

SPATIAL AND TEMPORAL CHANGES IN FYNBOS RIPARIAN VEGETATION ON SELECTED UPLAND RIVERS IN THE WESTERN CAPE

By

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DECLARATION

This thesis reports original research carried out during 2011 and 2012, at the University of Stellenbosch, South Africa. It has not been submitted in whole or in part for a degree at any other university. Data presented here are original, and any other sources of data acquired are acknowledged such as the use of historic data to which newly collected data sets were compared to.

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ABSTRACT

Restoration practices commonly make use of a reference condition in order to restore a site to a better ecological state than it is currently in. The selection process and relevance of the reference condition has not yet been tested in upland Western Cape rivers especially with relation to spatial and temporal scales. This thesis sought to evaluate whether space (longitudinal) and time (temporal) influence riparian plant community composition (laterally), how it influences the community composition and whether these differences impacts the selection of a reference condition used in restoration practices.

In order to investigate the role longitudinal position, sites were selected across three longitudinal zones: mountain stream, transitional and upper foothills. Historic sites used in a previous study on riparian vegetation of upland rivers were resampled and datasets used for temporal comparisons between undisturbed sites, sites recovering after clearing of invasive alien plants and sites affected by fire.

Riparian vegetation communities showed differences between longitudinal zones, basins and rivers. The species responsible for marginal zone identity (plants in close proximity to the active channel), determined using relative cover abundance varied, with *Isolepis prolifera* responsible for the group identity in the mountain stream and transitional sites but in the foothills *Calopsis paniculata*, *Drosera capensis* and *Metrosideros angustifolia* saplings were responsible for lateral zone identity. The lower dynamic (transitional between wet and drybank) had no similarities between different longitudinal zones across rivers. In the lower zone *Pteridium aqualinum* was mostly responsible for the identity. The upper bank had no single species responsible for group identity. The species described to be typical for the reference condition on these particular rivers by other studies were mostly present in the comparable lateral zone but it was however not always responsible for the identity of the specific lateral zone.

By comparing selected environmental variables such as horizontal distance from active channel, elevation and substrate calibre with different longitudinal zones' riparian vegetation species distribution, different combinations were produced. The mountain streams showed the strongest relationship with horizontal distance and elevation in combination to one another and the upper foothills horizontal distance from the active channel was linked most strongly to vegetation positioning. These results confirm the importance of space when attempting to assess, study or restore riparian communities.

Temporally, sites had stronger similarity to data collected during the same sampling period than with historic data. Also, the overall relative species abundance did not show significant change to be present at a site scale. The changes in community composition were found to be due to a lateral zone scale variation in species abundance. As expected the undisturbed rivers showed less variation in species responsible for temporal changes than the recovering and fire-exposed rivers. Species responsible for changes in relative abundance at a lateral zone scale were *Metrosideros angustifolia*, *Morella serrata*, *Brabejum stellatifolium*, *Isolepis prolifera*, *Elegia capensis*, *Prionium serratum* and *Calopsis paniculata*. Due to the species diversity not changing much temporally but the relative abundance of specific species showing much variation over time it can be concluded that the changes are not diversity based but instead driven by changes in relative abundances of species typical for a lateral zone.

The spatial and temporal variation in riparian vegetation community composition was found to be significant enough to suggest that the use of a fixed reference condition for all Western Cape rivers would not be feasible due to clear differences between basins. Secondly when selecting a reference site the spatial location of this site should be within the same longitudinal zone since bank shape does influence riparian plant species distribution. Finally the temporal comparison between sites showed high diversity in species abundances but small differences in diversity overall. This would suggest that a general community description specific to 1) where the site is situated and 2) based on the present riparian vegetation community composition within a specific basin may be more realistic and achievable for restoration and environmental management purposes as opposed to using site descriptions from the past and reference sites too far upstream or downstream from the restoration site.

SAMEVATTING

Herstel praktyke maak algemeen gebruik van 'n verwysing toestand om 'n terrein te herstel na 'n beter ekologiese toestand as wat dit tans is. Die keuringsproses en relevansie van die verwysing toestand is nog nie in die boonste gedeeltes van Wes-Kaap Riviere getoets nie, veral met betrekking tot ruimtelike en tydskaal nie. Hierdie tesis het gesoek om te evalueer of ruimte (longitudinaal) en tyd (temporaal) rivieroewers plant gemeenskap samestelling (lateraal) beïnvloed en of hierdie verskille die keuse van 'n verwysing toestand in die herstel praktyke beïnvloed.

Ondersoek terreine was oor drie longitudinale sones geselekteer: berg stroom, oorgangs en boonste hange terreine. Historiese terreine was weer ondersoek en die datastelle was gebruik vir die temporale vergelykings tussen onversteurde terreine, terreine wat herstel na die skoonmaak van indringer spesies en wat geraak was deur 'n brand.

Oewerplantegroei gemeenskappe het verskille tussen longitudinale sones, rivier-kom en rivier takke gewys. Die spesies wat verantwoordelik was vir marginale zone (plante in nabye afstand met die aktiewe rivier kanaal) identiteit, bepaal met behulp van relatiewe dekking hoeveelheid, het gevarieer met *Isolepis prolifera* verantwoordelik vir die groep identiteit in die berg stroom en oorgangs terreine, maar in die boonste hange was dit *Calopsis paniculata*, *Drosera capensis* en *Metrosideros angustifolia* boompies wat verantwoordelik was vir die laterale sone identiteit. Die laer dinamiese area het geen ooreenkomste tussen marginale gebiede van verskillende longitudinale sones gehad nie. In die onderste sone was *Pteridium aquilinum* meestal verantwoordelik vir die groepering se identiteit. Die boonste bank het nie 'n enkele spesie wat verantwoordelik was vir die groep identiteit gehad nie. Die spesies beskryf as tipies vir die laterale sone deur Reinecke et al. (2007) was meestal teenwoordig in die beskryfde laterale sone van hierdie studie, maar dit was egter nie altyd verantwoordelik vir die identiteit van die laterale sone gemeenskap nie.

Verskillende lengte sones het gekorreleer met verskillende omgewingsveranderlikes wat sterkste gekoppel kon word aan die verspreiding van spesies. Die bergstrome het die sterkste verhouding met horisontale afstand en hoogte in kombinasie met mekaar gehad en in die boonste hange was horisontale afstand van die aktiewe kanaal die sterkste gekoppel aan plantegroei posisie. Die belangrikheid van ruimte is onmiskenbaar ten opsigte van evaluering, bestudering en die herstel van rivieroewers gemeenskappe.

Terreine het sterker ooreenkoms met data gehad wat tydens dieselfde tydperk versamel was, as met historiese data. Die algehele relatiewe spesies hoeveelheid het egter nie beduidende verandering getoon op 'n terrein skaal nie. Soos verwag was het die onversteurde riviere minder temporale variasie in spesies getoon as die herstellende en brand blootgestelde riviere. Spesies wat verantwoordelik was vir die verandering in relatiewe hoeveelhede op 'n laterale sone skaal was *M. angustifolia*, *Morella serrata*, *Brabejum stellatifolium*, *I. prolifera*, *Elegia capensis*, *Prionium serratum* en *C. paniculata*.

As gevolg van die diversiteit van spesies wat nie baie verander het tydelik nie, maar die relatiewe hoeveelheid van spesifieke spesies wat heelwat variasie oor tyd getoon het, kan dit afgelei word dat die veranderinge nie diversiteit gebaseer was nie, maar eerder gedryf was deur veranderinge in relatiewe hoeveelhede van tipiese spesies in 'n laterale sone.

Die ruimtelike en tydelike variasie in oewerplantegroei gemeenskap samestelling was beduidende genoeg om voor te stel dat die gebruik van 'n vaste verwysing toestand vir alle Wes-Kaapse riviere nie haalbaar sou wees nie as gevolg van duidelike verskille tussen riviere. Tweedens, by die kies van 'n verwysing terrein moet die ruimtelike plek van hierdie terrein in dieselfde lengte sone wees aangesien bank vorm 'n invloed op rivieroewer plant verspreiding het. Laastens, het die tydelike vergelyking tussen terreine hoë diversiteit in spesies verspreidings maar klein verskille in algehele diversiteit gehad. Dit stel voor dat 'n algemene beskrywing van die gemeenskap wat spesifiek op 1) waar die terrein geleë is en 2) gebaseer op die huidige oewerplantegroei gemeenskap samestelling binne 'n spesifieke rivier netwerk dalk meer realisties en haalbaar vir hersteel en bestuurs doeleindes sou wees. Hierdie benadering word verkies bo die gebruik van 'n terrein beskrywings uit die verlede en verwysing terreine te ver stroomop of stroomaf van die herstel gebied.

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1 General Introduction

1.1 Background

Rivers are complex, multidimensional, dynamic ecosystems (Wilson and Imhof 1998). Their functioning is influenced by their size (Ward et al. 2002), position in the catchment, geology and hydrology (Naiman and Décamps 1997). Riparian vegetation occurs on the banks of rivers, ponds, wetlands and lakes and is associated with almost all continental freshwater bodies (Naiman et al. 2005) forming ecotones between terrestrial and aquatic ecosystems (Swanson et al. 1992). A transition is present in riparian vegetation moving from the active channel to the terrestrial habitat. The transition from aquatic to terrestrial is known as the riparian zone and forms part of the lateral dimension of interactions occurring in a riverine environment.

Riparian vegetation occurs in two main zones up the bank: wetbank and drybank. The wetbank and drybank can be segregated into smaller lateral zones, which have been described as being associated with flood recurrence levels (Boucher 2002; Reinecke and Brown 2013) and containing species that are associated with them specifically (Reinecke et al. 2007; Sieben et al. 2009).

Environmental factors affecting riparian areas operate on different temporal hierarchical scales (O'Neill et al. 1986) and also across three physical dimensions (Wilson and Imhoff 1998). These are:

1. Longitudinal, from source to mouth, for example, longitudinal changes in rivers along their length include those associated with the river continuum concept (Vannote et al. 1980), the nutrient spiralling concept (Webster and Patten 1979) and the hyporheic corridor concept (Stanford and Ward 1993).
2. Vertical, between the bank, fluvial aquifers and river bed, exemplified by studies on the vertical exchange in the hyporheos (Palmer et al. 1992).
3. Laterally across the floodplain, addressed in studies such as Junk et al. (1989), who described the riparian flood-pulse concept for floodplains.

The main drivers of change in these dimensions are hydrology and geomorphology (Lorenz et al. 1997), the effects of which should be considered within the appropriate temporal scale (Ward 1989; Ward et al. 2002, Figure 1.1).

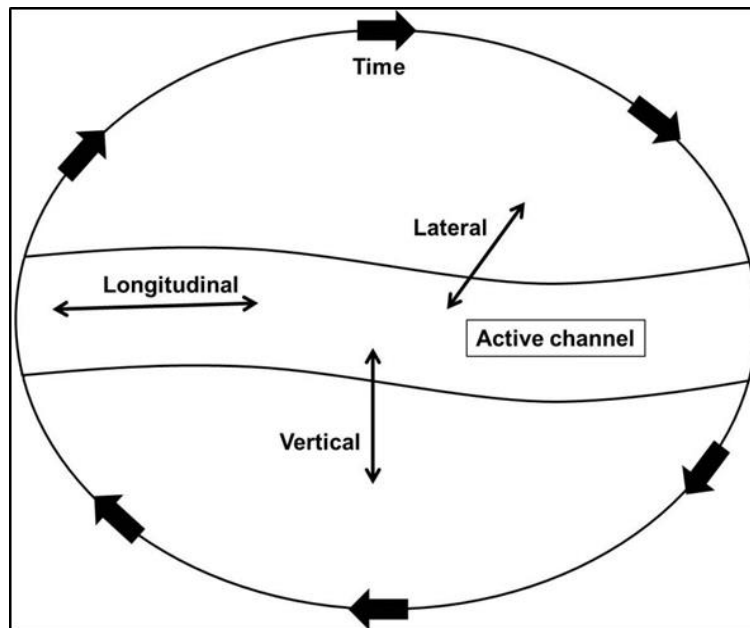


Figure 1.1 Diagrammatic representation of the four dimensions in which interactions and exchange occurs in riparian vegetation along rivers. Three are physical dimensions: lateral, vertical and longitudinal. The fourth dimension is time as indicated by the outside chain.

The prevailing hydrological regime drives riparian dynamics (Brinson 1990; Correll and Weller 1989; Tabacchi et al. 1998; Ward and Stanford 1995), directly influencing the riparian vegetation. Water moving downstream expends energy on the transport and re-arrangement of bed and bank sediment. The adjustment of channel form results in changes to channel width and depth that affect water velocity and sediment load. Riparian biota respond to such changes in the recruitment phase due to the influence channel and bank shape have on established species as well as the removal of individuals and succession processes that follow (Gordon et al. 1992).

The distribution of particle sizes on the river bed and banks has a major influence on the distribution of riverine plant and animals (Gordon et al. 1992). Local flow conditions have a sorting effect on sediment, as finer particles travel further downstream than larger material. Finer sediments are therefore often found in areas of deposition such as large pools and/or backwaters, whereas faster flowing areas are flushed clean of fine material. The distribution of substrate (especially coarser material) may only change at high flows, when flow velocities are sufficiently high to transport the bigger particles, and thus the spatial distribution of materials is often closely related to antecedent flood events.

Many authors have linked hydrology, or aspects thereof, to the zonation of riparian vegetation, resulting in various zonal definitions (Boucher 2002; Sieben et al. 2009; Taman 2001; Thayer et al. 2005).

Taman (2001), working on wetlands in the South-West of Western Australia used the volume and depth of water to define four riparian zones, whereas Thayer et al. (2005) described six zones based on a combination of elevation from the water's edge and flood recurrence intervals for South African rivers. Boucher (2002) described three main zones in Fynbos riparian ecosystems, comprised of seven-sub-zones based on a combination of elevation from the water's edge and flood recurrence intervals. In each case, lateral riparian zones were distinguished from one another by species grouped according to their different water requirements (Boucher 2002; Sieben et al. 2009; Thayer et al. 2005). Sieben et al. (2009) also found climatic gradients to be a significant factor influencing riparian vegetation patterns.

More recently, a simplified zonation structure was suggested by Reinecke et al. (2007) who described a reference condition for four lateral zones in Western Cape rivers: marginal, lower dynamic, lower and upper zones. Reinecke et al. (2007) collected their vegetation data from headwaters but did not distinguish between mountain stream, transitional or foothill sections of rivers. Thus, it is not clear how these lateral zones, and the species that define them, may differ between longitudinal zones of the rivers. There is thus scope to further explore the patterns they described at a finer scale i.e. lateral zone within longitudinal zone. Furthermore, because the Reinecke et al. (2007) data were available, and had been collected seven years prior to the start of this study, there was also scope to explore whether the zones changed over time in response to flood disturbance or succession.

Thus, in this study the description (reference condition) of Reinecke et al. (2007) for lateral riparian zones of relatively undisturbed upland rivers in the Western Cape was used to compare riparian vegetation communities across different longitudinal zones and at two different times (2004 and 2011).

1.2 Motivation and Hypotheses

Scale influences all ecological processes, within the same process operating at several scales, and observation of the same phenomenon at different scales resulting in different trends (Levin 1992). There is a need for increased knowledge of natural variability in plant community structure, composition and dynamics in order to better manage aquatic ecosystems. The scales at which changes occur influence conservation initiatives and

restoration practices. Increased knowledge on riparian ecology can thus inform management and restoration initiatives, which can be optimised and aligned with the characteristics of a river system at the appropriate spatial and temporal scale.

The research conducted in this thesis focussed on two dimensions, namely; spatial (longitudinal) and temporal. The overarching aims of the thesis were:

1. To investigate and describe differences in riparian vegetation at a lateral zone scale across longitudinal zones of selected upland¹ rivers in the Western Cape (the spatial dimension).
2. To assess changes in riparian vegetation communities over a relatively short time frame and with different disturbances impacting the communities between sample periods (the temporal dimension).

1.2.1 Changes in the longitudinal dimension

In terms of the River Continuum Concept (Vannote et al. 1980), biological communities adapt to the variable physical template of the riverine ecosystem, and it should be possible to predict and observe the resulting differences. Similarly, Naiman et al. (2005) contended that riparian ecologists should be able to explain longitudinal changes of biota and the mechanisms responsible for these changes. There are, however, as yet few if any comprehensive published studies that document these differences for Fynbos Riparian Vegetation² (Mucina and Rutherford 2006).

Elevation above the river has often been used to explain patterns in riparian vegetation communities (Nixon et al. 1977, Wall and Darwin 1999, Hupp 1983 and Bowman and McDonough 1991), although few studies have quantified this relationship. Small changes in horizontal distance and elevation can have significant influence on the flooding frequency (Lindsey et al. 1961; Sieben et al. 2009), changes in water table levels (Bowman and McDonough 1991), fluvial landform (Hupp and Osterkamp 1985) and soil and substratum type (Bowman and McDonough 1991). There should be some correlation between vertical and horizontal distance from the active channel and the nature of the riparian vegetation (Boucher 2002; Reinecke et al. 2007). Mountain stream sites are expected to have narrower riparian zones than foothill zone sites, and a change in vegetation structure is expected as

¹ Upland rivers are sections of rivers with steep channel slope and higher elevation than the lowland sections, usually somewhat unutilized for agricultural activities due to the positioning in narrower valleys and therefore relatively if not entirely undisturbed.

² Fynbos Riparian Vegetation as described by Mucina and Rutherford (2006) is a collective name for the riparian vegetation occurring in the Fynbos biome.

the river channel widens and deepens. Because bank shape, sediment deposition and inundation also differ between riffles, pools and rapids, these geomorphological units are expected to have different riparian characteristics.

The objectives for this part of the study were:

1. To identify and describe how plant community composition changes between longitudinal zones.
2. To evaluate and test the relationship between plant community composition and selected environmental variables.

The hypotheses were:

1. Riparian vegetation differs between longitudinal zones of upland rivers.
2. Horizontal distance, elevation and substrate composition influence species distribution and thus riparian zone community structure.

1.2.2 Changes in the temporal dimension

Apart from changes in riverine ecosystems down the length of a river, there are temporal changes occurring in riverine ecosystems. These temporal changes are encapsulated in the Flux of Nature paradigm (Pickett et al. 2007), which states that ecosystems are continually changing in response to external influences such as any combination of drought, fire, floods, erosion, climate change or anthropogenic impacts (Sousa 1984). This dynamic character is particularly expected in regions with extreme seasonal fluctuations, such as the Western Cape.

The Western Cape has a Mediterranean climate and biota of the Fynbos biome has adapted to the hot dry summer and wet cold winter seasons. The warm dry summer months coincide with fire disturbance and are essential for the successful reproduction and distribution patterns of fynbos vegetation. The wet winter conditions coincide with variable discharge patterns and flash floods that can lead to erosion and uprooting of riparian vegetation, with flood debris and large amounts of sediment being deposited downstream (Grubb and Hopkins 1986). Riparian vegetation, although part of the fynbos biome, do not rely heavily on fire for successful reproduction and distribution but is instead influenced greatly by flooding in the wet winter months and drought episodes in the warm summer months. Flow regimes have been linked to ecological and biological processes in the past (Palmer et al. 1997) and more recently hydrology has been shown to influence the positioning of riparian

species relative to the active channel, with the wetbank (marginal and lower dynamic later zones) being more reliant on regular inundation than the drybank (lower and upper lateral zones) (Reinecke and Brown 2013).

I focussed on the changes in riparian vegetation composition that occurred between sampling periods. Due to fire, floods and drought being difficult to track between seasons and different sites due to isolated locations, lack of species data (e.g. temperature, wind speeds, streamflow) and varying physical characteristics (geomorphology and altitude), less focus was placed on the specific changes driven by these disturbances and instead more focus was placed on disturbance impacts in general and on comparing disturbed sites to relatively undisturbed sites. I looked at the differences between undisturbed sites and sites subjected to two different types of disturbance: natural (fire) and unnatural (recovery after clearing of invasive alien trees) to assess whether sites subjected to disturbance show more or less change than undisturbed sites.

One of the biggest anthropogenically driven disturbance factors in South Africa is the invasion of woody alien species in riparian zones, particularly in the Fynbos biome. These woody alien species are known to have higher transpiration rates (Dye et al. 2001) and therefore use more water (Dye and Poulter 1995) compared to co-occurring native species. Invasive species have also been known to alter riparian canopy structure and the abundance and diversity of native species (Holmes et al. 2005). This empirical information has led to the Working for Water (WfW) programme that was initiated in 1995 of which one aim is to removing invasive species as to preserve water resources.

Restoration practices are aimed at restoring a degraded environment back to its historical state by using a reference condition (Bailey et al. 1998). The dynamic character of natural ecosystems often makes it difficult to pinpoint the state to which an impacted environment should be restored (Pickett and Parker 1994; Hobbs and Harris 2001). A more realistic approach is to restore an environment to a less disturbed state than it is currently in (Meek et al. 2013; Palmer et al. 1997). The recovery of disturbed riparian communities has been a popular area of research but the changes occurring over time in undisturbed sites have received less attention. This part of the study aimed to look at changes occurring in undisturbed sites and sites subjected to disturbance to see whether disturbed sites or undisturbed sites show more change over a relatively short period of time and what drives any changes that do occur.

The objective of this part of the study was:

1. To assess the change in riparian community composition over time.

The hypotheses were:

1. Disturbed sites (disturbed by fire and alien plants) exhibit greater change in species abundance when compared to natural sites over time.
2. If differences result from changes in relative species abundances then the wetbank should show greater change due to its close proximity to the active channel which is inundated more regularly.

1.3 General Description of Vegetation

The Fynbos biome, a unique part of the Cape Floristic Region, contains three distinct vegetation types; 1) Fynbos, 2) Renosterveld and 3) Strandveld (Mucina and Rutherford 2006). The Fynbos biome is situated in the Cape Fold Mountain Belt, South Africa, and, as such, is adapted to frequent natural disturbances, such as fire and floods. Within the Fynbos biome there are many specialised vegetation units, such as coastal vegetation and inland azonal vegetation, which includes freshwater wetlands, salt pans and alluvia (Mucina and Rutherford 2006). Fynbos Riparian Vegetation occurs on alluvial soils and is characterised by narrow belts of thicket on the banks of rivers from near sea level to 1300 meters above sea level (masl). Typical species include palmiet (*Prionium serratum*) and restios (*Calopsis paniculata* and *Elegia capensis*), while tall species such as *Metrosideros angustifolia* and *Brachylaena neriifolia* are also common (Holmes et al. 2005, Mucina and Rutherford 2006, Reinecke et al. 2007).

1.4 Geology

The main components of geology in the Fynbos biome are Table Mountain sandstone, Cape Supergroup shale and Cape granite. These components are broken down, leading to the alluvial sandy and silty soils distributed across Quaternary sediments found in the western part of the Fynbos area. The sites for this study were situated in the Cederberg Sandstone and the Hawequas Sandstone (Figure 1.2), which are both characterised by acidic lithosol soils from Ordovician sandstones from the Table Mountain Group (Mucina and Rutherford 2006).

Shale and granite typically erode into fertile soils, but sandstone erodes slowly, eventually forming nutrient poor soils that are coarse, well-drained and acidic with a pH ranging between 4.4 and 7.0 (Goldblatt and Manning 2000). The vegetation is usually scrubby on sandstone mountain slopes and they have physiological adaptations for water absorption and retention and nutrient uptake to survive the climate (warm dry summers) and geology (nutrient poor soils) (Goldblatt and Manning 2000, Mucina and Rutherford 2006). The positioning of a plant relative to a water source is thus very important in a nutrient poor and water scarce area.

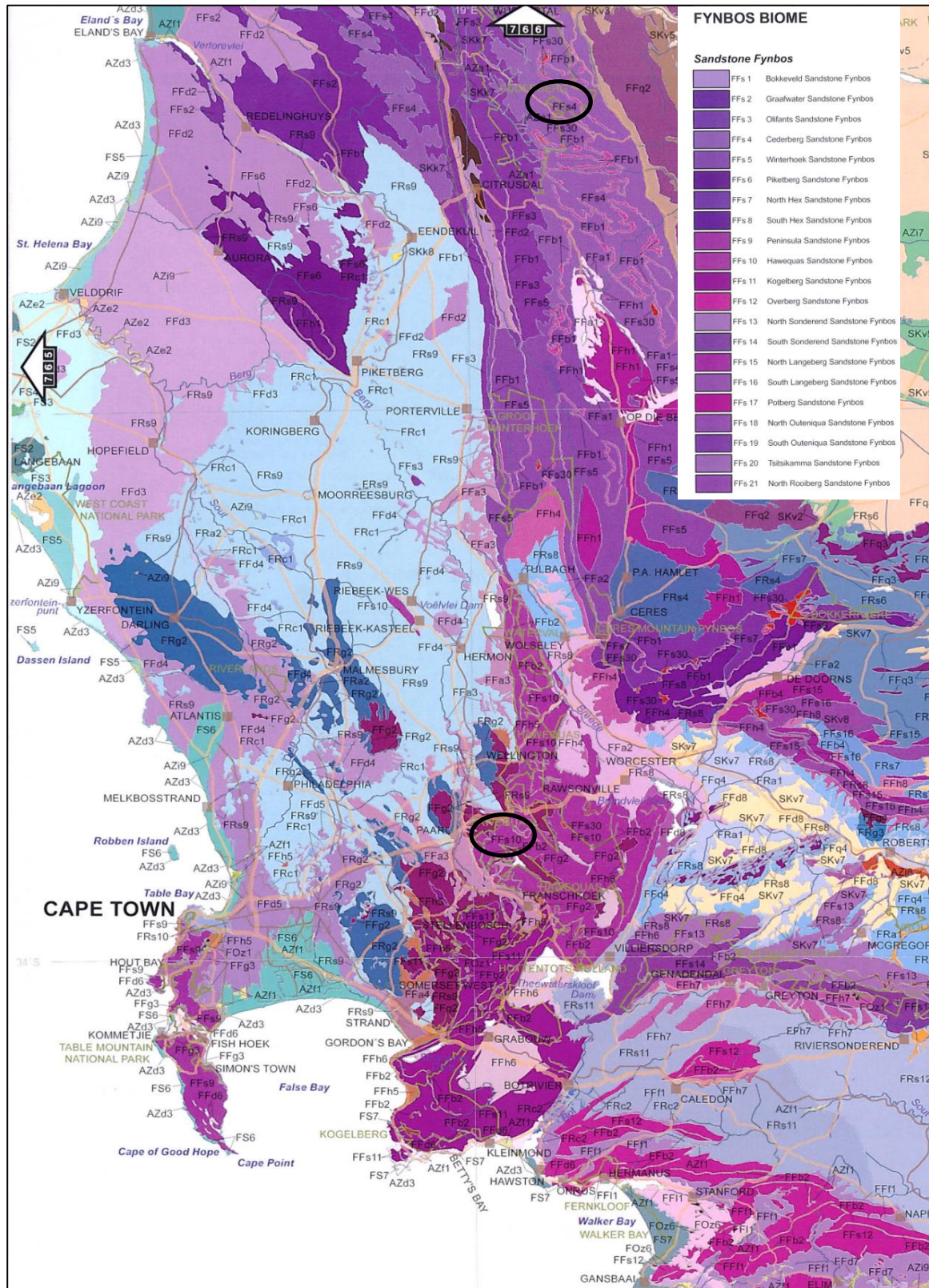


Figure 1.2 The South-Western section of the vegetation Map of South Africa, Lesotho and Swaziland indicating the different geological Fynbos types. FFs 4 = the distribution of Cederberg Sandstone Fynbos and FFs 10 = the distribution of the Hawequas Sandstone Fynbos type (SANBI 2005, Mucina and Rutherford 2006).

1.5 Climate

The Western Cape experiences a Mediterranean climate and supports one of the five Mediterranean Type Ecosystems found globally (Cowling and Richardson 1995; Cowling and Holmes 1992). These are characterised by hot dry summer months and wet cold winter months. The dry summer months coincide with fire disturbance and the wet winter months are known for flooding events occurring annually.

Streams and rivers are fed by winter rainfall and acidic seeps that are high in organic compounds (Mucina and Rutherford 2006). Some streams carry water year round (perennial) while others only flow during the rainy winter season (seasonal) and run dry during warm summer months. High rainfall, steep slopes and narrow gorges throughout the mountainous region contribute to the occurrence of violent floods during winter. Erosion, especially higher up in the catchment, leads to soil-poor substrate. The vegetation is adapted to uprooting, poorly vegetated patches are common (Mucina and Rutherford 2006).

Warm, dry summer months increase the risk of wildfires. Fynbos vegetation is dependent on fire for reproduction and distribution of seeds, and many trees are adapted to burning as they re-sprout after fire (Cowling 1992; Cowling and Richardson 1995). Riparian vegetation is sheltered from fire in the catchment due to headwater areas and narrow valleys acting as protection (Cowling 1992). If it does burn, riparian vegetation is known to re-sprout afterwards and is thus also believed to be fire adapted (Cowling 1992; Cowling and Holmes 1992).

The Cederberg Sandstone Fynbos vegetation occurs in an area with a mean annual rainfall of 395 mm, and mean daily maximum and minimum temperatures of 28.4°C and 4.0°C, respectively. The incidence of frost is 3 to 30 days per year (Mucina and Rutherford 2006). By contrast the Hawequas Sandstone Fynbos vegetation occurs where there is a higher mean annual rainfall (1200 mm) and milder temperatures. The mean maximum and minimum daily temperatures are 25.4°C and 4.4°C, respectively, and frost is less frequent, with 3 to 20 frost days per year (Mucina and Rutherford 2006).

The Western Cape Province has been identified as one of two South African provinces most at risk of climate-induced warming and rainfall reductions, both of which represent significant threats to upland Riparian Fynbos Vegetation (Mukheibir and Ziervogel 2006). Climate change threatens to increase the likelihood of extreme events, such as droughts, floods and fire, in the province. It also threatens to reduce water quality and annual runoff/stream flow (DEADP 2012).

1.6 Site selection and description

1.6.1 Site selection

The study sites are located in two Fynbos vegetation types: Cederberg Sandstone Fynbos and Hawequas Sandstone Fynbos (Figure 1.3).

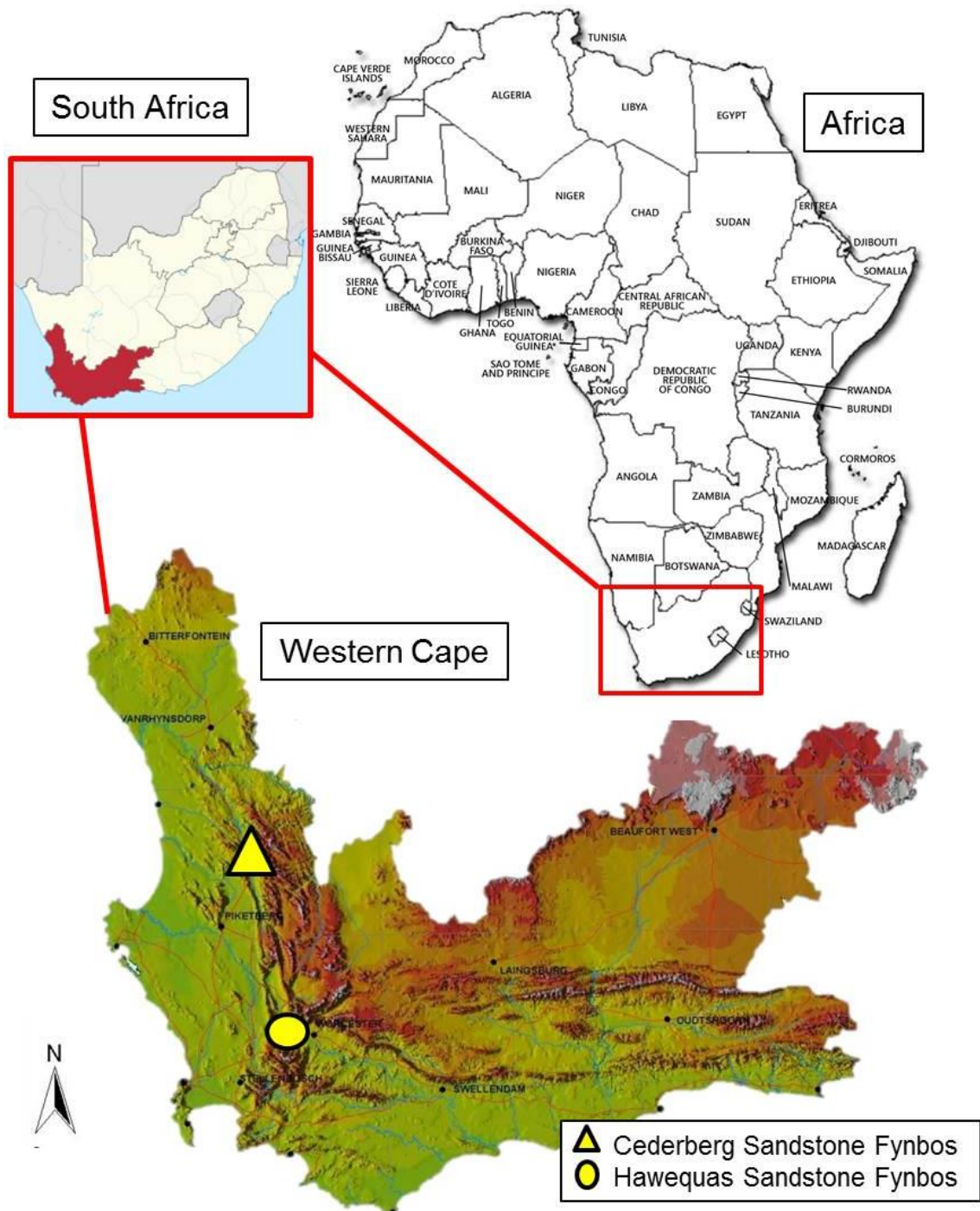


Figure 1.3 Location of study areas within Africa, South Africa and the Western Cape.

The sites were selected on the basis of:

1. The longitudinal zone (Rowntree et al. 2000) they were situated in which enabled a variation of longitudinal zones to be represented for comparisons to be made spatially.
2. Their condition i.e undisturbed vs disturbed. Undisturbed sites were used with the exception of two sites on the Molenaars River (Mol 1 and Mol 3).
3. The availability of historic vegetation data collected from sites used by Reinecke et al. (2007) making temporal sample plot level comparisons possible.

The location of study sites was important as the aim of the study was to draw spatial and temporal comparisons. Mountain stream, transitional and upper foothill longitudinal zones were used. Only upland rivers were used due to lower sections being too modified and disturbed.

Two sites were selected within each of the three longitudinal zones, adjacent to a pool and the second adjacent to an hydraulic control (riffle, rapid or run). An important consideration was the general condition of the site, as riparian communities in lower reaches are often disturbed by agricultural activities, invasion by exotic species or some other anthropogenic disturbance. The sites selected for this study were relatively undisturbed unless stated otherwise (two recovering sites are used in Chapter 4). Using riparian vegetation communities in a near-natural condition was important because it allowed for a better understanding of the natural characteristics of these communities, particularly for answering the questions on spatial differences of riparian community composition between longitudinal zones assessed in Chapter 3. Disturbances are also important, as they are known to drive change in community structure and functioning, and this is dealt with in Chapter 4.

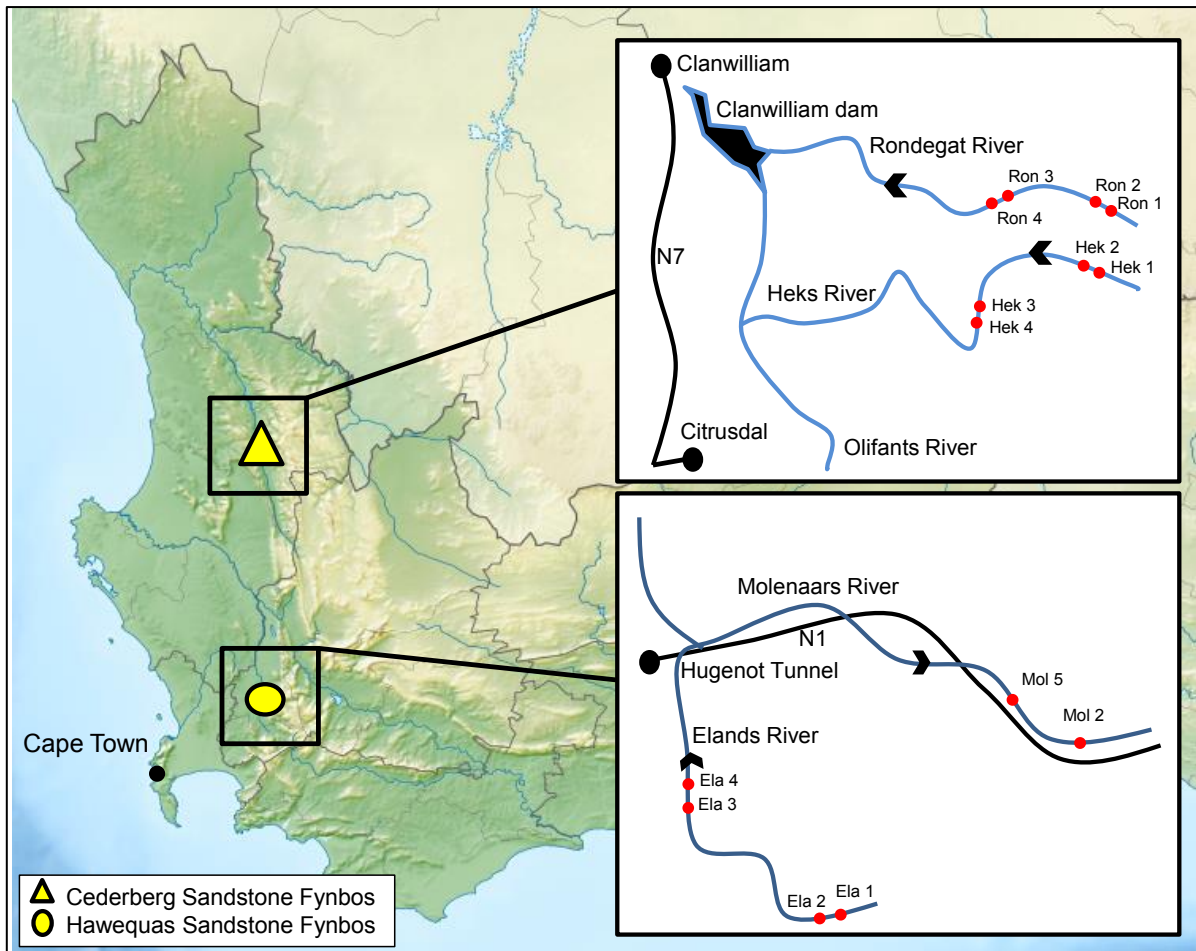


Figure 1.4 Location of paired sites (pool and hydraulic control combination) situated on four rivers in the Western Cape. The Rondegat (Ron), Heks (Hek), Molenaars (Mol) and Elands Rivers (Ela).

The third important consideration in site selection was availability of historic data that would allow for assessment of the temporal changes in riparian vegetation (Chapter 4). Historic data from Reinecke et al. (2007) were available for 13 sites on four rivers. These were the Elands/Molenaars River combination, the Heks River and the Rondegat River. In each case, permanently marked plots from Reinecke et al. (2007) enabled sample plot level accuracy in the re-sampling seven years later. This relocation level of sample plots was within a less than 2 m accuracy. Google Earth was used to establish the altitude at which the sites were located. This is done by entering the GPS coordinates into Google Earth and reading the altitude (in metres above sea level - masl) from the map.

1.6.2 Site Description

1.6.2.1 *Elands River*

The Elands River is in the Hawequas Mountain range. Four sites on the Elands River were sampled: two mountain stream (Ela 1 and Ela 2: Figure 1.5 A and B) and two transitional sites (Ela 3 and Ela 4: Figure 1.5 C and D). Ela 1 is situated next to a deep pool. The valley is narrow and the banks are rocky. Large boulders and slabs of exposed bedrock caused the riparian vegetation to be somewhat sparse and more scattered than that at the downstream sites. Ela 2 is situated downstream of Ela 1 next to a rapid. The valley and bank had very similar characteristics to upstream with steep banks and large boulders and exposed bedrock. Ela 3 was situated next to a cobble bar and plane bed. The banks were less steep than upstream and the valley wider. Ela 4 was situated next to a pool and downstream of Ela 3. The valley shape and character was much the same as at Ela 3.

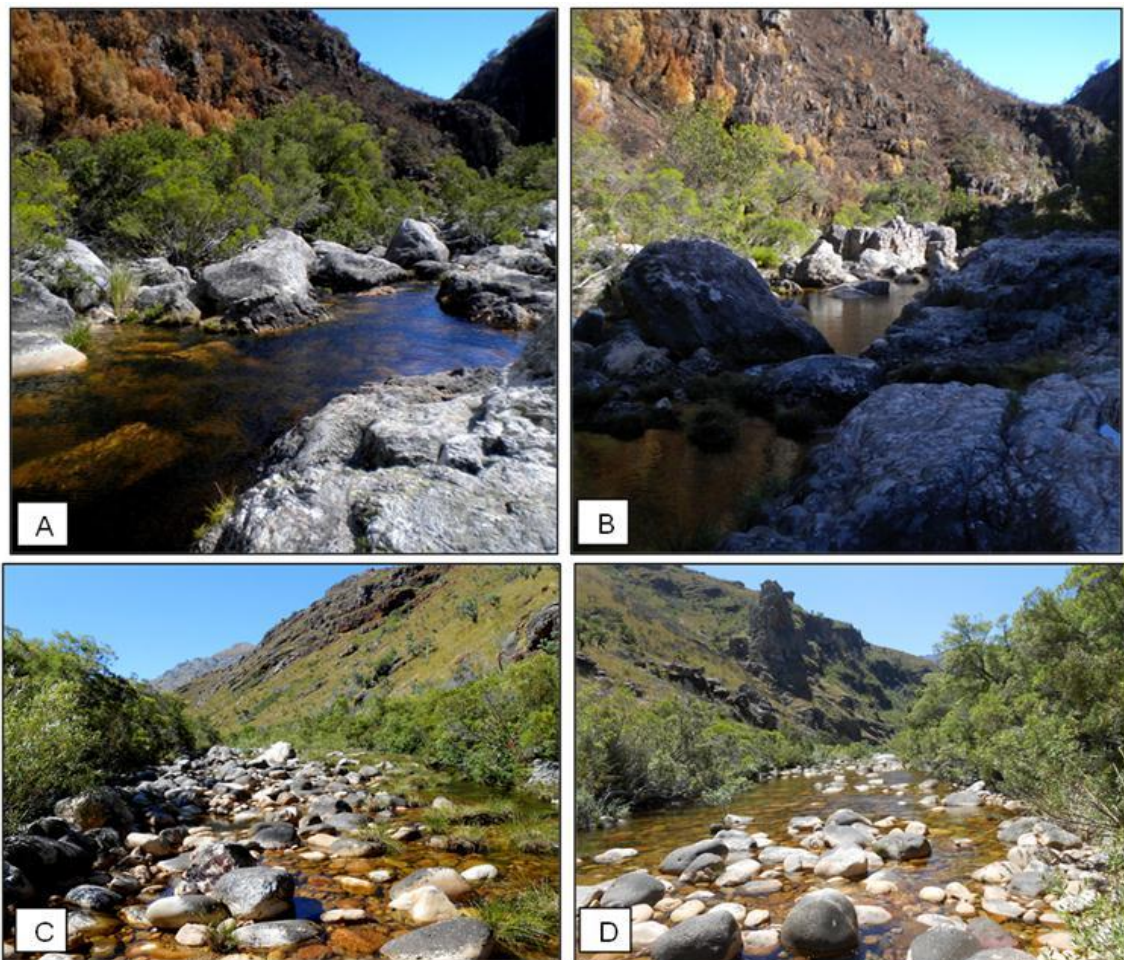


Figure 1.5 Sites on the Elands River during summer 2011: A - Ela 1 (pool); B - Ela 2 (rapid); C - Ela 3 (riffle); D - Ela 4 (pool).

1.6.2.2 Molenaars River

The Molenaars River is in the Hawequas mountain range, and the sites were located downstream of the confluence with the Elands River and the Krom River. Four sites were sampled along the Molenaars River (Figure 1.6), all of which were in the upper foothills longitudinal zone.

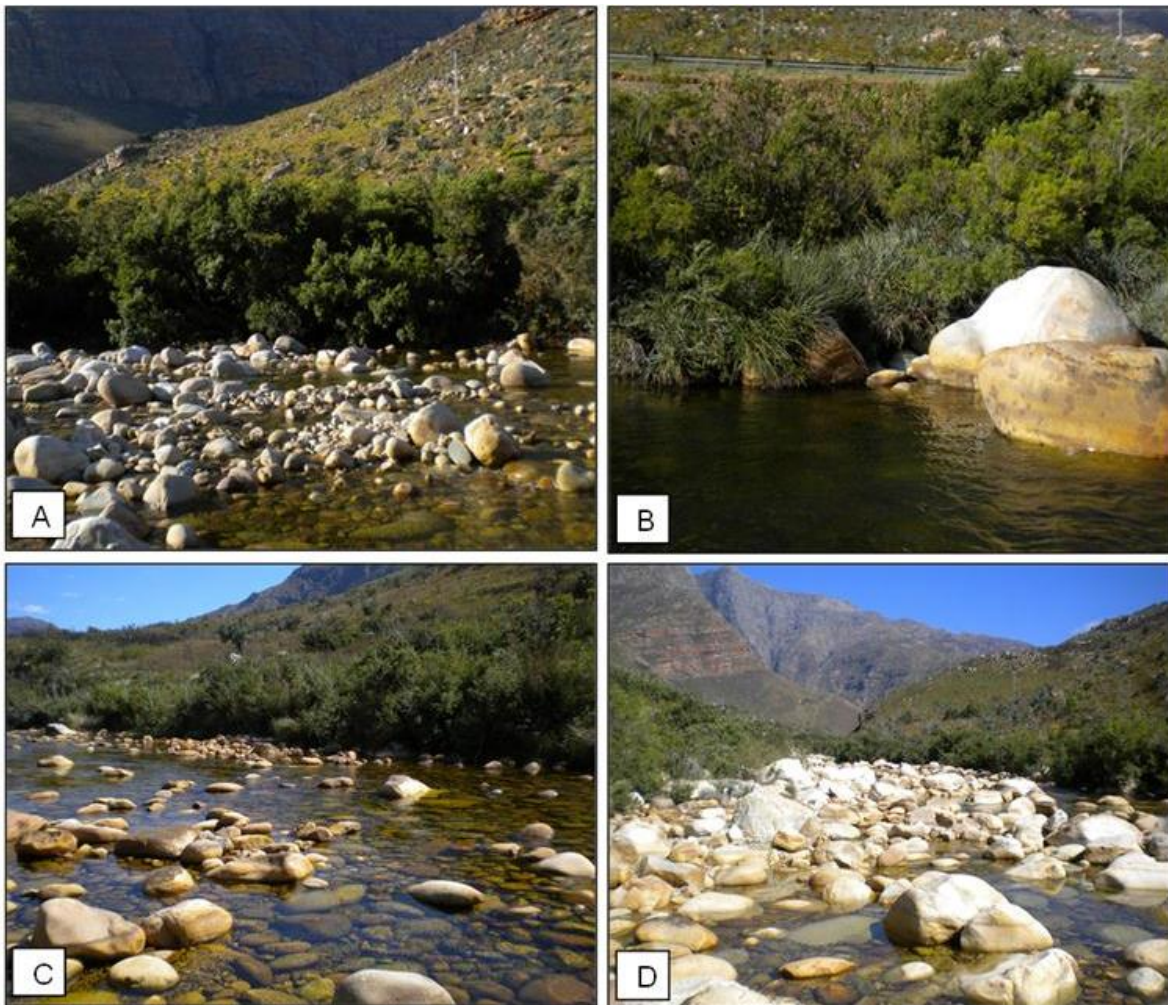


Figure 1.6 Sites on the Molenaars River during summer 2011: A - Mol 2 (riffle); B – Mol 5 (pool); C - Mol 1 (run); D - Mol 3 (riffle).

Mol 2 (Figure 1.6 A) was situated next to a riffle/plane bed in a much wider valley than the Elands River. The bank slope was more gradual and the riparian zone much wider than upstream. This site was upstream of the confluence with the Klip River in an area described to be in a near natural condition (Boucher 1988), although Reinecke et al. (2007) found this site to be more comparable with sites that had previously been cleared of *Acacia mearnsii*

even though disturbance at the site due to invasion was not very evident. The site contained a few small individuals of invasive species (*A. mearnsii* and *Parkia speciosa*) but overall it had few signs of disturbance and, for the purpose of this study, was considered relatively undisturbed. Mol 5 (Figure 1.6 B) was situated next to a deep pool upstream of Mol 2. The valley and banks had characteristics similar to Mol 2 with the exception of the right bank, which was near vertical along the pool edge.

Mol 1 (Figure 1.6 C) was the most upstream site on the Molenaars River. The site was cleared of woody invasive alien species (mainly *A. mearnsii*) in 1994 and Working for Water teams have continued removing invasives through successive follow-ups. Mol 3 (Figure 1.6 D) is situated downstream of Mol 2 and was first cleared of *A. mearnsii* in 1997, with regular follow ups thereafter. This site was more disturbed than Mol 1 when sampled by Reinecke et al. (2007) who found evidence of stack burning and hacked vegetation that was stacked on top of indigenous plants. There were also large sandy areas with little or no vegetation at that time which was no longer the case when sampled during 2011.

1.6.2.3 Rondegat River

The Rondegat River is situated in the Cederberg and forms part of the Olifants River system. It occurs in a neighbouring river basin of the Heks River (see 1.6.2.4). Four sites were selected on the Rondegat River: two in the mountain stream zone (Ron 1 and Ron 2), and two in the transitional (Ron 3 and Ron 4; Figure 1.7).

Ron 1 (Figure 1.7 A) was alongside a fast-flowing turbulent riffle. Ron 2 (Figure 1.7 B) was just downstream of Ron 1 next to a pool. The channel was very narrow and the riparian canopy extended over into the channel at both sites. The outer parts of the riparian zone had been burnt three years earlier when a fire swept the upland area. Ron 3 (next to a riffle; Figure 1.7 C) was situated upstream of Ron 4 (next to a pool; Figure 1.7 D). The valley was wider and flatter than at Ron 1 and Ron 2 and the stream was not shaded by the canopy. These sites had also been burnt three years earlier, and burnt trees and dead branches extended to the edge of the active channel.



Figure 1.7 Sites on the Rondegat River during summer 2012: A - Ron 1 (riffle); B - Ron 2 (pool); C - Ron 3 (riffle); D - Ron 4 (pool).

1.6.2.4 Heks River

The Heks River is in the Cederberg, adjacent to the Rondegat River, and forms part of the Olifants River System. Four sites were selected on the river: two in the transitional zone (Hek 1 and Hek 2), and two in the foothills (Hek 3 and Hek 4).

Hek 1 was next to a pool and Hek 2 was just downstream of Hek 1, next to a riffle. Both sites were confined within well-defined macro-channels. Hek 3 was next to a pool and Hek 4 was just downstream of Hek 3, next to a riffle. The valley was much wider at Hek 3 and 4 than at Hek 1 and Hek 2. There were some secondary channels present with riparian vegetation extending out into the floodplain. The outer edges of the riparian zone had burnt three years earlier.



Figure 1.8 Sites on the Heks River during summer 2012: A - Hek 1 (pool); B - Hek 2 (riffle); C - Hek 3 (pool); D - Hek 4 (riffle).

1.7 General Sampling Methods

There is some overlap in the use of sites and the methods applied for data collection in Chapters 3 and 4, which has led to some repetition between the chapters. Data collected during 2011/2012 are indicated with an asterisk (*) throughout the document and historic data used only in Chapter 4 are not indicated with an asterisk to make it clear which results relate to which data set. The methods used in this study were based on the same ones used to collect the historic data. This enabled temporal comparisons to be as accurate as possible.

1.7.1 Riparian Vegetation

The width of the sampled area was dependent on the width of the riparian zone. At some sites higher up in the catchment the width of riparian zone was only 5 m, while downstream in the foothill longitudinal zone the width was up to 12 m. Each site was 20 m long and laid out perpendicularly to the active channel (Figure 1.11), and was sub-divided into four transects of 5 m each, named A, B, C and D from upstream to downstream (Figure 1.9). Each transect was divided into 1 m sample plots up the bank (5 x 1 m sample plots).

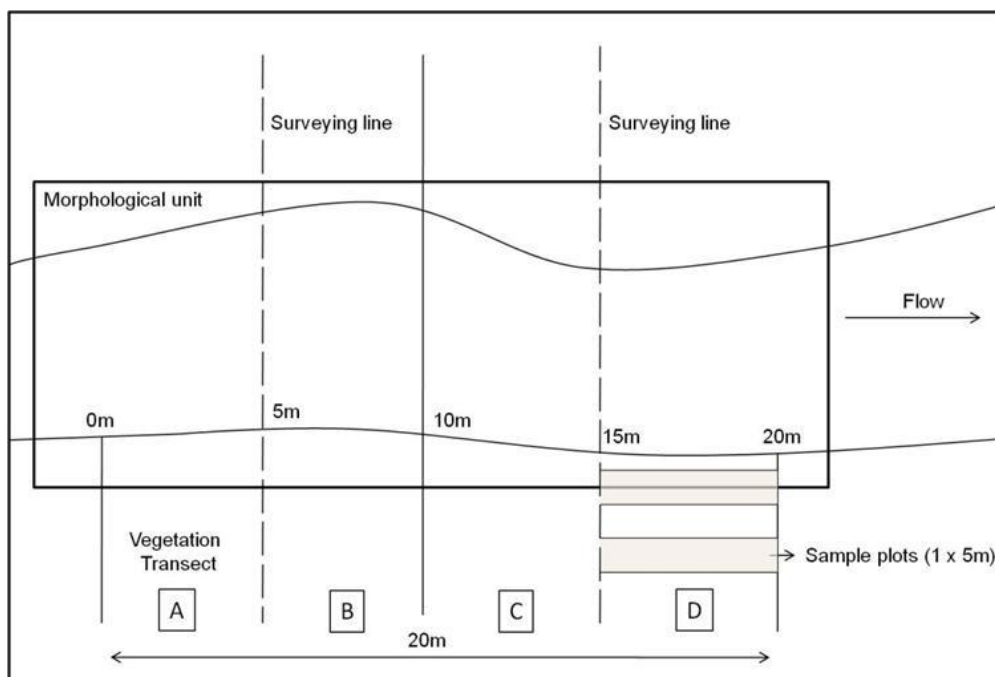


Figure 1.9 Site setup was done at a morphological unit scale (pool, riffle, run). Vegetation transects A – D were along the bank and vegetation plots of 5 m x 1 m up the river bank. Surveying lines were situated at 5 m (between vegetation plots A and B) and 15 m (between vegetation plots C and D).

Cover abundance of canopy and groundcovers were estimated visually (Kent and Coker 1992) for plants rooted in each sample plot. Species were collected and pressed according to standard plant identification protocols and sent to the Compton Herbarium at Kirstenbosch (South African National Biodiversity Institute) for identification. All species present were collected. Vegetation data were collected at the exact same locations as Reinecke et al. (2007), who had marked the transect boundaries when fieldwork was carried out in 2004/2005. In this study, additional punched metal washers were attached to each sample plots indicating the distance (in meters) of the sample plot from the edge of the active channel (water's edge). These markers were also the points that were surveyed. The spatial scale at which longitudinal comparisons were made was at the pool and riffle scale $10^1 - 10^2$ m and the temporal scale was 7 years (<10).

1.7.2 Cross-sectional Surveying

The shape of the river bank was surveyed using a Total Station (Leica TC307 model) (Figure 1.12). The horizontal distance from the active channel and the difference in height (elevation above active channel/water's edge) between two points (one of which was fixed by means of the total station's position) was measured across the channel. When these two points were plotted together on a graph the shape of the bank and active channel could be determined (Figure 1.10). This allowed for bank slope to be calculated and comparisons in bank shape to be made between different longitudinal zones, lateral zones and between the two sampling dates. The sample plots could also be related to the substrate at specific points on the bank.

1.7.3 Substrate

Sample-plot substrate information was estimated as the percentage of each substrate size-class relative to the sample plot's surface area (Wentworth scale, Gordon et al. 1992). This meant that the maximum total percentage substrate per sample plot was 100%. The substrate types were: bedrock, boulder, cobble, gravel and sand (Wentworth scale, Gordon et al. 1992). The presence of surface water was also recorded.

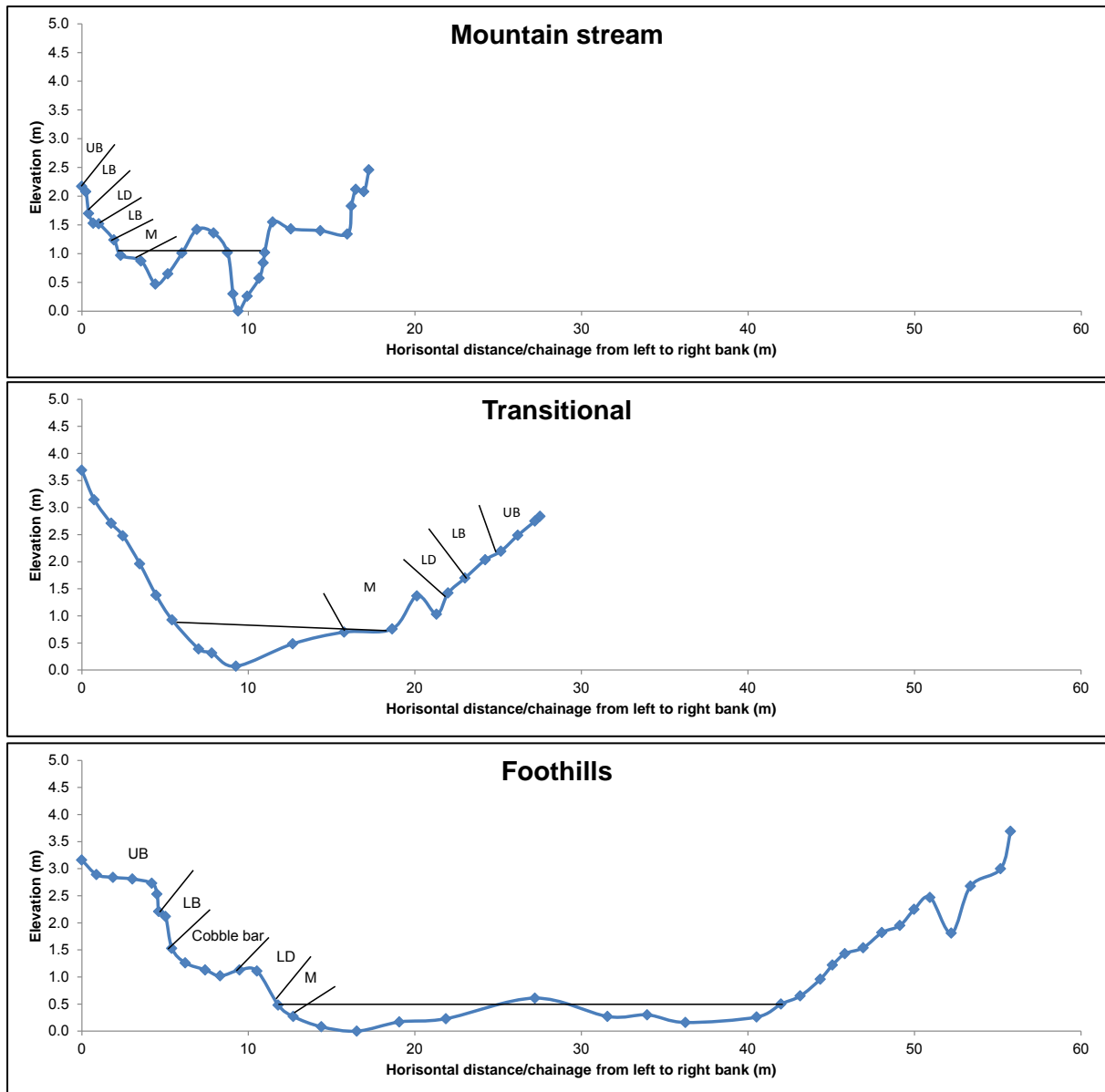


Figure 1.10 Cross-sectional survey graphs of bank shape across sites situated in different longitudinal zones: mountain stream (Ela 1), transitional (Ela 3) and foothills (Mol 2). The x-axes (horizontal distance) and y-axes (elevation) are recorded in m with M - marginal, LD - lower dynamic, LB - lower and UB - upper bank, indicating the approximate position of the lateral riparian zones.

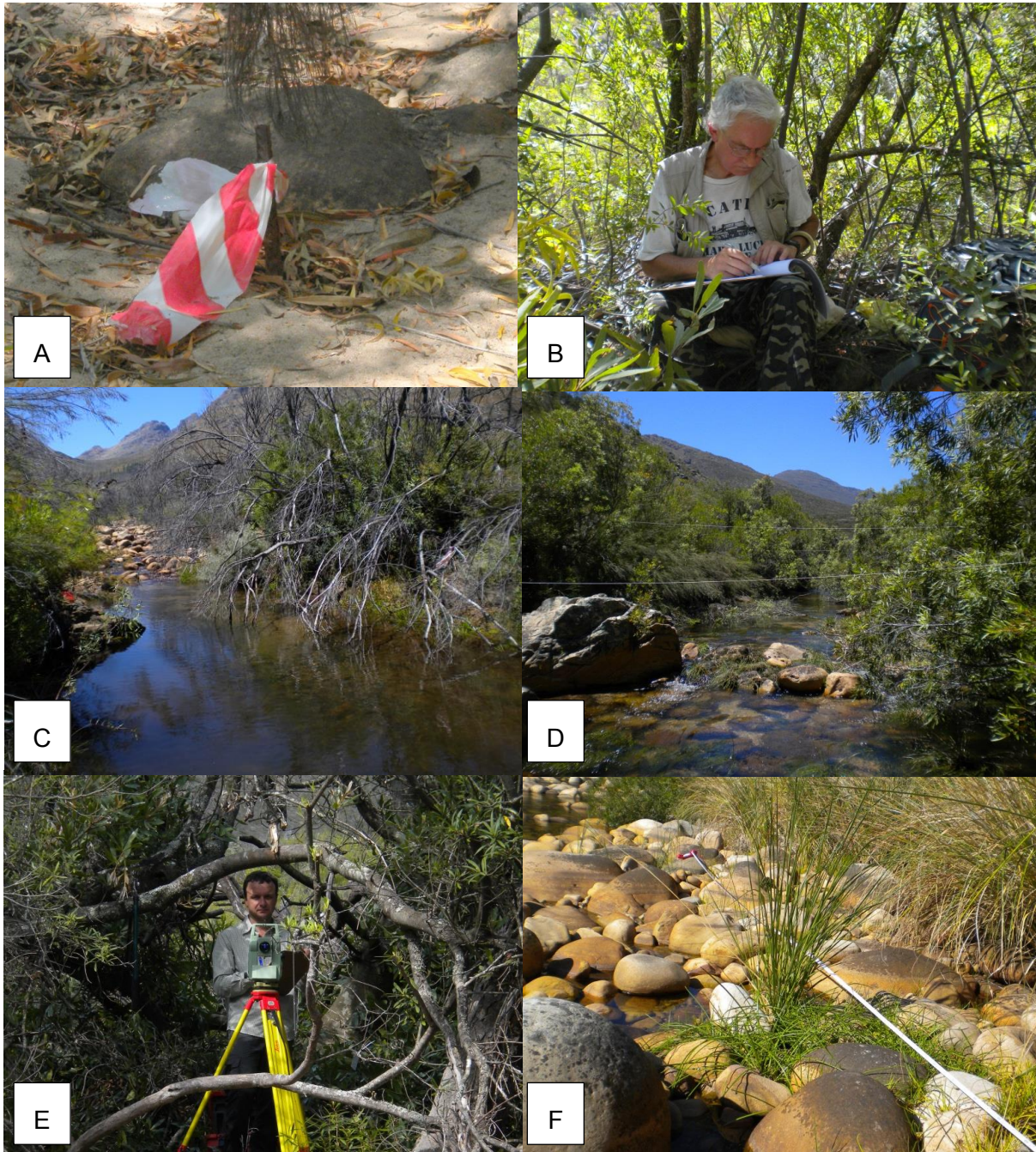


Figure 1.11 Fieldwork during the summers of 2011 and 2012. A - Permanent markers placed at sites during 2004 sampling, B - Dr Willem Otto recording vegetation data while assisting with fieldwork on the lower sites of the Rondegat River, C - Burnt branches of re-sprouting trees overhanging the active channel on the Rondegat River during 2012 sampling, D - Strings are put out spanning the cross-section to aid the surveying and sampling of vegetation, E - Karl Reinecke and the total station used to survey cross-sections across sites, F - Sites are set up by laying out a 50 m tape perpendicularly to the active channel.

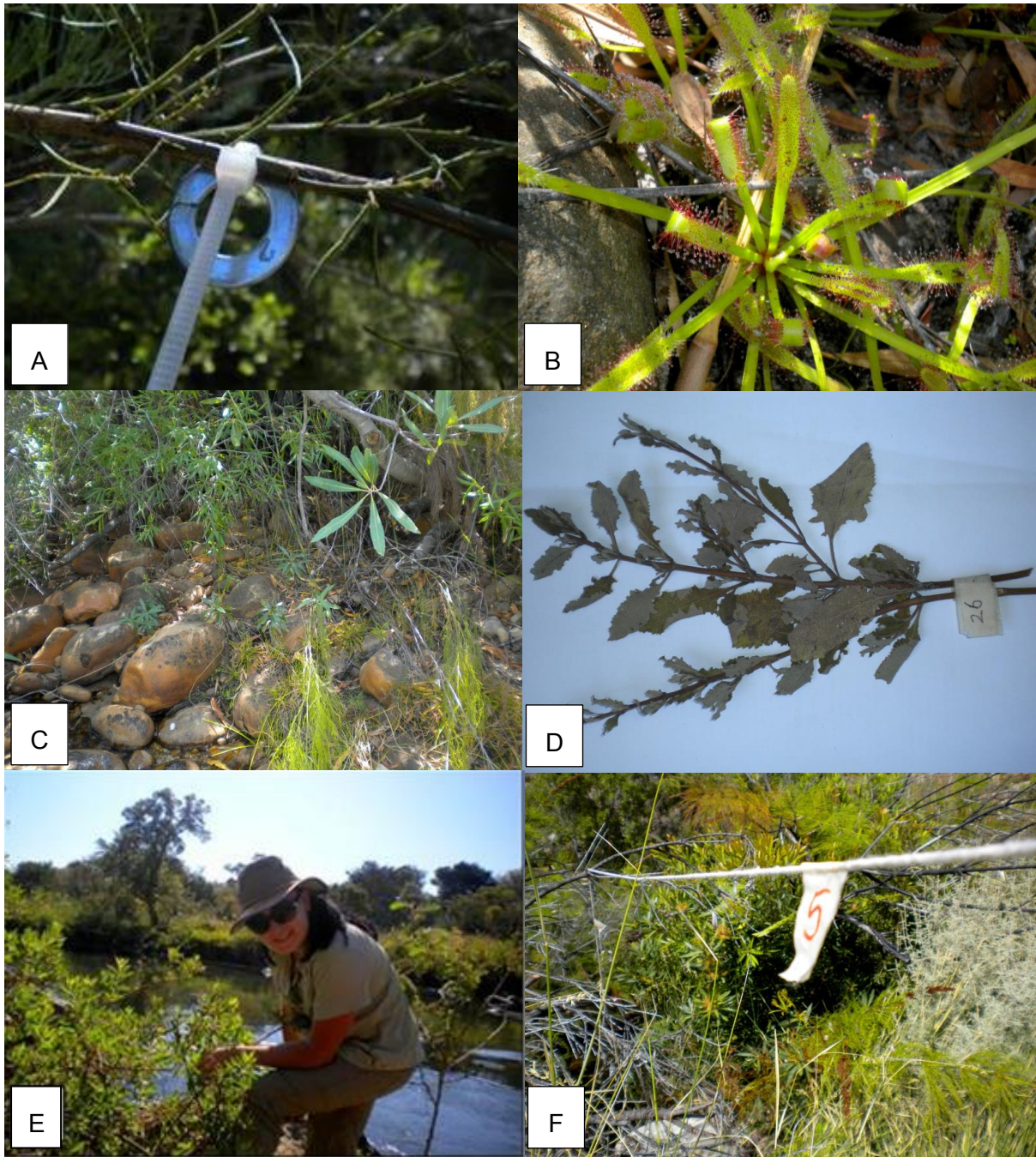


Figure 1.12 Fieldwork during summers of 2011 and 2012 continued. A - Permanent markers (number-punched washers) attached to vegetation at each sample plot up the bank, B - *Drossera capensis*, one of the many species collected, photographed and submitted for identification, C - Sediment calibre was estimated as percentage coverage per sample plot, D - Plant specimens were labelled, pressed and submitted to the Compton Herbarium at Kirstenbosch for identification, E - Vegetation collection during summer 2012, F - Strings are put up to measure 1 m sample plots up the bank.

1.8 Thesis Structure

The thesis is divided into five chapters, two of which are data chapters (Chapters 3 and 4). Chapter 3 addresses the spatial comparisons across longitudinal zones and Chapter 4 deals with the question of change over time in Fynbos Riparian Vegetation.

Chapter 1 – Introduction: This section contains the general outline and conceptual framework for the research study.

Chapter 2 - Literature Review: This chapter is an overview summarizing the foundation upon which the research study was based.

Chapter 3 - This is the first data chapter of the thesis and is focussed on the spatial differences in Fynbos Riparian Vegetation communities of the Western Cape.

Chapter 4 - This is the second data chapter of this thesis and deals with temporal changes in riparian Fynbos Riparian Vegetation communities.

Chapter 5 - Synthesis: The concluding chapter used the results to draw conclusions regarding Fynbos Riparian Vegetation communities over spatial and temporal scales. These include lateral zone characteristics, biodiversity and community composition. Recommendations for further studies are also made in this chapter.

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2 Literature Review

2.1 Introduction

Riparian vegetation is associated with nearly all continental freshwater bodies (Naiman et al. 2005) and forms diverse ecotones (Swanson et al 1992) between the aquatic and terrestrial environments. In this study, 'riparian zone' refers specifically to the plant community that is directly adjacent to, and dependent on, water in the river channel. This band of vegetation is often distinctly different from the adjacent terrestrial vegetation, which is located higher up the bank away from the active channel (Reinecke et al. 2007).

Riparian vegetation occurs in different zones on the bank of rivers (Boucher and Tlale 1999). This zonation pattern has been described by multiple authors in South Africa (Boucher 2002; Sieben et al. 2009; Taman 2001; Thayer et al. 2005). Boucher (2002) used hydrology, and more specifically the flood recurrence intervals to establish the positioning of riparian zones on the bank. He described three riparian areas broken down into seven zones with the transition between wetbank and drybank occurring at the 1:2 year flood recurrence level. Other authors have used similar methods in other parts of South Africa such as Hughes (1990); Van Coller (1992); Van Coller et al. (1997). Reinecke et al. (2007) identified four lateral zones on reference sites in the Western Cape, South Africa from which they also identified horizontal distance and elevation as good indicators for riparian zone. Throughout, hydrology and geomorphology has been the most effective approach used to describe riparian zones and community dynamics. Van Coller (1992) and Van Coller et al. (1997) used geomorphological characterises of the active channel linked it to vegetation communities of the floodplain. Boucher (2002), Hughes (1990) and Reinecke and Brown (2013, in press) used aspects of hydrology to explain riparian community structure and dynamics.

Rogers (1995) distinguishes riparian vegetation of rivers from that of other wetland ecosystems on the basis of (1) its linear form – as the communities track the course of the river, and (2) longitudinal connectivity – the river forms a hydrological connection between upstream and downstream areas for the movement of sediment, hydrochorous seeds, aquatic vertebrates, invertebrates and other fauna. Defining the correct temporal and spatial scales for ecological studies of riverine ecosystems is important (Levin 1992; Lowe et al. 2006; Wiens 2002). Scale is defined as an informal system to categorise changes in space and through time (Gibson et al. 2000). Lowe et al. (2006) emphasised the importance of using multiple scales in ecological management while Biggs et al. (2005) focussed on

different scales of flow events and the impacts these had on lotic system development and maintenance. Species are known to be sometimes restricted geographically and, such as the case with plants, to be relatively immobile, which emphasises the relationship between localized species and the local geographic scale (Poiani et al. 2000). Most spatial scale studies have focussed on invertebrate (instream) community dynamics leaving little known about the impact of ecological scales on plant (local-scale species³) dynamics. Levin (1992) described scale as a filter through which the observer investigates a particular piece of an ecosystem and how this filter changes in size depending on the specific dynamics and patterns investigated. Spatial and temporal scales are the two fundamental mechanisms driving and maintaining ecosystem development and population dynamics (Levin 1992).

There are three spatial dimensions across which exchange of ecological processes occur in a river ecosystem: longitudinal, vertical and laterally across the floodplain (Figure 1.1). Time is considered by many authors view as a fourth dimension (Lorenz et al. 1997, Ward et al. 2002). In this thesis, spatial and temporal changes in riparian vegetation characteristics were assessed separately. Riparian vegetation ecosystem development is influenced by structural processes (e.g. landforms) and disturbance events (e.g. fire) which varies in scale spatially and temporally. The largest spatial scale is the river basin catchment, which tends to change over a temporal scale of 10 to 1000 000 years (Table 2.1). The smallest scale is a particle the size of 10^{-8} ; which changes over <10 years (Sear 1994, Wissmar 1998). There are, however, numerous exceptions to these rules. The spatial and temporal scale at which research is conducted has always influenced ecosystem studies (O'Neill et al. 1986, Sieben et al. 2009) and was considered most important for this thesis. Since spatial and temporal scales influence the riparian vegetation communities in different ways (Table 2.1), these should be addressed separately.

³ Local-scale species refers to organisms unable to move as widely geographically. In this case when disturbances occur the species are unable to relocate or avoid the disturbance and are therefore more directly influenced and affected by localized disturbances of varying scales.

Table 2.1 Spatial and temporal scales that influence a river catchment. Highlighted rows are at the scale used in this study to sample and compare riparian communities. Adapted from Wissmar (1998) and Sear (1994).

Geomorphic Structure	Geomorphic Function	Spatial Scale (m)	Temporal Scale (years)
River basin network	Sediment and water transfer	$>10^4$	$10^1 - 10^6$
Valley floor	Sediment and water storage	$10^3 - 10^4$	$10^2 - 10^4$
Floodplain	Sediment and water storage	$10^2 - 10^3$	$10^1 - 10^3$
Riparian zone/corridor	Sediment and water storage, wildlife and habitat interactions	$10^1 - 10^2$	$10^0 - 10^3$
Channel meander	Sediment and water storage and transfer	$10^1 - 10^2$	$10^1 - 10^2$
Pools and riffles	Sediment and water storage and transfer	$10^1 - 10^2$	$10^1 - 10^2$
Depositional bars	Sediment transfer	$10^0 - 10^2$	$10^0 - 10^2$
Dunes and ripples	Sediment and water storage	<1	<1
Particles	Erosion product	$1 - 10^2$	<10

2.2 Spatial Change

The flow regime is the main driver of channel morphology through its influence over sediment transport and, through this, channel structure (Naiman et al. 2005). Seasonal inundation and flooding, and the erosion and deposition of sediments all exert an influence on the physical characteristics of the river channel and banks (Frissel et al. 1986) and the composition of the plant community that inhabits river banks (Tabacchi et al. 1998). The Western Cape's flash floods during the winter months have different impacts on channel morphology at different longitudinal positions in the river basin (Campbell 1983). For instance, in steep mountain streams with a boulder and cobble substrate one extreme flow event can substantially alter the channel morphology, whereas in a large low gradient channel, low intensity and frequently recurring flows are often responsible for channel form as they deposit sediment and change fluvial landforms (Frissel et al. 1986, Swanson et al. 1988). There are, however, exceptions to this. For instance, low channel gradient flooding during the 2000 flood in the Sabi River, Mpumalanga, South Africa, resulted in substantial channel modification. The geomorphological characteristics (slope, channel substrate and valley width) are important characteristics that influence the composition and structure of the riparian plant community.

Frissell et al. (1986) proposed a framework for the hierarchical classification of spatial variation in a basin that was based on several spatiotemporal scales and geomorphic features and events. This framework is presented in Figure 2.1 and is very similar to the

hierarchical classification system developed more recently by Rowntree et al. (2000) in terms of its spatial division of 5 clear riverine scales (catchment/basin, zone, segment, reach, morphological unit). Sullivan et al. (1987) describes three geomorphological provinces of physical factors operating in a river basin. The first of these is the erosional province that corresponds with headwaters where the channel gradient is $>4\%$, the valley is v-shaped and only minor lateral exchanges occur. The steep gradient results in a high carrying capacity so a variety of particles of different calibre are transported. The riparian community is generally narrow in this province (Tabacchi et al. 1998). The second province is transitional with a channel gradient of between 1 and 4%. Enough kinetic energy is available to transport particles of between 0.2 and 250 mm in diameter. This province is associated with wider valley areas and more stable channels than the erosion province. The riparian zone tends to be wider and spatially more complex in habitat diversity (Tabacchi et al. 1998). The depositional province is downstream, has a very low gradient ($>1\%$) and is characterised by meandering or braided channels and high sediment deposition, and a fragmented riparian zone (Tabacchi et al. 1998).

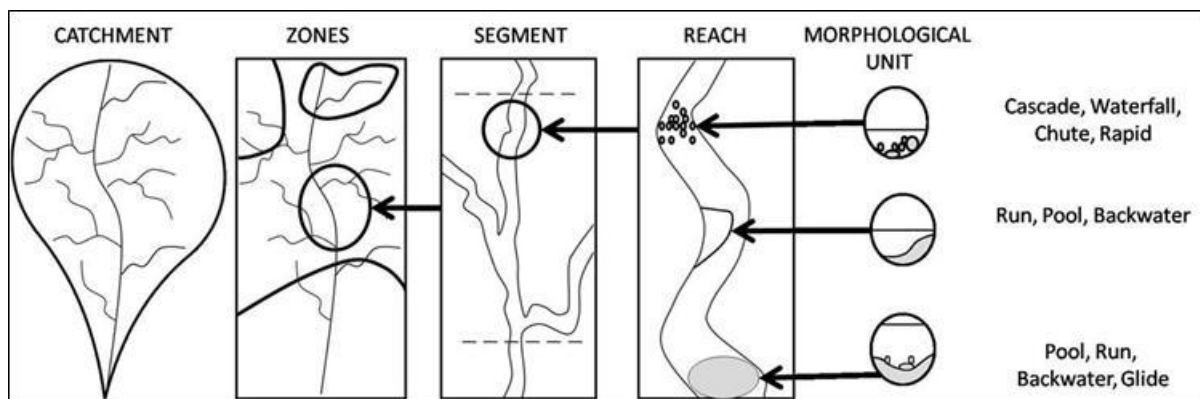


Figure 2.1 A hierarchical classification system for river basins which relates directly to the zonal classification system of Rowntree et al. (2000) (modified from Frissell et al 1986).

The geomorphological hierarchy and provinces described by Frissell et al. (1986) and Sullivan et al. (1987) correlate with the more recent zonal classification system of Rowntree et al. (2000). Rowntree et al. (2000) described different longitudinal zones for rivers in three different parts of the country: the Sabie River in Mpumalanga, the Buffalo River in the Eastern Cape and the Olifants River in the Western Cape. This zonal classification system identified five scales at which different physical characteristics dominate. These are (from

largest scale to smallest): 1) the catchment; 2) zones; 3) segments; 4) reaches; and 5) morphological units (Figure 2.1; Table 2.2).

The classification system of Rowntree et al. (2000) has become widely used in the Fynbos biome (e.g. within the eco-classification system of Kleynhans et al. (2007)). According to Rowntree et al. (2000), mountain streams are characterized by bedrock, boulders and large cobbles with a slope of 0.04 to 0.099. There is also a tendency toward abrupt gradient changes, such as at waterfalls and chutes, and outside of pools, the flow is fast and turbulent. Foothills, on the other hand, typically have a higher dominance of smaller stones, such as cobbles, gravel and sand, and although there are large pools, there are also long sections of relatively shallow riffles and runs. This longitudinal zone has a channel slope range of 0.005 to 0.0019.

Table 2.2 The zonal classification system for South African rivers. Highlighted rows are the longitudinal zones used in this study (Rowntree et al. 2000).

Zone	Range of slope	River characteristics
Source zone	Not specified	Low gradient, upland plateau or upland basin able to store water. Spongy or peaty hydromorphic soils.
Mountain headwater stream	>0.1	A very steep gradient river dominated by vertical flow over bedrock with waterfalls and plunge pools. Normally first or second order. Reach types include bedrock fall and cascades.
Mountain stream	0.04-0.099	Steep gradient river dominated by bedrock and boulders, locally cobble or coarse gravels in pools. Reach types include cascades, bedrock fall, step-pool. Approximate equal distribution of vertical and horizontal flow components.
Transitional	0.02-0.039	Moderately steep river dominated by bedrock or boulder. Reach types include plane-bed, pool-rapid or pool-riffle. Confined or semi-confined valley floor with limited flood plain development.
(Upper) foothills	0.005-0.0019	Moderately steep, cobble-bed or mixed bedrock-cobble bed channel, with plane-bed, pool-riffle, or pool-rapid reach types. Length of pools and riffles/rapids similar. Narrow flood plain or sand, gravel or cobble often present.
Lower foothills	0.001-0.005	Lower gradient mixed bed alluvial channel with sand and gravel dominating the bed, locally may be bedrock controlled. Reach types include pool-riffle or pool rapid, sand bars common in pools. Pools of significantly greater extent than rapids or riffles. Flood plain often present.
Lowland river	0.0001-0.0009	Low gradient alluvial fine bed channel, typically regime reach type. May be confined, but fully developed meandering pattern within a distinct flood plain develops in unconfined reaches where there is an increased silt content in bed or banks.

The role of riparian vegetation in upland-riverine ecosystem functioning received little attention (Tabacchi et al. 1998) until the publication of the River Continuum Concept (RCC)

(Vannote et al. 1980) and the Nutrient Spiralling Concept (Minshall et al. 1983 and Webster 1975), where after riparian zones were integrated more into such studies. The RCC states that biological communities adapt to the physical template of the riverine ecosystem, defined by changes in gradient, river width, sediment size and food resources from source to mouth. It should therefore be possible to predict and observe these differences in natural systems (Naiman et al. 2005).

Partly in response to the RCC, longitudinal changes in riverine ecosystems received considerable attention in studies, which focused on, *inter alia*, the influence of tributaries on mainstream ecosystems, river ecosystem classification (Hestir 2007; Statzner and Higl 1985), longitudinal and temporal variation in recovery of benthic invertebrate communities (Canton and Chadwick 1983; Larned et al. 2010), longitudinal distribution of macroinvertebrate assemblages (Carter et al. 1996; Miserendino and Pizzolon 2003; Nautiyal and Mishra 2012), the complexity of biological interactions (Thorp et al. 2006; Peckarsky et al. 1997) and organic matter processing in different river reaches (Navel et al. 2011). Together these have helped shed light on how populations, nutrient availability and abiotic characteristics change and interact with one another down the length of a river.

Although longitudinal studies on macroinvertebrate assemblages (e.g. Carter et al. 1996; Grubaugh et al. 1997; Miserendino and Pizzolon 2003; Nautiyal and Mishra 2012) tend to be more numerous than those on riparian vegetation communities, possibly because it is easier to collect large amounts of data for macroinvertebrates, some studies have focused on the riparian vegetation. Rot et al. (2000) found that large woody debris in the riparian zone was directly influenced by the age of riparian forest communities and by the geomorphological characteristics of the sample site, although they did not give detailed descriptions of riparian change from upstream to downstream.

Hupp (1986) recorded a change in geomorphological characteristics and associated tree species as the stream order changed. He described the changes recorded in the distribution of tree species in terms of changes in gradient downstream, bringing about morphological changes in the channel and landform type. He concluded this directly influenced riparian structure. Bredenkamp et al. (1991) also found that there was a gradient of different species assemblages along the length of the Sabie River in South Africa, which could be partially explained by geology. Van Coller (1992), working on the same section of the Sabie River suggested that factors other than geology influenced species distribution, since geological changes were abrupt, whereas changes in riparian communities tend to occur along a continuum.

At a local scale, elevation above the river has often been used to explain patterns in riparian vegetation communities, although few studies have been able to quantify this relationship (Bell 1973; Bowman and McDonough 1991; Hupp 1983; Nixon et al. 1977) until recently by Reinecke and Brown (2013). Small changes in horizontal distance and elevation can have significant influence on the flooding frequency (Bell 1973; Lindsey et al. 1961), changes in water table levels (Bowman and McDonough 1991), fluvial landform (Hupp and Osterkamp 1985) and soil and substratum type (Bowman and McDonough 1991). It is clear that there are some correlations between vertical and horizontal gradients of species distribution within the riparian zone and are likely to be due to a combination of physical influences and channel characteristics. Land use may also be a contributing factor to shaping riparian zones (Meek et al. 2010).

Rosgen (1994) contends that the shape of the active river channel (inundated during low flows) is mainly driven by floods with a return interval of 1.5 to 2.5 years. Different substrate compositions have different correlations with flooding frequency (Calow and Petts 1992). The marginal riparian vegetation zone is usually considered to be within the 1.5 to 2 year flooding area which means this area gets inundated regularly and has a lower drought tolerance than the other riparian vegetation zones higher up the bank as described by Boucher (2002) for South African rivers.

Fynbos Riparian Vegetation was described to comprise of four identifiable lateral zones (Reinecke et al. 2007). These zones were said to differ in species composition (Reinecke et al. 2007) and although there were no consistent indicators for any one lateral zone, species varied in abundance between lateral zones up the river bank. The marginal zone was characterised by *Isolepis prolifera* and *Pronium serratum*, the lower dynamic and lower zones by *Calopsis paniculata*, *Elegia capensis*, *Todea babara*, *Morella serrata* and *Metrosideros angustifolia* and the upper by *Searsia angustifolia*, *Diospyros glabra*, *Pteridium aquilinum* and *Brabejum stellatifolium* (Reinecke et al. 2007).

In Fynbos riparian vegetation, Reinecke et al. (2007) was able to describe general community patterns across lateral zones, and Boucher (2002) investigated the relationship between riparian community and distance and elevation from the water's edge but the relationship between riparian vegetation and longitudinal zone (Rowntree et al. 2000) has not yet been tested. This gap is investigated in this thesis.

2.3 Temporal Change

Riverine ecosystems also change over time, even in undisturbed environments. These temporal changes are encapsulated in the Flux of Nature paradigm⁴ (Pickett et al. 2007), which states that ecosystems are continually changing in response to external influences. These external influences can be any combination of drought, fire, floods, erosion, climate change and other natural or anthropogenic disturbances. This dynamic character is expected to be marked in regions with extreme seasonal fluctuations, such as the Western Cape, and in the Fynbos biome where fire is a major and frequent natural disturbance (Cowling and Holmes 1992).

The Western Cape has a Mediterranean climate that is characterized by hot, dry summer months and cold, wet winter months (Campbell 1985). The hot and dry summers mean that disturbances such as fire and drought are common, and it is expected that the riparian vegetation communities have a high level of resilience and resistance (Paskoff 1973). The wet winter conditions coincide with variable discharge patterns and flash floods that can lead to erosion, uprooting of riparian vegetation and deposition of large amounts of sediment and other flood debris downstream (Grubb and Hopkins 1986). Fire and flooding are probably the biggest drivers of natural disturbance in Fynbos Riparian Vegetation (Hupp and Osterkamp 1996; Rogers and van der Zel 1989; Stromberg et al. 1996).

Examining the history of climatic and other natural changes occurring within a basin is useful when trying to establish the ecological spatial and temporal scale at which disturbances occur (Tabacchi et al. 1998). Fire and flooding is of special interest due to the decadal basis on which they occur (Wissmar and Swanson 1990). All these disturbances alter the physical characteristics of the surface landform, thereby altering riparian and channel characteristics. Reinecke and Brown (2013) found that lateral zonation is linked to the hydrological regime at a wetbank and drybank scale. Disturbance driven change is therefore predicted to occur at this scale within a site.

Flooding alters the physical habitat and the biological composition for instance when macroinvertebrates are flushed downstream and vegetation gets uprooted (Grubb and Hopkins 1986). Flood debris may get caught in bank vegetation, causing sunlight and space limitations for established plant species to continue growing (Naiman et al. 2005). Flooding also changes the substrate characteristics, due to larger amounts and particle sizes of sediment being deposited downstream. Intra-annual floods have a smaller impact on

⁴ The Flux of Nature paradigm views the environment as a dynamic system rather than a static one. Whether disturbances, development or any other form of altering impacts occur or not, the habitat would not stay static it is ever changing as organisms act and react to one another and their immediate environment (Pickett et al. 2007).

bank structure and the biological communities than inter-annual flooding. This is because of the flood magnitude being considerably larger with inter-annual floods (larger floods occurring more than one year apart) than that of intra-annual floods (floods occurring every year/seasonal flooding). Large trees usually get uprooted in large scale floods, and even relatively small annual floods can uproot young individuals or cover them in debris, enabling further plant community development and recruitment (Reinecke and Brown 2013). Vegetation uprooting opens new niches for recruitment to occur, suggesting that the areas exposed to regular inundation should show greater changes than areas not regularly inundated over a relatively short temporal scale.

One of the biggest disturbance concerns in South Africa is the invasion of woody alien species in riparian zones. These woody alien species are known to have higher transpiration rates than the indigenous species (Dye et al. 2001) and therefore use more water (Dye and Poulter 1995). Invasive species have also been known to alter riparian canopy structure and the abundance and variety of species (Holmes et al. 2005). This led to the Working for Water (WfW) programme which was initiated in 1998 and is aimed at removing invasive species to preserve water resources. This programme has also secondarily created jobs and training opportunities for economically marginalised people (Van Wilgen et al. 1998).

Restoring previously invaded communities is a complicated and long process due to persistent seed banks left by different invasive species (Holmes et al. 2005). The restoration process therefore requires regular follow up clearings but has been shown to have made significant progress in the clearing and restoration of freshwater ecosystems nationally (Blanchard and Holmes 2008; Holmes et al. 2005). Woody invasive species are able to utilize the flooding events and anthropogenic disturbances to aid their recruitment (Galatowitsch and Richardson 2005) and ability to out-compete the indigenous species (Meek et al. 2010; Tabacchi et al. 1998). Sieben and Reinecke (2008) give a wetbank / drybank description to aid restoration by means of re-vegetation instead of natural recovery. Natural recovery is timely and has proven less successful as well as more expensive in the past (Blanchard and Holmes 2008; Galatowitsch and Richardson 2005; Pretorius et al. 2008).

The Western Cape has a Mediterranean climate and the Fynbos biome has adapted to the hot dry summer and wet cold winter seasons. The warm dry summer months coincide with fire disturbance that is essential for the successful reproduction and distribution of fynbos vegetation. Fire affects the community structure of Mediterranean vegetation (Arianoutsou 1998) and post-fire succession has been shown to cause an increase in species richness in

some cases at the two to three year temporal scale (Rutherford et al. 2011) due to the flush of germination triggered by fire disturbance (Purdie 1977).

The second part of this study was aimed at assessing the temporal changes occurring at undisturbed sites and sites subjected to fire and clearing of alien woody species. More focus has been directed towards studying the changes following burning and clearing and comparing these with undisturbed sites. The changes occurring in these “reference sites” was assessed and then compared with disturbed.

Authors such as Reinecke et al. (2007) and Reinecke and Brown (2013) addressed lateral zonation in riparian vegetation communities, but the issue of how vegetation differs from mountain stream to the upper foothill longitudinal zones has not been addressed. Also a temporal comparison between sites affected by different disturbances and sites not subjected to major disturbances has not yet been compared. The small temporal scale at which this comparison was made helped to assess whether sites change drastically over a relatively short period of time. The information on the spatial and temporal dimension of change is needed because the concept of reference sites or descriptions may be defined better if such information is available.

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3 Spatial differences of undisturbed Fynbos Riparian Vegetation communities longitudinally down Western Cape Rivers

3.1 Introduction

A river has three main dimensions across which exchange of nutrients and ecological interactions occur: 1) longitudinal; 2) lateral, and; 3) vertical (Ward and Wiens 2001). The distribution of vegetation growing alongside rivers is closely linked to these three dimensions. Longitudinal changes in nutrient input and sediment size affects longitudinal distribution of species with communities changing markedly from source to sea. Differential lateral inundation (Boucher 2002), scouring and seed dispersal affects zonation across the floodplain/river bank, as does the connection between roots (vertical dimension) and subsurface water (Richardson and Kruger 1990). Indeed, in recognition of the important influence of longitudinal factors on the distribution and life-histories of aquatic biota, spatial, often hierarchical classification of stream and rivers has become an important aspect of ecological studies on rivers (Downes et al. 2000; Frissell et al. 1986; Townsend and Hildrew 1994; Ward and Palmer 1994). The longitudinal dimension has also received considerable attention through frameworks such as the River Continuum Concept⁵ (Vannote et al. 1980).

Of all riverine biota, riparian plant communities show the most prominent lateral zonation patterns. These have been linked to the flow regimes of river system (Boucher and Tlale 1999, Boucher 2002) and, albeit to a lesser extent, to vertical exchange of water and nutrients (Correll 1999, Jacobs et al. 2007). This thesis used the most recent lateral zone description of Reinecke and Brown (2013), which described four lateral riparian zones: marginal, lower dynamic, lower and upper, based on differential species responses to a suite of abiotic factors that influence water availability and a species' dependence upon this. Three of these, marginal, tree-shrub and upper, correspond to the three zones described by Kleynhans et al. (2007) and are listed in Table 3.1.

The marginal plants are considered to be reliant upon regular inundation (Boucher 2002) and, as such, are expected to be less drought-tolerant and more flood-resistant than those in zones further from the water's edge (Reinecke and Brown 2013, in press). The lower dynamic zone is situated between the marginal and lower zones. It is therefore also considered to form a transition between these two zone types (marginal and lower zones) thus containing a mixture of species found in those zones (Reinecke et al. 2007). Plants in

⁵ The River Continuum Concept (RCC) states that biological communities adapt to the physical template of the riverine ecosystem defined by changes in gradient, river width, sediment size and food resources from source to mouth.

the lower zone were said to be reliant upon periodic inundation (Reinecke and Brown 2013) and usually comprise both obligate and facultative riparian woody trees and shrubs. Plant species in the lower zone are less drought-tolerant than upper zone species (Reinecke and Brown 2013, Reinecke et al. 2007). The upper bank species are relatively drought-tolerant but less resistant to flooding (Boucher 2002). The upper bank comprises of a mixture of lower bank and non-riparian species.

Table 3.1 A comparison of lateral zonation descriptions for South African riparian vegetation from different sources.

Bank position based on flow regime/inundation	Boucher (2002)	Reinecke et al. (2007)	Kleynhans et al. (2007)	Reinecke and Brown 2013
Aquatic	Permanent	Not addressed	Not addressed	Not addressed
	Rooted aquatic macrophytes			
Wet bank	Fringing sedge	Wet edge	Marginal	Marginal
	Shrub willow			
	Lower dynamic	Channel fringe	Not addressed	Lower dynamic
Dry bank	Tree shrub	Tree shrub	Lower	Lower
	Back dynamic	Outer transitional	Upper	Upper
Terrestrial				

Although species are often not confined to a single zone, they do tend to occur more frequently in some zones than others. To that end, Reinecke et al. (2007) described the distribution of indicator species for lateral zones of Fynbos rivers: *Isolepis prolifera* and *P. serratum* for the Marginal, *C. paniculata*, *E. capensis*, *T. babara*, *M. serrata* and *M. angustifolia* for the lower dynamic and lower and *S. angustifolia*, *D. glabra*, *P. aquilinum* and *B. stellatifolium* for the upper bank. The most comprehensive study on lateral zones in Fynbos Riparian Vegetation to date (Reinecke et al. 2007) described a reference condition for the four lateral zones that is applicable across three longitudinal zones; the mountain stream, transitional and upper foothills.

This study focused on disaggregating the differences between lateral zones situated in three longitudinal zones. The objective was to demonstrate changes in riparian vegetation

communities and the physical attributes linked to these differences between longitudinal zones.

The objectives of the study were:

1. To identify and describe how plant community composition changes between longitudinal zones.
2. To evaluate and test the relationship between plant community composition and selected environmental variables.

3.2 Methods

3.2.1 Site selection

Fourteen sites were selected on four rivers across three longitudinal zones in two different basins in the Western Cape Province, South Africa (Figure 3.1, Table 3.2). Each longitudinal zone contained two sites which were paired units consisting of a hydraulic control, such as a riffle or rapid, and a pool (Figure 3.2). These were:

- Elands Rivers in the Breede River Basin: two sites along the mountain stream and transitional;
- Molenaars River in the Breede River Basin: two sites in the upper foothills longitudinal zone;
- Rondegat River in the Olifants River Basin: two sites along the transitional and upper foothills;
- Heks River in the Olifants River Basin: two sites along the mountain stream and transitional.

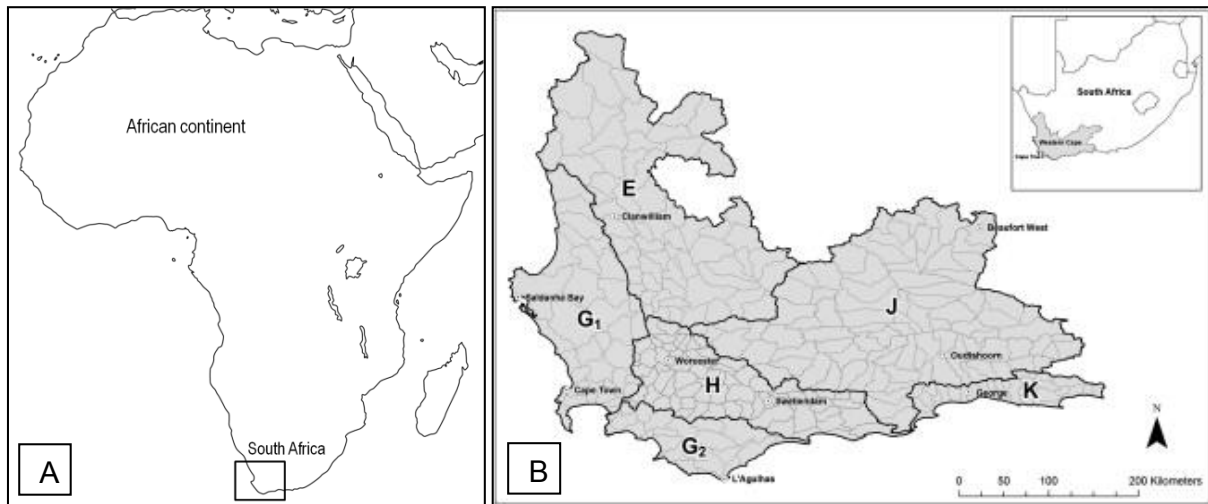


Figure 3.1 Position of rivers selected in context to the African continent (A) and within the Western Cape Province, South Africa (B). E indicates the Olifants River Catchment and H indicates the Breede River catchment.

Table 3.2 Location of paired sites in the two catchments with their corresponding zone - longitudinal zone: M - mountain stream, T - transitional, FH - upper foothills, unit - morphological units. Masl = Altitude in meters above sea level.

Catchment	River	Site	Coordinates	masl	Gradient	Zone	Unit
Breede	Elands	Ela 1	S33°45.654', E19°07.705'	519	0.054	M	Pool
		Ela 2	S33°45.636', E19°07.694'	505	0.054	M	Rapid
		Ela 3	S33°44.410', E19°06.791'	450	0.017	T	Riffle
		Ela 4	S33°44.361', E19°06.786'	446	0.017	T	Pool
	Molenaars	Mol 2	S33°43.387', E19°10.762'	375	0.012	FH	Run
		Mol 5	S33°43.398', E19°10.524'	382	0.012	FH	Pool
Olifants	Heks	Hek 1	S32°26.123', E19°00.530'	245	0.023	T	Pool
		Hek 2	S32°26.116', E19°00.518'	244	0.023	T	Riffle
		Hek 3	S32°26.187', E18°58.883'	175	0.018	FH	Pool
		Hek 4	S32°26.209', E18°58.872'	167	0.018	FH	Riffle
	Rondegat	Ron 1	S32°23.764', E19°05.384'	624	0.085	M	Riffle
		Ron 2	S32°23.762', E19°05.368'	624	0.085	M	Pool
		Ron 3	S32°22.599', E19°04.015'	501	0.029	T	Riffle
		Ron 4	S32°22.569', E19°04.002'	497	0.029	T	Pool

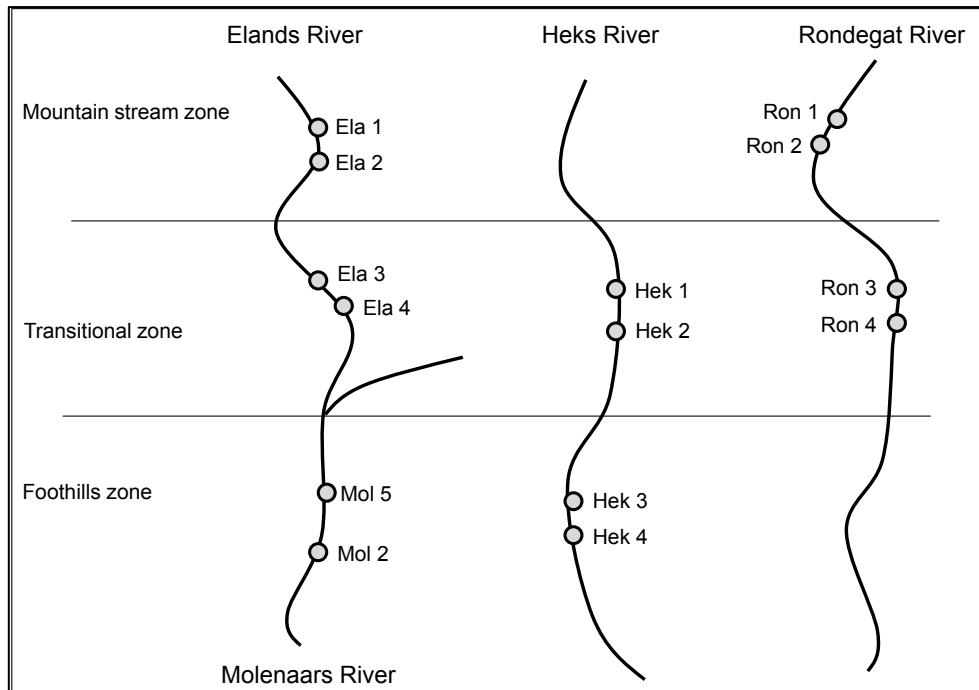


Figure 3.2 Distribution of sites across the three longitudinal zones; mountain stream, transitional and upper foothills. Paired sites (one hydraulic control and one riffle) were used in each longitudinal zone and the same longitudinal zone was used on at least two different rivers.

3.2.2 Data Collection

All data used in this chapter were collected during summer 2011/2012, these includes data on riparian vegetation cover, sediment calibre and cross-sectional surveys (see 1.7). Sites were classified into three longitudinal zones: mountain stream, transitional and upper foothills using the geomorphological classification of Rowntree et al. (2000).

Riparian vegetation cover was estimated per sample plot. This estimation was made as a percentage cover present within the three dimensional space in and above the 1 x 5 m sample plot. Overhanging individuals from neighbouring sample plots were excluded. The estimates also separated trees into three growth classes based on tree height: seedling = 0.01 – 0.3 m, sapling = 0.31 – 2 m and trees > 2 m in height. All ground cover and tree cover data were recorded and unknown species were collected and submitted to the Compton Herbarium at the South African National Biodiversity Institute (Kirstenbosch) for identification.

Sediment calibre was estimated as a percentage of surface substrate present in a sample plot (see 1.7). The soil/sediment size was recorded using the Wentworth scale (Gordon et al. 1992).

3.2.3 Data Analyses

The vegetation data were analysed using PRIMER (V6, Clarke and Gorley 2006) a multivariate statistical programme. An overall transformation of fourth root was applied to the data before CLUSTER analyses and non-metric Multi-Dimensional Scaling (MDS) ordinations were produced. The fourth root transformation function boosts the values of plants with smaller cover abundances recorded due to their small growth form. A Bray-Curtis (PRIMER V6, Clarke and Gorley 2006) similarity was applied before data was analysed further. Multi-dimensional scaling and CLUSTER analyses were used to determine similarity coefficients between sites (PRIMER V6, Clarke and Gorley 2006). Global one-way ANOSIM analyses (PRIMER V6, Clarke and Gorley 2006) were then applied to test the similarity/dissimilarity between sites based on assigned factors of basin, river and longitudinal zones. These results were used to indicate where differences worth investigating were present. As was indicated by the Global R values (ANOSIM results), comparative analyses for this chapter were then further conducted at the river scale.

A 40% similarity grouping value was used to distinguish differences between sample plots (Reinecke et al. 2007). Plots were allocated to a lateral zone on the basis of the outcome of the CLUSTER and MDS analyses (Clarke and Gorley 2006), and borderline sample plots were assigned to groups using plant life histories (Goldblatt and Manning 2000). Based on Goldblatt and Manning (2000) species were assigned one of three possible categories: obligate⁶, incidental⁷ and facultative⁸. These categories aided CLUSTER or MDS results for allocating a group to a specific lateral zone. Once sample plots had been allocated to a lateral zone, a one-way Bray-Curtis similarity (SIMPER) analysis (Clarke and Gorley 2006) was used to identify the species responsible for similarity and dissimilarity in a lateral zone of the specific longitudinal zones.

⁶ Species commonly found in seeps, rivers and watercourses, these are wet species associated with riparian communities

⁷ Species found on rocky outcrops, rocks, mountain slopes and other dry areas of the riparian zone, these are dry terrestrial species occurring on the outer edge of the riparian zone where the riparian vegetation transitions to a terrestrial community

⁸ Occurs in forest, woodland and bushy areas and are associated with water courses, these can be wet or dry species and are known to occur across the riparian zone however usually in higher abundances between the obligate and incidental species

Principle Component Analysis ordinations act on the same principles for environmental data as an MDS would for biological data. Distance, as plotted on a chart, is used as an indicator of the relationship between different environmental variables recorded for a sample plot. By using environmental data only, a PCA ordination was produced for each longitudinal zone on a river producing comparable graphs between longitudinal zones. By using the lateral vegetation zones as produced by MDS and CLUSTER diagrams, a colour was assigned to different zones making the relationship between environmental and biological visible if present. The distribution of sample plots was based on environmental attributes solely, while the colour is an indication of biological results.

BEST Bio-Env analysis (Clark and Gorley 2006) was used to test which combination of environmental variables best explained the vegetation assemblage/pattern. The environmental variables included horizontal distance of sample plot from water's edge, elevation above water level and substrate calibre (bedrock, boulder, cobble, gravel and sand). BIOENV analysis in PRIMER (V6, Clarke and Gorley 2006) produced a combination of environmental variables which shows the strongest relationship with the biological data (discriminant species).

3.3 Results

The species recorded at each site are given in Table 6.1. These data were used to generate a CLUSTER diagram that portrays the similarity/dissimilarity of species composition between sites (Figure 3.3 and Figure 3.4). At the first level of similarity, the sites grouped into the two river basins in which they occurred indicating catchment signatures being very prominently indicated. The Rondegat River grouped with the Heks, and the Elands River grouped with the Molenaars. The second level of similarity occurred at the river scale, where multiple sites on each river grouped together. The Molenaars River grouped separately from the Elands River, even though they are part of the same main stem, with only 30% similarity between the two rivers.

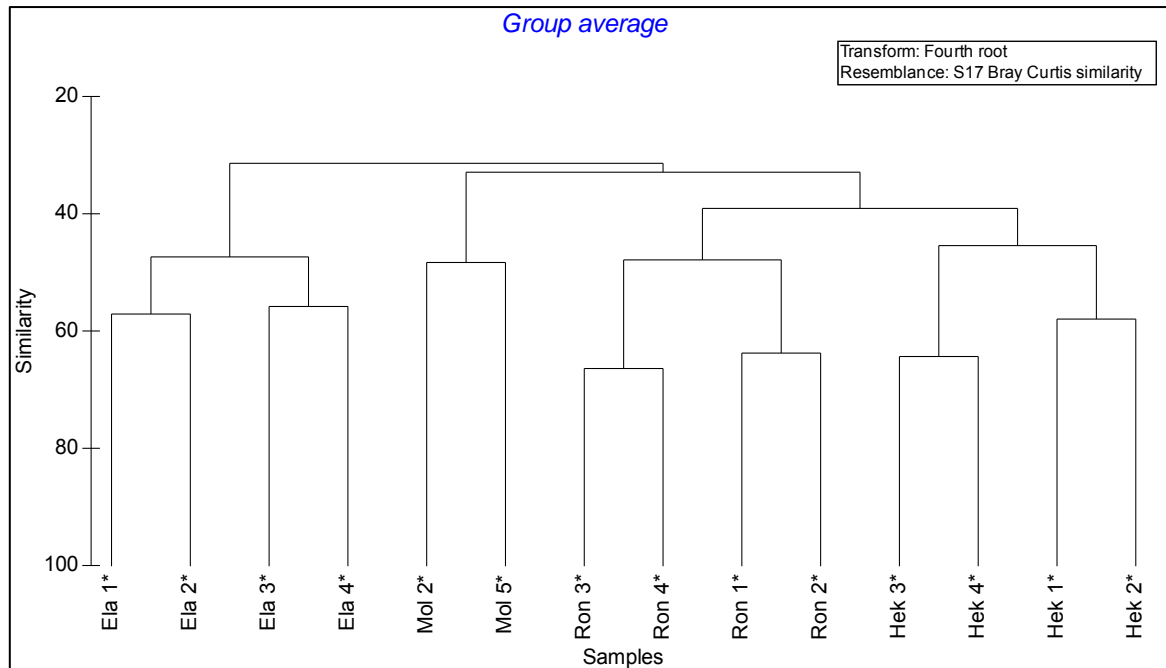


Figure 3.3 CLUSTER diagram of Bray-Curtis similarity between sites. Hek - Heks, Ron - Rondegat Mol - Molenaars and Ela - Elands Rivers with sites numbered 1 to 5.

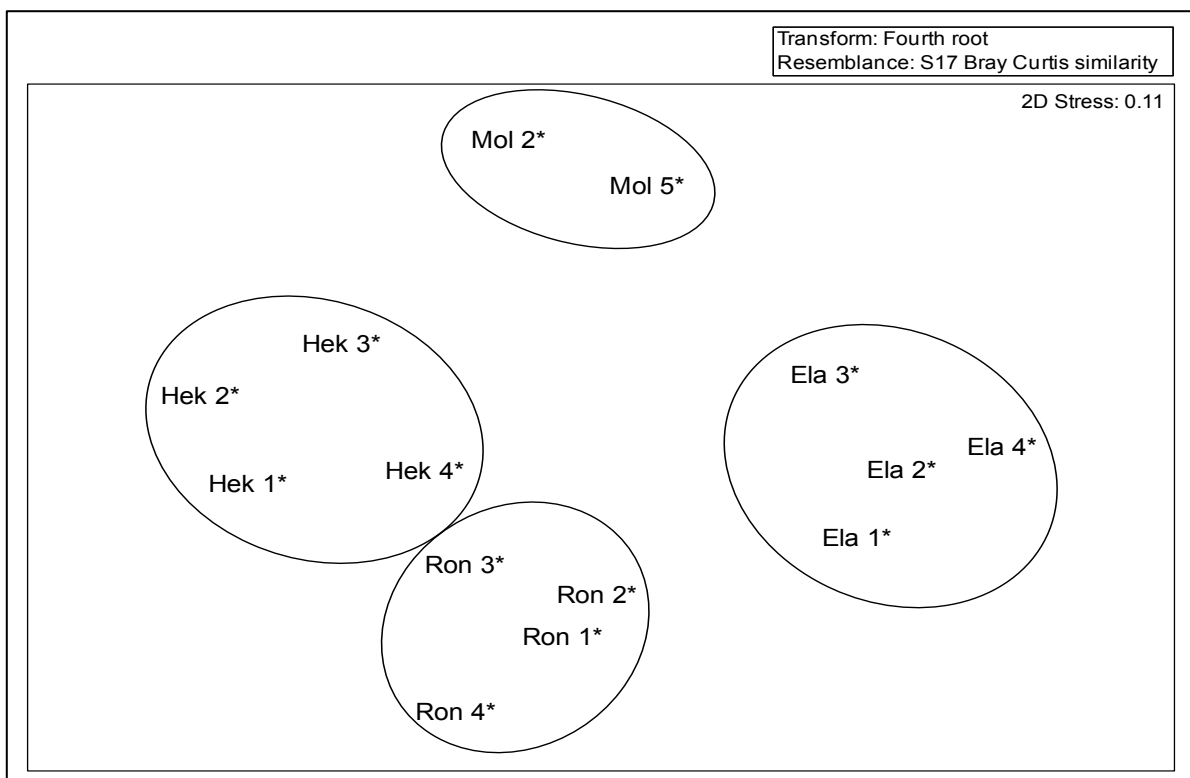


Figure 3.4 Non-metric MDS ordination of Bray-Curtis similarity between sites. Hek - Heks, Ron - Rondegat Mol - Molenaars and Ela - Elands Rivers with sites numbered 1 to 5.

The third level of separation was between longitudinal zones. Sites grouped according longitudinal zone rather than morphological unit. For instance, Ela 1 (pool) and Ela 2 (rapid) grouped together in the mountain stream while Ela 3 (riffle) and Ela 4 (pool) grouped together in the transitional zone. A Global one-way ANOSIM of species abundances conducted at three different scales⁹, the basin, river and longitudinal zone scales showed R values for the basin at 0.84, the river at 0.92 and longitudinal zone at 0.69 ($p < 0.01$).

3.3.1 Comparisons between riparian vegetation of longitudinal zones

Outputs from the MDS and CLUSTER analyses are presented for the Molenaars in Figure 3.5, Elands River in Figure 3.6, Heks River in Figure 3.7 and the Rondegat River in Figure 3.8.

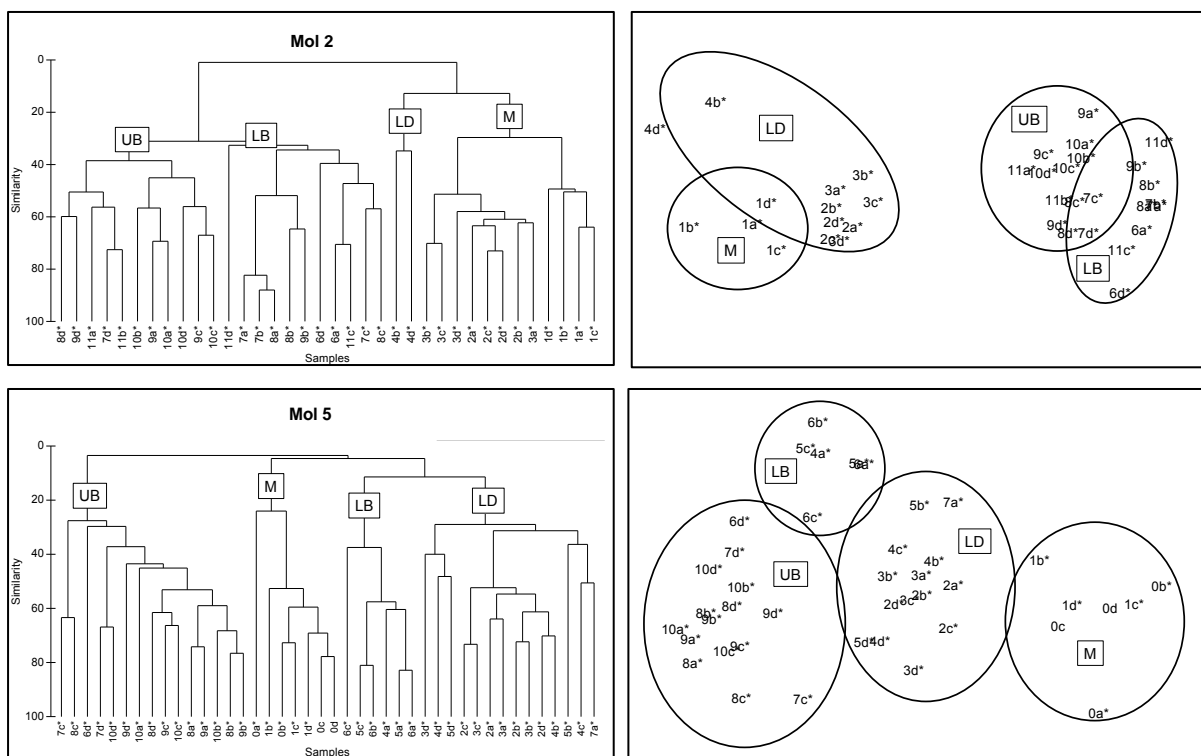


Figure 3.5 Cluster analysis (left) and Non-metric MDS ordinations (right) of Bray-Curtis similarity between species abundances of Mol 2 and Mol 5. The following lateral zones are indicated as follows: M - Marginal, LD - lower dynamic, LB - lower and UB – upper. Sample plot codes are indicated by a numeric (meters up bank) and alphabetic letter (a- upstream and d – downstream transect).

⁹ The scales (factors) used for the ANOSIM analyses were based on the geomorphological classification system by Rowntree et al. (2000).

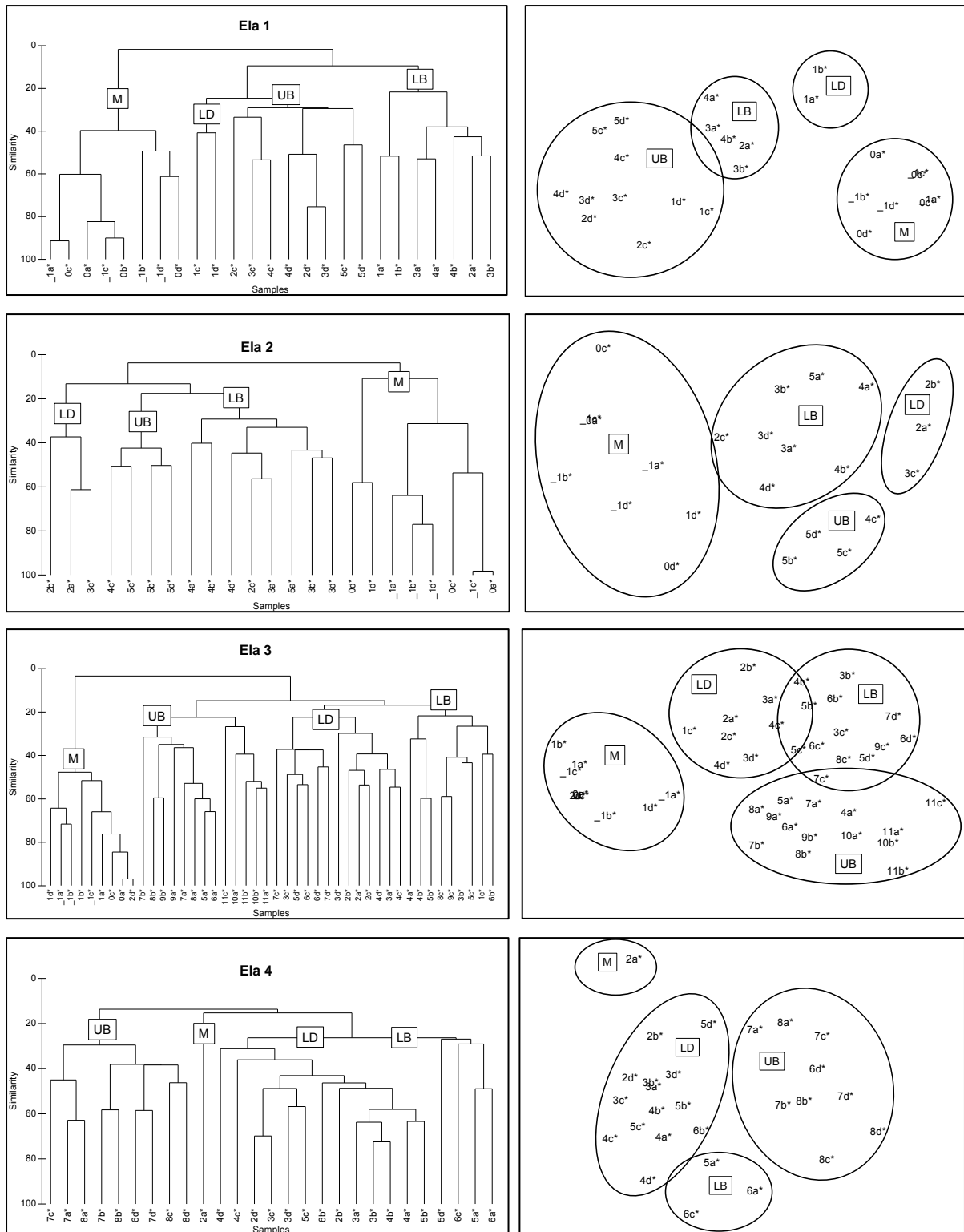


Figure 3.6 Cluster analysis (left) and Non-metric MDS ordinations (right) of Bray-Curtis similarity between species abundances of Ela 1 - 4. The following lateral zones are indicated as follows: M - Marginal, LD - lower dynamic, LB - lower and UB – upper. Sample plot codes are indicated by a numeric (meters up bank) and alphabetic letter (a- upstream and d – downstream transect).

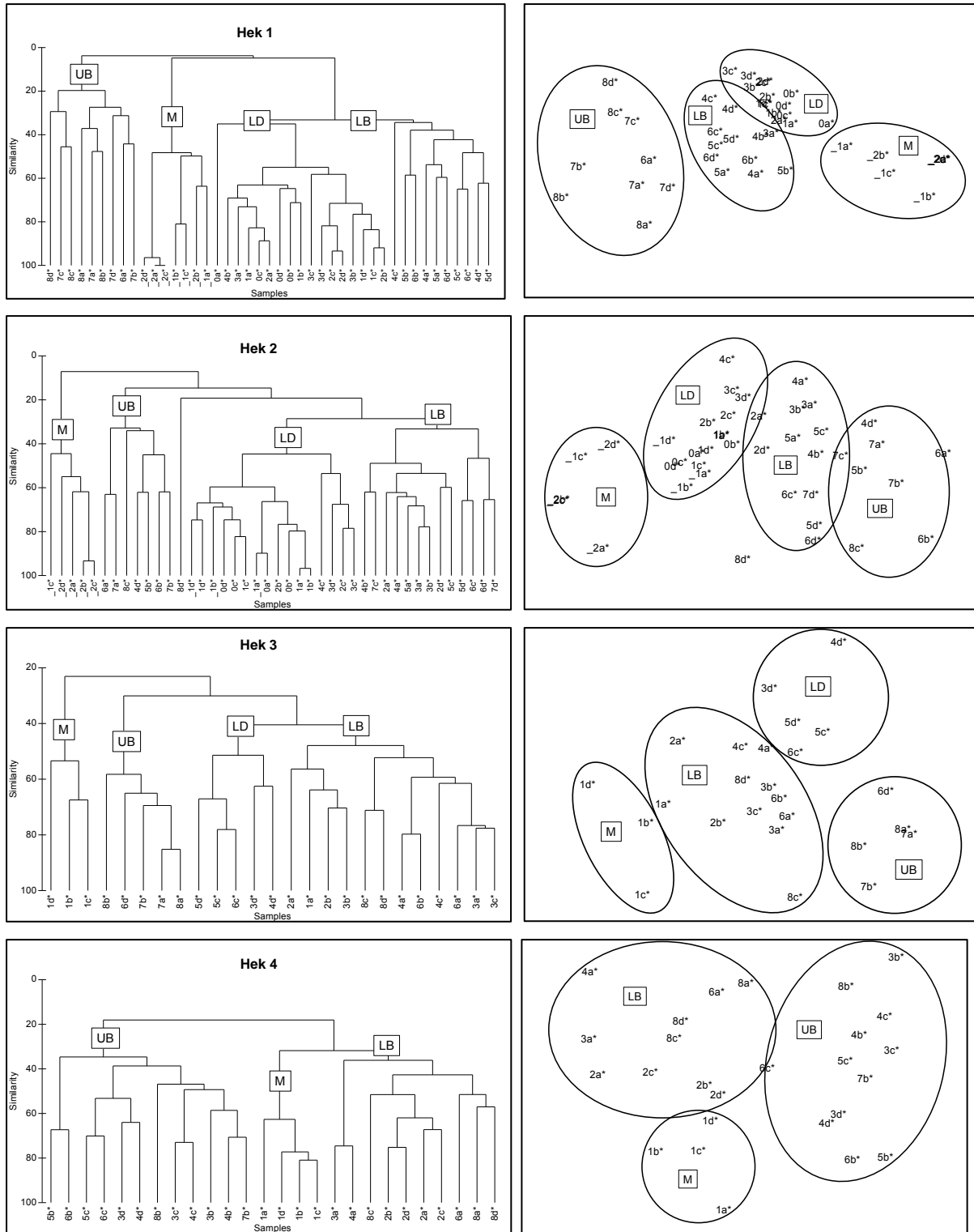


Figure 3.7 Cluster analysis (left) and Non-metric MDS ordinations (right) of Bray-Curtis similarity between species abundances of Hek 1 - 4. The following lateral zones are indicated as follows: M - Marginal, LD - lower dynamic, LB - lower and UB – upper. Sample plot codes are indicated by a numeric (meters up bank) and alphabetic letter (a- upstream and d – downstream transect).

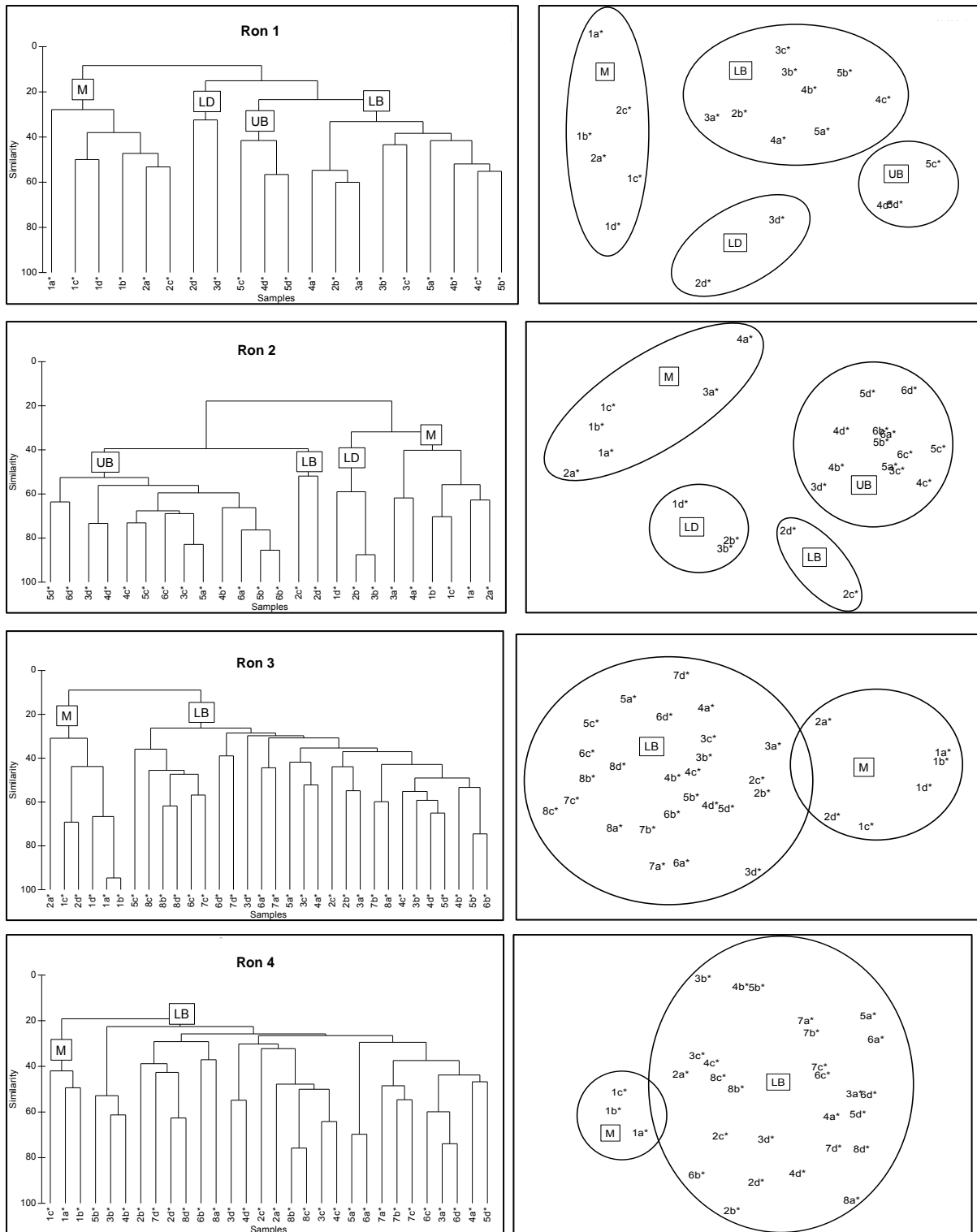


Figure 3.8 Cluster analysis (left) and Non-metric MDS ordinations (right) of Bray-Curtis similarity between species abundances of Ron 1 - 4. The following lateral zones are indicated as follows: M - Marginal, LD - lower dynamic, LB - lower and UB – upper. Sample plot codes are indicated by a numeric (meters up bank) and alphabetic letter (a- upstream and d – downstream transect).

3.3.1.1 Typical and differentiating species for lateral zones

Zones (marginal, lower dynamic, lower and upper) were assigned to sample plots in the mountain stream (Ela 1 and Ela 2) and transitional sites (Ela 3 and Ela 4). SIMPER was used to identify typical (Table 3.3) and differentiating (Table 3.4) species in and between sample plots for each longitudinal zone. Species with the highest values were selected and low valued species were discarded as a low value meant that the variation between longitudinal zones and rivers was too high. The species with the highest values are summarised in Table 3.3 and Table 3.4.

The most important species for the grouping of sample plots (based on SIMPER results) in the marginal zone of mountain stream and transitional sites was *I. prolifera*, while in the upper foothill sites it was either *M. serrata* saplings or a combination of *C. paniculata* and *D. capensis*. The lower dynamic zone was dominated by different species across rivers and longitudinal zones. Little consistency was present in species dominance with the exception of *Brabejum neriifolia*. Where indicated as dominant species, *M. angustifolia*, *M. serrata* and *B. stellatifolium* were usually adult trees and not juveniles or saplings.

The lower bank on the Rondegat River had the same species defining the lateral zone in both longitudinal zones: *P. aqualinum*. The other typical species occurring in the lower bank were *M. angustifolia*, *E. caffra* and *E. capensis*. The upper bank contained *P. distichophylla*, *A. capitata*, *S. angustifolia* and *D. glabra*. With the exception of *P. aqualinum* in the lower bank of the Rondegat River, each longitudinal zone presented a different species as typical and thus responsible for the grouping of a different lateral zone. The Molenaars River had no differentiating species because there were no other longitudinal sites selected to compare the foothills with. Species responsible for the dissimilarities between lateral zones were comparable with that of the species on the Elands River as presented in Table 3.3.

On the Elands River *I. prolifera* was responsible for the difference between the marginal zones of the mountain stream and transitional zone. *B. stellatifolium* trees and *B. neriifolia* saplings was responsible for the mountain stream being different from the transitional zone in the lower dynamic zone. The lower dynamic in the transitional sites on the Elands and Heks Rivers both showed *C. paniculata* as discriminant species. The differences in discriminating species continued up the bank and across the rivers with very little consistency in indicating and differentiating species present.

Table 3.3 Typical species for lateral zones on the Elands, Molenaars, Heks and Rondegat Rivers per longitudinal zone based on SIMPER analyses. Sim/SD = similarity coefficient divided by the standard deviation within groups.

Lateral zone	Mountain stream		Transitional		Foothills	
	Elands River					
	Sim/SD	Species	Sim/SD	Species	Sim/SD	Species
Marginal	1.18	<i>Isolepis prolifera</i>	-	None	No sites sampled	No sites sampled
Lower dynamic	0.62	<i>Brabejum stellatifolium</i> tree	0.62	<i>Calopsis paniculata</i>	No sites sampled	No sites sampled
Lower	0.77	<i>Erica caffra</i>	1.06	<i>Elegia capensis</i>	No sites sampled	No sites sampled
Upper	0.76	<i>Pentameris distichophylla</i>	1.12	<i>Aristea capitata</i>	No sites sampled	No sites sampled
	Molenaars River					
	Sim/SD	Species	Sim/SD	Species	Sim/SD	Species
Marginal	No sites sampled	No sites sampled	No sites sampled	No sites sampled	0.83	<i>Morella serrata</i> sapling
Lower dynamic	No sites sampled	No sites sampled	No sites sampled	No sites sampled	0.96	<i>Brachylaena nerifolia</i> sapling
Lower	No sites sampled	No sites sampled	No sites sampled	No sites sampled	0.5	<i>Pteridium aqualinum</i>
Upper	No sites sampled	No sites sampled	No sites sampled	No sites sampled	1.67	<i>Searsia angustifolia</i>
	Heks River					
	Sim/SD	Species	Sim/SD	Species	Sim/SD	Species
Marginal	No sites sampled	No sites sampled	2.57	<i>Isolepis prolifera</i>	6.8, 6.55	<i>Calopsis paniculata</i> , <i>Drosera capensis</i>
Lower dynamic	No sites sampled	No sites sampled	1.94	<i>Metrosideros angustifolia</i> tree, <i>Morella serrata</i> tree	2.62, 2.98	<i>Ehrharta ramosa</i> , <i>Metrosideros angustifolia</i> tree
Lower	No sites sampled	No sites sampled	1.55	<i>Metrosideros angustifolia</i> tree	1.56	<i>Metrosideros angustifolia</i> tree
Upper	No sites sampled	No sites sampled	0.43	<i>Diospyros glabra</i>	2.75	<i>Diospyros glabra</i>

	Rondegat River					
	Sim/SD	Species	Sim/SD	Species	Sim/SD	Species
Marginal	0.74	<i>Metrosideros angustifolia</i> tree	1.97	<i>Isolepis prolifera</i>	No sites sampled	No sites sampled
Lower dynamic	2.43	<i>Elegia capensis</i>	0	None	No sites sampled	No sites sampled
Lower	4.93	<i>Pteridium aqualinum</i>	2.06	<i>Pteridium aqualinum</i>	No sites sampled	No sites sampled
Upper	2.22	<i>Pelargonium scabrum</i>	0	None	No sites sampled	No sites sampled

Table 3.4 Differentiating species within lateral zones and between longitudinal zones on the Elands, Heks and Rondegat Rivers. Diss/SD = dissimilarity coefficient over standard deviation.

Elands River				
Lateral zone	Diss/SD	Mountain stream	Transitional	Foothills
Marginal	1.27	<i>Isolepis prolifera</i>	None	No sites sampled
Lower dynamic	1	<i>Brabejum stellatifolium</i> tree, <i>Brachylaena neriifolia</i> sapling	<i>Calopsis paniculata</i>	No sites sampled
Lower	1.21	<i>Erica caffra</i> , <i>Metrosideros angustifolia</i> tree,	<i>Diospyros glabra</i> , <i>Elegia capensis</i>	No sites sampled
Upper	1.21	<i>Pentameris distichophylla</i> , <i>Elegia capensis</i>	<i>Aristea capitata</i>	No sites sampled
Heks River				
Lateral zone	Diss/SD	Mountain stream	Transitional	Foothills
Marginal	5.45	No sites sampled	None	<i>Drosera capensis</i> , <i>Calopsis paniculata</i> , <i>Morella serrata</i> sapling
Lower dynamic	2.74	No sites sampled	<i>Calopsis paniculata</i> , <i>Panicum schinzii</i>	<i>Ehrharta ramosa</i> ,
Lower	1.17	No sites sampled	<i>Morella serrata</i> T	<i>Metrosideros angustifolia</i> tree, <i>Morella serrata</i> sapling
Upper	1.24	No sites sampled	<i>Rhus lucida</i> forma <i>eliptica</i>	<i>Morella serrata</i> sapling, <i>Diospyros glabra</i> , <i>Ehrharta ramosa</i>
Rondegat River				
Lateral zone	Diss/SD	Mountain stream	Transitional	Foothills
Marginal	1.86	<i>Metrosideros angustifolia</i> tree, <i>Elegia capensis</i>	<i>Pronium serratum</i> , <i>Isolepis prolifera</i>	No sites sampled
Lower dynamic		None	None	No sites sampled
Lower	1.94	<i>Phyllica oleaefolia</i> S	<i>Stoebe plumosa</i>	No sites sampled
Upper		None	None	No sites sampled

When typical species occurrence as described by Reinecke et al (2007) was compared to data collected for different longitudinal zones, a graphic comparison between species occurrence in lateral zones and across different longitudinal zones could be made (Figure 3.10; Figure 3.11; **Error! Reference source not found.**).

Most of the groundcover species followed the same trend produced by Reinecke et al. (2007). *Isolepis prolifera* and *Pronium serratum* in the marginal and *Calopsis paniculata* and *Elegia capensis* in the lower dynamic and lower zones was consistent with the reference description but had slight differences in abundances present longitudinally. The same was true for *P. macrourum*, *E. caffra* and *S. angustifolia* following the Reinecke et al. 2007 description for later distribution with variation in abundances longitudinally. There were however species that varied significantly in abundance between longitudinal and lateral zones. *Diospyros glabra*, for instance, showed higher abundances in the marginal of the mountain stream sites than in the upper lateral zone as described by the reference description. *Todea babara* had high occurrence frequency in the mountain stream marginal and lower zone, apart from that no clear distribution pattern was evident. *Pteridium aqualinum* was most frequently found in the lower zone of the transitional sites however the increase in abundance from marginal to upper was true for all longitudinal zones sampled.

Results from a comparison of typical tree species with the reference description made by Reinecke et al. (2007) are shown in Figure 3.12, Figure 3.13, Figure 3.14 and Figure 3.15. Tree growth class distribution varied greatly. The most variation was seen in seedling establishment with an overall trend towards the marginal zone having the most seedling activity. Where higher occurrence for *M. angustifolia* and *M. serrata* was found for the lower dynamic zone by Reinecke et al. (2007) a higher frequency of occurrence was found to be present in the marginal zone by data collected during this study. *Brabejum stellatifolium* was an exception with the highest frequency of occurrence¹⁰ being in the lower dynamic instead of the lower zone as predicted by Reinecke et al. (2007).

An overall increase in occurrence of *B. stellatifolium* seedlings was seen from mountain stream to upper foothills. Saplings and adult trees showed similar patterns in distribution but great variation in frequency of occurrence between longitudinal zones. The mountain stream zone tended to have a very different distribution of adult trees from that of the foothills. For instance *B. stellatifolium* which is usually found in the lower and upper lateral zones in the foothills, showed high abundance in the marginal and lower dynamic lateral zones of the mountain stream sites. Also in the case of *M. angustifolia* where there were hardly any trees

¹⁰ Frequency of occurrence is presented as relative cover abundance recorded.

recorded in the marginal during 2004/2005 sampling but during the present study high abundances of trees were recorded in the marginal lateral zone.

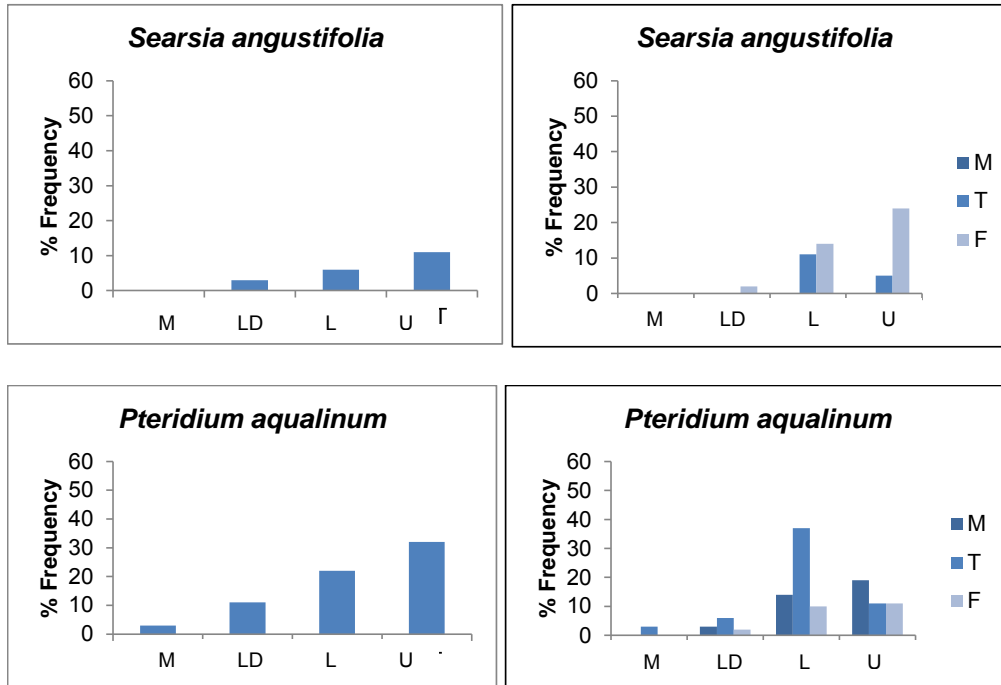


Figure 3.9 Comparison between results for typical groundcover species taken from Reinecke et al. (2007) presented on the left, and results produced by the present study distributed across three longitudinal zones presented on the right. M – mountain stream, T – transitional and F – upper foothills. Results are based on relative species abundances as % frequency of occurrence in a sample plot situated in the particular lateral zone. M – marginal, LD – lower dynamic, L- lower and U – upper lateral zone.

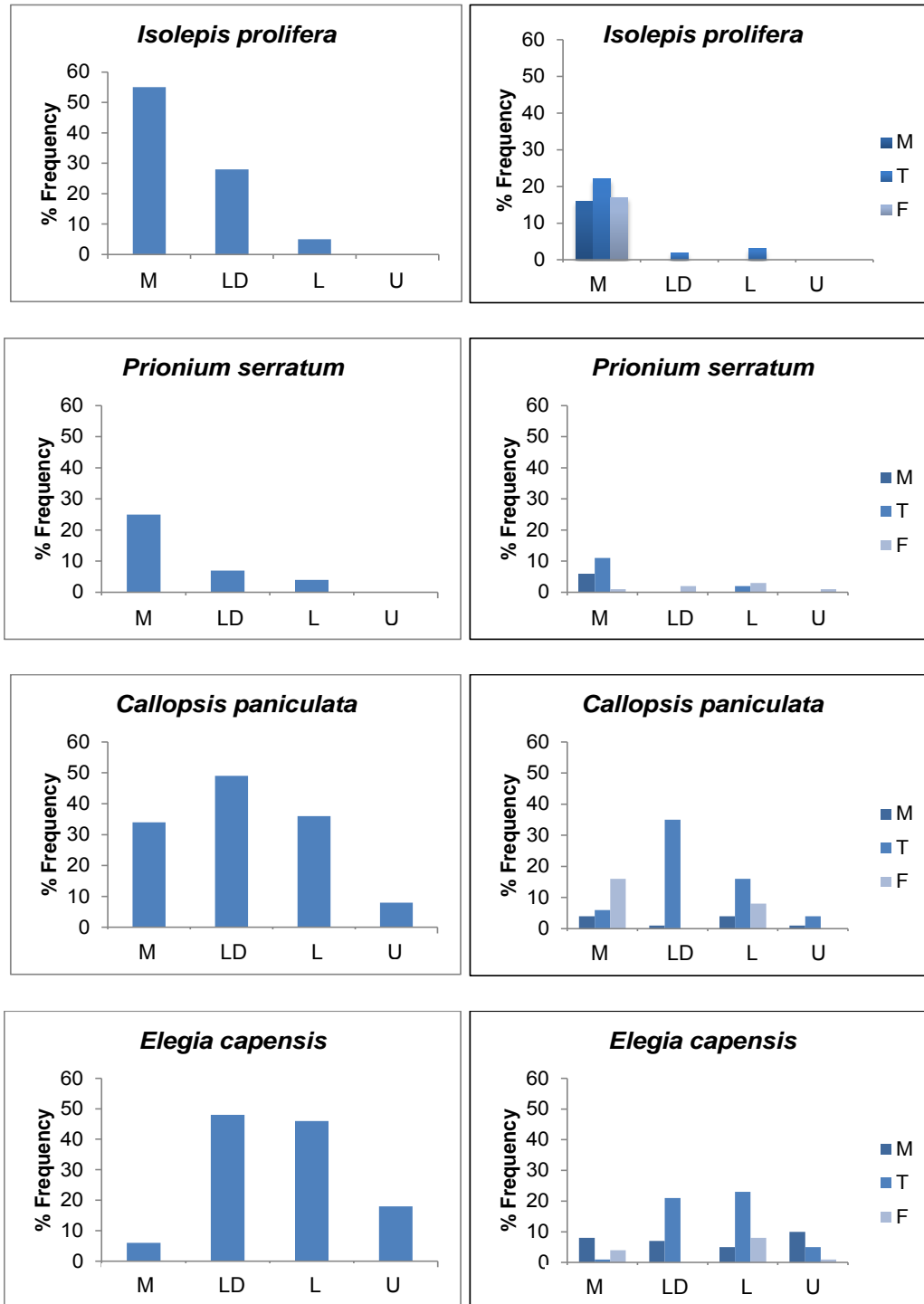


Figure 3.10 Comparison between results for typical groundcover species taken from Reinecke et al. (2007) presented on the left, and results produced by the present study distributed across three longitudinal zones presented on the right. M – mountain stream, T – transitional and F – upper foothills. Results are based on relative species abundances as % frequency of occurrence in a sample plot situated in the particular lateral zone. M – marginal, LD – lower dynamic, L- lower and U – upper lateral zone.

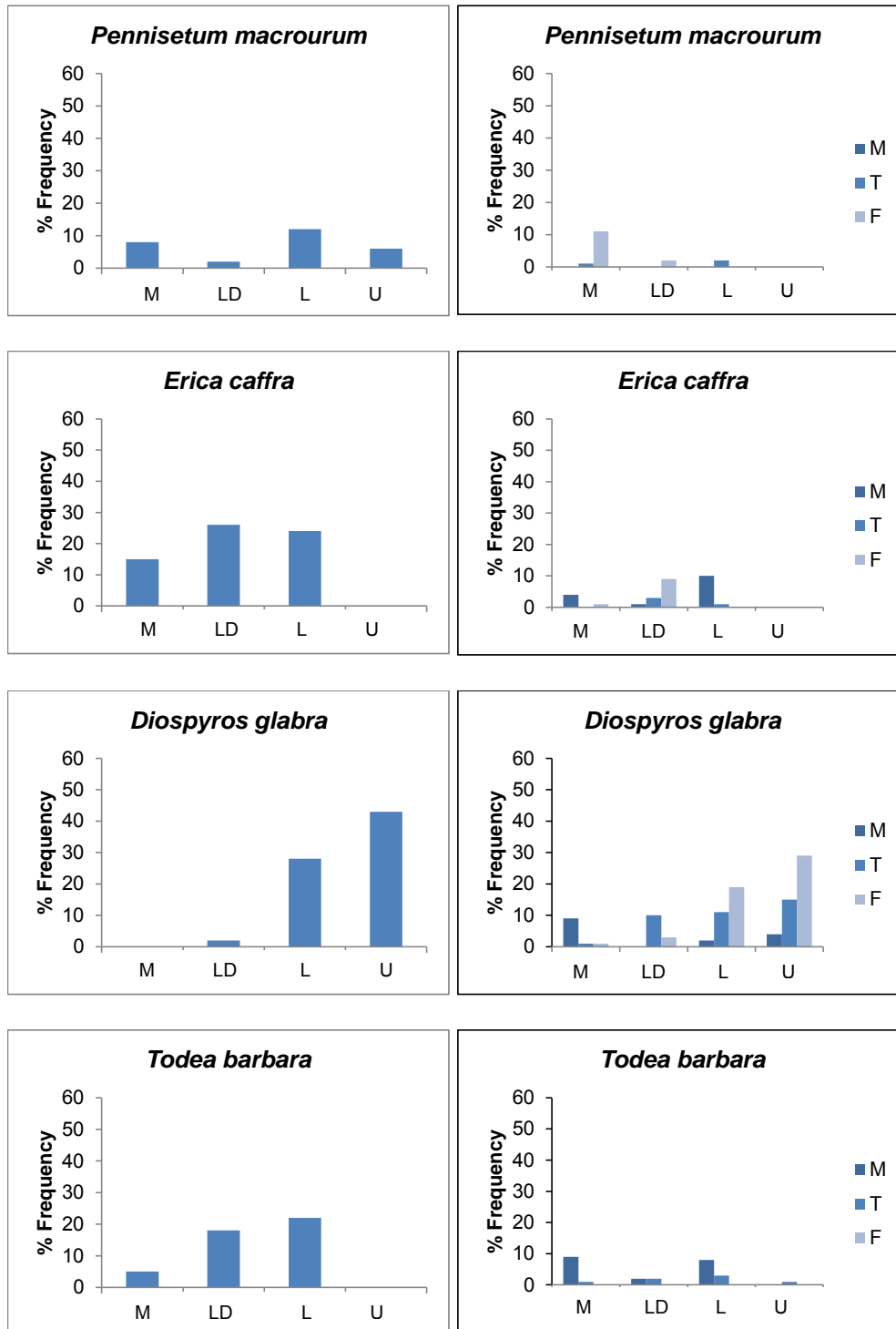


Figure 3.11 Comparison between results for typical groundcover species taken from Reinecke et al. (2007) presented on the left, and results produced by the present study distributed across three longitudinal zones presented on the right. M – mountain stream, T – transitional and F – upper foothills. Results are based on relative species abundances as % frequency of occurrence in a sample plot situated in the particular lateral zone. M – marginal, LD – lower dynamic, L- lower and U – upper lateral zone.

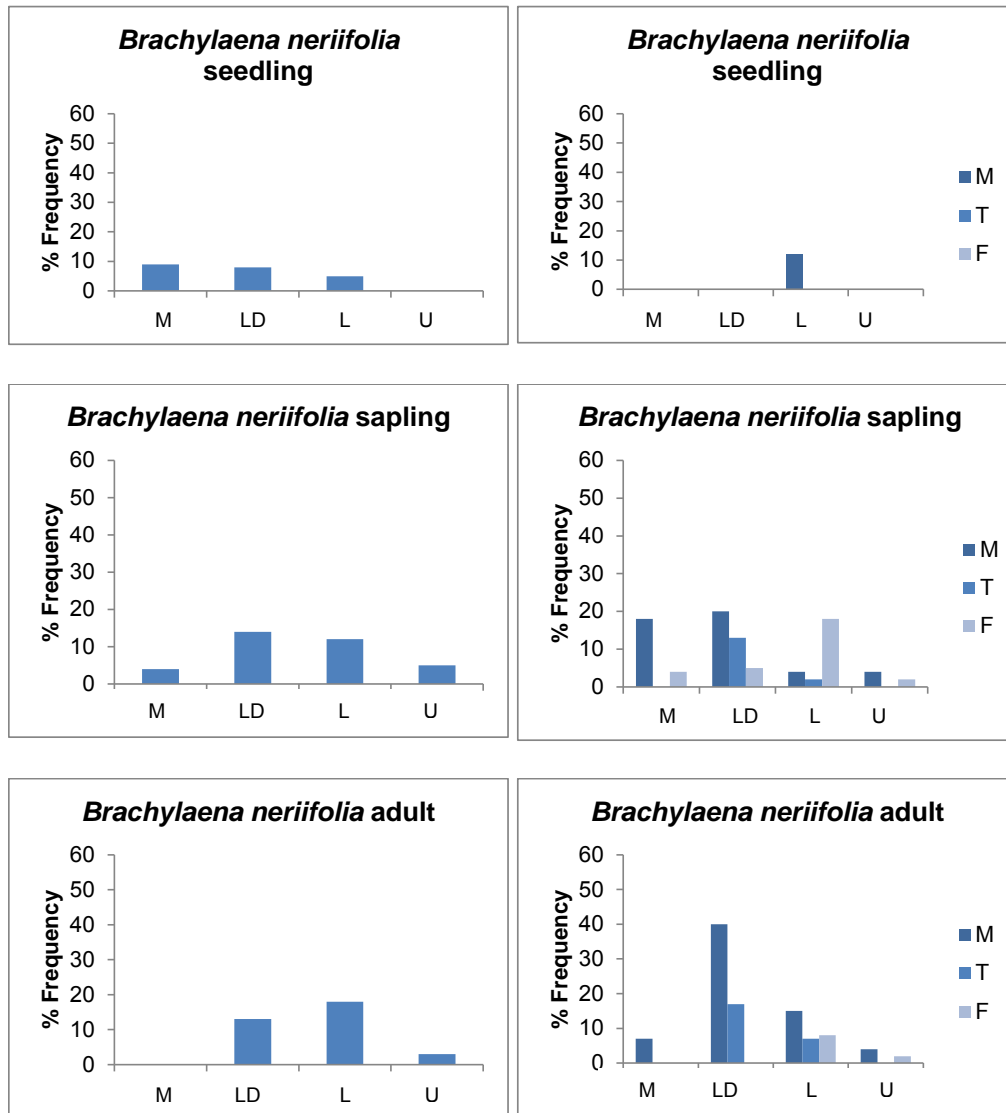


Figure 3.12 Comparison between results for typical tree species (separated into growth classes: seedling, sapling and adult) taken from Reinecke et al. (2007) presented on the left, and results produced by the present study distributed across three longitudinal zones presented on the right. M – mountain stream, T – transitional and F – upper foothills. Results are based on relative species abundances as % frequency of occurrence in a sample plot situated in the particular lateral zone. M – marginal, LD – lower dynamic, L- lower and U – upper lateral zone.

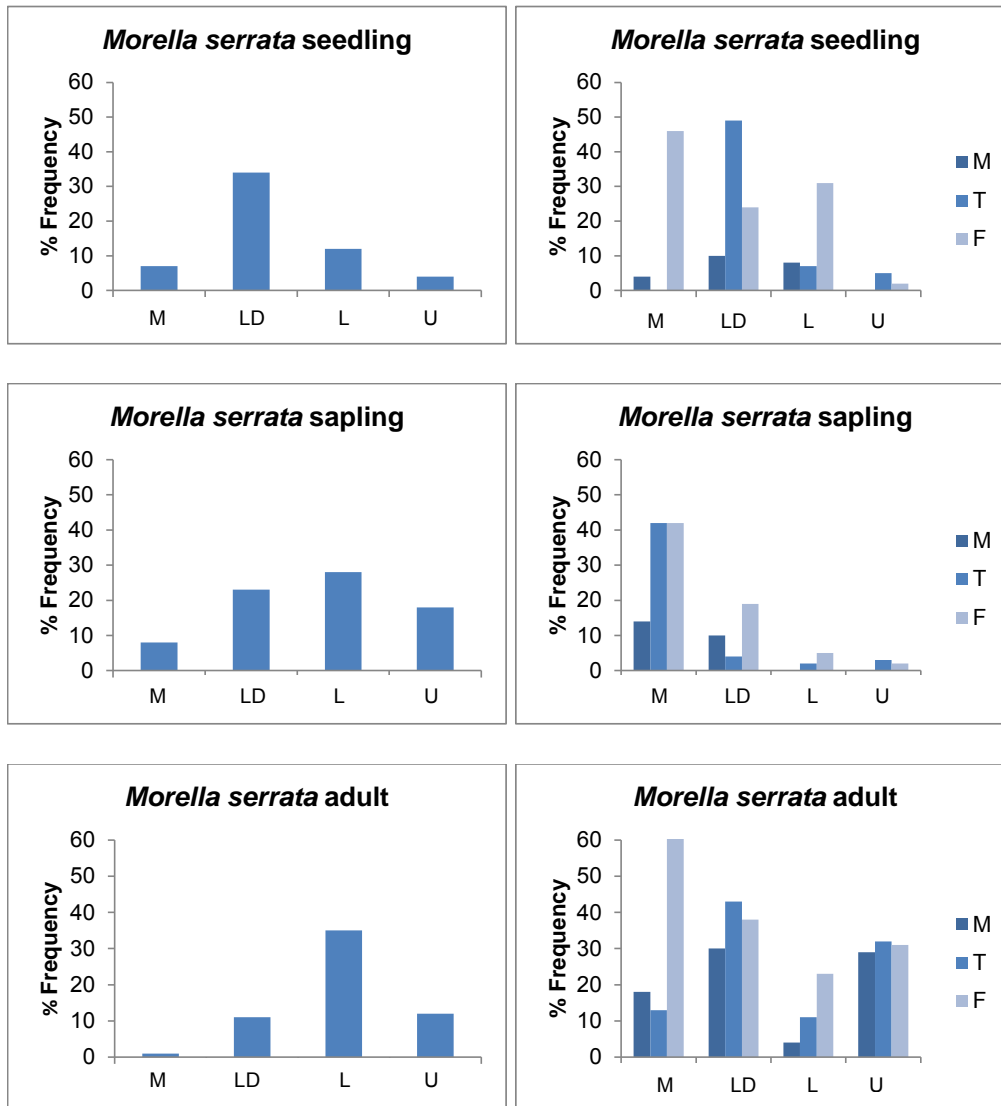


Figure 3.13 Comparison between results for typical tree species (separated into growth classes: seedling, sapling and adult) taken from Reinecke et al. (2007) presented on the left, and results produced by the present study distributed across three longitudinal zones presented on the right. M – mountain stream, T – transitional and F – upper foothills. Results are based on relative species abundances as % frequency of occurrence in a sample plot situated in the particular lateral zone. M – marginal, LD – lower dynamic, L- lower and U – upper lateral zone.

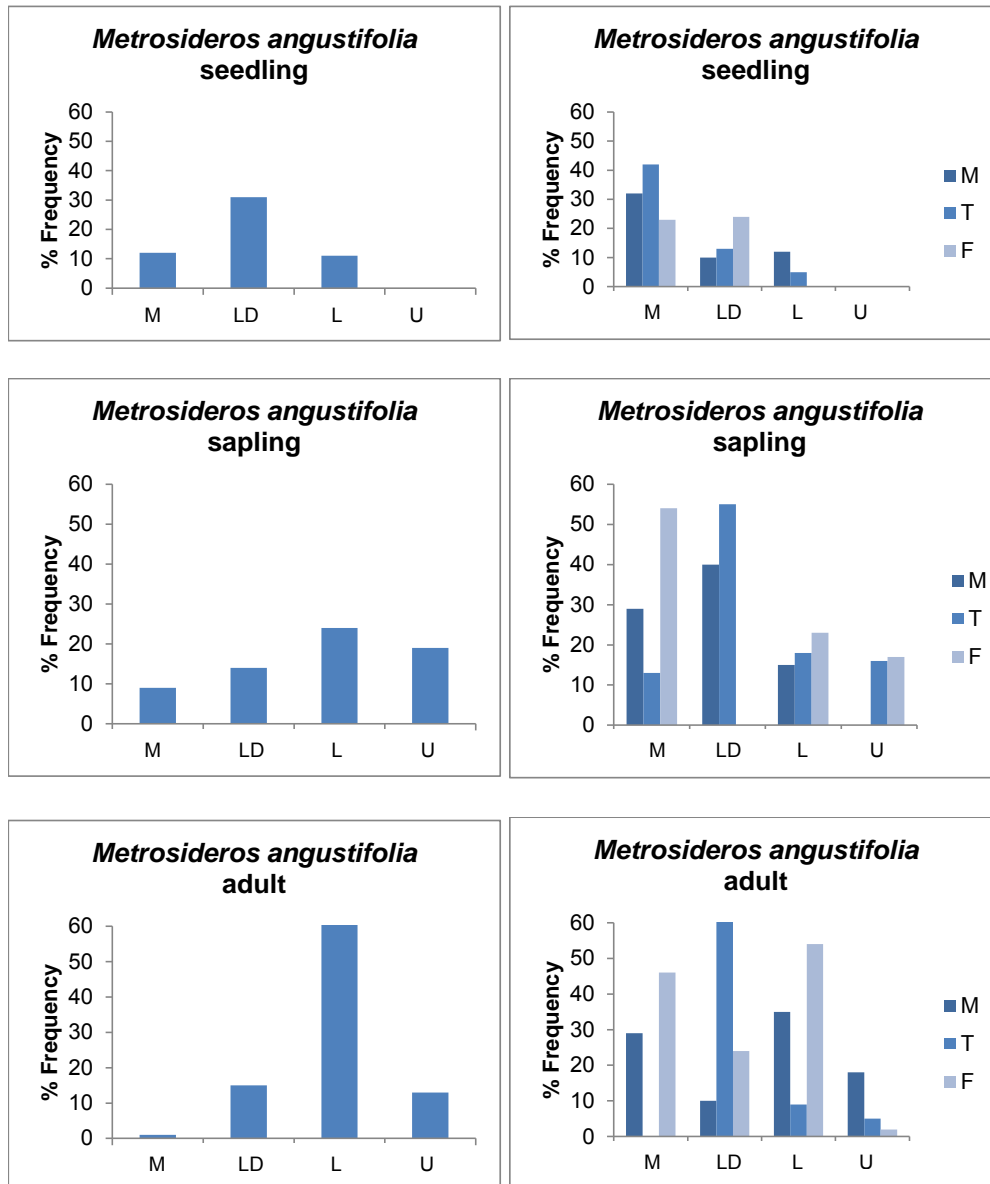


Figure 3.14 Comparison between results for typical tree species (separated into growth classes: seedling, sapling and adult) taken from Reinecke et al. (2007) presented on the left, and results produced by the present study distributed across three longitudinal zones presented on the right. M – mountain stream, T – transitional and F – upper foothills. Results are based on relative species abundances as % frequency of occurrence in a sample plot situated in the particular lateral zone. M – marginal, LD – lower dynamic, L- lower and U – upper lateral zone.

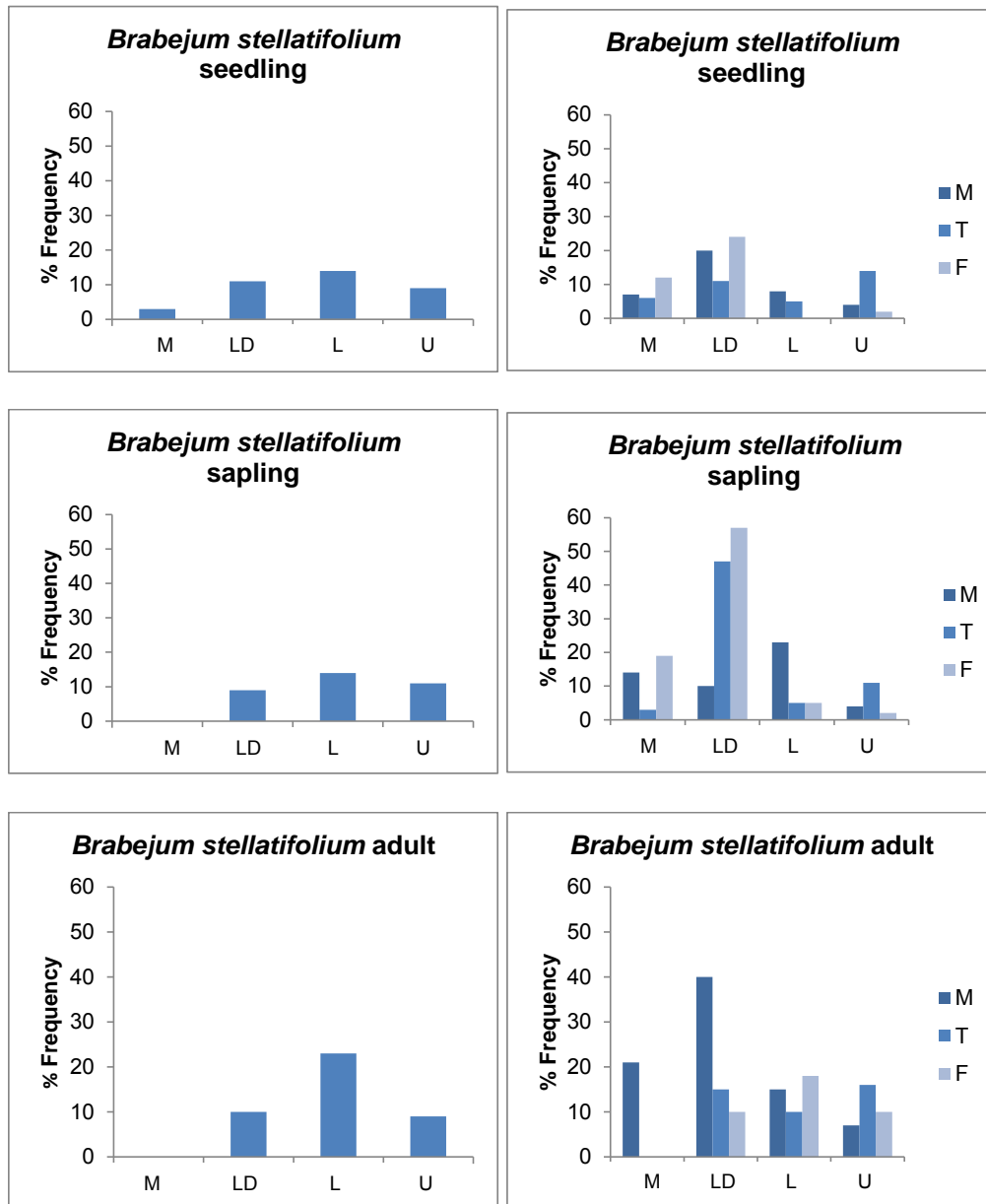


Figure 3.15 Comparison between results for typical tree species (separated into growth classes: seedling, sapling and adult) taken from Reinecke et al. (2007) presented on the left, and results produced by the present study distributed across three longitudinal zones presented on the right. M – mountain stream, T – transitional and F – upper foothills. Results are based on relative species abundances as % frequency of occurrence in a sample plot situated in the particular lateral zone. M – marginal, LD – lower dynamic, L- lower and U – upper lateral zone.

3.3.1.2 *Links between environmental variables and species assemblage*

To assess whether the differences in species composition between longitudinal zones is related to physical environmental variables, PCA ordinations were used to determine the relationships between sediment calibre, bank shape and riparian zonation.

Principle Component Analyses present the relationship between a sample plot and its different environmental variables in a diagram as ordination distance between samples and factors. In order to establish whether pre-selected lateral zones can be linked to environmental variables, the sample plots were labelled according to the vegetation pattern (lateral zonation) but the analyses were conducted using only environmental data: sediment calibre, horizontal distance and elevation. The PCA ordinations indicate a distinct relationship between environmental variables and riparian vegetation species distribution as seen by the distribution of different coloured lateral zone sample plots (Figure 3.16 and Figure 3.17).

Elevation and horizontal distance seem to be the best related to upper bank sample plots while one or more substrate type together with saturated soil was predominantly associated with marginal sample plots. The lower dynamic and the lower bank showed the most overlapping with varying combinations of environmental attributes associated with the sample plot distribution within the PCA ordination. There are some exceptions to the pattern described above such as the transitional zone on the Rondegat River. In this case the lower bank showed a strong relationship with elevation and horizontal distance. This could be because the site is situated in a braided channel and the upper bank and lower dynamic were not present.

The foothill sample plots on the Heks River were distributed across the PCA with little or no pattern. The upper bank and marginal zone tended to show divergent relationships to environmental attributes. The upper bank and the marginal zone sample plots are at opposite ends of the PCA in most diagrams, and while this may be due to the influence of horizontal distance and elevation growing stronger higher up the bank, the transitional sites on the Heks River for instance showed that the marginal had the strongest relationship with horizontal distance while still positioned at the opposite end of the PCA than the upper bank.

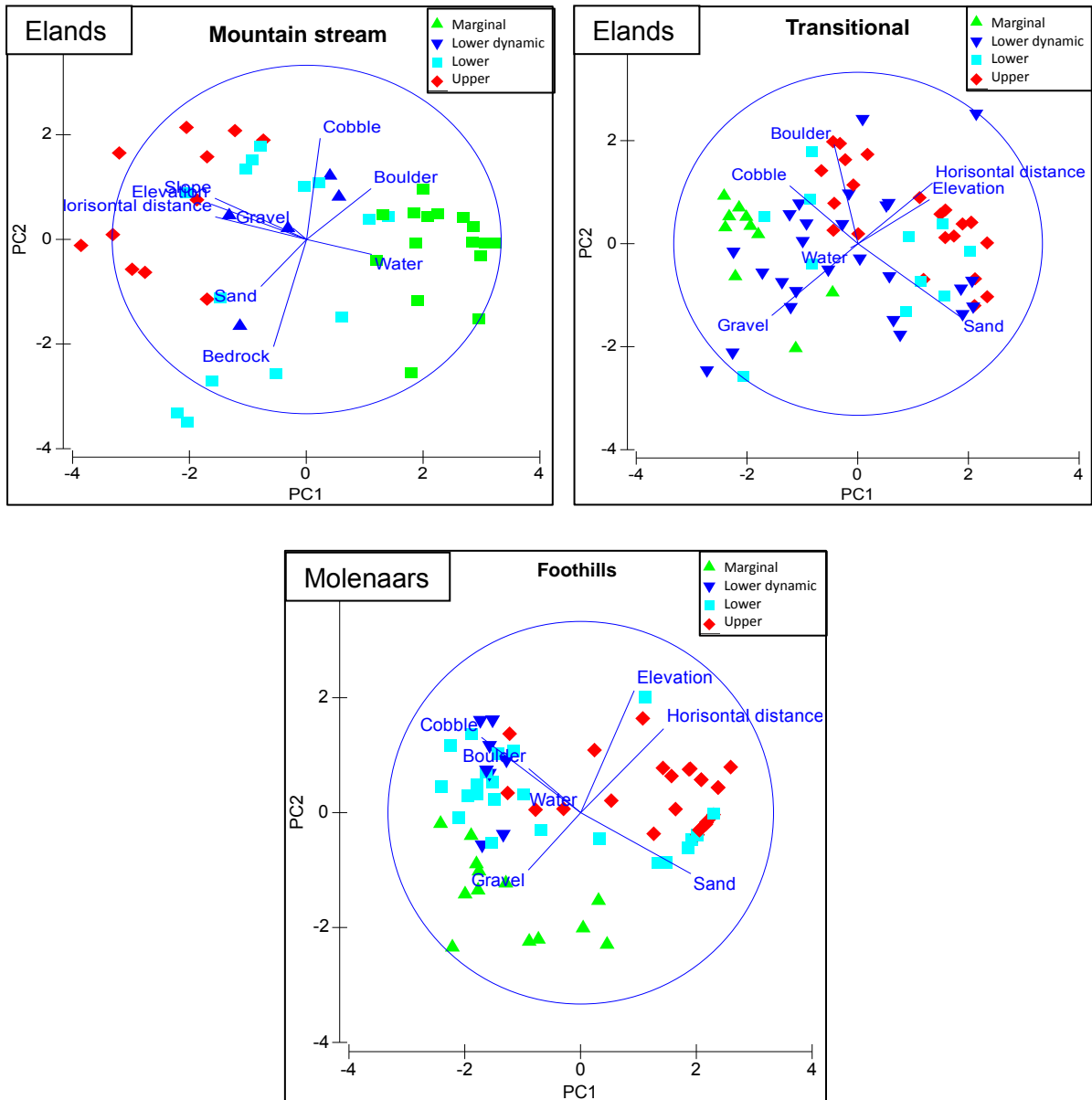


Figure 3.16 PCA ordination of ordination distance between sample sites of three longitudinal zones on the Elands and Molenaars Rivers. Sample sites are indicated by different colours: Green = marginal, blue = lower dynamic, turquoise = lower and red = upper bank zones.

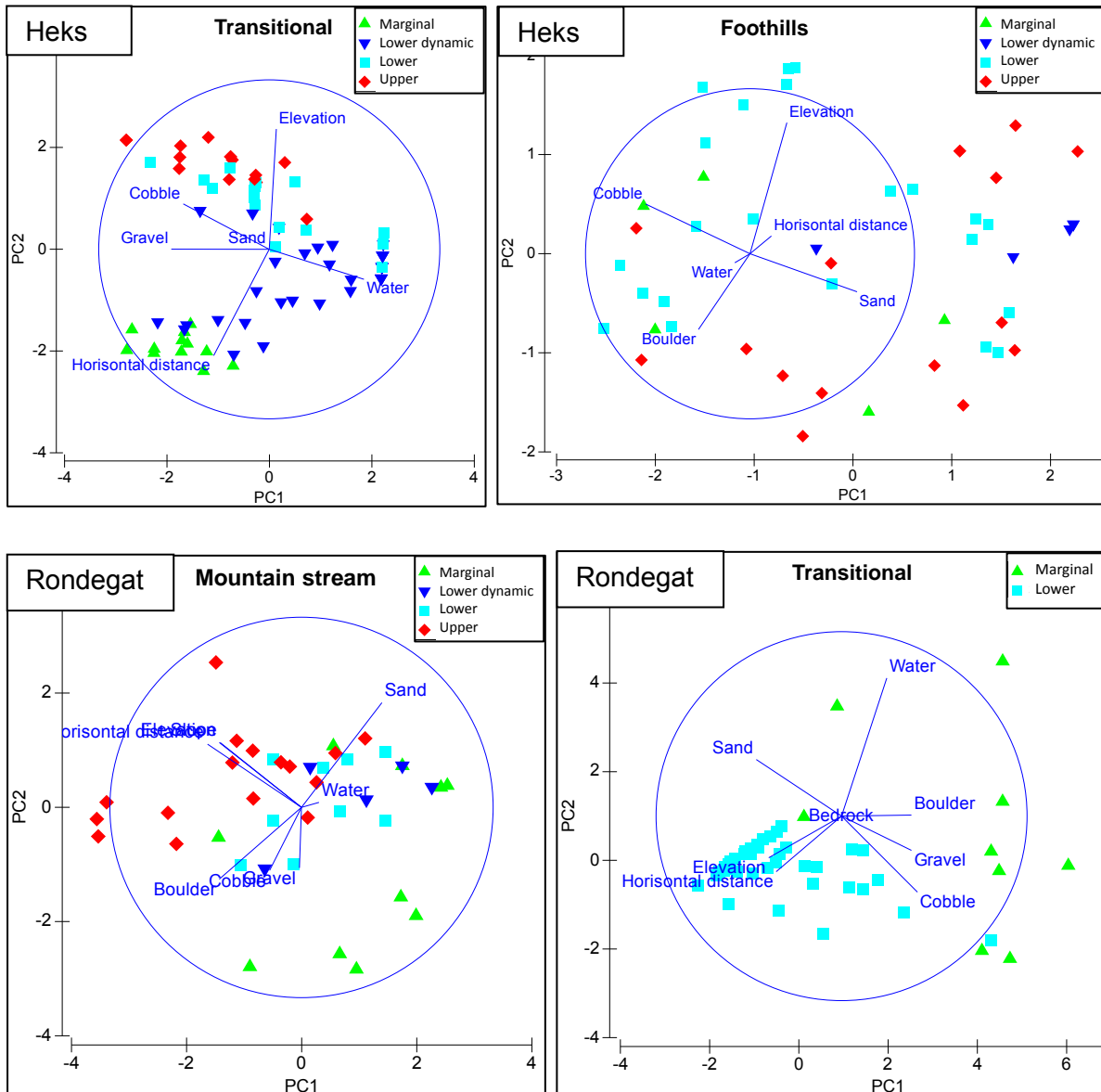


Figure 3.17 PCA ordination of ordination distance between sample sites of three longitudinal zones on the Heks and Rondegat Rivers. Sample sites are indicated by different colours: Green = marginal, blue = lower dynamic, turquoise = lower and red = upper bank zones.

Little species data overlapping occurred between the marginal and the upper bank while the lower dynamic and the lower zones did have some significant species overlapping present in the PCA ordinations. To test the relationship between these two patterns (environmental attributes with vegetation) a BEST analysis in Primer was run. The BEST test (Bio-Env) uses environmental attributes in different combinations in an attempt to best explain the biological pattern present. By using the MDS and CLUSTER results of species level data

together with detailed environmental variable information for each sample plot the best combination of environmental variables were produced (Table 3.5).

Table 3.5 BEST Bio-Env PRIMER (V6, Clarke and Gorley 2006) results representing the best combination of environmental variables responsible for the pattern presented in riparian vegetation.

Longitudinal zone	Sample Statistic (R^2)	Environmental variables
Elands River		
Mountain stream	0.40 ($p < 0.01$)	Horizontal distance and elevation
Transitional	0.53 ($p < 0.01$)	Boulder, cobble and elevation
Molenaars River		
Foothills	0.24 ($p < 0.01$)	Horizontal distance
Heks River		
Transitional	0.56 ($p < 0.01$)	Cobble and elevation
Foothills	0.24 ($p < 0.01$)	Horizontal distance
Rondegat River		
Mountain stream	0.50 ($p < 0.01$)	Horizontal distance and elevation
Transitional	0.48 ($p < 0.01$)	Horizontal distance and elevation

The BEST results show that the lateral riparian vegetation patterns in the mountain stream sites are linked to horizontal distance and elevation. For foothill sites horizontal distance is the most important environmental variable linked to riparian vegetation communities although the strength of this relationship is not very strong as indicated by the low values in Table 3.5. In the transitional sites one or more substrate type together with elevation was shown to be the best combination of variables linked to the riparian vegetation community pattern.

3.4 Discussion Does riparian vegetation community composition change between longitudinal zones?

Riparian vegetation communities did not just differ between longitudinal zones, but also showed significant differences between basins and rivers. This indicates the presence of river signatures (Roux et al. 2002) as previously described by King and Schael (2001) for macroinvertebrates. Other studies have also shown river signatures for fish and riparian vegetation (Hawkins 2000, King and Schael 2001, Roux 2002, Wishart et al. 2002; Sieben et al. 2009). This makes grouping riparian communities across basins and rivers inappropriate for comparative studies. Even though river signatures have been found to be present in multiple studies across a variety of disciplines, to date no explanation exists for these patterns between basins and rivers. What was interesting about the results obtained from this study was that the differences are not just present at a basin scale but also at a river scale. The Elands and Molenaars river sites were situated only a couple of hundred meters downstream and upstream from one another and yet very prominent separations were seen in the CLUSTER and MDS diagrams. This could indicate that a tributary, in this case the Krom River, influences the character of a river greatly and or that other ecological processes such as nutrients, sediment deposition and channel gradient greatly influences the overall character of the ecology over as little as a couple of hundred meters.

The logical next question was whether riparian species, and more specifically, the riparian community structure differ between longitudinal zones when looking at lateral zones? By comparing longitudinal zones on one uninterrupted stretch of river, it was found that although the species compliment did not differ substantially, the species responsible for the grouping of the lateral zone was different more often than not. For instance *Isolepis prolifera* was expected to be responsible for the grouping of the marginal zone as described by Reinecke et al. (2007) and Sieben and Reinecke (2008), but instead was not responsible for the grouping of marginal zone sample plots in the foothill zone. Instead the species responsible for marginal zone identity in the foothills were: *Calopsis paniculata*, *Drosera capensis* and *Morella serrata* saplings. This could be due to the valley widening and banks flattening out more gradually towards the terrestrial environments. A more gradual incline up the banks could mean that the overall marginal zone is wider and the species abundances recorded during sampling was larger for species with larger growth forms leading to a smaller ratio *I. prolifera* being recorded. *I. prolifera* were present at foothill sites but it wasn't responsible for the identity of the marginal zone. In the mountain streams and transitional zones however, *I. prolifera* was mostly responsible for the marginal zone group formation but one exception to this was the mountain stream sites on the Rondegat River where it was *M. angustifolia* adult trees. As for *Prionium serratum*, none of the longitudinal zones showed this species to be

responsible for the grouping of marginal zone sample plots, in many cases the species did not occur on the site. I suspect this to be due to site specific substrate differences rather than distribution patterns. Some species such as *P. serratum* was seen very abundantly on rivers with cobble/boulder substrate at the edge of the active channel. Most river sites used in this study had smaller substrate calibre at the outer edges of the active channel.

The lower dynamic had no similarities between different longitudinal zones. Each sample set had its own unique species responsible for the grouping of the lower dynamic zone. Since the lower dynamic zone is a transitional between the marginal (wetbank) and the lower bank zone (drybank), it was expected that there would be high variability in species composition. There were however similarities when the results were compared to what Reinecke et al. (2007) described as frequent species for the lower dynamic. These included *C. paniculata*, *E. capensis*, *E. caffra*, *M. serrata* and *M. angustifolia* seedlings. On the Elands River's transitional zone *C. paniculata*, on the Rondegat River's mountain stream zone *E. capensis* and on the Heks River's transitional and foothill zones *M. angustifolia* (however adult trees and not seedlings) were the species responsible for the grouping. *Brabejum stellatifolium* is described as an upper bank zone species (Reinecke et al. 2007; Sieben and Reinecke 2008) but occurred with quite substantial frequency in the lower dynamic and even marginal zones of mountain stream sites. This suggests that the lateral zone description of *B. stellatifolium* tree species is not that narrow. The occurrence of substantial cover of *B. stellatifolium* lower down the bank may be explained by the spatial constraints associated with mountain streams (steep banks and narrow valleys). And lower down the river where the banks widen and valley open up on the sides the positioning of *B. stellatifolium* may be more hydrology/drought influences than driven by competition for recruiting space. Also, it is possible that recruitment activities over the course of the past seven years could have been influenced by disturbances and or the size of the individuals recorded by Reinecke et al. (2007) changing from sapling to tree without any significant flooding events uprooting trees in the marginal zone.

In the lower bank, *P. aqualinum* was shown to be responsible for the lower bank identity in most cases, however, the Elands River had *E. caffra* in the mountain stream and *E. capensis* in the transitional zones. On the Heks River in the transitional zone *M. angustifolia* adult trees was responsible for the identity of the lower bank lateral zone identity. This is not entirely out of line with what Reinecke et al. (2007) and Sieben and Reinecke (2008) described for Western Cape Rivers. They identified *M. angustifolia*, *M. serrata* and *B. stellatifolium* adult trees together with *E. capensis* and *E. caffra* as the typical species present in the lower bank zone. Apart from *Pteridium aqualinum*, which was responsible for

zone identity in most cases, the other species were similar to what was expected to be found in the lower zone.

The upper bank had no single species indicated as responsible for the groupings of sample plots in this particular lateral zone. Each river and longitudinal zone had its own species responsible for the identity of the upper bank. The upper bank zone is a transition between the lower bank zone and terrestrial species so this is not entirely unexpected. The presence of different terrestrial species in different abundances could influence the upper bank significantly since the species complement is a mixture between the terrestrial area and riparian zone. Some species identified as responsible for the group identity were *P. distichophylla*, *A. capitata*, *S. angustifolia*, *D. glabra* and *P. scabrum*. This lateral zone shows great variability in species composition, most variability was however seen in the foothills. Again this could be due to more space being available for riparian and terrestrial species to establish.

Reinecke and Brown (2013) produced new indicator species for each lateral zone based on SIMPER results combined with hydrological data. For the marginal zone they suggest *P. serratum*, for the lower dynamic *C. paniculata* and *P. schinzii*, for the lower zone *E. capensis* and for upper zone *P. aquilinum* and *D. glabra*. Their sampling was conducted across more rivers and basins when they made this description, thus this may be why species such as *P. schinzii* and *P. serratum* did not feature significantly in the results of this study. However the aim of this research was not to identify indicators or even describe lateral zone identities, the aim was to assess whether a single riparian vegetation description based on species complement alone could be used across longitudinal zones. The description for lateral zones such as Reinecke et al. (2007) was based on riparian communities on river reaches high up in the valleys (upland) and used as a reference description for this study. This description was, however found to not always be consistent. The results showed that riparian zones did not always have the same species/group of species responsible for lateral zone identity in different longitudinal zones. The species described to be typical was, more often than not, present in the lateral zone of described preference, just not responsible for the identity of the group.

3.4.2 Is there a relationship between riparian species distribution and selected environmental variables?

A strong pattern was found to be present when overlaying lateral zones onto PCA diagrams consisting purely of environmental data analysis. Different longitudinal zones presented

different environmental variables most strongly linked to different lateral zones. The mountain stream sites were linked to horizontal distance and elevation, foothill sites were linked to horizontal distance and the transitional sites were linked to elevation and cobble/boulder. The strength of these relationships based on the statistical values were not always convincing such as the case with the foothills where the p value was 0.24 compared to the transitional and mountain stream sites producing p values higher than 0.5. Due to narrow valleys in the mountain streams the space for recruitment and establishment is limited, which explains why horizontal distance and elevation in combination to one another would be important for an individual's survival. In the foothills, where valleys are much wider than in the mountain streams, elevation was found not as important for riparian species position as horizontal distance from the active channel. This result makes sense since I would expect a species to be more vulnerable to drought in the foothills than in the mountain streams. In the mountain streams I would expect species to be more vulnerable to uprooting during floods. This explains the relationship of species positioning with different environmental variables in the mountain stream than that of the foothills.

When these results are compared to what Boucher (2002) and Reinecke and Brown (2013) found, the results supports their findings of riparian vegetation being hydrology linked. Both Boucher (2002) and Reinecke and Brown (2013) used hydrology to describe lateral zonation in riparian vegetation communities. Boucher (2002) used the two-year flooding mark on the bank as an indicator for wetbank (marginal and lower dynamic) and drybank (lower and upper zones) zones. Horizontal distance is an indication of inundation, and elevation is in direct relation to horizontal distance due to the shape of a river bank, both these environmental variables were linked to riparian vegetation in this study and therefore support the findings of other authors working in the fynbos biome (Reinecke et al. 2007; Reinecke and Brown 2013, Sieben and Reinecke 2008).

Cobble and boulder seems to be the most important sediment type related to species distribution, this could be due to the fact that species recruit in finer sediment calibre, and especially higher up the bank cobble bars and boulders are less vegetated (as seen at Mol 2) than the sand and gravel areas. A possible reason why the foothills did not show a significant relationship with any sediment type is due to the fact that the foothills contained more sandy areas and space for recruitment was not as big a constraint as in the mountain streams where space is limited and valleys are narrow with steep banks containing larger substrate such as boulders and bedrock. The mountain stream showed little relationship to sediment calibre, but in this case it might be due to the fact that species that survive on bedrock are adapted to do so and will most probably out-compete other species less adapted to surviving flash floods while rooted on bedrock. This was expected since the

amount of finer sediment in the mountain stream is less, perhaps due to the carrying capacity being higher and the channel slope being steeper than in the upper foothills. This clear relationship between bank shape, sediment calibre and species positioning suggests that more caution should be used when attempting to use a general riparian description for different basins and different longitudinal zones. Space is clearly a contributing factor to where a species recruits, grows and establishes. Care needs to be taken when attempting to study or manage these rivers as to not disregard the river signatures and longitudinal zonation in Western Cape Rivers.

3.5 Conclusion

These findings have implications for restoration and future research frameworks. Space is an important aspect which should be considered very carefully when conceptually developing ecological research and management programmes or projects. It is important to consider the differences in location relative to longitudinal zones of sample sites and reference conditions when attempting to access, study or restore riparian communities. The implication this has on our current understanding and use of reference sites should be questioned and studied further to ensure restoration practices are developed to suit each river individually as shown by river signatures (King and Schael 2001; Roux et al. 2002) and for each longitudinal zone shown by results produced in this study. A change in riparian plant community at this small spatial scale (longitudinal zone scale) questions the relevance of a reference condition in restoration practices. Furthermore future research conducted across the riparian vegetation types could be affected by basin, river and longitudinal zone scale site selections. Comparing lateral zone scale data across basins, rivers and even longitudinal zones could be ineffective with the variability in species abundance across lateral zones being very high.

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4 Temporal changes of Fynbos Riparian Vegetation communities on selected upland rivers in the Western Cape, South Africa

4.1 Introduction

Spatial and temporal scales have significant influence on the community composition of fynbos riparian structure and form an integral part of ecological theory, environmental management and restoration practices (Callicott 2002). The lateral riparian plant communities are shaped by many natural disturbances such as flood, fire and drought (Sousa 1984). These disturbance processes are important for nutrient cycling, primary production processes, competition (Connell 1978) and diversity and succession (Callicott 2002; Bailey et al. 1998) within ecosystems, especially in riparian ecosystems (Naiman et al. 2005). In rivers, physical interactions occur in three spatial dimensions: laterally across the floodplain, vertically between the surface and groundwater, and longitudinally down the river's length (See Chapter 3). These spatial interactions are embedded in a fourth dimension, which is time. Spatial and temporal scales are central to the framework of ecological inquiry (Callicott 2002; Chesson 2000), and the dynamic character of natural ecosystems often makes it difficult to pinpoint the state to which an impacted environment should be restored (Pickett and Parker 1994; Hobbs and Harris 2001).

A reference condition has been used in the past as template for restoration and to facilitate data interpretation while factoring in the regional differences of biotic factors (Dallas 2000). There are two types of reference conditions: a site-specific and a regional reference condition. A site-specific reference condition is usually used in upstream and downstream instances whereas a regional reference condition is based on a bigger scale such as ecoregions (Kleynhans et al. 1998), bioregions (Brown et al. 1996) and even a smaller scale based on geomorphological zones and river types (Brown et al. 1996). By using a site-specific reference condition an established site with the least amount of impacts can be compared to monitoring sites. When a less degraded site or suitable reference site and a regional template are unobtainable a historic description or ecological models are used (Kleynhans 1999).

A reference condition enables a measurement of deviation from the natural conditions and also assists with restoration initiatives (Dallas 2000). The aim of this study was to determine ecological changes over time and to ascertain what implications this has for use of reference conditions. Also, how does the change in reference conditions compare to changes in sites subjected to fire and sites recovering after clearing of woody alien invasive species?

When looking at changes and the processes linked to riparian community composition and disturbance regimes, hydrology is a very important contributor. Flow regimes have been linked to ecological and biological processes (Palmer et al. 1997) and more recently hydrology has been shown to influence the positioning of riparian species relative to the active channel (Reinecke and Brown 2013). The wetbank (marginal and lower dynamic later zones) is more reliant on regular inundation than the drybank (lower and upper lateral zones) and Reinecke and Brown (2013) found that riparian vegetation could be linked to hydrology at this scale. Impacts of hydrological disturbances on the riparian community composition are different for each of these two zones (wetbank and drybank). Based on this the smallest scale of temporal changes examined in this part of the study was at the wetbank-drybank spatial scale.

At a bigger scale climate, which also influences flow regimes also drives disturbances such as fire and drought. The Western Cape has a Mediterranean climate and the Fynbos biome has adapted to the hot dry summer and wet cold winter seasons. The warm dry summer months coincide with fire disturbance that is essential for the successful reproduction and distribution of fynbos vegetation. Fire affects the community structure of Mediterranean vegetation (Arianoutsou 1998) and post-fire succession has been shown to cause an increase in species richness in some cases at the two to three years temporal scale (Rutherford et al. 2011) due to the flush of germination triggered by fire disturbance (Purdie 1977). Recruitment of seedlings is favoured by the open patches created by fire, and also flooding and other riverine ecological impacts (geomorphology, sediment deposition, erosion and drought) (Ward and Stanford 1995).

The riparian community can be separated into lateral zones and these lateral zones usually consists of different life histories and growth forms. Goldblatt and Manning (2000) defines ten different growth forms, these descriptions are summarised in Table 4.1. Different growth forms have different life histories and may be responding differently to disturbances which would make an assessment of temporal change based on growth forms worth exploring. In this part of the study, the temporal changes of growth form frequency and distribution were assessed and compared in order to test whether change occurs at a site scale or perhaps at a smaller disturbance scale such as that associated with intra-annual flooding occurrences.

Table 4.1 Growth form definitions (Goldblatt and Manning 2000).

Growth form	Definition
Forb	A broad leafed herbaceous plant.
Geophyte	A perennial plant that propagates by underground bulbs or tubers or corms.
Rhizomatous perennial	Plants in the division Pteridophyta.
Rush	Plants in the family Juncaceae.
Sedge	Plants in the family Cyperaceae.
Grass	Plants in the family Poaceae.
Restio	Plants in the family Restionaceae
Small shrub	A low woody perennial plant often with multiple stems (<1m).
Shrub	A medium sized woody perennial plant often with multiple stems (1-2m).
Tree	A tall woody plant with main trunk, branches and a distinct elevated crown (>10m).

Apart from natural disturbances there are also unnatural disturbances acting on the riparian communities. In the Western Cape, water is a scarce commodity, especially in the hot dry summer months when fire and drought are common. In light of this water scarcity, one of the biggest disturbance concerns is the invasion of woody alien species in riparian zones. These woody alien species are known to have higher transpiration rates (Dye et al. 2001) and therefore use more water than indigenous riparian species (Dye and Poulter 1995). Invasive species have also been known to alter riparian canopy structure and the abundance and variety of species (Holmes et al. 2005). The need to control invasive species led to the Working for Water (WfW) programme which was initiated in 1995 and is aimed at removing invasive species as to preserve water resources. This programme has also secondarily created jobs and training opportunities for economically marginalised people (Van Wilgen et al. 1998). Restoring previously invaded communities is a complicated and long process due to the persistent seed banks left by different invasive species (Holmes et al. 2005). The restoration process therefore requires regular follow-up clearings but has been shown to have made significant progress in the clearing and restoration of freshwater ecosystems nationally (Blanchard and Holmes 2008; Holmes et al. 2005).

Restoration practices are aimed at restoring a degraded environment back to its historical state (Bailey et al. 1998). A more recently suggested approach is to restore an environment to a less disturbed state than it is currently in (Meek et al. 2013; Palmer et al. 1997). The recovery of disturbed riparian communities has been a popular area of research but to a lesser extent the changes occurring over time in undisturbed sites, the latter is the primary aim while the former is a secondary aim of this current study. I am expecting to see the

recovering sites on the Molenaars to be very similar to the reference site Mol 2 after such an extended period of recovery (more than 10 years).

Undisturbed sites are referred to in this study as sites at which no obvious disturbance, other than natural processes, occurred between sampling periods. Natural disturbances are constantly impacting these sites but could not be quantified; these include hydrology, geomorphology, climate, competition and others. These disturbances are encapsulated in an extension of the Intermediate Disturbance Hypothesis¹¹ (IDH) proposed by Svensson (2010) which proposed that smaller more frequent disturbances will have different (more unpredictable) effects on diversity than larger less frequent disturbances. The flux of nature paradigm states that an ecosystem is dynamic and ever-changing in response to different spatio-temporal impacts (Pickett et al. 2007). Even though riverine ecosystems are relatively hostile environments, riparian vegetation is adapted to these disturbances (Naiman and Decamps 1997) and little or no significant changes are expected to be present at sites not subjected to fire or clearing of alien woody invasives.

This chapter aims to look at both changes occurring in undisturbed sites and sites subjected to disturbance to see whether disturbed sites or undisturbed sites show more change over a relatively short period of time.

The objective for this part of the study was:

To assess the change in riparian vegetation community composition over time.

The key questions were:

1. Do fynbos riparian communities show change in community composition, at a site scale, over a relatively short period of time (within decadal at a seven year scale)?
2. Does riparian vegetation composition show significant changes at the wetbank and drybank scale (lateral zone scale) based on relative species abundances?

¹¹ Local plant species diversity is influenced by disturbance and these ecological disturbances should neither be too frequent nor infrequent. Intermediate levels of disturbance maximize diversity (Catford et al. 2012).

4.2 Methods

Methods and site selection was similar to that of Reinecke et al. (2007). This was done to make the present (indicated by an asterisk), and historic data sets comparable.

4.2.1 Site selection

In the summer 2004/2005 Reinecke et al. (2007) sampled 15 sites on four rivers in two basins in the Western Cape, South Africa. Seven sites were situated on the Elands/Molenaars River combination (Breede Basin) and four sites on each of the Heks and Rondegat Rivers (Olifants Basin, Table 4.2).

These sites were permanently marked during 2004/2005 (Reinecke et al. 2007) and re-sampled for this study during summer 2011/2012 (*). Two of the sites on the Molenaars River, Mol 1 and Mol 3, were cleared by Working for Water in 1994 (Mol 1) and 1997 (Mol 3). This means that when they were sampled during 2011 they have been recovering for 17 and 14 years respectively. The Rondegat River sites were affected by fire in 2009. The sites did not burn in entirety but the outer edges of the riparian zone did sustain fire damage which was evident from the black tree branches observed during re-sampling.

Situated between Mol 1 and Mol 3 is Mol 2 which was described as undisturbed by Boucher (1988). Although Mol 2 had been subjected to the practices of Working for Water it has never been necessary to clear all the vegetation at the site. Therefore even though Boucher's (1988) classification was done more than twenty years ago, this site on the Molenaars River was found to be still in a relatively undisturbed condition¹². Sprouting invasive species are hacked and removed before significant levels of invasion by mature trees are reached.

Table 4.2 is a summary of undisturbed and recovering sites re-sampled during 2011/2012 with their coordinates, ecological state/history, elevation, geomorphological location in the river and the basin within which they occur.

¹² An undisturbed condition is referred to as a site not subjected to habitat altering disturbances which include natural (fire, erosion, invasion by alien species) and anthropogenic (flow altering abstraction, damming and uprooting of natural vegetation for agricultural or mining activities). The site has a naturally flowing channel with unmodified riparian vegetation occurring on the banks.

Table 4.2 Sites selected in two catchments, and across four rivers in the Western Cape. E = Elevation in meters above sea level (masl), Z = longitudinal zone. M = Mountain stream, T = Transitional and F = Foothills

Basin	River	Site	Coordinates	Z	E	Date Sampled	Condition
Breede	Elands	Ela 1	S33°45.654', E019°07.705'	M	553	2004 & 2011	Undisturbed
		Ela 2	S33°45.636', E019°07.694'	M	553	2004 & 2011	Undisturbed
		Ela 3	S33°44.410', E019°06.791'	T	470	2004 & 2011	Undisturbed
		Ela 4	S33°44.361', E019°06.786'	T	470	2004 & 2011	Undisturbed
	Molenaars	Mol 1	S33°43.437', E019°08.863'	F	368	2004 & 2011	Cleared in 1994 and recovering
		Mol 2	S33°43.387', E019°10.762'	F	368	2004 & 2011	Undisturbed with periodic WfW activity
		Mol 3	S33°42.580', E019°11.848'	F	368	2004 & 2011	Cleared in 1997 and recovering
Olifants	Heks	Hek 1	S32°26.123', E019°00.530'	T	255	2005 & 2012	Undisturbed
		Hek 2	S32°26.116', E019°00.518'	T	255	2005 & 2012	Undisturbed
		Hek 3	S32°26.187', E018°58.883'	F	191	2005 & 2012	Undisturbed
		Hek 4	S32°26.209', E018°58.872'	F	191	2005 & 2012	Undisturbed
	Rondegat	Ron 1	S32°23.764', E019°05.384'	M	634	2005 & 2012	Undisturbed but Burnt Feb 2009
		Ron 2	S32°23.762', E019°05.368'	M	634	2005 & 2012	Undisturbed but Burnt Feb 2009
		Ron 3	S32°22.599', E019°04.015'	T	526	2005 & 2012	Undisturbed but Burnt Feb 2009
		Ron 4	S32°22.569', E019°04.002'	T	526	2005 & 2012	Undisturbed but Burnt Feb 2009

4.2.2 Data collection

Sites sampled by Reinecke et al. (2007) were re-located from permanent markers laid out during historic vegetation sampling in 2004/2005. The size of the site was dependant on the width of the riparian vegetation and by using the historic data set measurements. The length of all sites was 20 m, containing four transects of 5 m in length with vegetation sample plots of 5 x 1 m (Figure 1.9). Vegetation cover was estimated as percentage per sample plot. All this was done as to replicate the methods used by Reinecke et al. (2007). Also see section 1.7 for detailed sampling method description.

4.2.3 Data analyses

In Chapter 3 it was concluded that sites are more comparable within than between rivers which led to the temporal comparisons being made at a river scale rather than across river basins. Observing temporal changes in riparian fynbos vegetation community composition would have to be based on more sites and across more river basins than used in this study. Therefore, rivers are addressed separately in this study as to minimize the different environmental events and impacts acting on riparian vegetation of different basins (temperature, altitude, rainfall and more). This way the differences in disturbances are minimized thus focussing more on the community response to localized disturbance.

PRIMER Version 6 (Clarke and Gorley 2006) was used to run multivariate analyses on both the historic and the present data sets. A fourth root transformation was used to transform data sets to boost species with smaller cover abundances in general. A Bray-Curtis similarity resemblance analysis was applied which enabled CLUSTER and MDS ordination analysis to be made (PRIMER Version 6). Cluster and MDS ordinations were used to demonstrate the differences between riparian communities at two sampling periods (Clarke and Gorley 2006). This result was then tested for significance by doing an ANOSIM (PRIMER Version 6). The ANOSIM analyses were run using a one way design using sampling occasion as factor (2004/2005 and 2011/2012) (See section 3.2.3).

By combining sample plot data of total recorded percentage cover per species at a site, PRIMER Version 6 could be used to run biodiversity analyses (DIVERSE, PRIMER Version 6). These results included Shannon, Simpson, Fisher and other common measures of diversity and evenness in variation of cover abundance across the two sampling periods. Plant Functional types were used to compare the differences in average relative cover abundances between sampling periods. These results was tested using a paired T-test (Excel, statistical expansion package). A paired T-test is used to test the significance of difference between two samples.

SIMPER analyses (PRIMER Version 6) based on relative species cover abundance were used at a wetbank (marginal and lower dynamic) and drybank (lower and upper) scale within sites to identify the species responsible for the change between sample periods (See section 3.2.3). I expected the differences to be most evident at this scale since this is where the hydrological regime could influence the recruitment and establishment of riparian species. Disturbance driven changes at a small temporal scale was therefore expected to occur at this spatial scale. By separating the wetbank (marginal and lower dynamic) from the drybank (lower and upper) a comparison could be made between changes evident in both these areas of the riparian community if present. Lateral zone descriptions as used in

Chapter 3; marginal, lower dynamic, lower and upper, was grouped into the wetbank (marginal and lower dynamic) and drybank (lower and upper) as done by Reinecke and Brown (2013) when they were able to link hydrology to riparian vegetation zones. The historic data were assigned into lateral zones during 2004/2005 sampling (Reinecke et al. 2007). By combining the sample plots into wetbank and drybank, a comparison could be made between species compliment and relative abundances between sampling periods at a within site scale.

MDS ordinations (PRIMER Version 6, Clarke and Gorley 2006) were then used to compare the differences occurring at a lateral zone scale (wetbank and drybank) temporally. These ordinations were created by using sample plot scale data of relative species abundances categorised by lateral zone; marginal, lower dynamic, lower and upper.

4.3 Results

4.3.1.1 Do fynbos riparian communities show change in community composition, at a site scale, over a relatively short period of time?

4.3.1.2 *Elands River - undisturbed*

A comparison of sites sampled during 2004 and 2011 is presented in Figure 4.1. Based on Cluster and MDS analyses Ela 1 and 2 grouped spatially (i.e. Ela 1* and Ela 1 grouped together and similarly Ela 2* and Ela 2) but Ela 3 and 4 grouped temporally. This indicates greater change on Ela 3 and Ela 4 between sampling periods than upstream at Ela 1 and 2 (Figure 4.1 top). The MDS ordination however clearly shows a separation between sample periods down the middle (Figure 4.1 bottom) as indicated with the red line.

A Global one-way ANOSIM of species abundances conducted across a temporal scale (Ela 1-4 historic versus Ela 1-4 present data) showed an R value of 0.5 ($p < 0.01$). This indicates some differences being present at a river scale.

4.3.1.3 *Molenaars River – recovering after clearing*

The Molenaars River showed little or no pattern. The reference site (Mol 2) seems to have changed especially in relation to Mol 1 and Mol 3. In Figure 4.2 (top) Mol 2 seems more similar to new data collected from Mol 1 and Mol 3 which suggests that the recovering sites are becoming more similar in community composition compared to Mol 2 (reference site). However in Figure 4.2 (bottom) the MDS ordination shows the new data sets of all three

Molenaars sites moving closer to the middle and towards each other but then spreading out to the top and bottom of the ordination. This indicates change but not a trend to become more similar to one another as would have been expected.

A Global one-way ANOSIM of species abundances conducted across a temporal scale (Mol 1* - Mol 3* versus Mol 1 – Mol 3) showed an R value of 0.357 ($p < 0.01$), which is the lowest value of all rivers, indicating the least change.

4.3.1.4 *Heks River - undisturbed*

A comparison of sites sampled during 2004 and 2011 is presented in Figure 4.3. The Heks River sites grouped temporally (Hek 1* – Hek 4* together and Hek 1 – Hek 4 together). At the second level of grouping, sites followed a longitudinal zone trend with Hek 1 and Hek 2 grouping together in the transitional zone and Hek 3 and Hek 4 grouping together in the upper foothills (Figure 4.3 top). The MDS ordination also confirms this clear separation between sampling periods as shown by the line separating the groups (Figure 4.3 bottom). The historic data however did not show a longitudinal separation in the MDS ordination.

A Global one-way ANOSIM of species abundances conducted across a temporal scale (Hek 1* - Hek 4* versus Hek 1 – Hek 4) showed an R value of 0.917 ($p < 0.01$). This indicates substantial differences being present between sampling periods. This is the highest value for all rivers which means this river has the greatest difference temporally.

4.3.1.5 *Rondegat River – fire disturbance*

A comparison of sites sampled during 2004 and 2011 are presented in Figure 4.4. Similar to the Heks River the Rondegat river sample sites grouped more strongly according to sampling period than with historic data. Figure 4.4 (top) showed that there is a minimum of 40% similarity within sampling efforts and less than 40% similarity between sampling periods. The MDS ordination (Figure 4.4 bottom) shows a clear separation vertically down the middle of the diagram.

A Global one-way ANOSIM of species abundances conducted across a temporal scale (Ron 1* - Ron 4* versus Ron 1 – Ron 4) showed an R value of 0.823 ($p < 0.01$). This indicates substantial differences being present between sampling periods.

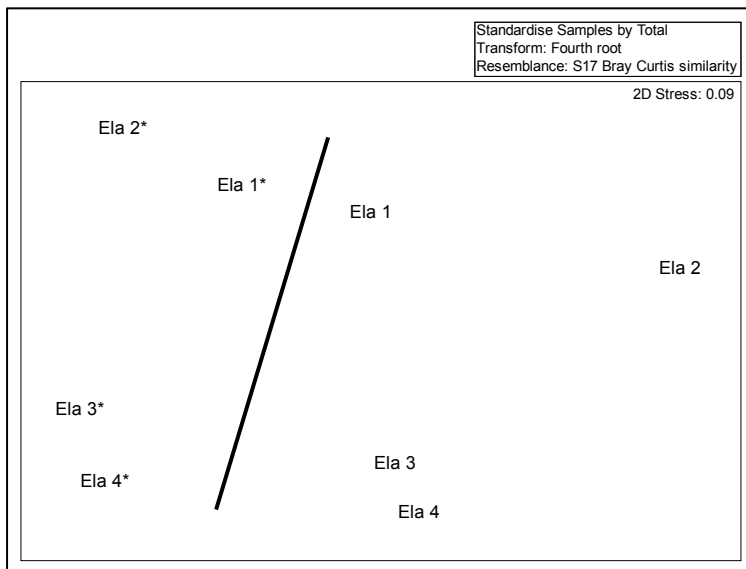
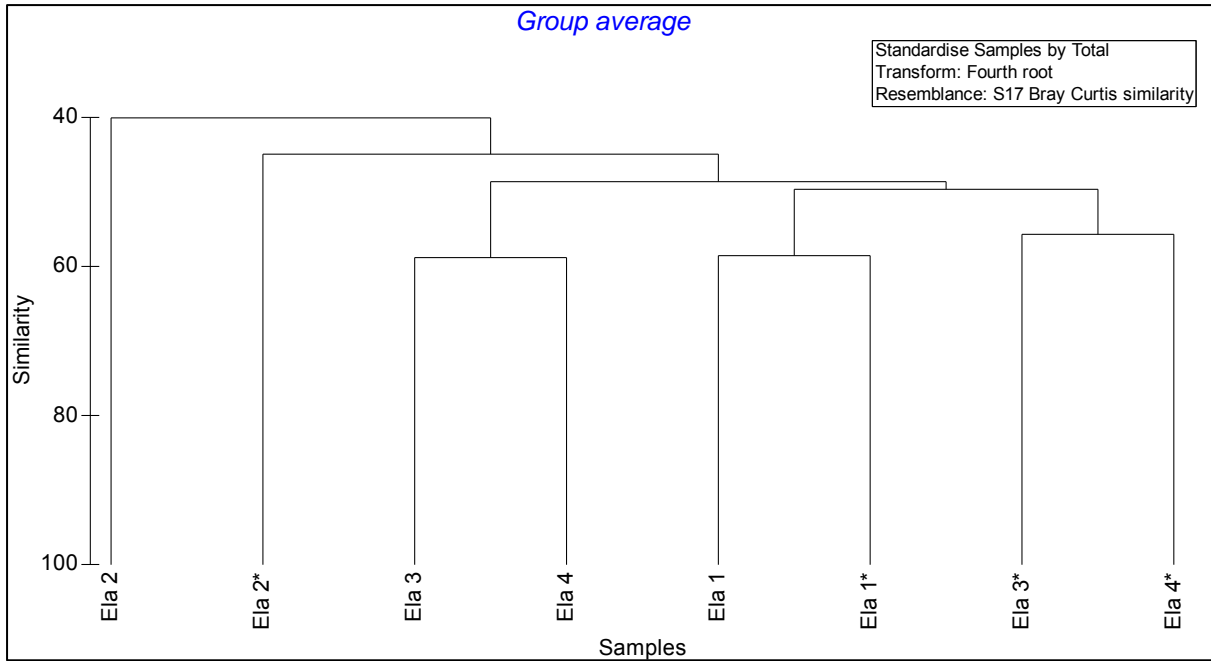


Figure 4.1 Cluster (top) and MDS (bottom) ordinations for sites on the Elands River sampled during 2004 and 2011(*). Line indicating the temporal separation present between sites. See table Table 4.2 for site codes and descriptions.

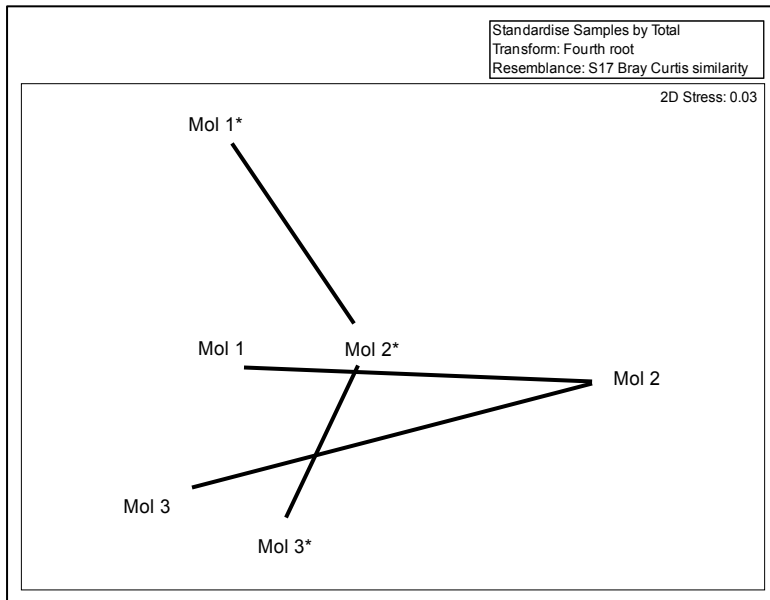
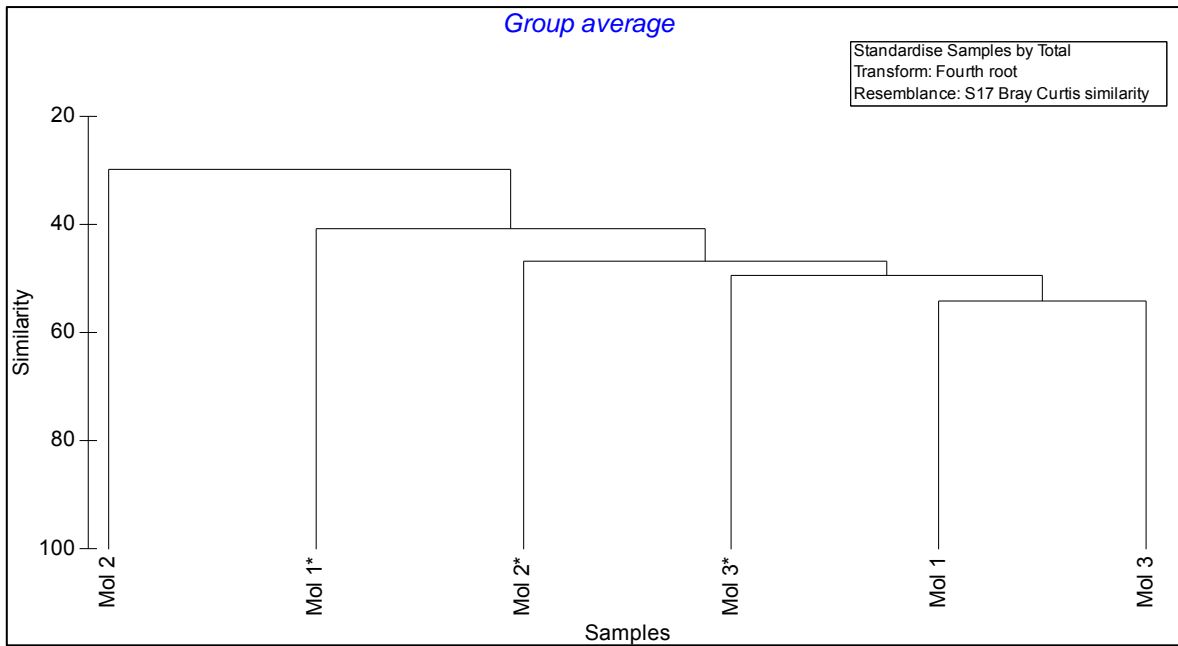


Figure 4.2 Cluster (top) and MDS (bottom) ordinations for sites on the Molenaars River sampled during 2004 and 2011(*). Lines indicating the present data moving towards the centre of the ordination but spreading out vertically around the reference site (*) and the distance between the same sites seven years ago.

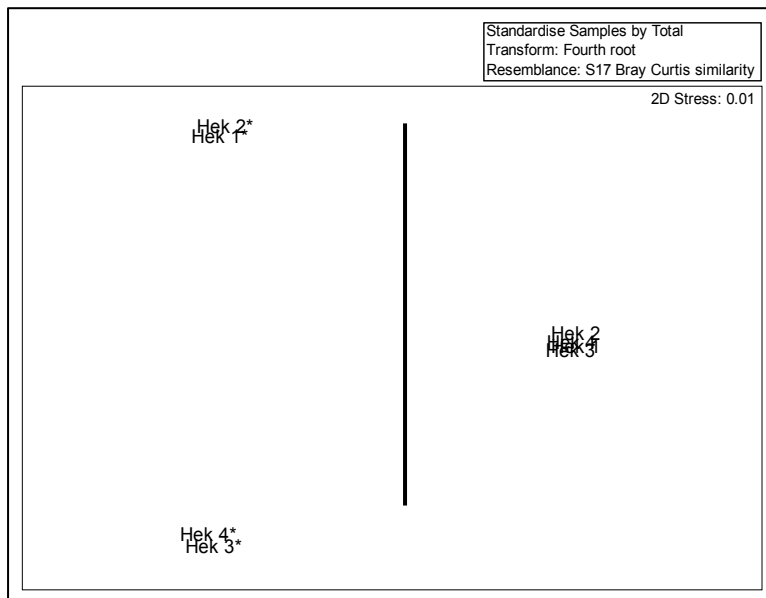
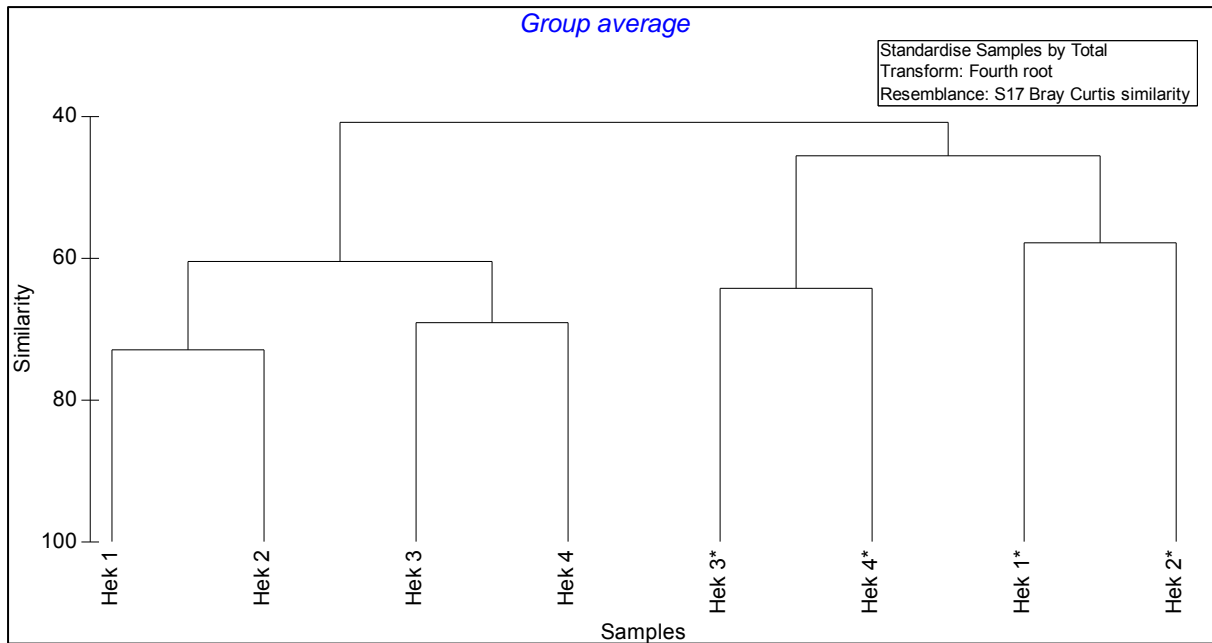


Figure 4.3 Cluster (top) and MDS (bottom) ordinations for sites on the Heks River sampled during 2004 and 2011(*). Line indicates the separation between sampling periods (temporal divide).

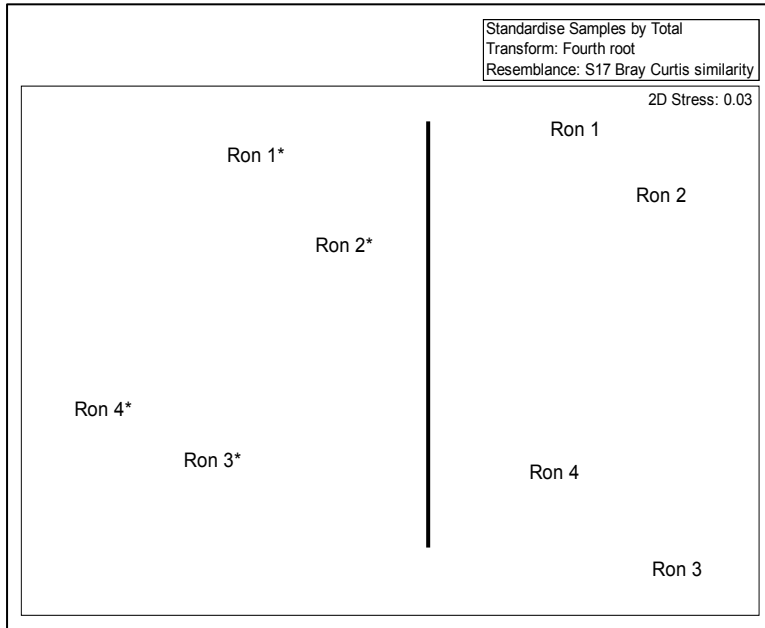
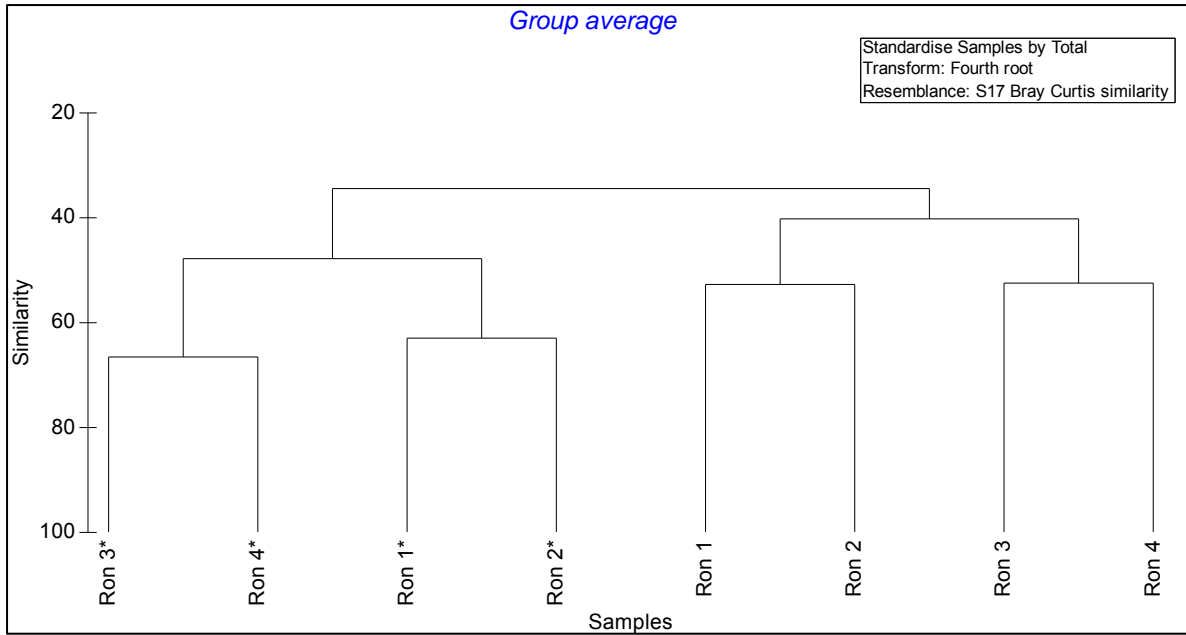


Figure 4.4 Cluster (top) and MDS (bottom) ordinations for sites on the Rondegat River sampled during 2004 and 2011(*). Line indicates the temporal separation between sample sites.

4.3.2 Diversity at a site scale

Plant diversity data are presented in Table 4.3. The Shannon diversity index (H') showed the Hex River to be very similar in diversity between sample periods. Mol 1 decreased in diversity while Mol 3 increased in diversity. On the Rondegat River the mountain stream sites Ron 1 and Ron 2 showed a decrease in diversity while the transitional sites Ron 3 and Ron 4 showed an increase in diversity.

Pielou's evenness showed that there was very little variation in cover abundance between sites temporally. Pielou's evenness ranges between 0-1 and the higher the value the less variation is present. All of the J' values in Table 4.3 are above 0.5 with some ranging as high as 0.9.

Fisher's coefficient describes the number of species expected to be recorded for every percentage cover recorded at a site. The number of species expected to be recorded per percentage cover increased on the Rondegat River. On the Elands, Molenaars and Heks Rivers the number of species expected to be recorded per percentage cover varied. In some cases it increased such as seen on Ela 1, Ela 3, Ela 4, Mol 2, Mol 3, Hek 1 and Hek 4. A decrease in number of species expected to be sampled was seen on Ela 2, Mol 1, Hek 2 and Hek 3. No consistent trend was evident at a site scale.

Table 4.3 Different standard biodiversity indices for historic and present (*) sample data per site with; S – total species, N – total cover, d – Species richness, J' – Pielou's evenness, H' – Shannon, 1 - Lambda' – Simpson, ES – Fisher's indication of the expected number of species from a percentage cover recorded.

Sites	S	N	d	J'	Fisher	H' (loge)	1-λ'
Ela 1	43	960	6.1	0.9	09.2	3.2	0.9
Ela 1*	46	1148	6.4	0.8	09.6	3.2	0.9
Ela 2	64	1163	8.9	0.8	14.6	3.5	1.0
Ela 2*	33	974	4.7	0.8	06.6	2.9	0.9
Ela 3	49	2369	6.2	0.8	08.7	3.0	0.9
Ela 3*	61	2448	7.7	0.8	11.3	3.2	0.9
Ela 4	45	1904	5.8	0.8	08.3	3.1	0.9
Ela 4*	53	2377	6.7	0.8	09.6	3.1	0.9
Mol 1	60	3218	7.3	0.8	10.5	3.3	0.9
Mol 1*	42	4162	4.9	0.6	06.5	2.4	0.9
Mol 2	51	2857	6.3	0.7	08.8	2.7	0.9
Mol 2*	55	2937	6.8	0.7	09.6	3.0	0.9
Mol 3	42	2636	5.2	0.7	07.1	2.5	0.9
Mol 3*	50	2293	6.3	0.8	09.0	3.0	0.9
Hek 1	40	3814.5	4.7	0.8	06.2	2.8	0.9
Hek 1*	49	3748	5.8	0.7	08.0	2.8	0.9
Hek 2	45	4031	5.3	0.7	07.1	2.7	0.9
Hek 2*	38	3800	4.5	0.7	05.9	2.7	0.9
Hek 3	29	2420	3.6	0.7	04.6	2.4	0.9
Hek 3*	27	2361	3.3	0.7	04.3	2.3	0.9
Hek 4	35	2221	4.4	0.8	05.9	2.9	0.9
Hek 4*	36	2244	4.5	0.8	06.1	2.8	0.9
Ron 1	46	1550	6.1	0.8	08.9	3.1	0.9
Ron 1*	50	1591	6.6	0.7	09.8	2.9	0.9
Ron 2	32	1813	4.1	0.8	05.5	2.6	0.9
Ron 2*	36	2166	4.6	0.6	06.1	2.2	0.8
Ron 3	41	1975	5.3	0.8	07.3	2.9	0.9
Ron 3*	55	1933	7.1	0.8	10.5	3.1	0.9
Ron 4	27	1870	3.5	0.7	04.5	2.2	0.8
Ron 4*	58	2188	7.4	0.8	10.9	3.1	0.9

A paired T-test analysis was done to establish if sites showed significant change in relative cover abundances for different functional types. These results are provided below in Table 4.4.

Table 4.4 Temporal results per site for t-test based on the percentage cover of each growth forms in river groups. Growth form categories see per Table 4.1. (n) = number of sample plots in each site. p =sample statistic for t-test (one-tailed). * = $p < 0.05$.

			Growth forms (p values)									
River	Sites	N - sample plots	Forb	Geophyte	Rhizome	Rush	Sedge	Grass	Restio	Shrublet	Shrub	Tree
Elands	Ela 1	n=28	0.1	0.1	0.4	0.3	0.1	0.5	0.07	0.1	0.2	0.2
	Ela 2	n=24	0.2	0.1	0.5	0.2	0.2	0.1	0.04*	0.2	0.5	0.3
	Ela 3	n=48	0.5	0.3	0.1	0.2	0.2	0.1	0.1	0.2	0.04*	0.009*
	Ela 4	n=32	0.2	0.2	0.5	0.3	0.5	0.2	0.06	0.001*	0.1	0.07
Molenaars	Mol 1	n=40	0.01*	0.08	0.4	0.5	0.04*	0.2	0.2	0.03*	0.2	0.01*
	Mol 2	n=48	0.06	0.1	0.5	0.2	0.1	0.1	0.2	0.1	0.2	0.2
	Mol 3	n=44	0.02*	0.08	0.5	0.2	0.006*	0.2	0.4	0.05*	0.5	0.5
Rondegat	Ron 1	n=20	0.2	0.1	0.5	0.03*	11.41	0.1	0.1	0.2	10.48	0.2
	Ron 2	n=24	0.5	0.2	0.3	0.1	11.41	0.03*	0.2	0.4	10.48	0.02*
	Ron 3	n=36	0.2	0.2	0.1	0.004*	11.41	0.006*	0.1	0.3	10.48	0.0001*
	Ron4	n=32	0.1	0.3	0.1	0.02*	11.41	0.1	0.1	3.92	10.48	0.06
Heks	Hek 1	n=40	0.1	0.2	0.1	0.005*	0.5	0.02*	0.1	0.2	0.008*	0.1
	Hek 2	n=43	0.2	0.4	0.1	0.1	0.2	0.2	0.1	0.2	0.1	0.5
	Hek 3	n=32	0.2	0.2	0.6	0.01*	0.2	0.2	0.1	0.5	0.04*	0.2
	Hek 4	n=32	0.3	0.2	0.4	0.2	0.2	0.1	0.5	0.3	0.1	0.2

There were growth forms that showed some changes over time. These differences are indicated by an * in Table 4.4. On the Elands River sites these were restios, shrublets, shrubs and trees. On the Molenaars River the changes were seen in forbs, sedges, shrublets and trees. Rushes, grasses and trees were responsible for change on the Heks River and on the Heks it was a combination of rushes, grasses and shrubs. The temporal differences in community composition are caused by differences in relative species abundance of different growth forms at different sites. There seems to be no specific pattern although trees, rushes, shrublets and shrubs seem to be the most regularly indicated growth form responsible for temporal differences at a site. A smaller scale analysis is needed to identify a more specific description of changes occurring at a site.

4.3.3 Does riparian vegetation composition show significant changes at the wetbank and drybank scale (lateral zone scale) based on relative species abundances?

Simper was used to identify small scale changes occurring at species level between the wetbank and drybank. This was done at a site scale and results obtained from each river are presented below. The Elands River results are summarised in Table 4.5, for the Molenaars River in Table 4.6, the Heks River in Table 4.7 and the Rondegat River in Table 4.8.

Table 4.5 SIMPER results for dissimilarity analysis = discriminant species on Elands River sites sampled during 2004 and 2011. Sample plots were grouped into wetbank and drybank. D – Dissimilarity/Standard Deviation, A – relative abundance.

WETBANK												
Species	Ela 1			Ela 2			Ela 3			Ela 4		
	D	2004	2011	D	2004	2011	D	2004	2011	D	2004	2011
		A	A		A	A		A	A			
<i>Isolepis prolifera</i>	1.18	0.79	1.29	0.79	0	0.73				0.25	0	0.08
<i>Metrosideros angustifolia</i> seedling	1.16	0.84	0.18	0.44	0	0.34				0.6	0.06	0.55
<i>Pseudobaeckia africana</i>	1.37	1.03	0.45				0.36	0	0.15	0.99	1.37	1.68
<i>Todea babara</i>	1.04	0.81	0.1				0.47	0.3	0.07			
<i>Metrosideros angustifolia</i> adult	0.43	0	0.32	0.58	0.98	0.4	0.52	0.6	0	1.08	0.89	1.46
<i>Salix macronata</i> saplings							0.73	0.61	0			
<i>Elegia capensis</i>	0.95	0.72	0.48				0.86	0.72	0.51	1.13	1.07	1
<i>Brabejum stellatifolium</i> adult				0.46	0.43	0				1.25	0.32	1.01
DRYBANK												
Species	Ela 1			Ela 2			Ela 3			Ela 4		
	D	2004	2011	D	2004	2011	D	2004	2011	D	2004	2011
		A	A		A	A		A	A			
<i>Pseudobaeckia africana</i>	1.22	1.1	0.69									
<i>Metrosideros angustifolia</i> adult	1.01	1.1	0	0.43	0	0.26				0.42	0.2	0.16
<i>Elegia capensis</i>	1.08	1.14	0.7	0.91	0.5	0.59	1.07	1.04	0.83	0.78	0.21	0.53
<i>Blechnum capense</i>				1.04	0.47	0.83	0.56	0.15	0.22			
<i>Pteridium aquilinum</i>	0.64	0.18	0.43	1.06	0.97	0.64	1.01	0.8	0.94			
<i>Erica caffra</i>				1.27	0.32	1.18						
<i>Pennisetum macrourum</i>							1.16	1.3	0.28	0.74	0.44	0
<i>Diospyros glabra</i>	0.73	0.41	0.29	0.59	0.29	0.1	0.81	0.17	0.51	0.92	0.26	0.67
<i>Erica pinea</i>										1.17	1.36	1.03

Table 4.6 SIMPER results for dissimilarity analysis on Molenaars River sites sampled during 2004 and 2011. Sample plots were grouped into wetbank and drybank. D – Dissimilarity/Standard Deviation, A – relative abundance.

WETBANK									
Species	Mol 1			Mol 2			Mol 3		
	D	2004	2011	D	2004	2011	D	2004	2011
		A	A		A	A		A	A
<i>Pennisetum macrourum</i>	1.59	1.48	0	1.35	1.96	1.32	1.1	0.56	0.6
<i>Isolepis prolifera</i>	1.2	1.34	1.78	0.84	1.87	1.04	1.38	1.1	0.46
<i>Salix macronata</i> seedling	1.13	0.25	0.88						
<i>Metrosideros angustifolia</i> sapling	1.1	0.81	0.24	0.91	1.15	0	0.84	0.67	0
<i>Metrosideros angustifolia</i> seedling	1.15	0.76	0.08				0.52	0.13	0.14
<i>Morella serrata</i> saplings	0.77	0.38	0.35	1.14	1.7	0	3.86	1.7	0
<i>Prionium serratum</i>				0.44	0.18	0	1.26	1.57	0.71
<i>Acacia mearnsii</i> seedling	0.66	0.22	0.23	0.43	0.25	0	1.04	0	0.63
DRYBANK									
Species	Mol 1			Mol 2			Mol 3		
	D	2004	2011	D	2004	2011	D	2004	2011
		A	A		A	A		A	A
<i>Brabejum stellatifolium</i> sapling	0.94	0.9	0.16				1.52	1.48	0.07
<i>Metrosideros angustifolia</i> sapling	0.96	0.83	0.12				0.79	0.55	0.28
<i>Calopsis paniculata</i>	0.82	0.31	1.31				0.54	0.13	0.39
<i>Searsia angustifolia</i>				1.59	2.59	1.6	0.27	0	0.12
<i>Pteridium aqualinum</i>	0.69	0.7	0	1.15	3.01	2.17			
<i>Stoebe plumosa</i>				0.83	0	1.63			
<i>Diospyros glabra</i>	0.55	0.45	0	0.88	1.15	0.49			
<i>Ehrharta ramosa</i> subsp. <i>aphylla</i>				0.48	0	0.43	0.61	0	0.46

Table 4.7 SIMPER results for dissimilarity analysis on Heks River sites sampled during 2004 and 2011. Sample plots were grouped into wetbank and drybank. D – Dissimilarity/Standard Deviation, A – relative abundance.

WETBANK												
Species	Hek 1			Hek 2			Hek 3			Hek 4		
	D	2004	2011	D	2004	2011	D	2004	2011	D	2004	2011
		A	A		A	A		A	A		A	
<i>Isolepis proliferata</i>	1.55	1.59	0.66	1.2	1.54	1.03	0.64	0.19	0.44	1.38	1	2.27
<i>Metrosideros angustifolia</i> seedling	1.44	0.18	1.46	1.45	0.45	1.42	1.3	0.35	1.91	1.36	0.45	1.79
<i>Metrosideros angustifolia</i> adult	1.13	0	0.95	0.44	0	0.3	1.05	0.8	0.64	1.07	0.46	0.65
<i>Morella serrata</i> adult	0.63	0	0.41	0.69	0.15	0.45	0.98	0.52	0.94	2.13	0.19	1.61
<i>Morella serrata</i> seedling	1.3	0.38	1.16	1.41	0.38	1.25	1.27	0.22	1.46	0.72	0.3	0.53
<i>Calopsis paniculata</i>	1.03	1.45	1.48	1.08	1.96	1.3	1.31	1.53	0.81	1.33	0.95	1.99
<i>Drosera capensis</i>				0.73	0	0.63	0.73	0	0.63	3.55	0	1.61
DRYBANK												
Species	Hek 1			Hek 2			Hek 3			Hek 4		
	D	2004	2011	D	2004	2011	D	2004	2011	D	2004	2011
		A	A		A	A		A	A		A	
<i>Metrosideros angustifolia</i> adult	2.43	2.25	0.23	1.12	1.35	0.08	1.15	1.35	0.21	0.99	1.03	0.53
<i>Metrosideros angustifolia</i> sapling	1.02	1	0	0.98	0	1.13	0.48	0.14	0.13	1.37	1.28	0
<i>Ehrharta ramosa</i>	1.08	0	1.34				0.95	0	1.2	0.49	0	0.38
<i>Calopsis paniculata</i>	1.15	1.16	0.09				0.46	0.22	0.09	0.75	0.47	0.38
<i>Morella serrata</i> adult	1.17	1.12	0.43	0.75	0.73	0.09	1.21	1.35	0.81			
<i>Morella serrata</i> sapling	0.95	0.76	0	0.65	0.51	0	0.78	0.53	0.13	1.35	1.21	0.12
<i>Morella serrata</i> seedling	0.73	0.13	0.56	0.66	0	0.69	1.31	0.14	1.29	0.55	0.24	0.05
<i>Ehrharta rehmannii</i>	0.8	0.76	0.12	1.55	1.36	0	0.62	0.48	0	0.4	0.28	0
<i>Searsia angustifolia</i>	0.74	0.47	0.33	1.01	0.73	0.95	0.7	0.43	0.32	0.32	0.06	0.14

Table 4.8 SIMPER results for dissimilarity analysis on Rondegat River sites sampled during 2004 and 2011. Sample plots were grouped into wetbank and drybank. D – Dissimilarity/Standard Deviation, A – relative abundance.

WETBANK												
Species	Ron 1			Ron 2			Ron 3			Ron 4		
	D	2004	2011	D	2004	2011	D	2004	2011	D	2004	2011
		A	A		A	A		A	A			
<i>Isolepis prolifera</i>	1.54	1.11	0.29	0.58	0.1	0.26	3.44	0	2.01	1.79	0.49	2.11
<i>Pronium serratum</i>							1.96	0	1.08	1.54	0.73	2.33
<i>Pteridium aqualinum</i>				0.87	0.53	0.63	0.81	0.75	0	1.57	1.47	1.55
<i>Metrosideros angustifolia</i> adult	0.72	0	0.66	1.01	0.64	0.87	0.76	0.13	0.45	0.85	0.52	0.44
<i>Metrosideros angustifolia</i> seedling	1.22	0.49	1.76	0.66	0.37	0.27	1.66	0.92	0			
<i>Brachylaena neriifolia</i> sapling	0.94	0.65	1.08	0.64	0.25	0.46						
<i>Elegia capensis</i>	0.9	0.34	1.02	1.33	2.15	2.55	1.68	1.3	0	0.83	0.35	0.4
<i>Calopsis paniculata</i>	1.22	1.18	0.57	0.99	0.8	0.36	1.29	0.95	0.49	0.98	0.63	0.4
<i>Todea babara</i>	0.89	0.4	0.42	1.06	1.95	1.46						
<i>Morella serrata</i> sapling	0.52	0.37	0	1.09	0.73	0.33						
<i>Brabejum stellatifolium</i> seedling	0.95	0.72	0.39	1.08	0.44	0.85						
<i>Stoebe plumosa</i>							0.62	0	0.42	1.21	0	1.28
<i>Erica caffra</i>	0.58	0.32	0.19	0.58	0.4	0				1.62	1.7	0.84
<i>Panicum cf. schinzii</i>										1.31	0	0.94
<i>Pelargonium grossularioides</i>										1.22	0	0.89
<i>Ursinia sericea</i>										1.33	0	0.89
DRYBANK												
Species	Ron 1			Ron 2			Ron 3			Ron 4		
	D	2004	2011	D	2004	2011	D	2004	2011	D	2004	2011
		A	A		A	A		A	A			
<i>Pteridium aqualinum</i>	1.49	0	1.22	1.13	1.79	1.77	0.95	1.28	1.64	1.28	2.03	1.77
<i>Brabejum stellatifolium</i> adult	0.98	1.17	0.11	0.26	0	0.13	0.91	0.91	0.05	0.77	0.79	0.11
<i>Metrosideros angustifolia</i> adult	0.79	0.76	0.34				1.17	1.19	0.82	1.23	1.36	0.28
<i>Metrosideros angustifolia</i> sapling	0.9	0.75	0	0.35	0.26	0	0.6	0.3	0.08	0.35	0.13	0.04
<i>Pelargonium scabrum</i>	1.12	0	0.92	1.23	0.91	1.34						
<i>Erharta ramosa</i> subsp. <i>aphylla</i>	0.93	0.78	0									
<i>Elegia capensis</i>	0.53	0.43	0	1.12	1.03	0.51	1.27	1.29	0.67	0.46	0.19	0.12
<i>Stoebe plumosa</i>	0.36	0.16	0	0.48	0	0.29	1.34	0	1.09			
<i>Morella serrata</i> adult	0.5	0.11	0.25	1.1	0.85	0.58	0.53	0	0.33			

On the Elands River sites, species responsible for temporal changes in the wetbank were a combination of trees and other functional types (Table 4.5). *Isolepis prolifera* abundance increased on most sites while *T. babara* and *E. capensis* decreased in abundance. *Brabejum stellatifolium* adults decreased in abundance on Ela 2 but increased in abundance on Ela 4. *Pseudobaeckia africana* decreased in abundance on Ela 1 but increased in abundance on Ela 3 and Ela 4. In the drybank changes were driven by *B. capense* which decreased in abundance on Ela 2 and Ela 3, *P. macrourum* which decreased in abundance on Ela 3 and Ela 4 and *D. glabra* which decreased in abundance on Ela 1 and Ela 2 but increased in abundance on Ela 3 and Ela 4. Some other species also contributing to the changes present on the wetbank and drybank were *M. angustifolia*, *S. macronata*, *E. caffra*, *P. aqualinum* and *Erica pinea*.

The species and life history stages responsible for changes in the wetbank on the recovering sites of the Molenaars River were *S. macronata* and *M. angustifolia* seedlings (Table 4.6). *Acacia mearnsii* seedlings was recorded at Mol 2 during historic sampling but was absent during present data collection. *Acacia mearnsii* went from being absent on Mol 3 during 2004/2005 to having a relative abundance of 0.63 during 2011/2012. Other species contributing to the changes in the wetbank were: *P. macrourum*, *I. prolifera*, *M. serrata* saplings and *P. serratum*. The drybank of recovering sites showed a decrease in *B. stellatifolium* and *M. angustifolia* saplings while species such as *C. paniculata* showed an increased abundance. Mol 2 had in a couple of different species responsible for the temporal change compared to that on the recovering sites (Mol 1 and Mol 3) these were: *Searsia angustifolia*, *S. plumosa* and *D. glabra*. Other species contributing to the temporal changes in composition were *P. aqualinum* and *E. ramosa* (subsp. *aphylla*).

Temporal changes in the wetbank on the Heks River (Table 4.7) were to a larger extent caused by *I. prolifera*, *M. angustifolia* seedlings, *Morella serrata* adults, *C. paniculata* and *Drosera capensis*. *Isolepis prolifera* decreased on sites Hek 1 and Hek 2 while the abundance increased on Hek 3 and Hek 4. The abundance of *M. angustifolia* seedlings and adults increased on all four sites with the exception of a decrease in adult abundance on Hek 3. *Drosera capensis* was not recorded on the Heks river sites during historic sampling but during 2011/2012 sampling the species was recorded on the wetbank of Hek 2, Hek 3 and Hek 4. The drybank had *M. angustifolia* saplings and adults together with *M. serrata* seedlings, saplings and adults causing temporal changes on sites (Table 4.7). *Metrosideros angustifolia* showed a decrease of abundance on all Heks River sites while sapling abundance varied. Abundances of *M. serrata* seedlings increased and that of adults decreased on sites Hek 1, Hek 2 and Hek 3. Species responsible for changes in abundance included *E. ramosa*, *C. paniculata*, *E. rehmannii* and *S. angustifolia*. *Erharta rehmannii*

decreased in abundance on all four sites while *E. ramosa* increased on Hek 1, Hek 3 and Hek 4.

The Rondegat River had the most diverse group of species responsible for temporal changes in composition (Table 4.8). The species driving changes on all sites sampled were *I. prolifera*, *M. angustifolia* adults, *E. capensis* and *C. paniculata*. Apart from these species there seemed to be a longitudinal difference (Chapter 3) present between species driving changes on the sites. In the mountain stream sites *B. neriifolia* saplings, *M. serrata* saplings and *B. stellatifolium* seedlings contributed to the changes in composition while in the transitional zone *P. serratum*, *S. plumosa*, *Panicum cf. schinzii*, *Pelargonium grossularioides* and *Ursinia sericea* were contributors to the temporal changes present. There were no clear trends present for species abundances. Some species increased on one site and decreased on the neighbouring site such was the case with *M. angustifolia* which increased in abundance on Ron 1 and decreased in abundance on Ron 2. *B. neriifolia* was one of the few species which showed a consistent trend with and increased abundance on Ron 1 and Ron 2. Another example of this was seen with *S. plumosa* in the transitional longitudinal zone which increased in abundance on Ron 3 and Ron 4. The changes were very diverse in the wetbank.

The temporal changes in composition were mostly driven by *P. aqualinum*, *B. stellatifolium* adults, *M. angustifolia* saplings and *E. capensis*. *Elegia capensis* decreased in abundance on all four sites sampled. *Pelargonium scabrum* increased in abundance on Ron 1 and Ron 2. On site Ron 1 *S. plumosa* decreased in abundance while on Ron 2 and Ron 3 the abundance increased. *Pteridium aqualinum* increased in abundance on Ron 1 and Ron 3 while the abundance decreased at Ron 2 and Ron 4. As with the wetbank, little or no trend was obvious in changes in species abundances. The sites exposed to fire disturbances and recovering after clearing of alien woody invasive species showed more diverse changes occurring in species abundances compared to natural sites. Rivers not subjected to disturbances such as fire and clearing of invasive species had less diversity in species responsible for the temporal changes in community composition. This was tested with MDS ordinations comparing the wetbank and drybank of sites temporally.

Based on the MDS ordination results, sites recovering after clearing and subjected to fire disturbance between sampling periods showed greater difference (ordination distance) than relatively undisturbed sites. The rivers undisturbed by recovering after clearing and not subjected to fire disturbances (Elands and Heks Rivers) showed more overlapping present in the wetbank and drybank sample plots. These results are present below in Figure 4.5 and Figure 4.6.

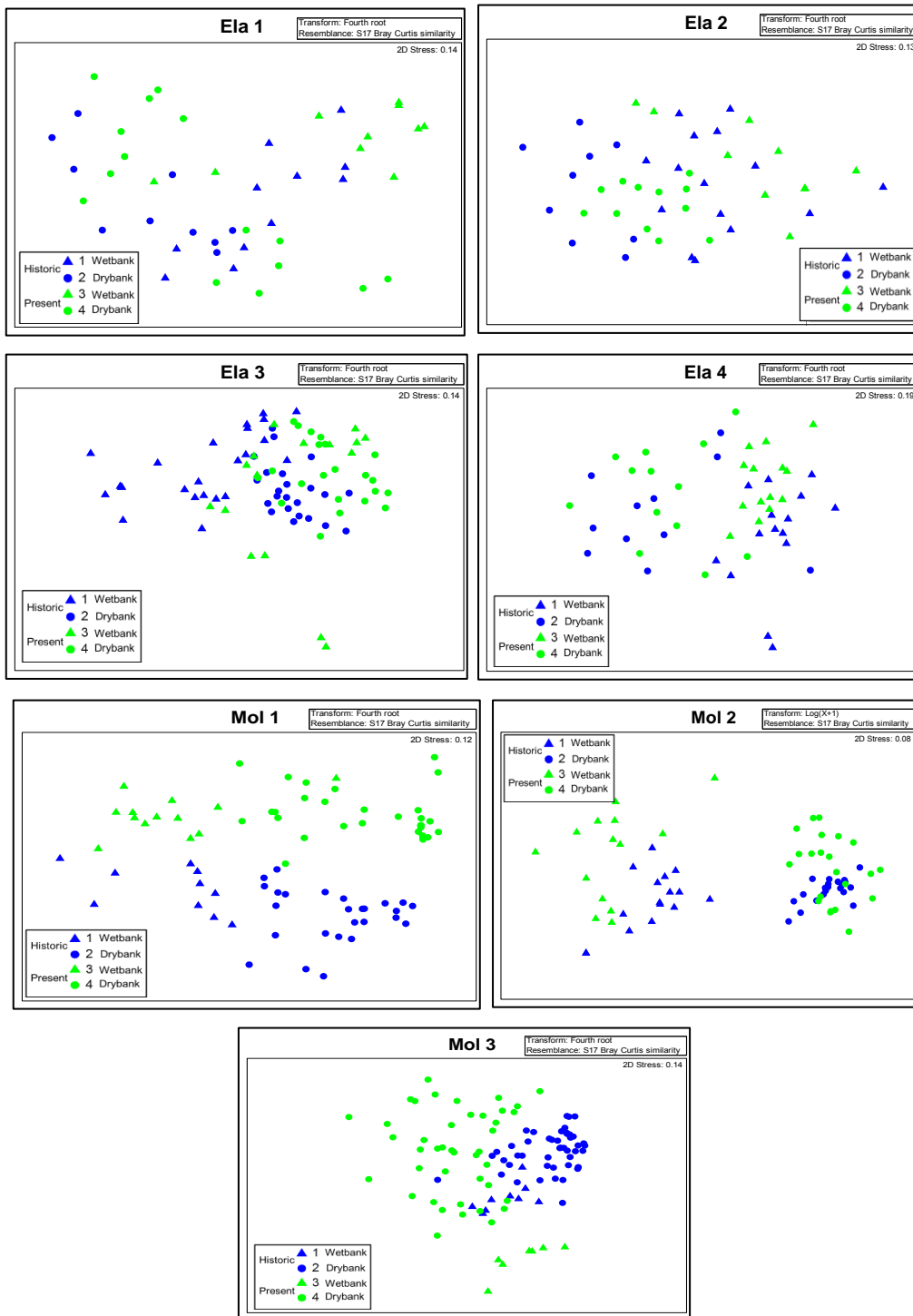


Figure 4.5 MDS ordinations of the wetbank and drybank compared temporally on sites of the relatively undisturbed Elands River (including Mol 2) and the recovering sites on the Molenaars River (Mol 1 and Mol 3). Blue – historic data, green – present data, 1 and 3 – wetbank, 2 and 4 – drybank.

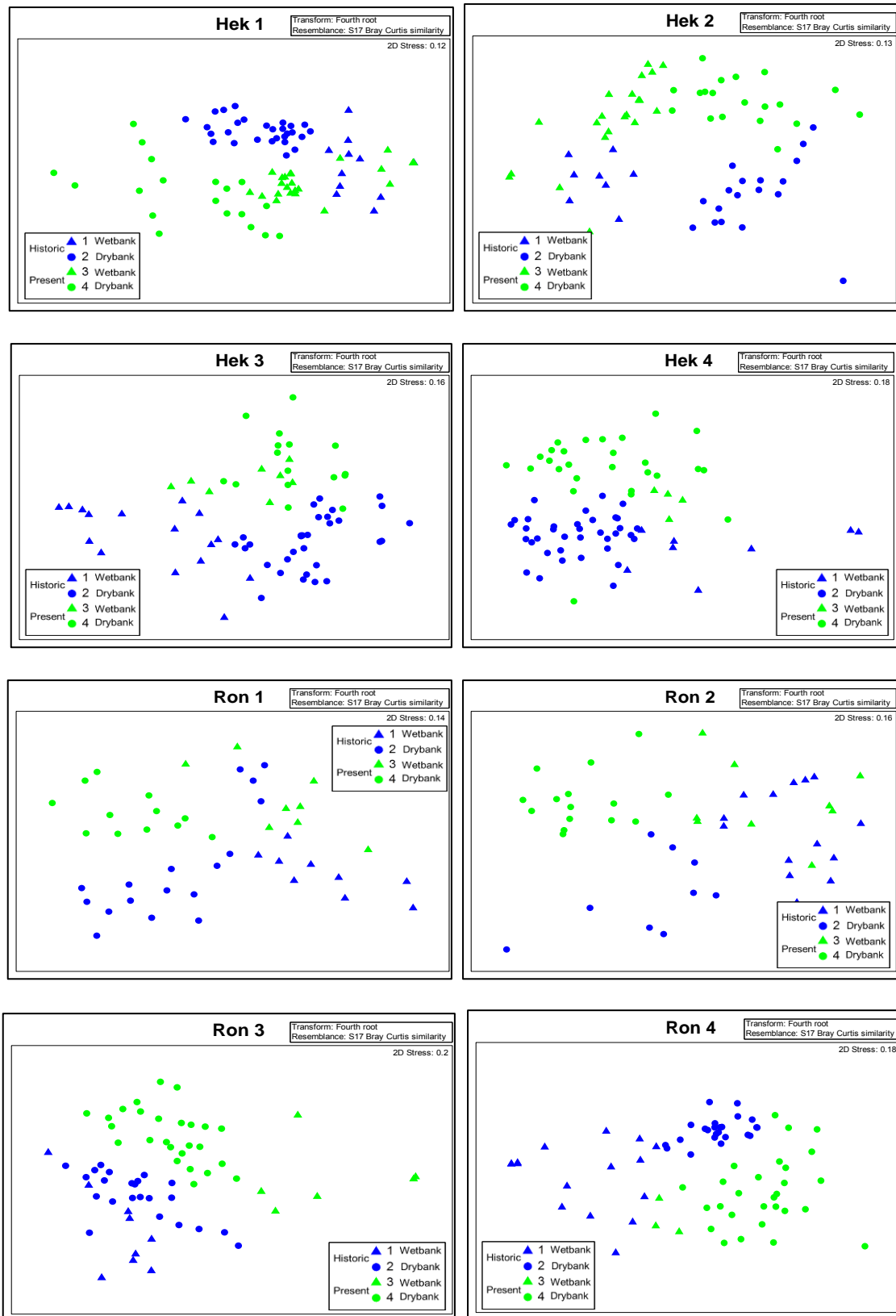


Figure 4.6 MDS ordinations of the wetbank and drybank compared temporally on relatively undisturbed sites of the Heks River (Hek 1-4) and sites subjected to fire disturbance on the Rondegat River (Ron 1-4). Blue – historic data, green – present data, 1 and 3 – wetbank, 2 and 4 – drybank.

4.4 Discussion

4.4.1 Do Fynbos Riparian communities (at a site scale) show significant change in community composition over a relatively short period of time?

One would expect a site to be more similar to its historic data than to a different site all together since the temporal scale was relatively small at seven years. This was however not the case, sites had stronger similarity to data collected during the same sampling period than with historic data collected from the same site. A bias due to different observers is a possibility, however this was potentially kept to a minimum by the presence during 2011/2012 observations of the historic sampler Mr. Reinecke. Temporal differences are evident at the river scale. Each river had a different pattern of change in plant community composition. Statistically, none of the sites showed significant differences regardless of their condition (recovering, burnt or undisturbed). The Elands River separated temporally during multivariate analyses of species composition data but showed little temporal change in plant diversity. The Molenaars River sites showed an increase in plant diversity while the Rondegat River, subjected to fire disturbances, had a decrease in overall plant diversity as shown by the same biodiversity indices (Shannon and Fischer). The Heks River like the Elands River, showed almost no change in diversity. Sites subjected to disturbance therefore changed more in terms of the biodiversity indices (Shannon and Fischer) at a relatively small temporal scale than undisturbed sites. This agrees with Callicott (2002) who describes temporal scales as being dynamic and reaching a climax community which after disturbance events restarts the successional processes till reaching equilibrium once more.

The overall relative species abundance, which was used to calculate the measures of biodiversity of sites did not show significant historical change. This could indicate that natural disturbance such as fire, in this case with overall biodiversity showing a slight decline temporally, does not change the overall community composition and diversity significantly. The sites on the Molenaars River that were recovering after clearing (Mol 1 and Mol 3) might not be exactly the same as the reference site (Mol 2) in terms of MDS ordinations but, no significant differences in species composition was noticeable between sampling periods at a site scale. It is important then to acknowledge the differences between sampling efforts as shown with Cluster and MDS results, but also how little has changed within a site scale in relation to overall species diversity.

The Western Cape fynbos is known for its resilience to disturbances such as fire and flooding (Cowling 1992) and thus the species diversity does not necessarily show major modifications in the medium term, while changes may be evident in the years immediately following disturbance. A t-test revealed within site differences being present of different

growth forms, but produced no clear trend that would explain the temporal changes. It appears that temporal changes are driven at a smaller scale within a site but not necessarily at the scale of the sites used in our study (approximately 200 m²).

4.4.2 Do riparian vegetation composition at the lateral zone scale (wetbank and drybank) show differences based on relative species abundance?

At a lateral zone scale, differences in species abundances over time were more apparent than at a site scale. Undisturbed rivers such as the Elands and Heks Rivers showed less variation in species responsible for temporal changes than the recovering and burnt sites on the Molenaars and Rondegat Rivers. Common species responsible for temporal changes in abundance were *M. angustifolia*, *M. serrata*, *B. stellatifolium*, *I. prolifera*, *E. capensis*, *P. serratum* and *C. paniculata*. These species were almost always suggested by Simper analyses as drivers of change on each river used in this study. Several other species were found to be drivers of change but mostly only on the Rondegat River. This was expected since the sites on this river were burnt three years ago. Most of the species not commonly indicated on the other rivers but on Rondegat River were either more terrestrial in nature such as *P. scabrum*, *S. plumosa*, *U. sericea*, *P. grossularioides* and *P. schinzii*, or known to resprout after fire such as *M. angustifolia* and *B. neriifolia*.

Temporally the wetbank and drybank on rivers relatively undisturbed showed fewer differences than that of sites subjected to disturbances (MDS ordination). The Molenaars sites showed Mol 1 and Mol 3 to have a clearer separation between the wetbank and drybank temporally than that of Mol 2. Similarly the Rondegat River sites had a greater distance (indication of difference) present in the MDS ordinations that those on the Heks and Elands Rivers.

4.5 Conclusion

Reference conditions used in restoration of rivers and riparian zones are typically, though not exclusively, based on a pre-disturbance state. The use of a medium term temporal reference condition is supported by the results of this study in that little variation in plant diversity at this scale was seen. These changes are due to changes in relative abundances of similar species. The species most commonly found to be drivers of changes are common species occurring in great abundances in most Western Cape Fynbos Riparian Vegetation communities, e.g. *M. angustifolia*, *M. serrata*, *B. stellatifolium*, *I. prolifera* and *E. capensis*.

The increased variation in species responsible for change at sites subjected to disturbances supports the theory that change is disturbance driven. This is in support of the Flux of Nature paradigm, which suggests that no ecosystem is static but an ever changing dynamic entity (Pickett et al. 2007).

In terms of environmental practices it is useful to use a reference condition of ecological conditions of particular sites in the past when the specific area or site was in a better ecological condition. It is however important not to ignore the results the Molenaars River produced in relation to its own reference condition (the natural site Mol 2). Mol 2 is situated within the same longitudinal zone and was never invaded or cleared of alien invasive species. The vegetation community at Mol 1 and Mol 3 might have recovered to a community consisting of dense canopy and large trees, but still diverged substantially from Mol 2. This is in comparison to the sites on other rivers, which were more similar to their longitudinally paired sites (Ela 1 and Ela 2, Ron 3 and Ron 4 etc.). This suggests that even though a site might be functionally recovered it will likely remain dissimilar to the reference condition. The more recent approach of restoring a site to a better condition that it is presently in rather than trying to get it to a state it was in previously makes more sense especially since all sites showed small-scale changes (Meek et al. 2013; Palmer et al. 1997). Sieben and Reinecke (2008) provides a wetbank drybank reference description to aid restoration by means of re-vegetation instead of using natural recovery which is timely and has proven less successful and more expensive in the past (Blanchard and Holmes 2008; Pretorius et al. 2008; Reinecke et al. 2008). This is in agreement with our results as the wetbank and drybank were found to be more comparable in their response to change as shown by MDS ordinations. A wetbank and drybank re-vegetation recovery approach is supported with these results as opposed to natural recovery which in the case of the Molenaars River sites did not return to the exact same community composition proposed by the reference site (Mol 2).

Even relatively undisturbed sites have ecological processes acting on the community. Hydrology for instance was not taken into account in this study but has been shown to impact the riparian community structure (Reinecke and Brown 2013). By looking at more types of disturbances acting on different scales it would be more realistic to gain a better understanding of disturbance driven changes in the very dynamic and resilient Fynbos Riparian Vegetation of the Western Cape. This is something that should be investigated further to aid the understanding of recovering dynamics and natural driven disturbances acting on the Fynbos Riparian community.

4.6 References

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5 Synthesis

5.1 Introduction

This study sought to investigate the changes in riparian fynbos community composition and diversity in space and time. This was based on the three physical dimensions (lateral, vertical and longitudinal) and the fourth temporal dimension (time) of interaction occurring on riverine habitats. In the past, lateral zonation has been used to assess and describe changes in riparian vegetation but no comparison of lateral zonation has been conducted between longitudinal zones in upper reaches of Western Cape rivers: mountain stream, transitional and upper foothills (Rowntree and Wadeson 1999).

The overarching aims of this study were to investigate and describe differences in riparian vegetation at a lateral zone scale across longitudinal zones of selected upland rivers in the Western Cape (the spatial dimension), and to assess changes in riparian vegetation communities over a relatively short time frame and with different disturbances impacting the communities between sample periods (the temporal dimension). Each part of the study (spatial and temporal) had its own objectives. For the spatial part, the objectives were: to identify and describe how plant community composition changes between longitudinal zones and secondly to evaluate and test the relationship between plant community composition and selected environmental variables. For the temporal part of the study the objective was to assess the change in riparian community composition over time

5.2 Spatial scale

Spatial and temporal changes were investigated in this study to assess whether longitudinal positioning of sites and temporal scale influences riparian vegetation community composition. Spatial changes in riparian vegetation were shown to occur at the river scale which supports the description of river signatures by King and Schael (2001). This makes comparing sites and data between different rivers difficult and unreliable depending on the scale and aim of the comparisons. Further a difference in species composition and abundances were evident at the longitudinal scale. These changes were not significant therefore previous descriptions made by Reinecke et al. (2007) cannot be discarded, it merely showed a high variability being present in community composition due to bank shape and to a lesser extent the bank substrate (sediment calibre). Mountain stream sites showed a strong relationship with elevation and the upper foothills with horizontal distance. This

makes sense due to narrow valleys upstream with steep inclines in contrast to the open flattened out bank shape of foothill rivers. Spatial constraints have a greater impact on the positioning and abundance of a species in the mountain stream than a species in the upper foothills. In the upper foothills there is more space, as shown when change was plotted against elevation, and thus less competition over recruitment space than in the foothills (Galatowitsch and Richardson 2005). This leads to better defined lateral zones and less overlapping in drybank and wetbank species. It is important to consider the differences in location relative to longitudinal zones of sample sites and reference conditions when attempting to access, study or restore riparian communities.

5.3 Temporal scale

Temporally, no significant change in plant diversity at a river or site scale was evident. At a lateral zone scale (wetbank-drybank scale), however, changes in species abundances were indicated as the drivers of temporal changes. The species responsible for the temporal changes were relatively common riparian species. These included *I. prolifera*, *C. capensis*, *E. ramosa*, *P. serratum*, *M. angustifolia*, *M. serrata* and *B. stellatifolium*. Sites subjected to clearing of invasive species have been recovering for more than fifteen years (relatively old site) and even though the community was mature and contained most of the species present on the reference site (Mol 2) there was still a difference evident when the sites were compared using multidimensional scaling.

Sites burnt in-between sampling periods showed more variation in the species responsible for changes. These species were either more terrestrial in nature such as *P. scabrum*, *S. plumosa*, *U. sericea*, *P. grossularioides* and *P. schinzii*, or known to resprout after fire such as *M. angustifolia* and *B. neriifolia*. When the wetbank and drybank were compared over time the burnt (Rondegat River) and recovering sites (Molenaars River) showed more variation in species abundances than the relatively undisturbed sites (Elands and Heks Rivers). Whether a site will ever be considered “recovered” depends on the reference condition. On the Molenaars River it was found that the recovering sites had a different community composition from that of the reference site Mol 2, but showed little difference in plant diversity temporally. Common riparian species were found to still be present but it was the abundances of these species that were different. For all intended purposes the Molenaars recovering sites could be classified as functionally recovered, but they do not show the same similarity in composition to Mol 2 than Ela 3 and Ela 4 for instance showed with Cluster and MDS analyses. Perhaps a site should be considered as permanently

altered once it has been disturbed, but functionally recovered once a diverse and mature indigenous plant community has returned?

5.4 Reference condition

Mol 2 showed changes present in species abundances indicating that no reference site is static (Flux of Nature paradigm). The relevance then of a temporally selected reference condition based on species abundances becomes questionable. A reference condition based on species presence or absence is more realistic since the diversity of species composition did not change significantly. This would mean that, based on the spatial and temporal results of this study, a reference description based on species composition would be more suitable than a reference site or historic description. The reason why species composition would be suitable across more basins, longitudinal zones and over time is that we found no evidence to suggest the absence of species but rather that the abundances of species varied greatly in space and time. In space the same lateral zone indicator (dominant) species may not occur with the same high level of abundance elsewhere but it is present in the community. Temporally species diversity may vary but the presence of the species is not lost. Sieben and Reinecke (2008) described a wetbank and drybank description for restoration which agrees with Reinecke and Brown (2013) who was able to link riparian zonation (wetbank and drybank scale) to hydrological regimes. If disturbance and recruitment driven changes occur at the wetbank and drybank lateral scale then a reference description based on species occurrence of these two lateral zones should be suitable for restoration practices aimed at restoring the degraded site to a functionally healthier state.

5.5 Restoration and management

Spatio-temporal scales are important for ecological restoration. Temporally, ecological processes act on the riparian community by means of disturbance regimes which can act spatially through landscapes and geomorphological changes, exchange of nutrients and biological provinces (Levin 1992; Sieben et al. 2009). Understanding ecological spatio-temporal scales can be useful for restoration practices for the process of developing scientific methods for recovery and the ultimate improvement of freshwater bodies (Bailey et al. 1998; Thorp et al. 2006). By incorporating spatio-temporal scales into ecological restoration more achievable and effective goals for conservation of biodiversity and ecosystem management can be developed.

Figure 5.1 is a diagrammatic representation of the spatio-temporal perspective. This shows that the scale of ecological study influences the time frame and space in which multidimensional changes in diversity occur. The diversity is also on the opposite side of disturbance since the magnitude of disturbance influences the degree of change occurring within plant communities. The smaller the temporal scale, the smaller the spatial scale of change as seen with changes of a within decadal scale (<10 years) only being evident at a lateral zone (wetbank drybank) scale and not at a site or river scale. The spatial functions over time and these two dimensions function within the dimension of space (Callicott 2002). They are inseparable as shown in this study by diversity, disturbances, longitudinal and lateral zones. These scale dimensions should be considered when attempting to develop and manage freshwater ecosystems, especially in a Riparian Fynbos Vegetation community. The smaller the spatial scale, the smaller the temporal scale at which changes occur as seen with wetbank drybank comparisons of species abundances. This relationship between the spatial and temporal dimension is depicted in Figure 5.1 which shows the scale of study influencing the time and space in which changes occur.

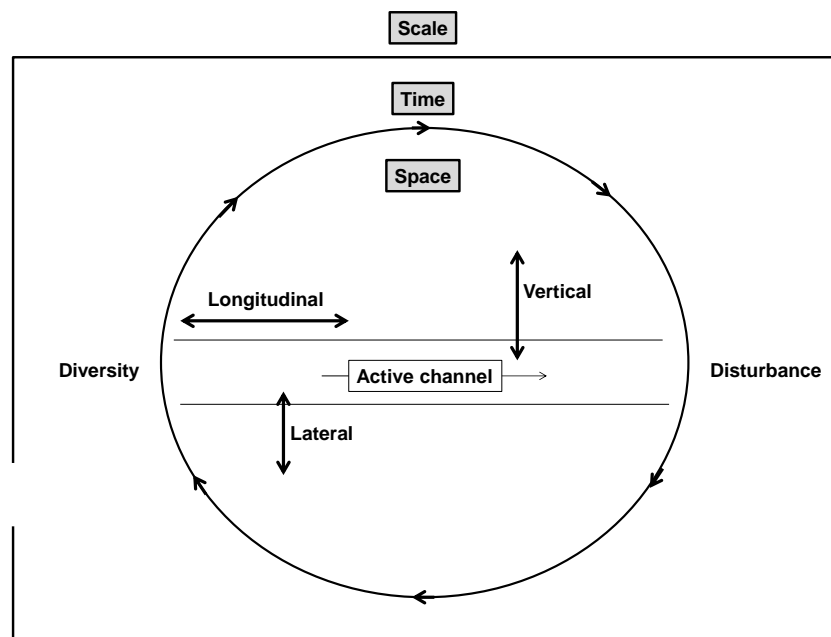


Figure 5.1 Spatio-temporal dimension of riverine environments. The three physical dimensions of interaction is encapsulated within the time over which these exchanges/interactions occur. The scale at which these interactions are studied influences the time and space at which they are observed and also the scale of changes driven by disturbance and diversity. The smaller the ecological scale the smaller the scale of disturbances influencing the vegetation community composition.

In terms of environmental practices a reference condition and reference sites are of great use especially when the aim is restoration of a degraded ecosystem to a better ecologically functioning state. Spatial and temporal templates then become very important especially when an area upstream or downstream sites seems to be in a better ecological state. Do we restore the degraded area to the closest possible template upstream or downstream? Do we use a previous description based on work previously done on a river? A more realistic approach would be to use a general riparian vegetation description or a reference description developed for that particular longitudinal zone than to use a specific site description situated on the neighbouring basin or even a couple of hundred meters upstream. This is in agreement with Sieben and Reinencke's (2008) wetbank drybank descriptions used to guide restoration practices involving re-vegetating a degraded riparian area.

The results support the use of a reference description for environmental management purposes but do not support the use of a static reference condition to be applied on all Fynbos Riparian Communities regardless of scale. A small scale temporal template is feasible for management and restoration purposes but the spatial scale at which these templates are applied should be assessed in more detail. Perhaps initiating a trajectory towards a more natural condition to that which it is presently in rather than trying to restore it to a previous or descriptive state makes more sense (Meek et al. 2013; Palmer et al. 1997).

5.6 Ecological Research and Recommendations

Spatial changes are more evident between basins than longitudinally and may make comparative ecological studies across basins less accurate than those based within one basin. When research is conducted on more than one basin these "catchment signatures" may have very significant and idiosyncratic influences on ecological processes, which should be carefully considered and cross-basin comparisons should be avoided when a sample size (site) is small in scale. Future research could look into basin/catchment signatures and the processes that cause these differences in plant species composition and spatial variation. Also this study did not take groundwater, climate, hydrology and soil ecology into account. These are important parts of the riparian riverine environment and play contributing roles in small scale disturbances, restoration initiatives and ecological wellbeing of an environment (Callicott 2002). Further incorporation of the environmental attributes acting on the riparian vegetation community could provide more information on inter-basin differences, spatio-temporal riparian scales and restoration initiatives for the future.

5.7 References

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	ELA 1	ELA 2	ELA 3	ELA 4	RON 1	RON 2	RON 3	RON 4	HEK 1	HEK 2	HEK 3	HEK 4
<i>Metalasia cf. Acuta</i>								*				
<i>Metalasia dregeana</i> DC.												
<i>Metrosideros angustifolia</i> tree	*	*	*		*	*	*	*	*	*	*	*
<i>Metrosideros angustifolia</i> sapling	*	*	*	*	*	*	*	*	*	*	*	*
<i>Metrosideros angustifolia</i> seedling	*	*	*	*	*	*	*	*	*	*	*	*
<i>Morella serrata</i> tree	*		*	*	*	*	*		*	*	*	*
<i>Morella serrata</i> sapling	*	*	*	*	*	*	*	*	*	*	*	*
<i>Morella serrata</i> seedlings	*	*	*	*		*	*		*	*	*	*
<i>Nemesia diffusa</i> Benth.							*	*				
<i>Notobubon tenuifolium</i>					*	*		*				
<i>Oftia africana</i>												
<i>Olea capensis</i> sapling										*		
<i>Othonna parviflora</i>								*				
<i>Panicum cf. schinzii</i>								*	*	*		
<i>Panicum schinzii</i>	*											
<i>Paraserianthes lophantha</i> tree												
<i>Paraserianthes lophantha</i> seedling												
<i>Passerina</i> sp.									*			
<i>Passerina vulgaris</i>			*									
<i>Pelargonium grossularioides</i>					*		*	*				
<i>Pelargonium scabrum</i>					*	*			*	*		*
<i>Pelargonium</i> sp.1												
<i>Pellaea pteroides</i>				*								
<i>Pennisetum macrourum</i>			*				*		*	*		
<i>Pentameris distichophylla</i>	*		*	*								
<i>Pentaschistis aurea</i>				*								
<i>Pentaschistis pallida</i>				*		*						*
<i>Pentaschistis patula</i>					*		*	*				*
<i>Phylica oleaefolia</i> sapling					*	*	*	*	*	*		*
<i>Platycaulos callistachyus</i>												
<i>Platylophus trifoliatu</i> s tree	*	*	*	*								
<i>Platylophus trifoliatu</i> s sapling			*									
<i>Platylophus trifoliatu</i> s seedlings			*									
<i>Poaceae</i> sp.2		*	*									
<i>Podalyria</i> sp.1	*	*	*	*								
<i>Pronium serratum</i>	*	*					*	*	*	*		
<i>Prismatocarpus fruticosus</i>							*	*				*
<i>Protea laurifolia</i>	*			*	*							
<i>Pseudobaeckia africana</i>	*		*	*								
<i>Pseudoselago recurvifolia</i>							*					

	ELA 1	ELA 2	ELA 3	ELA 4	RON 1	RON 2	RON 3	RON 4	HEK 1	HEK 2	HEK 3	HEK 4
<i>Pseudoselago sp.2</i>							*	*				
<i>Psoralea angustifolia</i>									*			
<i>Psoralea aphylla usitata</i>					*	*		*	*			
<i>Psoralea pinnata</i>	*	*	*	*								
<i>Psoralea sp.2</i>			*									
<i>Pteridium aquilinum</i>	*	*	*		*	*	*	*				
<i>Restio multiflorus</i>	*	*	*	*								
<i>Restio perplexus</i>												
<i>Restionaceae sp.1</i>												
<i>Restionaceae sp.2</i>												
<i>Restionaceae sp.4</i>												
<i>Restionaceae sp.6</i>			*	*								
<i>Restionaceae sp.7</i>												
<i>Searsia angustifolia</i>			*				*		*	*	*	*
<i>Searsia lucida forma elliptica</i>			*							*		
<i>Searsia tomentosa</i>							*	*				
<i>Rubiaceae sp.2</i>								*				
<i>Rubus sp. 2</i>				*								
<i>Salix mucronata tree</i>			*									
<i>Salix mucronata sapling</i>			*									
<i>Salix mucronata seedling</i>			*									
<i>Schizaea tenella</i>	*		*	*								
<i>Secamone alpinii</i>					*						*	*
<i>Senecio rigidus</i>										*		
<i>Species 100</i>			*	*								
<i>Species 101</i>												
<i>Species 102</i>									*	*		
<i>Species 103</i>									*			
<i>Species 104</i>									*			
<i>Species 105</i>					*	*	*	*	*	*		*
<i>Species 107</i>									*			
<i>Species 108</i>							*	*	*			
<i>Species 109</i>									*			
<i>Species 110</i>									*			
<i>Species 111</i>					*		*	*	*			
<i>Species 112</i>							*	*	*			
<i>Species 113</i>					*						*	*
<i>Species 114</i>							*	*				
<i>Species 115</i>						*	*	*			*	
<i>Species 116</i>					*	*	*	*				

	Ela 1	Ela 1*	Ela 2	Ela 2*	Ela 3	Ela 3*	Ela 4	Ela 4*	Mol 1	Mol 1*	Mol 2	Mol 2*	Mol 3	Mol 3*	Ron 1	Ron 1*	Ron 2	Ron 2*	Ron 3	Ron 3*	Ron 4	Ron 4*	Hek 1	Hek 1*	Hek 2	Hek 2*	Hek 3	Hek 3*	Hek 4	Hek 4*
<i>Euclea tomentosa</i>										*																				
<i>Euryops abrotanifolius</i>															*										*	*				
<i>Ficinia acuminata</i>																	*								*	*				
<i>Ficinia capitella</i>			*						*																					
<i>Ficinia indica</i>		*	*			*				*										*					*	*			*	
<i>Ficinia sp.2</i>	*																			*										
<i>flat white hair stringy leaf</i>												*																		
<i>Freylinia lanceolata 0.3-2</i>											*	*												*	*	*	*		*	
<i>Freylinia lanceolata 2-5</i>									*	*	*	*	*	*									*	*	*	*	*	*	*	
<i>Freylinia lanceolata seedlings</i>									*	*	*	*	*	*									*	*	*	*	*	*	*	
<i>Gnaphalium sp.1</i>									*		*	*	*	*																
<i>Hackea sericia</i>			*																											
<i>Halleria elliptica</i>									*										*		*		*							
<i>Halleria lucida 0.3-2</i>					*	*	*	*													*		*							
<i>Halleria lucida 2-5</i>						*	*	*	*	*	*	*	*	*							*		*							
<i>Halleria lucida seedling</i>						*	*	*	*	*	*	*	*	*							*		*							
<i>Hartogiella schinoides 0.3-2</i>		*	*	*			*								*					*		*								
<i>Hartogiella schinoides 2-5</i>		*	*	*			*								*					*		*								
<i>Hartogiella schinoides seedlings</i>	*		*	*			*	*							*					*		*								
<i>Hebenstretia lanceolata</i>															*			*	*			*								
<i>Heeria argentea 0.3-2</i>																	*	*	*			*								
<i>Helichrysum cf. odoratissimum</i>																			*		*		*							
<i>Helichrysum odoratissimum</i>					*															*		*							*	
<i>Helichrysum scabrum</i>																			*		*		*						*	
<i>Helichrysum sp.1</i>																			*		*		*						*	
<i>Hemarthria altissima</i>												*							*		*		*						*	
<i>Hermannia sp.</i>																		*	*		*		*						*	
<i>Homalanthus populifolius 0.3-2</i>																				*		*			*	*			*	
<i>Hymenolepis sp.1</i>											*	*		*					*		*		*						*	
<i>Ilex mitis 0.3-2</i>	*		*		*	*	*	*	*																				*	
<i>Ilex mitis 2-5</i>	*	*			*	*	*	*	*																				*	
<i>Ilex mitis seedlings</i>					*	*	*	*	*					*							*		*			*	*		*	
<i>Indigofera frutescens</i>																					*		*						*	
<i>Ischyrolepis fraterna</i>					*	*	*	*	*					*							*		*			*	*		*	
<i>Ischyrolepis gaudichaudianus.</i>					*	*	*	*	*					*							*		*		*	*		*	*	

	Ela 1	Ela 1*	Ela 2	Ela 2*	Ela 3	Ela 3*	Ela 4	Ela 4*	Mol 1	Mol 1*	Mol 2	Mol 2*	Mol 3	Mol 3*	Ron 1	Ron 1*	Ron 2	Ron 2*	Ron 3	Ron 3*	Ron 4	Ron 4*	Hek 1	Hek 1*	Hek 2	Hek 2*	Hek 3	Hek 3*	Hek 4	Hek 4*
<i>Restionaceae sp.2</i>									*	*	*	*		*																
<i>Restionaceae sp.3</i>									*	*	*	*		*																
<i>Restionaceae sp.4</i>			*						*	*	*	*		*																
<i>Restionaceae sp.6</i>						*			*	*	*	*		*																
<i>Rhamnaceae sp.1</i>																														
<i>Rhus angustifolia</i>						*				*	*	*		*						*	*			*	*	*	*	*	*	*
<i>Rhus lucida forma elliptica</i>						*				*	*	*		*					*	*			*	*	*	*	*	*	*	*
<i>Rhus tomentosa</i>																				*	*			*	*	*	*	*	*	*
<i>Rubiaceae sp.1</i>			*		*		*														*	*			*	*	*	*	*	*
<i>Rubiaceae sp.2</i>																					*	*			*	*	*	*	*	*
<i>Rubus sp. 2</i>								*		*	*	*		*								*	*			*	*	*	*	*
<i>Rubus sp.1</i>									*	*	*	*		*								*	*			*	*	*	*	*
<i>Salix mucronata 0.3-2</i>					*	*			*	*	*	*		*								*	*			*	*	*	*	*
<i>Salix mucronata 2-5</i>					*	*			*	*	*	*		*								*	*			*	*	*	*	*
<i>Salix mucronata seedling</i>					*	*	*		*	*	*	*		*								*	*		*	*	*	*	*	*
<i>Salvia sp.1</i>	*	*	*			*		*		*	*	*		*			*								*	*	*	*	*	*
<i>Schizaea tenella</i>	*	*	*			*		*		*	*	*		*			*													
<i>Secamone alpinii</i>																*											*	*	*	*
<i>Senecio rigidus</i>											*	*		*												*	*	*	*	*
<i>Setaria sp.2</i>											*	*		*																
<i>Solanum sp.1</i>																					*	*					*	*	*	*
<i>Stoebe plumosa</i>			*			*	*	*		*	*	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Stoebe sp.1</i>										*	*	*		*							*	*			*	*	*	*	*	*
<i>Stoebe spiralis</i>					*	*	*	*		*	*	*		*							*	*			*	*	*	*	*	*
<i>Struthiola myrsinites</i>												*		*							*	*					*	*	*	*
<i>Struthiola sp.1</i>														*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Taraxacum officinale</i>						*								*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Tetaria c.f. flexuosa</i>					*	*								*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Thamnochortus lucens</i>							*							*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Thesium nudicaule</i>																					*	*			*	*	*	*	*	*
<i>Thesium sp.1</i>															*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Todea babara</i>	*	*	*		*	*	*	*		*	*	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Tribolium uniolae</i>						*		*		*	*	*		*							*	*			*	*	*	*	*	*
<i>Ulmus sp. 1</i>	*																													
<i>Ursinia abrotanifolia</i>			*		*																*	*			*	*	*	*	*	*
<i>Ursinia sericea</i>																					*	*			*	*	*	*	*	*

