence in both biodiversity hotspots predate the late Miocene tectonic upheaval of the East African Rift Valley system (Bryja et al., 2017; Dupont et al., 2013; Maslin et al., 2014; Pound et al., 2012), with refugia established along windward mountain slopes continuously sequester moisture from Indian Ocean trade winds (Fjeldså et al., 2012). Comparatively stable equatorial conditions foster higher forest biodiversity in EA Hotspot forests than in the MPA Hotspot (Fjeldså & Bowie, 2008; Levinsky et al., 2013; Pinkert et al., 2020), which nevertheless retains considerable endemism (Geldenhuys & Macdevette, 1989; Levinsky et al., 2013; Perera et al., 2018). The MPA Hotspot lies at the confluence between tropical trade winds and southern westerlies, and the interactions between these two moisture systems ensured consistently high rainfall over this region during the late Pleistocene (Chase et al., 2017; Engelbrecht et al., 2019; Simon et al., 2015). At higher latitudes, however, mid-elevation (500-1800 m) Afromontane communities may have been more adversely affected by global cooling events than in the tropics (Combrink et al., 2020; Eeley et al., 1999; Stewart & Mitchell, 2018).

Subtropical Afromontane forests occur more readily at lower elevations than in the tropics, and integrate with the Indian Ocean coastal belt (IOCB) forest sub-biome to create a transitional, albeit largely Afromontane, forest-type known as scarp forest, established within sheltered terrain along a narrow zone of consistently temperate, humid lowland (Mucina, 2018; von Maltitz et al., 2003). Scarp forests appear relatively resilient to Palaeoclimatic shifts (Eeley et al., 1999), and are regarded as prominent climate refugia for both Afromontane, and IOCB forests within the MPA Hotspot, exhibiting higher species and genetic diversity than either sub-biome (Barnes & Daniels, 2019; Busschau et al., 2019a; Lawes et al., 2007a; Moir et al., 2020; Tolley et al., 2018). Mid-elevation Afromontane forests may harbour unique genetic complexity (Barnes & Daniels, 2019; Coetzer et al., 2020; da Silva & Tolley, 2017; Hughes et al., 2005; Kushata et al., 2020; Madisha et al., 2018), which suggests greater past forest persistence than currently appreciated.

To better understand the biogeography of Afromontane forest avifauna within the MPA Hotspot, we conducted a phylogeographic study on three songbird species inhabiting forest sky islands across the Eastern Cape and southern KwaZulu-Natal provinces of South Africa. Mitochondrial control region (mtDNA CR), and microsatellite data were generated for *Batis capensis*, *Phylloscopus ruficapilla*, and *Pogonocichla stellata*, three species with similar functional traits (small body size <30 g, insectivorous, occupy forest mid- and understoreys) (Hockey et al., 2005), but which differ in evolutionary history, and habitat specialisation. Two species, *P. ruficapilla*, and *P. stellata*, almost exclusively reside in forests (Berruti, 1997; Oatley, 1997b), and are thought to have proliferated within EA Hotspot during the late Pliocene/early Pleistocene, migrating into South Africa during forest expansions 0.9-0.8 mya

(Alström et al., 2018; Bowie et al., 2006). The origins of *B. capensis* is less certain, but this species a near endemic to South Africa (Wogan et al., 2016), occurring in temperate thicket and forest habitats across the south and east of the country (Johnson, 1997),

The last glacial maximum (LGM; ~21 kya), is thought to have severely constricted forests throughout the MPA Hotspot, imposing an extinction filter on less robust forest taxa (Eeley et al., 1999; Lawes et al., 2007a). We suspect, however, that the three focal species persisted through this event, given the recognition of distinct South African subspecies (Hockey et al., 2005). We further suspect that persistence through Palaeoclimatic shifts like the LGM were largely reliant upon scarp forest refugia, and so these forests should exhibit greater genetic diversity, and serve as source populations for other regional forests. Forest expansions, and upslope shifts during the current interglacial (<12 kya) (Eeley et al., 1999; Norström et al., 2014; Scott et al., 2012; Zhao et al., 2016) likely encouraged both population and range expansions within each species, as has been observed in regional forest-associated bats (Moir et al., 2020). Lastly, we anticipate *B. capensis* would possess the greatest genetic diversity of the three focal species, given the possibly more ancient presence of this species within South Africa, alongside a broader habitat generalisation that likely conferred greater resilience against past forest loss compared to the forest-exclusive *P. ruficapilla*, and *P. stellata*.

4.3 Methods

4.3.1 Field sampling and laboratory procedures

From 2017-2018, we visited eleven forests – six Afromontane, three scarp, and two IOCB – over three-week intervals across the Eastern Cape and southern KwaZulu-Natal provinces of South Africa (Figure 4.1). The study species were captured, and banded following a standardised mist-netting protocol (De Beer et al., 2001). Genetic material was sampled by collecting 20-50 µL of blood from the brachial vein using sterile hypodermic needles, and heparinised capillary tubes, complying with South African regulations (see Acknowledgments), and all birds were released on site. Blood was preserved in 95% ethanol, and DNA extraction followed a Nucleospin DNA extraction kit protocol (Macherey-Nagel, Germany). The complete mtDNA CR was amplified across two overlapping fragments, using species-specific primers (Appendix S4.1, Appendix S4.2) customised from Singh et al. (2017), as this hypervariable non-coding locus is situated between the *tRNA-glu* and *tRNA-phe* genes in *B. capensis* and *P. stellata*, and between *tRNA-thr* and *tRNA-pro* in *P. ruficapilla* (Ruokonen & Kvist, 2002; Singh et al., 2008). Each mtDNA CR fragment was amplified using polymerase chain reactions (PCR) in 25 µL volumes containing 1 x SuperTherm Taq buffer (Thermo Fisher

Scientific), 1.5 mM $MgCl_2$, 1 mM dNTPs, 1mM of each primer, 0.5 U SuperTherm Taq polymerase (Thermo Fisher Scientific), and 2 µL [100 ng/µL] template DNA. All mtDNA CR PCR protocols comprised an initial denaturation of 94 °C for 5 minutes, 35 cycles of 30 s at 94 °C, 30 s at T_{anneal} (Table S1), and 30 s at 72 °C, and a final extension of 72 °C for 7 min. Negative controls were used to monitor contamination, and all amplicons were screened using 1% agarose gel electrophoresis, and purified using a BioSpin Gel Extraction Kit protocol (Bioer Technology, China) prior to sequencing on an ABI 3730xl device (Central Analytical Facility, Stellenbosch University). Sequencing was conducted in a single direction using internal primers only (see Appendix S4.1) to circumvent complications arising from repeat regions flanking the mtDNA CR. Sequences were checked for base ambiguity in GENEIOUS 7.1.4 (©Biomatters), and aligned with CLUSTAL X (Larkin et al., 2007) in the same software. We additionally incorporated nuclear microsatellite data, based on genotypic profiles of eight species-specific loci generated for the same individuals (Chapter 3), to improve the phylogeographic inferences made from mitochondrial sequence data.

4.3.2 Intraspecific genetic diversity and genetic population structure

Forest-level genetic diversity based on mtDNA CR was assessed for each species according to number of haplotypes (*H*), haplotype- (*h*) and nucleotide diversity (π), and the number of private haplotypes (*PH*), estimated in ARLEQUIN 3.5 (Excoffier & Lischer, 2010), with statistical significance tested over 1000 permutations. Mitochondrial diversity values were compared to forest-level microsatellite diversity estimates obtained from Chapter 3. To visualise patterns of maternally determined population structure, we constructed statistical parsimony networks using POPART 1.7 (Leigh and Bryant, 2015). To compare differences in population differentiation according to biparentally- and maternally-inherited genetic markers within each species, we determined pairwise F_{ST} from mtDNA CR, and microsatellite (nuDNA) datasets in ARLEQUIN 3.5 (Excoffier & Lischer, 2010). We visualised population structures using pairwise F_{ST} values of these two genetic markers using both principal component analysis (PCoA) in GenAlEx 6.5 (Peakall and Smouse, 2012), and BARRIER 2.2 (Guerard and Manni, 2004) to identify where inter-forest geneflow is constrained. Finally, we observed underlying population substructures according to Bayesian Analyses of Population Structure (BAPS) 6.0 (Corander et al., 2013), using the ‘spatial clustering of groups’ approach for both mtDNA CR and microsatellites, and performed hierarchical analysis of molecular variance (AMOVA) in

ARLEQUIN 3.5 (Excoffier & Lischer, 2010) to measure the genetic differentiation between the population subdivisions identified by BAPS.

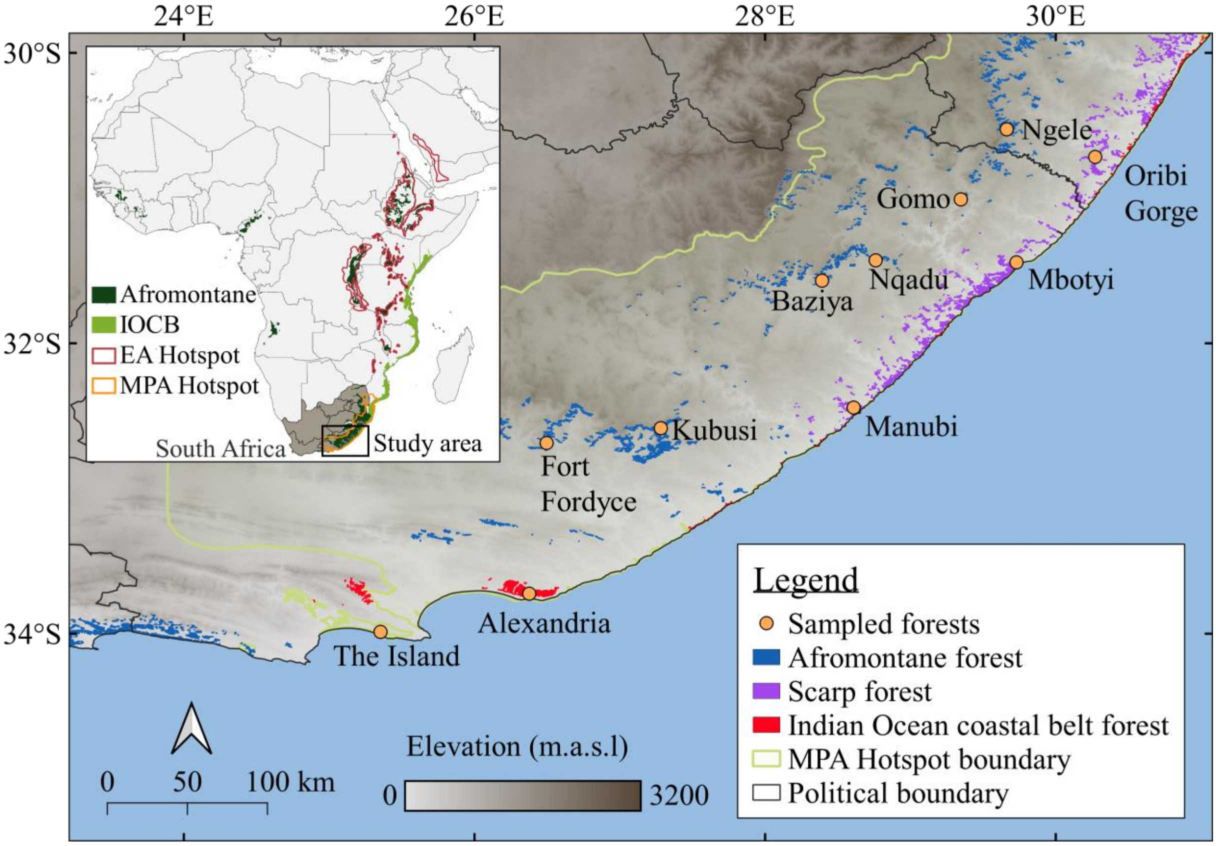


Figure 4.1 Sample locations within Afromontane (blue), scarp (purple), and Indian Ocean coastal belt (IOCB) (red) forests across the southern region of the Maputaland-Pondoland-Albany (MPA) Hotspot in the Eastern Cape and southern KwaZulu-Natal Provinces of South African. The inset map shows the delineation of the East Afromontane (EA), and MPA Hotspots, and the distribution of the Afromontane and IOCB forest sub-biomes across Africa.

4.3.3 Long-term demographic history

Past fluctuations in female effective population sizes (N_{ef}) were reconstructed from mtDNA CR sequences of each species using Bayesian skyline plots (BSPs), generated in BEAST 2.6.1 (Bouckaert et al., 2019). To perform coalescence modelling, we evaluated optimal nucleotide substitution models for the mtDNA CR of each species according to Akaike Information Criteria (AICc) in jMODELTEST 2.1.10 (Darriba and Posada, 2012): HKY+I+G (I = 0.913; G = 0.286) for *B. capensis*; HKY+I (I = 0.891) for *P. ruficapilla*; and HKY+I (I = 0.963) for *P. stellata*. Weak observed population substructuring permitted the pooling of individuals within each species without confounding BSP reconstruction (Heller et al., 2013). Three independent runs were conducted for 40 million Markov chain Monte Carlo (MCMC) steps, with a 10% burn-in period, and sampling every 10 000 chains. Given the uncertainty of mtDNA CR mutation rates within songbirds, we employed a strict molecular clock using three mutation rates: μ = 3.7% (Lerner et al., 2011), μ = 5.0% (Zhang et al., 2012), and μ = 12.0% per million years (Hansson et al., 2008; Hindley et al., 2018). Convergence of runs, BSP results, and 95% highest posterior densities, were visualised in TRACER 1.7 (Rambaut et al., 2018). We further investigated historic declines in total effective population size (N_e) (>100 generations, Zachariah Peery et al. 2012) using heterozygosity-excess tests on microsatellite data in Bottleneck 1.2 (Piry et al., 1999). We employed the single-step mutation model (SSM), and two-phase mutation (TPM) model (90% and 95% SMM), using a variance value of twelve (Piry et al., 1999) to accommodate a wider range of possible mutation dynamics in natural populations (Bhargava & Fuentes, 2010). Strong population declines were identified using a Wilcoxon signed-rank test (Luikart & Cornuet, 1998).

4.3.4 Modelling regional forest-level divergence

To elucidate forest demographic history, and divergence time estimates between genetically identified subpopulations of the three songbird species, we employed approximate Bayesian computations in DIYABC 2.1.0 (Cornuet et al., 2014). We iteratively tested the goodness-of-fit for a variety of plausible demographic scenarios hierarchically modelled from the two to five genetic subdivisions suggested by BAPS and BARRIER (see below), incorporating mtDNA CR and microsatellite datasets (see Appendix S4.10 for all tested demographic scenarios). For mtDNA CR analysis, we selected the summary statistics: number of haplotypes, number of segregating sites, mean pairwise differences, number of privately segregating sites, and F_{ST}. We selected the HKY mutation model for all three species, adjusting gamma shape (G) and proportion of invariant sites (I) according to optimal mutation models suggested by jMODELTEST 2.1.10 (Darriba and Posada, 2012), and used a uniform mutation rate ranging from $\mu = 3.7 \times 10^{-8}$ to $\mu = 12.0 \times 10^{-7}$ substitutions/site/year (s/s/y). For microsatellites, we selected the summary statistics: number of alleles, mean genetic diversity, mean size variance, F_{ST}, and shared allele distance. The default microsatellite mutation model was retained, with a uniform mean mutation rate ranging from $\mu = 1 \times 10^{-4}$ s/s/y standard in vertebrates (Bhargava & Fuentes, 2010), to $\mu = 1 \times 10^{-2}$ s/s/y observed in the songbird genus *Hirundo* (Anmarkrud et al., 2008; Brohede et al., 2002). Higher microsatellite mutation rates may be more applicable in smaller songbirds (Fan & Guo, 2018). We explored prior effective population sizes of N = 10-100000, and prior time intervals T = 10-100000 generations, assuming a generation time of two years in *B. capensis* and *P. ruficapilla* (Bird et al., 2020), and three years for *P. stellata*

(Oatley, 1982b). Following recommendations from Cornuet et al. (2014) for computational and statistical robustness, we simulated one million datasets per proposed demographic scenario. We compared relative model performance by computing posterior probabilities using logistic regression linear discriminant analysis components of the summary statistics. Following this, we estimated the posterior probabilities of parameters for the best performing model. Finally, we performed model checking on the chosen model using principal component analysis, and locating observed summary statistics amongst simulated summary statistics. These procedures were conducted in DIYABC 2.1.0 (Cornuet et al., 2014).

4.3.5 Modelling past changes in species distribution

To evaluate how the occurrence of each species may have varied within the study area during the late Pleistocene, we modelled species distributions for the present day, mid-Holocene climate optimum, (HCO; ~6 kya), LGM (~21 kya), and last interglacial period (LIG; 120-140 kya). Georeferenced species occurrence records were compiled from the South African Bird Ringing Unit (SAFRING, http://safring.birdmap.africa/, accessed 14 March 2020), BirdPix Virtual Museum (http://vmus.adu.org.za/, accessed 14 March 2020), and Southern African Bird Atlas Project 2 databases (SABAP2, http://sabap2.birdmap.africa/index.php, accessed 16 March 2020). We excluded occurrence records extra-limital to the study area, and which predate 1970 (before present day climate records), as well as duplicate records within 30 arc-second grid cells.

We used 19 bioclimate variables (Appendix S4.7) from WORDCLIM 2.1 (https://www.worldclim.org/) for present day (1970-2000), and WORLDCLIM 1.4 (https://www.worldclim.org/) to model species distributions during the HCO, LGM, and LIG (Fick & Hijmans, 2017). Variables were obtained at 30 arc-seconds and 2.5 arc-minutes resolution for the present-day models, 30 arc-second resolution for HCO models, 2.5 arc-minute resolution for the LGM models (the lowest resolution available), and 30 arc-second resolution for the LIG models. HCO and LGM variables were derived from the Model for Interdisciplinary Research on Climate Earth System Model (MIROC-ESM; Watanabe et al. 2011), and the Community Climate System Model 4 (CCSM4; Gent et al. 2011) to accommodate different interpretation of past climates (Beaumont et al., 2008), and LIG bioclimate were derived from Otto-Bliesner et al. (2006). All bioclimate datasets were trimmed to the study area in QGIS 3.10 (QGIS Development Team, 2018) to improved model accuracy.

MAXENT 3.4 (Phillips et al., 2017) was used to compute past and present SDMs for each species. The following model conditions applied: hinge features only; a regularisation multiplier of 1, 10 000 maximum background points; 10 cross-validated replicate runs; 500 maximum iterations; a convergence threshold of 0.0001 and assessment of model importance using jack-knife tests; use of hinge features alone for occurrence records >15 for more versatile approximations of species-climate relationships (Phillips & Dudík, 2008). Model training used 452 occurrence records of *B. capensis*, 305 of *P. ruficapilla*, and 266 of *P. stellata*, and tested 98, 72, and 55 records of each species, respectively. To improve model reliability, we used ENMTOOLS 1.4 (Warren et al., 2010) to find correlations coefficients among variables exceeding $R = 0.90$, removing the auto-correlated variables with the lowest model contributions to retain seven BIOCLIM layers (bio3, 6, 9, 12, 14, 15, 19; Appendix S4.8) to create the past and present species distributions.

4.4 Results

4.4.1 Intraspecific genetic diversity and population structure

Complete mtDNA CR were successfully sequenced for all individuals of each songbird species (Table 4.1): 116 *B. capensis* (1311 bp), 92 *P. ruficapilla* (1134 bp), and 200 *P. stellata* (1295 bp). *Batis capensis* exhibited high genetic diversity levels, according to both mitochondrial ($h = 0.964$, $\pi = 0.006$), and microsatellite (rarefied $AR = 10.625$) genetic markers (Table 4.1). By comparison, *P. ruficapilla* showed moderately high mitochondrial diversity ($h = 0.944$; $\pi = 0.007$), but remarkably low microsatellite diversity (rarefied $AR = 3.375$). *Pogonocichla stellata* displayed the lowest mitochondrial genetic diversity ($h = 0.769$; $\pi = 0.003$), despite having relatively high microsatellite diversity (rarefied $AR = 9.750$) (Table 4.1).

Statistical parsimony networks (Figure 4.2) indicated that many haplotypes in *B. capensis* are restricted to single forests patches, with no clear geographic pattern evident; *P. ruficapilla* also shows no clear phylogeographic pattern, but has more shared haplotypes among forest types compared to *B. capensis*. *Pogonocichla stellata* had the greatest degree of geographic clustering of related haplotypes between northeast forests (Ngele, Oribi Gorge, Gomo, Baziya), and southwest forests (Kubusi, Fort Fordyce, Alexandria, The Island), although this species also showed the highest proportion of shared haplotypes, including one haplotype common to 40% of individuals among all sampled forests. The BAPS analyses showed more mtDNA CR phylogeographic resolution, and identified two genetic clusters in *B. capensis* (Ngele, Oribi Gorge, Gomo vs Nqadu, Baziya, Manubi, Kubusi, Fort Fordyce, and The Island), but no geographic subdivisions within this species based on microsatellite data (Figure 4.3). BAPS further identified no population subdivisions for either genetic marker in *P. ruficapilla* (Figure 3). In *P. stellata*, however, BAPS detected three genetic clusters from mtDNA CR (Ngele, Oribi Gorge, Gomo vs Alexandria vs Baziya, Manubi, Kubusi, and Fort Fordyce), and two genetic clusters from microsatellites (Alexandria, The Island vs Ngele, Oribi Gorge, Gomo, Baziya, Manubi, Kubusi, and Fort Fordyce) (Figure 4.3).

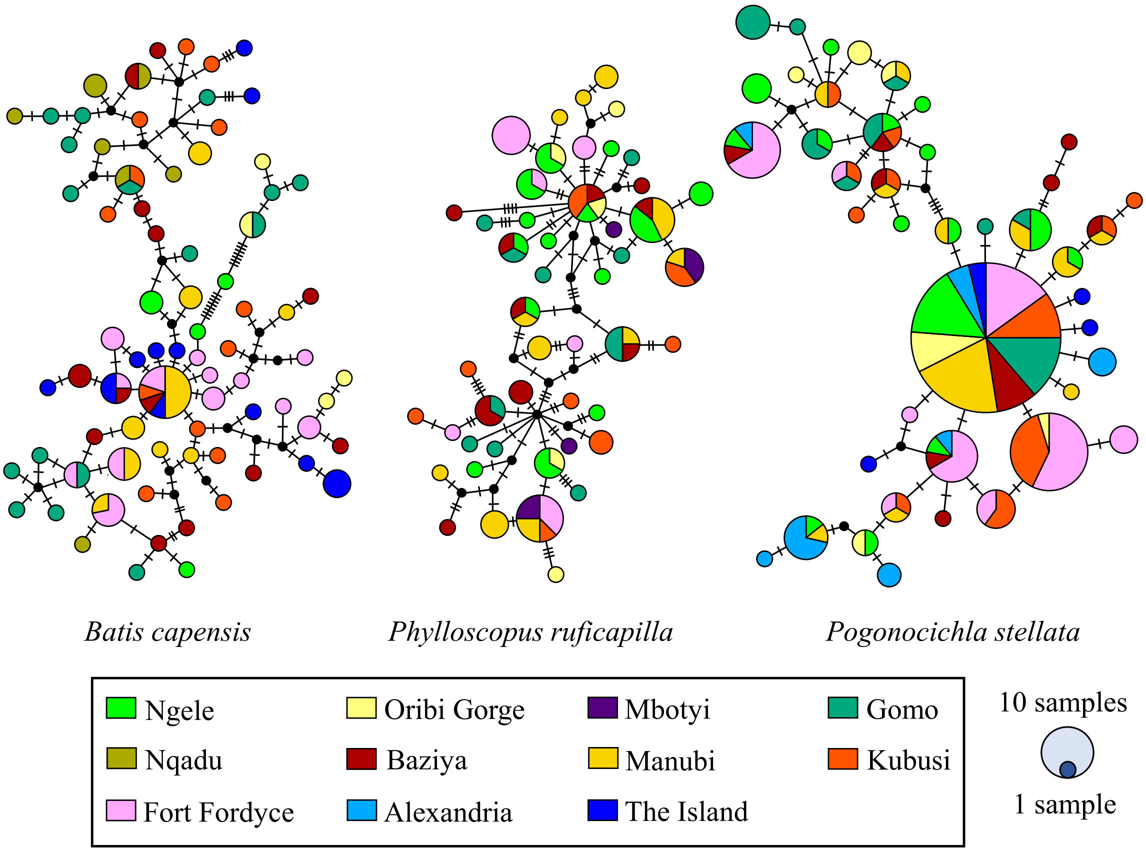

Batis capensis *Phylloscopus ruficapilla* *Pogonocichla stellata*

Figure 4.2 Haplotype networks of complete mtDNA control regions within three songbird species, with corresponding colour key for sampled forests. Haplotype relatedness is shown by connecting lines, with hatch marks indicating the number of mutational differences. Black dots represent missing haplotypes. Haplotype frequency is indicated by circle size.

Global population genetic differentiation as revealed by AMOVA analyses (Table 4.2) was highest in *P. stellata* (mtDNA: $F_{ST} = 0.054$, $p < 0.001$; nuDNA: $F_{ST} = 0.054$, $p < 0.001$), followed by *B. capensis* (mtDNA: $F_{ST} = 0.024$, $p < 0.001$; nuDNA: $F_{ST} = 0.013$, $p = 0.100$), and lowest in *P. ruficapilla* (mtDNA: $F_{ST} = 0.009$, $p = 0.322$; nuDNA: $F_{ST} = 0.006$, $p = 0.261$). Comparisons between pairwise F_{ST} values derived from mtDNA CR and microsatellite markers (Appendix S4.3-S4.5), revealed a higher level of significant differentiation based on mtDNA CR than microsatellites for both *B. capensis* (Appendix S4.3), and *P. stellata* (Appendix S4.5). Utilizing the phylogeographic group structure revealed by BAPS as *a priori* hypotheses in AMOVA, *B.*

capensis and *P. stellata* groups based on BAPS, showed shallow but significant variation among groups, with most genetic variation being present within forests for both species (Table 4.2). BARRIER identification of the three most prominent locations of constrained geneflow differed for mtDNA CR and microsatellites in *B. capensis*, showing mtDNA CR geneflow to be more constrained (Figure 4.3). Geneflow barriers derived from each genetic marker were similarly divergent in *P. ruficapilla* but also differ in their geographic positions, but of the three bird species included in here, BARRIER results were most congruent among methods and markers in *P. stellata* (Figure 4.3).

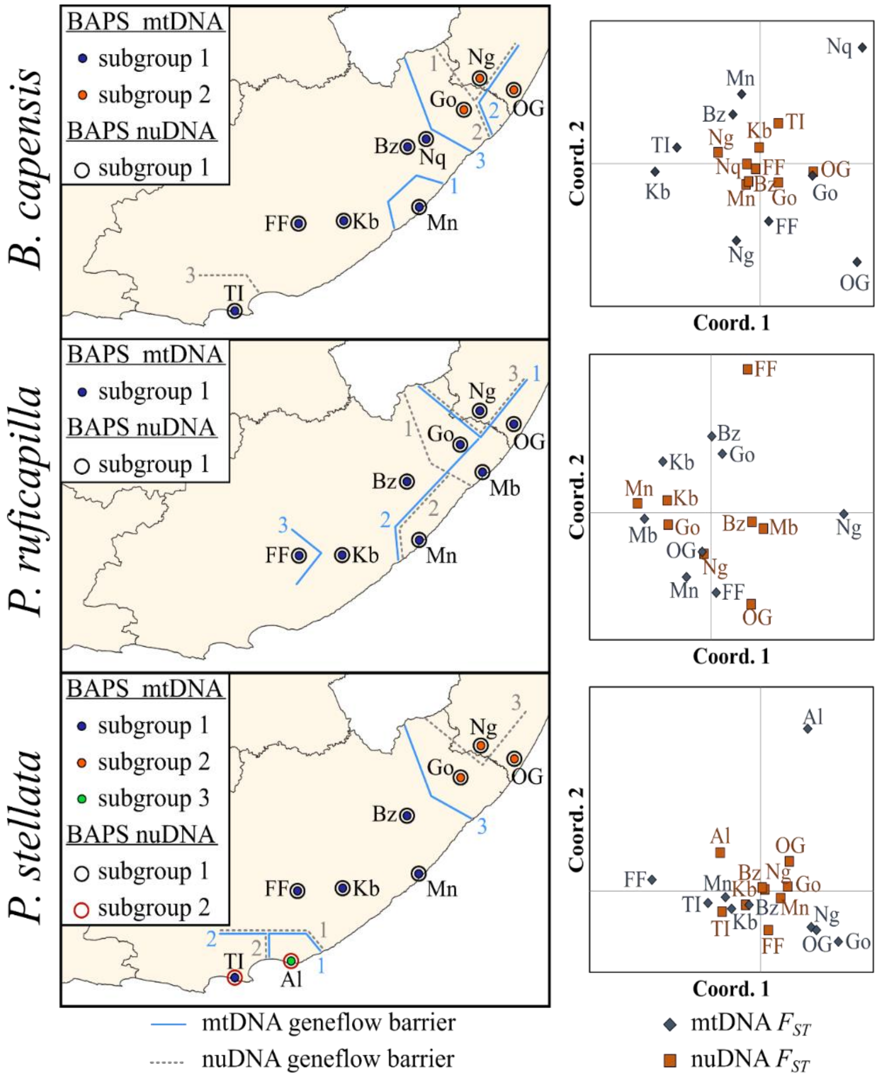


Figure 4.3 Genetic population structure of the three passerine bird species in the Eastern Cape. (a) Boundaries between BAPS subgroups inferred from mtDNA (small circles), and nuDNA (large circles), as well as BARRIER results for both mtDNA (dashed line), and nuDNA microsatellites (blue line). (b) principal coordinate analyses (PCoA) comparing species pairwise F_{ST} of mtDNA (blue diamonds), and nuDNA (orange squares).

Table 4.1 Estimates of forest-level genetic diversity within focal species, showing sample size (*N*), number of haplotypes (*H*), private haplotypes (*PH*), haploptype (*h*) and nucleotide (π) diversity of complete mtDNA control region. Shown alongside are the rarefied allelic richness (*AR*), and rarefied privatised allelic richness (*PrAR*) from eight microsatellites of each species. The respective sub-biomes are included for each forest locality: A = Afromontane, S = scarp, and I = IOCB

	Forest	*N*	*H*	*PH*	*h*	π	*AR*	*PrAR*
B. capensis	Ngele (A)	6	4	4	0.900	0.005	4.750	0.475
	Oribi Gorge (S)	8	8	4	1.000	0.013	4.250	0.035
	Gomo (A)	17	17	13	1.000	0.009	6.750	0.179
	Nqadu (A)	14	13	5	0.989	0.005	5.625	0.243
	Baziya (A)	8	7	10	0.964	0.003	6.500	0.253
	Manubi (S)	16	8	4	0.883	0.003	7.625	0.148
	Kubusi (A)	13	13	11	1.000	0.005	6.375	0.109
	Fort Fordyce (A)	18	16	10	0.983	0.009	7.125	0.252
	The Island (I)	16	11	9	0.956	0.004	5.625	0.070
	Overall	**116**	**79**	**71**	**0.964**	**0.006**	**10.625**	**0.196**
P. ruficapilla	Ngele (A)	20	14	7	0.963	0.005	1.429	0.104
	Oribi Gorge (S)	6	6	2	1.000	0.008	2.250	0.005
	Mbotyi (S)	6	5	2	0.900	0.008	2.375	0.050
	Gomo (A)	11	10	7	0.982	0.008	2.250	0.046
	Baziya (A)	14	10	4	0.970	0.007	2.500	0.032
	Manubi (S)	15	11	6	0.941	0.007	2.875	0.100
	Kubusi (A)	9	8	5	0.946	0.008	2.375	0.003
	Fort Fordyce (A)	11	6	4	0.849	0.007	0.286	0.002
	Overall	**92**	**48**	**37**	**0.944**	**0.007**	**3.375**	**0.043**
P. stellata	Ngele (A)	30	15	6	0.835	0.004	6.625	0.212
	Oribi Gorge (S)	13	4	2	0.561	0.004	4.875	0.122
	Gomo (A)	26	10	3	0.790	0.004	6.125	0.188
	Baziya (A)	15	8	3	0.791	0.003	5.875	0.181
	Manubi (A)	28	11	1	0.677	0.002	6.250	0.094
	Kubusi (A)	26	12	2	0.846	0.003	6.250	0.176
	Fort Fordyce (A)	39	8	2	0.785	0.001	5.875	0.058
	Alexandria (I)	17	6	3	0.833	0.002	4.750	0.070
	The Island (I)	6	4	3	0.800	0.001	4.375	0.319
	Overall	**200**	**42**	**25**	**0.769**	**0.003**	**9.75**	**0.185**

Table 4.2 Hierarchical analyses of molecular variance (AMOVA), based on complete mtDNA CR and eight microsatellite loci, respectively, for BAPS population subdivisions in *B. capensis*, *P* and *P. stellata* (see text). *F* = fixation index; * p <0.05

		mtDNA CR		Microsatellite	
Population subdivisions	Source of variation	% of variation	*F*	% of variation	*F*
B. capensis BAPS mtDNA CR	Among groups	0.29	0.002	0.07	0.001
	Within groups	2.32	0.023*	1.19	0.012
	Within forests	97.39	0.026*	98.74	0.013
P. stellata BAPS mtDNA CR	Among groups	3.02	0.030*	1.34	0.013*
	Within groups	3.34	0.035*	0.70	0.007*
	Within-forests	93.55	0.065*	97.95	0.020*
P. stellata BAPS microsatellites	Among groups	2.59	0.026	2.19	0.022*
	Within groups	4.68	0.048*	1.03	0.010*
	Within-forests	92.72	0.073*	96.78	0.032*

4.4.2 Long-term demographic history

Pronounced expansions in female effective population size during the late Pleistocene were evident in all three songbird species BSPs (Figure 4.4). In *B. capensis*, conservative mutation rates (μ = 3.7 % per my, and μ = 5.0% per my) suggest demographic expansion began ~50-60 kya, while faster rates (μ = 12.0%) estimate this expansion at around 20-25 kya (Figure 4.4). In *P. ruficapilla*, expansion in N_{ef} is varyingly placed between 35-50 kya (μ = 3.7 % per my), 25-35 kya (μ = 5.0 % per my), and 10-15 kya (μ = 3.7 % per my); across mutation rates, the $N_{ef\ of}$ *P. ruficapilla* was shown to plateau after demographic expansion, before declining from 5 kya – present (Figure 4.4). For *P. stellata* demographic expansion began either ~15 kya (μ = 3.7 % per my), or ~10 kya (μ = 5.0% per my; μ = 12.0 % per my) (Figure 4.4). Estimated time to the most recent common ancestor (TMRCA) along mitochondrial lineages within the study area, ranged from 120-350 kya in *B. capensis*, 28-90 kya in *P. ruficapilla*, and 28-48 kya in *P. stellata* (Figure 4.4).

Heterozygosity excess tests conducted in Bottleneck 1.2 on microsatellite data corroborated demographic declines observed in *P. ruficapilla*, detecting a decline in total N_e of this species across mutation models (Table 4.3); forest-level declines species were detected at Oribi Gorge, Mbotyi, Gomo, Kubusi, and Fort Fordyce (Appendix S4.6). In *P. stellata*, significant forest-level declines in N_e were detected at Ngele, Baziya, Manubi, Kubusi, and The Island, depending on the mutation model used (Appendix S4.6), whereas in *B. capensis*, no significant long-term population declines in N_e were detected.

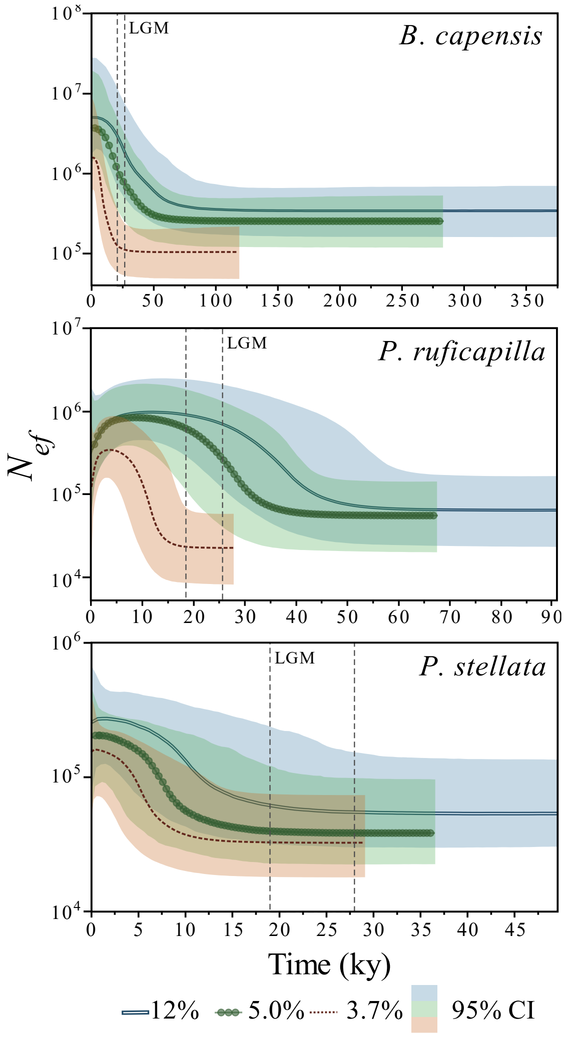


Figure 4.4 Bayesian skyline plots showing long-term fluctuations in female effective population size (N_{ef}), and time to the most recent common ancestor (TMRCA) for the three passerine species in the Eastern Cape, based on complete mtDNA CR sequences, and assuming a mutation rate µ = 12% per my, 5.0% per my, and 12% per my. Shown alongside is the LGM (black dashed line).

Table 4.3 Results of bottleneck tests of microsatellites for the three species in the Eastern Cape. For heterozygosity (H_e) excess tests, significance values after Bonferonni corrections ($p < 0.006$) are shown for one-tailed Wilcoxon signed-rank test applied to two-phase (TPM) and single-step (SSM) mutation models.

Test	*B. capensis*	*P. ruficapilla*	*P. stellata*
H_e excess (10 % TPM)	0.371	**0.004***	0.010
H_e excess (5 % TPM)	0.629	**0.004***	0.027
H_e excess (SSM)	0.980	**0.004***	0.156

4.4.3 Relationships among regional forests

ABC modelling suggested contrasting forest histories across the three songbird species (Figure 4.5a), although forest divergence probabilities were low in all three species (0.5%-9.5%), and divergence events were similarly estimated to have culminated 1.5-4.5 kya (Table 4.4). For both *B. capensis* and *P. stellata*, posterior probabilities were highest for demographic scenarios which treated the northeast BAPS subgroup (Ngele, Oribi Gorge, and Gomo) as the source population among regional forests, with hierarchical modelling supporting Oribi Gorge as the primary regional source population for both species (Appendix S4.10). The best-supported comprehensive demographic scenario for *B. capensis* suggested a predominate geneflow direction from northeast-southwest, and from lowland scarp forests to mid-elevation Afromontane forests (Figure 4.5b). Oribi Gorge (northeast, scarp forest) represents a demographic source population for Ngele and Gomo (northeast, Afromontane forest), while Manubi (central, scarp forest) serves as a demographic sink for the northeast BAPS subgroup, but is a source population for Nqadu, Baziya, Kubusi, Fort Fordyce (southwest, Afromontane forest), and The Island (southwest, coastal belt forest). The best-supported comprehensive demographic scenario for *P. stellata* (Figure 4.5b) similarly showed prevailing northeast-southwest geneflow direction: the northeast BAPS group (Ngele, Oribi Gorge, Gomo) serves as a source population for central-southwest forests (Manubi, Baziya, Kubusi, Fort Fordyce), which in turn are source populations for each of the two southern coastal belt forests (Alexandria, The Island). For *P. ruficapilla*, however, the best-supported demographic scenario posited southwest, mid-elevation Afromontane forests (Baziya and Kubusi) as the primary regional source population (Figure 4.5b), showing a contrasting predominate geneflow direction from southwest to northeast, and from mid-elevation Afromontane forests to lowland scarp forests.

Table 4.4 Divergence times (generations) between adjacent genetic forest subpopulations of each focal across the Eastern Cape. 95% confidence intervals are bracketed.

	B. capensis	*P. ruficapilla*	*P. stellata*
t1	1650 (540-3990)	772 (116-2140)	1080 (187-2970)
t2	2120 (860-4980)	1550 (528-3630)	1380 (340-3910)
t3	2460 (833-5460)	1680 (499-4670)	1740 (428-5740)
t4	2260 (1220-7300)	1030 (214-3800)	2860 (228-7540)
t5	3400 (1570-8100)	1380 (116-9610)	-

4.4.4 Past changes in regional species distributions

MAXENT modelling of present-day species distributions approximated the known regional ranges of the three songbird species (Figure 4.6). Mean area under the curve (AUC) values were 0.923 for *B. capensis* (*s.d.* = 0.008; training AUC range: 0.918-0.9226; test AUC range: 0.894-0.936), 0.952 for *P. ruficapilla* (*s.d.* = 0.013; training AUC range: 0.953-0.956; test AUC range: 0.930-0.971), and 0.960 for *P. stellata* (*s.d.* = 0.007; training AUC range: 0.959-0.961; test AUC range: 0.941-0.963). Model performance was therefore considered reliable given that AUC values >0.75 are informative (Elith, 2006). ‘Minimum temperature during the coldest month’ (bio6; 39.2% – *B. capensis*; 38.2% – *P. ruficapilla*; 42.8% – *P. stellata*); and ‘annual precipitation’ (bio12; 20.6% – *B. capensis*; 51.4% – *P. ruficapilla*; 45.4% – *P. stellata*) provided the largest contributions to model performance across all three species. Additionally, ‘precipitation during the driest month’ (bio14) was important for *B. capensis* (36.1%); and ‘mean temperature during the driest month’ (bio9) for *P. stellata* (5.8%). The remaining variables contributed <5% towards species distribution model performance.

Predicted regional distributions during the LGM indicated that these three songbird species were displaced to coastal lowland regions (Figure 4.6), suggesting high habitat suitability (0.70-0.98) over the area today associated with lowland scarp forests of the Wild Coast (Figure 1). By comparison, habitat suitability over areas today associated with mid-elevation Afromontane forests appeared to have low suitability during the LGM (0.20-0.50), although moderate habitat suitability (0.40-0.70) for *P. stellata* was predicted over the eastern Amatole mountains (Figure 4.6), and the central and northern escarpment of the Eastern Cape (Appendix S4.9) during this time. The MIROC-ESM model predicted a more extensive distribution for *B. capensis* across the southwest Cape during the LGM (Figure 4.6), although the CCSM4 model showed a more restricted distribution for this species at this time (Appendix S4.9). For all three species, habitat suitability was shown to have increased (0.60-0.90) across the mid-elevation areas during the HCO, according to both GCMs (Figure 4.6, Appendix S4.9). Both models further predicted that species distributions during the HCO were more extensive compared to the present day, suggesting greater forest connectivity throughout this period, especially for *B. capensis* (Figure 4.6, Appendix S4.9). Both models further showed that coastal lowland regions associated with present-day scarp forests continued to be suitable for *B. capensis* and *P. stellata* during the HCO, although the MIROC-ESM model suggested *P. ruficapilla* to have been absent from these lowland areas at this time Figure 4.6, Appendix S4.9). This latter species displayed the least extensive distribution during the HCO compared to the present day (Figure 4.6, Appendix S4.9Interestingly, predicted species distributions during the LIG suggested that *B. capensis* and *P. stellata* were absent from the coastal lowland regions associated with present-day scarp forests, and instead shifted further inland, whereas *P. ruficapilla* was present at these coastal lowlands (Figure 4.6).

4.5 Discussion

4.5.1 Subtropical Afromontane forest avifaunal glacial refugia

Our multi-locus study provides evidence that Afromontane and Scarp forests within the southern region of the Maputaland-Pondoland-Albany Biodiversity Hotspot showed resilience during climatic fluctuations of the late Pleistocene. Coalescence modelling of mitochondrial lineages within each species consistently estimates intra-population TMRCA to the last glacial period (Figure 4.4), well before the severe South African forest contractions, and subsequent extinction events previously associated with the LGM (Eeley et al., 1999; Lawes et al., 2007a). Additionally, the lack of sudden demographic population changes in all three bird species studied here, especially during the LGM (Figure 4.4), alongside the retention of high mitochondrial or nuclear genetic diversity (Table 4.1), signifies that the LGM climatic event was not especially detrimental to the regional population viability of these species within the region. It thus seems reasonable to conclude that during Pleistocene glacial cycles, Afromontane and scarp forests acted as refugia to many species dependent on forests in this region.

Forest source-sink demographic modelling for *B. capensis* and *P. stellata* (Figure 4.5), and species distributions modelled for the LGM (Figure 4.6, Appendix S4.9) affirm the glacial refugial role served by scarp forests as proposed by Lawes et al. (2007). Scarp forests within the study area were established ~130m below present-day sea levels during the LGM (Compton, 2011; Cooper et al., 2018). Palaeodistribution modelling further predicts reduced presence of *B. capensis* and *P. ruficapilla*, but not necessarily *P. stellata* (Figure 4.6, Appendix

S4.9), at higher elevation during the LGM (Figure 4.6, Appendix S4.9), yet mid-elevation (500-1800 m.) Afromontane forests yield comparatively high genetic diversity across all three species (Table 4.1).

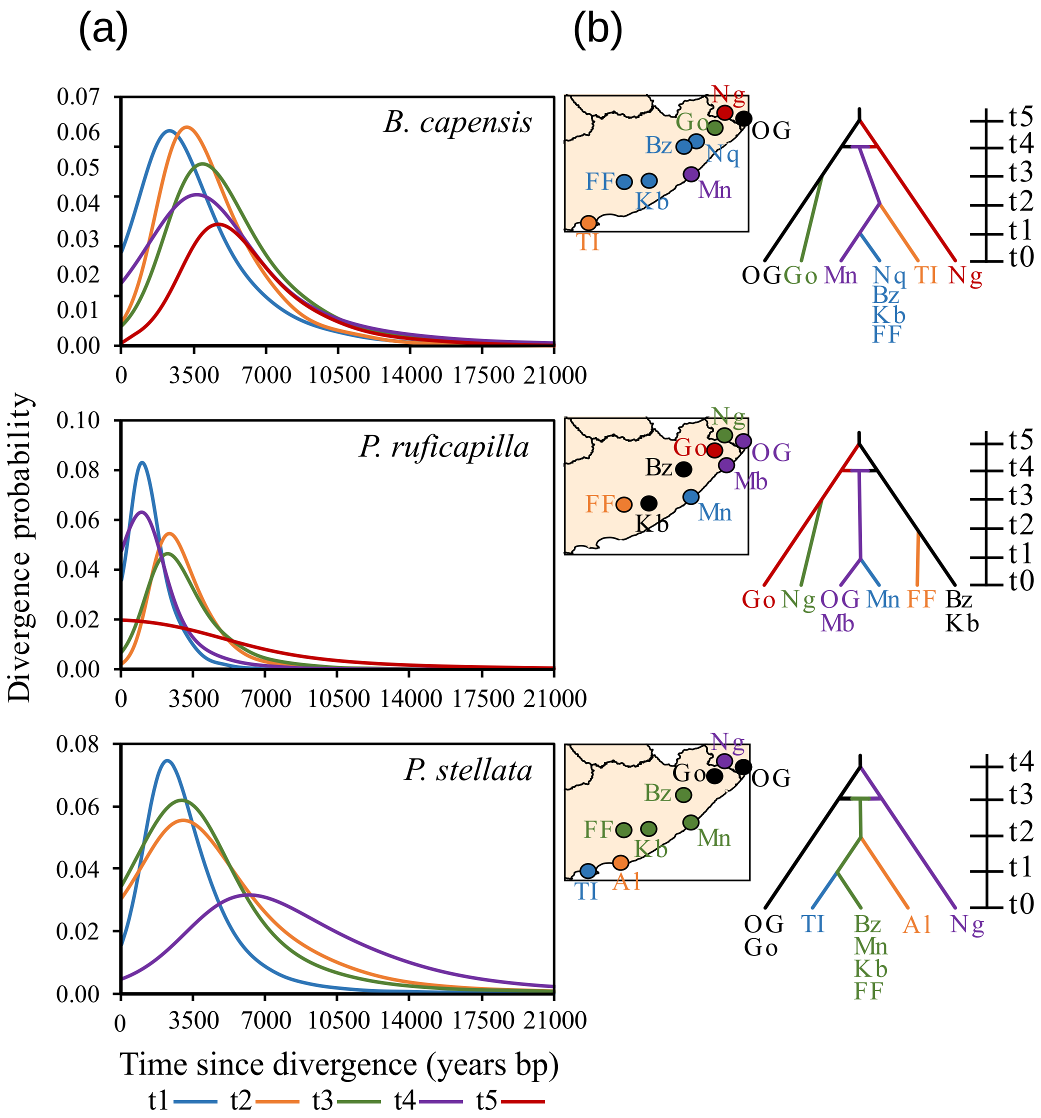


Figure 4.5 (a) posterior probability densities for the divergence times (in generations) between adjacent forest demes across the Eastern Cape for each focal species, based on combined mtDNA Control Region and microsatellite datasets. Divergence time estimates were derived from (b) the best-supported demographic scenario of dominant geneflow direction, and ancestral forest populations. Coloured branches depict genetically identified forest subgroups, with more ancestral/source subgroups predating divergence events t1-t5.

Additionally, source-sink population dynamics modelling suggests that the southern Afromontane forests – Amatole mistbelt, and Transkei mistbelt forests (von Maltitz et al., 2003) – served as the primary climate refugia for *P. ruficapilla* – if not during the LGM, then later during the current interglacial (Figure 4.5, Appendix S4.10). In *P. stellata*, these same southern, mid-elevation Afromontane forests do not function as important demographic sinks for adjacent scarp forests (Figure 4.5, Appendix S4.10), but in *B. capensis*, the mid-elevation Afromontane forests of Amatole mountains appear to be a genetic stronghold (Table 4.1). This suggests greater Palaeoclimatic resilience of the Afromontane forests than previously thought, but which is congruent with the endemic genetic diversity observed in other taxa (Barnes & Daniels, 2019; Coetzer et al., 2020; da Silva & Tolley, 2017; Hughes et al., 2005; Kushata et al., 2020; Madisha et al., 2018). This phenomenon may even have been underestimated by our palaeodistribution modelling, as the coarse spatial grain used likely could not distinguish the microclimates conducive to this sheltered habitat.

Past hydroclimatic variability across the MPA Hotspot may mean that these inferences are confined specifically to our study area (Engelbrecht et al., 2019; Miller et al., 2019, 2020). Recent work has argued that much of South Africa likely experienced increased precipitation during the LGM, following the equatorial advance of the southern westerlies alongside southward displacement of tropical trade winds (Combrink et al., 2020; Engelbrecht et al., 2019), challenging the notion of aridity-driven LGM contractions of KwaZulu-Natal forests presented by Eeley et al. (1999). Decreased summer rainfall over the central Maloti-Drakensberg escarpment, which constitutes the northeast boundary of the MPA Hotspot in KwaZulu-Natal, provides some support for this hypothesis (Engelbrecht et al., 2019). But increased winter rainfall likely mitigated summer aridity, and this aridity may not have been as extreme over the mid-elevation Afromontane and scarp forests of the Eastern Cape and southern KwaZulu-Natal (Combrink et al., 2020; Engelbrecht et al., 2019). Therefore, these southern forests may have been more important climate refugia during the LGM than elsewhere in eastern South Africa, with scarp forests being particularly important regional refugia during global glaciations.

4.5.2 Glacial-Interglacial subtropical Afromontane forest dynamics

Palaeodistribution models predict increased habitat suitability of inland, mid-elevation regions for the three songbird species during the HCO and LIG thermal maxima, while habitat suitability over the east coast lowlands either moderately or severely decreased (Figure 4.6, Appendix S4.9). These lowland displacements may be partly ascribed to the subtropical expansion of Indian Ocean coastal belt forests during the early-mid Holocene, 10-3.6 kya (Botha et al., 2003; Finch & Hill, 2008; Miller et al., 2019; Neumann et al., 2008, 2010; Scott et al., 2012), as all three species appear largely averse to this sub-biome (Berruti, 1997;

Johnson, 1997; Oatley, 1997b). Periodic advancement of Indian Ocean coastal belt forests into the Eastern Cape is similarly predicted during the LIG, especially 116 kya (Huntley et al., 2016). However, LIG climates over South African were markedly more arid than at present, due to weakened southern tropical trade winds lacking compensation from southern westerlies, challenging the expansion of regional forests at this time (Yeung et al., 2020). Despite these climatic fluctuations, palaeodistribution modelling supports the continuous presence of suitable forest habitats for the three songbird species within the MPA Hotspot throughout the late Pleistocene, suggesting altitudinal shifts in Afromontane and scarp forests following glacial-interglacial cycles, and hydroclimatic fluctuations (Figure 4.6, Appendix S4.9). Such shifts in regional forest distributions may have provided corridors through which the three species colonised the isolated lowland Afromontane (southern Afrotemperate) forest complex of the south coast, another suspected prominent forest avifaunal refuge (Figure 4.6, Appendix S4.9) which fell beyond the scope of the study.

Wetter conditions are projected over the MPA Hotspot during the Holocene Interglacial (Miller et al., 2020; Zhao et al., 2016). Extensive HCO distributions of suitable habitats for the three songbird species, particularly *B. capensis* (Figure 4.6, Appendix S4.9), are congruent with palaeoecological evidence. They suggest increased prevalence of mid-elevation Afromontane forests (Combrink et al., 2020; Neumann et al., 2014), and low-elevation Afromontane and scarp forests (Finch & Hill, 2008; Neumann et al., 2010) in KwaZulu-Natal at the advent of the Holocene (~12 kya), but especially from 6.8-3.6 kya, (Eeley et al., 1999). A lack of palaeoecological records within the Eastern Cape limits our understanding of how Holocene hydroclimates varied across the MPA Hotspot (Chase et al., 2017; Miller et al., 2020). However, the HCO expansion of suitable habitats indicated by palaeodistribution modelling (Figure 4.6, Appendix S4.9), as well as forest divergence time estimates presented here suggests the Afromontane forests within the Eastern Cape and KwaZulu-Natal portions of the MPA Hotspot were subject to overlapping climate regimes during the Holocene. The postglacial expansion of both subtropical Afromontane and scarp forests likely account for the population growth of N_{ef} observed in each of the three species (Figure 4.4). These indicate indirectly that faster mutation rates (μ = 12.0 % per my) are more likely to the evolution of mtDNA CR within *B. capensis* and *P. ruficapilla*, whereas for *P. stellata* this rate remains uncertain. Interestingly, the expansion of these forests under warm, mesic conditions contrasts the Afromontane forest expansions in the EA Hotspot during the LGM (Peterson & Ammann, 2013), and previous wet intervals within glacial periods (Ivory et al., 2018, 2019; Los et al., 2019), demonstrating the asynchrony in regional dynamics of this forest sub-biome across Africa.

4.5.3 Late Holocene forest divergence

Estimated forest group divergence times within forest-specialised *P. ruficapilla* and *P. stellata* (Figure 4.5, Table 4.4), as well as long-term demographic declines of N_e and N_{ef} in *P. ruficapilla* (Table 4.3, Figure 5.4), coincide with late Holocene forest subsistence in South Africa from 3.6-1.0 kya (Neumann et al., 2010). These are depicted by the predicted species range reductions from the HCO to the present-day (Figure 4.6, Appendix S4.9). This climatic event also negatively impacted the endemic forest-dependent parrot *Poicephalus robustus* (Coetzer et al., 2020). The earlier, more gradual divergence time estimates within the forest generalist *B. capensis* (Figure 4.5, Table 4.4), by contrast, may partly reflect the fynbos-to-grassland transition landscapes in the southern MPA Hotspot (Combrink et al., 2020; Neumann et al., 2014), in addition to forest contraction. Decreasing N_{ef} in *P. ruficapilla* is likely driven by the diminished extent of Afromontane forests since the HCO, given that low forest-level divergence probabilities across the three species (Figure 4.5), alongside weak multi-locus population genetic differentiation (Figure 4.3; Appendix S4.4), suggest relativity uninterrupted connectivity between forests maintained by these species to the present day during this forest subsidence event. Forest-level divergences, and declines in *P. ruficapilla*, appear to predate the arrival of Iron Age farmers to South Africa 1.2 kya (Fitchett et al., 2016; Neumann et al., 2008, 2010, 2014), and therefore these events cannot be attributed solely to increased anthropogenic forest clearance and altered fire regimes over the last millennium which offset forest re-emergence across the MPA Hotspot. However, past population declines can mask recent demographic disruptions (Cornuet & Luikart, 1996), potentially meaning that long-term declines in *P. ruficapilla* may be worsening under increasing anthropogenic forest exploitation, despite previous evidence showing this species to be impervious to such activity in South Africa (Chapter 3). Both *B. capensis* and *P. stellata* (Chapter 3), as well as *P. robustus* (Coetzer et al., 2020) show genetic stress – geneflow disruption and/or effective population decline – from increased pressures placed on South African forests since European contact after 1652, and *P. stellata* shows localised long-term population declines (Appendix S4.6). Similar population stress is reflected in range declines in half of the region's forest-dependent avifauna (Cooper et al., 2017), necessitating the need for effective conservation of the precariously small forest biome (0.5% total surface area, Low and Rebelo 1998) in South Africa.

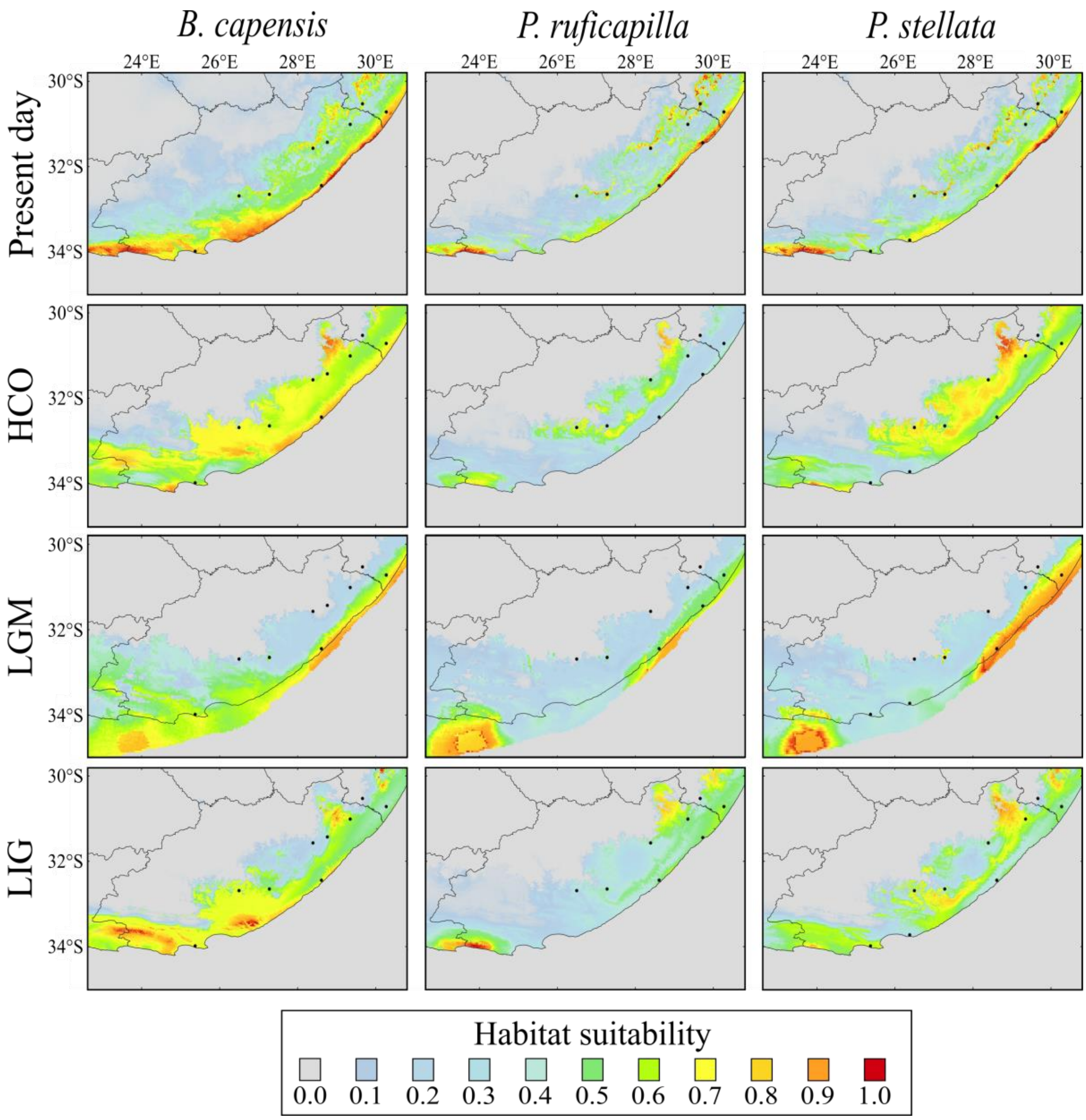


Figure 4.6 Maxent modelled distributions of *B. capensis*, *P. ruficapilla*, and *P. stellata* across the Eastern Cape and southern KwaZulu-Natal for the present day, mid-Holocene climate optimum (HCO), last glacial maximum (LGM), and last interglacial (LIG) periods. Habitat suitability ranges from 0.0 (low) to 1.0 (high), with warmer colours (yellow, orange, red) indicating higher habitat suitability. Shown projections for HCO and LGM species distributions were generated from the Model for Interdisciplinary Research on Climate (MIROC), while LIG projections were generated from global climate model of Otto-Bliesner *et al*. (2006).

4.5.4 Reconciling mitonuclear discordance within the three songbird species

Of the three songbird species, *B. capensis* exhibits similarly high nuclear and mitochondrial genetic diversities (Table 4.1), as well as the most divergent mitochondrial lineages (Figure

4.4), which together indirectly reflect a deeper evolutionary history of this species within these southern forests compared to *P. ruficapilla* and *P. stellata* (Figure 4.4), both of which originated in the tropics. As a greater habitat generalist, *B. capensis* could more readily persist through glacial periods – in smaller forest patches (Johnson, 1997) and Albany thicket refugia (Potts et al., 2013). Its range also extended into the dense Fynbos stands to the west of the study area that were more prevalent under winter-rainfall regimes during the LGM (Combrink et al., 2020; Huntley et al., 2016; Norström et al., 2014; Quick et al., 2016), and even across the then-exposed Agulhas bank (Marean et al., 2020). Therefore, *B. capensis* benefitted from a greater extent of suitable habitats during palaeoclimatic fluctuations (Figure 6, Figure S1), which both allowed for larger N_{ef} during the late Pleistocene, as well as better safeguarding against bottlenecks and genetic attrition compared to the forest-specialised *P. ruficapilla* and *P. stellata* (Figure 4.4). Source-sink demographic modelling for *B. capensis* suggests an underlying southward dispersal (Figure 4.5, Appendix S4.10), along coastal lowlands, and riparian corridors (Chapter 3). Although geographic clustering of nuclear and mitochondrial DNA within this species is weak (Figure 4.2, Figure 4.3), such a latitudinally-defined genetic gradient is corroborated by Chapter 3. Evidence of male biased dispersal within *B. capensis*, previously documented in Malawian populations (Dowsett, 1985), is revealed by greater mitochondrial vs nuclear population differentiation (Figure 4.3; Appendix S4.3), alongside concordant mitonuclear genetic diversities (Prugnolle & De Meeus, 2002), and 2:1 female:male ratio of sampled individuals, suggesting higher mortality of the dispersing (male) sex (Payevsky, 2016).

As with *B. capensis*, *P. ruficapilla* exhibits similarly weak geographic clustering of mitochondrial and nuclear genetic variations (Figure 4.2, Figure 4.3), and the total population appears homogenous. This lack of population structure undermines the recognition of two allopatric subspecies in the Eastern Cape, *P. r. ruficapilla* (Sundevall, 1850) and *P. r voelckeri* (Roberts, 1941), and suggests the recognition of the former subspecies only. Additionally, the population homogeneity of *P. ruficapilla* across the southern MPA Hotspot contrasts the forest insularity observed in the EA Hotspot (Burgess & Mlingwa, 2000; Callens et al., 2011), which may signify divergent dispersal behaviours across the species distribution of this songbird. Within the MPA Hotspot, the concordant strength of mitonuclear population differentiation, and high mitochondrial diversity suggest there an absence of sex-biased dispersal in *P. ruficapilla*. However, the peculiar disparity between the nuclear and mitochondrial genetic diversity within the regional *P. ruficapilla* population (Table 4.1) may reflect a strong bottleneck event in the distant past, from which mitochondrial DNA has recovered better than nuclear DNA. This derives from neutral mitochondrial variations, especially of the mtDNA CR, accruing faster than nuclear variations in sufficiently large avian populations (Allio et al., 2017; Eo & DeWoody, 2010; Nabholz et al., 2009; Zink & Barrowclough, 2008).

Of the three species, *P. stellata* exhibited the highest degree of multi-locus population structuring, despite possessing a higher proportion of shared mitochondrial haplotypes, including a single haplotype ubiquitous throughout the study area (Figure 4.2). This species shows an underlying southward geneflow direction, as with *B. capensis*, with notable mitochondrial and nuclear genetic differentiation between the southern coastal forests (Alexandria and The Island), and all other forests. This distinction may indicate recent colonisation of these coastal forests, which likely established only during the early-mid Holocene (Botha et al., 2003). Alternatively, dispersal may have been restricted across an arid corridor, the ‘Bedford Gap’, which isolates these coastal belt forests from the rest of the MPA Hotspot (Lawes et al., 2007a; Potts et al., 2013). This arid region may have impacted *B. capensis* less, as this species readily disperses through Albany thicket (Chapter 3), and over open spaces (Dane & Bolton, 2017; Oschadleus & Ranwashe, 2017).

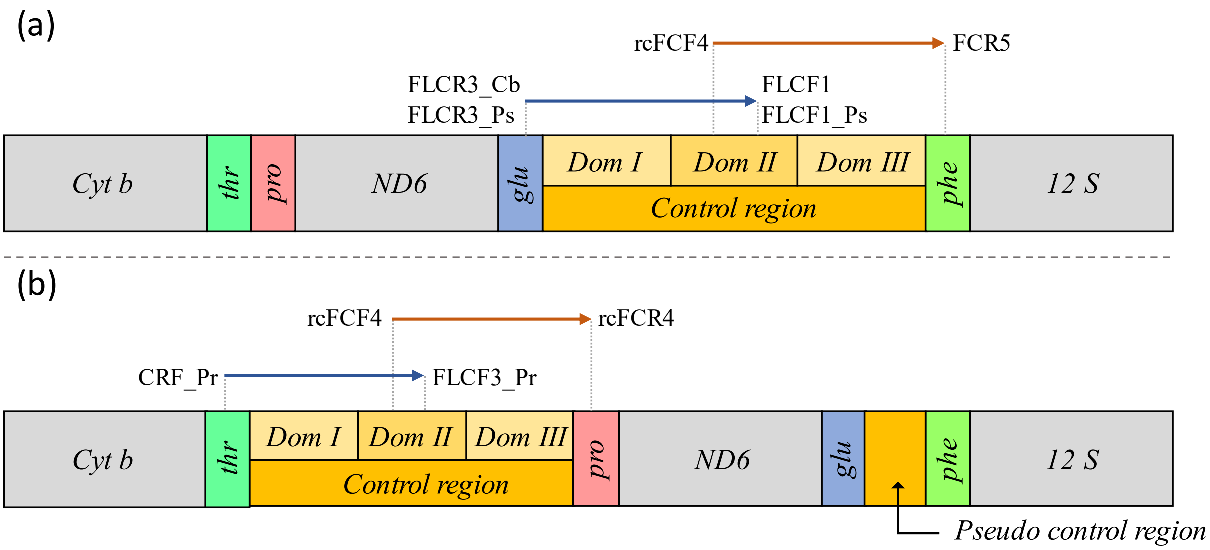
Despite moderately high nuclear diversity, *P. stellata* shows surprisingly low mitochondrial variation (Figure 4.3; Table 4.1), which may be an artefact of this species’ life history. This songbird is a range-wide altitudinal migrant (Oatley & Arnott, 1998), yet exhibits philopatry, and so migrating individuals typically seasonally return to previously occupied forests (Dowsett, 1985). Adult females appear to be obligate migrants with a higher mortality compared to the more sedentary males (Dowsett, 1985; Oatley, 1982a). Female:male sex ratios are reported here as 6:10, as recorded in KwaZulu-Natal by (Oatley, 1982b) in contrast to 9:10 ratio observed in Malawi (Dowsett, 1985). Female philopatry precludes mitochondrial geneflow (Pavlova et al., 2013), so geneflow contingent upon natal dispersal of immature males which disperse locally (Oatley, 1982b, 1982a), resulting in a gradual, stepwise dispersal patterns with near-congruent barriers to mitonuclear geneflow (Figure 4.3). Therefore, *P. stellata* may experience male-biased dispersal, despite higher female mortality. It is noteworthy that despite female-biased dispersal being more commonplace among songbirds (Arlt & Pärt, 2008; Dale, 2001; Payevsky, 2016), the evidence provided in this study does not strongly support this phenomenon, beyond potential migratory behaviour in *P. stellata*.

Winter visitation of migrating *P. stellata* to Indian Ocean coastal belt forests (Burgess & Mlingwa, 2000; Craig & Hulley, 2019; Oatley, 1997b), could have augmented Afromontane forest connectivity, and better facilitated colonisation of the MPA Hotspot compared to *P. ruficapilla*, which largely avoids Indian Ocean coastal belt forests (Berruti, 1997; Burgess & Mlingwa, 2000; Craig & Hulley, 2019). For this latter species, colonisation of the MPA Hotspot may have been limited, so the genetic bottleneck incurred by the regional population may reflect a founder effect. Lawes et al. (2007), proposed that expansions of Indian Ocean coastal belt forest served as a route through which many forest bird species migrated into South Africa, especially at the advent of the current interglacial period. Additionally they interpreted the periodic integration of Afromontane elements within these forests (Finch & Hill, 2008; Miller et al., 2019) to be conducive for the regional infiltration of steadfastly Afromontane forest species. Although this model remains plausible, the presence of Afromontane specialists in South Africa could be better reconciled by mid-earlier Pleistocene Afromontane forest integration into lowland forest communities (Dupont et al., 2011; Ivory et al., 2018), with the most recent continental expansion of Afromontane *Podocarpus* conifers ~200 kya (Migliore et al., 2020b). These mixed Afromontane-lowland forest expanses ostensibly ceased upon broad disturbance regime changes across lowland regions ~80 kya (Ivory et al., 2018, 2019; Los et al., 2019; Peterson & Ammann, 2013). Many Afromontane forest species within South Africa therefore may be relicts of these bygone forests with mixed characteristics, and have persisted within the region through the late Pleistocene by virtue of prominent subtropical Afromontane forest refugia.

4.6 Conclusion

In this study we provided phylogeographic and palaeodistribution evidence to support the existence of palaeoclimatic refuge Afromontane and scarp forests for three songbird species – *B. capensis*, *P. ruficapilla*, and *P. stellata* – within the southern Maputaland-Pondoland-Albany Hotspot. We further show that the last glacial maximum did not constrain the female effective population size of these species, and therefore is unlikely to have constricted the distributions of these subtropical Afromontane and scarp forests. However, substantial population growth of the three species at the advent of the Holocene Interglacial suggests that warm, mesic climates are conducive to regional forest expansion. We further show that the broader habitat generalisation of *B. capensis* conferred greater resilience against past forest contractions, compared to the forest specialists *P. ruficapilla* and *P. stellata*. Lastly, we provide indirect evidence to support the deeper evolutionary history of *B. capensis* within these subtropical forests, and that *P. stellata*, a seasonal altitudinal migrant to lowland forests, most likely colonised these forests from tropical east Africa more reliably than the steadfastly Afromontane *P. ruficapilla*.

4.7 Chapter 4 appendices



Appendix S4.1 The position of avian mitochondrial control region (mtDNA CR) within the mitochondrial genome. (a) The mtDNA CR of *P. stellata* and *B. capensis* resides between genes encoding tRNA-glu and tRNA-phe. (b) The mtDNA CR of P. ruficapilla has been transposed to between the genes encoding tRNA-thr and rRNA-pro. Species-specific primer pairs used in the PCR amplification of mtDNA CR for each species are including alongside.

Appendix S4.2 Species specific mtDNA CR primer pairs, depicted in Appendix S4.1, and the optimal annealing temperatures for PCR amplification of these respective primer pairs. '_Cb' identifies *B. capensis* specific primers, '_Ps' identifies *P. stellata* specific primers, and '_Pr' identifies *P. ruficapilla* specific primers.

F/R	Primer	Primer sequence (5´– 3´)	T_{anneal} (°C)
F	FLCR3_Cb	GGCACAAAAGAGCAAGTTG	57.0
R	FLCF1	GAATGGGGTCAAAGTGCATCAGT	
F	rcFCF4	TTCTCACGAGAACCGAGCTAC	54.3
R	FCR5	CTTGGCATCTTCAGTGCCATGC	
F	FLCR3_Ps	GGCGCCAAAGAGCAAGT	57.0
R	FLCF1_Ps	AAATGGGGTCAAAGTG CATCAGC	
F	CRF_Pr	CATTGGTCTTGTAAGCCAAAG	56.0
R	FLCF3_Pr	GGCGCAAAAGAGCAAGG	
F	rcFCF4	(see above)	56.3
R	rcFCR4	GCTTTGGGAGTTGGTGGTGAA	

Appendix S4.3 Pairwise F_{ST} values for 1311 bp mtDNA CR (above) and eight microsatellite loci (below) for *B. capensis*. Values in bold: $p < 0.05$ (mtDNA CR); $p < 0.00625$ after Bonferroni correction (microsatellites).

		F_{ST} (mtDNA CR)								
	Forest	Ngele	Oribi Gorge	Gomo	Nqadu	Baziya	Manubi	Kubusi	Fort Fordyce	The Island
F_{ST} (microsatellites)	Ngele	-	0.05	**0.04185**	0.06483	0.04859	**0.10994**	0.04267	0.0514	0.06742
	Oribi Gorge	**0.0811**	-	-0.01266	0.01938	0.00626	0.06851	0	-0.01121	0.02519
	Gomo	0.0450	0.0215	-	0.0089	0.00544	**0.05833**	-0.00483	-0.00102	**0.02175**
	Nqadu	0.0069	0.0394	0.0129	-	0.01381	**0.0798**	0.00738	0.02586	0.04011
	Baziya	0.0180	0.0492	0.0084	0.0084	-	**0.0431**	0.00003	0.00309	0.01236
	Manubi	0.0155	0.0371	0.0114	-0.0046	-0.0111	-	0.03624	0.0248	**0.0598**
	Kubusi	0.0137	0.0310	0.0080	-0.0061	0.0089	0.0036	-	0.0009	0.01671
	Fort Fordyce	0.0153	0.0310	0.0086	-0.0037	0.0031	-0.0007	0.0039	-	0.01566
	The Island	0.0428	0.0309	0.0201	0.0202	0.0263	0.0242	0.0200	-0.0016	-

Appendix S4.4 Pairwise F_{ST} values for 1134 bp mtDNA CR (above) and eight microsatellite loci (below) *P. ruficapilla*. Values in bold: $p < 0.05$ (mtDNA CR); $p < 0.00625$ after Bonferroni correction (microsatellites).

		F_{ST} (mtDNA CR)							
	Forest	Ngele	Oribi Gorge	Mbotyi	Gomo	Baziya	Manubi	Kubusi	Fort Fordyce
F_{ST} (microsatellites)	Ngele	-	-0.0305	**0.0625**	0.0089	**0.0235**	0.0206	**0.0365**	**0.0835**
	Oribi Gorge	0.0186	-	0.0500	0.0004	0.0102	0.0343	-0.0062	0.0875
	Mbotyi	0.0380	0.0087	-	0.0601	0.0536	0.0217	0.0020	0.0325
	Gomo	0.0330	0.0141	0.0254	-	-0.0141	0.0224	0.0276	**0.0909**
	Baziya	0.0470	0.0362	0.0361	0.0493	-	0.0296	0.0364	**0.0856**
	Manubi	0.0213	0.0512	0.0608	0.0200	0.0316	-	0.0373	**0.0776**
	Kubusi	0.0450	0.0406	0.0250	0.0300	0.0122	0.0410	-	**0.0827**
	Fort Fordyce	0.0447	0.0574	0.0227	0.0372	0.0342	0.0550	0.0375	-

Appendix S4.5 Pairwise F_{ST} values for 1295 bp mtDNA CR (above) and eight microsatellite loci (below) for *P. stellata*. Values in bold: $p < 0.05$ (mtDNA CR); $p < 0.00625$ after Bonferroni correction (microsatellites).

		F_{ST} (mtDNA CR)								
	Forest	Ngele	Oribi Gorge	Gomo	Baziya	Manubi	Kubusi	Fort Fordyce	Alexandria	The Island
F_{ST} (microsatellites)	Ngele	-	0.0365	0.0012	-0.0053	0.0046	**0.0679**	**0.0543**	**0.0604**	-0.0242
	Oribi Gorge	0.0042	-	0.0309	0.0162	-0.0090	**0.1304**	**0.1272**	**0.1567**	-0.0048
	Gomo	**0.0107**	-0.0071	-	-0.0011	0.0147	**0.0843**	**0.0670**	**0.0890**	-0.0185
	Baziya	0.0058	-0.0038	-0.0027	-	-0.0016	**0.0647**	0.0460	**0.0764**	-0.0367
	Manubi	**0.0187**	0.0031	0.0030	-0.0029	-	**0.0927**	**0.0840**	**0.1124**	-0.0236
	Kubusi	**0.0114**	0.0201	**0.0240**	0.0005	0.0085	-	-0.0172	**0.1140**	0.0604
	Fort Fordyce	**0.0185**	**0.0256**	**0.0130**	0.0023	0.0057	0.0083	-	**0.0947**	0.0447
	Alexandria	**0.0373**	**0.0394**	**0.0488**	**0.0152**	**0.0406**	**0.0188**	**0.0452**	-	0.0641
	The Island	0.0208	**0.0530**	**0.0348**	0.0113	**0.0390**	0.0124	**0.0316**	**0.0241**	-

Appendix S4.6 Bottleneck results on microsatellite data for the three focal birds, showing significance values (*p* values) from a one-tailed Wilcoxon signed-rank test for heterozygous excess using two-phase mutation (TPM) and single-step mutation (SSM) models. The Bonferroni correction was applied to all *p* values (*p* = 0.00625).

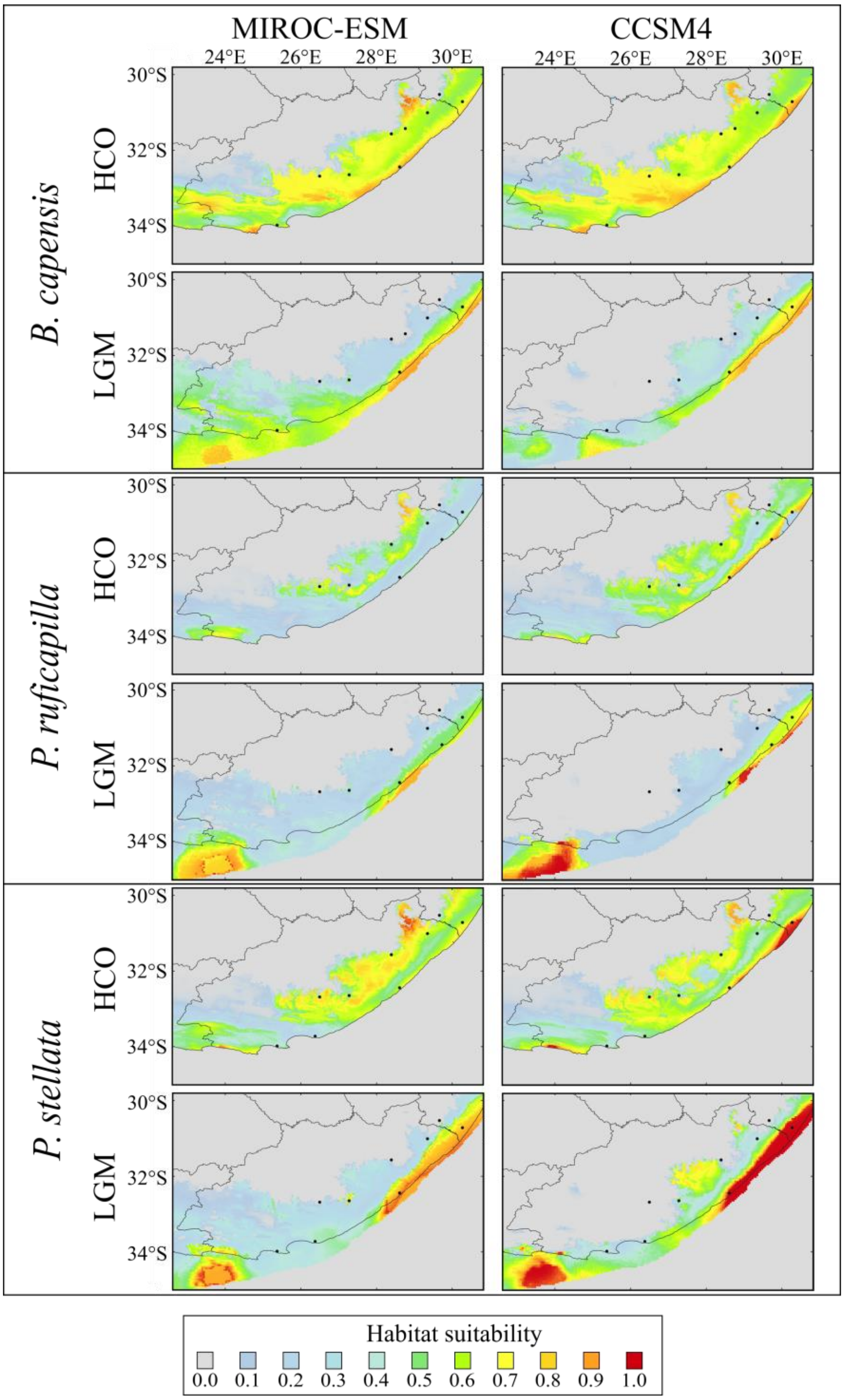
	Parameter	Ngele	Oribi Gorge	Mbotyi	Gomo	Nqadu	Baziya	Manubi	Kubusi	Fort Fordyce	Alexandria	The Island	Total
B. capensis	TPM 90 % SMM	0.469	0.371	-	0.289	0.344	0.578	0.371	0.711	0.527	-	0.422	0.371
	TPM 95% SMM	0.531	0.422	-	0.469	0.344	0.422	0.473	0.766	0.527	-	0.422	0.629
	SMM	0.766	0.527	-	0.656	0.594	0.680	0.527	0.852	0.809	-	0.473	0.980
P. ruficapilla	TPM 90 % SMM	0.010	**0.004***	**0.002***	**0.004***	-	0.014	0.010	**0.004***	**0.006***	-	-	**0.004***
	TPM 95% SMM	0.010	**0.004***	**0.002***	**0.004***	-	0.010	0.010	**0.004***	**0.006**	-	-	**0.004***
	SMM	0.010	**0.004***	**0.002***	**0.006***	-	0.010	0.010	**0.004***	0.098	-	-	**0.004***
P. stellata	TPM 90 % SMM	**0.002***	0.014	-	0.020	-	**0.004***	**0.002***	**0.006***	0.020	0.010	**0.002***	0.010
	TPM 95% SMM	**0.002***	0.014	-	0.027	-	0.010	**0.002***	0.010	0.020	0.014	**0.002***	0.027
	SMM	**0.004***	0.014	-	0.098	-	0.014	**0.006***	0.014	0.027	0.020	**0.002***	0.156

Appendix S4.7 Description of the 19 BIOCLIM bioclimatic variables utilised in this study, retrieved from https://www.worldclim.org/.

BIOCLIM code	Climate variable
bio1	Annual mean temperature
bio2	Mean diurnal range (mean of monthly maximum temperature minus minimum temperature)
bio3	Isothermality
bio4	Temperature seasonality (standard deviation of annual mean temperature × 100)
bio5	Maximum temperature of the warmest month (°C)
bio6	Minimum temperature of the coldest month (°C)
bio7	Temperature annual range
bio8	Mean temperature of the wettest quarter (°C)
bio9	Mean temperature in the driest quarter (°C)
bio10	Mean temperature in the warmest quarter (°C)
bio11	Mean temperature of the coldest quarter (°C)
bio12	Annual precipitation (mm)
bio13	Precipitation in the wettest month (mm)
bio14	Precipitation in the driest month (mm)
bio15	Precipitation seasonality (standard deviation of monthly precipitation values)
bio16	Precipitation in the wettest quarter (mm)
bio17	Precipitation in the driest quarter (mm)
bio18	Precipitation in the warmest quarter (mm)
bio19	Precipitation in the coldest quarter (mm)

Appendix S4.8 Correlation coefficients between the 19 bioclimatic variables (Appendix S4.8), determined in ENMTOOLS 1.4, for climates over the Eastern Cape and southern KwaZulu-Natal provinces of South Africa.

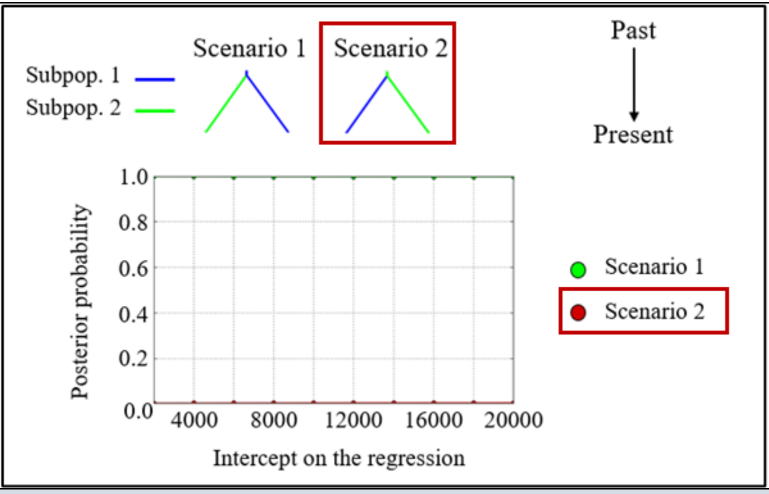
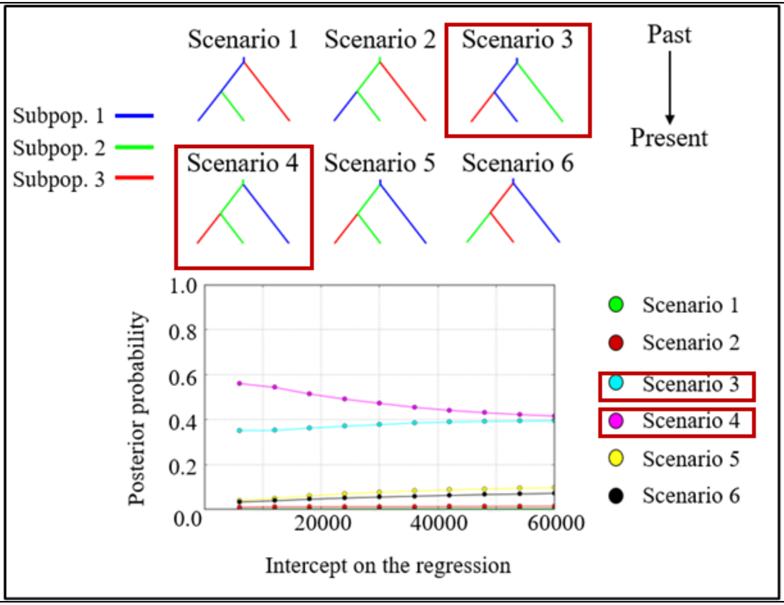
	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19
bio1	1.00	0.94	0.99	0.87	0.99	0.46	0.92	0.99	0.96	0.99	0.96	0.85	0.82	0.82	0.85	0.81	0.85	0.78	0.83
bio2	0.94	1.00	0.96	0.97	0.98	0.15	0.99	0.98	0.82	0.97	0.82	0.74	0.77	0.67	0.91	0.75	0.69	0.71	0.66
bio3	0.99	0.96	1.00	0.89	0.99	0.39	0.94	0.98	0.93	0.99	0.93	0.86	0.84	0.81	0.88	0.83	0.84	0.80	0.81
bio4	0.87	0.97	0.89	1.00	0.94	-0.02	0.99	0.93	0.70	0.92	0.70	0.65	0.70	0.58	0.89	0.67	0.60	0.63	0.57
bio5	0.99	0.98	0.99	0.94	1.00	0.32	0.97	1.00	0.90	1.00	0.91	0.81	0.81	0.76	0.89	0.80	0.79	0.76	0.76
bio6	0.46	0.15	0.39	-0.02	0.32	1.00	0.09	0.34	0.69	0.36	0.68	0.52	0.37	0.65	0.08	0.39	0.67	0.40	0.68
bio7	0.92	0.99	0.94	0.99	0.97	0.09	1.00	0.96	0.78	0.96	0.78	0.72	0.76	0.64	0.92	0.74	0.66	0.70	0.63
bio8	0.99	0.98	0.98	0.93	1.00	0.34	0.96	1.00	0.90	1.00	0.91	0.82	0.82	0.75	0.90	0.81	0.79	0.77	0.76
bio9	0.96	0.82	0.93	0.70	0.90	0.69	0.78	0.90	1.00	0.92	1.00	0.85	0.78	0.88	0.71	0.78	0.91	0.76	0.89
bio10	0.99	0.97	0.99	0.92	1.00	0.36	0.96	1.00	0.92	1.00	0.92	0.81	0.81	0.78	0.87	0.79	0.81	0.75	0.78
bio11	0.96	0.82	0.93	0.70	0.91	0.68	0.78	0.91	1.00	0.92	1.00	0.86	0.79	0.87	0.72	0.79	0.90	0.77	0.88
bio12	0.85	0.74	0.86	0.65	0.81	0.52	0.72	0.82	0.85	0.81	0.86	1.00	0.98	0.81	0.82	0.98	0.85	0.97	0.84
bio13	0.82	0.77	0.84	0.70	0.81	0.37	0.76	0.82	0.78	0.81	0.79	0.98	1.00	0.72	0.89	1.00	0.76	0.99	0.74
bio14	0.82	0.67	0.81	0.58	0.76	0.65	0.64	0.75	0.88	0.78	0.87	0.81	0.72	1.00	0.53	0.71	0.99	0.99	0.68
bio15	0.85	0.91	0.88	0.89	0.89	0.08	0.92	0.90	0.71	0.87	0.72	0.82	0.89	0.53	1.00	0.88	0.57	0.86	0.54
bio16	0.81	0.75	0.83	0.67	0.80	0.39	0.74	0.81	0.78	0.79	0.79	0.98	1.00	0.71	0.88	1.00	0.75	1.00	0.73
bio17	0.85	0.69	0.84	0.60	0.79	0.67	0.66	0.79	0.91	0.81	0.90	0.85	0.76	0.99	0.57	0.75	1.00	0.72	1.00
bio18	0.78	0.71	0.80	0.63	0.76	0.40	0.70	0.77	0.76	0.75	0.77	0.97	0.99	0.99	0.86	1.00	0.72	1.00	0.70
bio19	0.83	0.66	0.81	0.57	0.76	0.68	0.63	0.76	0.89	0.78	0.88	0.84	0.74	0.68	0.54	0.73	1.00	0.70	1.00

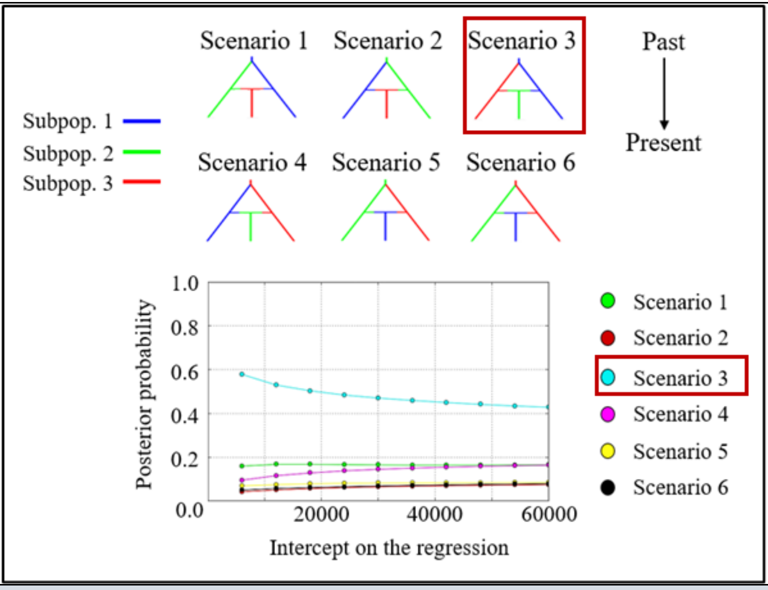
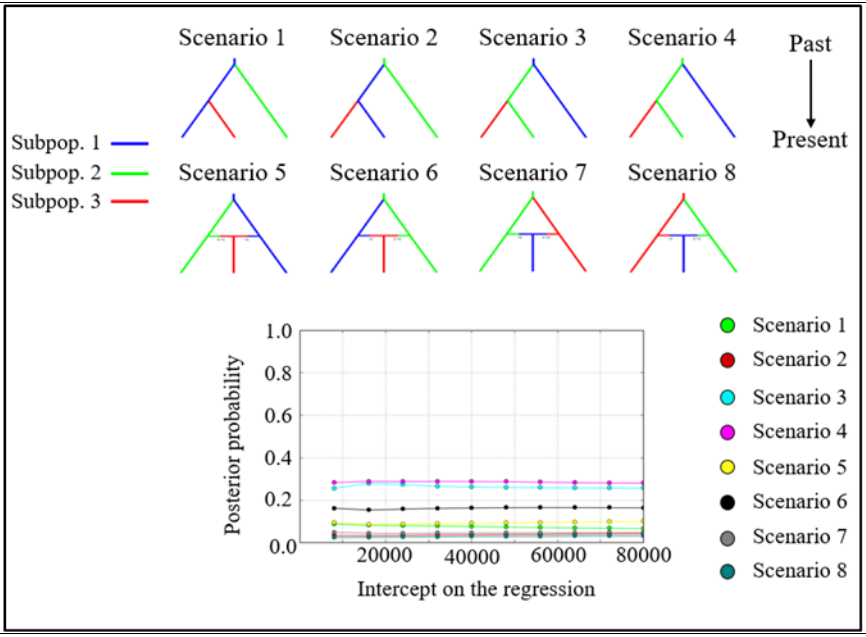


Appendix S4.9 Maxent modelled paleo-distributions of *B. capensis*, *P. ruficapilla*, and *P. stellata* across the Eastern Cape and southern KwaZulu-Natal during the mid-Holocene climate optimum (HCO), and last glacial maximum (LGM). Warmer colours indicate higher habitat suitability. Projections for HCO and LGM species distributions were generated from two global climate models [Community Climate System Model (CCSM) and Model for Interdisciplinary Research on Climate (MIROC)].

Appendix S4.10 Approximate Bayesian computations

Appendix S4.10 shows the approximate Bayesian computation outcomes of plausible demographic scenarios tested for *Batis capensis*, *Phylloscopus ruficapilla*, and *Pogonocichla stellata* populations across forests of the Eastern Cape and southern KwaZulu-Natal provinces of South Africa, determined in DIYABC 2.1.0 (Cornuet et al., 2014). For each species, a hierarchical approach was used to tested demographic scenarios of increasing complexity, first establishing the ancestral subpopulations between the two-three best-supported BAPS population subdivisions (Figure 4.3), before elaborating upon more comprehensive demographic scenarios which consider tall the population sub-divisions supported by BAPS and BARRIER analyses of both mtDNA CR and nuclear microsatellite datasets for each species (Figure 4.3). Each demographic scenarios tested includes alongside the number of subpopulations tested, as well as the individual forest locales incorporated into each group. Diagrams illustrating the chronology of demographic events are arranged from top (past) to bottom (present-day). The colour of each branch denotes the distinct population genetic subgroup. The more ancestral/source subpopulation are represented as continuing past coalescent events (t1-t6), while the subsequent derived/sink subpopulations are shown diverging from the source populations after each coalescent event. Subpopulations derived from admixture events between multiple ancestral subpopulations are depicted as emerging from horizontal lines connecting respective ancestral subpopulations. We evaluated relative model performance by computing posterior probabilities using logistic regression linear discriminant analysis components of the summary statistics. Subsequently, we performed model checking on the chosen best-supported demographic scenario model using principal component analysis (PCA), and locating observed summary statistics amongst simulated summary statistics. These procedures were conducted in DIYABC 2.1.0 (Cornuet et al., 2014).

Cape batis *Batis capensis*
BAPS mtDNA CR subdivisions (2 subpopulations)
Subpopulation 1: Ngele; Oribi Gorge; Gomo
Subpopulation 2: Baziya; Manubi; Kubusi; Fort Fordyce; The Island

BAPS mtDNA CR and BARRIER subdivisions (3 subpopulations; non-admixture)
Subpopulation 1: Ngele
Subpopulation 2: Oribi Gorge; Gomo
Subpopulation 3: Baziya; Manubi; Kubusi; Fort Fordyce; The Island


Cape batis *Batis capensis* (continued)
BAPS mtDNA CR and BARRIER subdivisions (3 subpopulations; admixture)
Subpopulation 1: Ngele
Subpopulation 2: Oribi Gorge; Gomo
Subpopulation 3: Baziya; Manubi; Kubusi; Fort Fordyce; The Island

BAPS mtDNA CR subdivision (3 subpopulations; northeast forests; series 1)
Subpopulation 1: Ngele (Afromontane forest)
Subpopulation 2: Oribi Gorge (scarp forest)
Subpopulation 3: Gomo (Afromontane forest)


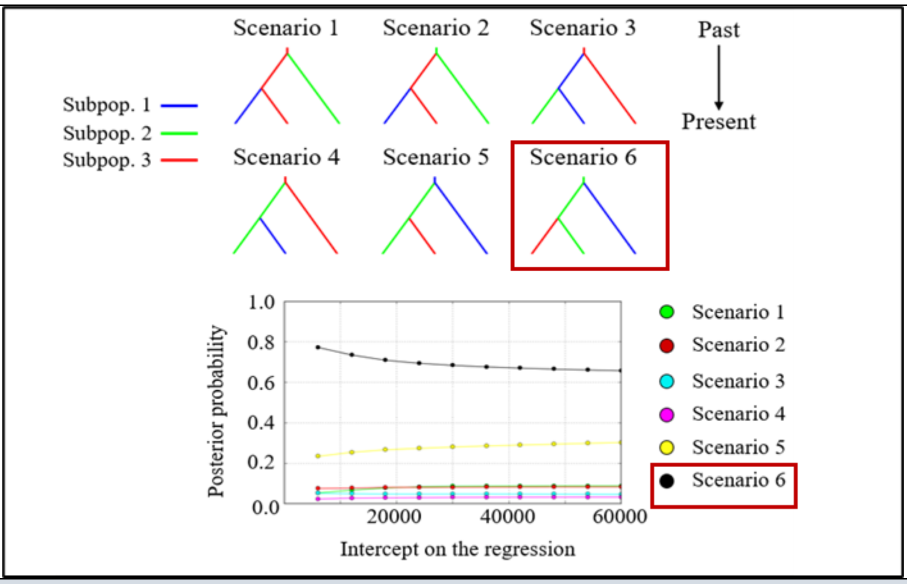
Cape batis *Batis capensis* (continued)

BAPS mtDNA CR subdivision (3 subpopulations; northeast forests; series 2)

Subpopulation 1: Ngele (Afromontane forest)

Subpopulation 2: Oribi Gorge (scarp forest)

Subpopulation 3: Gomo (Afromontane forest)

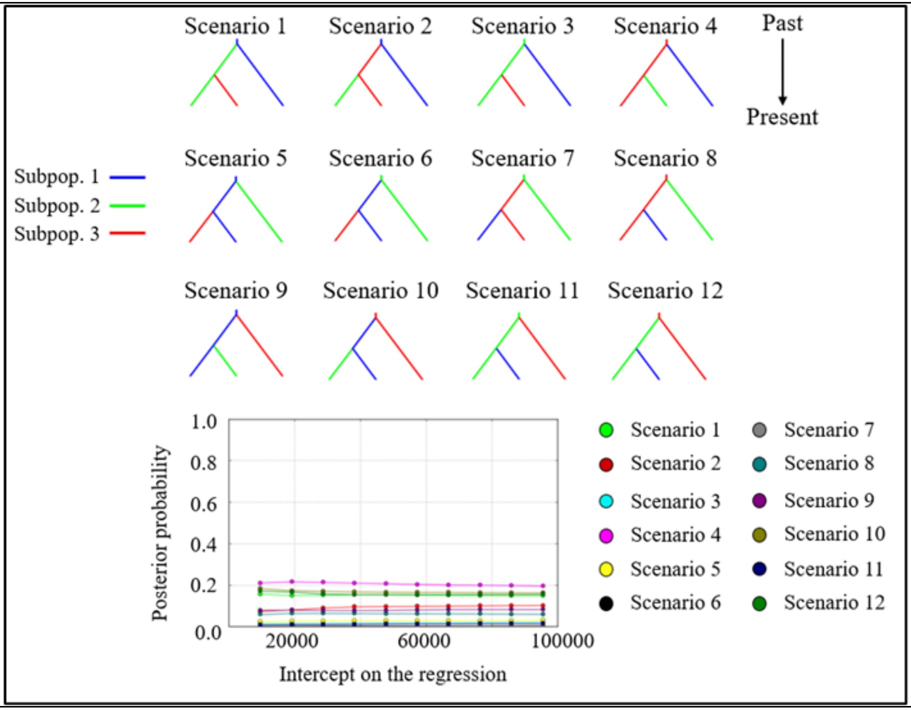


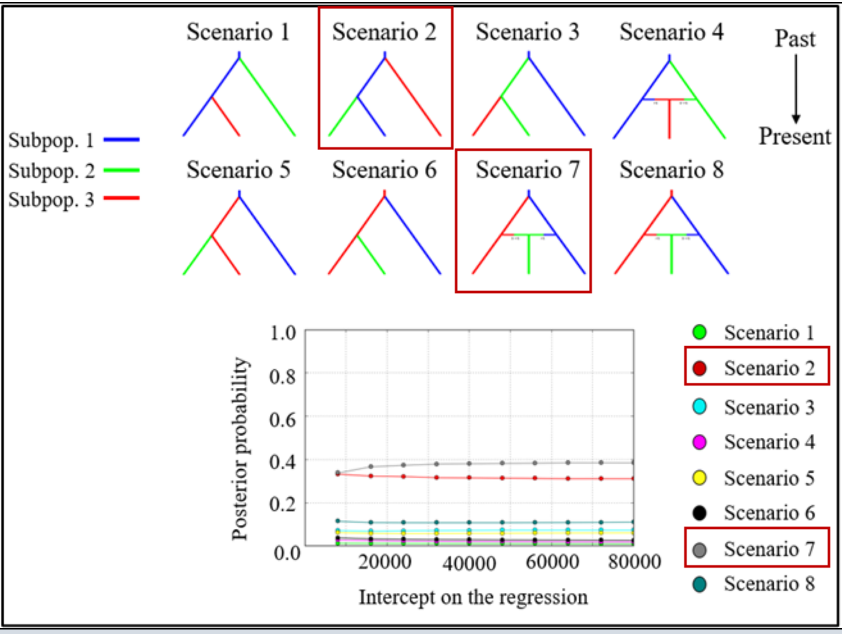
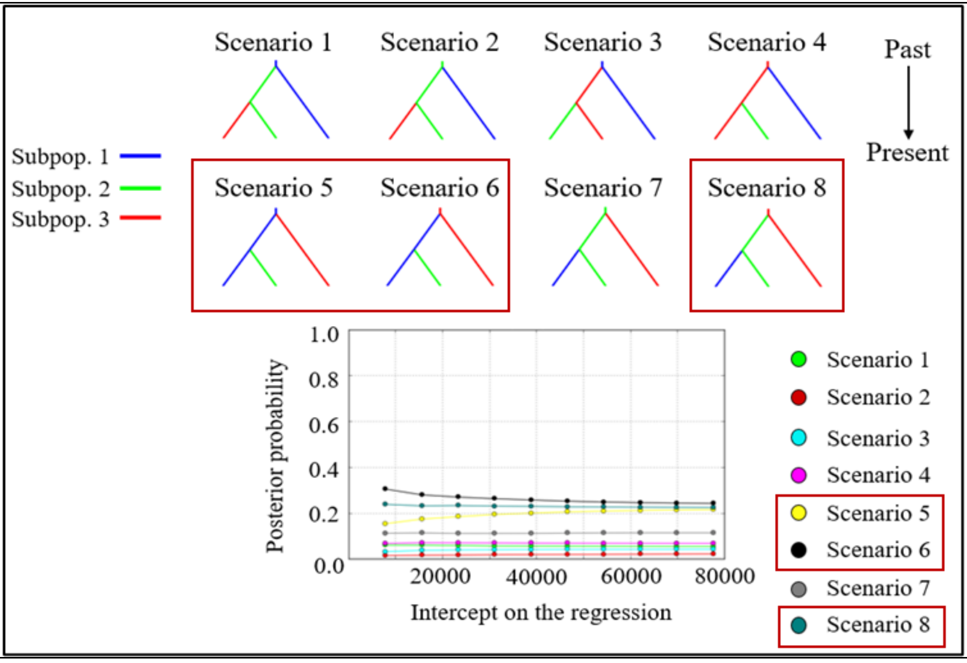
BAPS mtDNA CR subdivision (3 subpopulations; southwest forests)

Subpopulation 1: Manubi (scarp forest)

Subpopulation 2: Kubusi; Fort Fordyce (Afromontane forests)

Subpopulation 3: The Island (southern Indian Ocean coastal belt forest)



Cape batis *Batis capensis* (continued)
Scarp forests and Gomo (3 subpopulations)
Subpopulation 1: Oribi Gorge (scarp forest)
Subpopulation 2: Gomo (Afromontane forests)
Subpopulation 3: Manubi (scarp forest)

Southern mistbelt forests (excluding Ngele and Gomo) (3 subpopulations)
Subpopulation 1: Baziya; Nqadu
Subpopulation 2: Kubusi
Subpopulation 3: Fort Fordyce


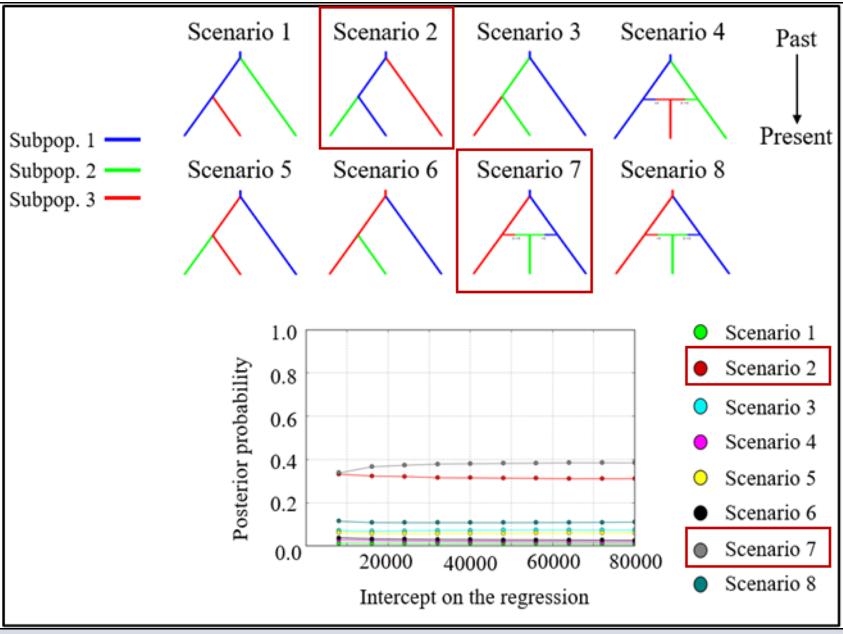
Cape batis *Batis capensis* (continued)

Scarp forests and Gomo (3 subpopulations)

Subpopulation 1: Oribi Gorge (scarp forest)

Subpopulation 2: Gomo (Afromontane forests)

Subpopulation 3: Manubi (scarp forest)

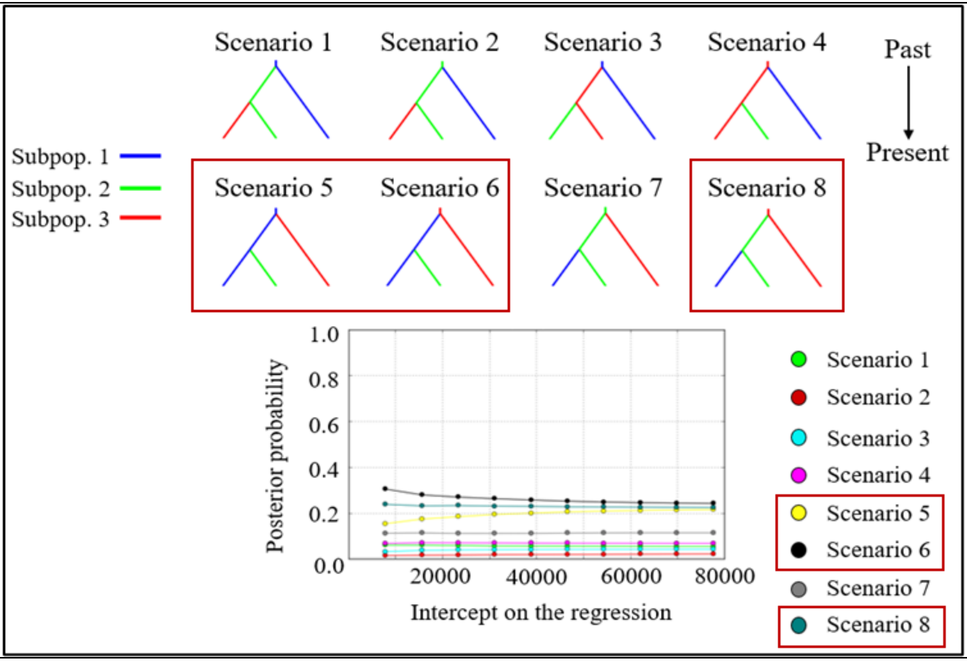


Southern mistbelt forests (excluding Ngele and Gomo) (3 subpopulations)

Subpopulation 1: Baziya; Nqadu

Subpopulation 2: Kubusi

Subpopulation 3: Fort Fordyce



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<tr><th>Cape batis <i>Batis capensis</i> (continued)</th></tr>
<tr><td>mtDNA CR BAPS, and BARRIER subdivisions (6 subpopulations; series 1)</td></tr>
<tr><td>Subpopulation 1: Ngele (Afromontane forest)</td></tr>
<tr><td>Subpopulation 2: Oribi Gorge (scarp forest)</td></tr>
<tr><td>Subpopulation 3: Gomo (Afromontane forest)</td></tr>
<tr><td>Subpopulation 4: Nqadu; Baziya; Kubusi; Fort Fordyce (Afromontane forest)</td></tr>
<tr><td>Subpopulation 5: Manubi (scarp forest)</td></tr>
<tr><td>Subpopulation 6: The Island (southern Indian Ocean coastal belt forest)</td></tr>
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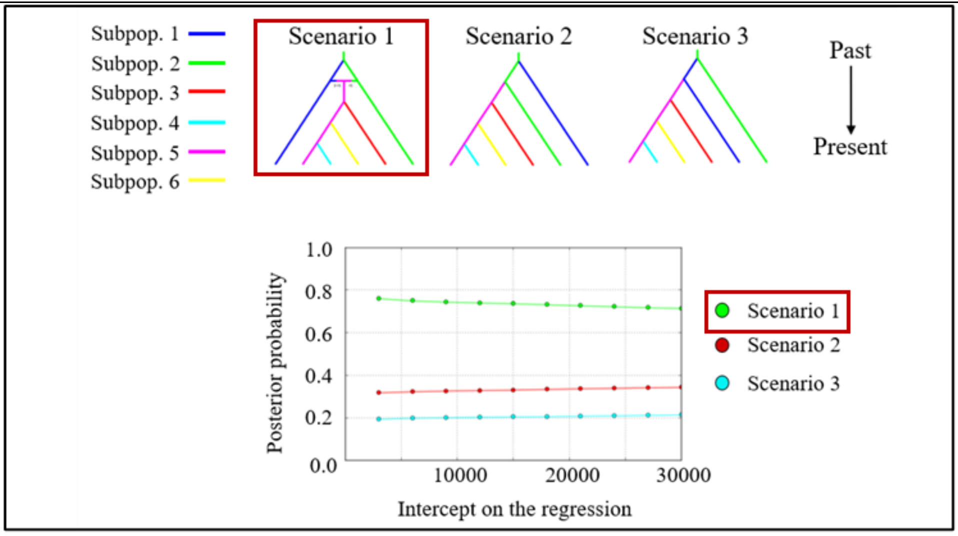

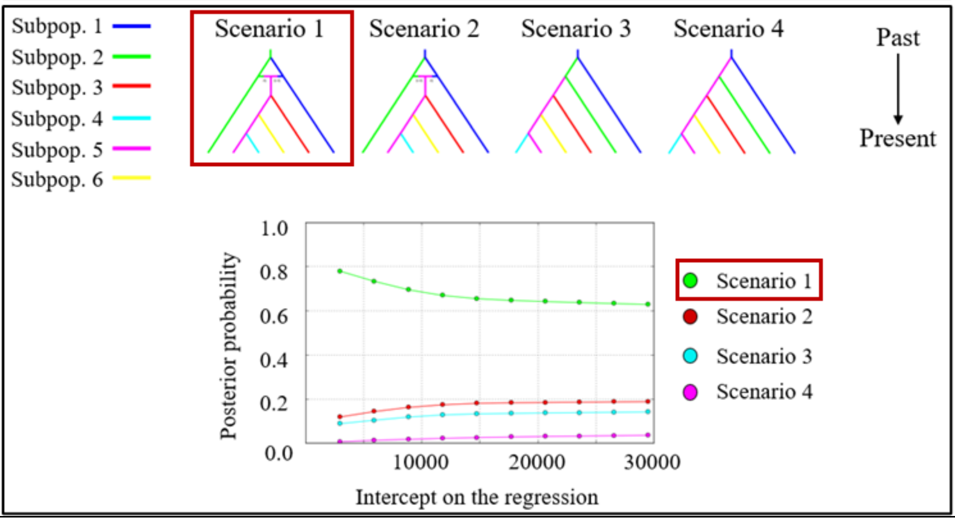

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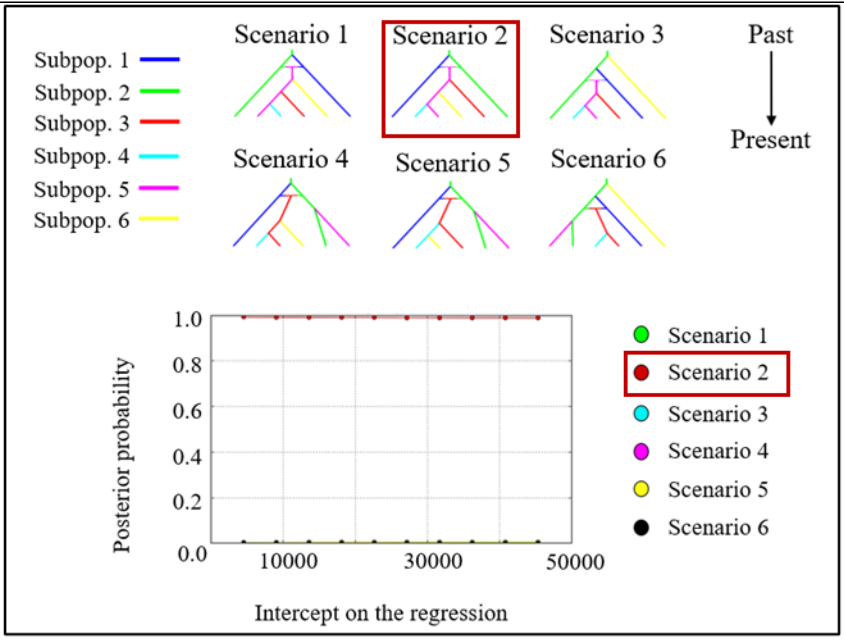
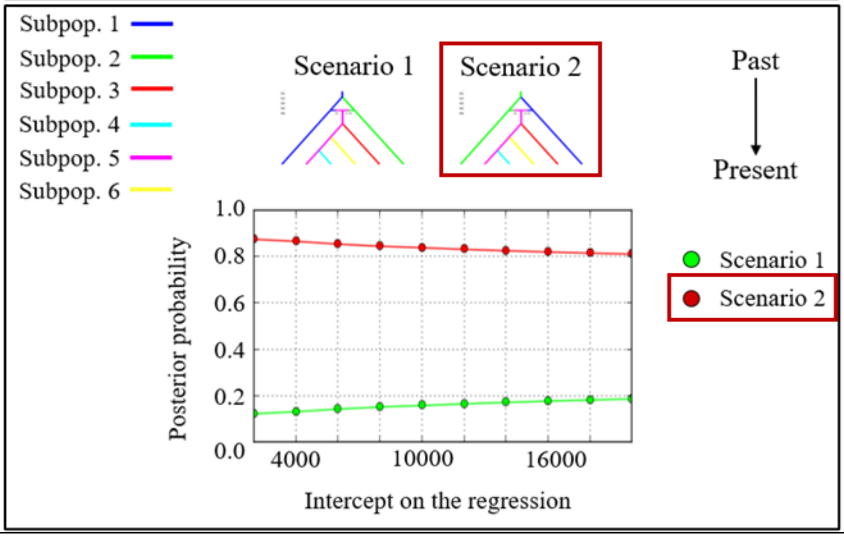
Cape batis *Batis capensis* (continued)
mtDNA CR BAPS, and BARRIER subdivisions (6 subpopulations; series 2)
Subpopulation 1: Ngele (Afromontane forest)
Subpopulation 2: Oribi Gorge (scarp forest)
Subpopulation 3: Gomo (Afromontane forest)
Subpopulation 4: Nqadu; Baziya; Kubusi; Fort Fordyce (Afromontane forest)
Subpopulation 5: Manubi (scarp forest)
Subpopulation 6: The Island (southern Indian Ocean coastal belt forest)
 

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<tr><th>Cape batis <i>Batis capensis</i> (continued)</th></tr>
<tr><td>mtDNA CR BAPS, and BARRIER subdivisions (6 subpopulations; series 2)</td></tr>
<tr><td>Subpopulation 1: Ngele (Afromontane forest)</td></tr>
<tr><td>Subpopulation 2: Oribi Gorge (scarp forest)</td></tr>
<tr><td>Subpopulation 3: Gomo (Afromontane forest)</td></tr>
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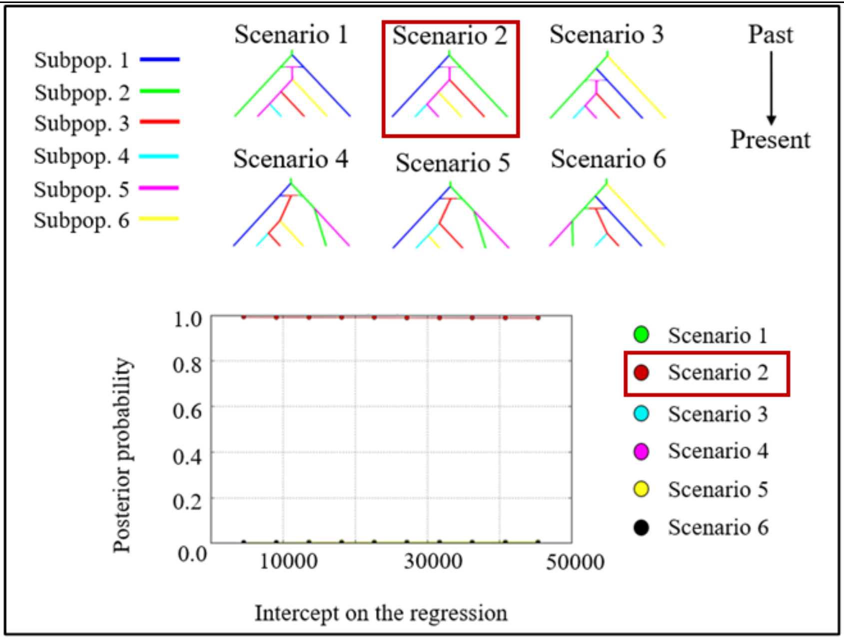

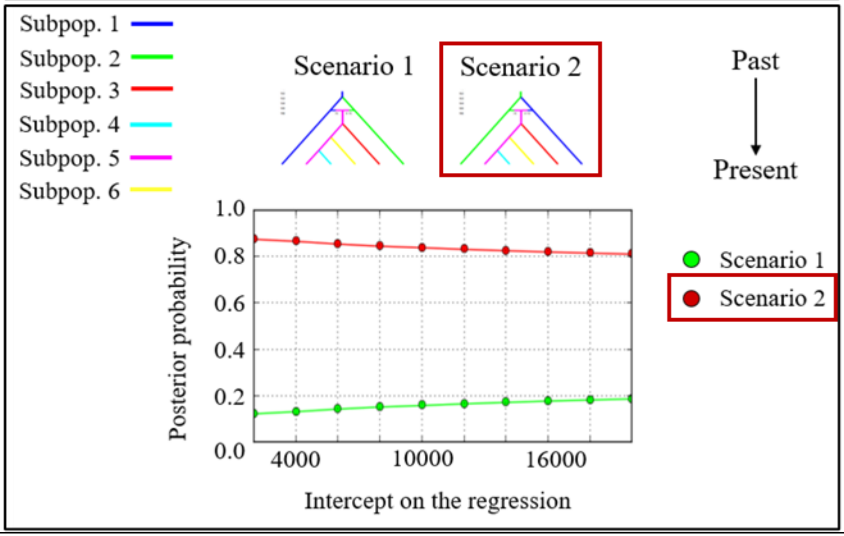

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Cape batis *Batis capensis* (continued)

mtDNA CR BAPS, and BARRIER subdivisions (6 subpopulations; series 2)
PCA of best supported demographic scenario model

Subpopulation 1: Ngele (Afromontane forest)

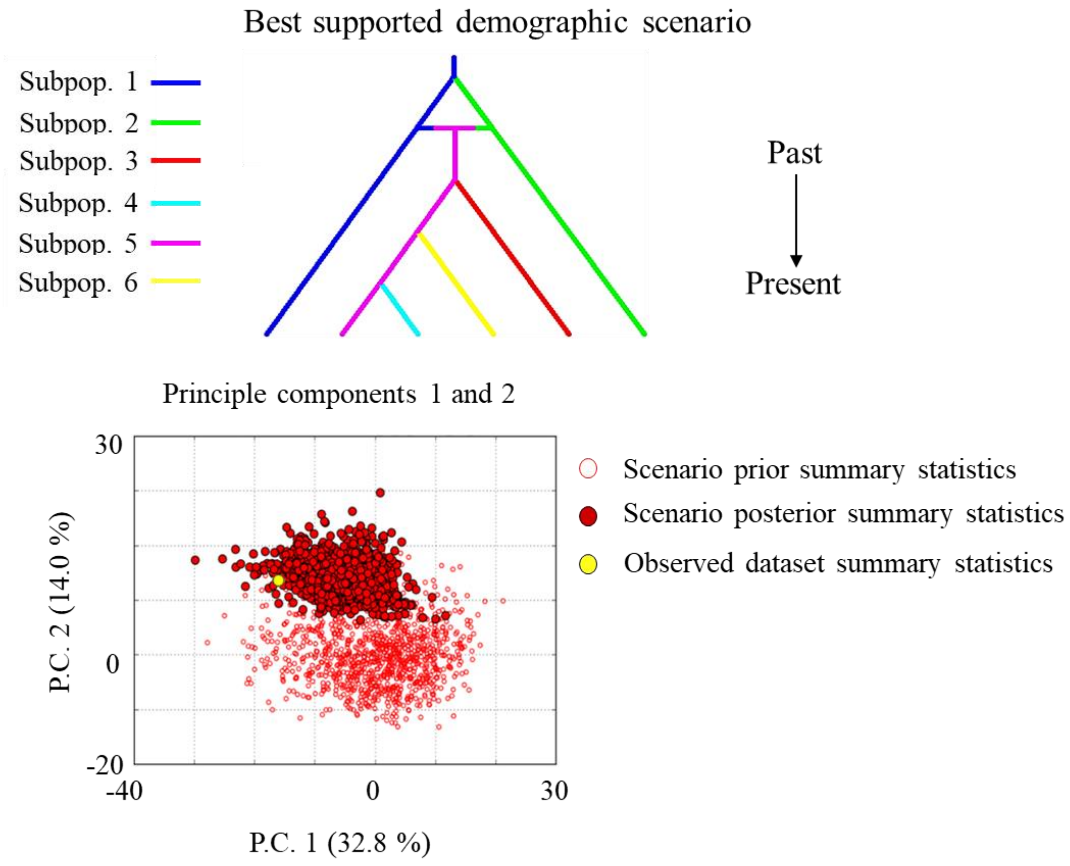
Subpopulation 2: Oribi Gorge (scarp forest)

Subpopulation 3: Gomo (Afromontane forest)

Subpopulation 4: Nqadu; Baziya; Kubusi; Fort Fordyce (Afromontane forest)

Subpopulation 5: Manubi (scarp forest)

Subpopulation 6: The Island (southern Indian Ocean coastal belt forest)



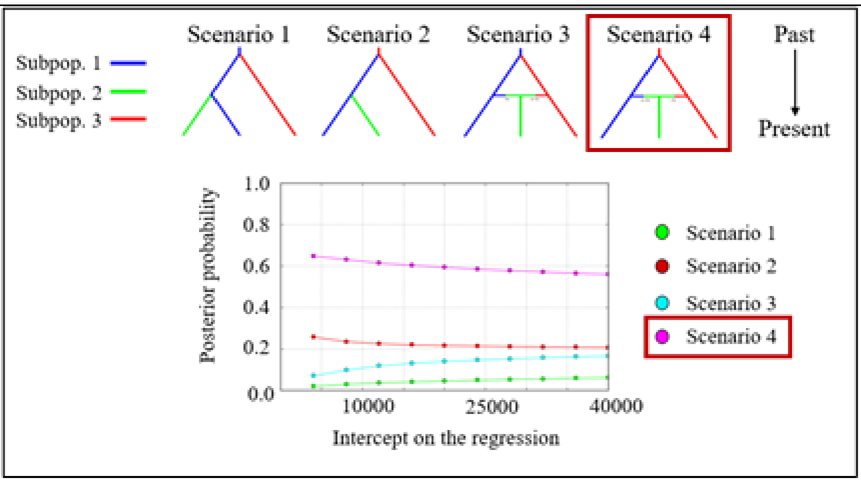
Yellow-throated woodland-warbler *Phylloscopus ruficapilla* (continued)

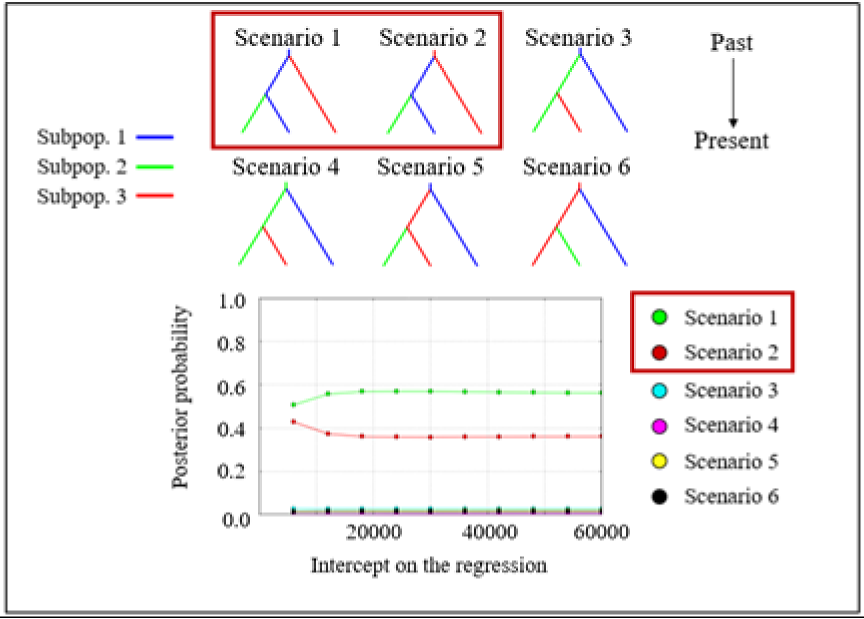
Northeast forests, excluding Gomo (3 subpopulations)

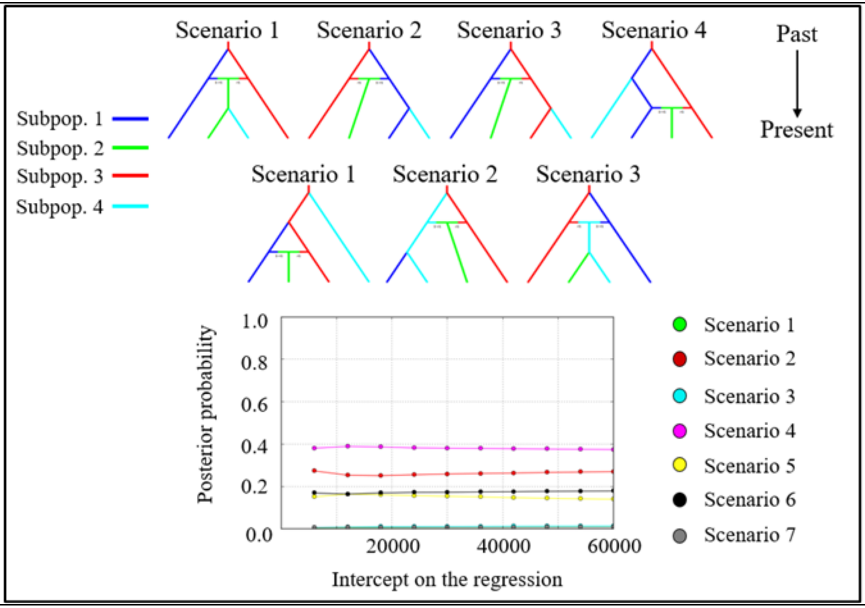
Subpopulation 1: Ngele (Afromontane forest)

Subpopulation 2: Oribi Gorge (scarp forest)

Subpopulation 3: Mbotyi (scarp forest)





Yellow-throated woodland-warbler *Phylloscopus ruficapilla* (continued)
Northeast forests, including Gomo (4 subpopulations)
Subpopulation 1: Ngele (Afromontane forest)
Subpopulation 2: Oribi Gorge (scarp forest)
Subpopulation 3: Mbotyi (scarp forest)
Subpopulation 4: Gomo (Afromontane forest)


Yellow-throated woodland-warbler *Phylloscopus ruficapilla* (continued)

BARRIER subdivisions, Gomo and Ngele combined (5 subpopulations, series 1)

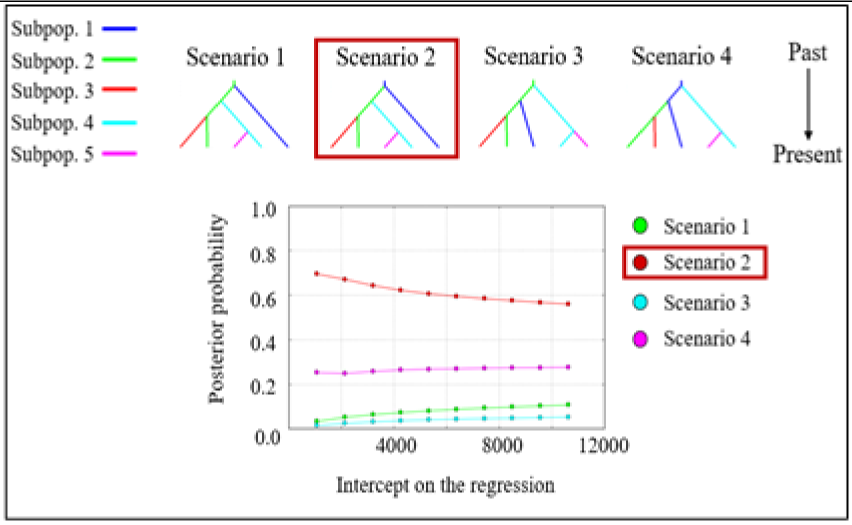
Subpopulation 1: Ngele; Gomo (Afromontane forests)

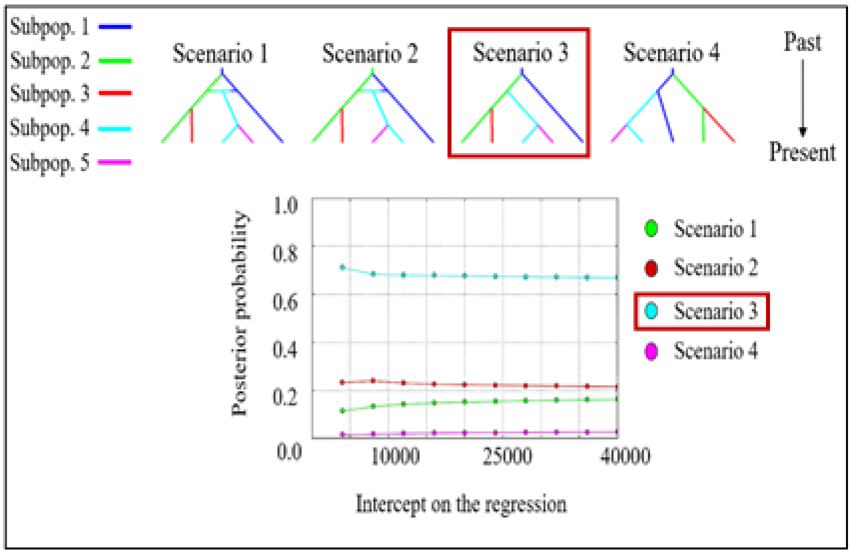
Subpopulation 2: Oribi Gorge; Mbotyi (scarp forests)

Subpopulation 3: Manubi (scarp forest)

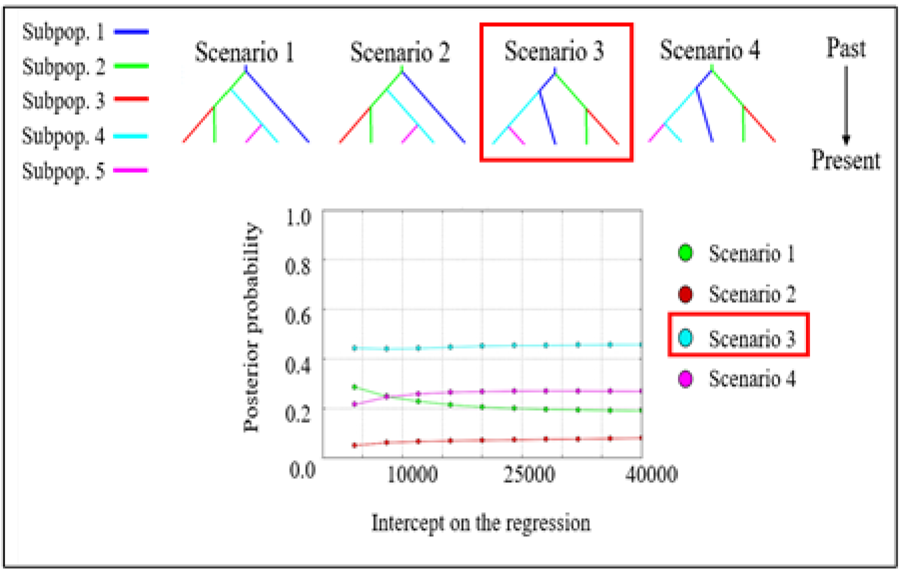
Subpopulation 4: Baziya; Kubusi (Afromontane forests)

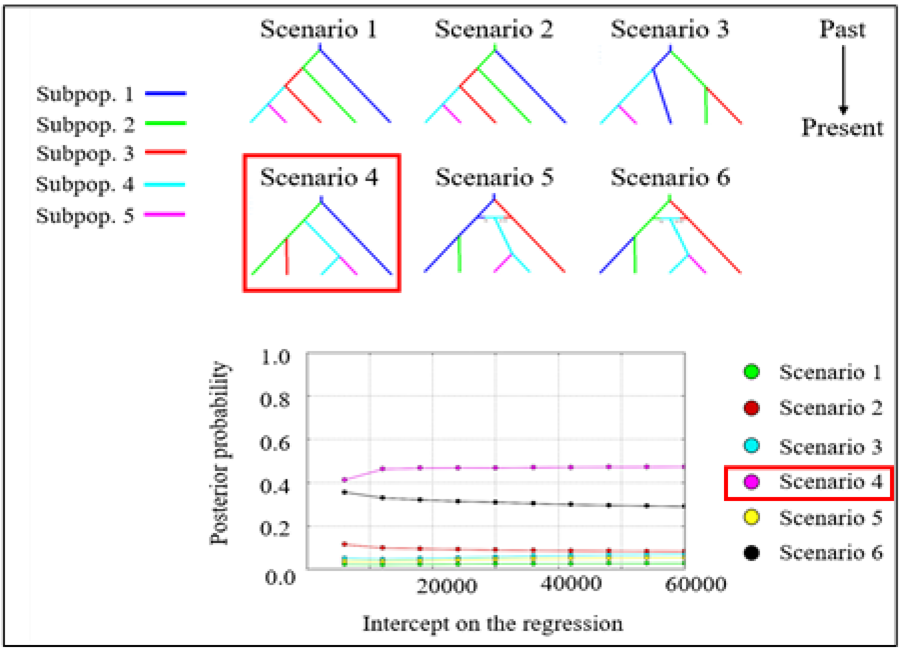
Subpopulation 5: Fort Fordyce (Afromontane forest)





Yellow-throated woodland-warbler *Phylloscopus ruficapilla* (continued)
BARRIER subdivisions, Gomo and Ngele combined (5 subpopulations, series 2)
Subpopulation 1: Ngele; Gomo (Afromontane forests)
Subpopulation 2: Oribi Gorge; Mbotyi (scarp forests)
Subpopulation 3: Manubi (scarp forest)
Subpopulation 4: Baziya; Kubusi (Afromontane forests)
Subpopulation 5: Fort Fordyce (Afromontane forest)





Yellow-throated woodland-warbler *Phylloscopus ruficapilla* (continued)

BARRIER subdivisions (6 subpopulations, series 1)

Subpopulation 1: Ngele (Afromontane forest)

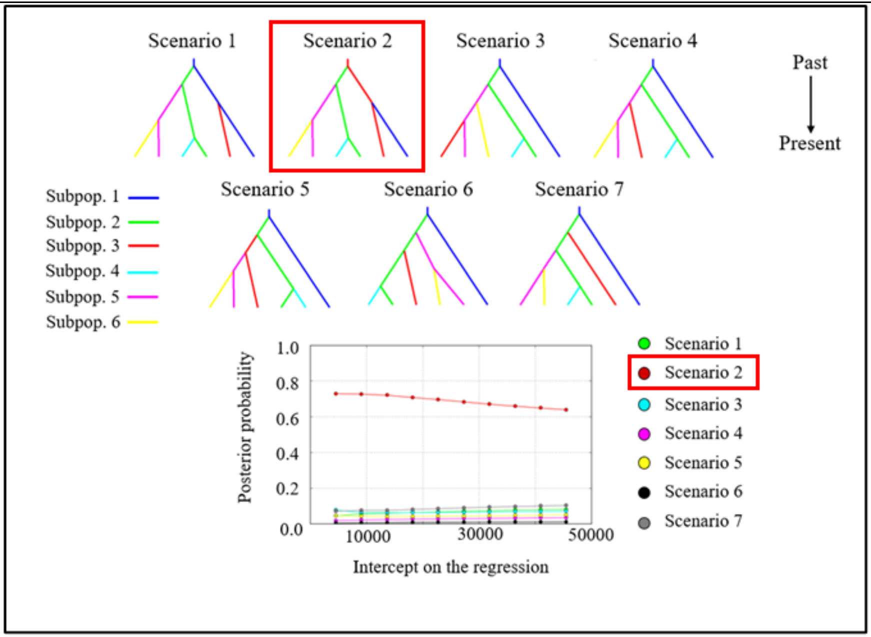
Subpopulation 2: Gomo (Afromontane forest)

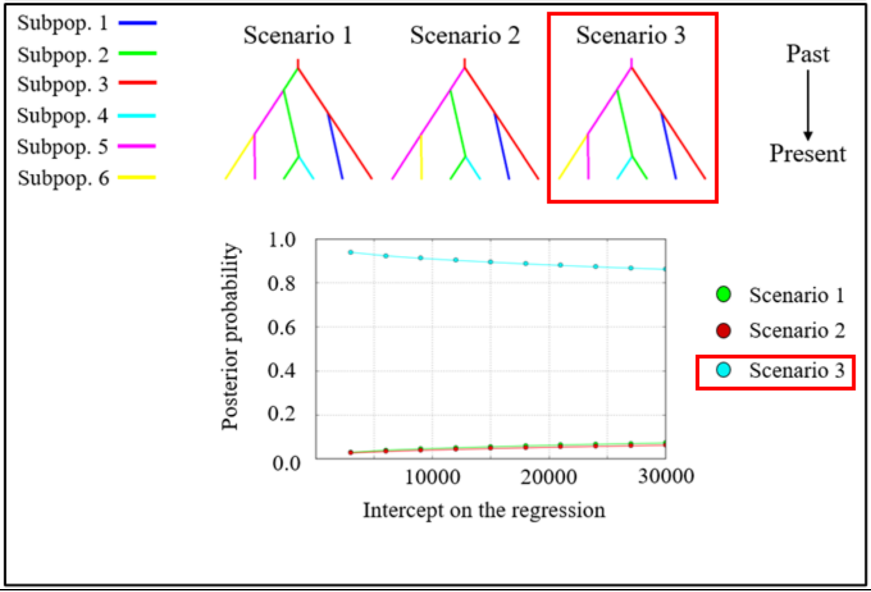
Subpopulation 3: Oribi Gorge; Mbotyi (scarp forests)

Subpopulation 4: Manubi (scarp forest)

Subpopulation 5: Baziya; Kubusi (Afromontane forests)

Subpopulation 6: Fort Fordyce (Afromontane forest)





Yellow-throated woodland-warbler *Phylloscopus ruficapilla* (continued)

BARRIER subdivisions (6 subpopulations, series 2)

Subpopulation 1: Ngele (Afromontane forest)

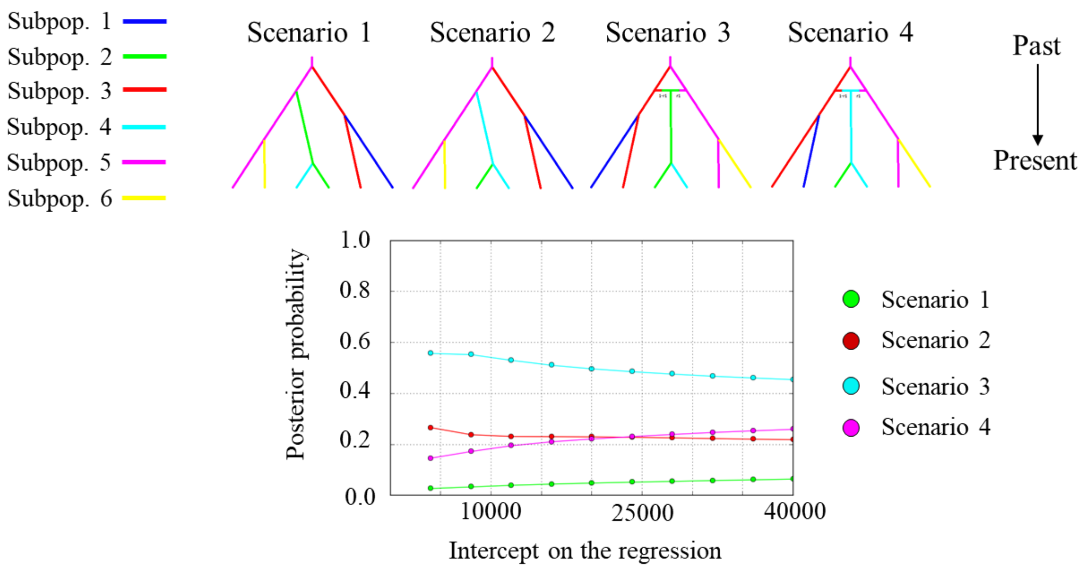
Subpopulation 2: Gomo (Afromontane forest)

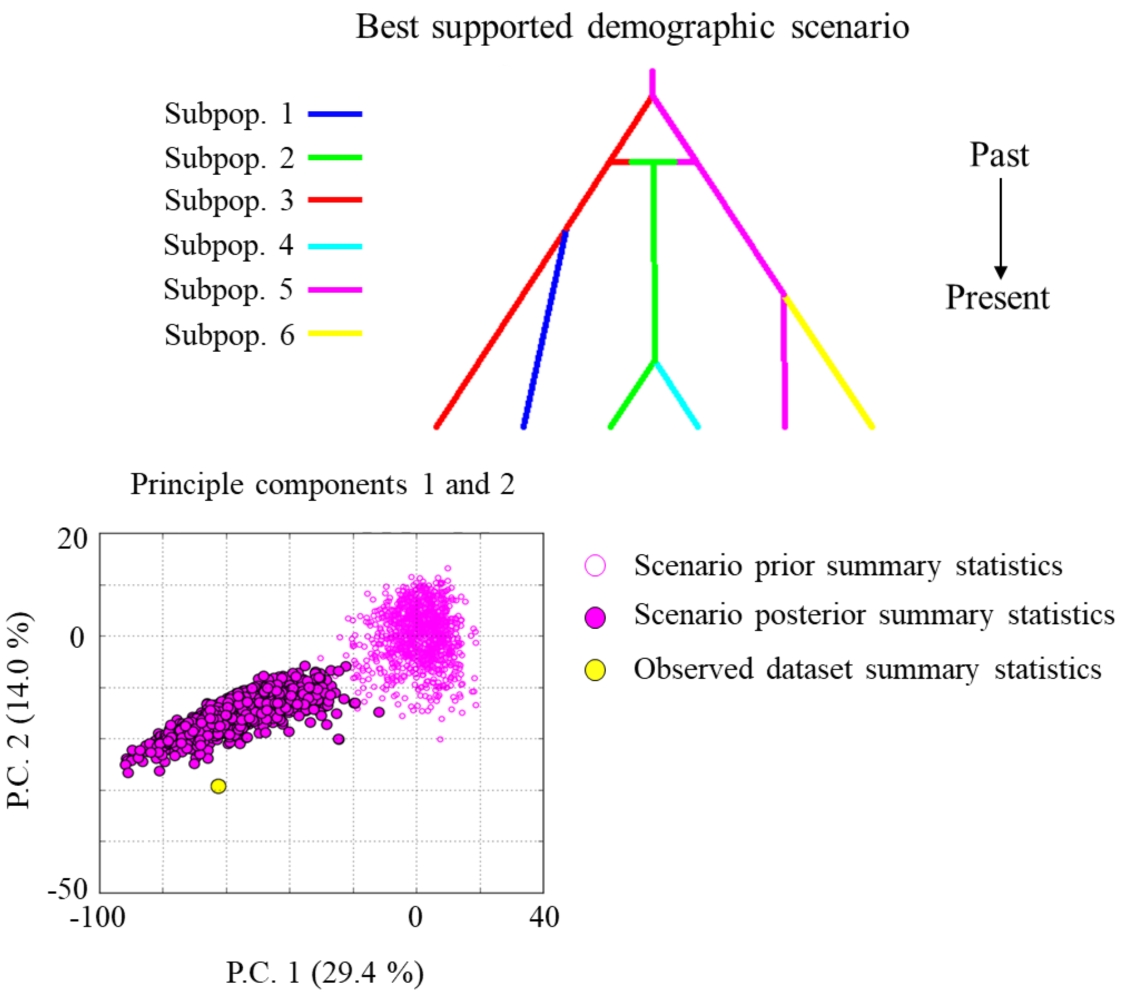
Subpopulation 3: Oribi Gorge; Mbotyi (scarp forests)

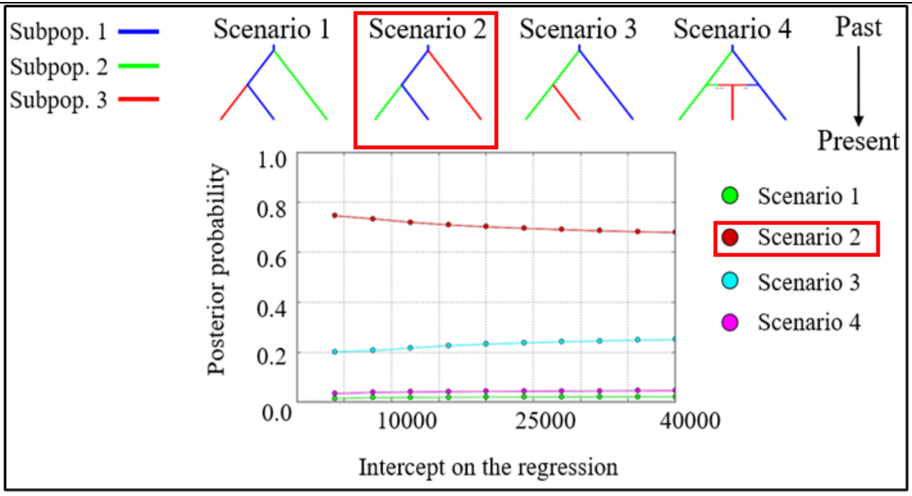
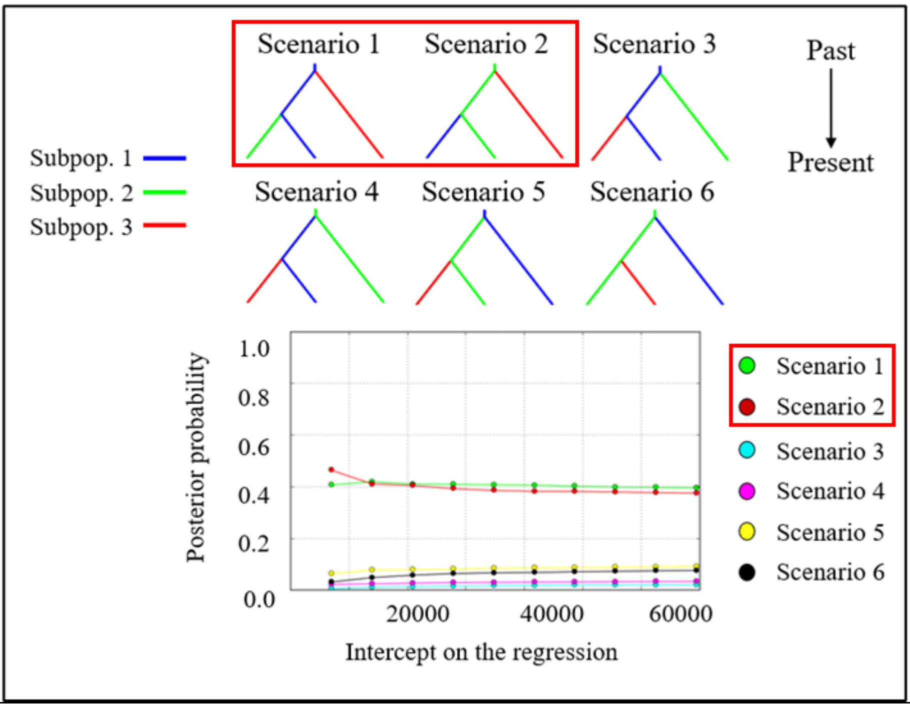
Subpopulation 4: Manubi (scarp forest)

Subpopulation 5: Baziya; Kubusi (Afromontane forests)

Subpopulation 6: Fort Fordyce (Afromontane forest)



Yellow-throated woodland-warbler *Phylloscopus ruficapilla* (continued)
BARRIER subdivisions (6 subpopulations, series 2) **PCA of best supported demographic scenario model**
Subpopulation 1: Ngele (Afromontane forest)
Subpopulation 2: Gomo (Afromontane forest)
Subpopulation 3: Oribi Gorge; Mbotyi (scarp forests)
Subpopulation 4: Manubi (scarp forest)
Subpopulation 5: Baziya; Kubusi (Afromontane forests)
Subpopulation 6: Fort Fordyce (Afromontane forest)


White-starred robin *Pogonocichla stellata*
BAPS mtDNA CR subdivision (3 subpopulations)
Subpopulation 1: Ngele; Oribi Gorge; Gomo
Subpopulation 2: Baziya; Manubi; Kubusi; Fort Fordyce; The Island
Subpopulation 3: Alexandria
 

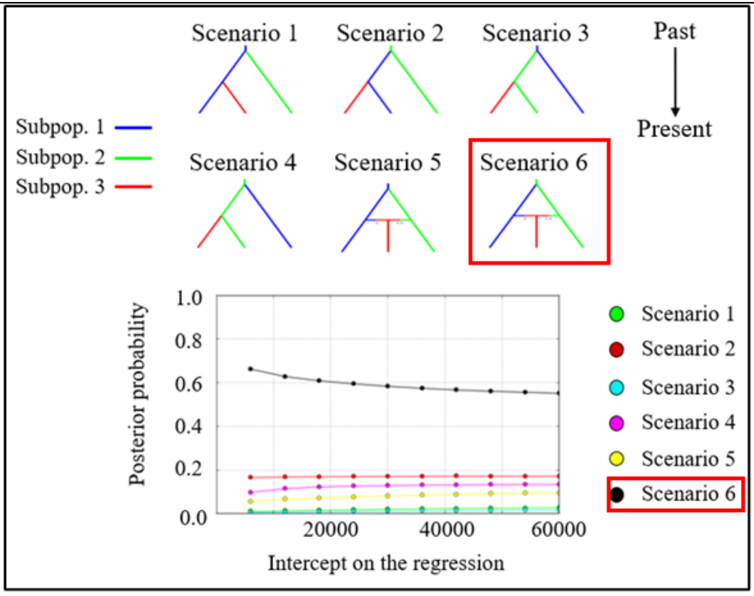
White-starred robin *Pogonocichla stellata* (continued)

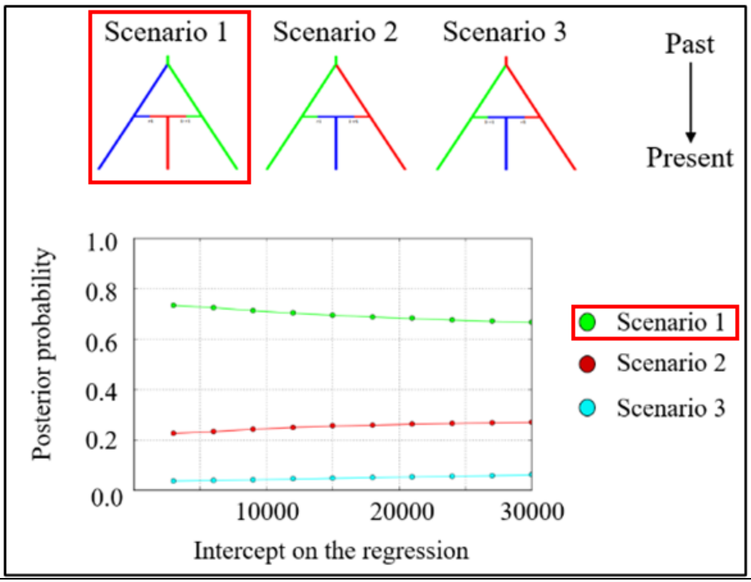
BAPS mtDNA CR: Northeast group (3 subpopulations)

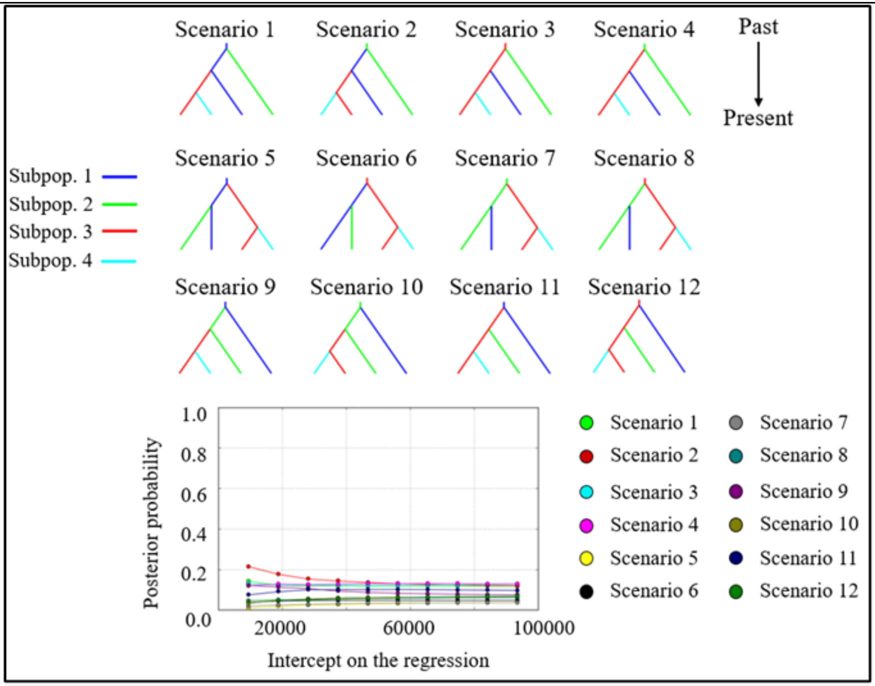
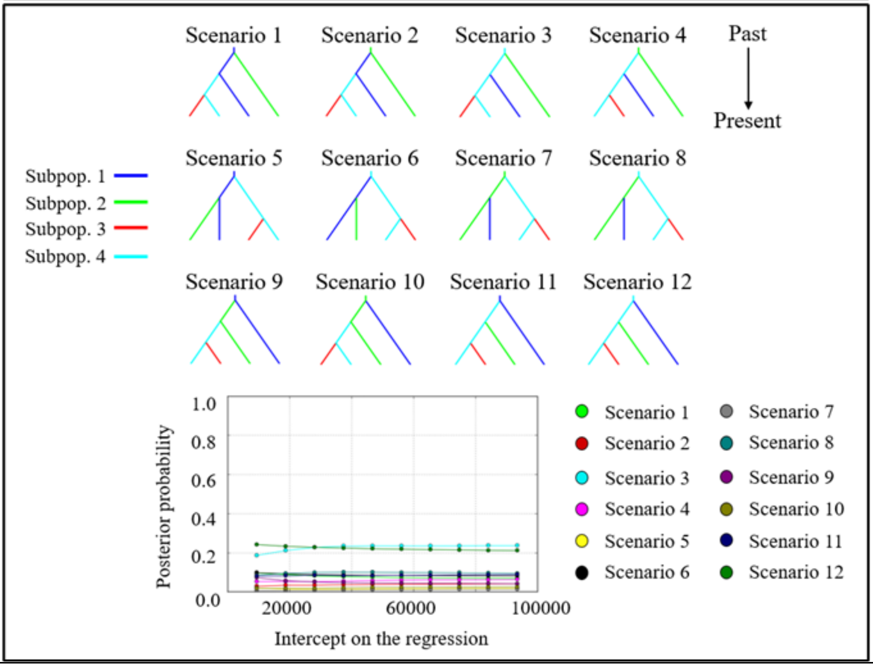
Subpopulation 1: Ngele (Afromontane forest)

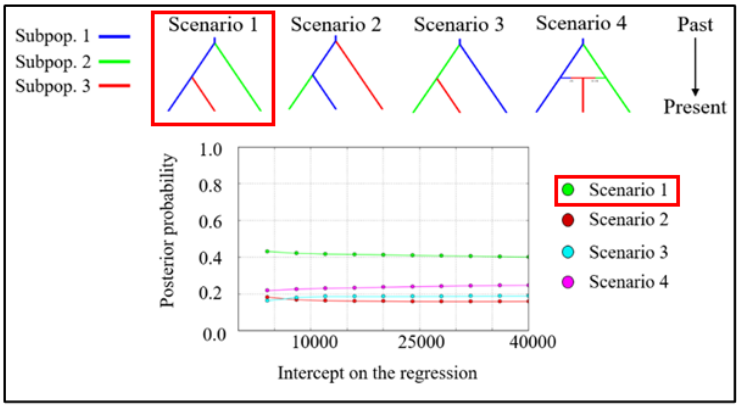
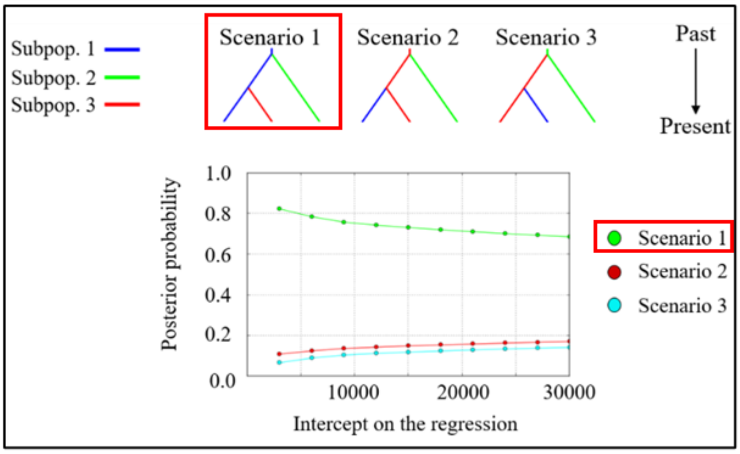
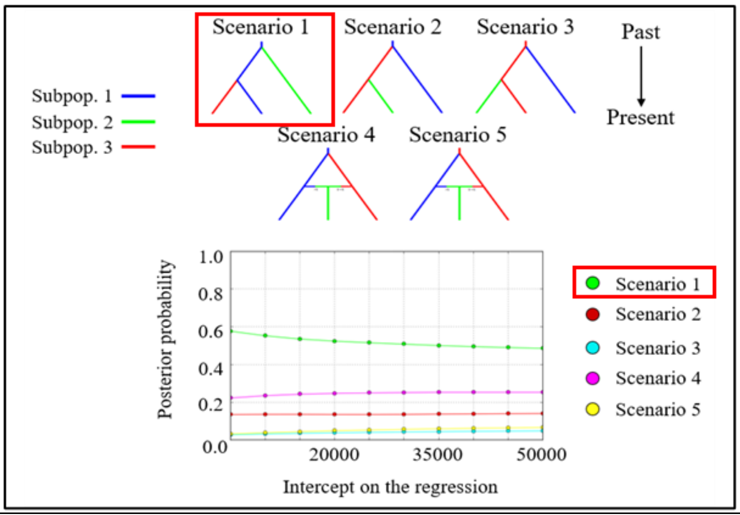
Subpopulation 2: Oribi Gorge (scarp forest)

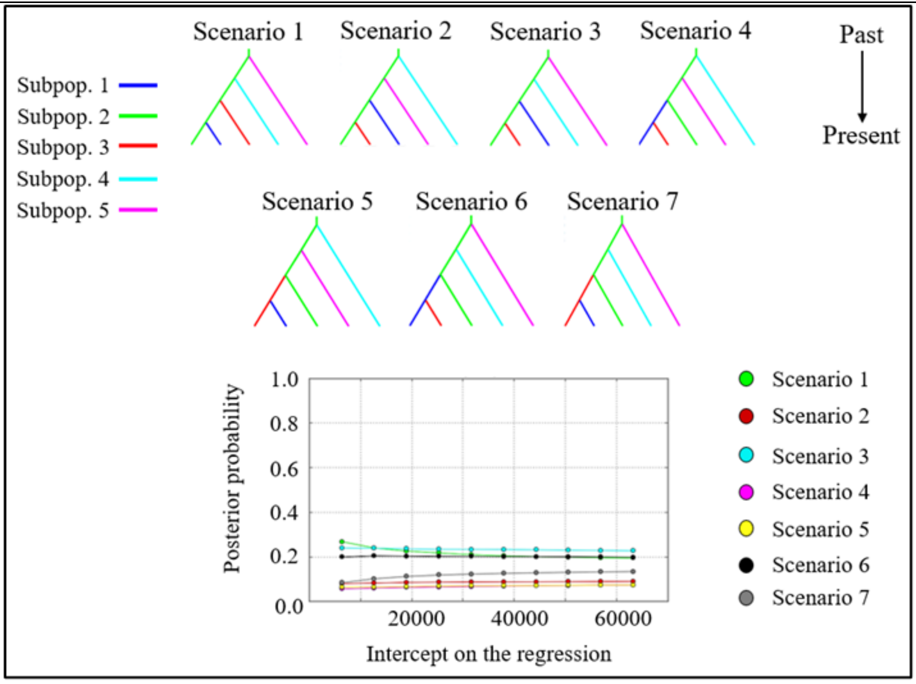
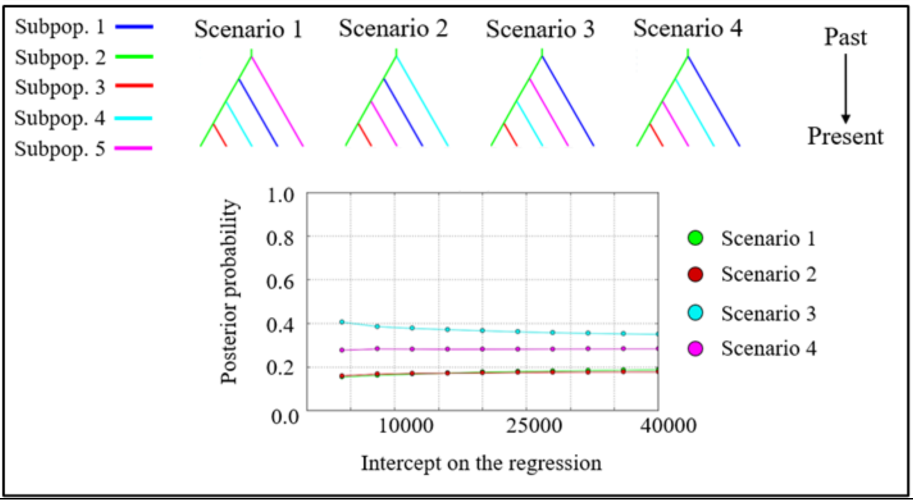
Subpopulation 3: Gomo (Afromontane forest)

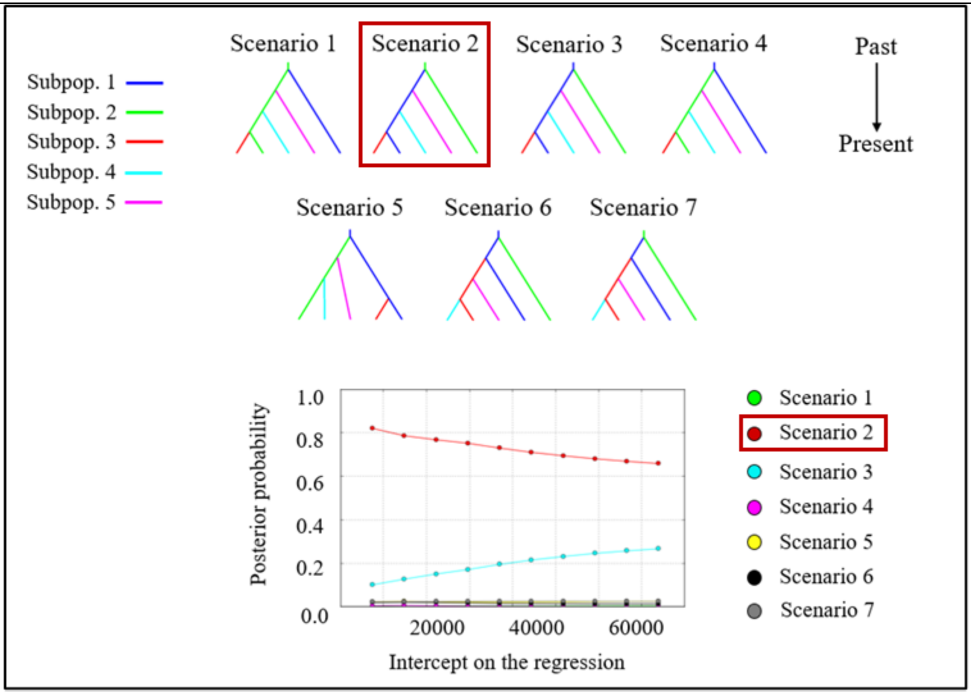


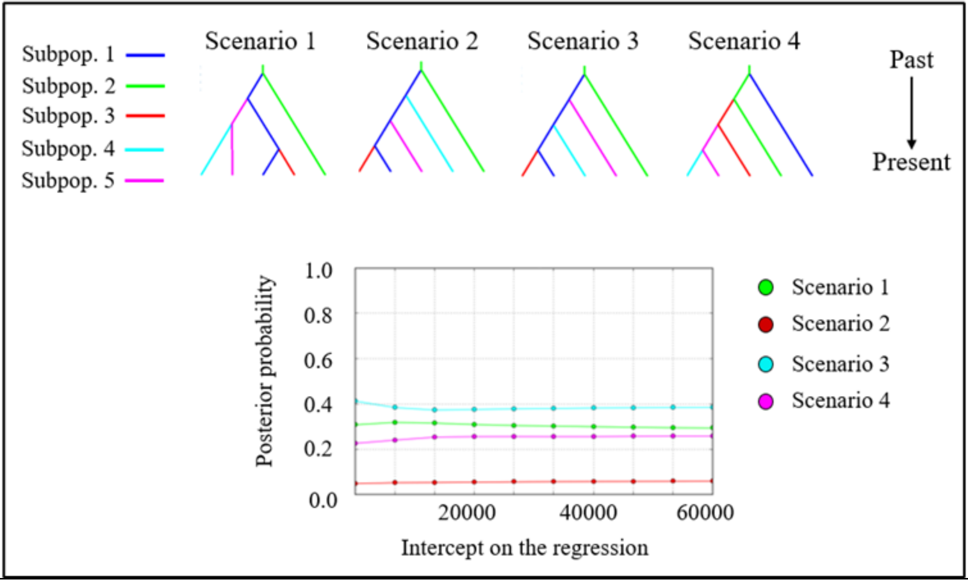


White-starred robin *Pogonocichla stellata* (continued)
BAPS mtDNA CR: Central group (4 subpopulations)
Subpopulation 1: Manubi (scarp forest)
Subpopulation 2: Baziya (Afromontane forest)
Subpopulation 3: Kubusi (Afromontane forest)
Subpopulation 4: Fort Fordyce (Afromontane forest)
 

White-starred robin *Pogonocichla stellata* (continued)
Scarp forests and Gomo (3 subpopulations)
Subpopulation 1: Oribi Gorge (scarp forest)
Subpopulation 2: Gomo (Afromontane forest)
Subpopulation 3: Manubi (scarp forest)
  

White-starred robin *Pogonocichla stellata* (continued)
mtDNA CR BAPS, and BARRIER subdivisions (5 subpopulations; series 1)
Subpopulation 1: Ngele (Afromontane)
Subpopulation 2: Oribi Gorge; Gomo (scarp, and Afromontane forests)
Subpopulation 3: Baziya; Manubi; Kubusi; Fort Fordyce
Subpopulation 4: Alexandria (southern Indian Ocean coastal belt forest)
Subpopulation 5: The Island (southern Indian Ocean coastal belt forest)
 

<table>
<tr><th>White-starred robin <i>Pogonocichla stellata</i> (continued)</th></tr>
<tr><td>mtDNA CR BAPS, and BARRIER subdivisions (5 subpopulations; series 2)</td></tr>
<tr><td>Subpopulation 1: Ngele (Afromontane)</td></tr>
<tr><td>Subpopulation 2: Oribi Gorge; Gomo (scarp, and Afromontane forests)</td></tr>
<tr><td>Subpopulation 3: Baziya; Manubi; Kubusi; Fort Fordyce</td></tr>
<tr><td>Subpopulation 4: Alexandria (southern Indian Ocean coastal belt forest)</td></tr>
<tr><td>Subpopulation 5: The Island (southern Indian Ocean coastal belt forest)</td></tr>
<tr><td>




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White-starred robin *Pogonocichla stellata* (continued)

mtDNA CR BAPS, and BARRIER subdivisions (5 subpopulations; series 3)

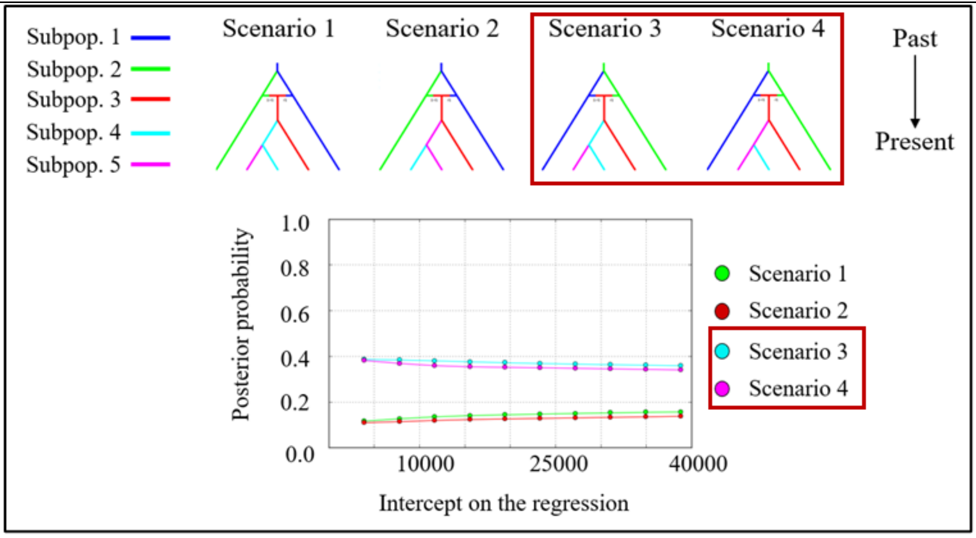
Subpopulation 1: Ngele (Afromontane)

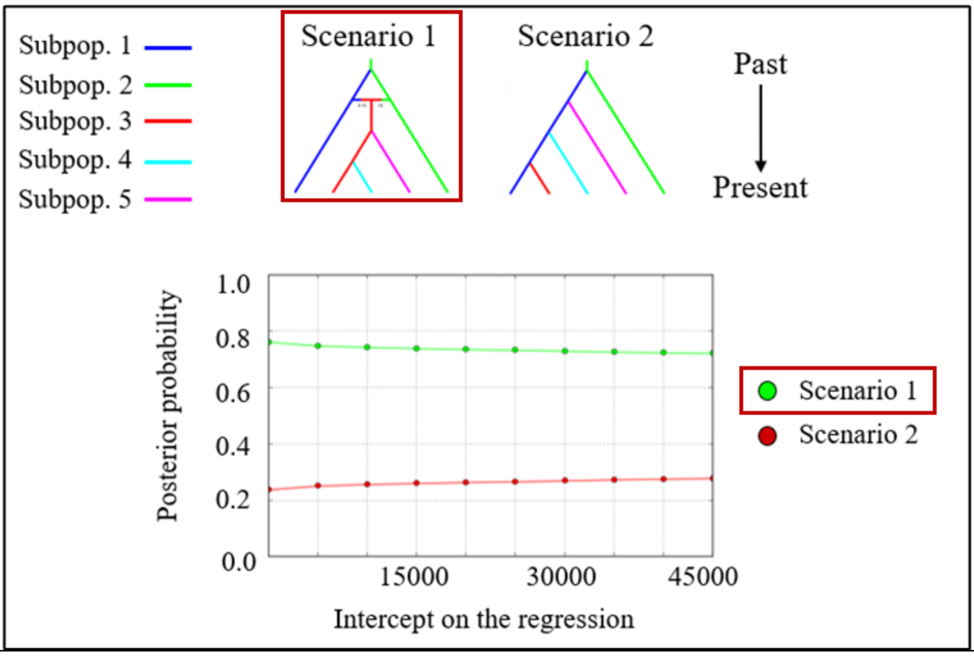
Subpopulation 2: Oribi Gorge; Gomo (scarp, and Afromontane forests)

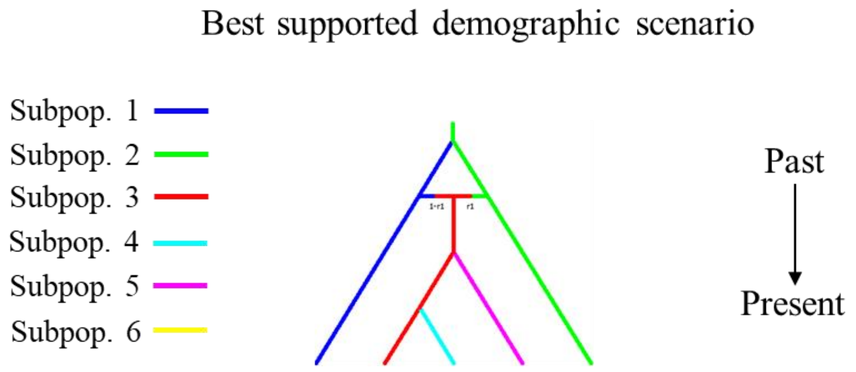
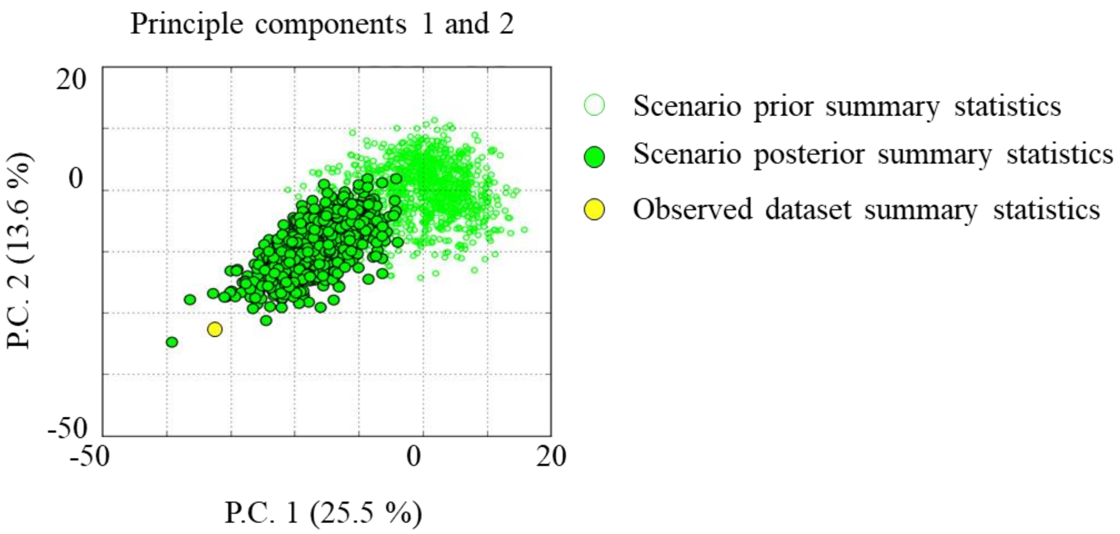
Subpopulation 3: Baziya; Manubi; Kubusi; Fort Fordyce

Subpopulation 4: Alexandria (southern Indian Ocean coastal belt forest)

Subpopulation 5: The Island (southern Indian Ocean coastal belt forest)





White-starred robin *Pogonocichla stellata* (continued)
mtDNA CR BAPS, and BARRIER subdivisions (5 subpopulations; series 3) **PCA of best supported demographic scenario model**
Subpopulation 1: Ngele (Afromontane)
Subpopulation 2: Oribi Gorge; Gomo (scarp, and Afromontane forests)
Subpopulation 3: Baziya; Manubi; Kubusi; Fort Fordyce
Subpopulation 4: Alexandria (southern Indian Ocean coastal belt forest)
Subpopulation 5: The Island (southern Indian Ocean coastal belt forest)
 

Appendix S4.10 Georeferenced species occurrence records (°S; °E) used to model the past and present species distributions of *B. capensis*, *P. ruficapilla*, and *P. stellata*.

B. capensis	***P. ruficapilla***	***P. stellata***
-29.926513; 29.849315	-29.921551; 29.853119	-29.817793; 29.817793
-29.927939; 29.83531	-29.928538; 29.841406	-29.926513; 29.849315
-29.974156; 29.738677	-29.954055; 29.815497	-29.927939; 29.83531
-29.979716; 29.67648	-29.955551; 29.816853	-29.974156; 29.738677
-30.003529; 30.08697	-29.97099; 29.73914	-29.979716; 29.67648
-30.016436; 29.633519	-29.978854; 29.676002	-30.003529; 30.08697
-30.121386; 29.57461	-29.97934; 29.726072	-30.016436; 29.633519
-30.145137; 29.555074	-29.979716; 29.67648	-30.121386; 29.57461
-30.149763; 29.5418	-30.016436; 29.633519	-30.145137; 29.555074
-30.152467; 29.776699	-30.017684; 29.630931	-30.149763; 29.5418
-30.173134; 29.738404	-30.121386; 29.57461	-30.152467; 29.776699
-30.296297; 29.63884	-30.145137; 29.555074	-30.173134; 29.738404
-30.310101; 29.862862	-30.148277; 29.544308	-30.296297; 29.63884
-30.334076; 29.54386	-30.152467; 29.776699	-30.310101; 29.862862
-30.35087; 29.50256	-30.153501; 29.786149	-30.334076; 29.54386
-30.359193; 29.847785	-30.153685; 29.777348	-30.359193; 29.847785
-30.45148; 29.639207	-30.173134; 29.738404	-30.434255; 30.326033
-30.455104; 29.608606	-30.180477; 29.674279	-30.43994; 30.273451
-30.460523; 30.237361	-30.186783; 29.658396	-30.45148; 29.639207
-30.475793; 29.651648	-30.237558; 29.59537	-30.452553; 30.267539
-30.48066; 29.74355	-30.24919; 29.614167	-30.455104; 29.608606
-30.48742; 29.42875	-30.263195; 30.476509	-30.460523; 30.237361
-30.487915; 29.736109	-30.264494; 30.467343	-30.475793; 29.651648
-30.496095; 29.720629	-30.269456; 30.477146	-30.487915; 29.736109
-30.50775; 29.65829	-30.296297; 29.63884	-30.496095; 29.720629
-30.50802; 29.67057	-30.310101; 29.862862	-30.517589; 29.716515
-30.517589; 29.716515	-30.314627; 29.871642	-30.526088; 29.685917
-30.5212; 29.71352	-30.334076; 29.54386	-30.52708; 29.662355
-30.526088; 29.685917	-30.352022; 29.842159	-30.527658; 29.699888
-30.52708; 29.662355	-30.45148; 29.639207	-30.627618; 29.663382
-30.52734; 29.66329	-30.455104; 29.608606	-30.632109; 29.653504
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-30.56858; 30.55909	-30.48723; 29.429027	-30.646787; 29.6874386
-30.584; 30.50312	-30.487915; 29.736109	-30.67487; 29.644458
-30.59642; 30.46835	-30.496981; 29.718961	-30.675655; 29.656869
-30.60117; 30.24884	-30.517589; 29.716515	-30.681225; 29.718301
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-30.627618; 29.663382	-30.523689; 29.683766	-30.691644; 30.268201
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-30.646787; 29.6874386	-30.540413; 30.288055	30.849477; 29.428107
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-30.65845; 30.50687	-30.578735; 30.512565	-30.969046; 29.379799
-30.67316; 30.32553	-30.579287; 30.514463	-30.98136; 29.362199
-30.67487; 29.644458	-30.582322; 30.516355	-31.009306; 29.344873
-30.675655; 29.656869	-30.58996; 30.52195	-31.021199; 30.167885
-30.67743; 28.34859	-30.609543; 30.5023	-31.28758; 29.946953
-30.681225; 29.718301	-30.610736; 30.501927	-31.28786; 29.939137
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-30.691644; 30.268201	-30.629227; 29.661217	-31.292301; 29.927257
-30.69673; 30.271	-30.632109; 29.653504	-31.305899; 29.813876
-30.714685; 30.271121	-30.634273; 29.636516	-31.330183; 28.665044
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Chapter 5: General conclusion

In this concluding chapter, I discuss the major findings of this thesis, which aimed to investigate the effects of species-landscape interactions, and species-climate relationships on the genetic diversity of forest-dependent birds in the Eastern Cape and KwaZulu-Natal provinces of South Africa, as well as to evaluate traditional survey approaches used to survey these forest bird communities. I further discuss how these findings can help inform future conservation efforts of forest-dependent birds in South Africa.

The key objectives and hypotheses of the previous chapters were:

i. To assess the effectiveness of point count and mist-netting ornithological field survey techniques representing South African forest bird community structures. Point counts were expected to outperform mist-netting, except for the detection of elusive mid- and understorey forest bird species. Mist-netting performance was further hypothesised to improve in lower canopy forests.

ii. To investigate the influence of the regional species-landscape interactions on the population trajectories of the four range-declining forest-dependent songbird species *B. capensis*, *C. dichroa*, *P. ruficapilla*, and *P. stellata* across the forests of the Eastern Cape and southern KwaZulu-Natal provinces of South Africa. It was hypothesised that landscape transformations of both forest and matrix habitats were driving the population declines of these bird species, particularly in *C. dichroa P. ruficapilla*, and *P. stellata*.

iii. To investigate the biogeographic histories, and forest climate refugia species-climate relationships for the forest-dependent birds species *B. capensis*, *P. ruficapilla*, and *P. stellata* within the study area of the Eastern Cape and southern KwaZulu-Natal. The hypotheses were that lowland scarp forests function as regional climate refugia for these species, and that broader habitat generalisation of *B. capensis* afforded this species greater palaeoclimatic resilience compared to the more forest specialised *P. ruficapilla* and *P. stellata*.

5.1 Key findings

5.1.1 Chapter 2

Fixed-radius point counts and mist-netting, two ornithological field survey techniques, were compared according to the ability of these techniques to detect forest-utilising bird species, and reliability represent bird community structures, with the forests of the Eastern Cape and south KwaZulu-Natal. Species detection by point counts outperformed that by mist-netting, detecting 79.2% vs 41.0% of forest-utilising bird species diversity, respectively. Additionally, point counts were better able to detect forest bird community structures than mist-netting, including elusive mid- and understorey foraging species that mist-netting is traditionally considered better able to detect. Mist-netting was adequate to detect bird species within these forest strata, but standard mist-nets (16 mm x 16 mm mesh) have limited applicability at detecting large-bodied birds. Point counts and mist-netting are frequently used in tandem to comprehensively survey bird communities within both Afromontane and Indian Ocean coastal belt forests, with the assumption that mist-netting improves the reliability of inferences made by point counts (Brown, 2006; Dulle et al., 2016; Engelen et al., 2017; Korfanta et al., 2012; Neuschulz et al., 2013; Newmark, 2009; Njuguna et al., 2014; Symes et al., 2000; Uwimbabazi et al., 2017). However, the time consuming, and laborious implementation of mist-netting was found to contribute only negligibly towards the species diversity observations made by point counts. Point counts therefore appear sufficient as stand-alone field survey technique to assess the bird community structures of these subtropical Afromontane and Indian Ocean coastal belt forests, although the effectiveness of this approach is dependent on the competency of the observer. Combined point count and mist-netting survey efforts were found to inadequately represent the following function groups: forest-edge foragers, woodland and grassland habitat generalists (both habitat generalist groups comprise ~63.6% regional forest-utilising bird species diversity), dispersive residents, large birds, Palaearctic migrants, and carnivores. The frequency to which avian functional groups interact with forests is poorly known, especially for dispersive, habitat generalists, and Palaearctic migrants. Nevertheless, care should be taken when inferring the status of avian functional groups within regional forests from the standard implementation of these two survey techniques. The findings of this chapter recommend the use of point counts alone to expedite future avifaunal community surveys within the South Africam forest sub-biomes. This chapter was further intended to contribute towards the global assessments point count and mist-netting surveys of forest bird communities (Blake & Loisille, 2001; Cavarzere et al., 2013; Derlindati & Caziani, 2005; Hatfield et al., 2018; Martin et al., 2010, 2017).

5.1.2 Chapter 3

In this chapter, a landscape genetics study was conducted to investigate the influence of the regional landscape on the contemporary population structures of four forest-dependent bird species *B. capensis*, *C. dichroa P. ruficapilla*, and *P. stellata* that have experienced range contractions across South Africa between 1997-2014 (Cooper et al., 2017). Contemporary population structures inferred from microsatellite data revealed that these four species have, to varying extents, historically been able to maintain functional connectivity among the fragmented forests habitats across the Eastern Cape and southern KwaZulu-Natal provinces of South Africa. The level of genetic differentiation between forests differed across the four species differed in unexpected ways. Surprisingly, *P. ruficapilla* forest populations were found to be almost panmictic throughout the study area, despite this species being perceived to be sedentary, with individuals thought to disperse only among local forest patches (Berruti, 1997; Craig & Hulley, 2019; Johnson & Maclean, 1994; Oatley, 2017). Similarly, *B. capensis* showed weak population structuring, despite this species also being assumed to be largely sedentary (Craig & Hulley, 2019; Johnson, 1997; Johnson & Maclean, 1994; Oatley, 2017), although this species can disperse reliably across open habitats (Dane & Bolton, 2017; Oschadleus & Ranwashe, 2017). By contrast, the two larger species, which are considered to be altitudinal migrants (Craig & Hulley, 2019; Johnson & Maclean, 1994; Oatley, 1982a, 1997a, 1997b; Oatley & Arnott, 1998), and should therefore be capable of effective dispersal over regional landscapes, showed the highest levels of population differentiation. This either suggests philopatry, whereby migrating individuals consistently return to forests they occupied in previous seasons, and so seasonal movements would not correspond to dispersal of genetic materials, or that regional populations are more sedentary than previously assumed. Philopatry is suspected in *P. stellata* (Dowsett, 1985; Oatley, 1982a), which likely does undergo altitudinal migrations within the study area (Craig & Hulley, 2019), while regional populations of *C. dichroa* is likely more sedentary than previously thought, as suggest by Wolmaran (2015).

Evaluation of the potential disruption between historic and contemporary geneflow, as well as the assessment of changes in effective population sizes within the most recent 100 generations of regional bird populations, showed that genetic responses of these species to anthropogenic activity did not closely correspond to reported range declines (Cooper et al., 2017). The forest generalist *B. capensis* underwent the lowest range contraction (-1.3%), yet showed the most substantial geneflow disruptions, alongside pronounced reductions in effective population size. More extensive range contractions reported for *P. ruficapilla* (-20.7%), and *P. stellata* (-23.0%) did not reflect the comparatively stable effective population sizes of either species, although geneflow restriction is evident in *P. stellata*. Only the South African endemic forest specialist *C. dichroa* showed both a decline in distribution (-19.5%), and effective population size, alongside geneflow disruption, and appears to be a species especially vulnerable to anthropogenic disturbance to regional forest ecosystems.

Landscape resistance modelling employed *a priori* evaluation of the associations between the genetic population structures of the four bird species, and regional landcover, freshwater systems, and topography. This approach allowed for insights into aspects of species relationships with the landscape which would otherwise have been difficult, or time-consuming to observe using field observations alone. All four species were shown to display associations between population structure and landscape features than could be explained by geographic distance alone. For *B. capensis*, *C. dichroa*, and *P. stellata* the extent and configuration of both forest and mesic/thicket landcover is important for maintaining connectivity between forests, and the loss and degradation of both habitats has likely contributed towards geneflow disruption in these three bird species, as well as populations declines in *B. capensis*, and *C. dichroa*. By comparison, *P. ruficapilla* appears to disperse stochastically across forests, but not seem reliant upon thicket vegetation to maintain forest connectivity. Freshwater systems appear important for dispersal of *P. stellata*, although this is likely true of both *B. capensis* and *C. dichroa*, which frequent riparian thicket (Johnson, 1997; Oatley, 1997a). Furthermore, *B. capensis* appears to be heavily influenced by landscape topography, alongside *P. ruficapilla*, and disperses along low-elevation regions of the eastern coastal plain of South Africa, relying upon ravines and gorges, sculpted by rivers, for dispersal into the mid-elevation Afromontane forests further inland.

The timing of effective population declines in *B. capensis* and *C. dichroa* implicates historic forest exploitation during the colonial era of South Africa as the main reason why these populations are taking strain, highlighting the risk of extinction debts culminating from past environmental disturbances. Fortunately, landscape resistance modelling highlighted the utility of implementing wildlife corridors along the most efficient dispersal routes though forest and coastal/mesic landcover, as well as prominent river systems/riparian corridors, as an effective conservation strategy to be employed in conjunction with preservation of core forest habitats, to ameliorate geneflow disruption within these species, and mitigate future population declines.

5.1.3 Chapter 4

This final research chapter was devoted towards investigating the biogeographic histories of *B. capensis*, *P. ruficapilla*, and *P. stellata*, and identifying prominent forest climate refugia within the Eastern Cape and southern KwaZulu-Natal provinces of South Africa. To assess the regional phylogeographic structures of these species, the complete mitochondrial control regions were sequenced, and used in conjunction with the microsatellite genotypes generated for these individuals from Chapter 3. As hypothesised, Bayesian skyline analysis of long-term fluctuations in female effective population size shows indirectly that these three species occurred in southeast South Africa prior to the last glacial maximum ~21 kya. Furthermore, this climate event did not adversely affect the regional populations of these bird species, despite the previously held notion that South African forests contracted substantially during this period in Earth's history (Eeley et al., 1999; Lawes et al., 2007a). Population expansion is evident in all three species in the advent of the current Holocene interglacial, and this, alongside palaeodistribution modelling, corroborates palaeoecological evidence that this climatic amelioration, particularly during the early-to-mid Holocene 11-3.6 kya, is associated with forest expansions across South Africa (Eeley et al., 1999; Lawes et al. 2007a; Miller et al., 2019, 2020; Scott et al., 2012). Postglacial population expansions have also been observed in sympatric forest-associated bat species (Moir et al., 2020a).

Palaeodistribution modelling, and forest demography analyses, affirmed the climate refugial role of scarp forests within southeast South Africa, especially for *B. capensis* and *P. stellata*. Scarp forests appeared to have been prominent near the coast in present day Pondoland, which shifted 130m below present-day sea levels (Compton, 2011; Cooper et al., 2018). This shift in sea levels likely has implications for the past establishment of coastal forests, which does not appear to have been considered in the palaeodistributions of KwaZulu-Natal forests presented by Eeley et al. (1999). Interestingly, however, forest demography analyses indicated that the mid-elevation Afromontane forests of the Amatole Mountains and Transkei escarpment may better serve as climate refugia for *P. ruficapilla*. The distribution of genetic diversity in all three species suggests that mid-elevation Afromontane forests across the study area were likely less diminished during cooler glacial periods than currently understood to have been the case. This is substantiated further by observations of genetic diversity endemic to these forests from more sedentary forest taxa (Barnes & Daniels, 2019; Kushata et al., 2020; Madisha et al., 2018).

High mitonuclear genetic diversity within *B. capensis* affirms the hypothesis that the broader habitat generalisation of this species likely conferred greater palaeoclimatic resilience, compared to the Afromontane forest-confined *P. ruficapilla* and *P. stellata*. Lower mitochondrial vs nuclear diversity in *P. stellata* corroborates higher female mortality within this species (Dowsett, 1985; Oatley, 1982a), whereas low nuclear vs mitochondrial genetic diversity in *P. ruficapilla* alludes to population recovery following a distant bottleneck event. The chapter provides indirect support for the long-term establishment of all three species within southeast South Africa, and highlights that palaeoclimatic resilience, and refugial potential of these southernmost Afrotropical forests is likely far higher than appreciated.

5.2 Study limitations and recommendation for future research

5.2.1 Chapter 2

The evaluation of ornithological field survey techniques in Chapter 2 was limited to only point counts and mist-netting. Although these two approaches are well utilised in forest bird community assessments, newer passive approaches, such as camera trapping and wildlife acoustic monitoring, are increasing being employed for forest community observations, including in South Africa (Ehlers-Smith et al., 2017, 2020; Maseko et al., 2017; Zungu et al., 2020). Fundamental limitations of point counts are that the effectiveness of this approach is dependent upon the observer competency, and human presence within forests may disturb avifaunal activity, introducing unwanted biases into avifaunal assessments. By comparison, mist-netting is a passive survey approach, but this technique is cumbersome, and the vegetation density within forests generally restricts the use of mist-netting; vegetation clearance for mist-netting transects are highly intrusive, and can disrupt the forest bird communities being monitored. Camera-trapping and wildlife acoustic monitoring circumvent the limitations of the previous two methods by being passive monitoring approaches which have greater flexibility of implementation throughout forest habitats (Leach et al., 2016; Navascués et al., 2017; Trolliet et al., 2014). Further evaluations of all availability ornithological survey techniques are therefore encouraged to optimise survey strategies of forest bird communities, both in South Africa, and globally.

Chapter 2 further highlights the importance of surveying transitional ecotones between forest-edge and surrounding matrix habitats, as these are of potentially high ecological importance for naturally fragmented forests that may rely on the surrounding landscape to maintain ecological integrity (Terraube et al., 2016). The lack of a comprehensive inventory of forest-utilising species in particular forests in South Africa made it difficult to determine the full composition of forest bird community structures sufficient for use in this study.

Finally, inter-regional, and inter-habitat variations in bird communities limit the inferences of point counts, and mist-netting performances to Afromontane (including scarp) and Indian Ocean coastal belt forests. Ideally, these evaluations should be conducted in more sites throughout both forest sub-biomes, as well as across different habitats of biomes outside of forests to improve the broader inferential power of these valuable ecological monitoring tools.

5.2.2 Chapter 3

The demographic responses of each species were assessed using generalised approximations of the mutation rates, and mechanisms for microsatellite loci of each species; the estimates used potentially may have been too conservative, given that smaller-bodied birds may have higher microsatellite mutation rates (Anmarkrud et al., 2008; Brohede et al., 2002; Fan & Guo, 2018). True timing of population declines within *B. capensis* and *C. dichroa* therefore may began closer in time to the present-day, although this still would not vindicate the impacts that historic forest exploitation had on these species, given the generational time-lag taken for population to manifest past environmental disturbances (Epps & Keyghobadi, 2015; Samarasin et al., 2017). This time-lag response may have precluded accurate detection of species response to contemporary anthropogenic interactions with forests. More inferentially powerful population genetic and demographic procedures are needed to detect recent population disturbances, and this potentially can be accomplished through integration of multiple field observation, and genetic datasets (Sirén et al., 2018).

The landscape-genetic association study conducted on the four focal species may be typical of similar small-bodied insectivorous birds, but does not represent the landscape associations of forest-dependent bird functional groups, as well as those of more sedentary taxa which could be far more sensitive to the quality of the landscape matrix (Eberle et al., 2017; Ehlers-Smith et al., 2017, 2020). Crucially, South African forest conservation is contingent upon up long-term viability floral diversity, which is far more sensitive to anthropogenically modified matrix conditions than birds (Botzat et al., 2015; Ivory et al., 2019). Therefore, it may be of greater imperative to improve understanding of landscape-species interactions in critical forest tree species to anticipate, and accommodate, future shifts in forest floral distributions. Anthropogenic climatically induced altitudinal shifts of Afromontane forest can already be detected (Los et al., 2019; Neate-Clegg et al., 2020), and this will invariably accelerate over the next century. Additionally, the relatively low sample sizes of each focal species within this study may have introduced type I error, precluding the detection of landscape associations critical for the forest connectivity and long viability of these populations (Winiarski et al., 2020). The low number of sample sites, too, may have limited adequate detection of matrix quality on the dispersal of these forest birds, which comprehensive sampling of forests across the study area may have otherwise revealed. Lastly, it may be worthwhile to conduct far broader landscape genetic associations across the wider distributions of these four bird species, as well as other forest-dependent species, especially across the species-rich forest mosaic landscapes of KwaZulu-Natal which likely support the most important forest climate refugia in South Africa (Lawes, et al., 2007a). This would be help to determine more comprehensively the impacts that anthropogenic landscape change has across the entire distribution of each forest-dependent species (Eberle et al., 2017).

5.2.3 Chapter 4

As with avian microsatellites, mutation rates of the mitochondrial control region are unknown among the focal birds of this study. Rate-variability of this hypervariable locus, alongside other genic mitochondrial loci, differs across avian taxa (Nguyen & Ho, 2016; Ruokonen & Kvist, 2002), and the lack of sufficiently recent passerine fossils (Mayr, 2013; Oliveros et al., 2019) precludes comprehensive calibrations on the mutation rates of this locus across avian groups (Ho & Duchêne, 2014; Lerner et al., 2011). The uncertainty surrounding the mutability of the mitochondrial control region unfortunately prevented accurate time estimates of long-term fluctuations in the effective population sizes within each focal species, and therefore made it difficult to determine appropriately certain aspects of response to past climate changes exhibited by each species. The combined uncertainty of rate-variability of both microsatellite loci and the mitochondrial control region could have potentially obfuscated inferences made from Approximate Bayesian Computations. Fortunately, the accommodation of multiple mutation rates for these genetic markers may have helped to mitigate uncertainties related to the timing of separate demographic events in the past (Cornuet et al., 2014). Thus, it is likely that forest divergence time estimates in Chapter 4 do accurately reflect the late-Holocene subsidence South African forests (Coetzer et al., 2020; Combrink et al., 2020; Finch & Hill, 2008; Miller et al., 2019, 2020; Neumann et al., 2010).

Despite the well-established ecological importance of scarp forests in the Pondoland centre of endemism in northeast Eastern Cape – Pondoland scarp forests (Mucina, 2018; Van Wyk & Smith, 2001; von Maltitz et al., 2003) – corroborated by the findings of Chapter 4 that these scarp forests served as important climate refugia (Lawes et al., 2007a), sampling of these forests was unfortunately low. This may have contributed towards under-estimating the refugial status of these forests. This study did not adequately explore the influence of the

Bedford Gap – an arid corridor between the Sundays River and Great Kei River in the southeast Eastern Cape which is a suspected dispersal barrier to forest-dependent taxa (Lawes, et al. 2007a). The Pondoland Plateau/Egossa Interval between Oribi Gorge and Port St Johns is another dispersal barrier to forest-dependent taxa (Busschau et al., 2020; Kushata et al., 2020; Moir et al., 2020a; Raphalo et al., 2021). Population differentiation in *Pogonocichla stellata* does appear to reflect the Bedford Gap, and it is likely that *P. ruficapilla* would be similarly affected by this biogeographic feature. Potentially, the Pondoland Plateau/Egossa Interval may contribute towards the mitochondrial population subdivisions observed in *B. capensis* and *P. stellata*.

The inferences on the regional biogeographic histories of these three species would greatly benefit from the extension of the scope of the study to include two areas. These are the forests further north in KwaZulu-Natal, many of which may be immensely important climate refugia for these forest-dependent birds (Lawes, et al. 2007a), as well as the Afromontane [southern Afrotemperate (Mucina, 2018; von Maltitz et al., 2003)] forest complex nestled between the Outeniqua and Tsitsikamma Mountains, and the south coast of the southwestern Cape. This forest complex also served as a climate refuge for forest dependent taxa (Daniels et al., 2017; Kushata et al., 2020; McDonald & Daniels, 2012).

Finally, this chapter serves as an invitation for future phylogeographic research exploring the colonisation mechanisms of South African forests from lower latitude Afrotropical forests. Divergence between the populations of these three species in South African and further north in Africa was not investigated, and may yield rich insights into forest history in South Africa. Afromontane (and Indian Ocean coastal belt) forest dynamics throughout the Pleistocene remain enigmatic (Ivory et al., 2012, 2018; Lézine et al., 2019; Peterson & Ammann, 2013; Singarayer & Burrough, 2015), and may have been greatly influenced by anthropogenically-induced fire region changes across swathes of the African continent <80 kya (Ivory et al., 2018). Colonisation of extant South African forest-dependent taxa from tropical Africa may have occurred earlier during the Pleistocene, utilising different dispersal mechanisms than those presented by Lawes et al. (2007a).

5.2.4 Species-genetic diversity correlation research

This thesis provides an opportunity to conducted research into correlations between species richness, community compositions, and neutral genetic diversity of focal taxa within the surveyed forests of the Eastern Cape. Species-genetic diversity correlation (SGDC) studies afford insights into how climatic factors, and resource availability may influence biodiversity patterns across emergent levels of biology – from the molecular to the regional landscape (Kahilainen et al., 2014; Lamy et al., 2013, 2017; Laroche et al., 2015). Additionally, SGDC studies can provide unique insights into how internal community factors – such as competitive exclusion, and mutual co-operation between species – impact the of genetic diversity of focal taxa. The influence of community ecology on genetic diversity patterns has largely been neglected in population genetic studies, but may be a major component shaping the genetic integrity and viability of many species' populations.

5.3 Insights into regionally intrinsic forest connectivity patterns of the focal songbird species

The genetic research components of this thesis have collectively been devoted towards understanding whether the focal forest-dependent bird species have been present in southeast South Africa since before the last glacial maximum. Further I have identified the climate refugial mechanisms which allowed these species to persist through palaeoclimatic shifts; how remote regional forest fragments came to be colonised by these species; and how these avian populations maintain functional connectivity between spatially isolated forest habitats. The utility of these insights, beyond appreciation of natural history, is to help inform South African conservation efforts on effective strategies to manage and preserve national forest resources (this is discussed in Section 5.4).

The overall results show that scarp forests are important climate refugia for forest-dependent birds in southeast South Africa, although Afromontane forests of the Transkei escarpment are important climate refugia too. Forest expansions during the early-mid Holocene likely facilitated the dispersal of many forest-dependent birds to colonise newly established forests in the region. Climate-induced forest contractions during the late Holocene subsequently fragmented forests across the study area, yet functional connectivity between forests could be maintained effectively either through high mobility, indiscriminate of extralimital matrix habitats, or through facultative dispersal through coastal/mesic thicket, and well-wooded riparian corridors. The establishment of these vegetation communities at lower elevations, along the east coastal plain of the Eastern Cape, and in ravines, gorges, and valleys created by freshwater systems, appears especially important for maintaining functional connectivity among certain forest-dependent bird species.

5.4 Contributions towards forest-dependent bird conservation in the Maputaland-Pondoland-Albany Biodiversity Hotspot

Population genetic, and phylogeographic studies undertaken in this thesis affirms the importance of conserving scarp forests in Pondoland, and along the Wild Coast of the Eastern Cape, as well as Afromontane forests of the Amatole Mountains, central Transkei escarpment, and KwaZulu-Natal midlands. These forests foster high genetic diversity, and collectively function as climate refugia for forest-dependent birds in south-east South Africa.

The four focal forest-dependent bird species utilised in this study appear to be in a state of population decline/population distress in south-east South Africa. This is attributable to a combination of: (i) historic, anthropogenically-driven loss, and degradation of both indigenous forests, as well as coastal/mesic thicket, especially within the Albany thicket biome; (ii) contemporary anthropogenic forest and thicket degradation; (iii) long-term climate-induced forest loss across southeast South Africa, a phenomenon likely exacerbated by anthropogenic activity.

Effective conservation efforts to mitigate future declines in these species, as well as other forest-dependent taxa, would be to carefully manage forest-utilisation practices to preserve and promote the ecological integrity of core forest habitats, especially for forests which function as important climate refugia; this recommendation further applies to conservation of the Albany thicket biome. Additionally, establishing wildlife conservation corridors designated along optimal dispersal routes through forest and coastal/mesic thicket habitats; alongside riparian corridors between the crucial forest habitats, may serve to mitigate geneflow disruption within forest-dependent taxa, and potentially provide opportunities for viable species responses to anthropogenic climate change. Altogether, these conservation efforts could help ameliorate past biodiversity losses culminating from extinctions debts, and promote species recovery from contemporary anthropogenic activity within South Africa.

5.5 Closing statement

This PhD thesis formed part of the Eastern Cape Forest Project, a research initiative spearheaded by Prof. Michael Cherry, and funded by the Foundational Biodiversity Information Programme (FBIP). This initiative aimed to survey the faunal species and genetic diversity within the poorly assessed forests of the Eastern Cape. Over the past five years, the Eastern Cape Forest Project has contributed towards zoological research into systematics, taxonomy, phylogenetics, phylogeography, population genetics, community ecology, landscape ecology, and human-forest relationships (Barnes & Daniels, 2019; Busschau et al., 2017, 2019, 2020; Cooper et al., 2017, 2020; Daniels, 2017; Daniels et al., 2017; Deng et al., 2020; Kushata et al., 2020; Leaver et al., 2019a, 2019b, 2020; Leaver & Cherry, 2020b, 2020a; Matamba et al., 2020; Moir et al., 2020a, 2020b, 2020c; Mulvaney & Cherry, 2020; Opperman et al., 2018; Raphalo et al., 2021). Research into the extraordinary forests of the Eastern Cape is ongoing, and is a vital component of South African zoological research which can help guide conservation efforts, and foster appreciation of our indigenous forests, and natural heritage.

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