Testing alternative stable state theory at Afromontane and Milkwood forest-fynbos ecotones

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Minor dissertation presented for the degree of Master of Science in Conservation Biology
In the Department of Biological Sciences
University of Cape Town

February 2023

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Walking through a milkwood forest, you grab a handful of the sandy, dark brown soil. You place it into a glass vial for your collection. Suddenly the sun streams through the canopy. You swiftly find yourself in a hot, uncomfortable thicket dominated by: Gymnosporia buxifolia, Euclea racemosa, Olea exasperata, Searsia lucida… But before finishing your thicket thoughts, you realise you are now in fynbos. Looking back, a forest regiment stands tall, holding a stark and strong boundary. Placing the vial on the ground, the disparity strikes you: the fynbos soil is sandy too, but the colour of very weak tea.

~ Thought ‘experiment’

Contents

Figures

Tables

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Abstract

Alternative stable state (ASS) and ‘sharpening switch’ theories provide a conceptual framework within which to understand abrupt ecotones between two (or more) contrasting ecosystem configurations. ASS theory is more suited for explaining ecosystems that exist within the same abiotic conditions. In the Greater Cape Region, forest-fynbos ecotones are often juxtaposed in landscapes where fire is the most important disturbance that maintains open canopy fire-prone fynbos and closed-canopy forests in fire refugia. Forest and fynbos ecotones are, however, additionally maintained by biotic feedbacks that result in edaphic differences between the contrasting ecosystems. Anthropogenic modifications to disturbance regimes alter the stability of forests and fynbos and may shift forest and fynbos into a degraded species-poor state. Conservation practitioners are concerned over perceived loss of forest habitat, and tree planting initiatives are common in parts of the Western Cape of South Africa. I hypothesised that diverse (e.g., Afromontane-and Milkwood-forests) forest and fynbos (e.g., different fynbos types) assemblages are ASS on the same nutrient-poor geology, and that biotic feedbacks with the soil result in edaphic discontinuities across the forest-fynbos ecotone. A sub-hypothesis is that anthropogenically altered disturbance regimes (e.g., timber harvesting, herbivory, fire management) have the potential to keep forest and fynbos in a transient state, so that a regime shift may be more likely. Soil samples (n=5 per vegetation type) were taken, and vegetation plot surveys conducted (n=3 per vegetation type) at seven study sites in Grootbos Private Nature Reserve (GPNR) and Platbos Forest Reserve (PFR) in South Africa. These data were collected in areas identified as forests, transitional vegetation, reforested areas (from conservation management), and the surrounding fynbos matrix.

Forests were floristically distinct from fynbos at all study sites (sharing max. = 5% spp. at one site). Most forests had similar soil texture to fynbos however, one site associated with an Afromontane Forest had a much higher silt: sand ratio (ca. 1: 0.9) than the fynbos matrix (ca. 1: 1.6), indicating differences in pedogenic processes in the forest compared to the surrounding fynbos. Forest soils had higher soil nutrient content (N, P, K, Mg, Ca, Fe, and loss-on-ignition) than fynbos soils. The edaphic nutrient differences across ecotones were not due to geological variability, indicating that edaphic differences are largely due to differences in nutrient cycling and vegetation-soil feedback mechanisms. The soil nutrient status of transitional vegetation was variable and not always intermediate between forest and fynbos. Historical imagery revealed that a complex history of disturbance has negatively affected all of the Southern Coastal/Milkwood Forests in the past, but that the forests have recovered in the absence of continued disturbances. Tree cover for most Southern Coastal/Milkwood forests has increased since 1938 (ca. 65% tree cover increase at one of the forests). Afromontane Forests have, however, not changed in extent or tree density since 1938. These findings add to the evidence that soil nutrient differences are sufficient to prevent a regime shift between forest and fynbos. The Southern Coastal/Milkwood Forests can be considered a fire-derived ASS, where edaphic differences reinforce the stability of forest and fynbos boundaries. Afromontane Forest-fynbos ecotones are perhaps better explained by a ‘sharpening switch’ model than ASS. Most existing transitional vegetation should not be considered a degraded vegetation state since transitional vegetation is a natural spatial and temporal gradation between fynbos and forest and also a natural buffer for forests against fire.

Keywords: alternative stable state, regime shift, bistability, multi-stability, hysteresis, tipping point, resilience, vulnerability, edaphic properties

Acknowledgements

From UCT, I would like to thank Prof. M. Timm Hoffman, without whom this study might not have been possible. I am also indebted to Prof. Michael D. Cramer for steering me in the right direction and being a most excellent supervisor. I am especially appreciative of his help and insights with wielding R and his ability to convey an understanding of the deeper underlying processes at play in natural systems. A shout out to my CB class of 2022/23, as we were always there for each other when times became stressful. I would like to thank the Grootbos Foundation and Plant Conservation Unit for funding this research. From the Grootbos Foundation, I would like to thank Sean Privett for his help identifying plants and help with vegetation survey design. Paula Strauss has also been an outstanding mentor who provided many insights, and who assisted with some of the data collection while I was based at Grootbos. From the Dyer Island Conservation Trust, I would like to thank Ralph Watson who gave up some of his time to help me with R. I would like to thank the FitzPatrick Institute of African Ornithology for the CB MSc course, and for the writing and presentation skills which proved rather useful during the writing of this thesis. Last, but not least, I would like to thank my parents and family for their support and motivation during my time as an MSc student.

"If I have seen further, it is by standing on the shoulders of giants."

~ Sir Isaac Newton

Abbreviations

ASS	Alternative stable states
CFR	Cape Floristic Region
GPNR	Grootbos Private Nature Reserve
PCoA	Principal Coordinate Analysis (also known as Metric Dimensional Scaling)
PFR	Platbos Forest Reserve
SCF	Southern Coastal Forest
SSMs	Sharpening Switch Models
WBFC	Walker Bay Fynbos Conservancy

Introduction

The theory of alternative stable states (ASS; Lewontin, 1969) explains how an abrupt turnover from one ecosystem configuration to a contrasting configuration can take place, despite both existing within the same abiotic environment (Lewontin 1969; Beisner et al. 2003; Mushet et al. 2019). ASS theory provides insight into the vulnerability of ecosystems to disturbances, as well as into its dynamics and early warning signals of approaching regime shifts (May 1977; Schröder et al. 2005). These ASS exist in a wide variety of open and closed ecosystems, although they are best understood within relatively closed systems. A common example of a closed system is an oligotrophic lake, which, having shifted to a eutrophic state, remains eutrophic even when nutrient inputs are reduced dramatically (Ardichvili et al. 2023). Understanding ASS is vital in the face of altered and rapidly changing disturbance regimes, particularly when a sudden regime shift between states can have profound impacts on ecosystem functioning (Heydenrych et al. 1999; Leverkus et al. 2021).

Identifying ASS is dependent on defining non-ASS systems in landscapes (Kéfi et al. 2016). Non-ASS ecotones may result from abiotic landscape heterogeneity, or larger scale climatic gradients. Within mountainous terrain, steep valleys, for example, are more protected from wind and solar irradiance and are often associated with higher water availability (Manders and Smith 1992), which can lead to non-ASS vegetation boundaries. Additionally, fire does not burn well downhill, which further separates the prevailing conditions of valleys from that of the surrounding vegetation (van Wagner 1988). It is no surprise that valleys often support vegetation (such as Afromontane Forests) that is very different from the vegetation of the surrounding landscape, even when the underlying geology is virtually identical (Luger and Moll 1993). This is especially important in the Cape Floristic Region (CFR), where fire refugia correlate with forest distributions (Luger and Moll 1993; Geldenhuys 1994).

ASS are separated by tipping points, or critical thresholds. Once a system has crossed a tipping point, it shifts into a new stable state. In contrast to the idea of ASS, sharpening switch models (SSMs) have been proposed to explain abrupt ecotone boundaries (Mount 1979; Wood and Bowman 2012). SSMs emphasise that the abiotic environment largely determines the distribution of vegetation patterns. Fire regimes that have remained relatively stable over long periods of time have been described by Wood and Bowman (2012) as a "one factor SSM", where fires sharpen ecotones that are, essentially, pre-determined by the abiotic environment of the vegetation. Vegetation types that are alternative stable states can undergo transitions, but the sharpening switch model of Mount (1979) suggests that vegetation patterns are largely controlled by the physical environment. Over long periods of time, forests that are an alternative stable state to fynbos may undergo state transitions if disturbance regimes are altered, but forests that fit more into the sharpening switch model cannot undergo state transitions with fynbos.

Geological discontinuities may also result in narrow non-ASS ecotones where the niches filled by certain vegetation types are bound to a specific geology (i.e., SSM applies). Indeed, many fynbos communities are named after the geology they are associated with (Mergili 2005; Adie et al. 2017; Dayaram et al. 2019). Additionally, old, climatically buffered, infertile landscapes (OCBILs) in the Cape that have been subjected to leaching over extended periods of time occur in a heterogeneous mixture with young, often-disturbed, fertile landscapes (YODFELs) in the CFR (Hopper 2009; Ingram 2010; Rundel et al. 2016). These geological boundaries in landscapes contribute to vegetation turnover.

Ecosystems (both ASS and non-ASS / SSMs) tend to maintain the niches that they occupy in both time and space, and their ability to resist change and competition translates to ecosystem resilience (MacPherson et al. 2019). While we may expect ecosystems to respond linearly to environmental change, long term biotic-abiotic feedbacks, which are pivotal to ecosystem resilience, often complicate the response of vegetation to environmental change (Fig. 1). For example, Camarero et al. (2021) predicted that high altitude alpine treelines become less predictable at the isotherm treeline, when it moves upslope due to mean annual temperature increases. Körner (2021) suggested that a better explanation is that biotic feedback, where trees enrich soil, results in sharp edaphic boundaries, and therefore a lag in tree recruitment along the new isotherm treeline (i.e., a non-linear response SSM example, creating the illusion of a non-responsive treeline; Fig. 1B). Studies have suggested that biotic feedbacks, over time, also reinforce the stability of closed-canopy forests within a matrix of open-canopy fynbos in the Cape Floristic Region (CFR) of South Africa (Coetsee et al. 2015; Cramer et al. 2019; MacPherson et al. 2019; Gillson et al. 2020). Therefore, the relatively long-term climatic stability in the CFR over the past ca. 5 million years (Cowling and Lombard 2002; Cowling et al. 2009) has likely entrenched resilience along some forest-fynbos ecotones in the CFR, which would mask the effects of shifting environmental gradients and disturbance regimes, unless near a threshold (Eby et al. 2016; Fig. 1C representing ASS ecosystems). Abrupt and seemingly non-responsive ecotones can only occur in ecosystems that respond non-linearly to change in the environment (Kéfi et al. 2016; Körner 2021).

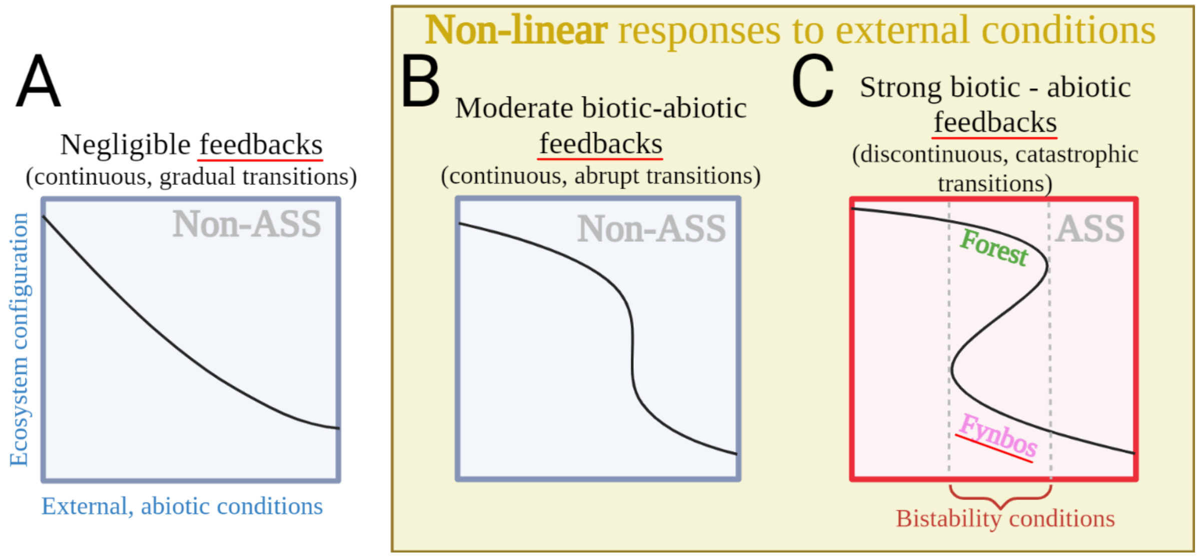

Figure 1: Three main ecosystem responses to external change are depicted (after Kéfi et al. 2016). The resilience of an ecosystem depends on the strength of biotic-abiotic feedback mechanisms. Imagine a gradual change in an external abiotic condition e.g., mean annual temperature, then A) without feedback loops, the ecosystem responds linearly to gradual changes in an external environmental condition. B) Positive biotic feedbacks would result in less predictable non-linear responses of ecosystems to abiotic gradients, so that an abrupt SSM ecotone between two ecosystems appears (e.g., alpine treelines), and C) in ecosystems with near identical physical environments, biotic feedback loops resulting in hysteresis allows for the existence of various ASS, so that it will take considerable effort to shift the ecosystem to an alternative state where the same abiotic conditions prevail.

Forest ecosystems are present in many Mediterranean type ecosystems (MTEs) around the world, including their limited distribution in the CFR of South Africa (Rundel et al. 2016). However, there was a time when forests dominated landscapes in the Cape. The Cretaceous Period (ca. 145.5 to 68.5 mya), sometimes referred to as the “Glasshouse world”, was a period of hotter and more humid climate worldwide (Bond and Scott 2010). Open canopy, ‘proto-fynbos’ vegetation in the Cape was limited to mountainous terrain, where seasonal aridity and oligotrophic quartzitic soils were found. During the Oligocene (ca. 33.9 to 23 mya), glacial conditions returned in Antarctica, and a period of cooling took place. However, fynbos was still mostly restricted to nutrient-poor mountainous terrain (Liu et al. 2009; Byrne et al. 2011). It was likely only during the Miocene (ca. 23 to 5.3 mya), when aridification continued, and landscapes became more fire prone, that forest distribution in the Cape changed (Rundel et al. 2016). The changed conditions after the early Miocene created novel lowland conditions, opening niches that fynbos vegetation could invade and diversify into, while forests retreated into fire refugia (Cowling et al. 2009; Verboom et al. 2015). Since the Miocene, the Cape region has enjoyed a long period of tectonic and climatic stability (i.e., since ca. 5.3 mya, a period which included the Pliocene, Pleistocene, and most of the current Holocene epoch), which has facilitated the evolution of exceptional floral diversity in the region today (Rundel et al. 2016).

Forest-savanna ecotones, as well as forest and fynbos distributions, are inadequately explained by climate-informed species distribution models (SDMs) (Staver et al. 2011; Magadzire et al. 2019). Fire and herbivory are the most important disturbances that maintain forest-savanna ASS (Dantas et al. 2016); and fire is also essential for maintaining forest-fynbos ecotones in the CFR. More recently, anthropogenic disturbances have also increased the level of herbivory as a disturbance in forest-fynbos systems (Kruger 1994), so that insights on the effect of herbivory on forest-savanna systems may now help to predict the effect that herbivory disturbance may have on forest-fynbos boundaries (Sankaran et al. 2008; Staver et al. 2011). Given the similarity between these two systems, it is no wonder that the ASS research of savanna-forest systems has sparked new questions regarding forest-fynbos ecotones too. Like studies on savanna-forest systems, fynbos-forest systems are also sometimes referred to as "bistable systems" albeit at smaller spatial scales (Hoffmann et al. 2012; Dantas et al. 2013; Veenendaal et al. 2015). Fire frequency and intensity has been used to explain how inflammable open-canopy ecosystems may shift towards fire resistant closed-canopy vegetation (Pausas 2015; Power 2018).

For landscapes with identified ASS, such as forest-savanna or forest-fynbos systems, hysteresis (where ecosystem dynamics depend on past processes) adds to the complexity, and unpredictability, of ecosystem responses to disturbance regimes (May 1977; Beisner et al. 2003; Kéfi et al. 2016). For ASS ecosystems, the threshold for a regime shift from ecosystem A (e.g., a forest) to B (e.g., fynbos) follows a different trajectory of change than a shift from state B to A (Beisner et al. 2003; Fig. 2). Allee effects are a simple explanatory tool for how multiple stable states can arise. Allee effects help us to explain the role of hysteresis by highlighting the difficulty of preventing and/or reversing population collapses (Wallach et al. 2010; Winter et al. 2020). Before an Allee effect, a system exists within a stable state, well adapted to the prevailing environmental conditions. However, vegetation cover reduction below a threshold can lead to an Allee effect where reduced recruitment in the affected ecosystem is observed. For example, forest fragmentation, or reduced fire return intervals in fynbos can lead to lowered recruitment success because of factors such as reduced reproductive success, limited genetic exchange, and increased plant stress. These negative effects then become self-reinforcing feedback loops beyond a certain point, so that Allee effects are observed as an ecosystem nears a critical threshold. Strong dissimilarities in soil nutrients between forest and fynbos (Richards et al. 1997; Bond 2010; Cramer et al. 2019), with narrow transitional zones means that short-term switches between forest and fynbos states following disturbance events is unlikely (i.e., indicating strong, stable ASS). The identification of ASS depends on the application of ecologically relevant timescales (Mushet et al. 2019), but this is tricky to determine. This timescale can be very short (e.g., coastal tidal systems), or involve long processes taking place over decades or even centuries. Anthropogenic disturbance regimes, that affect entire sections of forest (felling, herbivory and trampling by cattle) introduce spatial patches of disturbed vegetation that increases ecosystem heterogeneity, alters ecosystem responses to change, and may help facilitate ecosystem collapse in bi- or multi-stable systems (Zelnik et al. 2018). The temporal duration and spatial extent of disturbances is therefore essential to predicting dramatic ecosystem responses to change.

There is a need is to better understand the role of the "the leading edge" of forest expansion or contraction, i.e., the transient (less stable) transitional vegetation along forest-fynbos ecotones in the CFR (Cramer et al. 2019; Manders, 1990; Richards et al. 1997; Fig. 2). Transitional vegetation may show the first signs of a loss of resilience in ecosystems (Cramer et al. 2019; Manders, 1990; Richards et al. 1997), whether that be a shift between forest and fynbos, or to a disturbed ecosystem state. Transitional vegetation is subject to edge effects, which means that community structure and species composition is different from either forest or fynbos, so that generally, the transition is associated with high species diversity. Invasions or other degradations of this transitional vegetation may result in reduced species diversity (Frank 2021), and consequently reduced ecosystem resilience due to negative edge effects associated with established invasive plant stands. Relatively new disturbance regimes may keep the transitional vegetation of ecotones in a transient state (Fukami and Nakajima 2011). Some novel disturbances may have the ability to shift forest or fynbos ecosystems into a species-poor degraded state which may be considered as a third potentially stable state (Fig. 2). An example of disturbed states in the CFR is where alien invasive plants (such as *Acacia* spp., *Pinus* spp., and *Hakea* spp.) proliferate and become a monoculture, causing numerous negative effects, such as allelopathic chemical release, reduced habitat suitability, altered pollination and dispersal for native species, biodiversity loss, higher fire intensity, and negative impacts on hydrological cycles and nutrient dynamics (van Wilgen et al. 2022).

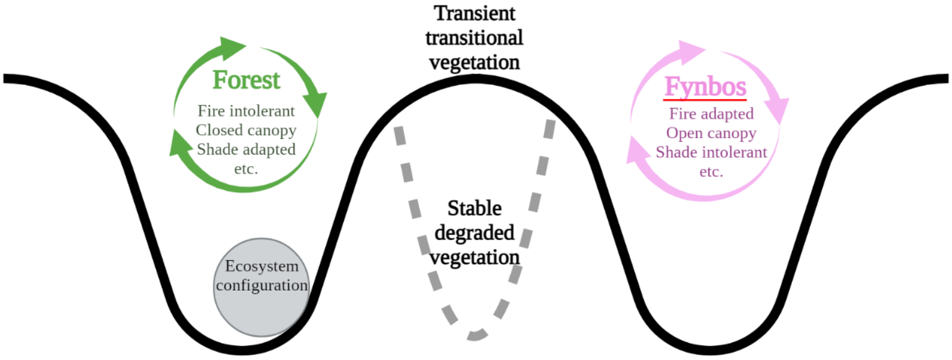

Figure 2: Ball in cup diagram representing forest and fynbos as two stable states, with a degraded vegetation state as a possible third stable state. Transitional vegetation is depicted as an unstable transient state between forest and fynbos. Critical slowing down (CSD) occurs as the community (green ball) approaches the edges of a basin of attraction. CSD translates to a reduction in the ability of an ecosystem to absorb the negative effects, i.e., reduced resilience as it approaches a threshold (Eby et al. 2016).

Currently, there is a lack of data showing forest distributions and tree cover density pre-dating 1938 in the Overberg, which is the date of the oldest aerial photographs available. 1938 is still in the relatively 'recent' past, but also represents a century within which vegetation would have faced unprecedented anthropogenic disturbance regimes. Apart from the natural heterogeneity inherent in CFR landscapes, anthropogenic modification and transformation modify and add layers of complexity to landscapes and the theoretical understanding of ASS (Kruger 1994; Karatayev and Baskett 2019). Historical imagery can reveal more about the effect of anthropogenic disturbance on forests over the past century, and to what extent the forests and surrounding vegetation was affected by these disturbances. Some researchers suggest that the forests of the CFR have shrunk in extent due to novel anthropogenic pressures. Conservationists today are concerned about the loss of fynbos and forest species due to threats such as the spread of alien invasive plants, agricultural transformations, developments, and changes in fire frequency (Luger and Moll 1993; Kruger 1994). Currently, several independent organisations within the Walker Bay Fynbos Conservancy (WBFC) have started expanding forests by planting trees in areas previously thought to have been occupied by forest. There is a need to better understand how different disturbance regimes may affect ecosystem trajectories and to translate ecological knowledge on ASS to aid decision making related to forest restoration initiatives.

Coetsee et al. (2015) argued that, if ASS exist, then fire is the main disturbance maintaining the contrasting vegetation states. The argument is that forest species are able to establish outside of the forest boundary when fire frequency is reduced in a given system. However, fire dynamics alone do not fully explain the co-occurrence of these two contrasting vegetation types (Pausas and Keeley 2009; Moncrieff et al. 2016). Fire regimes help shape ASS, but edaphic differences also maintain ecotone boundaries between forest and fynbos. The restricted distribution of closed-canopy forests in the CFR is associated with low soil nutrient status, especially P, in most types of fynbos vegetation (Brown et al. 1984; Witkowski and Mitchell 1987; Manders 1990; Wood and Bowman 2012; Coetsee et al. 2015;

Cramer et al. 2019). P, a non-renewable resource in the soil, is sometimes referred to as the "ultimate limiting nutrient" (Vitousek et al. 2010). Strong edaphic boundaries across forest-fynbos ecotones are a sign of strong biotic feedback between the vegetation and the soil, where forests are more dependent on and accumulate P in the topsoil, while fynbos plants have evolved to cope well in nutrient-poor environments that lack P (MacPherson et al. 2019). One of the methods some fynbos species have evolved to cope with limited P are cluster roots that improve the bioavailability of limited P (Allsopp et al. 2014; Lu et al. 2022). Differences in soil [P] is an example of how edaphic differences can play an important role in the establishment and maintenance of ASS.

Forests soils also contain higher levels of C, N, and K relative to fynbos soils, even where both are derived from the same geology (Manders 1990; Cramer et al. 2019). Organic matter build-up in forests also facilitates moisture accumulation in the topsoil, which is important because sandy soils under many Southern Coastal/Milkwood Forests lack a meaningful clay component (feldspar and micas) (Soderberg and Compton 2007) to help hold soil moisture. Organic matter therefore helps the forest to resist leaching and bind nutrients that can then concentrate in the topsoil (Jobbagy and Jackson 2000). Even if a fire manages to decimate part of a fire-intolerant forest, an established edaphic boundary should persist (Veenendaal et al. 2015; Power 2018). This is important where forests, like the surrounding fynbos matrix, occur on deep aeolian sandy soils that are inherently prone to leaching (Mucina and Rutherford 2006). In fynbos, organic matter does not accumulate in the soil as in forests, and recurring fires are likely to deplete soil nutrients through volatilisation (Witkowski and Mitchell 1987; Dantas et al. 2013; Pausas 2015). Even though nutrient loss occurs after a fire, N temporarily becomes more readily available in fynbos (Richards et al. 1997; Allsopp et al. 2014). Different disturbance regimes in forests as compared with fynbos affect plant biomass and life-history strategies (Dantas et al. 2016), so that plants associated with contrasting stable states are also associated with very different eco-physiological adaptations (Allsopp et al. 2014).

While past studies have evaluated edaphic differences between forest and fynbos, and related this to ASS, few have also included transitional thicket and historical aerial photographs in their analysis. This study fills this gap and addresses the need to better conserve landscapes using ecologically sound approaches. The first hypothesis is that forest and fynbos vegetation are not different successional stages of the same stable state / vegetation type. The first objective was to determine if forest and fynbos vegetation types at the various sites are floristically and structurally distinct from each other. The main hypothesis is that forest and fynbos are likely ASS if they occupy the same abiotic environment and are derived from the same nutrient-poor substrate. If this hypothesis is not rejected, then differences in soil substrate (e.g., soil nutrient content and organic matter) are likely derived from internal feedback mechanisms (the biotic environment). The second objective was to test for the possible presence of geological variation across forest-fynbos ecotones to determine if soils are derived from the same geological parent material (which if true, indicates that edaphic differences are more likely due to vegetation-soil feedback mechanisms). The third objective was to test whether biotic-soil feedback mechanisms are responsible for the alteration of edaphic properties by analysing essential elements for plants in topsoil.

The implications of this are that restoration of forest outside of edaphic boundaries will be more at risk of failure. Despite equally poor geology, the emergent edaphic cumulative nutrient status will aid in identifying the previous extent of forests. However, along narrow ecotones reforestation following fire events may upset the natural vegetation succession along ecotones. An additional hypothesis is that areas considered forest, and/or fynbos are currently in unstable/transient states, so that one, or both of these vegetation types are susceptible to a regime shift. This situation could merit active restoration and further prevention of degradation. The fourth objective was to use historical aerial imagery to show whether forest extent and transitional vegetation has changed in landscapes in the recent past, and whether novel disturbance regimes affect boundaries between open fynbos and lowland Southern

Coastal/Milkwood Forests differently to those with Afromontane Forests (often associated with mountainous terrains). Should novel disturbances (i.e., anything besides fire and mild herbivory) be detected, major disturbances causing the instability will need to be identified and managed. This study included ecotones along four Milkwood Forests, one Southern Coastal Forest, and two Afromontane forests. For each site, edaphic properties, vegetation surveys, and historical aerial photograph analyses were used to assess the relationships between forest, transitional vegetation, reforested areas, and fynbos.

Methods

Study sites

Six study sites were in the Grootbos Private Nature Reserve (GPNR, ca.2 550ha) and one in Platbos Forest Reserve (PFR ca.27ha; Fig. 3, and general locations of sites in Appendix; Table 4). Four of the sites were originally called Milkwood Scrub Forests, and the Southern Coastal Forest of PFR resembles Milkwood Forests. The remaining two sites included Afromontane Forests. Since two of the study sites are on Witvoetskloof, the site associated with a Milkwood Forest is referred to as “Witvoetskloof M”, while the site associated with an Afromontane Forest is called “Witvoetskloof A”. These study sites are not treated as replicates of each other because they each occur in distinct ecological settings.

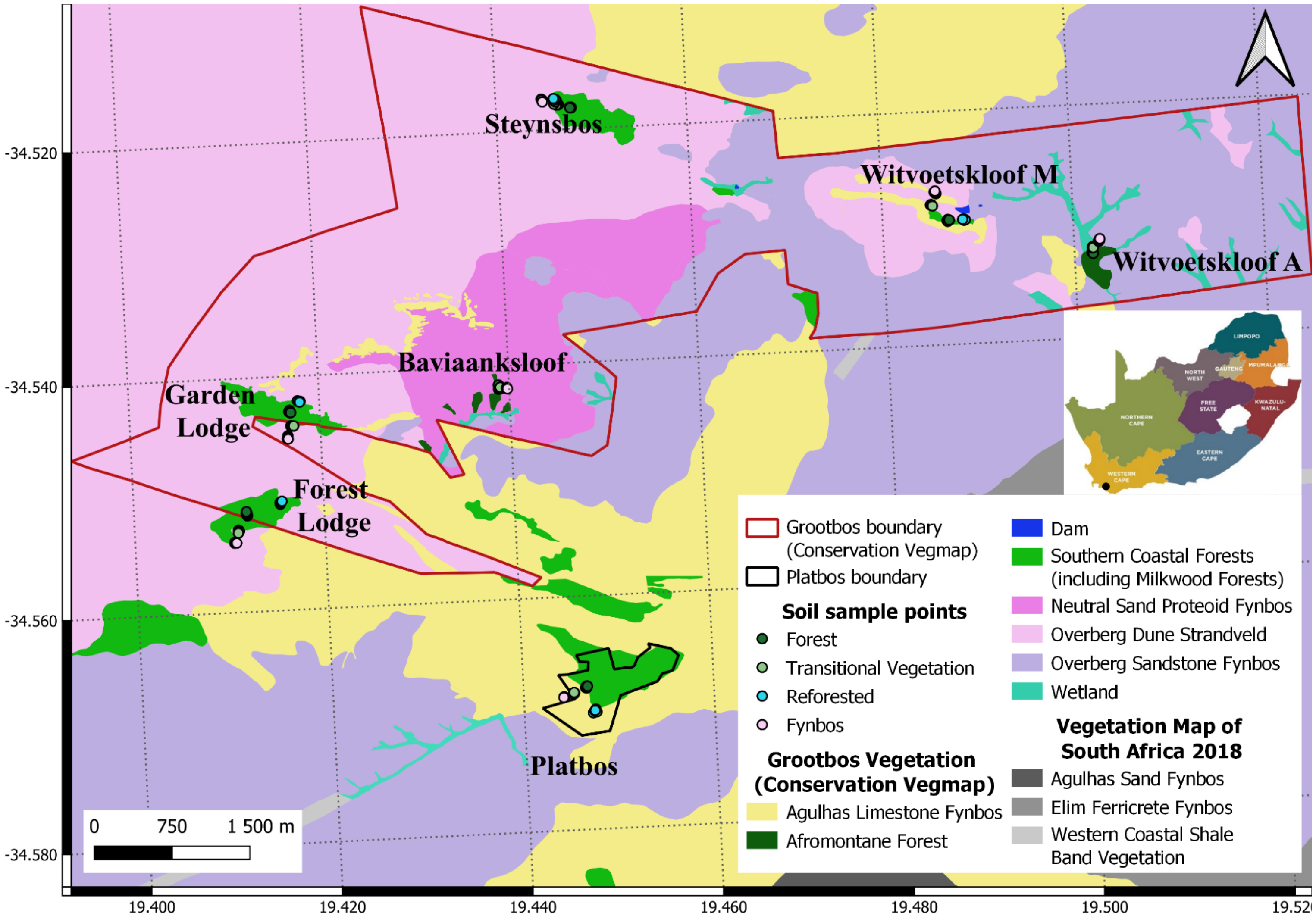

Figure 3: Map of the study area showing the vegetation units and different forest types and points where sampling took place. The Afromontane Forests included in the study are found at the Baviaanskloof and Witvoetskloof A sites. The rest of the sites are associated with Southern Coastal/Milkwood Forests. Vegetation types within the red Grootbos Private Nature Reserve (GPNR) boundary were defined by the Grootbos conservation team, and vegetation types mapped outside of the boundary are from the 2018 Vegetation Map of South Africa (Adie et al. 2017; Dayaram et al. 2019). Additional Vegmap 2018 vegetation types on the map, that are not associated with any of the study sites, are highlighted in grey in the map.

In total, eight vegetation types (including two transitional thicket types) were sampled, where Milkwood Forests form part of the broader Southern Coastal Forests vegetation type. Following Cowling et al. (1988), Mergili (2005) created a local vegetation classification for GPNR, which included a description of soil characteristics for each of the vegetation complexes identified. Transitional thicket (Table 2) has a unique species composition (distinct from subtropical thicket), although it also contains elements from both forest and fynbos, and is associated with a decreased incidence of fire, acting as a buffer to fire for forests (Mergili and Privett 2008). The Platbos forest is surrounded by fire breaks, with a wild olive thicket along the north-western edge of PFR.

Table 1: The eight vegetation types included in this study (after Mergili, 2005). Milkwood Scrub Forests are a type of Southern Coastal Forest, and reforested areas are not considered a vegetation type (rather reforested areas will form part of one of the vegetation types listed).

Forest vegetation types	**Transitional vegetation types**	**Fynbos vegetation types**
Afromontane Forest	Transitional Thicket	Dune Asteraceous Fynbos[1]
Southern Coastal Forest (including Milkwood Scrub Forests)	*Pteris dentata* Shrubland	Agulhas Limestone Fynbos
		Neutral Sand Proteoid Fynbos
		Overberg Sandstone Fynbos

[1] Mergili designated Dune Asteraceous Fynbos (adopted for this study), while vegetation maps for the area classify the same vegetation as Overberg Dune Strandveld.

Afromontane Forests in GPNR are associated with rocky, shallow, neutral to slightly acidic soils rich in K and Mg occurring in steep valleys (Fig. 4) protected from south easterly winds (Mergili and Privett 2008). The canopy is usually over 10 m tall, commonly dominated by *Rapanea melanophloeos*, and surrounded by transitional *Pteris dentata* Shrubland (Mergili and Privett 2008). In Baviaanskloof, the forest occurs in three parallel valleys associated with ephemeral streams. To the west, north and east of the valleys, the forest transitions abruptly into Neutral Sand Proteoid Fynbos (Fig. 4), with a wetland to the south. In contrast to Baviaanskloof, the Witvoetskloof forest has a permanent stream running through its centre and is also furthest from the coast even though it occurs at a low elevation (Table 1). Overberg Sandstone Fynbos occurs on the mountainous terrain surrounding the Afromontane Forest valley at Witvoetskloof (Fig. 4).

Sandy soils of Milkwood Forests are deep, likely derived from marine aeolian sand deposits, with slightly acidic to alkaline soils that are rich in Ca and K (Mergili and Privett 2008). The dominant tree species, *Sideroxylon inerme* (Fig. 5 and 6), can grow up to 6 m tall, with an understory typified by *Droguertia iners*, and the shrub *Myrsine africana* (Mergili and Privett 2008). *Chionanthus foveolatus,* and *Euclea racemosa* are also common tree species of the Southern Coastal Forest and Milkwood Forests. The Platbos forest has a heterogeneous species make-up, with *Apodytes dimidiata, Curtisia dentata*, *Ilex mitis*, and *Cunonia capensis* occurring in some places. The grasses *Ehrharta erecta*, *Melica racemosa* and *Festuca scabra* are also dominant in the understory. The southern boundaries of the Garden Lodge and Forest Lodge forests are bisected by the boundary of GPNR.

The Milkwood Forests of Garden Lodge, Forest Lodge, Steynsbos, and Witvoetskloof are also surrounded by transitional thicket, within a predominantly Dune Asteraceous Fynbos matrix, reaching about 2.5 m in height as depicted in Fig. 5. Agulhas Limestone Fynbos occurs along the northeast margin of the Steynsbos forest, the southern outcrop of the Witvoetskloof Milkwood Forest, the eastern boundary of the Forest Lodge forest, and in patches around the Garden Lodge forest. At Steynsbos, Dune Asteraceous Fynbos is only found along the west of the forest boundary (Mergili 2005), and the widest transitional thicket zone of all the Milkwood Forests also occurs along its western boundary (Mergili 2005). The southern and eastern forest boundaries of Steynsbos are surrounded by *Protea repens* Proteoid Fynbos (Mergili 2005), although this is not reflected in the vegetation map of GPNR (Fig. 3).

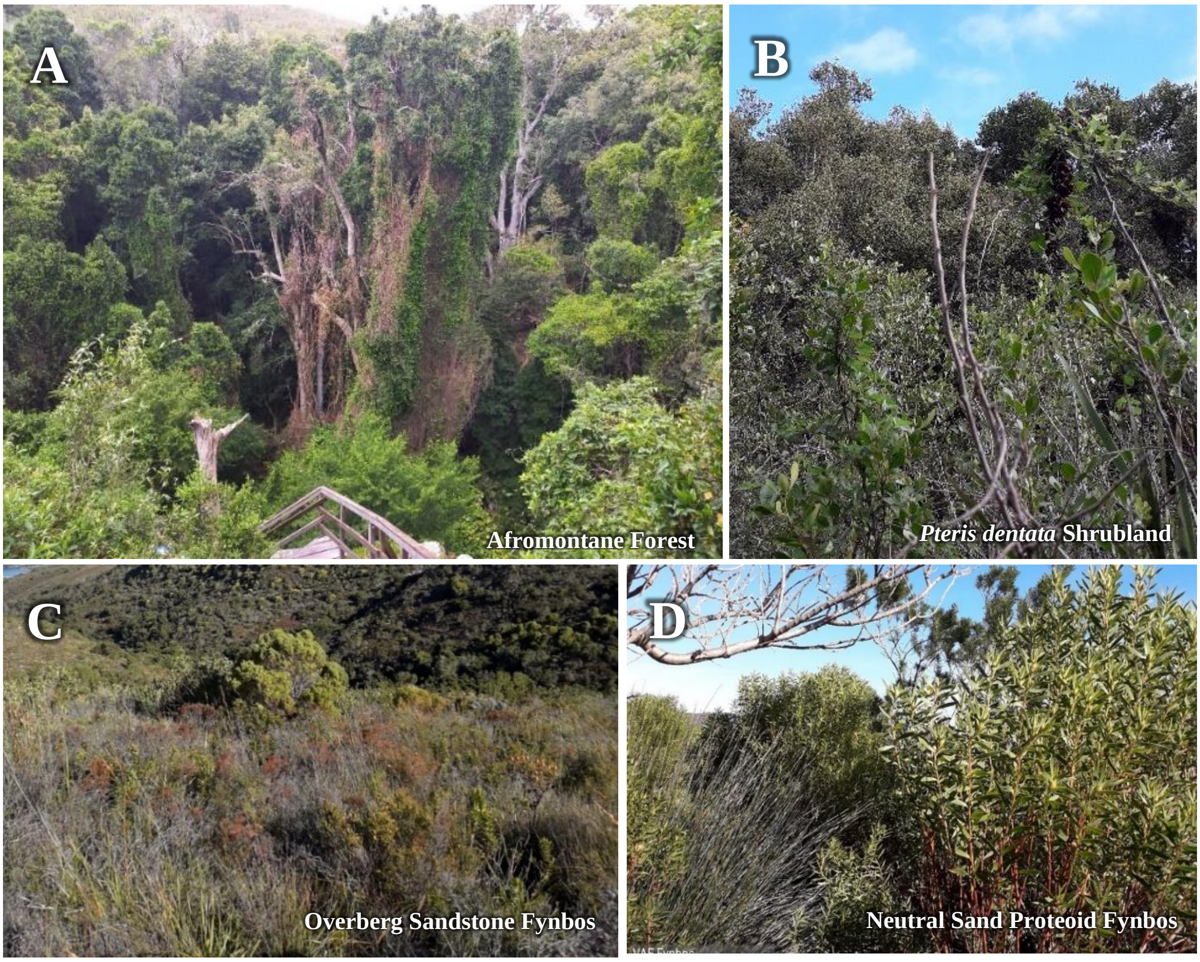

Figure 4: Vegetation types found at the two sites that are associated with A) Afromontane Forests. Both Baviaanskloof and Witvoetskloof A have transitional vegetation called B) *Pteris dentata* Shrubland. The fynbos matrix of Witvoetskloof A is C) Overberg Sandstone Fynbos, and at Baviaanskloof the fynbos is D) Neutral Sand Proteoid Fynbos.

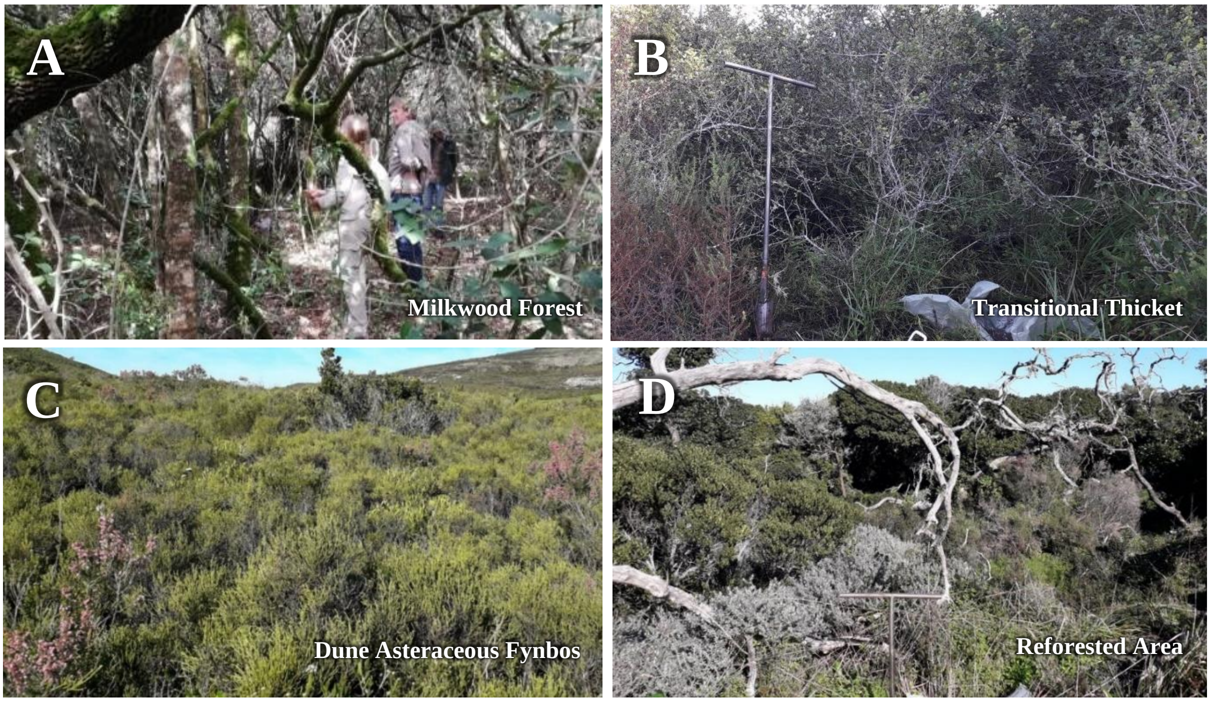

Figure 5: Vegetation types found at the four sites that are associated with A) Milkwood Scrub Forests. The forest transitional vegetation is called B) transitional thicket. The fynbos matrix is C) Dune Asteraceous Fynbos. Sites associated with Milkwood Forests all have designated D) reforested areas, where trees have actively been planted.

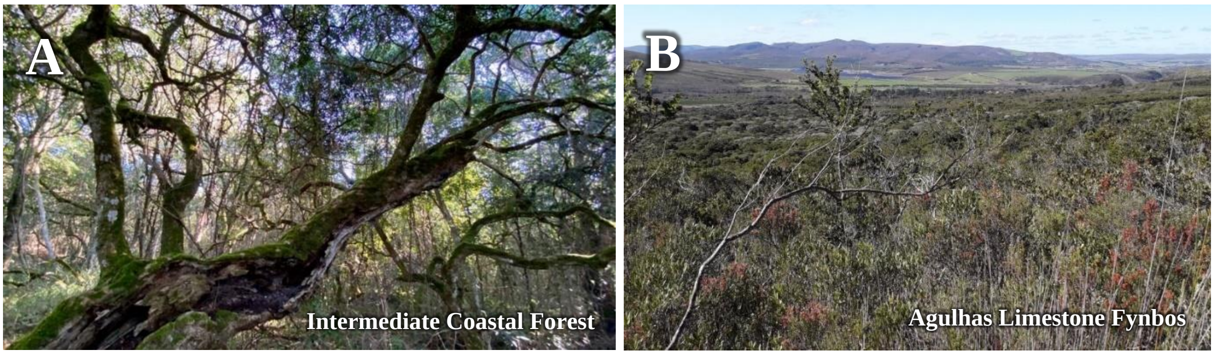

Figure 6: A) Southern Coastal Forest and surrounding B) Agulhas Limestone Fynbos at PFR (as assigned in the 2018 Vegmap of South Africa; *(Mucina and Rutherford 2006; Dayaram et al. 2019)*. The left image (A) shows an old milkwood tree in the foreground, with *Euclea racemosa* and *Chionanthus foveolatus* in the background.

Objective 1: Vegetation surveys and analysis

Rectangular relevé vegetation surveys (5 m x 10 m) were conducted in each vegetation type per site (n=3; following Goldblatt and Manning, 2000; Kent and Coker, 1992; Mergili, 2005). Each relevé plot was divided into 10 cells of 2 x 2.5 m, within which floristic composition was analysed (Fig. 7). Average percentage plant species cover, tree canopy cover, dead material, and bare ground for the relevés were recorded. A field herbarium was compiled for reference voucher specimens that were collected.

Figure 7: A vegetation survey in progress at Witvoetskloof, with help from the Grootbos Foundation conservation team.

The Shannon Wiener α-diversity index was calculated using the *diversity* function in the “vegan” library in R (Oksanen et al. 2022). Simpsons and Pielou’s evenness indices were also calculated. Post-Hoc Tukey HSD test letters were generated using the “emmeans” library (Lenth 2022). Sørensen’s dissimilarity coefficient, as well as nestedness and species turnover was used to determine beta diversity and to compare species turnover within and between the different vegetation types (or zones). This was done using the *beta.sample* function in the “betapart” library (Baselga et al. 2022).

The vegetation types of GPNR have been well studied and classified in the past (Mergili 2005), and therefore the k-means cluster analysis only serves to highlight similarities and differences between the vegetation surveys of this study. A Manhattan distance metric was used to create the dendrogram, using the *ward.D2* clustering method in R. The Manhattan distance metric is based on the distance of absolute values (Sunge et al. 2020), and is usually more robust than the Euclidean distance metric, minimising the effect of outliers in the vegetation data. The R libraries “NbClust”, “indicspecies”, “dendextend”, and “cluster” were used in this analysis (De Caceres and Legendre 2009; Charrad et al. 2014; Galili 2015; Maechler et al. 2022). The “indicspecies” library (De Caceres and Legendre 2009) was used to conduct an indicator species analysis, to identify diagnostic species within the number of clusters chosen (n=9, based on the vegetation types in the study, where Southern Coastal and Milkwood Scrub Forests were each treated as a separate vegetation type).

PCoA (synonymous with Metric Dimensional Scaling) analysis was chosen over Non-Metric Multidimensional Scaling (NMDS), as the NMDS analysis resulted in an extremely low stress value for most sites (Palmer 2013). To assess the importance of edaphic factors and their relationship to the four vegetation 'zones' (forest, fynbos, transitional vegetation, and reforested), a PCoA was conducted. This analysis compliments the k-means clustering analysis. The function *vegdist* in "vegan" was used to compute the standard Bray-Curtis dissimilarity index (Oksanen et al. 2022). The function *betadisper* of "vegan" was then used to test for homogeneity of variances and as a method of assessing β-diversity. The base R function *cmdscale* was used to calculate the PCoA. The *envfit* function from "vegan" was used to fit the environmental variables onto the PCoA plot. Only environmental variables that had a significant relationship ($p<0.05$) with the vegetation clusters were retained. The *scores* function was then used to create species and site scores from the ordination.

Objectives 2 and 3: Soil sampling and analysis

For each study site, a) forest, b) transitional vegetation, c) fynbos, and d) reforested vegetation (where it existed) were identified. The reforested vegetation was identified in areas that had previously been planted with trees. The two Afromontane Forests had never been part of tree planting initiatives, and therefore do not have reforested vegetation. Surface leaf litter was removed prior to sampling. An auger with a diameter of 0.07 m was used to sample the top 0.3 m of soil of the soil profile. Soil samples were placed on a plastic sheet, where they were homogenised before being placed into paper bags (Schumacher et al. 1990). Within each of the vegetation zones mentioned, five soil samples were taken within a 15 m x 15 m area (i.e., 20 samples per site with Milkwood Forests, and 15 samples per site with Afromontane Forests = 130 soil samples in total). Coordinates, and elevation were recorded for each sample.

Infiltration was measured adjacent to the locations from which soil samples were taken (n=5 per vegetation type at each site). The infiltration of water through the soil was measured using a single ring infiltrometer with a diameter of 12.8 cm (McCarthy 1934). The mineral soil was exposed by first removing any surface litter. The soil was then covered with a cloth, wetted with 150 ml water and the infiltrometer inserted into the soil to a depth of 3 cm and filled with 400 ml water replenished from a Mariotte's bottle (McCarthy 1934). The time taken for the volume in the Mariotte bottle to drop by 3 cm was recorded, and the infiltration rate calculated as in Herrick et al. (2005).

All soil samples were air-dried for 14 days prior to sieving through a 2 mm sieve. The sieved soil samples were homogenised using a soil quartering method, and then submitted to the Elsenburg Laboratory (Western Cape Department of Agriculture, Western Cape, South Africa) for nutrient analysis. The following variables were quantified per soil sample: pH (M KCl), extractable P (1% w/v of citric acid), K (1M NH_4OAc), Ca, Mg, Na, and extractable Fe. A portion of the dry sieved soil samples was analysed at the University of Cape Town to determine the organic matter content of the soil using the gravimetric loss-on-ignition (LOI) method. About 20 g of air-dried soil was placed into crucibles, weighed, and combusted at 450°C for three hours. The soils were weighed again to obtain the difference in soil sample weight before and after the LOI process. Mass spectrometer analyses were also conducted in the Department of Archaeometry at UCT. The soil samples were placed into small tin capsules (Elemental Microanalysis Ltd, Devon, UK) containing ca. 40 mg of the sieved, dry soils. The soils were fed into a Delta Plus XP isotope ratio mass spectrometer (Thermo Electron Corporation, Milan, Italy) and combusted in a Thermo Flash EA 1112 series elemental analyser. An IAEA

(International Atomic Energy Agency) standard, as well as two standards from UCT were used to calibrate the results.

Soil particle-size distributions were determined using a Malvern Master-Sizer 2000 (Malvern Instruments Ltd, Malvern, UK) on < 2 mm sieved soils. The samples were suspended in water and underwent ultrasonic dispersal to break up all natural soil aggregates. Soil samples were then moved to the laser diffractometer with a Malvern Hydro 2000G wet dispersion unit. Floating organic matter was removed by hand. The result shows the proportion of soil particles present of various particle-size ranges. These proportions were summarised into broad particle-size classes, namely clay, silt, and sand, using the Udden-Wentworth grain size chart (Terry and Goff 2014).

All statistical analyses were completed using R version 4.2.1, (2022). The "R-stats" library was used to run linear models (*lm* function) for each site. Vegetation type was the explanatory variable, and various soil characteristics (elevation, pH, and various soil nutrients) were the response variables. The results from the linear models were used to test for significant ($p < 0.05$) differences between vegetation types per site. A one-way ANOVA was run to test how the particle-size distributions varied by textural class (sand, silt, and clay), and vegetation 'zone' (forest, transitional vegetation, fynbos, and reforested). Post-Hoc Tukey HSD (honest significant difference) tests were run using the "emmeans" library (Lenth 2022). The "multcomp" and "multcompView" libraries were used to generate compact letter displays (*cld* function) indicating significant differences between vegetation types found at each study site (Hothorn et al. 2008; Graves et al. 2019).

Objectives 3 and 4: Analysis of historical aerial photographs

Historical aerial imagery was analysed to assess forest cover and distribution changes over the past century. Insight into past disturbances over the landscape, especially anthropogenic disturbances, is an important insight that can help to better understand forest-fynbos ecotones today. High resolution scans of historical aerial photographs for this study were obtained from the Chief Directorate: National Geospatial Information (CD: NGI), based at the General Surveys and Mapping section of the Department of Agriculture, Land Reform, and Rural Development in Mowbray, Cape Town (Appendix; Table 6). The earliest available historical imagery for GNPR and PFR was from 1938, then 1961, 1973, 1980, 1989, 1998, 2005, and 2022. Current high resolution satellite imagery was obtained from the ArcGIS Map Service (Redlands, California), using the "World Imagery" Layer (from Maxar Technologies Inc. in Westminster, Colorado, with 0.5 m resolution), which ESRI updated on the 22nd of September 2022.

Analysis of the historical imagery obtained was completed using Arc GIS Pro version 2.9.0 (Redlands, California). Each image was georeferenced using the 'spline' method requiring > 10 control points. The historical images were clipped using rectangular 'site polygons' ($n = 7$, one per study site) with the "Extract by Mask" geoprocessing tool to represent an area within which to conduct the cover analysis at each study site. The clipped images were then classified into various land cover classes, using the "Create Feature Class" geoprocessing tool. The classes defined were bare ground, the built environment, cultivated land, "unknown trees" (which are likely invasive alien plant species, or planted trees), wetlands, dam areas, cultivated land, fire breaks, Agulhas Limestone Fynbos, Dune Asteraceous Fynbos, Neutral Sand Proteoid Fynbos, Overberg Sandstone Fynbos, transitional thicket, scattered trees (<50% tree cover estimate), open forest (50-80% tree cover estimate), and closed forest (>80% tree cover estimate). Once classified, the "Calculate Geometry Attributes" tool was used to calculate the geodesic area (in square meters) of each cover class per site.

Within each 'site polygon', a series of points were scattered, with a minimum distance of 60 m between points giving a uniform density of points. Random points that were created within bare ground, built environment, cultivated, and dam area categories were consequently selected and deleted. This means that points were left scattered within land cover classes including forests, transitional vegetation, wetlands, fynbos, and unknown trees present within the photos. The points were then buffered with a 20 m radius buffer and clipped to the extent of the ‘site polygons’. The attribute table was then used to delete all incomplete buffers. Each buffer was assigned a visual assessment of percentage tree cover across eight historical aerial photograph timestamps. A predefined aid (Anderson 2008) for visually assessing canopy was used to improve the accuracy of the tree cover assessment (Jennings et al. 1999). A Mann-Kendall test using the “Kendall” library and *MannKendall* function in R was run to assess tree cover trends for each buffer (McLeod 2022). This analysis was then used to label polygons that are associated with significant increases or decreases in tree cover over time since 1938 (Appendix; Fig. 30 and 31).

Results

Objective 1: Vegetation characteristics and differences

Fynbos was associated with higher species turnover between plots than was the case in forest plots (Fig. 8). Within each vegetation type, species turnover between plots (as opposed to nestedness) was the greatest contributor towards the Sørensen beta diversity. Transitional, and reforested plots generally had relatively high turnover between plots, similar to fynbos (Fig. 8). Reforested sites had a similar species turnover to the transitional vegetation, and species diversity was similar to transitional vegetation. Fynbos plots had the highest plant species diversity of all vegetation types, although transitional vegetation and reforested areas also had high plant diversity (Fig. 9). For example, at Garden Lodge the transitional thicket was found to have a greater species diversity (41 spp. recorded) than the adjacent fynbos vegetation plots (31 spp.). The transitional vegetation between forest and fynbos supports plant species from both forest and fynbos in addition to several unique species. The *Pteris dentata* Shrubland of Baviaanskloof shared 27% of its plant species with the forest and 14% with fynbos, and the transition along the Witvoetskloof Afromontane Forest transitional vegetation shared even fewer species with both forest (9%) and fynbos (1%). Garden Lodge was the only exception; the reforested area had a floral composition similar to the forest, sharing 52% of species recoded there with the forest, while only 13% of species were shared with the adjacent fynbos plots. Reforested areas at other sites shared fewer species with forest sites. At Forest Lodge, 26% of the spp. recorded in the reforested area were shared with the forest and 21% with fynbos plots. At Steynsbos the reforested site shared over a third of species with fynbos, and only approximately a sixth with the forest.

Species turnover between forest and fynbos were very high (Appendix; Table 5). Fynbos vegetation types were all floristically distinct from the forest plots, sharing almost no plant families (Fig. 10). Only 5% of all species at Baviaanskloof were shared between forest and fynbos, which is the highest percentage overlap of all seven sites, and the Witvoetskloof Afromontane Forest shared no plant species with the surrounding fynbos plots (Appendix: Table 5).

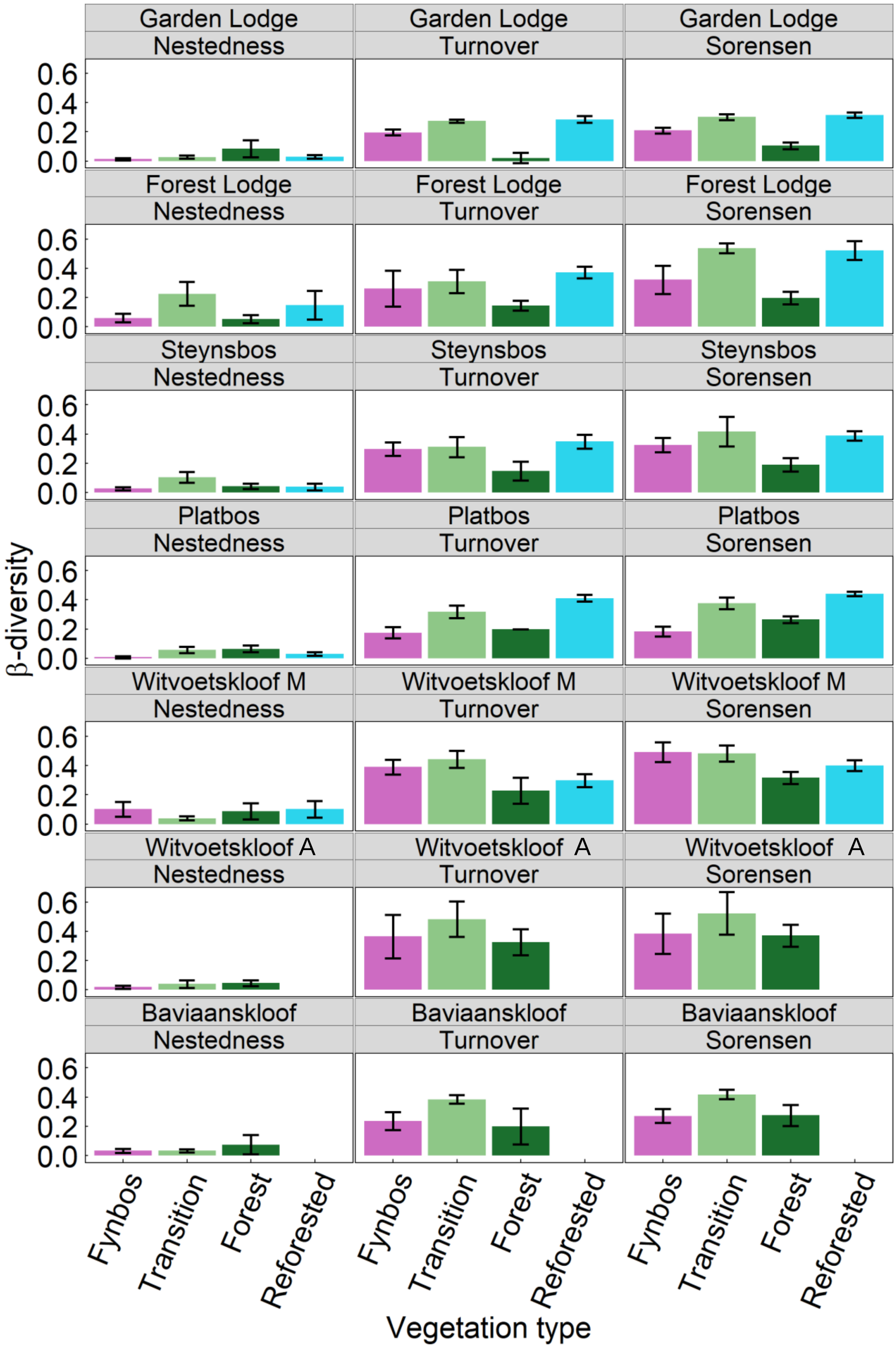

Figure 8: Beta diversity between the three vegetation surveys within each vegetation type. The Sørensen coefficient (right plots) is shown alongside its components, species nestedness (left plots) and species turnover (middle plots). Standard deviation bars are plotted over the average bar plot values. The top five plots refer to sites that are associated with Southern Coatal/Milkwood Forests, while Witvoetskloof A and Baviaanskloof are associated with Afromontane Forests.

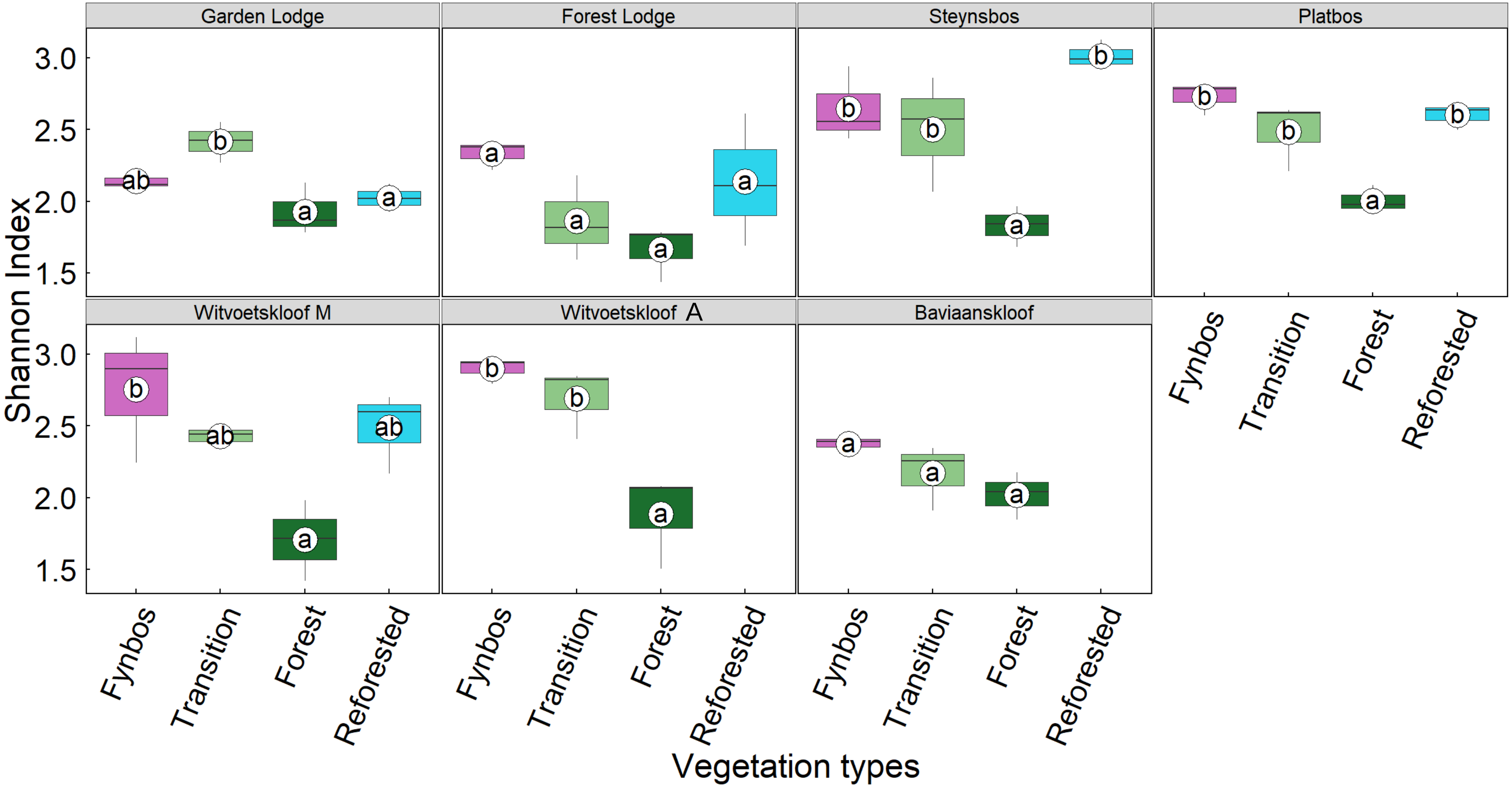

Figure 9: Plant species α diversity (Shannon-Wiener diversity index) for the seven study sites. Broad vegetation categories are depicted along the x-axis. The boxplots represent the first quartile (lowest line), median (middle line), and third quartile (highest line) and the "whiskers" represent the interquartile range times 1.5. Outliers in the data are shown as points outside of the boxes. The white circles on the plot represent means, and the letters show if there are significant differences (based on ANOVA with Post-Hoc Tukey tests) between the means of the vegetation types for each site (each site analysed separately).

A hierarchical cluster analysis, using the best performing "Ward" method and Manhattan distance (agglomerative coefficient = 0.90) was used to differentiate the clusters of vegetation present from the vegetation surveys (Fig. 11). Since the vegetation types were previously described based on floristic and environmental data (Mergili 2005), the number of clusters (n=9) represented reflect the number of vegetation types (excluding the reforested category, as it represents areas where trees have been planted). The results from the hierarchical cluster analysis compliments the results from the PCoA above. Both cluster and PCoA analyses revealed that the two sites associated with Afromontane Forests are distinct from the Southern Coastal/Milkwood Forests. Agulhas Limestone Fynbos at Platbos Forest Reserve (PFR) forms part of the cluster representing Dune Asteraceous Fynbos. Transitional Thicket and reforested areas do not form clear clusters apart from the forests, which is again very similar to the PCoA result (Figs. 10 and 11).

Each cluster identified was associated with specific plant species. In reality, some of the species in Table 2 (associated mostly with the two sites with Afromontane Forests) are also found in Southern Coastal Forests (pers. obs.), and this analysis could be made more representative of vegetation types with increased sampling effort. The trees *Curtisia dentata* and *Ocotea bullata* are also found in the Afromontane Forests and are absent from Southern Coastal/Milkwood Forests. The second cluster represents Neutral Sand Proteoid Fynbos and the Baviaanskloof *P. dentata* shrubland, and the third cluster represents only Overberg Sandstone Fynbos, with several species that were only associated with this vegetation type (Table 2). The fourth cluster included only transitional vegetation types, including *P. dentata* Shrubland of Witvoetskloof, Transitional Thickets and some reforested areas. No species were very strongly associated with this cluster.

Transitional vegetation is not as easily defined as other vegetation types (Fig. 11). All four fynbos vegetation types are, however, clearly different from forests. Where transitional and reforested areas were included in clusters containing Southern Coastal/Milkwood Forests too, they are likely a successional stage of forest recovery. Clusters 4 and 5, however, are associated only with transitional vegetation and reforested areas, and are distinct from forest vegetation. Few species were consistently associated with clusters four and five because of the higher variability in species composition. *Olea exasperata* and *Stachys aethiopica* are highly likely to be found in cluster five but are not indicator species for the cluster (low specificity). The sixth cluster represents the forests of Platbos, Forest Lodge, and Steynsbos, as well as from transitional thickets and reforested areas. Graminoid species *Ehrharta erecta* and *Festuca scabra* are forest understory grasses that were highly associated with this cluster. This cluster was also associated with milkwood (*Sideroxylon inerme*) and pock ironwood trees (*Chionanthus foveolatus*), the two most abundant tree species in Milkwood Scrub Forests. Cluster seven also represents forests, transition, and reforested vegetation, and is associated with the forest understory species *Droguetia iners* (association statistic = 0.90) and *Myrsine africana* (0.60), which corresponds to forest patches sampled where tree cover is discontinuous. Clusters eight and nine represent only Dune Asteraceous Fynbos and the Agulhas Limestone Fynbos (at Platbos). It is likely that the fynbos of Platbos, called Agulhas Limestone Fynbos in the vegetation map of South Africa is actually also Dune Asteraceous Fynbos.

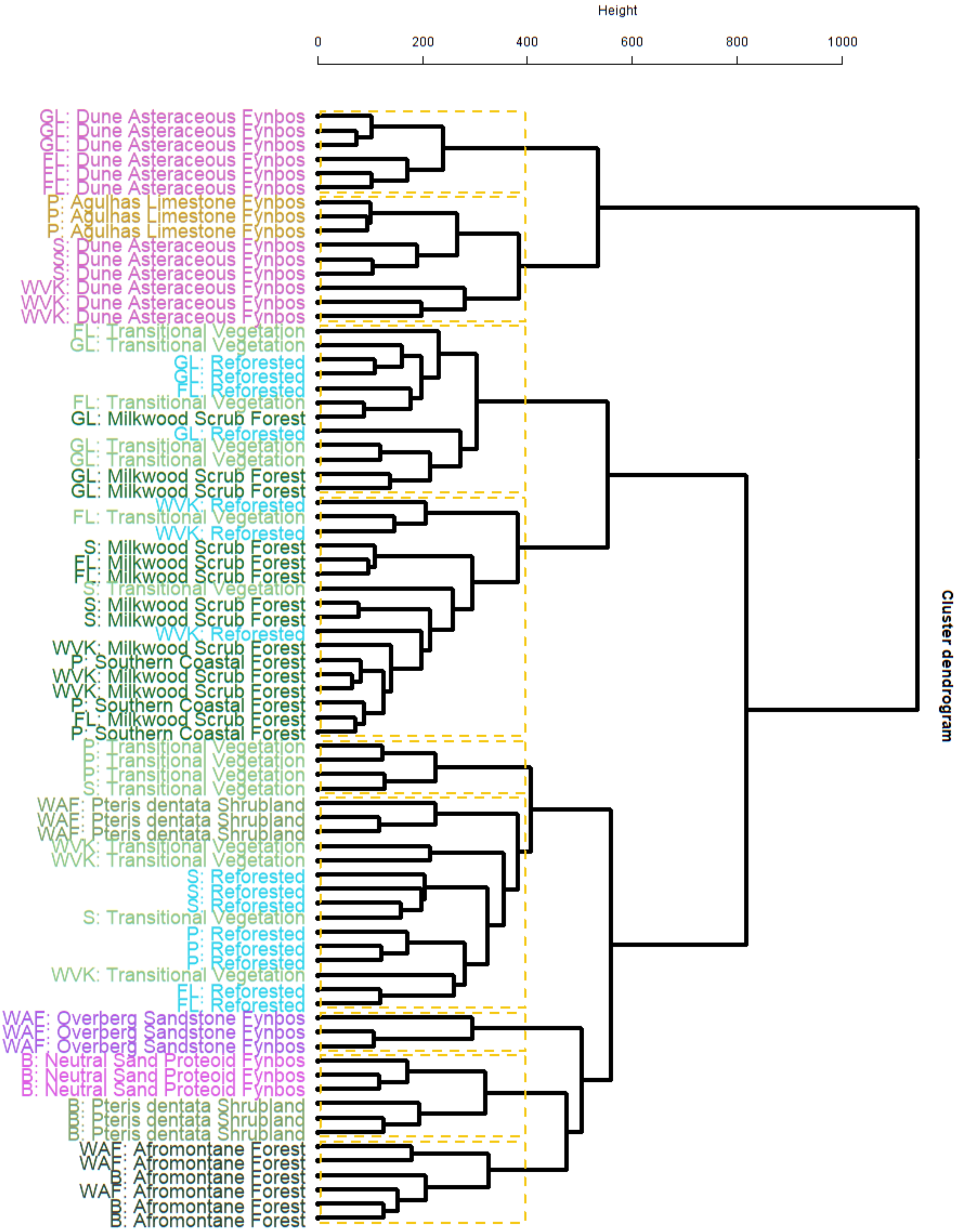

Figure 10: Ward hierarchical clustering dendrogram with nine clusters (yellow dotted boxes). Pre-defined vegetation types (for the 78 vegetation surveys) are colour coded along the end points of the dendrogram. The number of clusters were chosen to represent the pre-existing vegetation types as well as possible. The height indicates the Manhattan distance between clusters. Small differences in height indicate short distances that translate to higher similarity between plots. The height (c. 400) split the dendrogram into nine clusters. Site codes are given before each vegetation type label, so that Baviaanskloof is B, Witvoetskloof site associated with an Afromontane Forest is WAF, Witvoetskloof site associated with a Milkwood Forest is WVK, Platbos is P, Steynsbos is S, Forest Lodge is FL, and Garden Lodge is GL.

Table 2: Species that are likely to be found in the vegetation types at the Baviaanskloof and Witvoetskloof A sites (associated with Afromontane Forests). The Ward clustering method, and Manhattan distance was used to differentiate the clusters. Species associated with p-values <0.01 (i.e., 99%) are listed. Specificity refers to the probability that a plot belongs to the cluster given the species present in the plot whereas fidelity is fundamental to interpreting the association of species with a vegetation type under the Braun-Blanquet approach. Together fidelity and specificity are used to calculate the association statistic.

Species	**Specificity**	**Fidelity**	**Association statistic**	**P-value**
Cluster 1				
Afromontane Forests (Baviaanskloof and Witvoetskloof)				
Rapanea melanoploeos	0.87	1.00	0.93	0.001
Secamone alpini	0.83	1.00	0.91	0.001
Diospyros whyteana	0.73	1.00	0.85	0.001
Asparagus scandens	0.90	0.50	0.67	0.005
Oxalis incarnata	0.67	0.50	0.58	0.005
Cluster 2				
Neutral Sand Proteoid Fynbos and *Pteris dentata* Shrubland (Baviaanskloof)				
Restio leptoclados	0.73	1.00	0.85	0.001
Leucadendron coniferum	0.86	0.67	0.76	0.001
Searsia laevigata	0.56	0.67	0.61	0.004
Metalasia densa	0.61	0.50	0.55	0.007
Cluster 3				
Overberg Sandstone Fynbos (Witvoetskloof)				
Aspalathus ciliaris	1.00	1.00	1.00	0.001
Dimorphotheca nudicaulis	1.00	1.00	1.00	0.001
Drosera cistiflora	1.00	1.00	1.00	0.001
Elegia thyrsifera	1.00	1.00	1.00	0.001
Erica corifolia	1.00	1.00	1.00	0.001
Erica glabella	1.00	1.00	1.00	0.001
Erica imbricata	1.00	1.00	1.00	0.001
Indigofera angustifolia	1.00	1.00	1.00	0.001
Oxalis truncatula	1.00	1.00	1.00	0.001
Pelargonium elegans	1.00	1.00	1.00	0.001
Penaea mucronata	1.00	1.00	1.00	0.001
Protea scabra	1.00	1.00	1.00	0.001
Searsia rosmarinifolia	1.00	1.00	1.00	0.001
Serruria fasciflora	1.00	1.00	1.00	0.001
Wachendorfia paniculata	0.79	1.00	0.89	0.001
Adenandra viscida	1.00	0.67	0.82	0.001
Disparago anomala	1.00	0.67	0.82	0.003
Leucadendron salignum	1.00	0.67	0.82	0.003
Lobelia coronopifolia	1.00	0.67	0.82	0.003
Metalasia brevifolia	1.00	0.67	0.82	0.003
Muraltia cf. rubiacea	1.00	0.67	0.82	0.001
Tetraria bromoides	1.00	0.67	0.82	0.003
Erica plukenetii	0.80	0.67	0.73	0.003
Gnidia juniperifolia	0.75	0.67	0.71	0.005
Trichocephalus stipularis	0.67	0.67	0.67	0.006
Cluster 4				
Pteris dentata Shrubland (Witvoetskloof), Transitional Thicket (Platbos, Steynsbos, Witvoetskloof), and Reforested (Platbos, Steynsbos, and Forest Lodge).				
Searsia lucida	0.89	0.53	0.69	0.002
Searsia glauca	0.66	0.60	0.63	0.002
Oxalis stellata	0.82	0.47	0.62	0.002
Olea europaea	0.82	0.40	0.57	0.005

Table 3: Species that were likely to be found at the five sites associated with Southern Costal/Milkwood Forests. The Ward clustering method, and Manhattan distance was used to differentiate the clusters. Species associated with p-values <0.01 (i.e., 99%) are listed. Specificity refers to the probability that a plot belongs to the cluster given the species present in the plot whereas fidelity is fundamental to interpreting the association of species with a vegetation type under the Braun-Blanquet approach. Together fidelity and specificity are used to calculate the association statistic.

Species	**Specificity**	**Fidelity**	**Association statistic**	**P-value**
Cluster 5 Transitional Thicket (Platbos and Steynsbos)				
Olea exasperata	0.47	1.00	0.69	0.001
Stachys aethiopica	0.42	1.00	0.65	0.004
Cluster 6 Milkwood Scrub Forest (Forest Lodge, Witvoetskloof, Steynsbos), Southern Coastal Forest (Platbos), Transitional Thicket (Forest Lodge, Steynsbos), and Reforested (Witvoetskloof)				
Ehrharta erecta	0.75	0.88	0.81	0.001
Festuca scabra	0.76	0.82	0.79	0.001
Sideroxylon inerme	0.54	1.00	0.73	0.001
Chionanthus foveolatus	0.56	0.94	0.72	0.001
Euclea racemosa	0.93	0.88	0.62	0.002
Asparagus aethiopicus	0.37	0.88	0.57	0.003
Cluster 7 Milkwood Scrub Forest (Garden Lodge), Transitional Thicket (Garden Lodge, Forest Lodge), and Reforested (Garden Lodge, Forest Lodge)				
Droguetia iners	0.81	1.00	0.90	0.001
Melica racemosa	0.93	0.83	0.88	0.001
Zantedeschia aethiopica	0.71	0.83	0.77	0.001
Myrsine africana	0.37	1.00	0.60	0.002
Cynanchum obtusifolium	0.38	0.92	0.59	0.002
Cluster 8 Dune Asteraceous Fynbos (Steynsbos, Witvoetskloof), and Agulhas Limestone Fynbos (Platbos)				
Otholobium bracteolatum	0.857	1.000	0.926	0.001
Agathosma serpyllaceae	0.897	0.889	0.893	0.001
Muraltia saturioides	1.000	0.778	0.882	0.001
Passerina paleacea	1.000	0.667	0.816	0.001
SMF Sparse grass	1.000	0.667	0.816	0.001
Thamnochortus erectus	0.659	1.000	0.812	0.001
Zaluzianskia villosa	0.952	0.667	0.797	0.001
Erica irregularis	0.698	0.889	0.788	0.001
Ficinia bulbosa	0.915	0.667	0.781	0.001
Crassula fascicularis	1.000	0.444	0.667	0.001
Diosma subulate	1.000	0.444	0.667	0.003
Indigofera incana	1.000	0.444	0.667	0.003
Oxalis luteola	1.000	0.444	0.667	0.002
Hermannia ternifolia	0.963	0.444	0.654	0.004
Pterocelastrus tricuspidatus	0.397	1.000	0.630	0.001
Ficinia ramossisima	0.446	0.889	0.630	0.001
Chaenostoma hispidum	0.492	0.667	0.573	0.001
Pelargonium myrrhifolium	0.667	0.444	0.544	0.003
Cluster 9 Dune Asteraceous Fynbos (Garden Lodge and Forest Lodge)				
Oxalis depressa	1.000	0.833	0.913	0.001
Passerina corymbose	0.826	1.000	0.909	0.001
Pelargonium betulinum	0.846	0.833	0.840	0.001
Satyrium carneum	0.914	0.667	0.780	0.001
Oxalis lindaviana	0.688	0.833	0.757	0.001
Cliffortia obcordata	0.647	0.833	0.734	0.001
Zaluzianskia capensis	1.000	0.500	0.707	0.002
Phylica ericoides	0.456	1.000	0.675	0.001
Metalasia muricata	0.769	0.500	0.620	0.005
Indigofera brachystachya	0.458	0.667	0.553	0.003

Objectives 1 to 3: Principle Coordinate Analysis

The PCoA also showed that Afromontane Forests are different from the Southern Coastal and Milkwood Scrub Forests (Fig. 10). The fynbos adjacent to the two Afromontane forests (i.e., Neutral Sand Proteoid Fynbos at Baviaanskloof and Overberg Sandstone Fynbos at Wtvoetskloof A) were distinct from fynbos vegetation types adjacent to Milkwood Forests (i.e., Dune Asteraceous Fynbos and Agulhas Limestone Fynbos). The Southern Coastal Forest of Platbos Forest Reserve (PFR) plotted together with the Milkwood Scrub Forests in the PCoA, suggesting that these forests are floristically similar to each other (hereafter referred to as Southern Coastal/Milkwood Forests; Fig. 10). The Dune Asteraceous Fynbos plots of Witvoetskloof M (i.e., associated with a Milkwood Forest) formed a poorly defined cluster in the PCoA and diverged from the fynbos plots at other sites (Fig. 10).

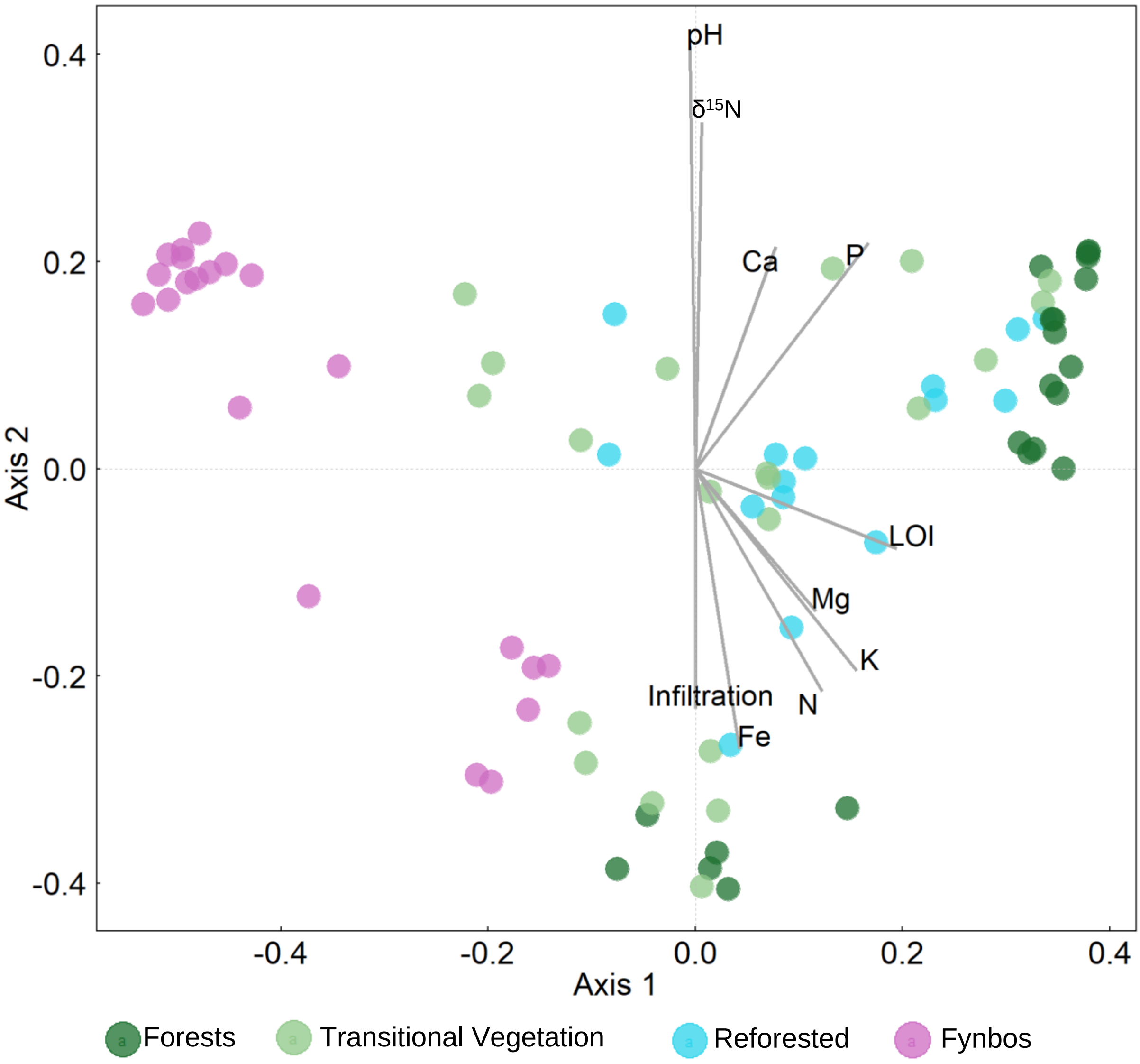

Figure 111: A PCoA ordination based on a Bray-Curtis dissimilarity matrix was used to calculate the separation of the 78 vegetation plots of this study. An ordination showing clusters formed by the forests, ecotone transitional vegetation, fynbos, and reforested vegetation. The key to the various vegetation types is given below the figure. Soil variables with a significant association with the separation of vegetation types is also illustrated. PCoA plots for individual sites are available in Appendix; Figs. 20 and 21.

Objective 2: Soil particle-size distribution

Soil texture (divided into sand, silt, and clay fractions) is similar across vegetation types at most of the study sites (Fig. 12). The clay fraction was almost non-existent in all of the soils sampled and did not vary significantly between vegetation types (Figs. 13 and 14). The main differences in soil texture between vegetation types were linked to the silt and sand textural classes. When silt and sand fractions differed, forests were associated with a greater silt fraction than the surrounding fynbos (Garden Lodge, Forest Lodge; Fig. 13). While there are no significant differences between sand and silt fractions at Baviaanskloof, the Neutral Sand Proteoid Fynbos had a finer sand fraction compared to soils from the Afromontane Forest and transitional *Pteris dentata* Shrubland (Fig. 12).

Baviaanskloof vegetation types have similar soil textures, but at Witvoetskloof A, the Afromontane Forest soil contains more silt than sand in soil samples. The surrounding Overberg Sandstone fynbos soils are composed of mostly sand, with a smaller silt fraction. The transitional *Pteris dentata* Shrubland from Witvoetskloof A has a soil texture that follows the same general pattern as the surrounding Overberg Sandstone Fynbos, i.e., with the sand fraction being proportionally higher than silt. Transitional vegetation of Afromotane forests occurred along the crest of the valleys within which the forests occurred. Despite the similar elevation, *P. dentata* shrubland has a larger silt and smaller sand fraction compared to the surrounding fynbos. The Afromontane Forest of Witvoetskloof is also the only forest in this study that has a perennial river flowing through it.

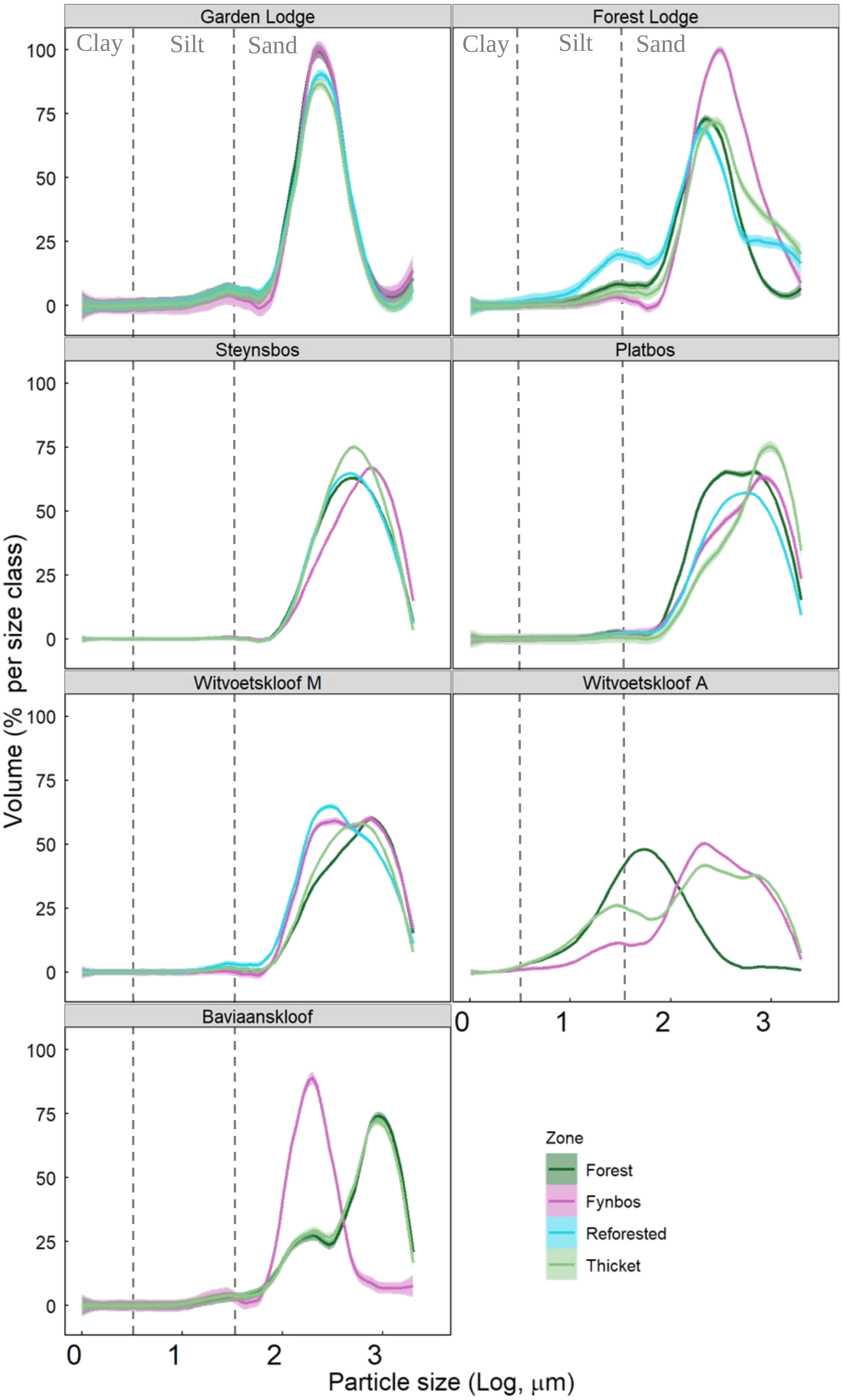

Figure 12: Soil particle-size distributions for all seven study sites. For each site, particle-size distributions are compared between forest, transitional vegetation, reforested areas, and fynbos. "Witvoetskloof M" refers to the site with a Milkwood Scrub Forest, while "Witvoetskloof A" and "Baviaanskloof" are the two sites where Afromontane forests were sampled. Ribbons represent 95% confidence intervals.

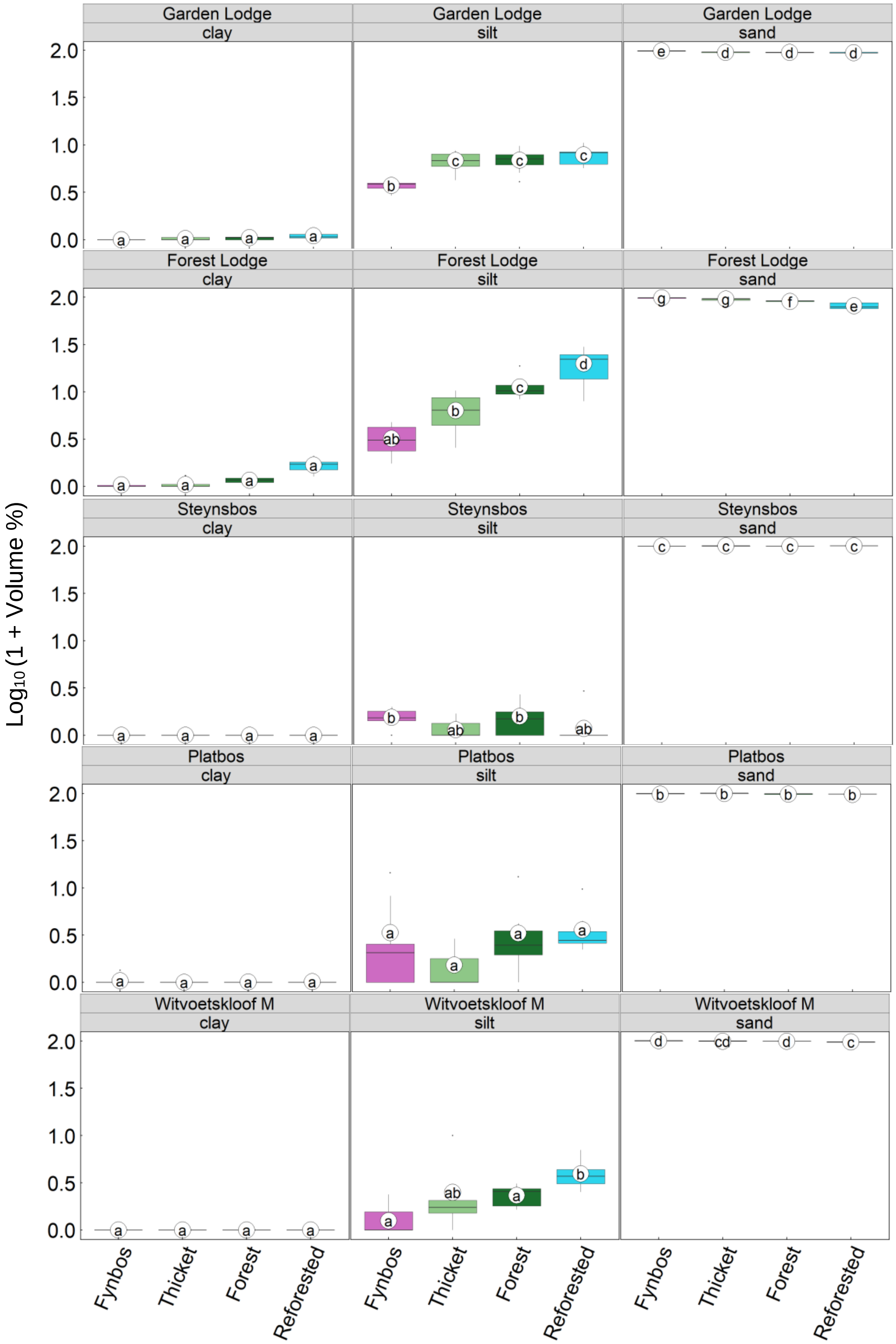

Figure 13: Average clay, silt, and sand particle-size distributions for the sites associated with Southern Coastal/Milkwood Forests. Pink boxplots in the left panels represent fynbos vegetation, light green boxplots are transitional vegetation, dark green is forest, and the blue boxplots are from reforested areas. Letters in the boxplots represent significant differences between means (based on a Post-Hoc Tukey test), so that different letters indicate a significant difference, while identical letters indicate means that are not significantly different. The three lines of the boxplots represent the first quartile (lowest line), median (middle line), and third quartile (highest line). The "whiskers" represent the interquartile range times 1.5, and points represent outliers.

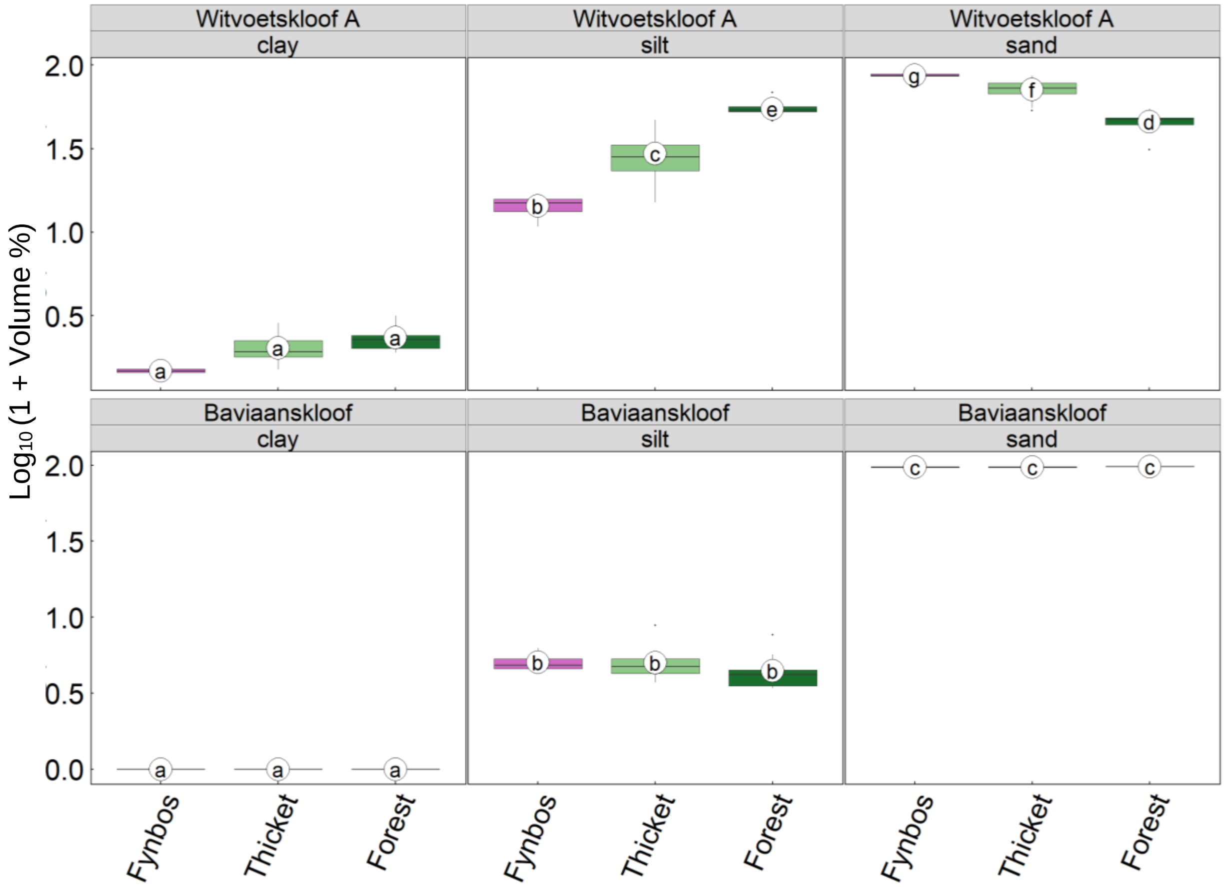

Figure 14: Average clay, silt, and sand particle-size distributions for the two sites associated with Afromontane Forests (which includes Milkwood Forests). Pink boxplots in the left panels represent fynbos vegetation, light green boxplots are transitional vegetation ("thicket"), and dark green is forest. Other details as in Fig. 13.

Objective 2 and 3: Soil nutrients and chemical properties

When comparing surface soils at each site, the forests generally had higher N, P, and K compared to fynbos soils (Fig. 15). The only exception to this rule was that P at Garden Lodge and Witvoetskloof M did not significantly differ between forest and fynbos (Fig. 15). Soil P at Garden Lodge is similar in fynbos, the transition, reforested area, and in the forest, showing higher variation in the amount of extractable P found. Interestingly, the forest of Witvoetskloof M had similar P to the surrounding fynbos, but the transitional thicket and reforested areas both have higher P than both forest and fynbos. The Forest Lodge forest had the highest P of all the forests in the study (ca. 300 mg kg^{-1}, where other forests all had <160 mg kg^{-1}). Both Afromontane Forests had the lowest level of P (ca. 20-40 mg kg^{-1}) compared to the Southern Coastal/Milkwood Forests (similar to the findings of Coetsee et al. 2015). However, the Afromontane Forest of Witvoetskloof contained the highest K and N compared to all of the other forests.

Unlike the results reported by Cramer et al. (2019), most forests had lower soil pH than the surrounding fynbos, with transitional soil pH being intermediate between forest and fynbos (Fig. 15). The only exception was Baviaanskloof where fynbos soil had a lower pH (ca. 5.4), than the forest (ca. 5.9). Generally, N in transitional vegetation and reforested areas was intermediate between forest and fynbos, however this is not always the case in the heterogeneous transitional areas. Transitional thicket generally contains similar N to the reforested areas, with the exception of soils sampled at Witvoetskloof M, where the Transitional Thicket resembled fynbos and reforested area resembled forest N. At Steynsbos the N of the reforested vegetation was also similar to that of the surrounding fynbos, but this is an exception. N was intermediate between forest and fynbos (resembling neither) at only three of the study sites.

The Southern Coastal/Milkwood Forests (on deep > 1m deep aeolian calcareous soils) were distinct from Afromontane Forests (on shallow <0.5m deep sandstone derived soils, as illustrated in Appendix; Fig. 22) in soil nutrient content as revealed by the PCoA (Fig. 10). The Afromontane Forests soils had the highest levels of N, K, Mg, and Fe in the topsoil compared to the Southern Coastal/Milkwood Forests (Fig. 10). The topsoil within the Afromontane Forest at Witvoetskloof A contained considerably higher soil nutrient status than the surrounding fynbos, and also than any other forest sampled (Fig 15, 16, and 17). Soils from Afromontane Forests contained more than double the N recorded in the topsoil of any of the other forests (ca. 1.2%; Fig. 15), and by far the highest loss-on-ignition, Mg, and Na of all the sites (Figs. 16 and 17). $\delta^{15}N$, soil pH, P, and Ca were generally higher in the deep aeolian, and calcareous soils associated with the five sites that feature Southern Coastal/Milkwood Forests than sites associated with Afromontane Forests (Fig 10). Forest soils tend to have higher loss-on-ignition (LOI) than fynbos soil, yet at Steynsbos and Witvoetskloof M the forest LOI is not significantly higher than that recorded in the surrounding fynbos soils (Fig. 17). Soil infiltration rate did not differ significantly across the vegetation types of the study sites, with the exception of Baviaanskloof where the transitional vegetation had the highest average infiltration rate. The sandy soils at all of the seven study sites meant that the infiltration rate of water was especially fast. Despite the similar soil textures along the forest-fynbos ecotones of six of the study sites (as Witvoetskloof A had mismatching soil texture between forest and fynbos), the overall soil nutrient content was significantly higher in forests compared to fynbos (where Witvoetskloof M is the only exception).

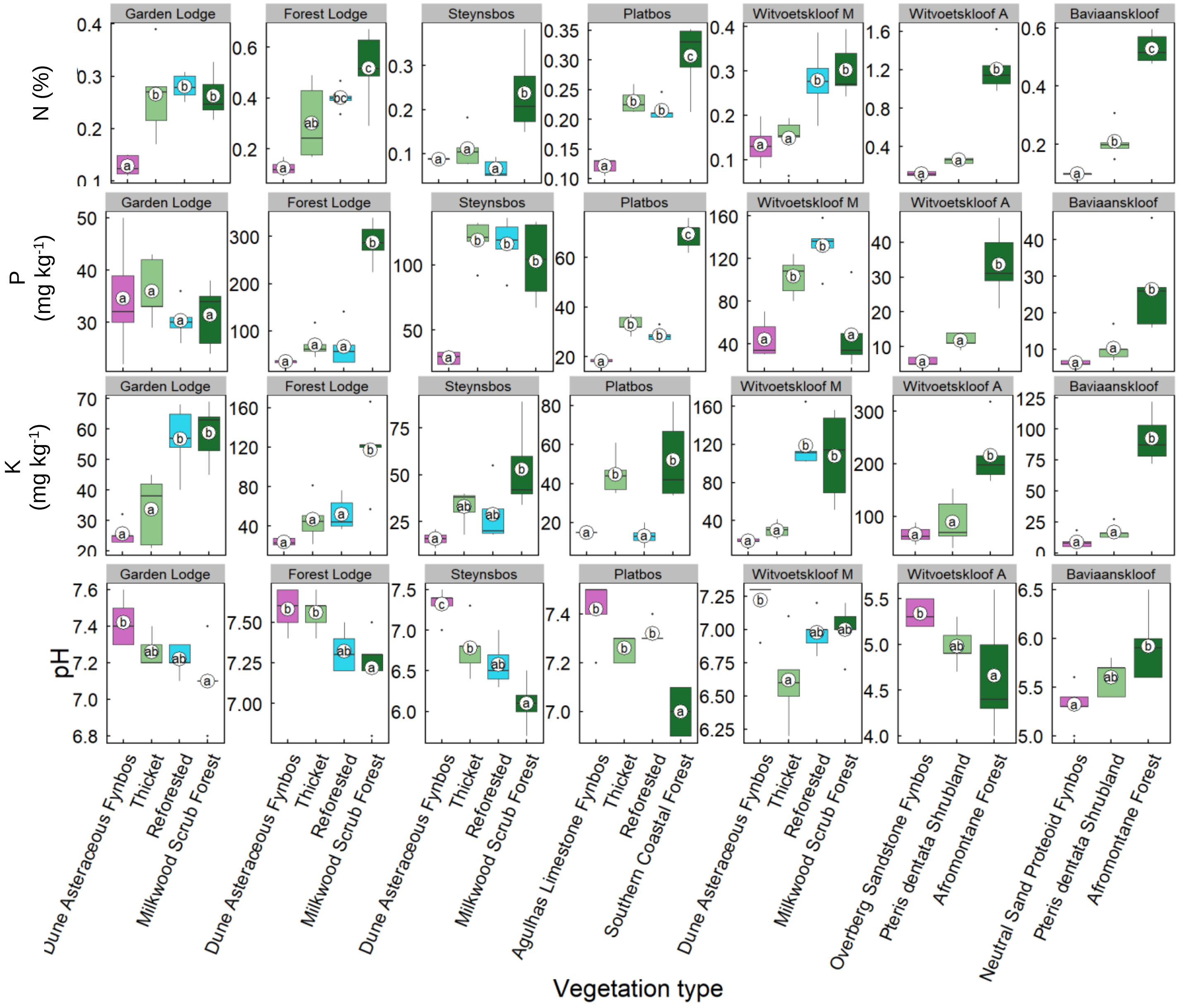

Figure 15: The topsoil (30 cm) total N, P, K, and pH from the seven study sites. Differences are illustrated between vegetation types where soil was sampled at each site. Pink boxplots represent fynbos, light green is transitional vegetation, blue is reforested areas, and dark green is forest. Please also note that y-axis minimum and maximum values differ between plots to account for larger variations in soil nutrient content between the various study sites. Plot details as in Fig. 13.

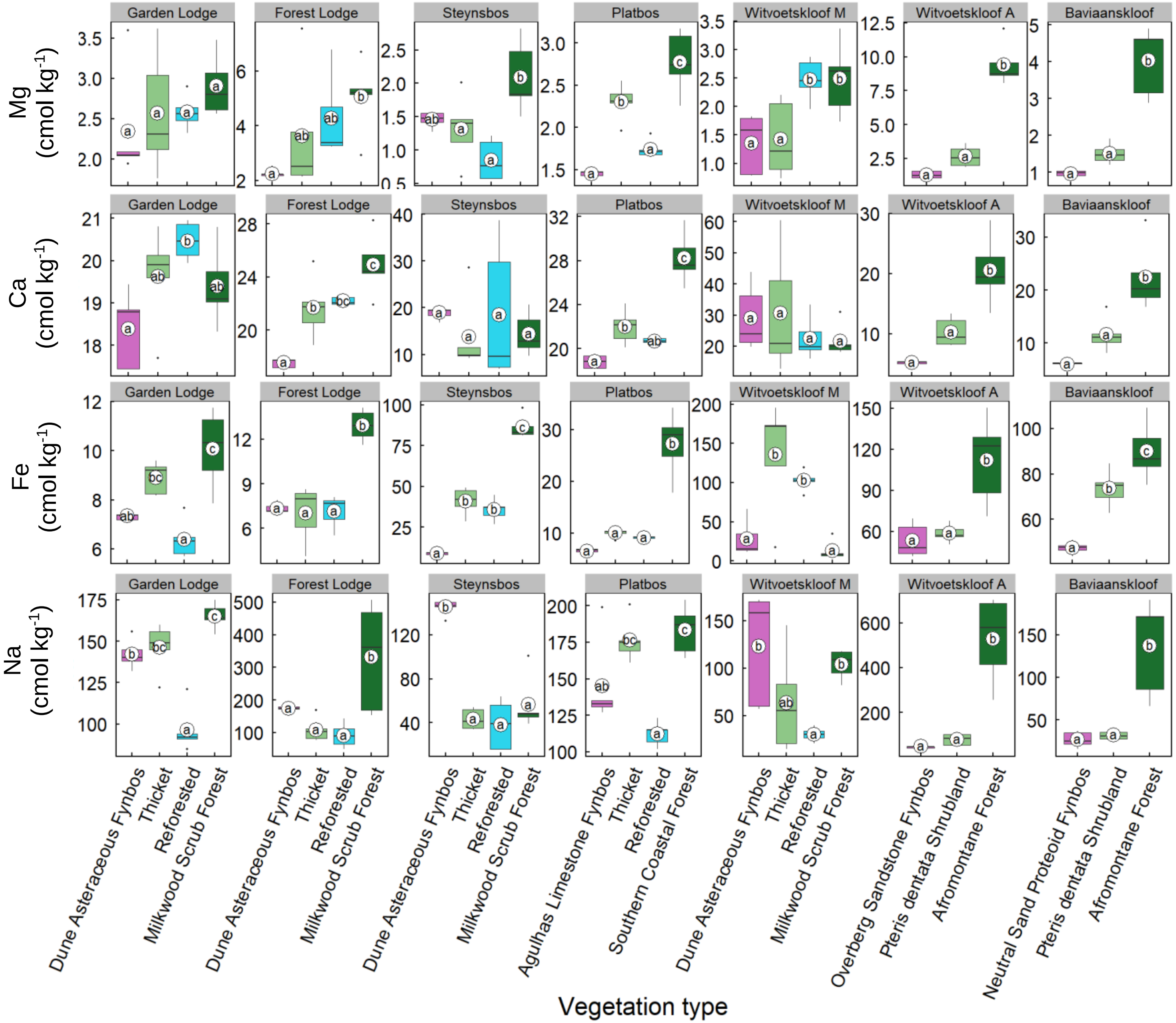

Figure 16: The topsoil (30 cm) Mg, Ca, Fe, and Na from seven study sites. Significant differences are illustrated between different vegetation types sampled for each site. Pink boxplots represent fynbos, light green is transitional vegetation, blue is reforested areas, and dark green is forest. Please also note that y-axis minimum and maximum values differ between plots to account for larger variations in soil nutrient content between the various study sites. Further plot details as in Fig. 13.

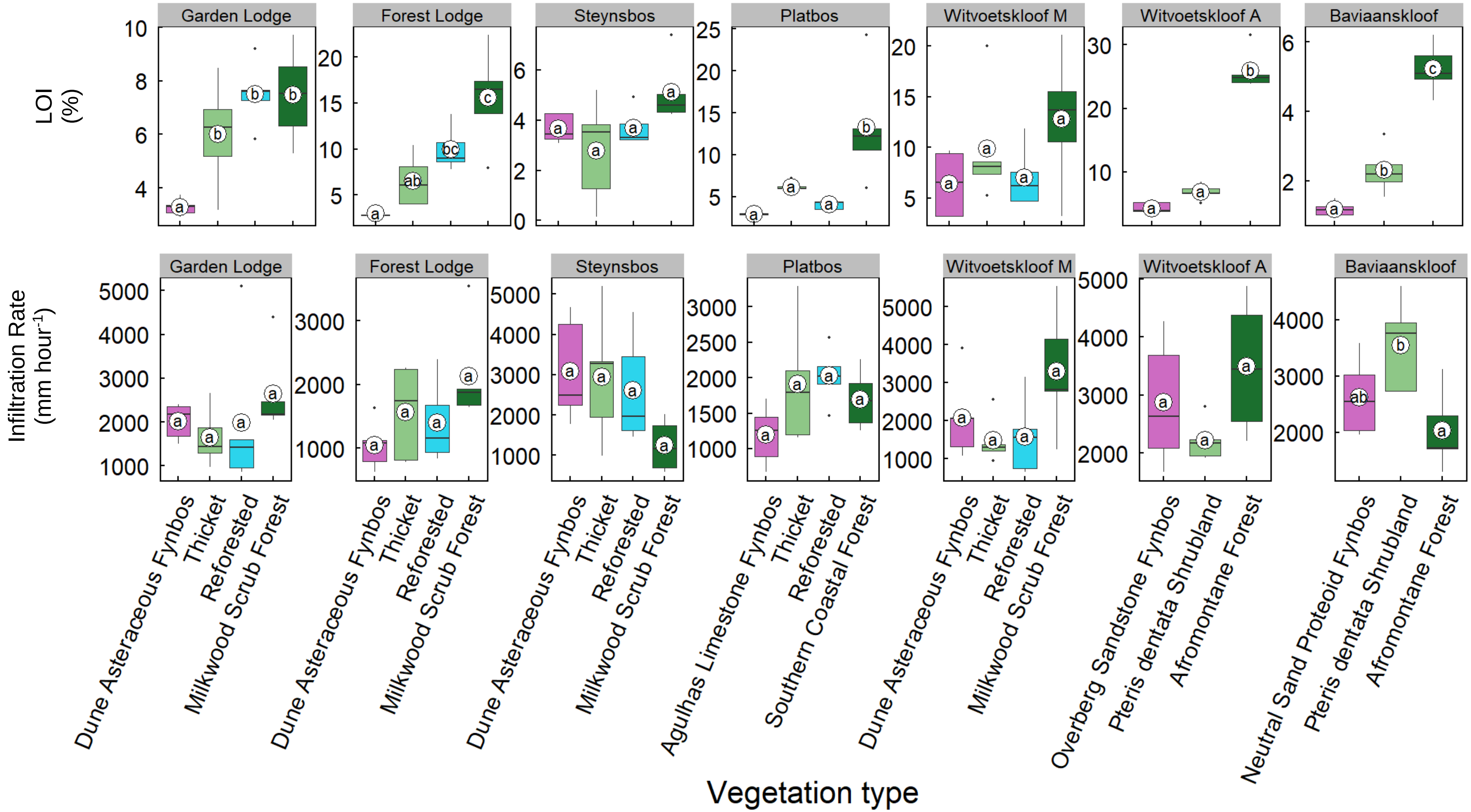

Figure 17: The topsoil (30 cm) loss-on-ignition (a proxy for soil organic matter) and the infiltration rate of water through the soil from seven study sites. Significant differences are illustrated between different vegetation types sampled for each site. Pink boxplots represent fynbos, light green is transitional vegetation, blue is reforested areas, and dark green is forest. Please also note that y-axis minimum and maximum values differ between plots to account for larger variations in soil nutrient content between the various study sites. Further plot details as in Fig. 13.

Objectives 3 and 4: Historical analysis of forest change

Unlike the findings of Cramer et al. (2019) for Afromontane forests, woody cover for most of the Southern Coastal/Milkwood Scrub Forests significantly increased between 1938 to 2022. The forests were more fragmented in 1938 compared to 2022. For example, Forest Lodge Milkwood Scrub Forest more than doubled in canopy cover between 1938 and 2022 (ca. 50 to 55%; Fig. 18). The 1938 imagery shows large-scale woodcutting in the Forest Lodge forest, but this had started to regrow by 1961 and had almost fully regenerated by 1973 to 1980 (Fig. 18). However, the previously felled section of forest contains some *Acacia* invasives and still has not achieved full canopy closure after almost a century of regeneration (pers. obs. of the Forest Lodge forest in 2022). At Steynsbos forest cover increased by over 65% from 1938 to 2022 reaching a stable forest cover by ca. 1998 (Fig. 19). Today, Steynsbos has the widest Transitional Thicket, indicating that although tree cover has increased, the forest-fynbos ecotone has not yet fully recovered from past anthropogenic disturbance. The Witvoetskloof M forest was also influenced by human activities over the past 85 years. The Witvoetskloof dam first observed in the 1973 imagery (Fig. 19), when a small water body was visible. There is a lack of data predating the historical photographs, and that this is a limitation for understanding the location of original boundaries of forests. “Original forest boundaries” are unknown, which is why this analysis was done to figure out if they have likely been stable or not, at least over the short period of the last century.

Like all of the Southern Coastal/Milkwood Forests, PFR also has a complex history, with visible woodcutting in the earlier images, agricultural fields in or on the edge of the forest at different points in time (Fig. 19; Appendix; Figs. 23-29), and potential alien invasive species that seem to have been present in the area around the forest for quite some time (called “Unknown trees” in Figs. 18 and 19). Continuous canopy cover was not seen in the 1938 imagery, due to extensive herbivory, trampling, and logging activities. The forest had started to densify by 1961, and by 1973 trees had already established and taken over the agricultural field from the 1938 imagery. However, by 1973 more agricultural fields had been established along the northern boundaries of the forest. By 1980, both the new fields had been abandoned, and trees were establishing again. However, this was short lived, as the same two fields are seen as cleared areas again in the 1989 imagery, with an additional cleared field showing up in the 1998 imagery. In 2022 the agricultural fields have shrunk dramatically in their extent along the north of the forest. It is likely (from the historical photographs) that the herbivory pressure had decreased by the 1980s, but that unfortunately the plants that regrew were likely invasive alien species. Alien invasive plants within the Platbos forest has been cleared between 1338 to 2022, while invasive alien stands surrounding the forest has increased in cover, especially since 1998 (Fig. 18, 19 and Appendix; Figs. 23-29 and 32), with extensive *Acacia longifolia* stands that are still present to the south of PFR, and spider gums (*Eucalyptus conferruminata*) in a section to the north of the forest (pers. obs.).

Apart from the effect of fire, forest cover has been adversely influenced, at least over the past century, by relatively novel anthropogenic pressures including woodcutting, agricultural crop planting, herbivory and trampling, and invasive alien plants. Since 1938, the Southern Coastal/Milkwood Forests of Forest Lodge, Steynsbos, Platbos, and Witvoetskloof M have significantly increased in canopy cover. Stands of invasive alien stands were cleared in the Garden Lodge Forest (Fig. 18 and 19). “Open forest”, where tree canopy cover is discontinuous (tree cover ca. 50 to 80%; Appendix; Figs. 23-29) was more common in the past. In Forest Lodge, Platbos, and Steynsbos, the forests had been cleared via logging, so that only a few “scattered trees” were visible in early 1938 aerial imagery. In the same areas where scattered trees were found in the 1930’s, forest has managed to return in less than a century.

Both Afromontane Forests of Baviaanskloof and Witvoetskloof show that the extent of forest canopy cover has not changed significantly between 1938 to 2022 (Appendix; Figs. 23-29). The Afromontane Forests, unlike the Southern Coastal/Milkwood Scrub Forests, are found in steep valleys on mountainous terrain. The relatively constant distribution of the various forests over landscapes, and the demonstrated densification of trees within areas that had been disturbed and cleared supports the hypothesis that forests are stable states within a wider fynbos matrix.

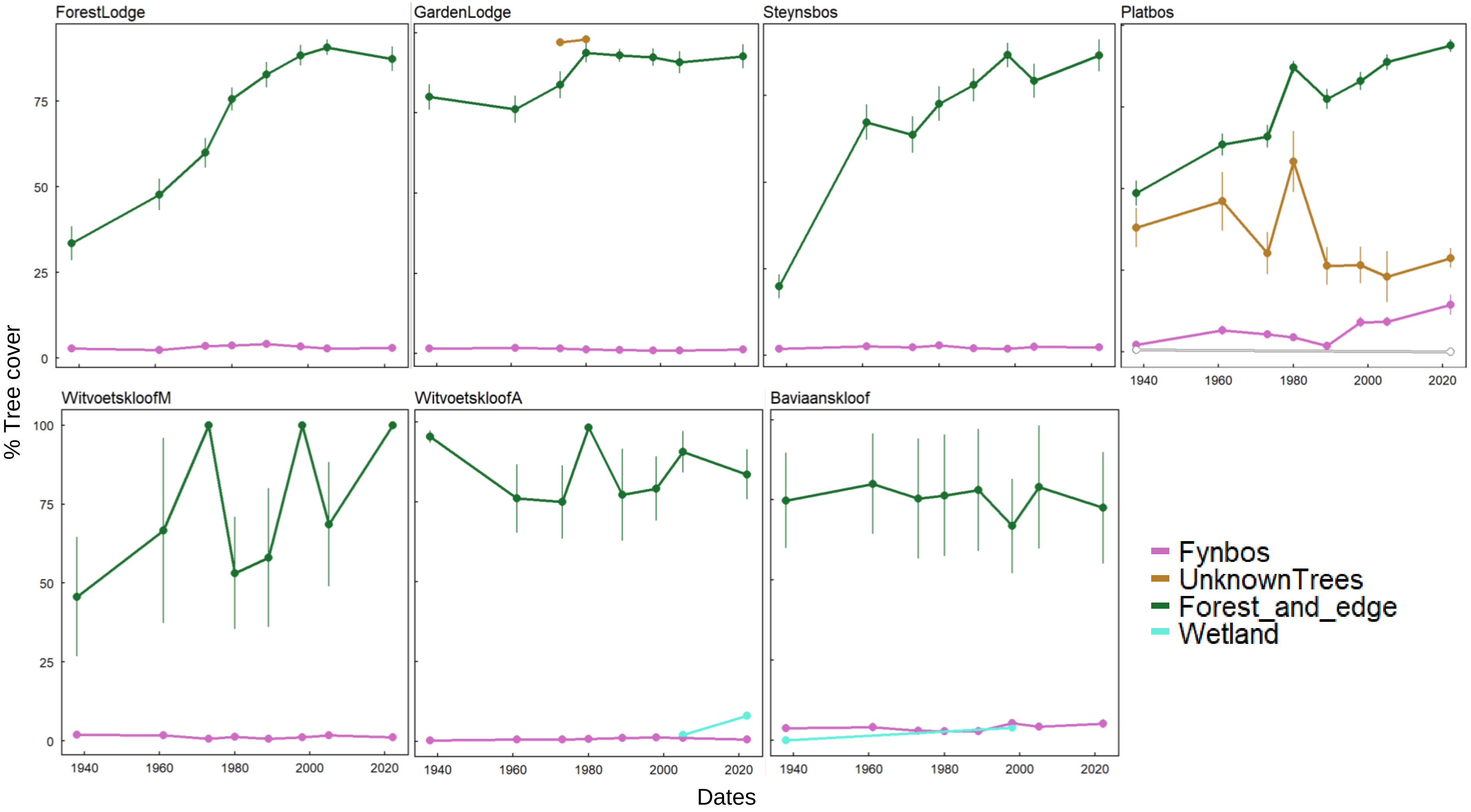

Figure 18: The change in tree cover between 1938 and 2022 averaged over the randomly sampled points within four broad vegetation categories, namely 1) forests and the forest transitional vegetation, 2) “unknown trees”, which represents invasive plants and cultivated trees, 3) fynbos vegetation, and 4) wetlands. The data presented here refers to tree cover assessments within areas that have remained within one of these four classified categories over all eight of the historical images that were analysed, in order to track tree cover change that correspond only to that vegetation category. Results from polygons that covered more than one category are illustrated in the Appendix; Fig. 32. The line graphs represent the average assigned tree cover% within the various vegetation categories across the eight historical layers (1938, 1961, 1973, 1980, 1989, 1998, 2005, and 2022). Standard error bars are shown per line graph to illustrate the variation in tree cover that was assigned within each of the vegetation categories for a given point in time.

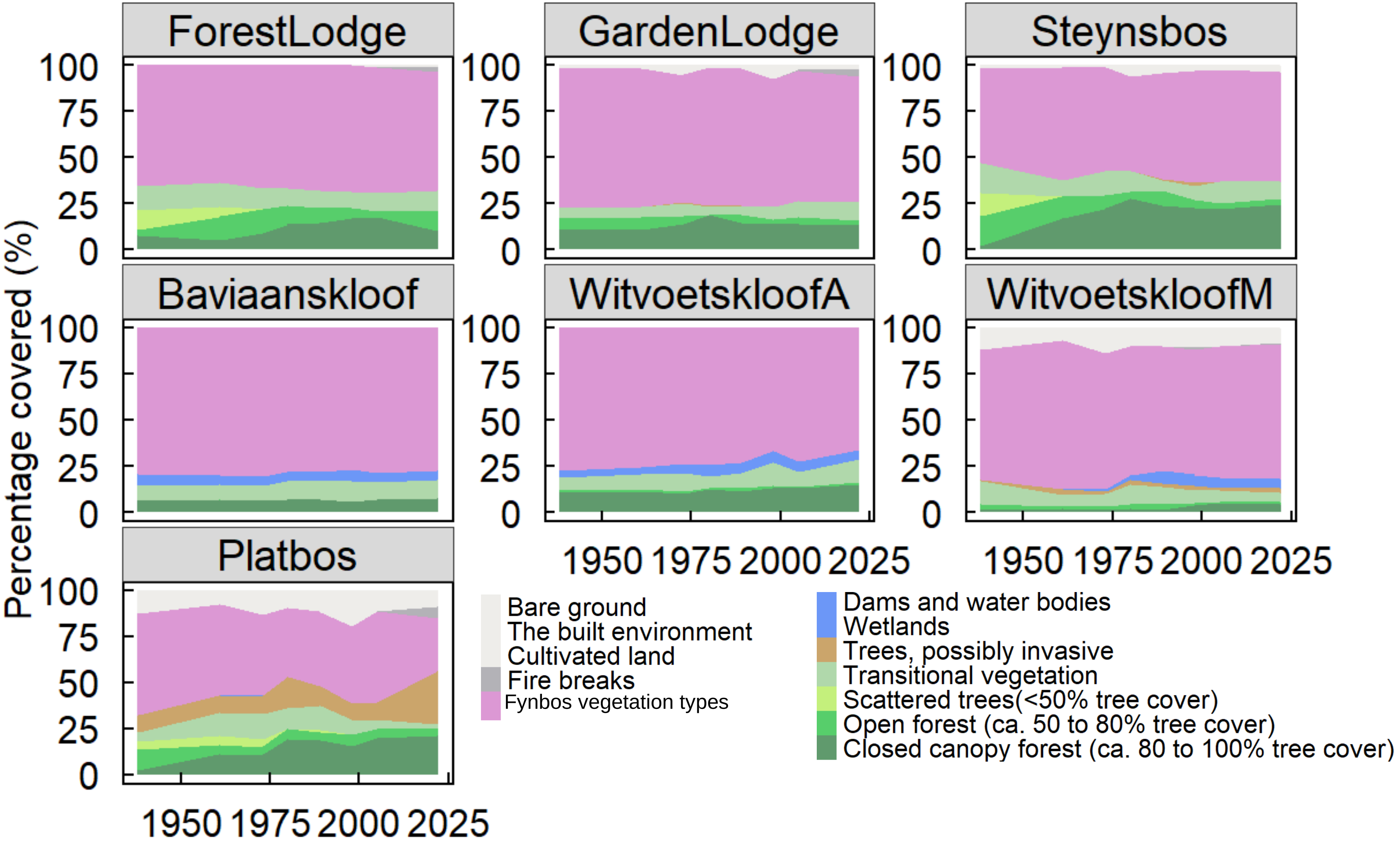

Figure 19: The manually classified land cover categories are plotted to illustrate changes in their extent from 1938 to 2022. Each facet in the figure represents one of the seven study sites. The forests at each site were divided into three tree cover categories, namely "Forest", which represents sections that have over 80% continuous canopy cover. Then the "Open forest" category represents discontinuous canopy cover, where trees covered between 50 to 80% of the classified area. "Scattered trees" were identified in areas where only a few discontinuous trees (<50% cover) were visible from the aerial images. The "Trees, possibly invasive" category refers to unknown and miscellaneous tree cover that fell outside or on the periphery of forests. Four fynbos vegetation type categories are also plotted.

Discussion

Almost no species, nor plant families were shared between forest and fynbos vegetation surveys at the study sites, which is consistent with the findings of previous studies such as Coetsee et al. (2015 and Cramer et al. (2019). The Southern Coastal/ Milkwood Forests tend to occur in flatter depressions in lowland regions than do Afromontane Forests (Geldenhuys 1994; Adie et al. 2017). Even where Southern Coastal/Milkwood forests are at different elevations to the surrounding fynbos (e.g., Garden Lodge, Platbos, and Witvoetskloof M), the change in elevation is small and gradual (see Appendix; Table 4). The lack of strong differences in soil texture across vegetation types indicates that the soils sampled are derived from a similar geological parent material. Soil nutrient-limitation plays a significant role in maintaining forest-fynbos ecotones (Power 2018; Cramer et al. 2019; Lu et al. 2022). The theory of alternative stable state (ASS) more likely applies along Southern Coastal/Milkwood Forest-fynbos ecotones than ecotones of Afromontane Forests. Afromontane Forest boundaries are more consistent with a sharpening switch model, where the physical environment largely determines the distribution of vegetation. The analysis of historical imagery confirms that forest distributions have not changed despite past disturbances, and that ecotone boundaries are especially clear in images following more recent major fire events. However, not all disturbance regimes are equal, and too much disturbance and fragmentation can lead to an increased risk of invasion by invasive species and diversity loss (Denslow 1980; Hobbs and Huenneke 1992; Holmes 2001; Laurance et al. 2002).

The floristic distinction between forest and fynbos is an important part of establishing whether these are in fact ASS (e.g., Weiher and Keddy 1999, Midgley and Rebelo 2016). While milkwood trees (*Sideroxylon inerme*) occur in transitional vegetation surrounding forest they are not found in fynbos. Similarly, common Dune Asteraceous Fynbos species such as *Erica irregularis* and *Indigofera brachystachya* do not occur in forests. Common plant families associated with fynbos vegetation, e.g., Bruniaceae, Restionaceae, Ericaceae, Proteaceae, Rutaceae, and Iridaceae, were entirely absent from forests, where families like Oleaceae, Sapotaceae, Ulmaceae, Ebenaceae, and Achariaceae commonly feature (Geldenhuys 1993; Kruger 1994; Mucina and Rutherford 2006). The low light conditions in forests mean that open-canopy fynbos species are disadvantaged while forest plants do not survive on nutrient-poor soils under fynbos (Power 2018). The highest percentage of shared species between forest and fynbos was only 5% at Baviaanskloof (Appendix; Table 5). The evolutionary and life-history strategy contrasts between forest and fynbos species are the reason that their feedback processes with the environment are also rather different (Barraclough 2006; Wood and Bowman 2012).

ASS theory is a reasonable explanation for the juxtaposition of entirely different ecosystems found in near identical abiotic environmental conditions (Beisner et al. 2003; Schröder et al. 2005). However, the question is whether ASS is an acceptable conceptual framework for understanding all forest-fynbos ecotones in the Overberg, and wider CFR. Some ambiguity exists around when the ASS concept is truly applicable to terrestrial systems (Wood and Bowman 2012; Karatayev and Baskett 2019; Mushet et al. 2019). In aquatic systems where ASS are well studied, the system is often closed, where terrestrial ecosystems are more open and complex. The ability to fully separate out vegetation effects from geological effects is tricky, and therefore these is some uncertainty regarding cause-and-effect. However, in landscapes where the underlying geology is constant, minor soil textural differences can be expected because of the interplay of the biotic and abiotic landscape properties (Sinowski and Auerswald 1999). For example, soil particle-size analysis revealed that the soil texture of the Afromontane Forest of Witvoetskloof A differed from the surrounding Overberg Sandstone Fynbos. The forest there had a higher proportion of silt than sand in the topsoil and is also the only forest with a permanent stream running through its centre. The most likely explanation for the textural mismatch between forest and the surrounding vegetation is due to long-term sediment transport and alluvial deposition (van Breemen and Buurman 1998; Aslan 2013) in the valley by the perennial stream that flows through it. The distinction between the soils textures raises the question for this site as to whether ASS applies.

Sand and silt content differences across forest-fynbos ecotones complicate the identification of ASS, even if these differences are likely not due to the presence of underlying geological boundaries (Brady and Weil 2014). Even without permanent streams, many of the other study sites (e.g., Forest Lodge) contained a greater silt and smaller sand fraction than the surrounding fynbos, which is similar to the findings of Masson and Moll (2010) and Cramer et al. (2019). Sedimentary processes (such as erosion, weathering, dissolution, precipitation, and lithification; van Breemen and Buurman 1998) have likely added to the development of soil differences between forest and fynbos, and therefore the diverse set of niches that are common in CFR landscapes (Cowling et al. 2009). Vegetation type can also play a role in sediment trapping. It was hard to properly tease apart cause and effect given the scope of this thesis, however the soil monoliths collected (Appendix; Fig. 22) provided a rough estimate of soil texture lower down in the soil profiles. If the textures lower down in the well-drained soil profiles are similar, it is likely because the parent geologies are the same.

Soil-textural differences at the various study sites likely result from a combination of mechanical landscape sedimentary processes and vegetation sediment and dust trapping by forests (e.g., Soderberg and Compton 2007, Cowling et al. 2009). These processes are likely to cause silt accretion in forests and silt loss through weathering and leaching in the fynbos matrix (Wood and Bowman 2012; Brady and Weil 2014). Additionally, ferricrete lenses resulting from long-term synergistic iron-concentrating processes (e.g., water table fluctuations) in the soil (van Breemen and Buurman 1998; Brady and Weil 2014) are present at some of the Southern Coastal/Milkwood Scrub Forests. Nevertheless, the abiotic environment currently occupied by Southern Coastal/Milkwood Forests may support fynbos, and vice versa if fire frequency and intensity is altered over long enough periods of time. This is similar to the ideas presented by Manders (1990), Luger and Moll (1993) for Afromontane Forests, however, forest expansion and contraction may apply more readily to Southern Coastal and Milkwood Scrub Forests, than to Afromontane Forests in steep valleys.

Both of the Afromontane Forests in this study occur in steep valleys (Mucina and Rutherford 2006), with a fynbos matrix on the surrounding mountainous terrain. Because of this, and the mismatch in soil textures between forest and fynbos, a “sharpening switch” model is likely a more appropriate conceptual framework than alternative stable states to describe Afromontane Forest boundaries where they occur in valleys found on highly heterogeneous mountainous terrains (Fig. 1B; Mount 1979, Wood and Bowman 2012, Kéfi et al. 2016). The “sharpening switch” model implies that differences in flammability across a landscape are partly due to vegetation mosaics (which are largely predefined by the physical environmental), and not an effect of them. According to this model, ecotone boundaries are sharpened by fire, but the distribution of contrasting vegetation types is, fundamentally, environmentally determined (Fig. 1B). Steep valleys generally have shallower depth to water tables, provide refuges from fire, wind, and have lower solar radiation (Manders 1990; Adie et al. 2017). Steep valleys also have space for the growth of vertical tree roots in otherwise very shallow soil. The micro-climatic differences arising from sudden changes in topography (and perhaps hydrology as well; Araya et al. 2011) within mountainous terrain may reflect conditions unsuitable for ASS ecosystems, i.e., there is no set of abiotic niches that can support either forest or fynbos. As a result, forests establishing outside of the valley, and fynbos thriving in the valley are highly improbable for the current climate associated with the sites (Adie et al. 2017).

Unlike Coetsee et al. (2015) this study supported the idea of the nutrient-limitation hypothesis. Forest and fynbos ecotones are maintained by “fire-vegetation-soil” feedbacks (Allsopp et al. 2014;

MacPherson et al. 2019). The idea is that there are different pedogenic and nutrient cycling pathways between different vegetation types (Hobbie 2015), such as forest and fynbos (van Wilgen and le Maitre 2010). Forests in this study generally tended to have higher concentrations of N, P, K, Fe, Mg, and organic matter, although there were some outliers. Afromontane Forests (particularly the Witvoetskloof A forest) were associated with higher N, K, Fe, and Mg, but lower P, Ca and pH compared to the Southern Coastal/Milkwood Forests. As soils age, P is lost from the system (Lambers et al. 2008; Turner and Condron 2013; Sulieman et al. 2018), and generally forests with low P (e.g., Witvoetskloof A) recycle it as efficiently as possible (Rastetter et al. 2013; Lang et al. 2016). The Southern Coastal/Milkwood Forests in this study may have more P in the soil, but have lower levels of other essential nutrients, and are associated with species that have lower water requirements compared to the Afromontane Forests. Even where fires have managed to penetrate into forests (e.g., Garden Lodge and Forest Lodge), the historical imagery revealed that forests recover and densify again within a relatively short period of time. Only when fire frequency and intensity changes significantly is it probable that a breakdown of emergent edaphic boundaries along ecotones will occur (Luger and Moll 1993; Kraaij et al. 2013; Cramer et al. 2019).

The resulting emergent edaphic boundaries along forest-fynbos ecotones are especially important where forest and fynbos share the same nutrient-poor geology and occur at relatively similar elevation (Coetsee et al. 2015; Cramer et al. 2019). Furthermore, micronutrients and clay are more likely to be trapped by forests, where the majority of clay may be from aeolian sources (Soderberg and Compton 2007). Apart from sedimentary and hydrological processes that concentrate nutrients from sources into nutrient sinks (van Breemen and Buurman 1998; Cowling et al. 2009), the organic carbon in the topsoil of forests also contributes to the accumulation of nutrients (Manders 1990). Organic matter content was higher in forests than the surrounding fynbos for five out of the seven study sites. Steynsbos and Witvoetskloof M were the exceptions, where the forest, transitional vegetation, reforested areas, and fynbos all had similar organic matter content. Even so, other soil nutrients (e.g., K and N) differed significantly between forest and fynbos at Witvoetskloof M and Steynsbos.

Where ASS exist along forest-fynbos ecotones, fire has been identified as the most important disturbance determining forest distributions over the landscape (Coetsee et al. 2015; Pausas 2015). Evidence from past studies suggest that fires have affected the forests of the CFR long before the oldest aerial imagery for the region (Geldenhuys 1994; Magadzire et al. 2019). This suggests that forests demonstrate a degree of resilience to the presence of fire, as the forest vegetation is able to recover and densify within a relatively short period of time following fire events (Luger and Moll 1993; Poulsen 2013; Poulsen and Hoffman 2015). However, since fire history prior to 1991 on Grootbos is not known, fire extent was assessed visually for most of the historical imagery analysed. Fire presence also inhibits forest expansion by burning until it reaches the forest transitional vegetation, and by reducing the nutrient status of the surrounding fynbos soils (Manders 1990; Power 2018; Magadzire et al. 2019). In fynbos, fire leads to the mineralisation of nutrients within fynbos plants (Stock and Lewis 1986). After a fire, more nutrients are available, but with time the majority of nutrients are lost via leaching or assimilation (Manders 1990; Allsopp et al. 2014).

Edge effects play a key role in fragmented forests. In already small forest patches, fragmentation negatively affects their stability, due to altered species richness, species composition, forest nutrient cycling dynamics, trophic structures, and microclimate (Laurance et al. 2002; Fischer et al. 2021). These new disturbances affected the forests of GNPR and PFR very differently from natural fire disturbance. With official land deeds merely ca. 200 years old (Scheffler 1993), anthropogenic land-use and transformation likely increased significantly from the 1800s onward. The historical imagery analysed covers a period of altered fire regimes and relatively novel disturbance regimes. Despite the disturbances, it is obvious that forests have returned relatively quickly with minimal human intervention as reforestation events mostly started in the area after 2010.

Forest and fynbos are almost always separated by a transition zone, despite this not being reflected on vegetation maps, such as the vegetation map of South Africa (Dayaram et al. 2019). Indeed, the hierarchical cluster analysis (Fig. 11) illustrates that differences between transitional vegetation types and forests are not clear cut. Natural systems, in the majority of cases, do not simply exist as either forest or fynbos, and the finer scale vegetation categorisations are only constructs that help to make sense of the natural world (Mergili and Privett 2008). Although transitional vegetation of the various sites displayed considerable variation in terms of soil nutrient content and floristic composition, this does not mean that transitional vegetation of forests is degraded (Sayer et al. 2004; Sasaki and Putz 2009; Putz and Redford 2010). Degraded vegetation is usually associated with severe vegetation fragmentation, or species-poor, invasive plant dominated vegetation. 'Healthy' transitional vegetation plays a role as a buffer against fire for forests, and as a leading edge for forest expansion when fire frequency is reduced. Transitional vegetation usually occupies a narrow region due to non-linear "fire-vegetation-soil" feedbacks (Power 2018). The transitional vegetation sometimes has a soil nutrient status which is intermediate between forest and fynbos (Shurin et al. 2004; Coetsee et al. 2015; Power 2018; Cramer et al. 2019), but this was not always the case, perhaps because the transition was very narrow in some cases. The unique micro-environment of transitional vegetation means that unique community structure and edaphic properties occur at the boundary of forests and fynbos. The presence of legumes like *Psoralea arborea* in the transitional vegetation (Mergili 2005; Coetsee et al. 2015) occurs because they require more sunlight than forest species, but usually also higher nutrient status than is available in fynbos soils. These pioneer species enrich the soil (N fixation, organic matter input, etc.) and can facilitate forest expansion when fire is excluded over long periods of time (Coetsee et al. 2015; Cramer et al. 2019; MacPherson et al. 2019). Additionally, the transitional vegetation of Steynsbos was very wide along the western edge of the forest. However, a wide transition, such as at Steynsbos, may be a sign of reduced stability of either the forest, or fynbos (Poulsen 2013; Poulsen and Hoffman 2015).

Forest and fynbos distributions have been relatively stable and resilient for centuries, if not millennia, due to the climatic (and even longer geological) stability of the CFR (Cowling and Lombard 2002). The ecologically relevant time-scale for forest-fynbos ASS is therefore likely of the order of centuries to millennia (Thomas et al. 2010), depending on when the macro-environment changes sufficiently to promote either forest expansion, or retreat (Power 2018; Cramer et al. 2019). It is possible that Southern Coastal/Milkwood Forests and the surrounding fynbos are ASS.Despite this knowledge, the timescales and effort required to shift the system between states is unknown (Allsopp et al. 2014; Coetsee et al. 2015; Cramer et al. 2019). The rate of change in ecosystems can vary, and it is therefore challenging to distinguish between regime shifts (such as the classic abrupt example where a clear lake shifts into a eutrophic state (Ardichvili et al. 2023) and more gradual shifts in ecosystem boundaries (Zelnik et al. 2018; Michaels et al. 2020). This is because both regime shifts and gradual environmental change result in altered ecosystem structure and function, and both can exhibit non-linear responses to environmental conditions, such as a change in temperature. Furthermore, the limited availability of long-term data on ecosystem dynamics makes it challenging to accurately attribute vegetation change to specific ecosystem drivers. The timeframe of this study affects the interpretation of the results. However, the concept of ASS is especially important in the face of novel disturbance regimes that have clearly impacted entire (or large sections of) forests over at least the last century.

The stability of forests has more recently been affected by anthropogenic disturbance regimes (Scheffler 1993; Kruger 1994; Poulsen 2013; Poulsen and Hoffman 2015). In addition to fire, disturbances like trampling, woodcutting, herbivory, agricultural expansion, and invasive alien plants have caused forest fragmentation in all of the Southern Coastal/Milkwood Forests studied. The geographic context (i.e., steep mountainous terrain) of the Afromontane Forests means that they would have been more difficult to access and exploit than the Southern Coastal/Milkwood Forests. The Afromontane Forests had no noteworthy change in woody cover over the last century, which is similar to the findings for the Afromontane forest-fynbos boundaries of Blinkwater and Orange Kloof on Table Mountain (Cramer et al. (2019).

Establishment of alien invasive species or sustained modification of soils in a fragmented system might precipitate a regime shift to a third stable state that would displace both forest and fynbos as a result of nucleation in a fragmented system, as described by Michaels et al. (2020). The resilience of a degraded system is unknown, due to the fact that anthropogenic disturbances along forest-fynbos ecotones are relatively new. For similar reasons it is not known if regime shifts to degraded ecosystem states are more likely to occur over shorter periods of time than shifts between forest and fynbos stable states. Understanding if anthropogenic disturbance regimes will lead to a shift from forest to fynbos, or to a degraded state is not yet well understood. Furthermore, how much harder would it be to return an ecosystem to either forest or fynbos once the system is in a degraded state, given that allelopathy, erosion, and nutrient inputs would affect the stability of the degraded state (Holmes et al. 2020)? The Greater CFR has also experienced increases in mean annual temperatures due to climate change, but the effect on precipitation is less clear (Allsopp et al. 2014). The impacts of climate change in the GCFR are complicated, and varies depending on site-specific ecological conditions, so that reforestation based on the notion of climate induced forest shrinkage is largely unfounded, and hard to prove (Yates et al. 2010; Allsopp et al. 2014).

Recommendations for forest-fynbos ecotone management in the Overberg include keeping the heterogeneous and diverse transitional vegetation between forest and fynbos intact. Reforestation of transitional vegetation zones would disrupt the natural successional dynamics of the ecotone, even if native trees are planted. A loose association of open and closed vegetation must be avoided when restoration of vegetation is required (Sasaki and Putz 2009; Putz and Redford 2010). Rather, management should focus on interventions that will maintain the natural dynamics of the ecotone, such as clearing of invasive alien species and prescribed ecological burning (Putz and Redford 2010). Reforestation with native species should only be taking place where transitional vegetation is absent, e.g., after removing stands of alien invasive species, or where an agricultural field is being restored. Planting native trees in a forest transitional area that has previously been burned can also lead to disruptions in the natural dynamics and successional stages at the ecotone between forest and fynbos. Because fire plays an obvious ecological role in fynbos, and in maintaining forest-fynbos ecotones, tree planting post-fire may actually prevent the ecosystem from returning to its natural state and can negatively affect soil and water resources available to other plants and animals (Wilson et al. 2015). Before any restoration action is taken, conservation practitioners need to be very careful not to disrupt natural processes (Sasaki and Putz 2009; Wilson et al. 2015). It is also important to remember that every forest-fynbos ecotone is unique, and ‘behaves’ differently, so that universal guidelines telling conservation practitioners when to reforest is not reasonable.

Conclusion

Afromontane Forests found in valleys within mountainous terrain may not be representative of ASS, especially where the soil texture of the forest is different from that of the surrounding fynbos. Instead, “fire-vegetation-soil” feedbacks along Afromontane Forest-fynbos ecotones result in a “sharpening switch”, where the underlying abiotic environmental conditions initially determine the vegetation community, with fire and biotic feedback mechanisms reinforcing the stability and abrupt ecotonal boundary between Afromontane Forests and the surrounding fynbos. Under this model, fynbos cannot switch to forest, and forest cannot switch to fynbos. Southern Coastal/Milkwood Scrub Forests in this study more accurately fit into the ASS model, as abiotic conditions such as elevation, climate, and soil texture are all similar across the forest-fynbos ecotones. Forest-fynbos ecotones studied here show a degree of resilience to novel anthropogenic disturbance regimes, with rapid tree cover densification after the removal of disturbances over the past 85 years. This indicates that Southern Coastal/Milkwood Forests are resilient to intense disturbances, at least over approximately a century. However, the effect of continued anthropogenic disturbance regimes along forest-fynbos ecotones is largely unknown. Forest fragmentation in the long term would likely result in a species-poor degraded vegetation state. This degraded state must not be confused with natural transitional areas between forest and fynbos. Where alien invasive species, and other anthropogenic disturbances (excluding fire) are absent, best practice may be to wait for a few months, without active tree planting, to allow the vegetation to regenerate. This may help conservation practitioners to see if the area was previously forest, transitional vegetation, or fynbos, allowing them to take more appropriate action from there. It is difficult to identify the appropriate restoration action, and therefore such actions should be approached with due caution. Perhaps the only time when reforestation should be permitted is in areas where vegetation does not return on its own, where soils reflect the nutrient status of the forest, and where the patch is clearly part of a larger forest. Considering historical landscape stability, the stabilising effect of fire, and edaphic differences between forest and fynbos, the contrasting forest and fynbos vegetation types are unlikely to shift in distribution, or experience a regime shift, unless disturbances that severely fragment forests persist for long periods of time.

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Appendix

Site and sample locations

The general locations of each of the study sites are provided in Table 4. The specific locations of soil samples and vegetation surveys conducted can be obtained from the author. All of these locations were chosen at sites with relatively similar elevations, and where elevation differences between vegetation types are minimal. Generally, fynbos occupied slightly higher points in landscapes compared to forests, with the exception of Garden Lodge. The Baviaanskloof study site occupied the highest elevation of all study sites. Differences in elevation between Southern Coastal/Milkwood Forests and the surrounding fynbos occurred gradually. Elevation differences between Afromontane Forests and the surrounding fynbos occurred far more abruptly, as these forests were located in steep valleys.

Table 4: Information for the seven study sites of this study. The study sites include four Milkwood forests, two Afromontane forests and one intermediate Southern Coastal Forest. The elevation is given as a range.

Forest Types	**Site**	**Latitude (decimal)**	**Longitude (decimal)**	**Elevation (m)**	**Aspect (degrees)**	**Distance from coast (km)**
Afromontane Forest	Baviaanskloof	-34.5422	19.4393	290 - 340	SW, S	5.5
Afromontane Forest	Witvoetskloof	-34.5325	19. 502	70 - 140	E, W, SW	11.5
Southern Coastal Forest	Platbos	-34. 5682	19.4453	80 - 160	NE, E	5.5
Milkwood Forest	Forest Lodge	-34.5514	19.4133	200 - 235	NW, W	3.2
Milkwood Forest	Garden Lodge	-34. 5433	19. 4175	150 -250	SW	3.1
Milkwood Forest	Steynsbos	-34. 5176	19. 4466	160 - 225	W	6.7
Milkwood Forest	Witvoetskloof	-34.5284	19.4855	190 - 230	NE, E	10.1

Species richness comparison tables

Table 5: A comparison of species richness for forest (Fo), transitional vegetation (T), reforested areas (R), and the surrounding fynbos (Fy) at the seven study sites. The diagonal greyed out background is the observed species richness of each community. Above the diagonal is the shared richness between different vegetation types. Below the diagonal is a pooled species richness for different vegetation types. In total Witvoetskloof A had 138 species, Witvoetskloof M had 124 species, Baviaanskloof 63 species, Platbos 97 species, Steynsbos 112 species, Forest Lodge 90 species, and Garden Lodge had 71 species. The percentage of species at each site within a specific vegetation type is indicated in the right four columns.

		Number of Species				Species (%)			
Site	Vegetation	Fo	T	R	Fy	Fo	T	R	Fy
Steynsbos	Fo	18	14	12	3	16	12	11	3
	T	53	49	32	14	47	44	29	12
	R	68	76	62	20	61	68	55	18
	Fy	74	89	97	60	66	79	87	54
Garden Lodge	Fo	15	12	12	2	21	17	17	3
	T	43	41	16	8	61	58	23	11
	R	27	49	24	3	38	69	34	4
	Fy	43	63	51	31	61	89	72	44
Forest Lodge	Fo	17	10	10	1	19	11	11	1
	T	40	36	19	8	44	40	21	9
	R	44	50	38	8	49	56	42	9
	Fy	64	76	78	49	71	84	87	54
Platbos	Fo	23	11	10	2	24	11	10	2
	T	54	46	14	9	56	47	14	9
	R	50	67	38	5	52	69	39	5
	Fy	58	73	69	37	60	75	71	38
Witvoetskloof M	Fo	21	12	15	4	17	10	12	3
	T	61	54	26	12	49	44	21	10
	R	56	78	51	10	45	63	41	8
	Fy	81	104	101	64	65	84	81	52
Witvoetskloof A	Fo	21	13		0	15	9		0
	T	71	63		1	51	46		1
	Fy	92	130		71	67	94		51
Baviaanskloof	Fo	21	17		3	33	27		5
	T	42	38		9	67	60		14
	Fy	54	60		37	86	95		59

PCoA plots per site

In addition to the PCoA plot for all of the study site presented in this thesis, plots for all seven study sites were created (Figs. 20 and 21). Only soil variables with a significant effect ($p<0.05$) are shown in the plots. All ordination plots were made using a Bray-Curtis dissimilarity matrix.

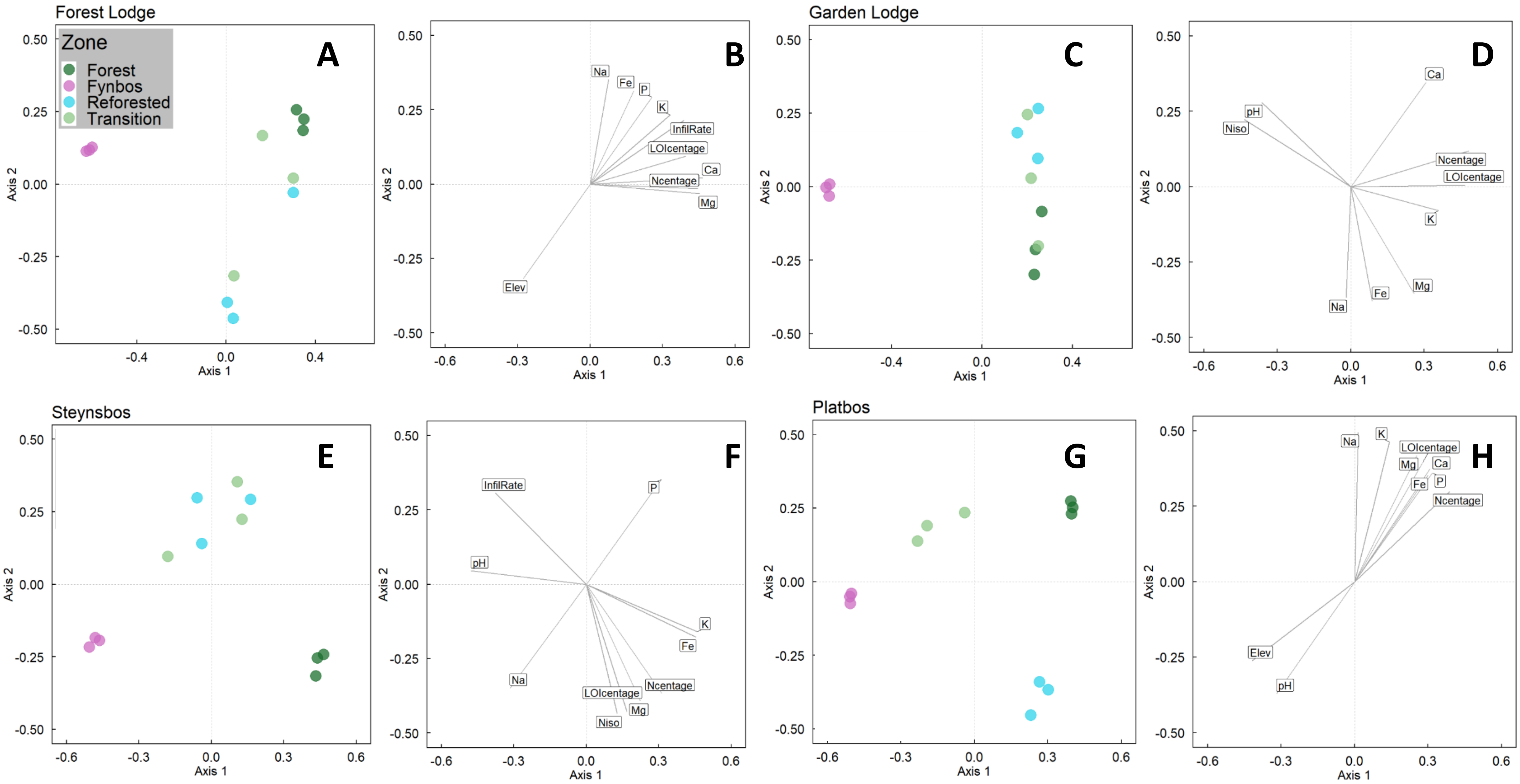


Figure 20: Ordination plots for Forest Lodge, Garden Lodge, Steynsbos, and Platbos study sites. Each pair of figures illustrate clusters formed by the forest, transitional, fynbos, reforested areas, and fynbos vegetation surveyed (A, C, E, and G), with the effect of only significant soil variables (B, D, F, and H). Elevation is "Elev", infiltration of water through the soil is "InfilRate", $\delta^{15}N$ is "Niso", and loss-on-ignition is "LOIcentage").

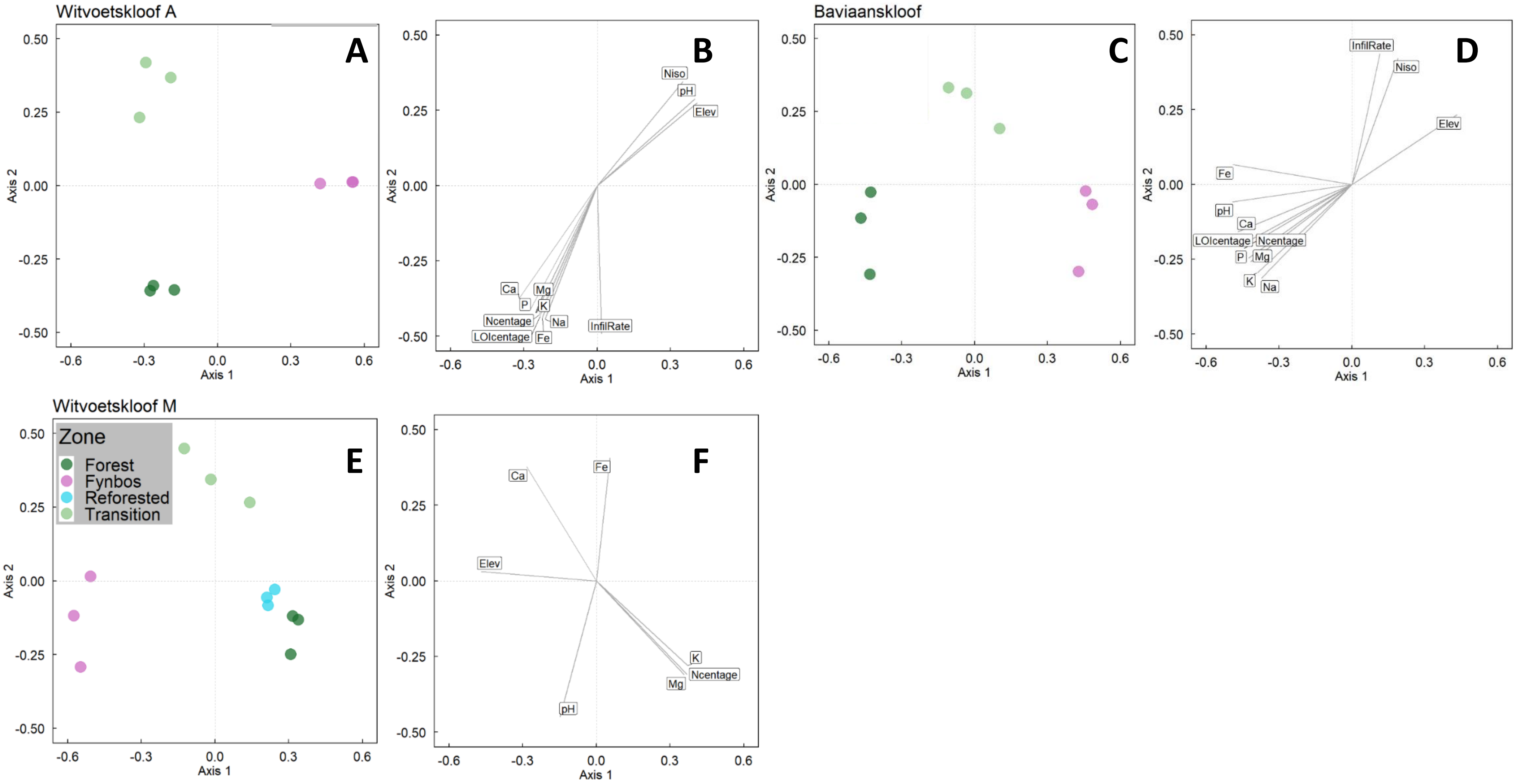


Figure 21: Ordination plots for Witvoetskloof A, Baviaanskloof, and Witoetskloof M study sites. Each pair of figures illustrate clusters formed by the forest, transitional, fynbos, reforested areas, and fynbos vegetation surveyed (A, C, and E), with the effect of only significant soil variables (B, D, and F). Elevation is "Elev", infiltration of water through the soil is "InfilRate", $\delta^{15}N$ is "Niso", and loss-on-ignition is "LOIcentage".

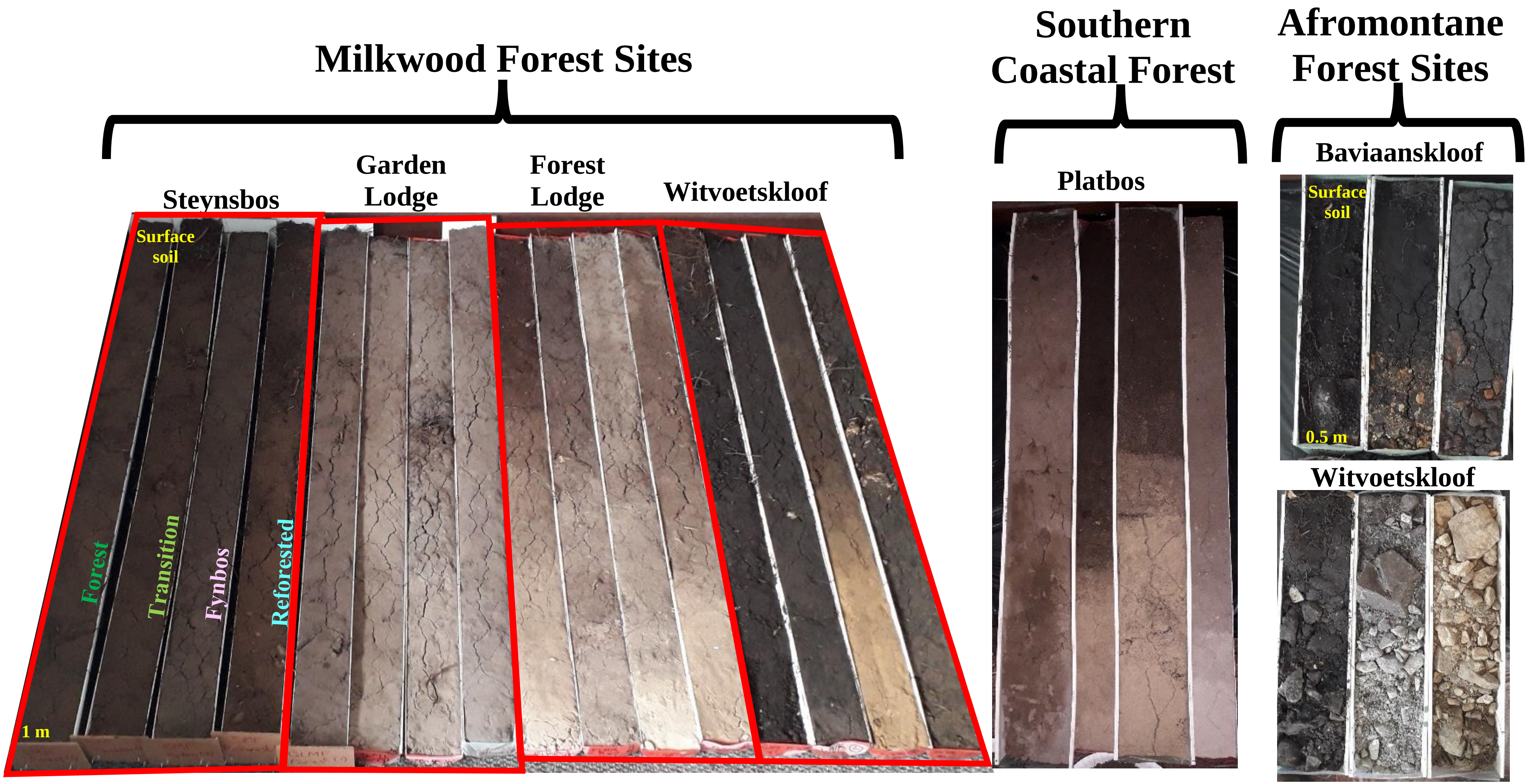


Figure 22: The soil monoliths collected on GNPR and PFR. Monoliths from sites with Milkwood Forests and the Southern Coastal Forest at Platbos were one meter deep, and those from the Afromontane forests were 0.5meters deep. Each site is represented by four monoliths, with the order from left to right being forest, transitional vegetation, fynbos, and the reforested area. These act as a visual aid for the display of differences between soil profiles. Soil horizons in the deep sandy aeolian soil profiles are not well developed for any of the milkwood forests, however organic matter has accumulated in the top few cm of the soil for most of the sites. Monoliths collected from Steynsbos are all very similar to each other, with no real visual differences between soil collected in forest vs. fynbos. The same is true for Garden Lodge soils, however these soils are much lighter in colour (with wet Munsell colours of very dark grey, very dark greyish brown, or dark grey) than the Steynsbos soils (with wet Munsell colours of very dark brown or black).

Historical images classified

High resolution historical aerial imagery that was obtained were classified over eight timestamps, the earliest of which is 1938 imagery. Following from 1938, imagery from 1961, 1973, 1980, 1989, 1998, 2005, and 2022 was analysed (list of images used in Table 6).

Table 6: Historical imagery used in the analysis. All these photographs were obtained from the Department of Agriculture, Land Reform, and Rural Development using their National Geospatial Information (NGI). The georeferencing method used is 'spline' in ArcGIS Pro.

Job	**Flight**	**Photo ID**	**Year**	**Date**	**Time of the day**	**Photo scale or height**
130	043	20436	1938	23 Dec.	ca.13h00	11 500 ft
130	043	20439	1938	23 Dec.	ca.13h00	11 500 ft
130	045	20447	1938	23 Dec.	ca.13h10	11 500 ft
130	045	20450	1938	23 Dec.	ca.13h10	11 500 ft
130	045	20453	1938	23 Dec.	ca.13h10	11 500 ft
130	046	20461	1938	23 Dec.	ca.13h20	11 500 ft
130	046	20464	1938	23 Dec.	ca.13h20	11 500 ft
461	011	08593	1961	02 Dec.	ca.11h45	1:36 000
461	011	08595	1961	02 Dec.	ca.12h00	1:36 000
461	012	08607	1961	02 Dec.	ca.12h00	1:36 000
719	030	01778	1973	21 Feb.	ca.13h50	12 000 ft
719	031	02103	1973	26 Feb.	ca.11h50	12 000 ft
498	148_001	01000	1980	08 April	ca.14h50	1:30 000
498	148_001	01269	1980	05 June	ca.12h30	1:30 000
498	148_002	01275	1980	05 June	ca.12h30	1:30 000
931	007	02107	1989	08 Dec.	ca.10h05	1:50 000
1004	024	03373	1998	19 Feb.	ca.11h30	1:60 000
1109	010	00388	2005	19 Nov.	ca.12h30	1:20 000
1109	011	00399	2005	19 Nov.	ca.12h40	1:20 000
1109	011	00400	2005	19 Nov.	ca.12h40	1:20 000
1109	011	00403	2005	19 Nov.	ca.12h40	1:20 000
1109	012	00434	2005	19 Nov.	ca.14h00	1:20 000

The maps presented in Figs. 22 and 23 below show the imagery from 1938, 1980, and 2022. 1980 imagery is also illustrated in this appendix as it represents an intermediate between 1938 and 2022 and is close to the year 1989, which is the comparison date included in the imagery analyses by (Kruger 1994). A legend of all the classified land cover categories is presented in Fig. 22 below and can be used as a reference for all of the maps that follow in this section. The author recognises that the classifications presented are not perfect, and can be further refined, and can incorporate far more information than they do at present.

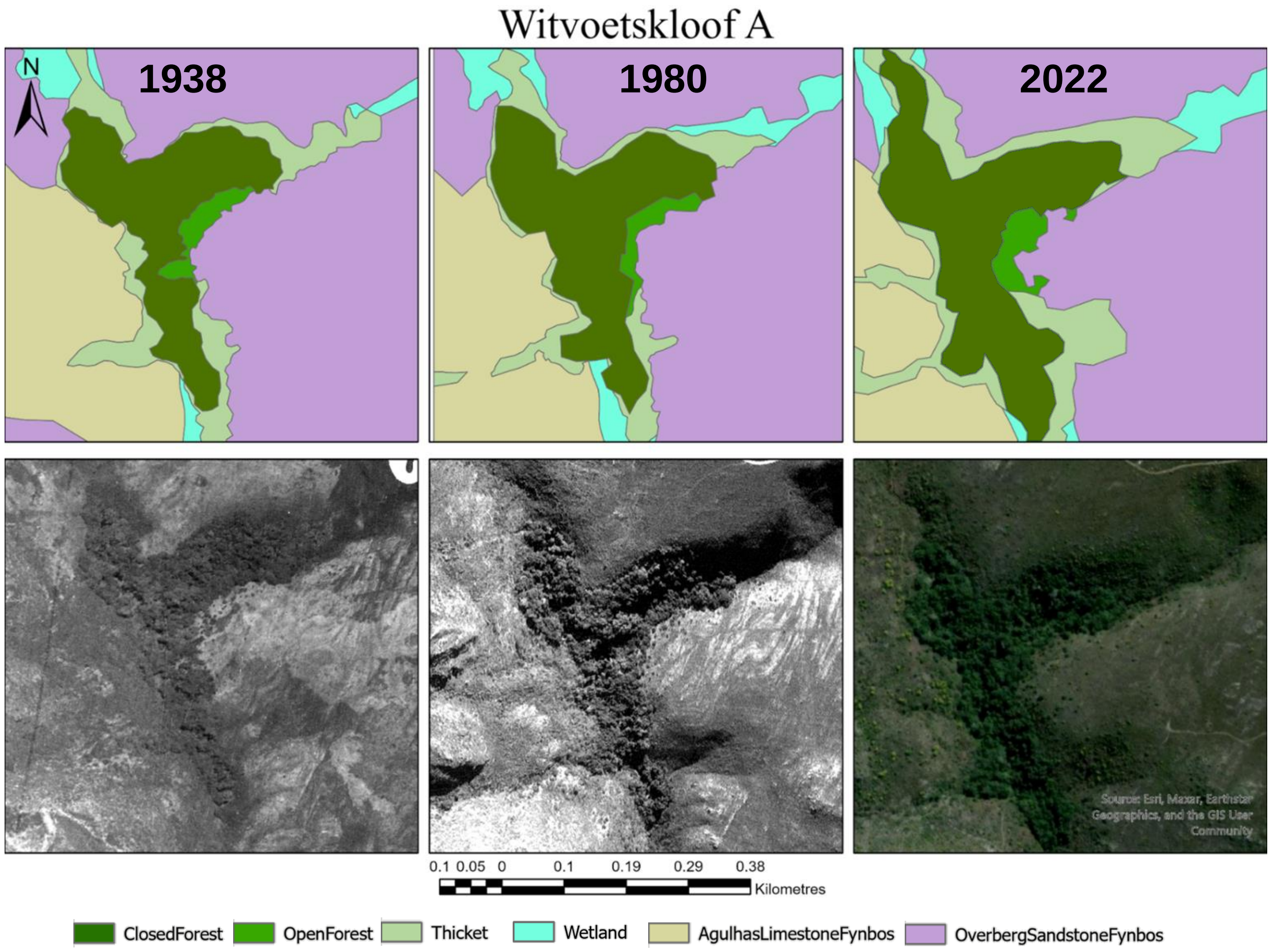


Figure 23: A subset of the historical images (bottom row) that were classified, and the corresponding land cover classification (top row) of 1938, 1980, and 2022 are illustrated for Witvoetskloof A. A legend for all colours represented in the classified images is below the figure. The dark green classification represents a closed canopy Afromontane Forest, and slightly lighter green represents open canopy forest (ca. 50 – 80% tree cover). The light green represents transitional *Pteris dentata* Shrubland vegetation.

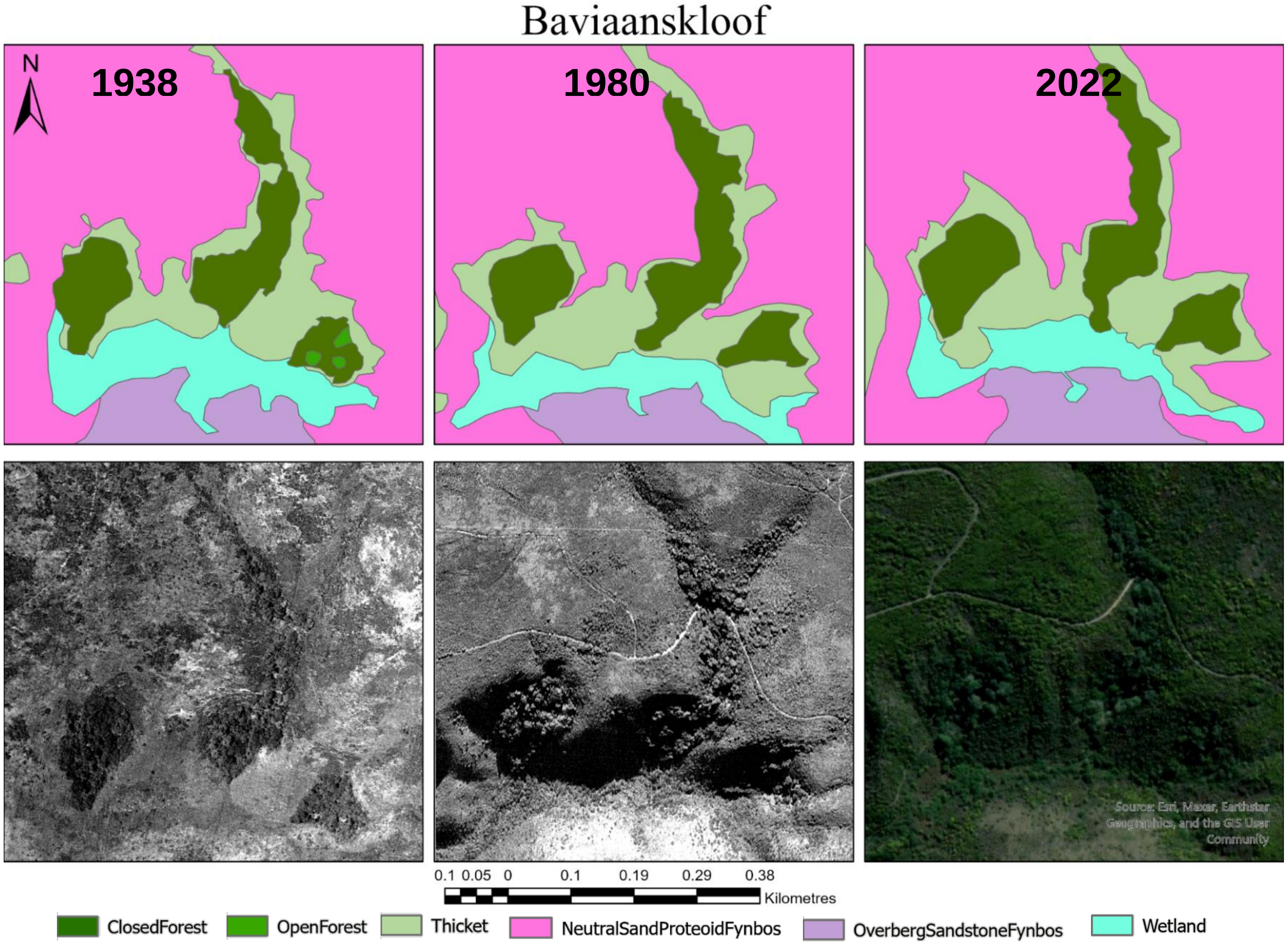


Figure 24: A subset of the historical images (bottom row) that were classified, and the corresponding land cover classification (top row) of 1938, 1980, and 2022 are illustrated for Baviaanskloof. A legend for all colours represented in the classified images is below the figure. The dark green classification represents a closed canopy Afromontane Forest, and slightly lighter green represents open canopy forest (ca. 50 – 80% tree cover). The light green represents transitional *Pteris dentata* Shrubland vegetation.

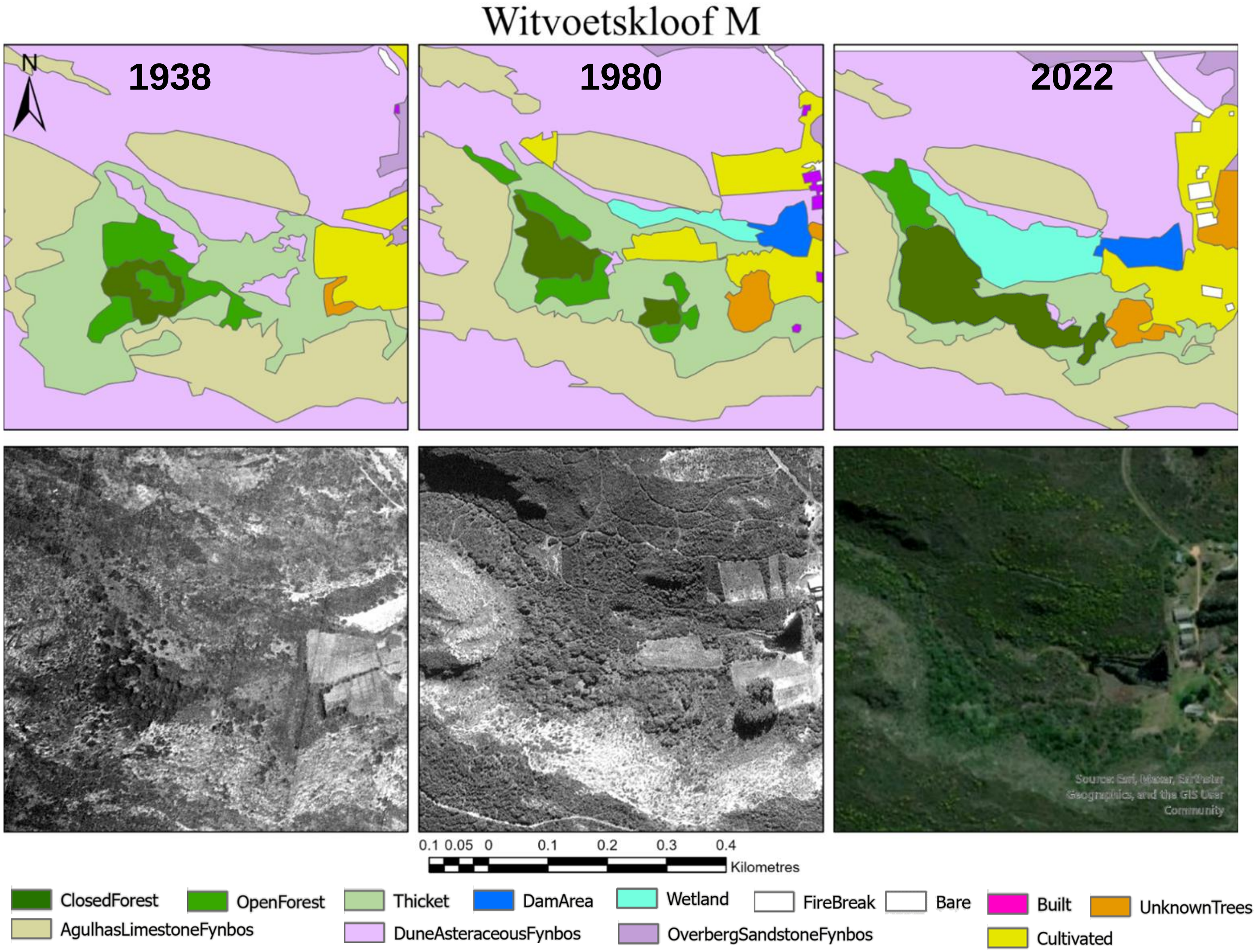


Figure 25: A subset of the historical images (bottom row) that were classified, and the corresponding land cover classification (top row) of 1938, 1980, and 2022 are illustrated for Witvoetskloof M. A legend for all colours represented in the classified images is below the figure. The dark green classification represents a closed canopy Milkwood Scrub Forest, and slightly lighter green represents open canopy forest (ca. 50 – 80% tree cover). The light green represents the Transitional Thicket vgeetation. "Unknown Trees" in these images represent mostly *Eucalyptus* trees.

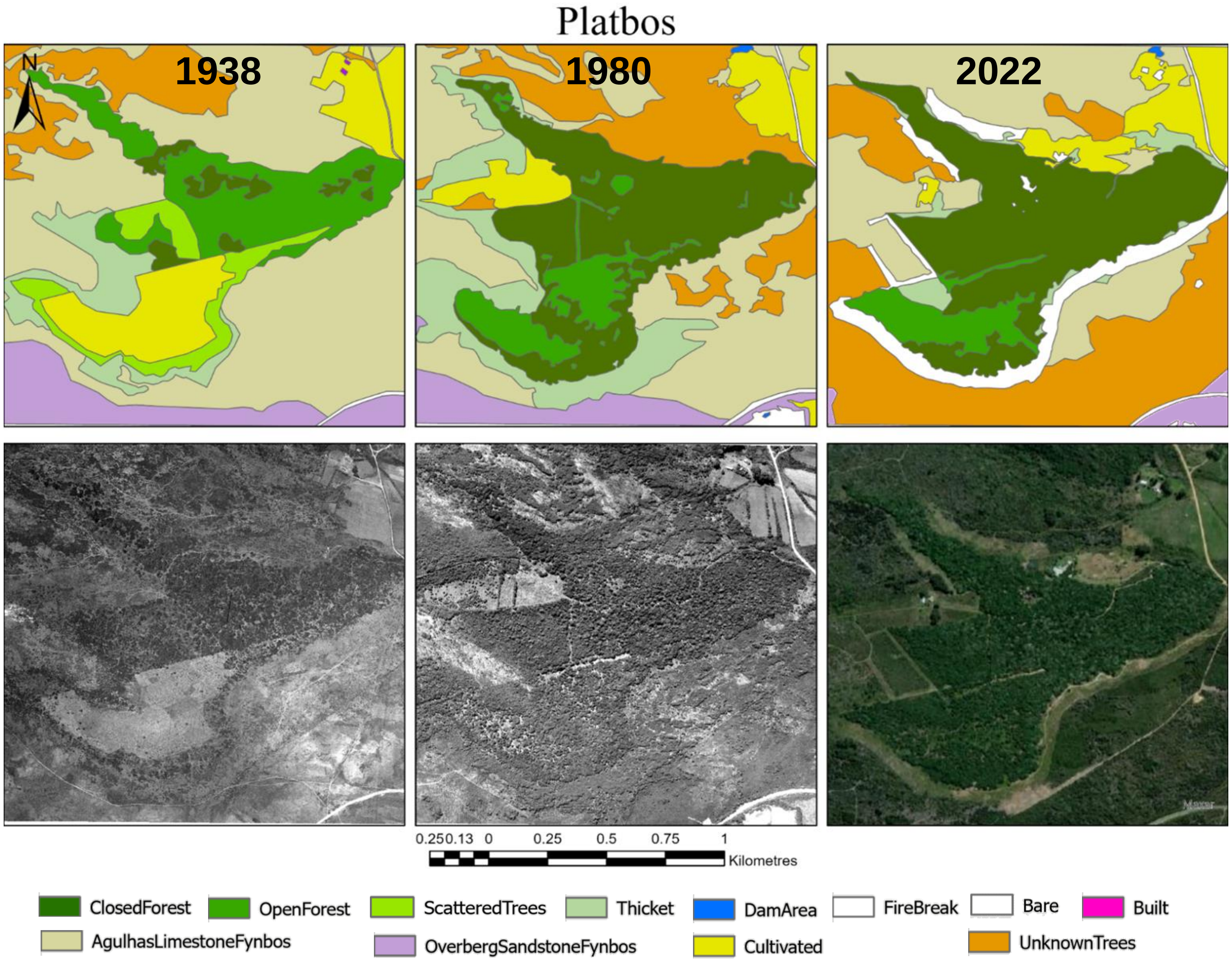
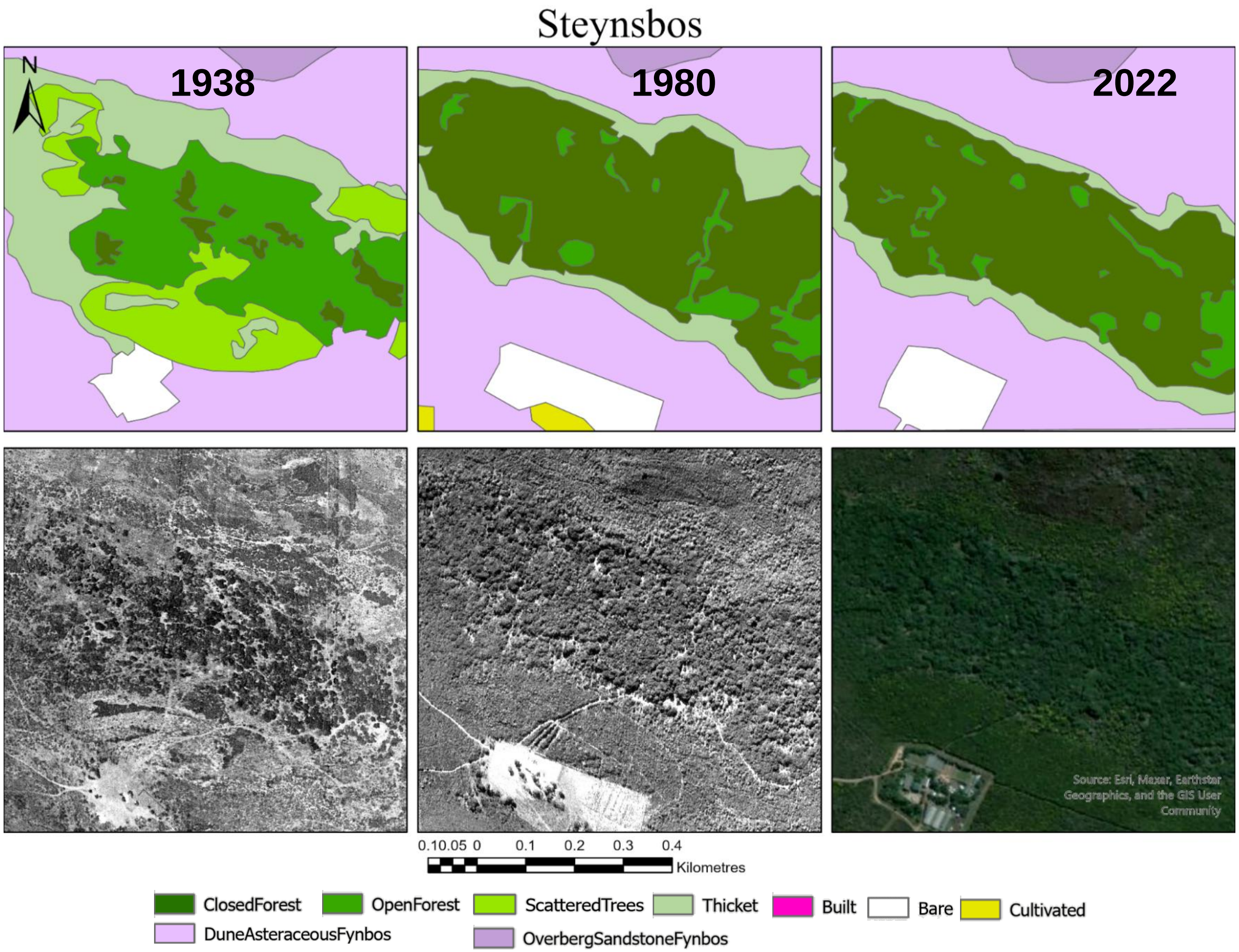


Figure 26: A subset of the historical images (bottom row) that were classified, and the corresponding land cover classification (top row) of 1938, 1980, and 2022 are illustrated for Platbos. A legend for all colours represented in the classified images is below the figure. The dark green classification represents a closed canopy Southern Coastal/Milkwood Forest, and slightly lighter green represents open canopy forest (ca. 50 – 80% tree cover). Scattered trees represent an estimated tree cover <50%. The light green represents the Transitional Thicket vegetation. “Unknown Trees” in these images represent mostly *Eucalyptus conferruminata*, and *Acacia lognifolia*.



Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community

Figure 27: A subset of the historical images (bottom row) that were classified, and the corresponding land cover classification (top row) of 1938, 1980, and 2022 are illustrated for Steynsbos. A legend for all colours represented in the classified images is below the figure. The dark green classification represents a closed canopy Milkwood Scrub Forest, and slightly lighter green represents open canopy forest (ca. 50 – 80% tree cover). Scattered trees represent an estimated tree cover <50%. The light green represents the Transitional Thicket vegetation.

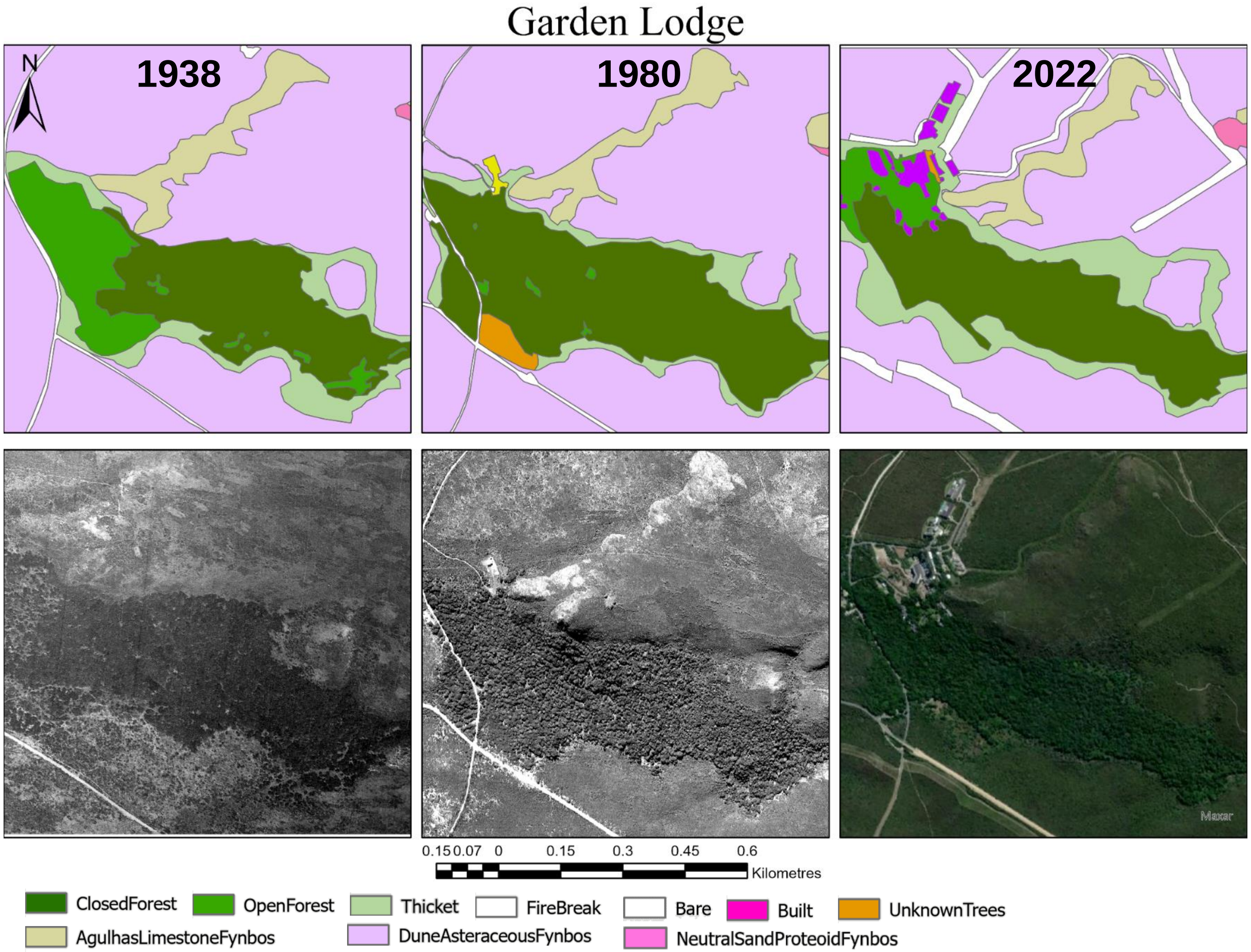


Figure 28: A subset of the historical images (bottom row) that were classified, and the corresponding land cover classification (top row) of 1938, 1980, and 2022 are illustrated for Garden Lodge. A legend for all colours represented in the classified images is below the figure. The dark green classification represents a closed canopy Milkwood Scrub Forest, and slightly lighter green represents open canopy forest (ca. 50 – 80% tree cover). The light green represents the Transitional Thicket vegetation.

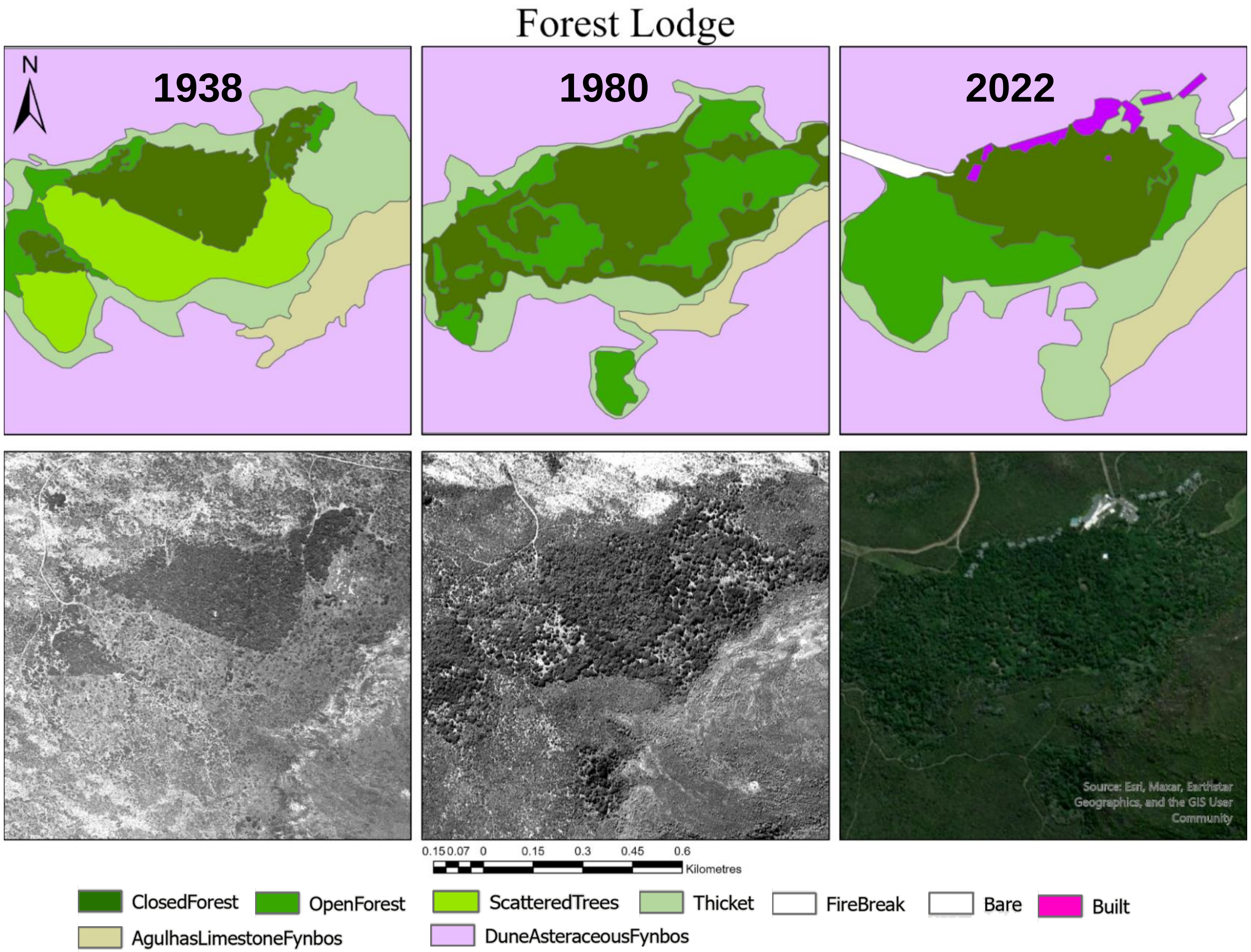


Figure 29: A subset of the historical images (bottom row) that were classified, and the corresponding land cover classification (top row) of 1938, 1980, and 2022 are illustrated for Forest Lodge. A legend for all colours represented in the classified images is below the figure. The dark green classification represents a closed canopy Milkwood Scrub Forest, and slightly lighter green represents open canopy forest (ca. 50 – 80% tree cover). Scattered trees represent an estimated tree cover <50%. The light green represents the Transitional Thicket vegetation.

Mann-Kendall trend analysis

Tree cover for historical imagery was manually assigned to each of the circular polygons presented in the maps below (Figs. 30 and 31). A Mann-Kendall non-parametric analysis of trends was used to assign colours to find significant relationships where tree cover either increased, decreased, or had no significant change since 1938. Note tha the fire break of Platbos (Fig. 31) is recent feature in the landscape, having only been made before 2012. It is therefore only about a decade old, and is absent in the earlier images.

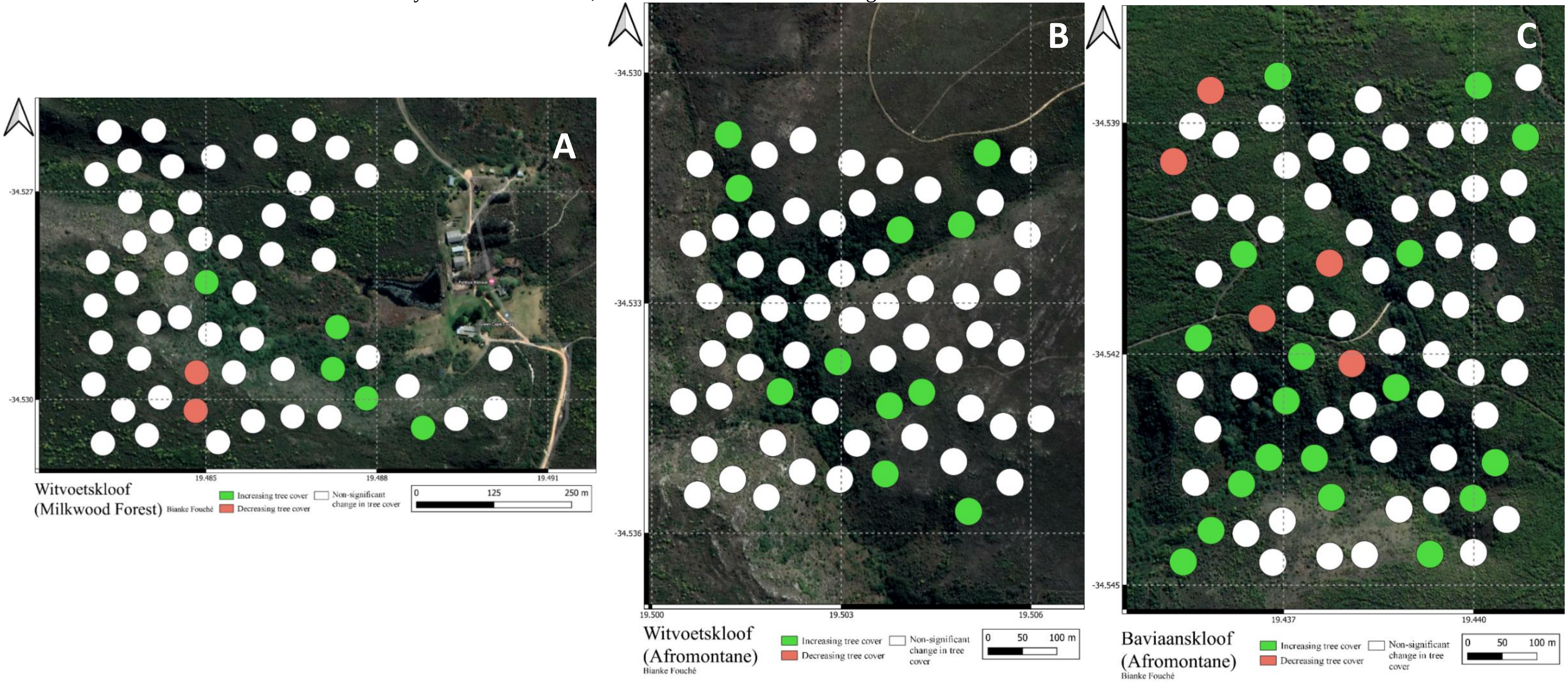


Figure 30: Results from a Mann-Kendall trend analysis to detect tree cover change over eight timestamps for Witvoetskloof M (A), Witvoetskloof A (B), and Baviaanskloof (C). The images analysed for input into the model were from 1938, 1961, 1973, 1980, 1989, 1998, 2005, and 2022. Green circles represent areas that show a significant positive trend for increasing tree cover, while red indicates a significant negative trend. White circles indicate there was no significant change in tree cover.

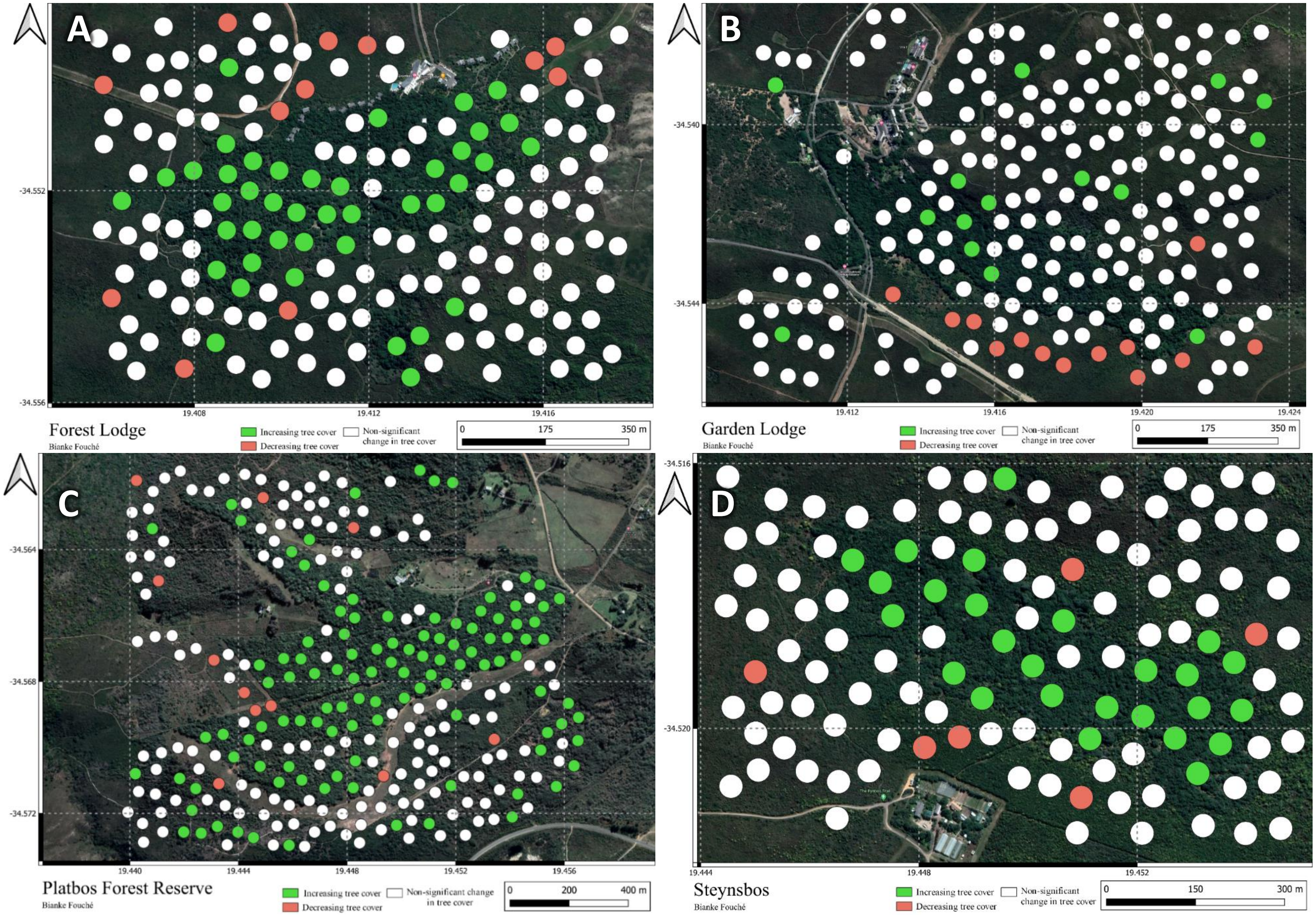


Figure 31: Results from a Mann-Kendall trend analysis to detect tree cover change over eight timestamps for Forest Lodge (A), Garden Lodge (B), Platbos (C), and Steynsbos (D). The images analysed for input into the model were from 1938, 1961, 1973, 1980, 1989, 1998, 2005, and 2022. Green circles represent areas that show a significant positive trend for increasing tree cover, while red indicates a significant negative trend. White circles indicate there was no significant change in tree cover.

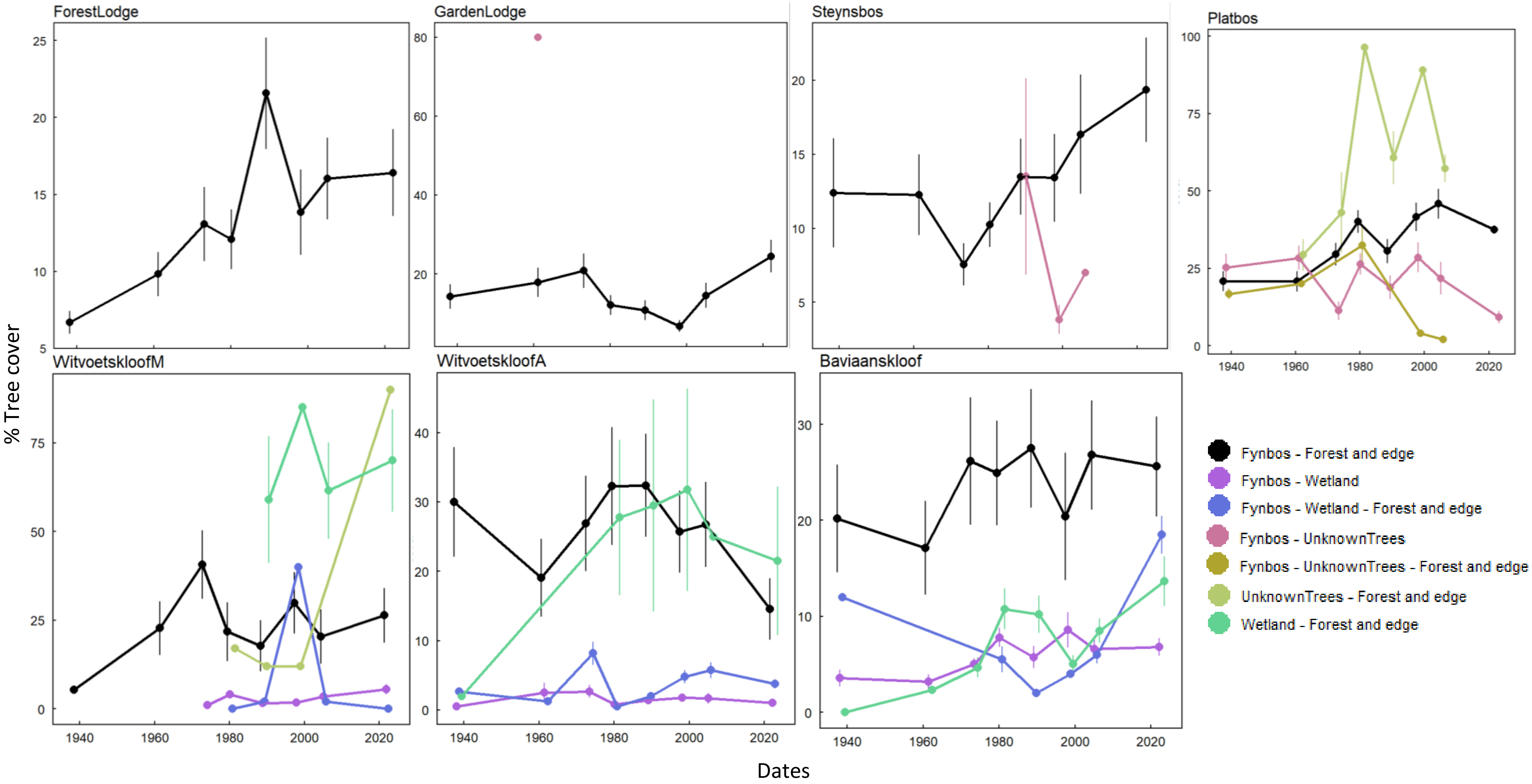


Figure 32: The change in tree cover between 1938 and 2022 averaged over the randomly sampled points within four broad vegetation categories, namely 1) forests and the forest transitional vegetation, 2) “unknown trees”, which represents invasive plants and cultivated trees, 3) fynbos vegetation, and 4) wetlands. The data presented here refers to tree cover assessments within areas that covered two or more of these vegetation cover categories over all eight historical images that were analysed. The combination of categories that is represented is shown in the legend of this figure, in order to show how tree cover has changed along the boundaries of each vegetation cover category. The line graphs represent the average assigned tree cover% within the various vegetation categories across the eight historical layers (1938, 1961, 1973, 1980, 1989, 1998, 2005, and 2022). Standard error bars are shown per line graph to illustrate the variation in tree cover that was assigned within each of the vegetation categories for a given point in time.