Can hydrological niche segregation explain species distributions in an aquifer-dependent wetland?

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Abstract

Aim: To investigate post-fire succession in fynbos wetland plant communities, test whether these species segregate along fine-scale hydrological gradients and to identify species potentially most sensitive to groundwater abstraction.

Intro: Hydrological gradients, which form between permanently inundated wetlands and adjacent dry habitats, are key drivers of vegetation community composition and structure, promoting opportunities for adaptive speciation and community coexistence. In the seasonally arid fynbos region of South Africa, the occurrence of permanently inundated, groundwater-fed wetlands suggests that fine-scale hydrological gradients may significantly shape floristic diversity in this region. The extent to which fine-scale hydrological gradients influence community composition and species segregation requires further testing in fynbos but has important implications for understanding the potential impacts of groundwater abstraction in these fire-prone systems as well as identifying potentially sensitive species.

Methods: I analyzed plant community composition and abundance data, along with soil volumetric water content collected across three transects in an aquifer-fed wetland, from 2011 to 2022. Non-parametric multivariate tests were used to quantify spatial and temporal changes in community composition, highlighting general patterns of community clustering across transects and changes related to post-fire succession. The hydrological niche space was quantified across an aquifer-dependent wetland by representing soil moisture data along two hydrological axes: the sum of exceedance values for flooding (SEVa) and drought (SEVd). Using a subset of persistent species, species locations were fitted to these hydrological axes based on their proximity to soil moisture probes. Species were ranked in accordance with their position on this gradient, indicating a preference for flooded or drier sites on the wetland.

Results: Successional changes were observed in the vegetation at different ages post-fire as well as shifts in early post-fire community composition between fire events. A robust test of the hydrological niche concept using several species that persisted over the post-fire successional trajectory shows that wetland community composition is spatially structured along hydrological gradients. It was also determined that species display some degree of hydrological niche segregation, with preference for either waterlogged or dry niches within the wetland.

Discussion: The results suggest that species segregate along hydrological gradients defined by the number of days under flooding and dry conditions and can thus be ranked according to their preference for inundated or dry hydrological niches. The occurrence of several species with a strong preference for, or dependence on, permanently inundated niches, highlights the potential impacts of

groundwater abstraction on species composition, abundance and distribution, which may affect this hydrological niche. The study takes proactive steps in monitoring ecologically sensitive ecosystems before groundwater abstraction, to ensure that appropriate vegetation management and conservation strategies are in place and can be implemented when necessary.

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1 Introduction

1.1 Groundwater-dependent ecosystems

Groundwater-dependent ecosystems (GDEs) are ecosystems whose composition and function are maintained through direct or indirect access to groundwater (Kløve *et al.*, 2011; Rohde *et al.*, 2017). GDEs can occur in the subterranean environment, occurring within the aquifer, and also above the land surface, including wetlands (including seeps and springs), riparian zones, riverbeds, and estuaries (Colvin *et al.*, 2007, fig. 2.4; Eamus *et al.*, 2015; Nevill *et al.*, 2010).GDEs that occur above the land surface tend to have unique physical and chemical characteristics that are a reflection of the hydrogeology of the primary water source which they are fed by (Castaño *et al.*, 2018; Ramsar Convention Secretariat, 2010). Consequently, this creates conditions that promote high endemism and a rich biodiversity (Aldous and Bach, 2014; Kløve *et al.*, 2011). There has therefore been growing interest in how these ecosystems will be affected by groundwater abstraction. Each GDE also has specific hydrological requirements that are a function of depth, water quality and quantity, as well as flow dynamics (Custodio, 2000; Rohde *et al.*, 2017). Any stress-inducing alterations to the groundwater regime will alter the ecosystem's structure and function by reducing the growth, recruitment and productivity of the affected vegetation (Glanville *et al.*, 2023).

The manner in which GDes depend on groundwater is unique to each ecosystem and is often reflected by the biodiversity dynamics that are characteristic of each ecosystem (Rohde *et al.*, 2017). The extent of groundwater dependence varies and can be observed at different spatial and temporal scales (Aldous and Bach, 2014). The spatial extent of dependence can vary at large scales between biomes, regions and even continents, but it can also be highly localized at fine scale (Colvin *et al.*, 2002). The extent of dependence can also vary through time, being either perennial, seasonal or intermittent (Colvin *et al.*, 2002; Kløve *et al.*, 2011). However, the complexity of these ecosystems often means that the exact nature of groundwater dependency is only realized once an ecosystem has been stressed beyond its range of tolerance of change (Colvin *et al.*, 2009; Kløve *et al.*, 2011). Therefore, it is important to work with parameters that encapsulate the ecohydrological complexities of each ecosystem when investigating how they will be affected by changes in groundwater availability.

Figure 1.1. Classification of aquifer-dependent ecosystems and where they could potentially be located within a landscape. Classification and description by (Colvin *et al.*, 2007) for the Water Research Commission.

The current study focuses specifically on wetlands, which can be highly isolated in rainfall limited regions, with an important influence on hydrology and biodiversity in semi-arid regions. Wetlands are habitats that experience some degree of inundation which is caused either by an accumulation of surface water or discharge of groundwater to the surface (Collins, 2006). Those that have a primary source of water from an aquifer are classified as aquifer dependent ecosystems (ADEs) (Colvin *et al.*, 2007), distinguishing them from other GDEs which may have primary water sources from rainfall or other water sources (Colvin *et al.*, 2007; Rohde *et al.*, 2017). Aquifer-dependent wetlands usually occur as part of larger wetlands that may sometimes have a different hydrological regime (Custodio, 2000). These wetland systems often form a gradient of dry to wet areas (Malan *et al.*, 2015), the wettest core area being dependent on a permanent source of water, such as an aquifer (Custodio, 2000).

1.2 Interaction between wetland hydrology and wetland vegetation

The hydrological characteristics of a wetland are critical in shaping the composition and function of wetland ecosystems (Collins, 2006; Yan *et al.*, 2020). This makes wetland habitats an ideal setting to study the interaction between vegetation and the hydrological regime. These interactions provide insights into how hydrological conditions influence the establishment and persistence of niches and therefore also drive community dynamics (Konar *et al.*, 2013). These interactions are also more prominent on a local scale where plant distribution patterns are primarily influenced by local environmental factors. In wetland ecosystems, particularly those that experience seasonal flooding, the hydrological characteristics that influence vegetation are water depth and hydroperiod (Goslee *et al.*, 1997; Konar *et al.*, 2013). The hydroperiod refers to the duration, depth and frequency of inundation (Bartholomew *et al.*, 2020; Brinson, 1993; Goslee *et al.*, 1997); it essentially accounts for the seasonal changes in the amount of water flowing in and out of the ecosystem. The hydroperiod is directly influenced by the water source that supports the wetland, and since the water source will shape the landscape within which a wetland is found, the hydroperiod will also significantly influence the structural and functional characteristics of that wetland (Collins, 2006; Yan *et al.*, 2020).

Any alteration to a wetland's hydroperiod will have an impact on vegetation dynamics, influencing both temporal and spatial distribution patterns (Collins, 2006; Yan *et al.*, 2020). Water level depth and fluctuations, which are key aspects of the hydrological regime, significantly affect the growth of wetland vegetation and contribute to varying patterns across different wetland types (Orsholm and Elenius, 2022; Yan *et al.*, 2020). This is because individual species have different tolerance ranges for water levels, often adapting to specific conditions within that range (Orsholm and Elenius, 2022; Yan *et al.*, 2020). Consequently, one of the most defining features of wetland vegetation is the way communities are structured along hydrological gradients (Gaberščik *et al.*, 2018; National Research Council, 1995; Orsholm and Elenius, 2022; Sandi *et al.*, 2019; Silvertown *et al.*, 1999). Vegetation-hydrology interactions can be complex – they can exist in a feedback loop where the hydrological regime determines species composition and distribution (Malan *et al.*, 2015) while the vegetation can also alter the hydrology by decreasing water levels and flow (National Research Council, 1995). Quantification of hydrological thresholds that are a combination of the hydrological requirements of individual species and the characteristics of the hydroperiod (Saco *et al.*, 2020; Sandi *et al.*, 2019) can help us to better understand these interactions on a site-by-site basis.

All wetland plants are adapted to some degree of seasonal inundation; however, individual species are adapted to different periods of inundation. (Araya, 2007; Malan *et al.*, 2015). Additionally, each community is maintained by a specific set of hydrological conditions. If these conditions are disrupted both the structure and function of the ecosystem will be altered (Araya and Walker, 2009; Saco *et al.*, 2020). Individual plants adopt different ecological and physiological strategies that contribute to their success within a specific tolerance range (Zelnik and Čarni, 2008). The common mechanism is a trade-off for tolerance for either soil aeration stress or soil drying stress (Silvertown *et al.*, 1999). Stress-tolerance adaptations are witnessed in waterlogged conditions and competitive ability is more prevalent in the drier sites (Gaberščik *et al.*, 2018). Species tolerate water-related stress differently and will therefore respond differently to waterlogging and drought induced stress (Born and Linder, 2018; Sand-Jensen *et al.*, 2022; Zelnik and Čarni, 2008). Plants found in waterlogged conditions evolve morphological adaptations that enable them to either avoid or tolerate anoxia through structures (e.g. aerenchyma) that still facilitate oxygen exchange even when under waterlogged conditions (Araya, 2007). Similarly, plants found in drought-stressed conditions must evolve morphological adaptations to deal with low soil water potentials, such as xylem resistance to embolism (West *et al.*, 2012), as well as manage a trade-off between water conservation and carbon acquisition (Born and Linder, 2018; McDowell *et al.*, 2008; Skelton *et al.*, 2015) Plants may also adopt various methods of water acquisition to alleviate surface soil drought, for example deep roots, fog or dew uptake and hydraulic lift (Colvin *et al.*, 2002; Hawkins *et al.*, 2009; Skelton *et al.*, 2023; West *et al.*, 2012)

1.3 Hydrological niches and hydrological niche segregation

Hydrological niche segregation (HNS) is a concept initially brought forth by Silvertown *et al.* (1999). The concept was originally developed in English Meadows by demonstrating how fine-scale hydrological gradients create hydrological niches which promote species co-existence in species-rich habitats. HNS was based on species exhibiting a trade-off between drought and flooding tolerance, and that their response to either condition could be estimated from the range of hydrological conditions of their respective habitats(Silvertown *et al.*, 1999). The findings of the initial study have since been expanded to understand species coexistence in a diversity of habitats, including but not limited to alluvial meadows (Zelnik and Čarni, 2008), forests (Bonetti *et al.*, 2017) and fynbos (Araya *et al.*, 2011).

Hydrological niche segregation assumes that species are distributed within a hydrological niche that exists between two environmental axes. One axis represents soil aeration stress induced by waterlogged conditions whilst the second axis represents soil drying stress induced by drought conditions (Silvertown *et al.*, 1999). These axes are calculated using an index known as the sum exceedance value (SEV). These SEVs define the hydrological niches that species occupy due to their tolerance for soil aeration stress and soil drying stress (Araya, 2007). The SEVs incorporate fluctuations in water levels, changes in water table depth and duration that surface soils are flooded (see Figure 1.2a) (Araya, 2007; Borde *et al.*, 2020; Orellana *et al.*, 2012), in order to evaluate the influence of the hydrological regime on vegetation (Borde *et al.*, 2020). The method relies on two threshold values that are calculated for each of the two environmental axes between which the hydrological niche exists (see Figure 1.2b). The first threshold is for the depth at which soil conditions trigger aeration stress (Araya, 2007), which is usually the depth at which soils become waterlogged. Responses to waterlogging stress are often triggered at depths when air-filled pore space < 10% of total soil volume (Araya, 2007; Araya *et al.*, 2011; Silvertown *et al.*, 1999). The second threshold is for the depth at which soil drying becomes detectable by plants (Araya, 2007), which is any depth that gives 5kPa tension at the soil surface (Araya, 2007; Araya *et al.*, 2011; Silvertown *et al.*, 1999).

The SEVs indicate the degree to which the water table depth exceeds each threshold (Araya *et al.*, 2011; Orellana *et al.*, 2012; Silvertown *et al.*, 1999). Each calculation uses field measurements made over the duration of a specified hydrological period, which often coincides with the growth season of a site (Borde *et al.*, 2020; Orellana *et al.*, 2012). The hydrological conditions that meet each threshold are specific to a site which makes SEV calculations applicable in a diverse range of ecosystems, from the English meadows in the groundbreaking study by Silvertown *et al.* (1999) to the fynbos of the Cape Floristic Region (Araya *et al.*, 2011; Ayuk *et al.*, 2019; Guo *et al.*, 2015). The SEV has had practical applications in ecological restoration, where it has been used to delineate and characterize spatial distribution of vegetation zones (Diefenderfer *et al.*, 2013), as well as to predict the presence of both native and invasive species at a site (Borde *et al.*, 2012).

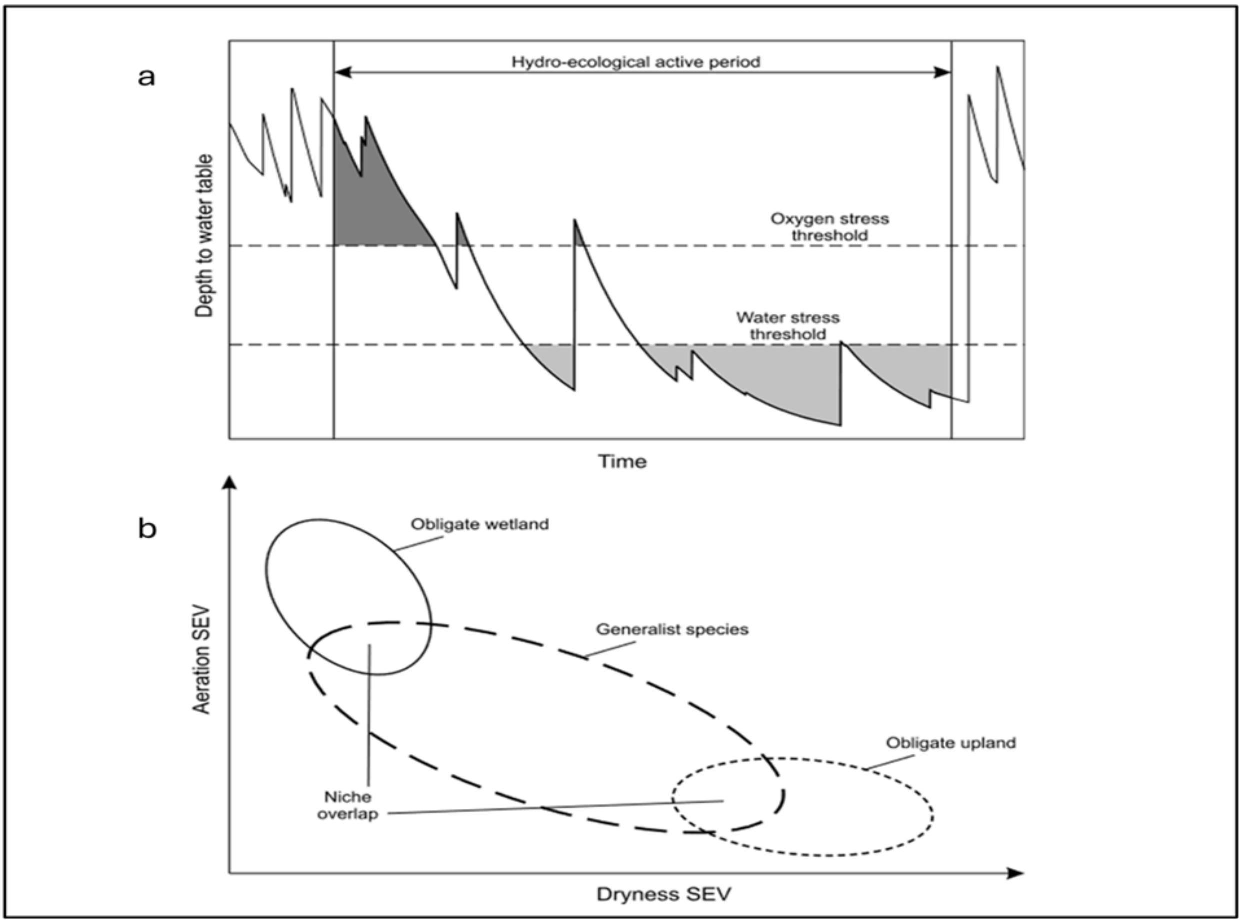

Figure 1.2. Description of the variables (depth, time, thresholds) when calculating the sum exceedance value (top figure, and the exes produces from those calculations (bottom figure) (Orellana *et al.*, 2012).

1.4 Wetlands under threat

Wetlands, including those that are not GDEs, are highly productive ecosystems. Most wetland ecosystems have a unique biodiversity which contributes to their ecological, social, and economic benefits (Dalu and Wasserman, 2022). These benefits are known as ecosystem services.

Unfortunately, these ecosystem services render wetland ecosystem even more vulnerable to a wide array of threats that are caused by anthropogenic activities (Magee and Kentula, 2005; Thamaga *et al.*, 2022) and climate change (Kløve *et al.*, 2014). Most of these threats have been ongoing for decades and approximately 35% of wetlands have been lost globally since the 1970s (Eyvaz and Albahnasawi, 2023). As a result, most wetlands present today are fragments of what were once intact and vast wetland habitats (Eyvaz and Albahnasawi, 2023) The fragility of these ecosystems, mounting pressures and threats, as well as the low protection status they are assigned, increase the risk of more losses over the next coming years. In South Africa, wetland habitats have been reduced by approximately 50-64%, with the remaining covering just about 2.4% of the land surface (Adeeyo *et al.*, 2022; Department of Forestry, Fisheries and the Environment, 2021). The threats to wetlands continue to increase due to mismanagement and a lack of conservation urgency. According to Department of Forestry, Fisheries and the Environment (2021), only 11% of South Africa's wetlands are protected, 48% are Critically Endangered, 12% are Endangered, 5% are Vulnerable, and 35% are Least Threatened. This makes wetlands one of the most threatened yet least protected ecosystems in South Africa (Skowno *et al.*, 2019). Without a protection status, wetlands continue to be even more vulnerable to degradation, which may be exacerbated by unregulated development and unsustainable use of the associated ecosystem services (Thamaga *et al.*, 2022).

Particularly concerning is the increasing focus on groundwater abstraction in South Africa. Plans to increase bulk water supply from the Table Mountain Group Aquifer (City of Cape Town, 2021; TMG Aquifer Alliance, 2019) have the potential to impact aquifer-dependent wetlands in the Western Cape. The most prominent example of the long-term effects of groundwater abstraction on ecosystems from the aquifer comes from long-term studies on the Klein Karoo Rural Water Supply Scheme (KKRWSS). Cleaver *et al.*(2003) found that continued abstraction resulted in either permanent or temporary drying of groundwater-fed springs in the Little Karoo. The drying of springs affected vegetation community dynamics and increased the risk of extinction of the Cape Mountain Zebra as it's natural water sources became scarce. Results from the KKWRS reports have raised concerns over what can be regarded as sustainable volumes of water that can be abstracted. Adding to the apprehension on abstraction of the TMGA is that most of the literature available focuses on testing water quality and understanding the geohydrology of the aquifer, with little emphasis on the ecological impacts of abstraction on ecosystems. The findings of Cleaver *et al.*(2003) emphasize the importance of improving our knowledge on species response to hydrological conditions. Knowing this might help us anticipate the potential impacts of groundwater abstraction on ecologically sensitive ecosystems, like those found in Steenbras Nature Reserve, and ensure that we have appropriate response measures to maintain and conserve the biodiversity of these ecosystems (Ewart-Smith and Boucher, 2019; Magee and Kentula, 2005).

1.5 Study aims, objectives and predictions.

1.5.1 Study Problem

The combined effects of water-scarcity, increase in drought occurrence because of climate change and urbanization have increased the pressure and demand on water sources. In situations where groundwater abstraction is seen as being a viable and a potential source of bulk water supply, it is important to understand how doing so can affect the local biodiversity and functioning of ecosystems that depend on that groundwater.

1.5.2 Aim and key questions

The aim of this study was to explore the influence of a fine-scale hydrological gradient on species composition and distributions in an aquifer-dependent fynbos wetland, in order to provide an improved understanding of vegetation sensitivity to groundwater abstraction.

I asked the following questions:

1. How does wetland vegetation community composition change during post-fire succession?
2. Is wetland community composition structured spatially across a hydrologically diverse wetland?
3. Can the hydrological niche concept explain species distributions within this ecosystem?
4. Can species' sensitivity to groundwater be ranked in order to improve monitoring and risk assessment?

1.5.3 Hypotheses

I hypothesized that that there would be:

1. a clearly defined post-fire successional trajectory, with age since fire being the key variable explaining these changes.
2. segregation of species into distinct niches along the hydrological gradient that persists through successional time.

2 Methods

2.1 Study site

The vegetation surveys and soil moisture data were collected from a wetland that has been designated as an ecological monitoring site as part of the Table Mountain Group Aquifer Ecological and Hydrogeological Monitoring project. The study site (Figure 2.2) is a perennial inland wetland that is approximately 1300 square meters in extent (Musungu *et al.*, 2024). The hydrology of the wetland fluctuates such that it is wettest at its centre (T1_SM4, T2_SM2-4) and the lower areas next to the stream (T3) (Figure 2.1 B and C).). It is an aquifer-dependent wetland that is fed by the Skurweberg formation of the Nardouw Aquifer, which forms part of the larger Table Mountain Group Aquifer (City of Cape Town, 2021). The wetland is situated south of the upper Steenbras Dam within the Steenbras Nature Reserve (SNR) (Musungu *et al.*, 2024); the reserve is a part of the protected areas that make up the Kogelberg Biosphere Reserve. There are five fynbos vegetation types that have been identified within the reserve (Figure 2.2). The most prominent vegetation type is the critically endangered Kogelberg Sandstone Fynbos. This vegetation type is characterized by low, closed shrubland and scattered emergent tall shrubs, and is dominated by proteoid, ericoid and restioid fynbos species (City of Cape Town, 2011). The Cape Winelands Shale Fynbos is the second most prominent vegetation type in the reserve and is classified as Vulnerable. This vegetation is classified by moderately tall and dense shrublands, dominated by proteoid and other closed-shrub fynbos (City of Cape Town, 2011). Present in much smaller patches are the Critically Endangered Elgin Shale Fynbos that occurs in the dam, the Western Coastal Shale Band vegetation as well as Boland Granite Fynbos (City of Cape Town, 2011). The wetland is inhabited by several common fynbos families, including, *Restio versatilis, Erica serrata, Berzelia alopecuroides, Erica intervallaris, Erica campanularis, Grubbia rosmarinifolia and Tetraria thermalis* (City of Cape Town, 2021; Musungu *et al.*, 2024).

The reserve is vulnerable to a variety of threats, and most of the ecosystems associated with the vegetation types mentioned above are threatened (Figure 2.2, right). The wetland is specifically threatened by potential groundwater abstraction, because it is an aquifer-dependent system that is in proximity to the Steenbras Wellfield that is located within the reserve (City of Cape Town, 2011; Musungu *et al.*, 2024). The Wellfield is situated in the Steenbras River basin, next to the Steenbras Dam, into which the water from the wellfield will be pumped (Steyn, 2023). After the drought that occurred from 2015-2018, plans to develop and upgrade various wellfields were fast-tracked, including the Steenbras Wellfield (TMG Aquifer Alliance, 2019; City of Cape Town, 2021).

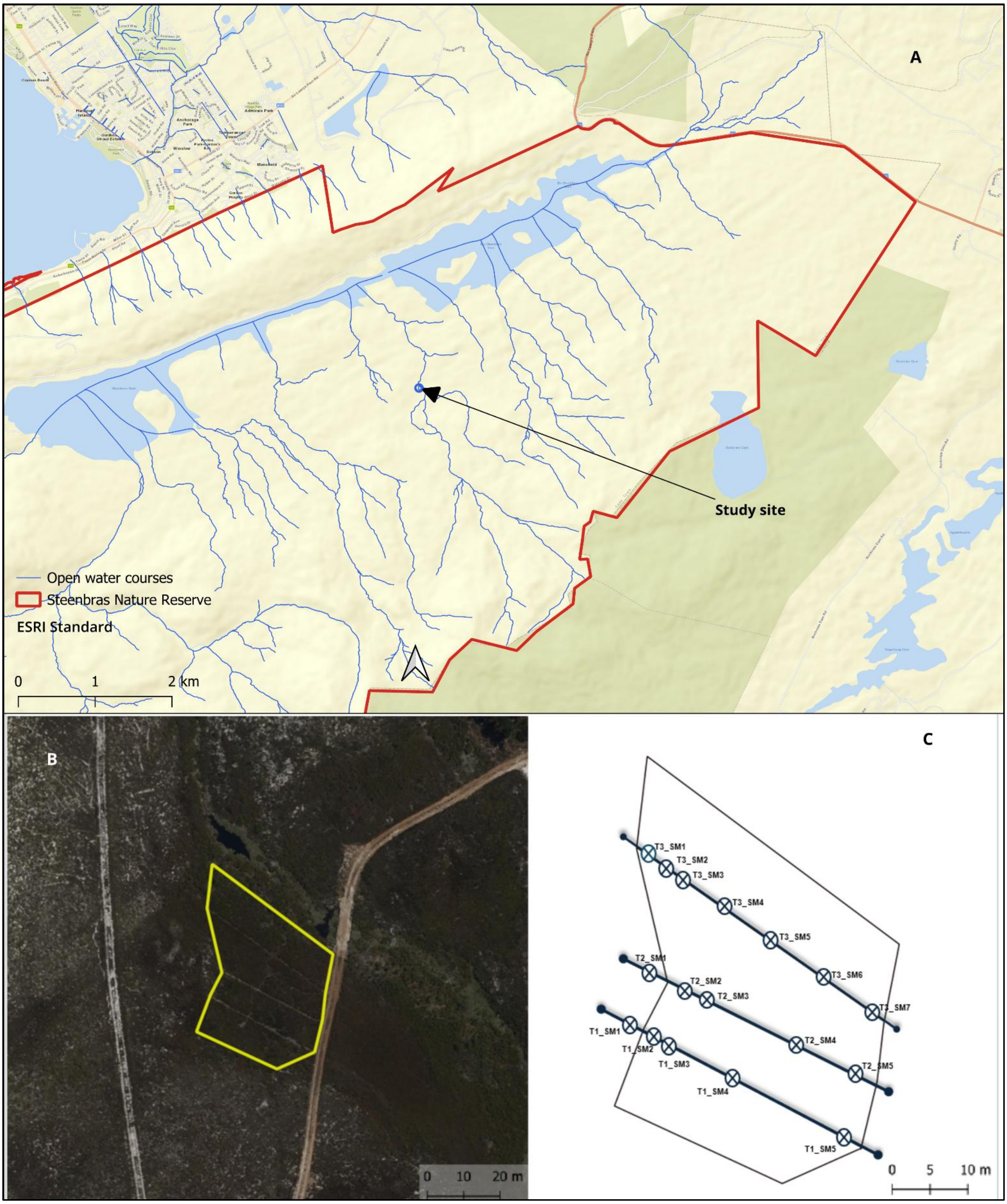

Figure 2.1. A: Location of the study site inside Steenbras Nature Reserve, also known as H83B for monitoring purposes. B: an outline of the wetland site C: position of the transects and soil moisture probes used in the collection of vegetation and soil moisture data, T = transect , SM = Soil moisture probe.

The Steenbras Wellfield will extract water from the Nardouw Subgroup of the aquifer, which is made up of the Goudini, Skurweberg and Rietvlei formations (City of Cape Town, 2021; Colvin *et al.*, 2009; Steyn, 2023). This part of the aquifer is characteristically shallow and smaller in thickness in comparison to Peninsula portion of the TMGA (Aston, 2007; City of Cape Town, 2021; Colvin *et al.*, 2009). Generally, shallow and unconfined aquifers are more likely to be sensitive to changes in groundwater levels (Kløve *et al.*, 2014). When abstraction happens from these types of aquifers, the concern is that the impacts will also affect ecosystems that are not directly at the site of abstraction (Aston, 2007). The location of the wetland (Figure 2.1A) on the south side of the upper Steenbras dam, makes it an ideal ecological monitoring point for ecosystem responses to potential groundwater abstraction.

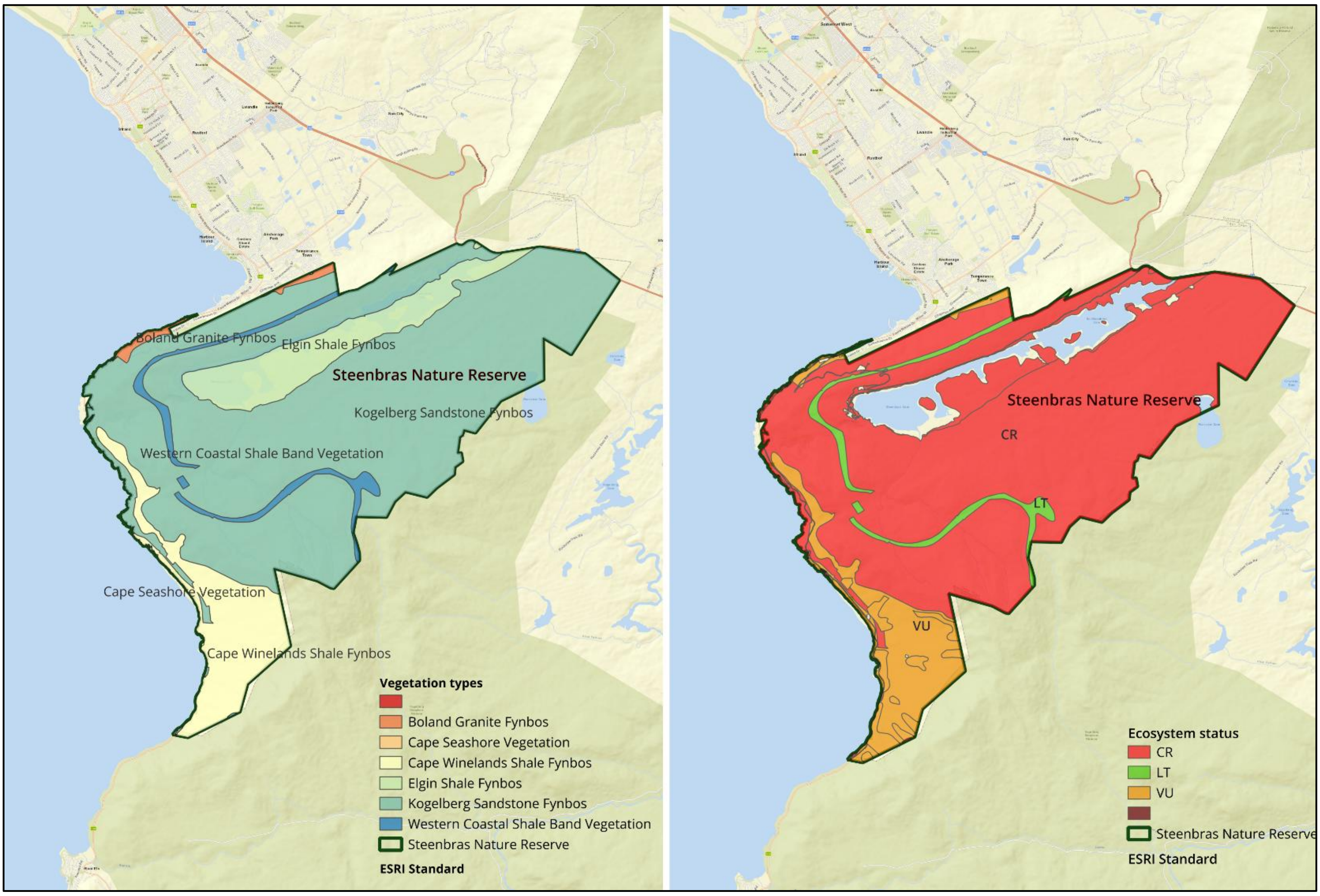

Figure 2.2. The extent and distribution of the vegetation types of Steenbras Nature Reserve as well as their RedList status, according to the City of Cape Town.

2.2 Data collation

Vegetation surveys were conducted as part of the long-term monitoring programme by TMG Aquifer Alliance (2019) and City of Cape Town (2021) every spring (October) from 2011 to 2022. Data were not collected in 2014, 2015 and 2021 due to contractual issues. Three transects were laid out at the wetland and 1x1m^2 plots were placed along the length of each transect. The abundance of plant species in each plot was recorded as a percentage cover in each year. The wetland has burnt twice. The first fire was in 2009, which affected vegetation that were in the plots along the boundary of the wetland (City of Cape Town, 2021); the second was in April of 2022, which completely burnt down the entire site. Soil moisture data were collected during the hydrological year, which ran from October to September of the following year, ending before the Spring period when vegetation surveys were conducted. The soil moisture was expressed as volumetric water content (VWC), which was measured monthly from soil moisture probes. The VWC measurements were taken at 10cm depth intervals, either up to maximum 1m or the greatest depth that the probe could be installed. There were 17 soil moisture probes – five each in the first and second transect, and seven in the third transect. The point where a probe was installed depended on whether the stratum allowed for the probe to be installed to a depth of 1m, and depth varied from 80cm to 1m.

2.3 Data analysis

The analysis was done in two parts – the first analysis describes the relationship between plant communities with respect to time since fire, and the second part links the distribution patterns of species to volumetric water content as the hydrological variable. The first analysis was done using non-parametric multivariate and univariate tests in PRIMER-e (version 6.1.6) (Clarke *et al.*, 2014; TMG Aquifer Alliance, 2019). The second part of the analysis was done in the R statistical environment (version 4.3.2).

2.3.1 Post-fire succession patterns

2.3.1.1 Relationship between vegetation of different ages post-fire

I ran a one-way ANOSIM (analysis of similarity) test that assessed the strength and significance of the differences between immediate post-fire vegetation with mid to late post-fire vegetation. The ANOSIM test is a non-parametric permutation test that checks for differences in species composition and abundance between subsequent years by using the Bray-Curtis similarity coefficient on species abundance data, such as percent cover. It runs a test statistic R^2, that represents some degree of differentiation in species composition between years. The R^2 value ranges between 0 and 1, with 0 representing years that are similar and 1 representing years that are dissimilar. For this study, I used the same metrics for R^2 that were used by TMG Aquifer Alliance (2019): $R^2 < 0.3$ = no differences, $0.65 > R^2 > 0.5$ = weak differences and $R^2 > 0.7$ = strong differences.

I then ran a SIMPER (similarity breakdown procedure) routine for all pairs of years where the pairwise tests from the ANOSIM showed that there were significant differences between those years. The SIMPER routine identified species and their contribution to the dissimilarity between years by disaggregating the similarities in the Bray-Curtis similarity matrix that the ANOSIM runs on (Clarke *et al.*, 2014). The SIMPER routine produced two lists. The first list consisted of species that characterize the community composition for each year. The list also showed the average contribution of each species to the total average similarity, its average abundance as well as the ratio

$\frac{average\ similarity}{\substack{standard\ deviation \\ of\ the\ sample\ pairs\ that\ make\ up\ the\ average\ dissimilarity}}$ or $\frac{SIM}{SD}$ (Clarke *et al.*, 2014).

The second list consisted of species which were responsible for the differences between years. This list also showed the average abundance for each species in the two years being compared, the average contribution of each species to the total average dissimilarity, as well as the ratio

$\frac{average\ dissimilarity}{\substack{standard\ deviation \\ of\ the\ sample\ pairs\ that\ make\ up\ the\ average\ dissimilarity}}$ or $\frac{DISS}{SD}$ (Clarke *et al.*, 2014).

The species that the SIMPER produced as key contributors to the differences observed between years were selected based on two values, the average contribution to the total average dissimilarity as well as the values of $\frac{SIM}{SD}$. The former shows which species contribute to the dissimilarity whereas the latter shows which ones do so consistently (Clarke *et al.*, 2014). The more practical and preferred value is the standard deviation ratio, which generally ranges from 0.5-10 but can also be greater than 10. The values of $x > 1.5$ are considered to contribute meaningfully and values of $x < 1.0$ are considered insignificant (Clarke *et al.*, 2014; TMG Aquifer Alliance, 2019).

I then ran a CLUSTER analysis to show when and where changes in species composition and abundance, as mean percent cover, occurred between vegetation of different ages post-fire. I started by performing a square-root transformation on the data to ensure an inclusive contribution from both rare and common species when the Bray-Curtis similarity coefficient was automatically applied in the next step. The transformed data was then used to run a hierarchical agglomerative CLUSTER analysis using the group-average linkage option, recommended by Clarke *et al.* (2014) for its ability to segregate groups with distinct community structure. The CLUSTER analysis treated each year as an individual cluster; the clusters were grouped or separated from each other based on the similarities between species composition and abundance between the two years being compared. (Clarke *et al.*, 2014). The CLUSTER was run simultaneously with a SIMPROF (similarity of profile) routine, a test applied to assess whether there is a significant structure within a set of samples (Clarke *et al.*, 2008). The null hypothesis of the SIMPROF is that species distribution patterns are homogenous across years and is based on the assumption that each year does not have a pre-existing structure, (Clarke *et al.*, 2014, 2008). These two tests produced a dendrogram which showed which years were alike, in terms of vegetation composition and distribution, at $p<0.05$ of the SIMPROF test (Clarke *et al.*, 2014, 2008).

2.3.1.2 Identifying community structures and species composition

I ran a CLUSTER analysis that broke down vegetation composition from each year - 2011, 2012, 2013, 2017, 2018, 2019, 2020 and 2022 - into distinct communities that were present in the wetland. The first step was to perform a square-root transformation to the data, to ensure evenness and contribution from both common and rare species when the Bray- Curtis similarity coefficient was applied (Clarke *et al.*, 2014). I then ran a hierarchical agglomerative CLUSTER analysis using the species-average linkage option (Clarke *et al.*, 2014; Clarke and Warwick, 2001). The CLUSTER analysis treats each plot as an individual "cluster"; the plots will be grouped together to form a community based on the Bray-Curtis similarity coefficient on patterns of species composition and percent cover (Clarke *et al.*, 2014; Clarke and Warwick, 2001). The CLUSTER analysis required a similarity threshold - an arbitrary value which restricts the similarity between clusters (Clarke *et al.*, 2014). The threshold was selected in accordance with the transformation method used and suitability to this ecosystem (Clarke *et al.*, 2014). I set the similarity threshold at ≥40% for this study, similar to what was used by TMG Aquifer Alliance (2019).

This CLUSTER analysis was also run simultaneously with the SIMPROF routine to check for groups of plots. These two tests produced a dendrogram that shows which sample plots were alike at $p<0.05$ of the SIMPROF test as well as the similarity threshold (Clarke, Somerfield and Gorley, 2008; Clarke *et al.*, 2014; Jack *et al.*, 2019). The SIMPROF assigns each plot a factor level, and plots that form part of one cluster will have the same factor level (Clarke and Gorley, 2015). If individual clusters of sample plots aggregated into a larger cluster within the similarity threshold of ≥40% and the same species contributed comparably to the total average within group similarity of the individual clusters, the sample plots of the smaller individual clusters were merged to represent one group (TMG Aquifer Alliance, 2019). The SIMPER routine was used to identify species that are characteristic of each community as well as those that were responsible for dissimilarity between communities.

2.3.2 Testing the hydrological niche

2.3.2.1 Establishing the hydrological niche at Steenbras

I worked with soil moisture data from six hydrological years – 2012, 2013, 2017, 2018, 2019 and 2020. These years were selected because they had unbroken records of soil moisture for the entire hydrological year, and corresponding vegetation surveys (see Table 2.1). I defined thresholds for conditions that would induce aeration or drought stress. This was informed by previous research that found that the range of VWC readings reflects the soil moisture conditions that the species can tolerate in the location where they are found (Silvertown *et al.*, 1999). The threshold for aeration stress was set as VWC≥40% at 10cm depth (i.e. a fully saturated soil profile with minimal gas diffusion). For each complete hydrological year, and for each probe, the number of days between two sampling points during which the threshold was exceeded were summed up and this would give the sum exceedance value for aeration stress (SEVa). The assumption with adding up the days in this manner is that the soil moisture conditions between two sampling points remain constant. The same procedure was followed to calculate the sum exceedance value for soil drying stress (SEVd). The difference was the threshold for soil drying stress, which was defined as VWC≤30% at 30cm depth. The depth was selected based on findings of (City of Cape Town, 2021), where two combined soil moisture parameters, namely duration of saturation and minimum soil saturation over an annual period at 20-30cm accounted for 38% of the variability in vegetation. Thus, for each hydrological period, I calculated an SEVa and SEVd for each probe. The distribution of each probe within the two SEV axes demarcates the shape of the hydrological niche and the potential space where species might be found.

Table 2.1. The setup for the soil moisture and vegetation data that was available for use in the analysis. Table adapted from City of Cape Town (2021).

Hydrological year	**Year**	**Vegetation data**
October 2011- September 2012	2012	Spring 2012
October 2012- September 2013	2013	Spring 2013
October 2016- September 2017	2017	Spring 2017
October 2017- September 2018	2018	Spring 2018
October 2018- September 2019	2019	Spring 2019
October 2019- September 2020	2020	Spring 2020

2.3.2.2 Species selection

The vegetation data that I used was collected in the spring after the hydrological year ended (see Table 2.1). In order to maintain full representation of species in each community whilst also ensuring that the data will highlight the vegetation's sensitivity to soil moisture conditions, I worked only with a subset of vegetation plots that were within 2m of the soil moisture probes , as also recommended by City of Cape Town (2021). Common species were defined as those occurring in four or more years over the succession period. Using these common species allowed for a focus on the most stable ecological indicators which are likely to persist in a given hydrological niche due to their physiological and competitive performance in specific hydrological conditions, whereas species that are only present briefly during succession may be influenced by transitional conditions and stochastic events.

2.3.2.3 Classifying species' hydrological niche

I used the Principal Component Analysis to determine the location of a species in the hydrological niche as well as the range of each species niche. The PCA identified the longest axis of variation within the two-dimensional space defined by the SEVa and SEVd axes. The results of the PCA were used to order species from those that are tolerant of dry conditions to those that are tolerant of waterlogged conditions. They were ordered on the increasing PC1 values - an increase of values from negative to positive demonstrates change from species that occupy dry to wet areas along the hydrological gradient. These species were then classified into four groups, using the same classification made by Malan *et al.* (2015) and adapted by City of Cape Town (2021). These are: 1) obligate wetland species that almost always grow in wetlands and rarely occur in non-wetland areas 2) facultative wetland species that usually grow in wetlands but also occur in non-wetland areas; 3) facultative dry species that usually grow in non-wetland areas but sometimes grow in wetlands and 4) dry species that almost always grow in drylands. I then compared the results of the classification based on the PCA analysis with habitat descriptions from Manning and Goldblatt (2012), and wetland affiliation from Van Ginkel and Hitchcock (2011) and TMG Aquifer Alliance (2019). Working with this, I could conclude whether the way the SEV analysis was used in this study could also be used to pick out potential indicator species.

3 Results

3.1 Post-fire succession patterns

3.1.1 Relationship between vegetation in different post-fire succession stages

The results of the global ANOSIM test (R^2 = 0.198, p<0.01) showed that overall, from 2011-2022, when assessing species composition and abundance, the vegetation at the wetland remained relatively stable over time as indicated by a low R^2 value (that is, low dissimilarity) (Table 3.1). Despite this, successional changes as well some differences in species composition and abundance were observed when comparing vegetation that was burnt in two separate fire cycles. There were significant yet weak differences between the immediate post-fire vegetation (2022) with the early to intermediate post-fire vegetation (2011-2013) – $R^2>0.4$ and $p<0.01$. The differences in species composition and distribution between vegetation from the earlier years when compared to that from 2022 became significantly stronger as the vegetation became more mature, especially from 2017 - 2020 ($0.65>R^2>0.5$, $p<0.01$). The strongest differences between vegetation of different ages post fire were observed in 2017 and 2018 (R^2 = 0.59 and 0.589 respectively, $p<0.01$), and the weakest difference was in 2016 ($R^2=0.395$, $p<0.01$) (Table 3.1).

Table 3.1. Global and Pairwise Tests from ANOSIM showing the strength (R^2) of the differences in species composition and abundance between vegetation of different ages post-fire as well as the significance of those differences. 2022 was compared with previous years because it represents a community from a new fire cycle, separate from 2011-2020

Global Test
Sample statistic (Global R): 0,198
Significance level of sample statistic: 0,001
Number of permutations: 999 (Random sample from a large number)
Number of permuted statistics greater than or equal to Global R: 0

Pairwise Tests

Groups	Dissimilarity R^2 Statistic	Significance Level
2022, 2011	0,479	p<0.01
2022, 2012	0,441	p<0.01
2022, 2013	0,487	p<0.01
2022, 2016	0,395	p<0.01
2022, 2017	0,59	p<0.01
2022, 2018	0,589	p<0.01
2022, 2019	0,556	p<0.01
2022, 2020	0,555	p<0.01

The results of the SIMPER (Table 3.2) showed that *Ehrharta rupestris, Erica campanularis, Restio leptostachyus* and *Cassytha ciliolata* were the primary contributors to changes in community composition over the observation period, with changes in their abundance increasing the dissimilarity in community composition between different years. *E. rupestris* increased in abundance towards the end of the observation period, especially in the immediate post-fire vegetation community (2022). *E. campanularis* increased in abundance from 2013 to 2020 but was absent in the immediate post-fire community (2022). The abundance of *R. leptostachyus* declined to zero by 2022 after fluctuating in previous years, while *C. ciliolata* appeared in 2017 and showed variable abundance in subsequent years, with a lower abundance in 2022 compared to earlier years. The SIMPER was conducted for 2012, however the Diss/SD < 1.5 (dissimilarity threshold value) for all species and they were therefore not included in the list in Table 3.2.

Table 3.2. List of species that contributed to the dissimilarity in plant communities between 2022 and each year between 2011-2020.

Year	Total Average Dissimilarity	Species	Average Abundance		Average Dissimilarity	Dissimilarity/ Std. Deviation
2022/2011	79.46		**2011**	**2022**		
		***Ehrharta rupestris* Nees ex Trin.**	0	3.58	8.41	1.7
2022/2013	74.57		**2013**	**2022**		
		***Erica campanularis* Salisb.**	4.73	0	6.70	1.6
		***Ehrharta rupestris* Nees ex Trin.**	0	3.58	5.39	1.9
		***Restio leptostachyus* Kunth**	3.34	0	4.99	1.5
2022/2017	77.85		**2017**	**2022**		
		***Erica campanularis* Salisb.**	4.61	0	7.55	1.5
		***Restio leptostachyus* Kunth**	3.82	0	6.38	1.7
		***Ehrharta rupestris* Nees ex Trin.**	0.03	3.58	6.00	1.9
		***Cassytha ciliolata* Nees**	2.24	0.44	3.36	1.5
2022/2018	77.40		**2018**	**2022**		
		***Erica campanularis* Salisb.**	4.76	0	7.39	1.6
		***Ehrharta rupestris* Nees ex Trin.**	0.11	3.58	5.60	1.9
		***Restio leptostachyus* Kunth**	3.42	0	5.44	1.6
		***Cassytha ciliolata* Nees**	3.14	0.44	4.57	1.8
2022/2019	75.97		**2019**	**2022**		
		***Erica campanularis* Salisb.**	4.87	0	7.33	1.6
		***Ehrharta rupestris* Nees ex Trin.**	0.12	3.58	5.50	1.8
		***Cassytha ciliolata* Nees**	2.73	0.44	3.80	1.7
2022/2020	75.61		**2020**	**2022**		
		***Erica campanularis* Salisb.**	5.17	0	7.64	1.7
		***Ehrharta rupestris* Nees ex Trin.**	0.15	3.58	5.34	1.8
		***Cassytha ciliolata* Nees**	2.81	0.44	3.84	1.8

The CLUSTER analysis showed that community composition differed between years (Figure 3.1). The SIMPROF test produced three distinct clusters of vegetation from different years that were grouped together because of a high similarity in species composition and abundance. The highest level of similarity in species composition and abundance was found in the first group, which was made up of vegetation data from 2019 and 2020, as seen by the red dashed lines connecting these years (Figure 3.1). Vegetation from these two years were also most similar and combined with vegetation from 2018 into one cluster. The second group was a cluster that was made up of vegetation from 2016 and 2017. The third group was a cluster made of vegetation from 2012 and

2013. The early post-fire years, 2022 and 2011, were outliers which did not form any significant structures with and were therefore significantly different from the vegetation of 2013-2020. Species composition and abundance remained stable from 2012-2020, as seen by the similarity and formation of one big group between these years and their separation from the 2011 and 2020 vegetation. The highest similarity between vegetation was between the more mature years – 2016-2020.

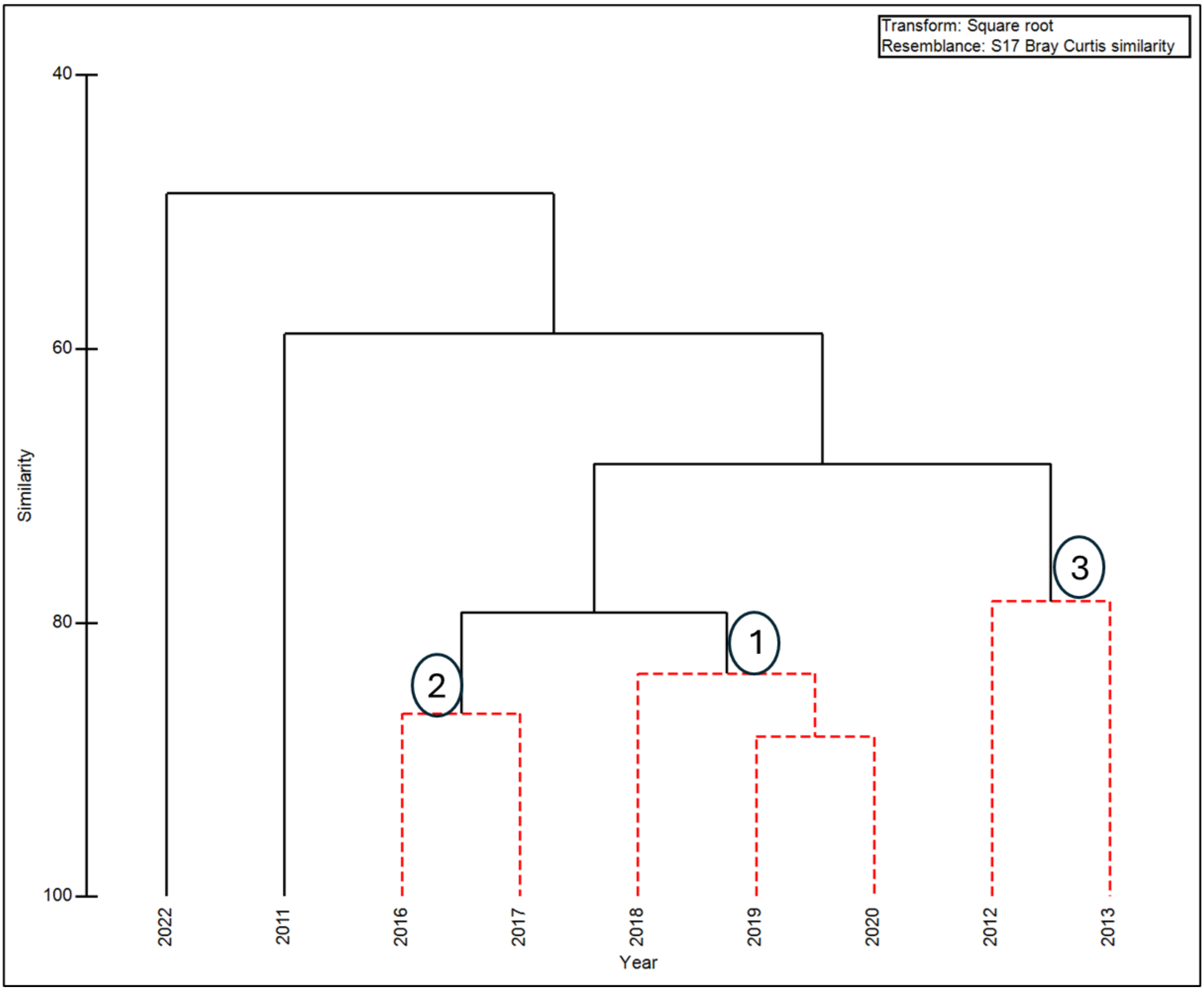

Figure 3.1. Hierarchical CLUSTER analysis displaying the relationship between vegetation of different ages-post fire, The 2022 vegetation is 6 months old post a 2022 fire and the 2020 vegetation is approximately 11 years old post a 2009 fire. Red dashed lines group vegetation whose structure was not separated at p<0.05 by the SIMPROF routine while the solid black lines separate vegetation that for which the null hypothesis of the SIMPROF test was rejected, signifying differences in species composition and abundance in those years.

3.1.2 Identifying community structures and species composition across the wetland for vegetation of different ages post-fire

For the years 2011, 2012, 2013, 2017, 2018, 2019, 2020 and 2022, each group formed by the CLUSTER analysis consisted of a combination of plots from either one, two or all three transects. Each group was formed as a result of the high similarity in species composition and abundance between those plots; these groups were representative of how the communities appeared in the wetland. (Figure 3.2). There were eight communities in 2020, an older post-fire vegetation, and seven communities in the immediate post-fire vegetation of 2022. In both years, the wettest plots (usually T3 and some T2), formed broader clusters, and thereby one big community. The drier plots (mostly T1 and edge of T2), were segregated into a larger number of smaller communities. The similarity in clustering patterns observed in both old (2020) and young (2022) vegetation suggests that there is an environmental gradient that separates species into distinct communities early during succession.

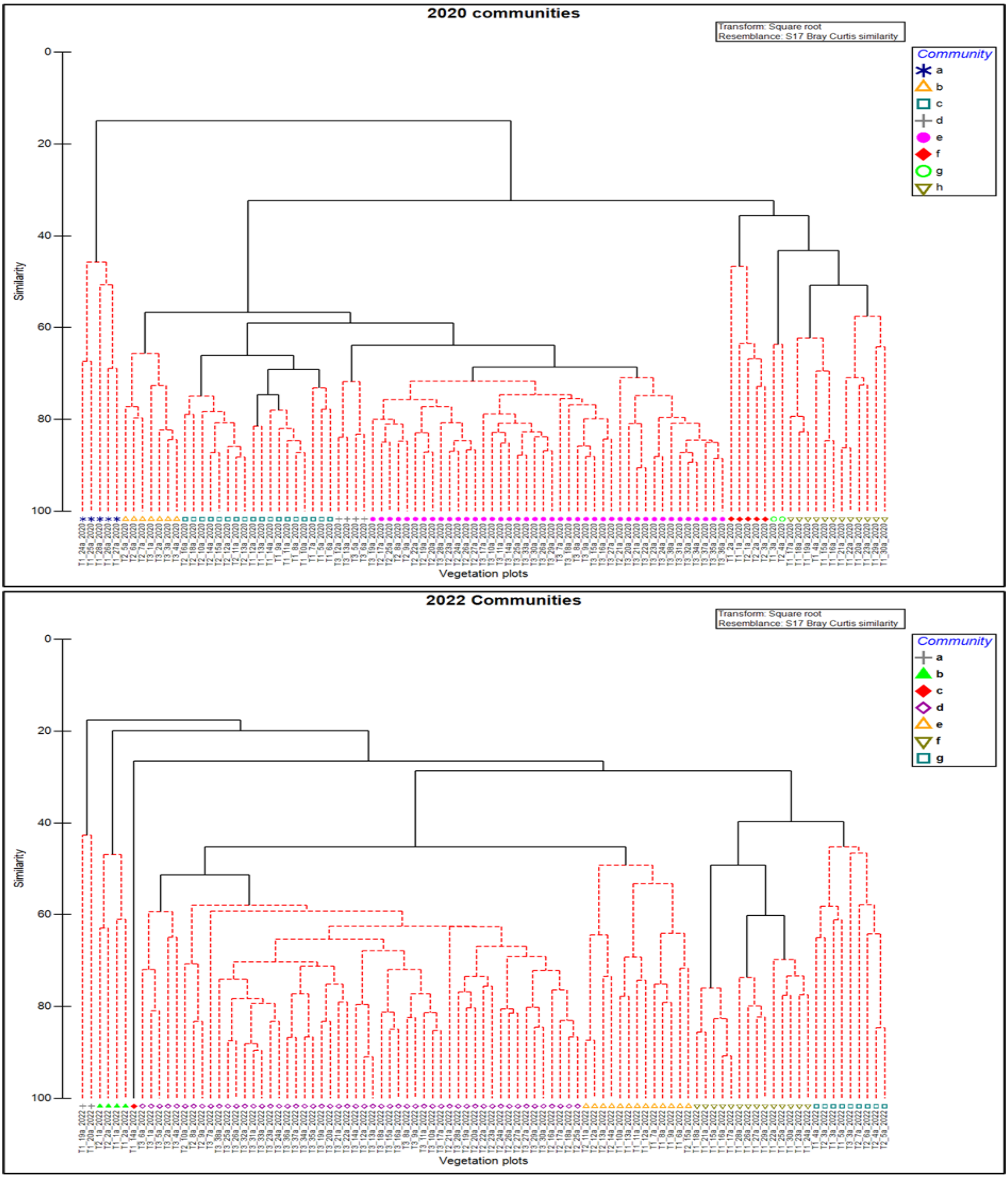

Figure 3.2: Hierarchical CLUSTER analysis displaying how communities clustered in young (2022) and old (2020) vegetation, using Bray-Curtis similarity of species composition and abundance. The symbols were superimposed to represent distinct communities. The red dashed lines in the dendrogram group vegetation plots for which the SIMPROF did not detect distinct clustering at $p<0.05$ of the SIMPROF routine; these plots form part of one community. The solid, black lines separate groups for which the null hypothesis of the SIMPROF test was rejected signifying differences in their structure, representing distinct communities.

3.2 Testing the hydrological niche

3.2.1 Calculating SEVa and SEV

Over the course of each hydrological year (Figure 3.3), there was spatial variation in volumetric water content as seen by differences in how and when changes in volumetric water content at each probe met the conditions of the threshold for either SEVa or SEVd. In most instances, for example, T1_SM1, VWC met the thresholds of both SEVa and SEVd, however this occurred at alternating days in the hydrological year. What was also noticeable is that conditions for SEVd were more prominent around the soil moisture probes in transects one (T1) and two (T2) whereas those for SEVa were more prominent in transect three (T3), except for T3_SM1 and T3_SM2 in 2011, and T3_SM4, T3_SM5 and T3_SM7 in 2016, which were drought recovery years.

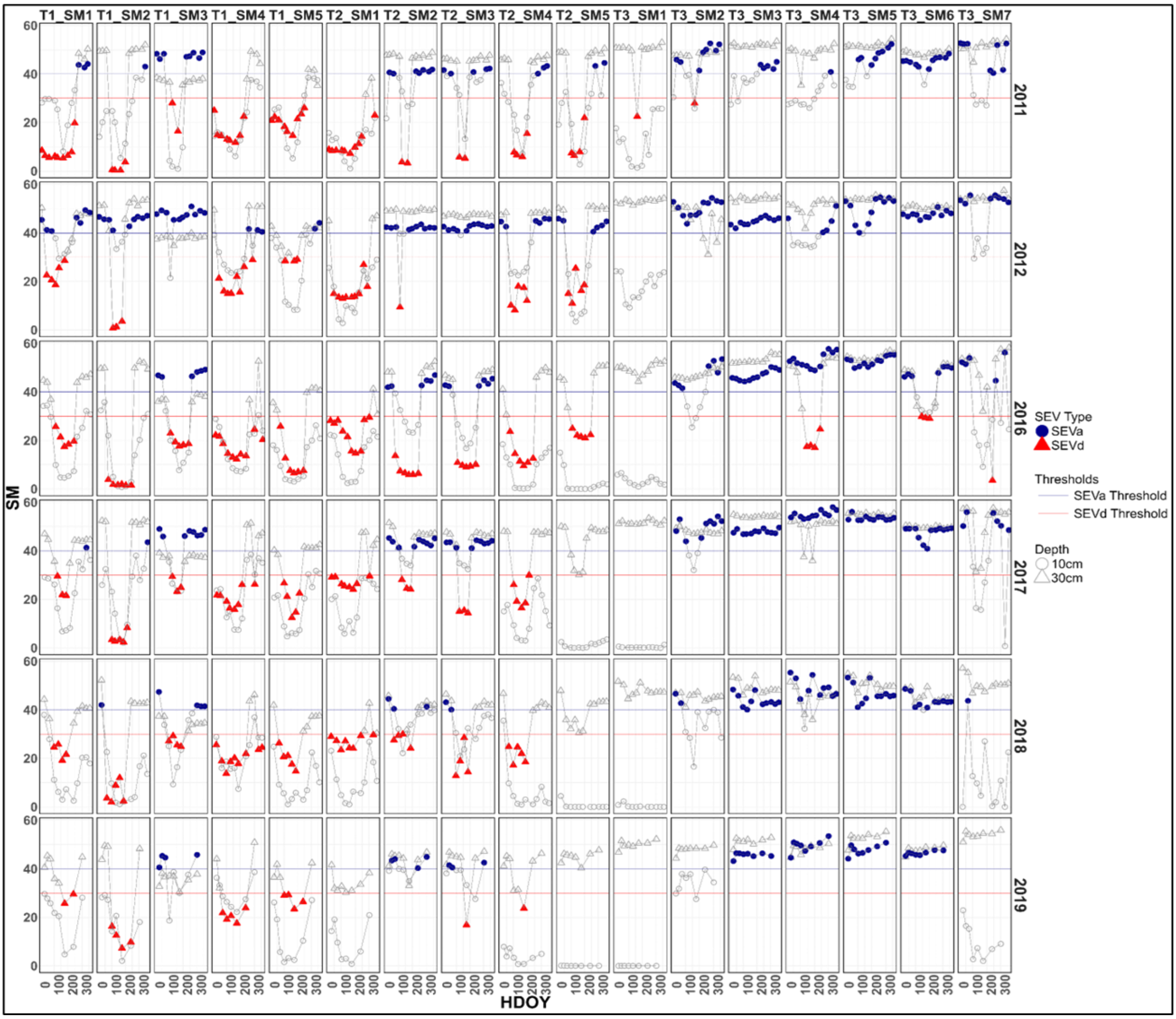

Figure 3.3. Days in the hydrological year (HDOY) when VWC was greater than or equal to 40% at 10cm (blue circles), as well as days when VWC was equal to or less than 30% at 30 (red triangles).

3.2.2 Establishing the niche space of the wetland

Each point in Figure 3.4 represents the total number of days for each probe, in each year, that VWC was either greater than or equal to 40% at 10cm depth, exceeding the threshold for waterlogged conditions (SEVa), or less than or equal to 30% at 30cm depth, exceeding the threshold for dry conditions (SEVd). The distribution of these points between these two axes defines the hydrological niche space. The hydrological niche space did not extend to where soils would experience both waterlogged and drought stress. These results are similar to what was found by Araya *et al.* (2011, fig. 1) . The upper left consists of niches that were prone to waterlogged conditions; these were the wetter parts of the wetland. These were all found in transect 3 and the center of transect 2; this area was permanently inundated and has been identified as the wet core of the wetland (City of Cape Town, 2021). The bottom right consists of niches that were prone to dry conditions; these were the drier parts of the wetland. These were areas in transect 1 as well as the edges of transect 2. The remainder of the niches that occurred between these two extremes experienced variations of intermediate levels of both soil drying and soil aeration stresses. We know from Figure 3.3 that these stresses occurred at different times in the year without overlapping. This is also why the hydrological niche did not extend to the upper right hand between the two axes, where soils would experience extreme levels of both soil aeration stress and soil drying stress.

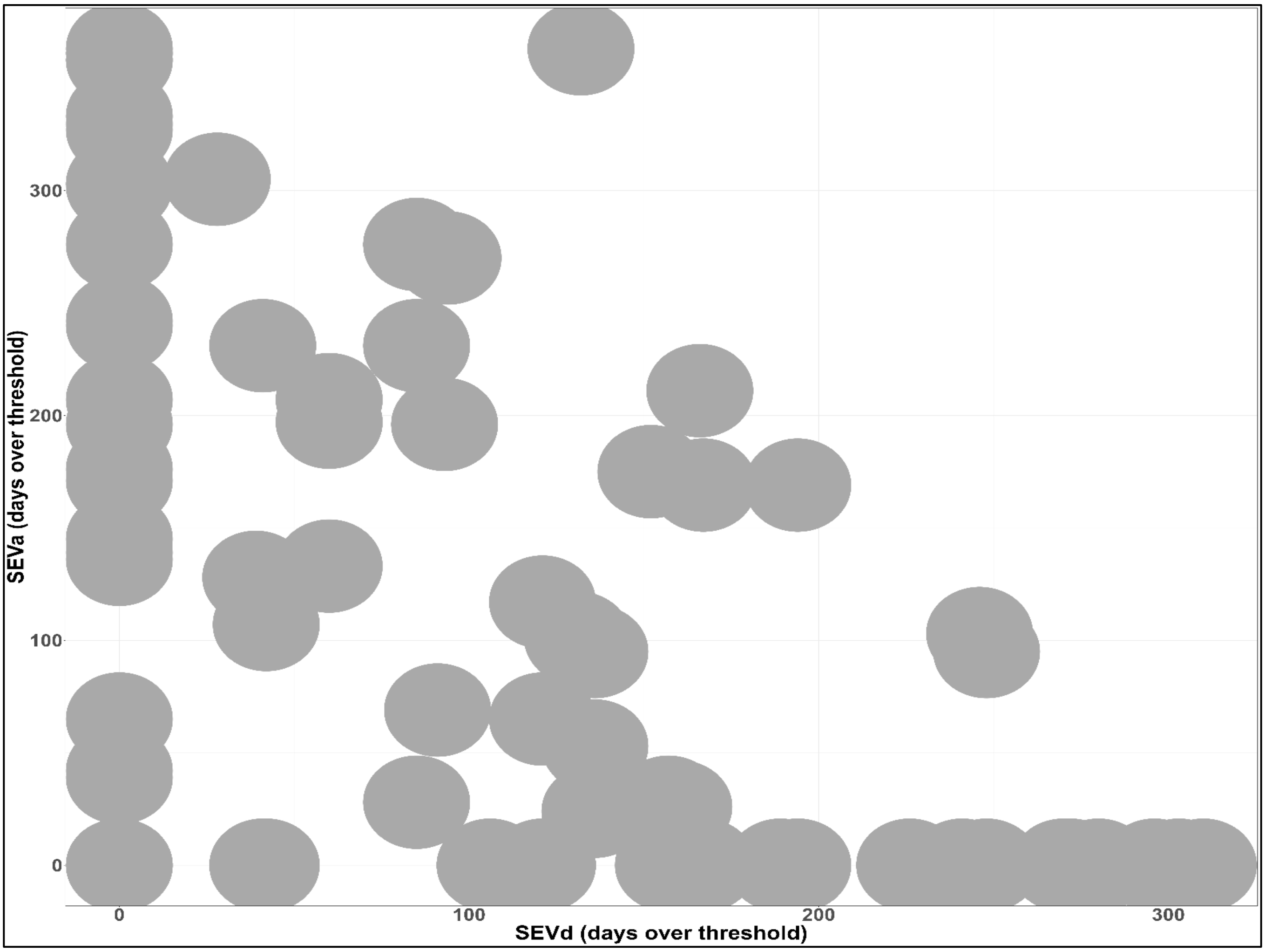

Figure 3.4: The hydrological niche space is defined by soil moisture probes and a combination of the number of days when VWC was above 40% at 10cm (SEVa) and below 30% at 30cm (SEVd)

The average SEVa and SEVd values at each probe over the duration of the six hydrological periods, represent average soil moisture conditions (Figure 3.5) that were prominent at locations within 2m of the probes. High SEVa was indicative of waterlogged conditions whereas high SEVd was indicative of dry conditions. Most soil moisture probes at transect 1, with the exception of T1_SM3, were in areas in the hydrological niche where SEVd>SEVa, and therefore soil moisture conditions at this transect were mostly dry. The soil moisture probes at transect 2 were more spread out over both wet and dry conditions in the hydrological niche space in comparison to those of both transects 1 and 3. Soil moisture conditions at T2_SM2 and T2_SM3 were waterlogged whereas they were dry at T2_SM1, T2_SM4 and T2_SM5. The soil moisture conditions at transect 3 were mostly waterlogged, as seen by soil moisture probes occurring in the hydrological niche space where SEVa>SEVd.

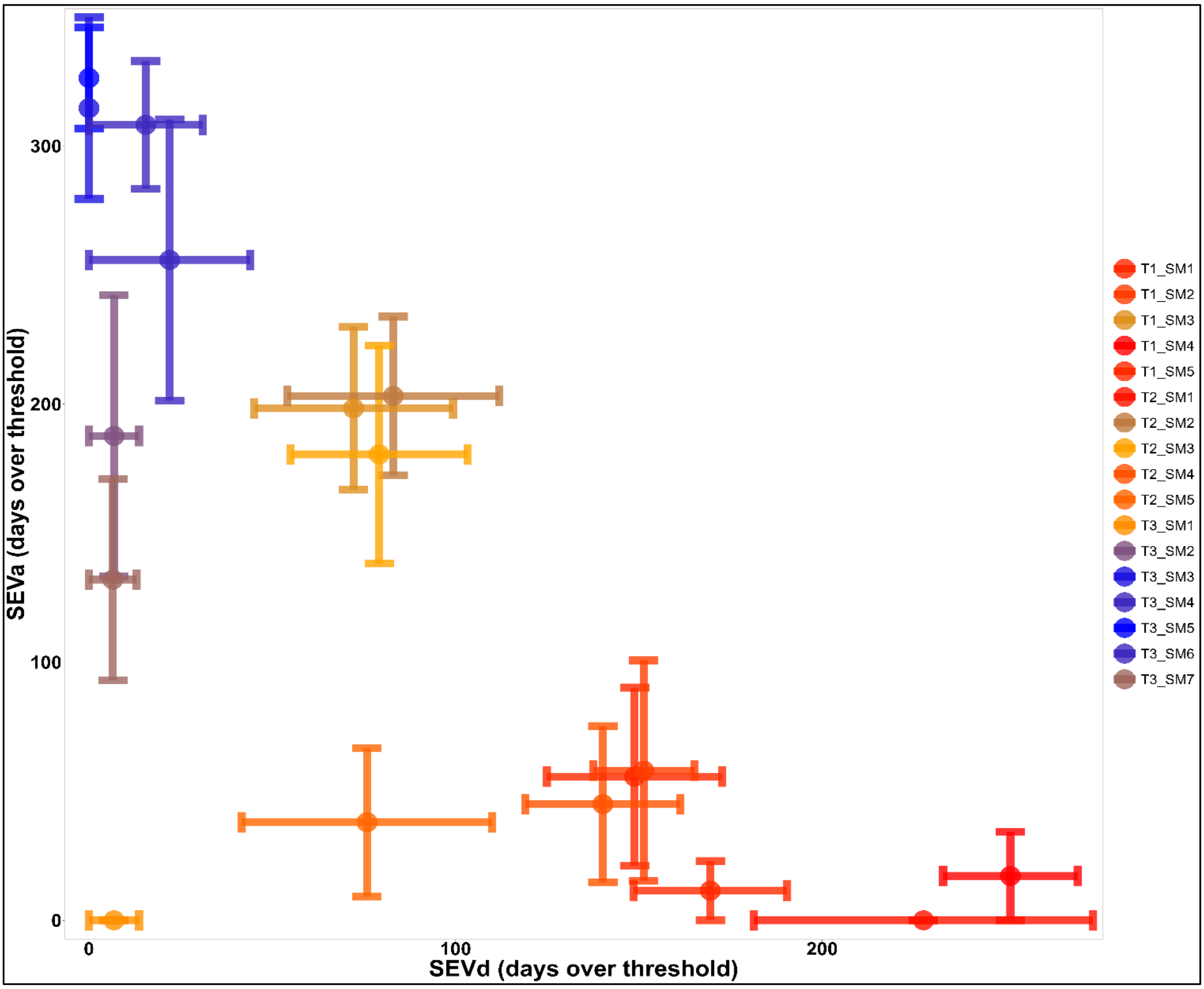

Figure 3.5.The hydrological conditions at each soil moisture probe show the occurrence of distinct niches defined by sum of exceedance values for flooding (SEVa) and drought (SEVd) during a hydrological year. Points represent mean yearly values for each probe while bars represent the standard error over the included years (2012, 2013, 2017, 2018, 2019 and 2020).

3.2.3 Species distribution in the niche space

Using the subset of common, persistent species chosen to test hydrological niche segregation, it was observed that species had different distributions within the hydrological niche space (Figure 3.6). Species such as *Restio versatilis, Erica serrata*, *Tetraria fasciata*, *Pentamaris colorata*, and *Erica hispidula* were distributed in the predominantly drier parts of the hydrological niche. *Anthochortus ecklonii*, *Lycopodiella caroliniana* and *Neesenbeckia punctoria* were at the other end of the hydrological gradient, and their distribution was confined mostly to waterlogged-prone parts of the hydrological niche. Then there were species that had a much wider distribution in the hydrological niche space, occupying areas that experienced, at varying degrees, a wide range of both waterlogged and dry conditions. These included *Erica intervallaris, Villarsia manningiana, Tetraria capillacae, Nevillea obtusissima, Bobartia gladiata, Berzelia alopecuroides*, *Drosera aliciae*, *Restio leptostachyus*, *Erica campanularis*, and *Cyathacoma hexandra*.

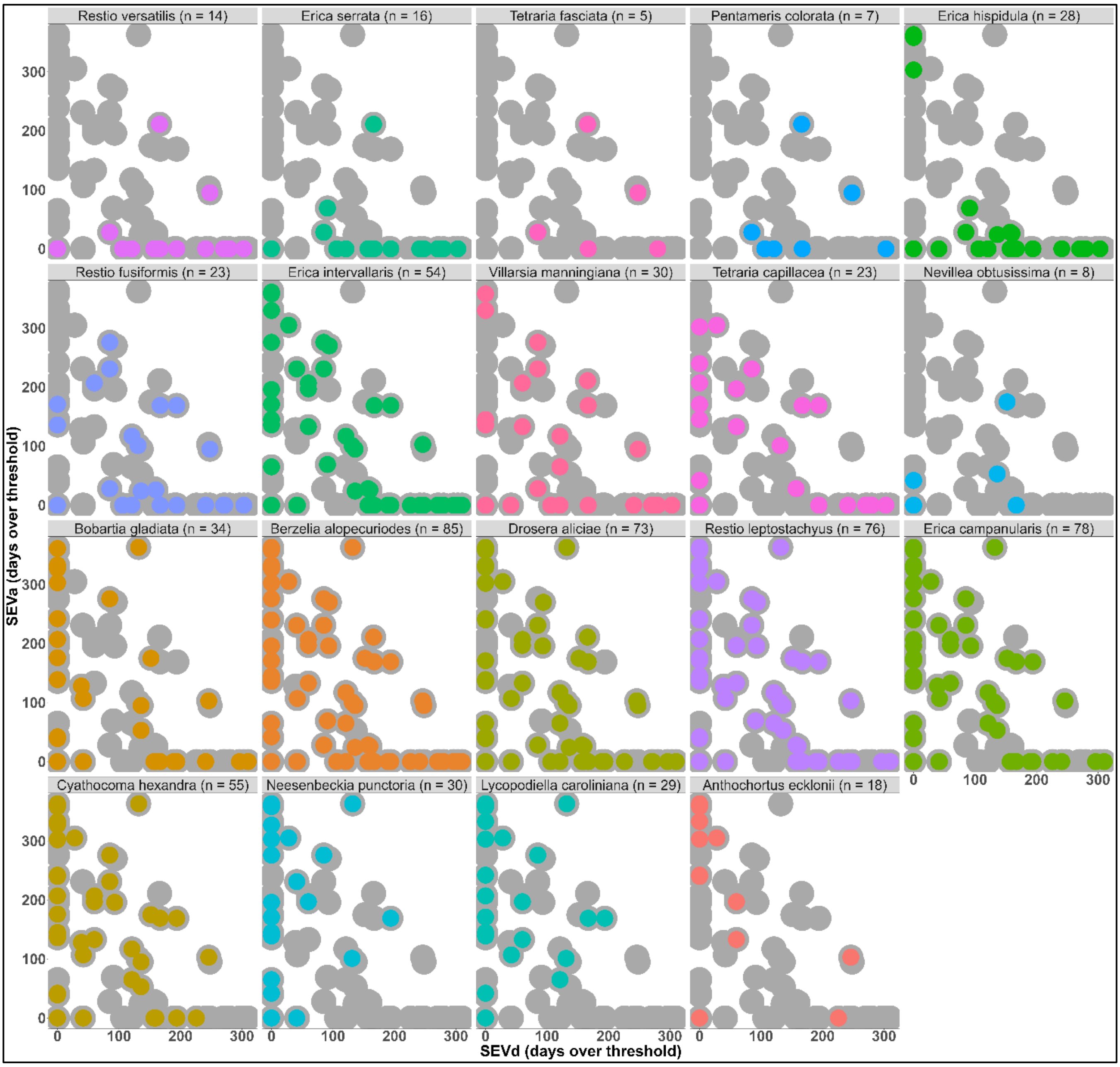

Figure 3.6. Hydrological niche for 19 commonly occurring species, including observations for years 2012, 2013, 2017, 2018, 2019 and 2020. The grey area represents the hydrological niche space in Figure 3.4, and the different colors represent the hydrological niches of each species.

While most species occupied a relatively broad range of positions within the hydrological niche space (Figure 3.6), the peak hydrological niche position for each species was best represented by the mean position of species occurrences along the SEVa and SEVd axes (Figure 3.7). Following this approach, species segregated strongly along a gradient from areas of high aeration stress (SEVa), for example, *A. ecklonii*, to areas of high drought stress (SEVd), for example, *R. versatilis*. An increase in values on one axis corresponded to a decrease of values on the other, highlighting a preference for either wet or dry conditions based on where the species falls within the hydrological niche space. These results indicate a tradeoff between tolerance for either soil aeration (high SEVa) or soil drying (high SEVd) stress, and therefore occupation of distinct hydrological niches by each species.

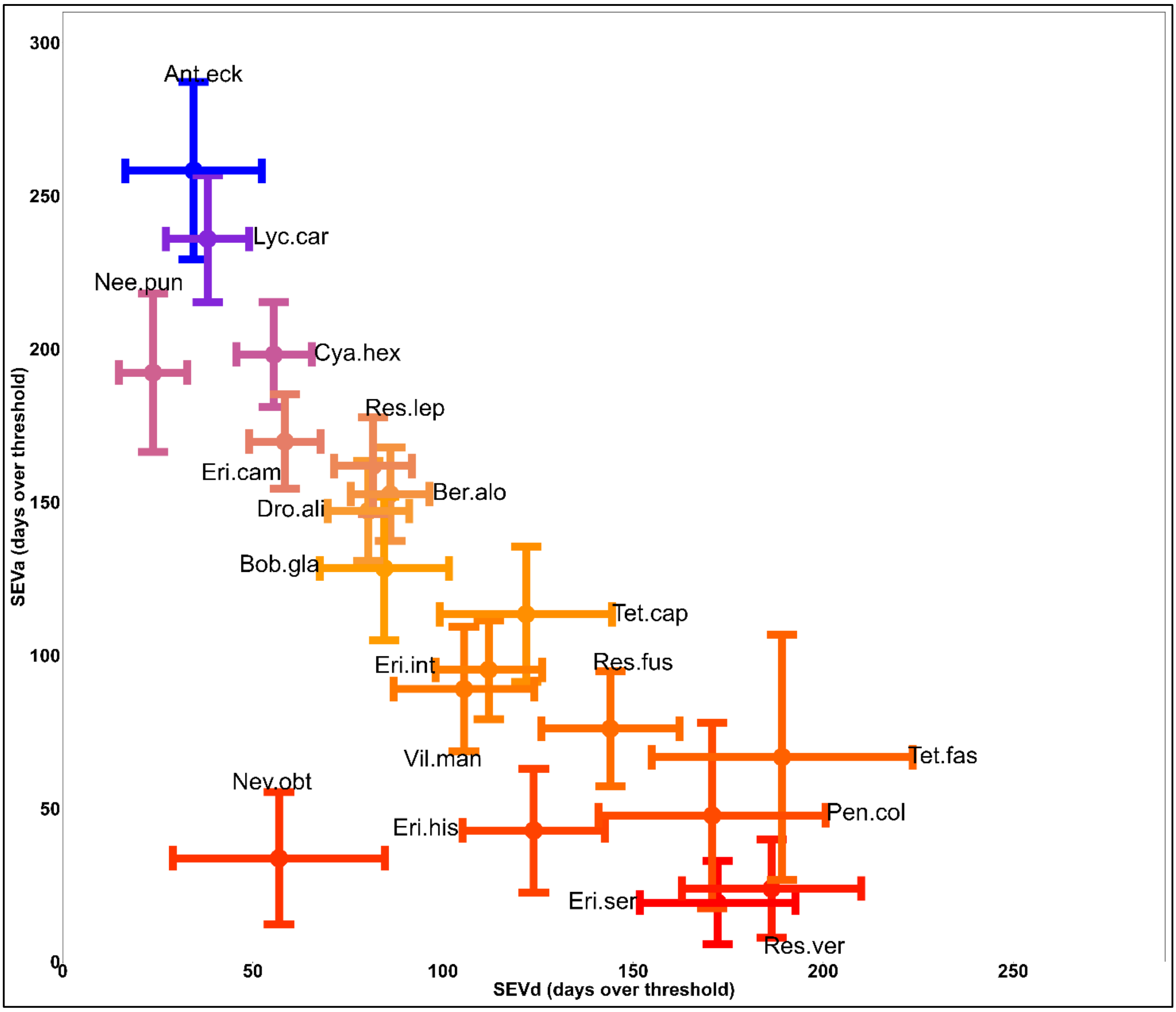

Figure 3.7. The SEVa and SEVd values of each species in Figure 3.6 were summarized to show the hydrological niche of each species as well as peak distribution within the hydrological niche space (Figure 3.4). Points represent mean positions and bars represent standard error.

Species key: Ant.eck = *Anthochortus ecklonii,* Lyc.car = *Lycopodiella caroliniana*, Nee.pun = *Neesenbeckia punctoria*, Cya.hex = *Cyathocoma hexandra*, Eri.cam = *Erica campanularis*, Res.lep = *Restio leptostachyus*, Dro.ali = *Drosera aliciae*, Ber.alo = *Berzelia alopecuriodes*, Bob.gla = *Bobartia gladiata*, Tet.cap = *Tetraria capillacea* , Eri.int = *Erica intervallaris*, Vil.man = *Villarsia manningiana*, Nev.obt = *Nevillea obtusissima*, Eri.his = *Erica hispidula*, Res.fus = *Restio fusiformis*, Tet.fas = *Tetraria fasciata*, Pen.col = *Pentameris colorata*, Eri.ser = *Erica serrata*, Res.ver = *Restio versatilis*

3.2.4 Classifying species' hydrological niches

The PCA quantified the longest axis of variation within the SEVa SEVd plot-space (Figure 3.8), thus distinguishing between species occurring in parts of the wetland with high SEVd but low SEVa values (dry) and those in parts of the wetland with high SEVa but low SEVd values (wet). The PCA showed that 76.8% (Figure 6.3) of the variation in species distribution can be explained by the PC1 axis, contributed to by both SEVa and SEVd. This allowed for species to be ranked in terms of their hydrological niche preference using PC1 values, where a shift from negative to positive values indicate a shift from high SEVd (dry niches) to high SEVa (wet niches) (Figure 3.8). The differences in the location and sizes of the boxplots indicate differences in both location and range of the hydrological niches of the species.

The PC1 values of *R.versatilis*, *E. serrata*, *T. fasciata* and *P. colorata* were all below zero. These species were, therefore, distributed, with a restricted range, in the dry hydrological niche (high SEVd). These species were therefore obligately associated with the drier transects of the wetland. The results also show two groups of facultative species, whose boxplots were distributed over both negative and positive PC1 values, and the hydrological niches of both the species in these groups were distributed in areas that experienced intermediate levels of both waterlogged and dry conditions. The first group consisted of *E. hispidula*, *R. fusiformis*, *E. intervallaris*, *V. manningiana*, *T. capillaceae*, *N. obtusissima*, *B. gladiata*, *B. alopecuroides* and *D. aliciae;* these species were facultatively associated with the drier areas. The second group consisted of *R. leptostachyus*, *E. campanularis*, *C. hexandra* and *N. punctoria*, and these species were facultatively associated with waterlogged areas. The location of the boxplots of *L. caroliniana* and *A. ecklonii* was restricted to positive PC1 values, however their range extended to some negative PC1 values (as seen by the whiskers). The hydrological niche of these species was therefore predominantly located in the waterlogged prone areas (high SEVa).

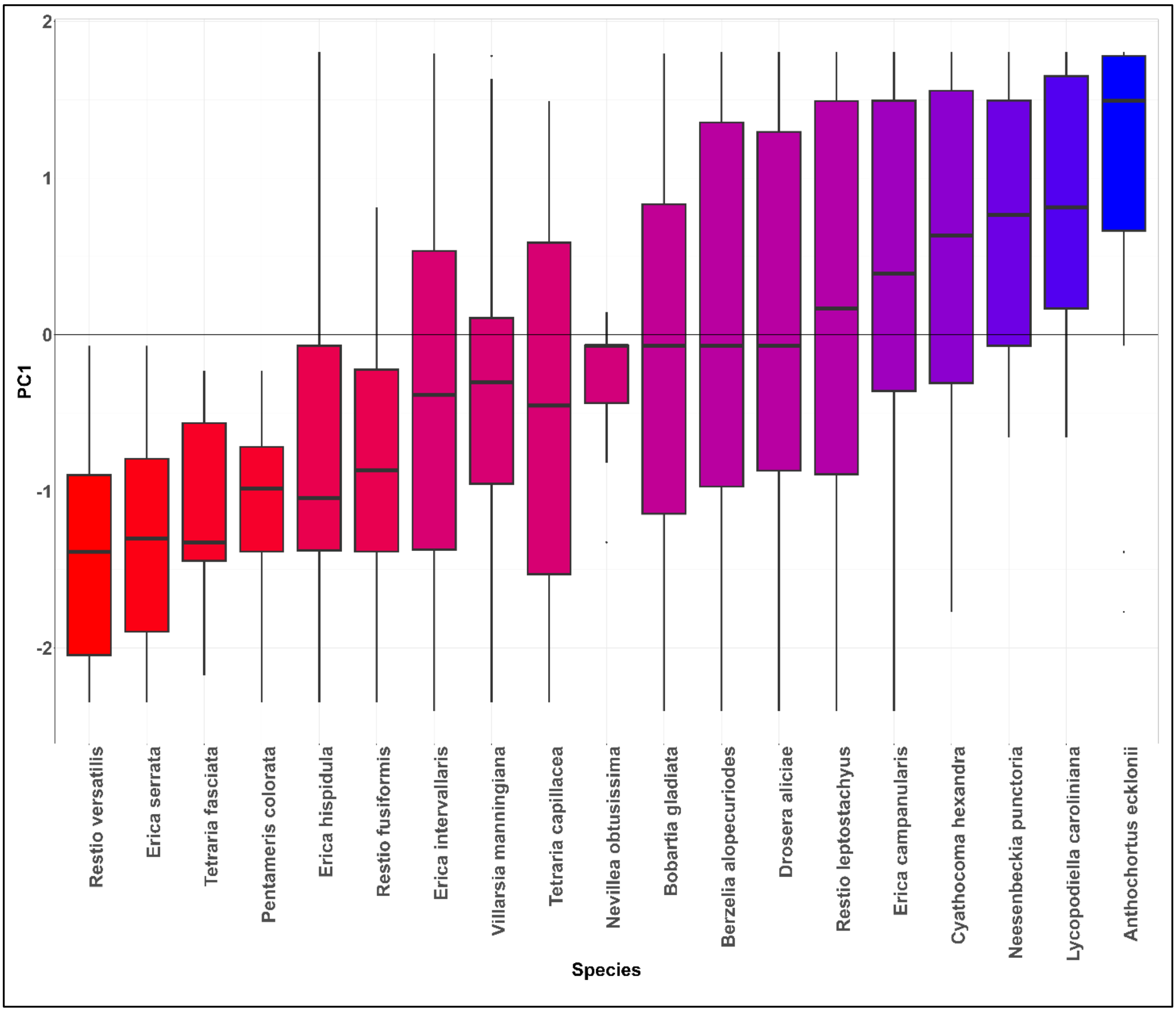

Figure 3.8: Location and range of species in the hydrological niche. Species with negative PC1 values are found in drought-prone areas (red), species with positive values (blue) are found in waterlogging-prone areas, and the species in between (purple) are the two types of facultative groups. The solid lines inside the box represent the median PC1, the boundaries of the box represent the upper and lower quartiles of PC1, the whiskers represent the highest and lowest PC1 values, and the black dots are the outliers.

4 Discussion

4.1 Overview

This study demonstrates that community composition at this wetland is a function of two drivers, time since fire and the hydrological niche. I documented successional changes in species composition and abundance with increasing age of vegetation post-fire, as well as similarities in patterns of community assemblage for each year. I also found that these communities are usually structured along hydrological gradients across the wetland, and species showed some degree of hydrological niche segregation, preferring either waterlogged or dry niches within the wetland. This community segregation appeared to establish early during post-fire succession. The potential reliance by several species on permanently inundated groundwater-fed niches, and the influence of hydrological gradients on community composition highlights the potential negative impacts of groundwater abstraction in the region.

4.2 Post-fire successional change

The analysis of vegetation data revealed a post-fire successional change in species composition and abundance as vegetation matures. Most of the changes occurred during the pioneer stages after fire in the years 2022 and 2011 (Figure 3.1),and vegetation began to show stability as early as five years post-fire. As the process of post-fire succession occurs, the different phases reflect changes in life-cycles and growth forms of species as they happen over time (Kruger, 1977). Therefore, any similarities or differences in species composition and abundance between vegetation are a reflection of the post-fire succession stage the vegetation is in (Privett *et al.*, 2001). Additionally, the majority of the species that are recorded during succession are present from within the first year of recovery and most will remain in the system for the entire fire cycle (Campbell and van der Meulen, 1980; Kruger, 1977; van der Merwe and van Rooyen, 2011). In this wetland, this was evident in the relatively low dissimilarity between the pioneer stages and the climax stages(Table 3.1). However, some of the species may be fire ephemerals that senesce within three to four years post-fire (Kruger, 1977; Privett *et al.*, 2001), which corresponds with the time when delayed regenerating species such as reseeding *Restio* species (Rutherford *et al.*, 2011) start to emerge (Privett *et al.*, 2001). Therefore, the differences observed in species composition and abundance between young and mature vegetation, as well as the stability that emerges approximately five years after fire, are a result of the fire ephemerals dying out of the system and the long-lived species establishing themselves.

I also found that community assembly was similar in young (2022) and older (2020) vegetation, i.e. the same plots grouped together to form communities because they were similar in terms of species composition and abundance (Figure 3.2). The main difference in how the vegetation indifferent post-fire succession stages assembled was that the communities were more clumped together in the young vegetation and comparatively more segregated in older vegetation (Figure 6.2). In this case, fire seems to be fundamental in explaining interannual changes in species composition and abundance at the whole ecosystem level. However, when these two attributes of community structure begin to stabilize after five years post-fire, any observed differences and/or similarities in community assembly might be better explained by fine-scale environmental variables such as hydrology.

4.3 Hydrological niche segregation

This study provides new evidence for hydrological niche segregation in diverse fynbos wetland plant communities. It shows that co-occurring graminoid, as well as shrub species, are structured along fine-scale hydrological gradients, which was previously only demonstrated with the graminoid restios (Araya *et al.*, 2011; Ayuk *et al.*, 2019; Guo *et al.*, 2015). This study was able to show that these hydrological niches occur according to the hypotheses of Araya *et al.* (2011) and Silvertown *et al.* (2015), and also confirms that they are not necessarily independent of each other. The first hypothesis is that these niches can occur when the hydrological gradient divides the system into distinct compartments, each with its own set of hydrological conditions. The evidence of this hypothesis is evident in Figure 3.5, where each soil moisture probe has its own set of SEVa and SEVd values reflecting the soil moisture conditions of any area with 2m of the probe. This type of niche partitioning is often most prominent on a fine-scale setting, similar to this wetland (Araya *et al.*, 2011; Fox, 1981; Silvertown *et al.*, 2015). The second hypothesis is that the niche occurs on the basis of resource availability and plants will occupy distinct niches (Figure 3.6) as a result of differences in their specialized water-use and acquisition strategies (Araya *et al.*, 2011; Silvertown *et al.*, 2015). The third hypothesis is that temporal fluctuations in hydrological niche parameters influence recruitment patterns of species, and this is directly influenced by species life-history traits, how individual species respond to these hydrological fluctuations as well as species' competitive ability (Angert *et al.*, 2009; Chesson, 2000; Silvertown *et al.*, 2015; Stump and Vasseur, 2023). This type of response to dynamic niches is known as the temporal storage effect, and both flooding and drought tolerant species would be induced into dormancy when soil moisture conditions are not favorable (Collins, 2006; Silvertown *et al.*, 2015). This is a phenomenon that could be of relevance in fire-prone systems such as the Fynbos.

The findings of this study, along with previous research, indicate that species distributions are likely governed by a trade-off between tolerance for stress induced by wet or dry conditions (Araya *et al.*, 2011; Silvertown *et al.*, 1999). Figure 3.3 shows that conditions that trigger waterlogging or drying stress in plants occur at different times within each hydrological year, sometimes even alternatively at one soil moisture probe. This not only highlights how dynamic the hydrological niche can be but that species in this wetland might have some physiological adaptations to both types of stresses (Born and Linder, 2018; Renziehausen *et al.*, 2024). Species distribution in this case could be driven by species having adapted various and often contrasting water-use strategies which enable them to regulate how they respond to changing soil moisture conditions (Bonetti *et al.*, 2017; Renziehausen *et al.*, 2024; Yao *et al.*, 2023). Which response prevails is a species-specific response (West *et al.*, 2012) that is triggered by the intensity of the stress (Renziehausen *et al.*, 2024). Although all the species in this wetland appeared to be tolerant, to varying degrees, of both wet and dry conditions, Figure 3.7 and Figure 3.8 show that they have characteristic soil moisture conditions, and their preference for a specific niche is most likely governed by these trade-offs.

Species found in the dry niches experience resource-related stresses caused by water deficiency (Bartelheimer *et al.*, 2010) that trigger either a drought-avoidance or a drought-tolerance response (Brum *et al.*, 2019). Drought avoidance responses occur in isohydric plants (Yao *et al.*, 2023). Isohydric plants respond to dry conditions by closing their stomata to maintain a constant water potential, which enables them to minimize water loss and ensure that they maintain hydraulic conductivity (West *et al.*, 2012; Yao *et al.*, 2023). This response is common in restioids that are often found in the drier parts of the hydrological niche (Cowling *et al.*, 1997), as well as deep-rooted Proteacaeae (West *et al.* 2012). On the other hand, anisohydric species, such as shallow-rooted *Erica* species (West *et al.* 2012), do not tightly regulate water potential, but rely on large hydraulic safety margins to prevent the onset of embolism in their xylem as their water potential falls (Brum *et al.*, 2019; West *et al.*, 2012; Yao *et al.*, 2023). Another form of drought adaptation was demonstrated by Hawkins *et al.* (2009), who found evidence that shallow-rooted *Leysera gnaphalodes* cohabitates with deep-rooted *Protea* Sylvia, and this enables *L. gnaphalodes* to survive drought conditions by accessing water that is redistributed from deep to shallow soils through a process known as hydraulic lift (Colvin *et al.*, 2007). Ericoid shrubs are facultative species that can be found in both wet and dry niches (Figure 3.8) (Cowling *et al.*, 1997). The City of Cape Town (2021) found that community composition in the drier parts of the wetland was significantly affected by rainfall variability, and the ericoid shrubs would therefore be affected too. Skelton *et al.* (2023) found that exposure to dry conditions for extended periods can lead to xylem embolism in *Erica* species. However, what enables them to survive dry conditions is that they have roots that function in shallow soil layers and this enables them to access and use water during summer rainfall events.

Species found in the wet niches are either completely (anoxia) or partially (hypoxia) deprived of oxygen (Banach *et al.*, 2009; Blom and Voesenek, 1996; Nakamura and Noguchi, 2020). Their tolerance of permanent or extended waterlogged conditions is facilitated by their capacity to form aerenchyma tissue (Blom and Voesenek, 1996; Nakamura and Noguchi, 2020). Aerenchyma tissue has multiple functions, which include improving the porosity of both the shoots and roots (Pan *et al.*, 2020), facilitating the transport of oxygen from non-waterlogged organs to the roots (Pan *et al.*, 2021), and discharging toxic substances from waterlogged tissues (Pan *et al.*, 2021). They are also able to develop adventitious roots that tend to have a greater concentration of aerenchyma compared to the primary lateral roots (Nakamura and Noguchi, 2020). Additionally, waterlogging stress signals hormonal regulation, and accumulation or reduced concentrations of hormones such as ethylene and auxins will aid in the aforementioned morphological adaptations (Blom and Voesenek, 1996; Pan *et al.*, 2021).

Species that have inundated niches may be most sensitive to groundwater abstraction. Over extended periods, abstraction will reduce the amount of water the aquifer can discharge into the wetland. Eventually, this will alter the frequency and duration of soil inundation, as well as the water chemistry of this wetland (Cronk and Fenessy, 2001; Le Maitre *et al.*, 1999). These changes to the hydrological characteristics will result in changes in community abundance and diversity (Collins, 2006; Cronk and Fenessy, 2001). Species that will most likely be affected by reduced water availability due to groundwater abstraction are *A. ecklonii L. caroliniana*, *E. campanularis*, *C. hexandra*, and *N. punctoria* (Figure 3.8). This is because the competitive ability of species found in the wet niches is contingent on the maintenance of waterlogged conditions (Bakker *et al.*, 2007). Disrupting the conditions that they are adapted to, even when non-lethal, results in diminished health and function of the plants, and potentially in their displacement from the system (Araya and Walker, 2009; Bakker *et al.*, 2007; Skelton *et al.*, 2023). If dry conditions extend over long periods and expand to the where the wet core once was, species in dry niches - *R. versatilis*, *E. serrata*, *T. fasciata* and *P. colorata* – might become dominant in the wetland through a process known as terrestrialization (Colvin *et al.*, 2009; Mason *et al.*, 2023). These dry niche species are therefore best suited to be used as potential indicators to monitor changes in species composition and abundance in response to groundwater abstraction.

I also found that communities of both mature and young vegetation were distributed similarly along the wetland's hydrological gradient. The similarities in this pattern of species distribution and community formation suggest that segregation of species could occur before competitive exclusion operates, due to physiology and specialization of different species to specific hydrological conditions. This also suggests that hydrological niche preferences may be established during the sensitive post-fire stage. This is particularly relevant to this fynbos ecosystem, where post-fire species richness (Privett *et al.*, 2001) and recruitment of seedlings of both reseeding and resprouting seedlings are sensitive to changing soil moisture conditions caused by rainfall patterns (Rutherford *et al.*, 2011; van Blerk *et al.*, 2021; van der Merwe and van Rooyen, 2011). If groundwater availability can influence the occurrence of different plant growth types along the hydrological gradient (Le Maitre *et al.*, 1999), it is possible that similar sensitivities of post-fire seedling recruitment to soil moisture in response to rainfall might be observed when changes to the timing and frequency of soil saturation are reduced by groundwater abstraction. It is also possible that the combined effects of fire and hydrological disruptions caused by abstraction would, to varying degrees, ultimately influence the processes of post-fire succession (Mason *et al.*, 2023; Zweig and Kitchens, 2009). Therefore, abstraction could have particularly large impacts on species composition and diversity in the wetland.

The mechanisms of species and community distribution through niche segregation in this wetland are potentially more complex than just physiological adaptations, and could also be attributed to competitive effects (Silvertown *et al.*, 2012, 2005; Zelnik and Čarni, 2008), as well as succession processes caused by environmental triggers such as fire (Dwyer *et al.*, 2021; Silvertown *et al.*, 2012). This complexity adds to the lack of knowledge we have on how this ecosystem will respond to groundwater abstraction. With regard to the TMGA, of great concern is that ecosystem responses to abstraction are often slow and impacts were only witnessed once thresholds had been breached (Aston, 2007; Cleaver *et al.*, 2003). Additionally, the impacts of abstraction are most likely to extend beyond the areas closest to the wellfields (Aston, 2007), which could have detrimental effects in ecologically sensitive areas such as the Steenbras Nature Reserve. Therefore, studies such as this one that aim to gain understanding on the potential ecological ramifications of groundwater abstraction are essential. This study shows that fine-scale hydrological gradients facilitate species coexistence at the community scale and therefore enhance species diversity. Reductions in the groundwater-fed niches could have implications for the diversity and richness of the area, as well as the integrity and function of the wetland.

5 Conclusion

Our study showed that Fynbos species' distributions were strongly segregated along fine-scale hydrological gradients. Hydrological niche segregation appeared to be mediated by the physiological trade-off between flooding and drought tolerance and manifested within the first few years of post-fire succession. Since groundwater is likely to play an important role in creating and maintaining permanently inundated hydrological niches, our study points to the potential sensitivity of flooding-tolerant species to forces that could be impacted by activities such as groundwater abstraction. Additionally, this study provides a mechanistic basis for identifying indicator species that can highlight changes to groundwater abundance. Future work to be done needs to focus on the potential impacts of groundwater abstraction, including improving the estimation of the points of aeration and drought stress using soil specific parameters (as per Silvertown 1999), identifying key plant traits that confer tolerance to these stresses, and linking these to community-level characteristics, to inform relevant management strategies before reaching tipping points.

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Appendix A. SUPPLEMENTARY MATERIAL

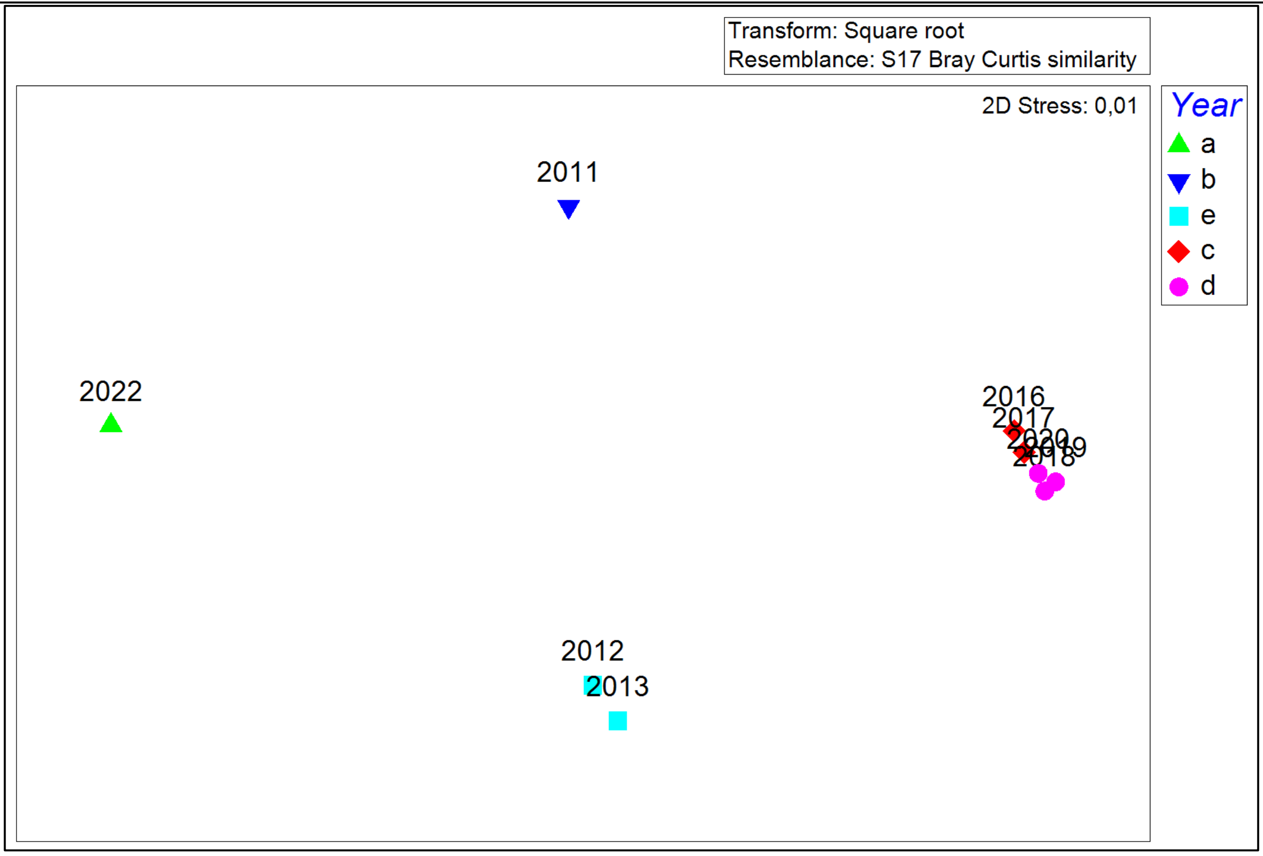

Figure 6.1. MDS showing shifts in species composition abundance and in vegetation of different ages post-fire. Corresponds with Figure 3.1.

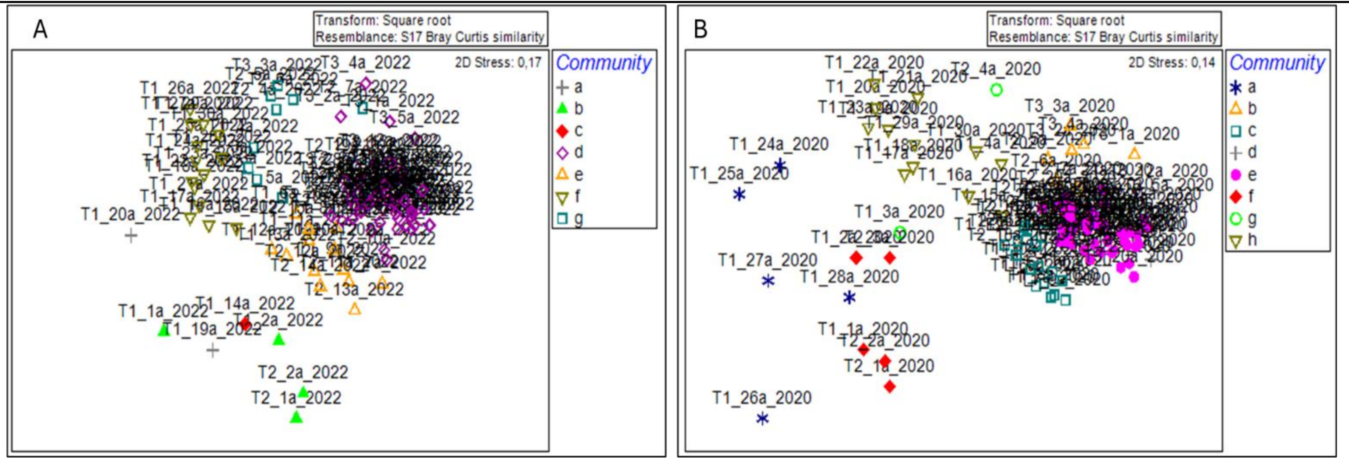

Figure 6.2. MDS showing clustering patterns of vegetation plots of all three transects to form communities based on similarity between species composition and abundance between those plots. The MDS plots correlate with clustering patterns in Figure 3.2, for young (2022, A) and mature (2020, B) post-fire vegetation.

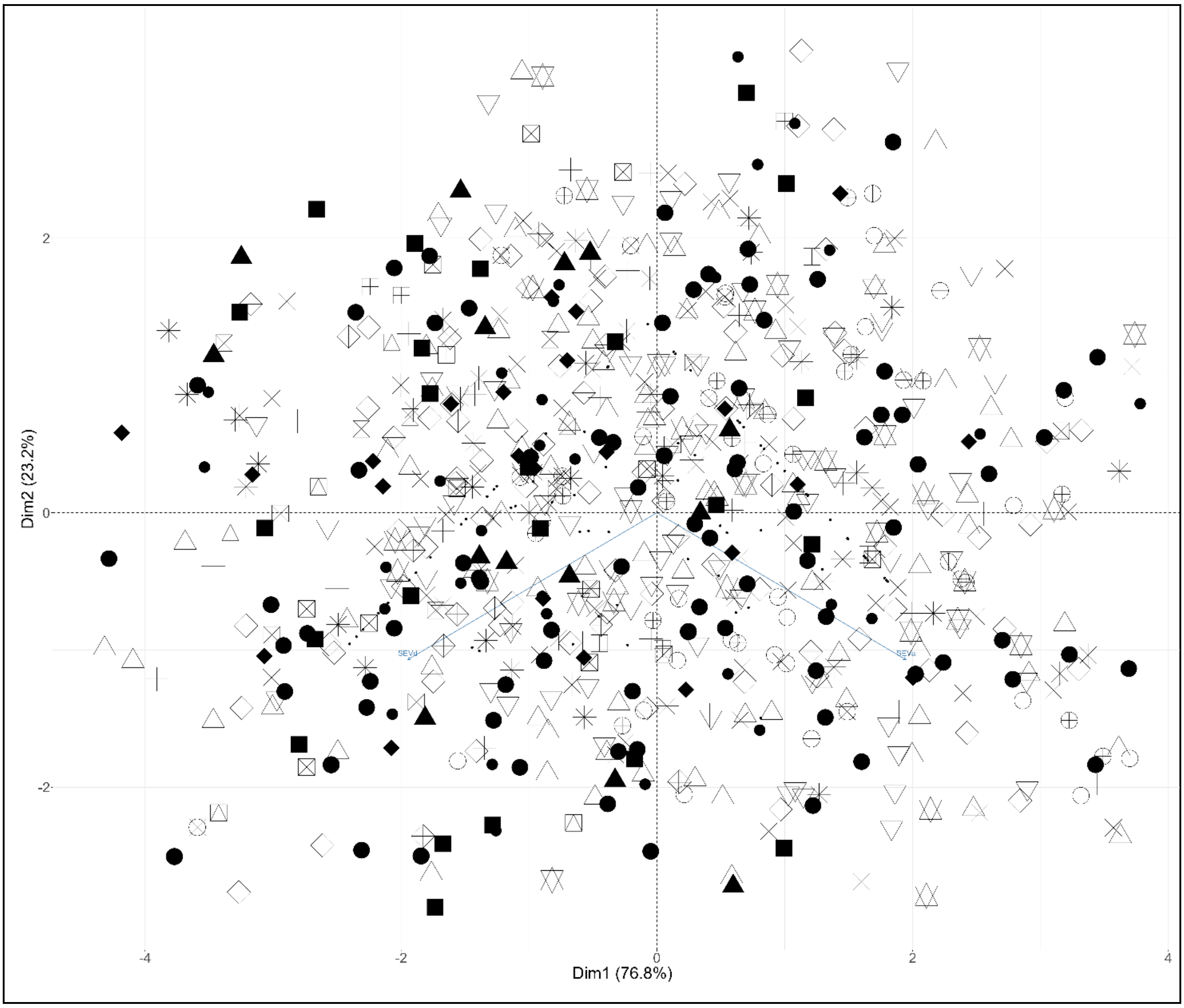

Figure 6.3: Biplot showing results of PCA analysis for SEVa and SEVd. High negative means high SEVd and low SEVa, high positive PC1 means high SEVa and low SEVd. When PC = 0, it means equal contribution from both SEVa and SEVd to the distribution of species in the hydrological niche

Table 6.1. PC values of species (negative PC value correlated to high SEVd value of species and positive PC1 value correlates to high SEVa value of species). The table also shows the wetland affiliation of a species as either obligate terrestrial, obligate wet facultative (generalist) designated according to its habitat Goldblatt and Manning (2002), Van Ginkel and Hitchcock (2011) and TMG Aquifer Alliance(2019).

species	**growth form**	**habitat description**	**wetland affiliation (literature)**	**pca classification**
Anthochortus ecklonii Nees	Restioid	seepages and on the wet steep upper south-facing slopes	obligate wetland /facultative	facultative wet
Berzelia alopecuriodes (Thunb.) Sond.	Shrub	sandstone slopes	dryland	facultative dry
Bobartia gladiata (L.f.) Ker Gawl.	Rhizomatous geophyte	mountain slopes and coastal flats	dryland	facultative dry
Cyathocoma hexandra (Nees) Browning	Cyperoid	marshes and watercourses on mountain slopes below 800m	obligate wetland	facultative wet
Drosera aliciae Raym.-Hamet	Carnivorous	peaty sandstone/marsh plant is usually found in damp, peaty, exposed areas on stream and riverbanks or in seeps.	obligate wetland	facultative dry
Erica campanularis Salisb.	Shrublet	marshes and stream banks, lower to mid-slopes	obligate wetland	facultative wet
Erica hispidula L.	Shrublet	flats to high altitude	dryland	facultative dry
Erica intervallaris Salisb.	Shrublet	moist places and slopes, mid-high altitude	facultative	facultative dry

Erica serrata Thunb.	Shrublet	mountain slopes	dryland	dry
Lycopodiella caroliniana (L.) Pic.Serm.	Prostrate	perennial or seasonal seeps or marshy areas in montane grassland and fynbos, montane streambanks and flat wet rocks.	obligate wetland	facultative wet
Neesenbeckia punctoria (Vahl) Levyns	Cyperoid	streamsides on lower slopes/seepages	Obligate wetland	facultative wet
Nevillea obtusissima (Steud.) H.P.Linder	Restioid	marshy slopes, valley bottoms	Obligate wetland	facultative dry
Pentameris colorata (Steud.) Galley & H.P.Linder	Graminoid (Poaceae)	sandstone slopes, seeps sometimes	facultative	dry
Restio fusiformis Pillans	Restioid	marshes in wetland, and along stream-margins/seepage areas above 300m	obligate	facultative dry
Restio leptostachyus Kunth	Restioid	seepages and south-facing rock ledges/Restricted to marshy or wet areas; commonly wet rock ledges	obligate	facultative dry
Restio versatilis H.P.Linder	Restioid	sandy flats and slopes	dryland/facultative	dry
Tetraria capillacea (Thunb.) C.B.Clarke	Cyperoid	dry to moist mountain fynbos	facultative	facultative dry
Tetraria fasciata (Rottb.) C.B.Clarke	Cyperoid	sandy lower or mid slopes	dryland	dry
Villarsia manningiana Ornduff	Herb	marshy sandstone	obligate	facultative dry