A palaeoecological approach to savanna dynamics and shrub encroachment in Namibia

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Abstract

The spread of shrubs in Namibian savannas raises questions about the resilience of these ecosystems to global change. This makes it necessary to understand the past dynamics of the vegetation, since there is no consensus on whether shrub encroachment is a new phenomenon, nor on its main drivers. However, a lack of long-term vegetation datasets for the region and the scarcity of suitable palaeoecological archives, makes reconstructing past vegetation and land cover of the savannas a challenge.

To help meet this challenge, this study addresses three main research questions: 1) is pollen analysis a suitable tool to reflect the vegetation change associated with shrub encroachment in savanna environments? 2) Does the current encroached landscape correspond to an alternative stable state of savanna vegetation? 3) To what extent do pollen-based quantitative vegetation reconstructions reflect changes in past land cover?

The research focuses on north-central Namibia, where despite being the region most affected by shrub invasion, particularly since the 21st century, little is known about the dynamics of this phenomenon.

Field-based vegetation data were compared with modern pollen data to assess their correspondence in terms of composition and diversity along precipitation and grazing intensity gradients. In addition, two sediment cores from Lake Otjikoto were analysed to reveal changes in vegetation composition that have occurred in the region over the past 170 years and their possible drivers. For this, a multiproxy approach (fossil pollen, sedimentary ancient DNA (*seda*DNA), biomarkers, compound specific carbon ($\delta^{13}C$) and deuterium (δD) isotopes, bulk carbon isotopes ($\delta^{13}Corg$), grain size, geochemical properties) was applied at high taxonomic and temporal resolution. REVEALS modelling of the fossil pollen record from Lake Otjikoto was run to quantitatively reconstruct past vegetation cover. For this, we first made pollen productivity estimates (PPE) of the most relevant savanna taxa in the region using the extended R-value model and two pollen dispersal options (Gaussian plume model and Lagrangian stochastic model). The REVEALS-based vegetation reconstruction was then validated using remote sensing-based regional vegetation data

The results show that modern pollen reflects the composition of the vegetation well, but diversity less well. Interestingly, precipitation and grazing explain a significant amount of the compositional change in the pollen and vegetation spectra. The multiproxy record shows that a state change from open *Combretum* woodland to encroached *Terminalia* shrubland can occur over a century, and that the transition between states spans around 80 years and is characterized by a unique vegetation composition. This transition is supported by gradual environmental changes induced by management (i.e. broad-scale logging for the mining industry, selective grazing and reduced fire activity associated with intensified farming) and related land-use change. Derived environmental changes (i.e. reduced soil moisture, reduced grass cover, changes in species composition and competitiveness, reduced fire intensity) may have affected the resilience of *Combretum* open woodlands, making them more susceptible to change to an encroached state by stochastic events such as consecutive years of precipitation and drought, and by high concentrations of pCO_2. We assume that the resulting encroached state was further stabilized by feedback mechanisms that favour the establishment and competitiveness of woody vegetation.

The REVEALS-based quantitative estimates of plant taxa indicate the predominance of a semi-open landscape throughout the 20th century and a reduction in grass cover below 50% since the 21st century associated with the spread of encroacher woody taxa. Cover estimates show a close match with regional vegetation data, providing support for the vegetation dynamics inferred from multiproxy analyses. Reasonable PPEs were made for all woody taxa, but not for Poaceae.

In conclusion, pollen analysis is a suitable tool to reconstruct past vegetation dynamics in savannas. However, because pollen cannot identify grasses beyond family level, a multiproxy approach, particularly the use of *seda*DNA, is required. I was able to separate stable encroached states from mere woodland phases, and could identify drivers and speculate about related feedbacks. In addition, the REVEALS-based quantitative vegetation reconstruction clearly reflects the magnitude of the changes in the vegetation cover that occurred during the last 130 years, despite the limitations of some PPEs.

This research provides new insights into pollen-vegetation relationships in savannas and highlights the importance of multiproxy approaches when reconstructing past vegetation dynamics in semi-arid environments. It also provides the first time series with sufficient taxonomic resolution to show changes in vegetation composition during shrub encroachment, as well as the first quantitative reconstruction of past land cover in the region. These results help to identify the different stages in savanna dynamics and can be used to calibrate predictive models of vegetation change, which are highly relevant to land management.

Zusammenfassung

Die Ausbreitung von Sträuchern in der namibischen Savanne wirft Fragen nach der Resilienz dieser Ökosysteme gegenüber globalen Veränderungen auf. Dies macht es notwendig, die Vegetationsdynamik in der Vergangenheit zu verstehen, da kein Konsens darüber besteht, ob die Verbuschung ein neues Phänomen ist oder über ihre Haupttreiber. Aufgrund des Mangels an Langzeitvegetationsdatensätzen für die Region und des Mangels an geeigneten paläoökologischen Archiven bleibt die Rekonstruktion der früheren Vegetation und der früheren Landbedeckung der Savannen eine Herausforderung.

In diesem Zusammenhang befasst sich diese Studie mit drei Hauptforschungsfragen: 1) Ist Pollenanalyse ein geeignetes Instrument, um die Veränderung der Vegetation widerzuspiegeln, die mit der Verbuschung von Savannen verbunden ist? 2) Entspricht die derzeitige verbuschte Landschaft einem stabilen Zustand der Savannenvegetation? 3) Inwieweit entspricht die quantitative Rekonstruktion der Vegetation auf der Grundlage fossiler Pollendaten der früheren Vegetationsbedeckung der Savanne?

Um diese Fragen zu beantworten, konzentrierte sich diese Forschung auf Nord-Zentral-Namibia, da diese Region insbesondere seit dem 21. Jahrhundert am stärksten von Verbuschung betroffen ist, über die Dynamik dieses Phänomens in der Region ist jedoch wenig bekannt.

Im Rahmen dieser Studie wurden feldbasierte Vegetationsdaten mit modernen Pollendaten verglichen, um das Potenzial moderner Pollen zu bewerten, die Vegetationszusammensetzung und -vielfalt entlang von Niederschlags- und Weideintensitätsgradienten widerzuspiegeln. Zusätzlich wurden zwei Sedimentkerne aus dem Otjikoto-See analysiert, um die Veränderungen der Vegetationszusammensetzung in der Region in den letzten 170 Jahren und ihre möglichen Treiber zu dokumentieren. Hierzu wurde ein Multiproxy-Ansatz (fossiler Pollen, sedimentäre alte DNA, Biomarker, verbindungsspezifische Kohlenstoff- ($\delta^{13}C$) und Deuterium- (δD) Isotope, Kohlenstoff-Isotope ($\delta^{13}Corg$), Korngröße, geochemische Eigenschaften) mit hoher taxonomischer und zeitlicher Auflösung angewendet. Schließlich wurde der REVEALS-Ansatz auf den fossilen Pollendata des Otjikoto-Sees angewendet, um die Vegetationsbedeckung der Vergangenheit quantitativ zu rekonstruieren. Dazu wurden zunächst die Pollenproduktivitätsschätzungen (PPE) der relevantesten Savannentaxa in der Region unter Verwendung des erweiterten R-Wert-Modells und zweier Pollenausbreitungsmodelle (Gaußsches Federmodell und Lagrange-Stochastikmodell) berechnet. Die auf REVEALS basierende Vegetationsrekonstruktion wurde dann unter Verwendung von auf Fernerkundung basierenden regionalen Vegetationsdaten validiert.

Die Ergebnisse zeigen, dass moderner Pollen die Zusammensetzung der Vegetation gut widerspiegelt, jedoch weniger die Diversität. Interessanterweise machen Niederschlag und Beweidung einen signifikanten, aber geringen Anteil der Änderung der Zusammensetzung in den Pollen- und Vegetationsspektren aus. Die Multiproxy-Analyse zeigt, dass ein Zustandswechsel von der offenen *Combretum* Baumsavanne zum *Terminalia* Buschland über ein Jahrhundert stattfinden kann und dass der Übergang zwischen den beiden Zuständen etwa 80 Jahre dauert und durch eine einzigartige Vegetationszusammensetzung gekennzeichnet ist.

Dieser Übergang wird durch allmähliche Umweltveränderungen unterstützt, die durch das Management (z.B. großflächige Abholzung für den Bergbau sowie selektive Beweidung und

verringerte Feueraktivität verbunden mit intensivierter Landwirtschaft) und damit verbundene Landnutzungsänderungen hervorgerufen werden. Abgeleitete Umweltveränderungen (z.B. verringerte Bodenfeuchtigkeit, verringerte Grasbedeckung, Änderungen der Artenzusammensetzung und Konkurrenzfähigkeit, verringerte Feuerintensität) können die Resilienz der offenen *Combretum* Baumsavanne beeinträchtigt haben und sie anfälliger machen, durch stochastische Ereignisse wie aufeinanderfolgende niederschlagsreiche Jahre, Dürre, und durch hohe Konzentrationen von $p\mathrm{CO}_2$, in einen verbuschten Zustand zu wechseln. Der daraus resultierende verbuschte Zustand wird durch Rückkopplungsmechanismen aufrechterhalten, welche die Etablierung und Konkurrenzfähigkeit der Holzvegetation begünstigen.

Schließlich deuten die auf REVEALS basierenden Deckungsschätzungen auf das Vorherrschen einer halboffenen Landschaft während des gesamten 20. Jahrhunderts und eine Verringerung der Grasbedeckung unter 50% seit dem 21. Jahrhundert hin, die mit der Verbreitung von Verbuschungstaxa verbunden ist. Deckungsschätzungen zeigen eine enge Übereinstimmung mit regionalen Vegetationsdaten, wodurch die aus der Multi-Proxy-Analyse abgeleitete Vegetationsdynamik bestätigt werden kann. Die PPE-Berechnung war für alle holzigen Taxa erfolgreich, für Poaceae jedoch fehlgeschlagen.

Zusammenfassend ist die Pollenanalyse ein geeignetes Instrument zur Rekonstruktion der Vegetationsdynamik in Savannen. Aufgrund der geringen taxonomischen Auflösung von Pollen zur Identifizierung von Gräsern ermöglicht ein Multiproxy-Ansatz, insbesondere die Verwendung von *seda*DNA, die Unterscheidung stabiler verbuschte Zustände von bloßen Waldphasen sowie die Identifizierung von Auslösern und Treibern von Zustandsänderungen. Darüber hinaus spiegelt die auf REVEALS basierende quantitative Vegetationsrekonstruktion trotz der Einschränkungen bei der Berechnung von PPEs deutlich das Ausmaß der Veränderungen in der Vegetationsbedeckung wider, die in den letzten 130 Jahren aufgetreten sind.

Diese Forschung liefert neue Einblicke in die Pollen-Vegetations-Beziehungen in Savannen und unterstreicht die Bedeutung von Multiproxy-Ansätzen zur Rekonstruktion der Vegetationsdynamik in semi-ariden Landschaften. Es bietet auch die erste Zeitreihe mit ausreichender taxonomischer Auflösung, um die Veränderungen der Vegetationszusammensetzung im Verlauf der Verbuschung sowie die erste quantitative Rekonstruktion der früheren Landbedeckung in der Region aufzuzeigen. Diese Ergebnisse können dazu beitragen, die verschiedenen Stadien der Savannendynamik besser zu identifizieren, und können auch zur Kalibrierung von Vorhersagemodellen für Vegetationsänderungen verwendet werden, die für die Landbewirtschaftung von großem Wert sind.

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1 General introduction

Sustainable management of savanna ecosystems requires a desirable balance of grass and woody vegetation (Archer et al., 2017). Shrub encroachment upsets this balance, which is a major concern for land managers and policy makers, not only because encroachment threatens the livelihoods of livestock-dependent households (70% of Namibia's population is involved in the agricultural sector, of which livestock production represents 75% of total agricultural production; Sweet and Burke, 2006), but also because it affects other ecosystem services. This is a challenge, as climate change and human impact can result in a change in ecosystem structure and function that will be difficult to reverse on a management time scale (Joyce et al., 2013; Polley et al., 2017). Furthermore, the rapid growth of the human population in Namibia increases the demand for ecosystem services that must continue to be provided.

Although shrub encroachment affects savannas worldwide (Saha et al., 2015; Stevens et al., 2017; Tian et al., 2017), generalizations about their pathways are difficult, as encroachment involves the interaction between climate, species-specific adaptations, and land use history (Joubert et al., 2008). Such interactions make it difficult to discern natural fluctuations in the abundance of woody vegetation, from a change to an encroached state, posing a challenge for land managers and policy makers in identifying problems and developing appropriate solutions (Archer et al., 2017).

A long-term perspective on savanna dynamics is therefore needed, particularly to assess the resilience of these ecosystems to changing environmental conditions. This thesis contributes to understanding the dynamics of shrub encroachment in the past, by combining different methodological approaches. The motivation for this thesis is to provide a detailed analysis of a sediment record, which allows us to reconstruct the compositional changes that have occurred in the last 170 years in the Namibian savannas, as well as to infer the triggers and drivers of encroachment, and its stabilizing feedback mechanisms. By providing a quantitative reconstruction of land cover over time, this study contributes to understanding the state and functioning of current ecosystems and enables a more refined prediction of future environmental change.

1.1 The background problem: shrub encroachment

Shrub encroachment is a wide-spread phenomenon in southern African savannas with far-reaching ecological and economic consequences (De Klerk, 2004; Moyo et al., 1993; O’Connor et al., 2014). Shrub encroachment is assumed to indicate a savanna state change from open woodlands and grasslands, characterized by a dominance of C_4 grasses, to a bush-thickened savanna (Joubert et al., 2008; Meyer et al., 2007). However, a mere increase in woody cover, as reported by several studies since the 20th century (Hoffman et al., 2019; van Rooyen et al., 2018; Wiegand et al., 2005), does not necessarily mean shrub encroachment, since the African savannas are characterized by grassland/woodland phases that occur with a periodicity of 250–600 years (Gil-Romera et al., 2010; Gillson, 2004). Instead, the identification of shrub encroachment as an alternative state implies the increasing cover of encroacher species and the suppression of palatable perennial grasses (Gil-Romera et al., 2010, and references therein).

Shrub encroachment has different impacts on ecosystems, particularly on species richness (Grellier et al., 2013; O’Connor and Chamane, 2012), community composition (Blaum et al., 2007; Skarpe, 1986), and rangeland sustainability (Belayneh and Tessema, 2017). Although long-term effects of shrub encroachment are projected under different future scenarios (Aleman et al., 2016; Midgley and Bond, 2015), little is known about the resilience of savannas in the past (Gil-Romera et al., 2010), or about how fast a transition to an encroached state can occur.

African savannas are assumed to be constrained by climate, soil properties and disturbances (Azihou et al., 2013; Bond, 2008; Staver et al., 2011). Due to the prevailing arid conditions, the Namibian savannas are characterized by low tree density, which in turn decreases along a north-south precipitation gradient with an average annual precipitation range of 600–200 mm (Mendelsohn et al., 2010). At the lower end, savannas are mainly constrained by precipitation (Joubert et al., 2008; Sankaran et al., 2005), while disturbances such as fire and herbivory mainly determine the grass-tree balance with increasing precipitation (Bond, 2008; Sankaran et al., 2005; Scholes, 1997). Therefore, changes in precipitation regimes associated with changes in fire frequency and intensity are expected to upset the balance between trees and grasses and promote the recruitment and spread locally of encroacher species (Case and Staver, 2017; Devine et al., 2017; Joubert et al., 2012). Interestingly, Namibian rangelands are most affected by shrub encroachment, which has been attributed to fire and grazing mismanagement (i.e. fire suppression and overgrazing; De Klerk, 2004; Rohde and Hoffman, 2012).

Despite the fact that precipitation, $p\mathrm{CO}_2$, vegetation fires, and land use are recognized as triggers and/or drivers of shrub encroachment (Aleman et al., 2016; Berry and Kulmatiski, 2017; Buitenwerf et al., 2012; Case and Staver, 2017), there is still no clarity on how these factors interact at global and local scales, or at different timescales. This is important, because such interactions have different effects on the encroacher species (Joubert et al., 2013, 2012, 2008), which affects the stability of the savannas.

1.2 The study area: an encroachment hotspot

The study sites are located along a north-south precipitation gradient in north-central Namibia (Fig. 1-1; detailed descriptions of the sites are provided in Chapters 2–4). This area has an average annual precipitation range of 212–460 mm (Harris et al., 2014), and an aridity range of 0.11–0.26, which places the area within the range of the arid to semi-arid ecosystems (UNEP, 1997).

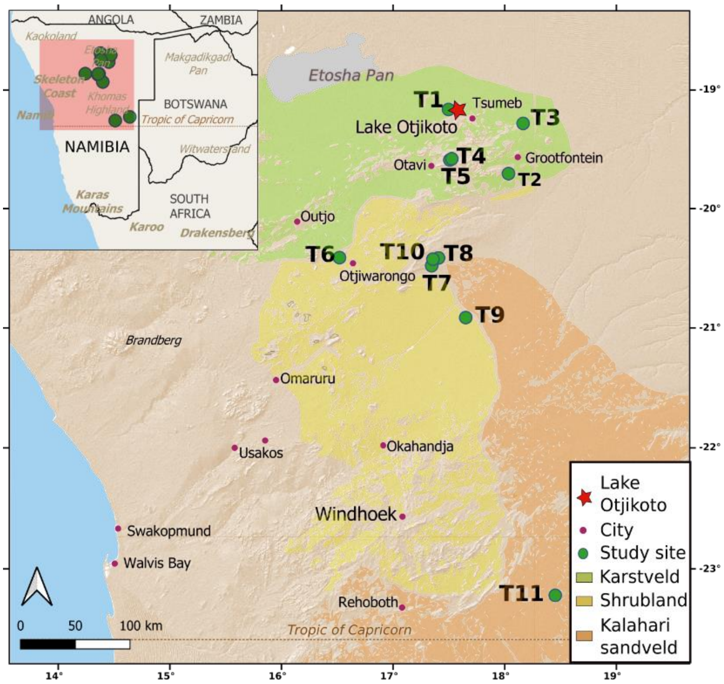

Figure 1-1. Map of the study area in Namibia. Relevant landscapes displayed after Mendelsohn et al, 2010.

The study area covers three different landscapes: the Karstveld in the north, the thornbush shrubland, and the Kalahari sandveld in the south (Mendelsohn et al., 2010). These landscapes are defined by distinctive vegetation and geological contrasts. The main vegetation types are mixed woodlands dominated by broadleaf taxa in the Karstveld, and *Acacia* shrublands and woodlands in the southern landscapes (Mendelsohn et al., 2010). The dominant encroacher species are *Terminalia prunioides* and *Dichrostachys cinerea* in the Karstveld and *Senegalia mellifera* in the thornbush and Kalahari areas (De Klerk, 2004).

North-central Namibia is the region most affected by shrub encroachment in the country (De Klerk, 2004). It is estimated that 30 million hectares in Namibia are being invaded by shrubs, which are found mainly within a rainfall range of 300–600 mm, particularly on loamy and clayey soils (De Klerk, 2004; Mendelsohn et al., 2000). In the Karstveld, more than 90% of the Tsumeb rangeland area has been invaded by shrubs, of this about 30% at very high densities, losing approximately 50–80% of the carrying capacity (Mendelsohn et al., 2000). This is a major concern for land managers, as shrub encroachment reduces agricultural productivity and therefore reduces the economic value of agricultural land (Mendelsohn et al., 2010).

Understanding the dynamics of shrub encroachment in the region is essential to predict possible ecosystem responses to future environmental changes in Namibia, in particular to increased temperatures and decreased rainfall (Mapaure, 2011). Under this future scenario, low water availability for plants, combined with population growth and human impact, can have a major impact on the ecosystem (Midgley et al., 2005). Therefore, to understand the current dynamics of the savanna and to be able to make reliable predictions about its resilience in the future, it is necessary to investigate the dynamics of vegetation in the past and its responses to a changing environment.

1.3 The analytical frame: savanna state transitions

State transition models are based on the multiple stable state concept (Holling, 1973; May, 1977) and the non-equilibrium paradigm (Ellis and Swift, 1988; Wiens, 1984). Accordingly, a state differs qualitatively from other states within the same system, and a transition implies a qualitative change in a given state induced by changes in the magnitude of external forces to the system (*exogenous factors* sensu D’Odorico et al., 2012; Li, 2002). These forces in turn prevent the system from reaching an equilibrium state (Briske et al., 2005; Li, 2002).

State transition models were originally developed to explain vegetation dynamics, particularly in rangelands (Dougill and Thomas, 2004; Westoby et al., 1989). Applied to savanna environments, these models allow us to interpret savannas as bistable systems, where vegetation fluctuates between herbaceous and woody states as alternative stable states (D’Odorico et al., 2012; Gil-Romera et al., 2010; Gillson, 2004). However, resilience of savanna ecosystems seems to be scale dependent. For example, savanna seems to be resilient to changes at a centennial timescale, as the vegetation fluctuates between grassland and woodland phases with a periodicity of 250–600 years (Gil-Romera et al., 2010; Gillson, 2004). Conversely, savanna seems to be less resilient at a decadal scale, as encroachment may occur within a century and without regression to a grassy state even at a patch scale (Rohde and Hoffman, 2012). Similarly, African landscapes are predicted to shift to woodland states, with abrupt transitions at the local scale, but smoother at the continental scale (Higgins and Scheiter, 2012).

Different models have been proposed to explain shrub encroachment according to the specific environments where it takes place and the encroacher species involved (Brown and Archer, 1999; Roques et al., 2001). In Namibia, the encroachment caused by *Senegalia melllifera* has been explained with a state-transition model, which takes into account the specific phenological cycle of the species, the timing of different environmental and anthropogenic events, as well as animal/plant interactions (Joubert et al., 2008). The validation of this model with field experiments showed that the savannas constitute a mosaic of herbaceous and woody patches, with grasses forming the matrix on the landscape scale. This enables savannas to experience multiple different states and transitions at a patch scale. During transition to an encroached state on the landscape scale, the herbaceous patches degrade or become bare until the woody patches become the matrix. Surprisingly little is known about the duration of such transitions (Higgins and Scheiter, 2012; Joubert et al., 2008) or the compositional changes they entail (Joubert et al., 2008; Liao et al., 2018).

Impact of triggers/drivers on ecosystem variables

The triggers and drivers of savanna state change are generally associated with broad-scale changes, such as increasing atmospheric $p\mathrm{CO}_2$ concentrations, changes in precipitation or temperature regimes, growth of the human population and large-scale management (Aleman et al., 2016; Buitenwerf et al., 2012; D’Odorico et al., 2012). They are considered not to be coupled with, but to modify, ecosystem feedback mechanisms (Briske et al., 2005; Li, 2002). Therefore, a continuous change in the magnitude of a driver can alter ecosystems in such a way that a threshold (or critical point) will be reached, which once passed can lead to an irreversible change of state (Li, 2002).

Ecological systems are assumed to be regulated by control variables, which are buffered by feedback mechanisms and thus stable over time (Briske et al., 2017). Control variables comprise the main ecological processes (i.e., primary production and nutrient cycle, biodiversity, functional groups, fire and grazing regimes; Briske et al., 2017). These variables have a controlling influence on fast variables (e.g., seasonal plant and animal production, compositional shifts in annual and transient species, soil water availability, pathogen, and insect dynamics; Briske et al., 2017), which are characterized by dynamic and rapid responses to external drivers.

Modifying control variables either directly by drivers or indirectly by feedback mechanisms is the main way in which resilience is modified (Briske et al., 2017). When a driver of sufficient magnitude (e.g., drought) modifies one or more control variables (e.g., fire and grazing), they in turn affect numerous rapid variables (e.g., grass growth and livestock numbers), establishing the threshold conditions necessary to change to an alternative stable state (Briske et al., 2017, 2005). Management legacies for example are assumed to affect the properties of temperate woodland responses to current environmental change up to 200 years after disturbance (Perring et al., 2018). Similarly, shrub encroachment of Namibian savannas has been related to management strategies during colonial administration (Moyo et al., 1993; Rohde and Hoffman, 2012; Verlinden and Kruger, 2007). However, it remains unclear to what extent management may have affected species composition and thus savanna stability in Namibia.

Environmental feedbacks

Feedback mechanisms (*endogenous mechanism*s sensu D'Odorico et al., 2012) describe the interaction between ecological variables to amplify (positive feedbacks) or buffer (negative feedbacks) the rate of change in a system (Briske et al., 2017). Stabilizing (negative) feedbacks reduce the rate of change in the system. For example, a high perennial grass cover provides abundant continuous fuel loads, allowing frequent fires to prevent the establishment of encroacher woody species, thus maintaining a grass-dominated landscape (D'Odorico et al., 2012; Joubert et al., 2012).

In contrast, amplification (positive) feedback accelerates change between variables. A change in the composition of plant species (e.g., spread of *Senegalia mellifera*), may be induced by an external driver (e.g., consecutive years of high precipitation), but be sustained by internal positive feedbacks that reinforce the initial change in vegetation (Joubert et al., 2008). Shrub encroachment, has been associated with feedback mechanisms that involve, among others, interactions of vegetation cover with fire dynamics, and interactions between soil erosion, loss of soil nutrients, water resources and microclimate (D'Odorico et al., 2012; Joubert et al., 2012; Ravi et al., 2009).

The interaction between positive and negative feedback mechanisms may induce the bistability observed in African savannas at centennial scales (Gil-Romera et al., 2010; Gillson, 2004). When the relative strength of the amplifying feedback exceeds that of the stabilizing feedback, one or more control variables can be modified enough to create threshold conditions and initiate the transition to an alternative state (Briske et al., 2017). Once an alternative state has been reached, resilience is established through a unique set of control variables and feedback mechanisms, preventing a reversal over the thresholds (Briske et al., 2005; Scheffer et al., 2001). This would explain why debushing may have limited success in some encroached areas (Rango et al., 2005; Wilcox et al., 2017).

Thresholds

Thresholds represent limits between alternative stable states (Li, 2002; Scheffer et al., 2001). A threshold can be triggered by a specific disturbance or event, which induces changes in the ecosystem, which in turn are reinforced by positive feedbacks (Briske et al., 2017, 2005). As thresholds involve interactions between external drivers, control variables, and feedback mechanisms on different time and space scales, it is difficult to identify ecological indicators that allow them to be anticipated or described (Briske et al., 2017). For example, in the highland savannas of Namibia, which are invaded by *Senegalia mellifera*, high grazing pressure and consequent loss of grass cover does not directly result in a transition to an encroached state if there is not enough rain for seed production and seedling establishment (Joubert et al., 2013, 2008). However, the probability of reaching a threshold in the future is high if the rain events become more frequent. Therefore, it seems unlikely that high grazing pressure alone will cause a shift from grass to shrub-dominated landscapes, but the stability of an encroached state can be clearly enhanced by grazing (e.g., shrub encroachment may perpetuate itself as it forces farmers to overgraze existing open patches; Joubert et al., 2008).

1.4 The methodological challenge: palaeoecological research in semi-arid savannas

Palaeoecological research in semi-arid environments is challenged by the poor preservation of macro and microfossil material, as well as the scarcity of adequate archives and continuous fossil records. The reconstruction of past dynamics in these environments involves the use of different proxies, generally applied to sediment cores and animal middens. In particular, the analysis of pollen and spores has been shown to be useful for documenting past and present vegetation composition in savannas (Schüler et al., 2014; Scott et al., 2012, 1991; Valsecchi et al., 2013), as well as climate-related environmental change (Gajewski et al., 2002; Hely et al., 2006; Lézine et al., 2009; Watrin et al., 2007), and human impact (Ekblom and Gillson, 2010; Mighall et al., 2012; Msaky et al., 2005). This is because pollen types allow plants to be identified at different taxonomic levels, and thus environmental changes that alter the composition of vegetation will also be reflected in the pollen record. Pollen records can therefore also be indicators of climate- or human-induced disturbance.

The identification of shrub encroachment in the long-term, however, is limited by the low taxonomic resolution of the pollen types. In particular, the Poaceae pollen type cannot capture changes in the composition of grass species, especially perennial/annual grasses. As an alternative, analysis of sedimentary ancient DNA (*seda*DNA) in palaeoecological studies provides improved taxonomic resolution that allows better inference of vegetation composition and diversity in African tropical forests (Boessenkool et al., 2014; Bremond et al., 2017). Furthermore, ancient DNA provides a stronger signal of changes in the plant community than plant microfossils, which has been demonstrated in arid environments with ancient DNA from coprolites (Murray et al., 2012) and in other environmental settings (Epp et al., 2015; Parducci et al., 2015).

Although fossil pollen and *seda*DNA are useful complementary proxies in paleoecology, it is still a challenge to know to what extent these proxies can reflect regional vegetation in the savannas, considering that most woody species are pollinated by insects or other animals and DNA is of local origin. Recent studies estimate the DNA source area to be a few hundred metres or perhaps a few kilometres from the catchment area (Alsos et al., 2018). Accordingly, DNA not only reflects local, shore and aquatic vegetation well, but also the dominant regional vegetation, because the greater the biomass, the greater the possibility of deposition. It is assumed that erosion provides most of the plant DNA to the lake sediments (Giguet-Covex et al., 2019). For this reason, high erosion rates, as reflected by end-members in the present study (Chapter 3) for example, can positively affect the representation of regional flora, especially through runoff. With respect to the relative source area of pollen (RSAP) for savanna vegetation, it is estimated that the animal-pollinated taxa have an RSAP of approximately 1 km

(Duffin and Bunting, 2008; Mariani et al., 2016), but depending on the dispersal model used, this area can extend up to 10 km (Mariani et al., 2016).

In addition to pollen and *seda*DNA, the use of proxies such as charcoal, isotopes and geochemical proxies have demonstrated their potential to relate vegetation change to fire dynamics (Colombaroli et al., 2018; Gillson and Ekblom, 2009), vegetation structure and hydrological variability (Garcin et al., 2018; Miller et al., 2019; Walther and Neumann, 2011) in savannas. Therefore, detailed analysis of a sedimentary record with a multiproxy approach is necessary to clearly identify shrub encroachment in the past and infer the interaction between their triggers and drivers. Such a study requires suitable sedimentary archives, which are rare in Namibia. In this sense, Lake Otjikoto, a sinkhole lake located in the Karstveld, represents a unique environmental archive (Scott et al., 1991). Due to its depth and lack of inflow, it provides favourable conditions for the conservation of organic material (particularly sedaDNA; Alsos et al., 2018) despite its alkalinity.

Estimating the magnitude of human and climatic impact on landscape opening and its consequences on savanna resilience, requires pollen-based quantitative reconstructions of past land cover. Pollen reconstructions assume that pollen deposition at a site is related to the abundance of the associated species in the surrounding vegetation (Davis, 1963). However, pollen deposition in the savanna is characterized by over-representation of wind-pollinated grasses and under-representation of insect-pollinated shrubs and trees that dominate the vegetation (Duffin and Bunting, 2008; Mariani et al., 2016). Consequently, the interpretation of pollen records needs to consider the poor representation of woody taxa (Lézine et al., 2009; Vincens et al., 2006), and the variable pollen productivities among the species of grasses fused under the Poaceae pollen type (Groenman-van Waateringe, 1993; Prieto-Baena et al., 2003). An understanding of modern pollen-vegetation relationships is thus essential to provide confidence in the interpretation of fossil pollen records regarding vegetation composition and diversity. In addition, making pollen productivity estimates (PPEs) for encroacher taxa is required to quantify changes in landscape cover from pollen data.

1.5 Aims of this thesis

As a part of the OPTIMASS (options for sustainable geo-biosphere feedback management in savanna systems under regional and global change) project, this PhD research focuses on understanding the vegetation-environmental feedbacks in the Namibian savanna over the long term. Due to the challenges associated with doing palynology in arid and semi-arid environments, this thesis also aims to assess the potential of pollen to track vegetation change under changing environmental conditions.

This study addresses three main research questions: 1) is pollen analysis a suitable tool to reflect the vegetation change associated with shrub encroachment in savanna environments? 2) Does the current encroached landscape correspond to an alternative stable state of savanna vegetation? 3) To what extent do pollen-based quantitative vegetation reconstructions reflect changes in past land-cover?

Based on these questions, this study pursues the three following aims:

1. To validate whether pollen analysis is a suitable tool for reconstructing vegetation composition and diversity under changing climate and land-use in savanna environments.

2. To reconstruct past vegetation dynamics at Lake Otjikoto and assess the potential of multiproxy approaches to document savanna state changes, and to identify potential triggers and drivers and related feedbacks of vegetation change.

3. To make pollen productivity estimates (PPEs) for the major plant taxa characteristic of the Namibian savanna and to identify the potentials and limitations of applying REVEALS to reconstruct past land cover from the fossil pollen record of Lake Otjikoto.

An overview over the methods, data and materials used in this research is given in figure 1-2.

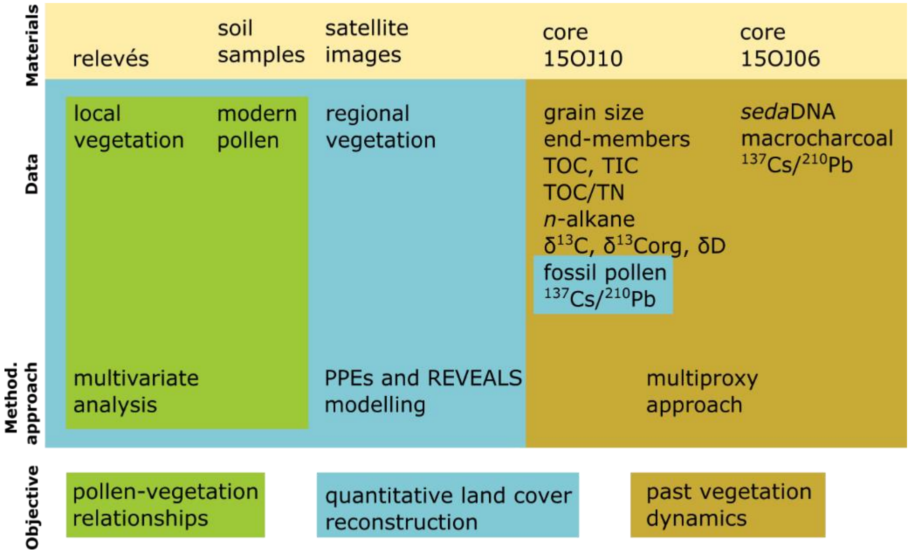

Figure 1-2. Overview over the methods, data and materials.

1.6 Outline

This thesis consists of five chapters and is designed as a cumulative dissertation. The first chapter presents the general introduction, discussing the main research problem, the analytical framework, the methodological challenges and the objectives of this research. Chapters 2 to 4 were prepared as manuscripts for publication in peer-reviewed scientific journals and constitute the main content of this thesis. Chapter 5 summarizes the main results of this research, discussing its implications and perspectives. All data supporting this research are archived in Pangaea.

Manuscripts included in this thesis and contributions from the authors are as follows:

Chapter 2 – Manuscript 1 published in *Review of Paleobotany and Palynology* in 2018:

Tabares, X., Mapani, B., Blaum, N., Herzschuh, U., 2018. Composition and diversity of vegetation and pollen spectra along gradients of grazing intensity and precipitation in southern Africa. Rev. Palaeobot. Palynol. 253, 88–100. doi:10.1016/j.revpalbo.2018.04.004

XT and UH conceived the ideas and designed methodology; XT performed vegetation surveys and pollen analysis; XT performed statistical and diversity analysis; under supervision of UH, XT wrote a first draft of the manuscript that all coauthors commented on. All authors gave final approval for publication.

Chapter 3 – Manuscript 2 published in *Ecology and Evolution* in 2020:

Tabares, X., Zimmermann, H., Dietze, E., Ratzmann, G., Belz, L., Vieth-Hillebrand, A., Dupont, L., Wilkes, H., Mapani, B., Herzschuh, U., 2020. Vegetation state changes in the course of shrub encroachment in an African savanna since about 1850 CE and their potential drivers. Ecol. Evol. 10, 962–979. doi:10.1002/ece3.5955

XT and UH conceived the ideas and designed methodology; XT and LD performed fossil pollen and macrocharcoal analyses; XT and HZ performed sedaDNA analyses; XT and ED performed grain-size and end-member modeling analysis; LB, AV-H, HW, and XT performed biogeochemical and sedimentological analyses. Under supervision of UH, XT wrote a first draft of the manuscript that all coauthors commented on. All authors gave final approval for publication.

Chapter 4 - Manuscript 3 submitted to *The Holocene* in 2020:

Tabares, X., Ratzmann, G., Kruse, S., Theuerkauf, M., Mapani, B. and Herzschuh, U. 2020. Relative pollen productivity estimates of savanna taxa from southern Africa and their application to reconstruct shrub encroachment during the last century. *Submitted.* ID: HOL-20-0065.

XT and UH conceived the ideas and designed methodology; XT performed field vegetation surveys and pollen analysis; GR, SK and XT performed remote-sensing based vegetation analysis; XT and MT made pollen productivity estimates and performed quantitative vegetation reconstruction. Under supervision of UH, XT wrote a first draft of the manuscript that all coauthors commented on. All authors gave final approval for submission.

2 Manuscript 1

Composition and diversity of vegetation and pollen spectra along gradients of grazing intensity and precipitation in southern Africa

Review of Palaeobotany and Palynology 253 (2018) 88–100

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Abstract

Understanding vegetation–modern pollen relationships is essential to provide confidence in fossil pollen reconstructions of long-term vegetation changes in savanna ecosystems. In this paper we compare the taxonomical composition and the diversity (Hill N0, N1, N2) of vegetation and modern pollen along precipitation and local grazing-intensity gradients in Namibian savannas. Modern pollen was extracted from surface soil samples collected from 5x5 m plots distributed along four 500 m gradients. Vegetation was surveyed in each plot. The results show a high correspondence between vegetation and pollen data in terms of composition. Precipitation and grazing explain a significant although low proportion of compositional change in the vegetation and pollen spectra. We identified pollen taxa as indicators of grazing pressure such as *Limeum, Alternanthera,* and particularly *Tribulus*. Correspondence between vegetation and pollen data in terms of taxa richness (N0) is limited, probably because of the influence of landscape heterogeneity and openness, as well as low pollen concentrations. In contrast, the effective numbers of common and dominant taxa (N1, N2) are consistent among the different datasets. We conclude that in spite of limitations, modern pollen assemblages can reflect changes in vegetation composition, richness and diversity patterns along precipitation and grazing gradients in savanna environments.

2.1 Introduction

Recent global climate change correlates with an increase of woody cover in savannas worldwide (Stevens et al. 2016; Tian et al. 2016; Saha et al. 2015). In African savannas, woody encroachment is a major concern for land managers and policymakers because of the various effects on ecosystem structures and services such as species richness (Grellier et al., 2013; O'Connor and Chamane, 2012), community composition (Blaum et al., 2007; Skarpe, 1986), and rangeland sustainability (Belayneh and Tessema, 2017). Surprisingly, while long-term effects of woody encroachment are projected under different future scenarios (Aleman et al., 2016; Midgley and Bond, 2015), there is limited knowledge about vegetation dynamics in the past (Rohde and Hoffman, 2012; Wigley et al., 2009). Understanding past vegetation changes is important since there is no consensus about the major drivers of shrub encroachment. It is assumed that increasing atmospheric CO_2 (Bond et al., 2003; Buitenwerf et al., 2012), changes in precipitation regimes, soil nutrient availability (Sankaran et al., 2008; Ward, 2005), fire suppression, and grazing release (Scholes and Archer, 1997; Skarpe, 1990) support the expansion of trees and shrubs. However, understanding the interplay among the different drivers remains a challenge (Synodinos et al., 2018). An absence of long-term vegetation datasets from Africa hinders such research (Muche et al., 2012).

Previous studies have shown that pollen analysis of sedimentary archives is a suitable tool to depict past vegetation change in African savannas (Valsecchi et al. 2013; Scott et al. 2012, 1991; Dupont 2006). However, the interpretation of fossil pollen records with respect to quantitative vegetation composition and diversity remains challenging because of restricted understanding of vegetation–pollen relationships. For example, Schüler et al. (2014) find approximately similar trends in taxa composition and diversity between pollen and vegetation records along an elevational gradient on Kilimanjaro, but they note that complex wind patterns complicate the quantification of the relationships. Vincens et al. (2000) tracked the successional stages of forest colonisation of open savannas using modern pollen spectra and also note a highly non-linear relationship between pollen and vegetation composition, probably as a result of the various pollen production and dispersal strategies among plant species.

Modern pollen records have also been used to study pollen–climate relationships at broad regional scales (Gajewski et al., 2002; Hély et al., 2006; Lézine et al., 2009; Watrin et al., 2007), but the low taxonomic resolution of major African pollen taxa limits their value as climate indicators since, in many cases, an individual pollen taxon encompasses a number of plant species that grow in climatically different habitats (Watrin et al., 2007). Furthermore, studies that assess the indicator value of modern pollen spectra for different types of land-use in African savannas, such as cropland, livestock farming, and settlements are lacking, even though the potential of palynology to track long-term land-use change has long been recognised (Ekblom and Gillson, 2010; Mighall et al., 2012; Msaky et al., 2005). Several studies performed in mesic and humid environments show that modern pollen–vegetation relationships in fragmented landscapes are particularly complex (Bunting et al., 2016; Groenman-van Waateringe, 1993; Lézine et al., 2009). The underrepresentation of key entomophilous taxa in disturbed tropical forests (Lézine et al., 2009; Vincens et al., 2006), the background pollen load in cleared temperate forests (Bunting et al., 2016), and contrasting pollen productivities in temperate grasslands (Groenman-van Waateringe, 1993) contribute strongly to the observed biases.

While previous approaches show the relevance and challenges of using modern pollen data to investigate climate, land-use, and vegetation, studies that explore the relationship between vegetation and modern pollen along both precipitation and grazing gradients in southern African savannas are still missing. This is particularly important because modern pollen analogues are needed to interpret and to validate fossil pollen-based reconstructions of past vegetation, climate change, and human impact in arid and semi-arid environments.

Our study investigates vegetation–modern pollen relationships along precipitation and grazing intensity gradients in Namibian savannas. We performed vegetation surveys and collected pollen from surface soil samples to test whether modern pollen reflects: (1) vegetation richness and diversity patterns and (2) vegetation compositional change along precipitation and grazing intensity gradients. The results allow us to assess the potential of pollen to track changes in vegetation composition and diversity under changing climate and land-use.

2.2 Methods

2.2.1 Study area

We selected four study sites in three different landscape types (Mendelsohn et al., 2010) located along a north–south precipitation gradient in northern central Namibia (Fig. 2-1) to infer the influence of precipitation and grazing on the diversity and composition of vegetation. The distance between the northernmost and the southernmost sites is approximately 440 km.

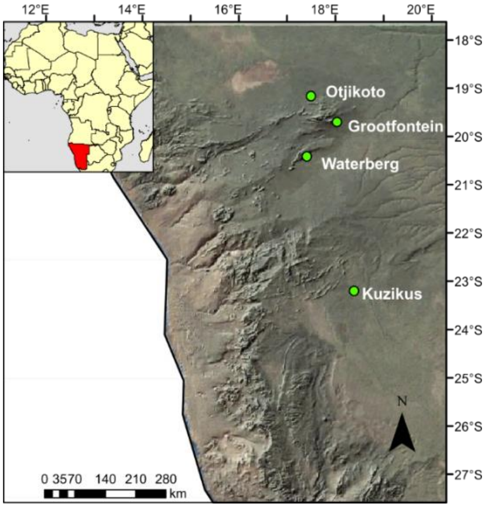

Figure 2-1. Map of the study site locations in Namibia.

The two northern and more humid sites (Otjikoto, Grootfontein) are in the Karstveld south of the Etosha Pan. Mean annual precipitation is 456 mm (Tsumeb climate station; Harris et al., 2014). Local substrate is dominated by soluble dolomite and limestone, while the main top soils are cambisols and chromic luvisols along with rock outcrops. Vegetation is mixed woodland dominated by *Colophospermum mopane, Combretum imberbe, Dichrostachys cinerea,* and *Terminalia prunioides* (Mendelsohn et al., 2010, 2000). Otjikoto is encroached and has a low ground cover (Table 2-1).

Table 2-1. Overview of the four study sites including GPS coordinates of the first plot in each transect. Mean annual precipitation (MAP) was estimated from climate station data (Harris et al., 2014), vegetation structure and landscape according to Mendelsohn et al. (2010), and mean ground cover was estimated on the basis of the vegetation survey data.

Site	**Farm**	**Latitude S**	**Longitude N**	**Elevation (m)**	**MAP (mm)**	**Vegetation structure**	**Landscape**	**Mean ground cover (%)**
Otjikoto	Otjiguinas	-19.16549	17.49638	1212	456	Mixed woodland	Karstveld	59
Grootfontein	John Pandeni Research Station	-19.70722	18.03505	1426	455	Mixed woodland	Karstveld	83
Waterberg	Okomumbode Breeding Farm	-20.41629	17.4066	1398	342	Acacia shrubland	Inselberg	91
Kuzikus	Kuzikus Wild Farm	-23.2012	18.38646	1350	212	Open Acacia woodland	Kalahari sandveld	23

The third study site, Waterberg is a sandstone formation located on the west border of the central western plains. Mean annual precipitation is 342 mm (Omambonde climate station; Harris et al., 2014). Local substrate is dominated by sands originating from the Etjo formation and from aeolian transport of Kalahari sands. Main top soils are arenosols, which have a higher clay content than those of the Kalahari sandveld (Jankowitz, 1983). Vegetation comprises a mosaic of mixed woodland growing on the plateau and along the margins of ephemeral rills, and *Acacia* shrubland that grows especially below the plateau. This distinction is presumed to reflect differences in clay and humus content in the soil (Wahl, 2003). The mixed woodland comprises broad-leaved taxa such as *Terminalia sericea, Burkea africana,* and *Baiquiaea plurijuga* while *Acacia* shrubland is dominated by *Acacia erioloba*. Scree slopes are dominated by grasses and forbs (Wahl, 2003).

The southern and most arid site is located at Kuzikus in the Kalahari sandveld. Mean annual precipitation is 212 mm (Dornenpfanne climate station; Harris et al., 2014). The sandveld is composed of deposits of sands, clays, and calcretes and the dominant top soil is ferralic arenosol. Vegetation corresponds to open *Acacia* woodland and includes species such as *Acacia mellifera, A. erioloba, Boscia albitrunca,* and *Grewia flava* (Mendelsohn et al., 2010).

Aside from a few national parks, most of the area between the four study sites is currently used for herding. All sites are situated on farms with either cattle or game and none were subject to clearance or chemical treatments (pers. comm.with the farmers). Wildfires have not occurred for at least the last 10 years.

2.2.2 Sampling design

At each site we investigated 11 plots of 25 m^2 with a distance of 50 m between each plot along a 500 m transect. Each transect started at an artificial livestock watering point and was set so that no buildings or further watering points occurred in the vicinity. We make the assumption that grazing intensity decreases along the transect because animals tend to remain close to watering points due to restricted water availability (Brits et al., 2002; Werger, 1977).

For each of the 44 plots, surface soil samples (approx. 60 gr) were collected from six subplots and pooled for subsequent pollen analysis.

Vegetation was recorded for every plot following Braun-Blanquet (Braun-Blanquet, 1964). For each plot a species list (Table 2-2) was compiled and aerial cover of each species was visually estimated at ground and tree layers. We assigned scores from one to four so as to infer the relative percentage cover of each species as follows: 1<5%, 2=5–25%, 3=25–50%, 4>50%. Aerial cover is used as a proxy for species abundance. Species identification followed (Mannheimer, 2012; Mannheimer et al., 2009; Müller, 2007), with critical identifications being made at the Botanical Institute of the University of Namibia in Windhoek. Surveys were conducted in April (Otjikoto, Grootfontein, Waterberg) and November 2015 (Kuzikus). Identification of some herbaceous taxa to species level was impossible due to drought and overgrazing, especially at Kuzikus.

Table 2-2. Summary of the taxa of the vegetation surveys and the corresponding plants as pollen-equivalents. Crosses indicate the presence of taxa at the study sites: Otj (Otjikoto); Grt (Grootfontein); Wat (Waterberg); Kuz (Kuzikus).

Species	**Otj.**	**Grt.**	**Wat.**	**Kuz.**	**Pollen equivalent**
Acacia ataxacantha			x		*Acacia*
Acacia erioloba			x	x	*Acacia*
Acacia fleckii			x		*Acacia*
Acacia hebeclada	x		x	x	*Acacia*
Acacia haematoxylon	x				*Acacia*
Acacia hereroensis			x		*Acacia*
Acacia karroo			x	x	*Acacia*
Acacia mellifera	x	x	x	x	*Acacia*
Acacia nilotica	x				*Acacia*
Achyranthes sp.			x		Chenopodiaceae/Amaranthaceae
Albizia anthelmintica			x		*Acacia*
Aloe sp.		x			*Aloe*
Alternanthera pungens	x				*Alternanthera*
Aptosimum sp.		x	x		Scrophulariaceae
Aristida congesta			x		Poaceae
Aristida sp.			x	x	Poaceae
Asparagus sp.				x	*Asparagus*
Asteraceae undeff.			x	x	Asteraceae
Bauhinia petersiana			x		*Bauhinia*
Bidens shimperii			x		*Senecio*
Boscia albitrunca			x		*Boscia*
Brachiaria sp.			x		Poaceae
Catophractes alexandrii			x		Bignoniaceae
Cenchrus ciliaris		x	x		Poaceae
Cleome monophylla			x		*Cleome*
Combretum hereroensis		x			Combretaceae
Combretum imberbe		x			Combretaceae
Commiphora angolensis		x	x		*Commiphora*
Commiphora glandulans	x				*Commiphora*
Crotalaria sp.		x			*Crotalaria*
Croton gratissimum	x		x		*Croton*
Croton sp.			x		*Croton*
Cucurbitaceae undeff.			x		Cucurbitaceae
Cyperaceae		x		x	Cyperaceae
Dichrostachys cinerea	x	x	x		*Dichrostachys cinerea*
Enneapogon sp.		x			Poaceae
Eragrostis sp.	x	x			Poaceae
Eriocephalus sp.		x			*Pentzia*
Euclea divinorum		x			*Euclea*
Euclea undulata		x			*Euclea*
Euclea sp.		x	x		*Euclea*
Geigeria ornativa		x			Daisy
Grewia falcistipula	x		x		*Grewia*
Grewia flava	x	x	x	x	*Grewia*
Grewia flavescens	x	x	x	x	*Grewia*

Species	**Otj.**	**Grt.**	**Wat.**	**Kuz.**	**Pollen equivalent**
Grewia sp.	x	x		x	*Grewia*
Grewia villosa	x	x			*Grewia*
Heliotropium sp.		x	x		*Heliotropium*
Helichrysum sp.		x			*Senecio*
Heteropogon sp.			x		Poaceae
Hibiscus sp.			x		Malvaceae
Indigofera sp.			x		*Indigofera*
Ipomoea sp.	x				*Ipomoea*
Justicia betonica			x		*Justicia/Monechma*
Laggera sp.				x	*Senecio*
Limeum	x	x	x		*Limeum*
Lamiaceae undeff.			x		Lamiaceae
Lantana sp.		x			*Lantana*
Marsdenia sp.	x				Apocynaceae
Melinis repens		x	x		Poaceae
Monechma sp.	x		x		*Justicia/Monechma*
Montinia caryophyllaceae	x				*Montinia caryophyllaceae*
Nidorella resedifolia			x		*Senecio*
Ozoroa sp.		x			*Heeria*
Panicum sp.			x		Poaceae
Pavonnia sp.			x		Malvaceae
Pergularia daemia	x				Apocynaceae
Philenoptera nelsii			x		*Philenoptera*
Poaceae undeff.	x	x	x	x	Poaceae
Pogonarthia squarrosa		x			Poaceae
Ptycholobium biflorum			x		*Ptycholobium*
Rhigozum brevispinosum			x		Bignoniaceae
Rhynchosia minima	x				*Rhynchosia*
Rhynchosia sp.	x				*Rhynchosia*
Schmidtia sp.			x		*Poaceae*
Searsia sp.		x	x		*Rhus*
Setaria verticulata	x		x		Poaceae
Sida ovata		x			*Sida*
Solanum sp.			x		*Solanum*
Spirostachys africana	x				*Spirostachys*
Stipagrostis sp.		x	x	x	Poaceae
Stipagrostis uniplumis		x			Poaceae
Tarchonanthus camphoratus		x			*Tarchonanthus*
Tephrosia purpurea			x		*Tephrosia*
Tephrosia sp.			x		*Tephrosia*
Terminalia prunioides	x	x			Combretaceae
Terminalia sericea			x		Combretaceae
Thiraphis sp.			x		Poaceae
Tribulus sp.	x				*Tribulus*
Vangueria sp.	x	x			*Vangueria*

Species	Otj.	Grt.	Wat.	Kuz.	Pollen equivalent
Vernonia fastigiata			x		*Vernonia*
Waltheria indica			x		*Waltheria*
Ximenia americanum			x		*Ximenia*
Ziziphus mucronata	x	x	x	x	*Ziziphus*

2.2.3 Modern pollen analyses

Surface soil samples were prepared for pollen analysis following standard procedures (HCl, KOH, HF – including 4 hours boiling – and acetolysis) (Faegri and Iversen, 1989; Moore et al., 1991). We added one *Lycopodium* tablet to each sample to calculate the pollen concentration (Stockmarr, 1971). The samples retained a large minerogenic fraction after standard treatment, so samples were stirred and decanted and the sediment subsequently controlled for absence of pollen. A minimum of 400 pollen grains were counted per sample using a microscope of x400 magnification, but in some cases this was not achievable due to low pollen concentration. Taxonomical identification (Table 2-3) was performed at x1000 magnification and based on standard literature (Bonnefille and Riollet, 1980; Gosling et al., 2013; Leźine, 2005; Reille, 1995; Scott, 1982). Pollen percentages were calculated relative to the total terrestrial pollen sum. Pollen diagrams were drawn using Tilia software (Grimm, 2004).

Table 2-3. List of identified pollen and spore types.

Pollen and spore types

Abutilon
Acacia
Acanthaceae
Adenium
Aloe
Alternanthera
Anacardiaceae
Anthoceros
Arctotis
Asparagus
Asteraceae
Barleria
Bauhinia
Bignoniaceae
Blepharis
Boscia
Baikiaea
Burkea
Cadaba
Canthium
Capparaceae
Caryiophyllaceae
Chascanum
Cleome
Combretaceae
Commelina
Commiphora
Convolvulaceae
Corchorus
Cordia
Corymbium
Crotalaria
Croton
Cucurbitaceae
Cyperaceae
Daisy
Dichrostachys
Euclea
Euphorbia
Evolvulus
Ficus
Gisekia
Gnidia
Grewia
Heeria
Heliotropium
Indigofera
Ipomoea
Justicia/Monechma
Kedrostis
Kirkia
Kohautia
Lannea
Leucas
Liliaceae
Limeum
Loranthaceae
Lycium
Malvaceae
Maytenus
Montinia
Mopane
Olea
Ophioglossum
Parkinsonia africana
Pentzia
Philenoptera
Phyllanthus
Poaceae
Prosopis africana
Pteris
Rhus
Rhynchosia
Salsola
Salvadoraceae
Scrophulariaceae
Sclerocarya
Searsia
Securinega
Senecio
Sida
Solanum
Spirostachys
Stoebe
Tarchonanthus
Tephrosia
Tragia
Tribulus
Vangueria
Verbenaceae
Vernonia
Waltheria

Pollen and spore types			
Chen./Amar.	*Hermannia*	*Podocarpus*	*Ximenia*
Cichorioideae	*Hypoestes/Dicliptera*	*Poligala*	*Ziziphus*
		Portulacaceae	Zygophyllaceae

2.2.4 Data analyses

We built three datasets from the original vegetation and pollen data. First, the vegetation survey dataset, containing all surveyed plant taxa. Second, the plants as pollen-equivalents dataset (PEq), where all plant taxa are translated into their taxonomically equivalent pollen taxa (Table 2-2). Translation was performed according to Vincens et al. (2007) in order to reduce taxonomical biases. Third, the pollen dataset, which contains all identified pollen and spore taxa.

We calculated the "effective number of taxa" for each dataset using Hill numbers (N0, N1, N2) (Hill, 1973). In this approach N0 is species richness, N1 is the effective number of common taxa, and N2 is the effective number of dominant taxa. We calculated richness and diversity measures for the vegetation survey data and for PEq with the full set of values. To avoid count-size biases, we rarefied the pollen data following Chao et al. (2014) to the smallest sample count size (231 grains). For all analyses we used R software, version 3.1.2 (R Core Team, 2014) and the R package iNext (Hsieh et al., 2016).

A set of multivariate analyses was conducted on the PEq and pollen datasets in order to make comparisons at the same taxonomic level. To reduce noise in the analyses, we selected only taxa which occur with a minimum frequency of 0.5% in at least three samples or with a singular frequency of 10%. The data were square-root transformed prior to analysis to homogenise the size of the residuals. First, we ran a hierarchical agglomerative cluster analysis to identify characteristic associations of specific vegetation types using the CONISS for unconstrained data function of the Tilia software (Grimm, 1987). We also applied a partitional cluster analysis using *k*-means (MacQueen, 1967) to cut the dendrogram tree into *k* clusters (*k*=4). We set 25 random starts and chose the cluster solution with the smallest sum of squared errors. The *k* value was previously calculated with the R package NbClust using the within cluster sums of squares method (Charrad et al., 2014). Second, we ran a detrended correspondence analysis (DCA) to estimate the compositional turnover in the datasets and to assess whether to use linear- or unimodal-based ordination methods (Legendre and Birks, 2012). Since the compositional turnover in the pollen dataset was lower than 2.5 standard deviation (SD) units and larger in the PEq data, we applied both methods to all data. After comparing our results we decided to use the linear-based ordination methods for interpretation because a) we could establish that the high compositional change (5.9 SD) in the PEq data was determined by the influence of two outliers (Fig. S1; Chapter 6.1), and b) because linear methods explained more variance in both datasets than unimodal methods. In this order, we ran a principal component analysis (PCA) to highlight the directions of the largest variations in the datasets and to assess the species–species relationships. Procrustes rotation analysis and Protest permutation tests were then applied to the PCA results to assess the comparability between paired PEq and pollen taxa. We also performed redundancy analyses (RDA) using precipitation as a constraining variable (Table 2-4). The precipitation variable was defined as the mean annual precipitation (MAP) for each study site (Harris et al., 2014). Since MAP probably does not reflect moisture availability to plants, we ran RDA with an aridity index (*AI*) as a constraining variable: the results were quite similar (Table S1; Chapter 6.1). Lastly, we ran RDA for local subsets (corresponding to the four study sites) using grazing intensity as a constraining variable. We defined grazing as an arbitrary variable with a range from 1 to 11, with 11 corresponding to the first plot (watering point) of the grazing transect and to the highest value of grazing intensity. All analyses were implemented using the R packages vegan (Oksanen et al., 2016) and BiodiversityR (Kindt and Coe, 2005).

Table 2-4. Explained variance (adjusted (Adj.) r^2) and significance coefficients (p) for Redundancy Analysis of plants as pollen-equivalents (PEq) and pollen for a) precipitation and b) grazing at the four sites.

a. Precipitation			**b. Grazing**	**Otjikoto**		**Grootfontein**		**Waterberg**		**Kuzikus**	
	Adj. r^2	**p**		**Adj. r^2**	**p**	**Adj. r^2**	**p**	**Adj. r^2**	**p**	**Adj. r^2**	**p**
PEq	0.062	0.001	PEq	0.263	0.001	0.119	0.008	0	0.535	0.082	0.1
Pollen	0.214	0.001	Pollen	0.169	0.014	0.078	0.022	0.235	0.006	0.172	0.006

2.3 Results

2.3.1 Compositional change of vegetation and pollen along the precipitation gradient

We recorded a total of 94 plant taxa. After translating the vegetation data into plants as pollen-equivalents (PEq), the dataset comprised 50 taxa (Table 2-2). Subsequent threshold criteria removed rare taxa and resulted in a final dataset of 28 taxa for multivariate statistical analysis.

We identified four vegetation types derived from the cluster analysis (Fig. 2-2). Cluster 1 comprises plots dominated by grazing-tolerant taxa such as *Alternanthera pungens, Limeum, Solanum,* and *Tribulus*. Cluster 2 comprises two subclusters: the first includes plots from open Acacia woodland, which are dominated by Poaceae and *Acacia*; the second comprises plots from mixed woodland, which have high abundances of Poaceae and shrubs such as *Euclea* and *Tarchonanthus camphoratus*. Cluster 3 comprises plots from mixed woodland characterised by low Poaceae abundance and dominance of *Dichrostachys cinerea, Croton,* and Combretaceae. Cluster 4 comprises plots from *Acacia* shrubland dominated by *Acacia, Grewia,* Bignoniaceae, and *Waltheria indica*.

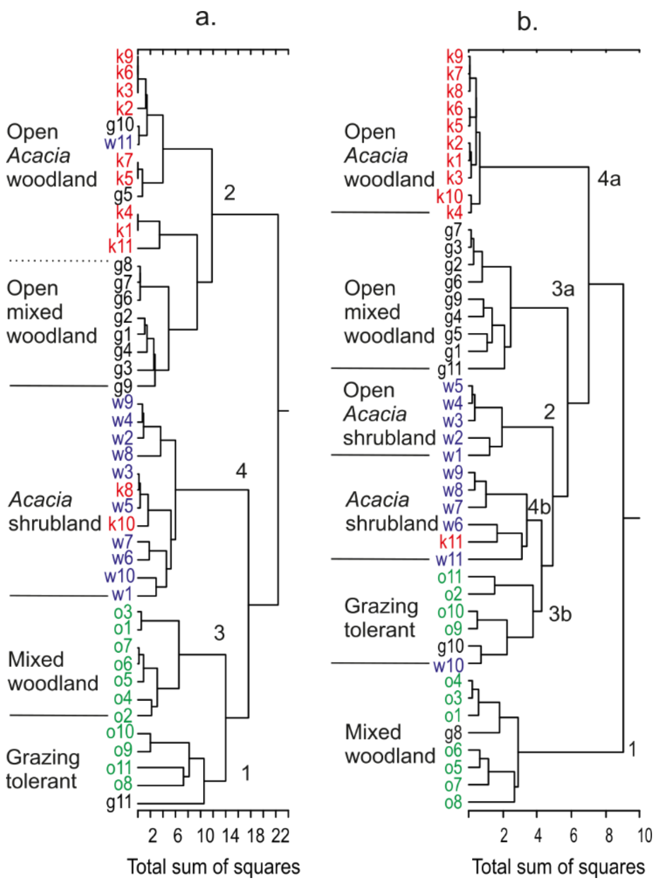

Figure 2-2. Unconstrained hierarchical cluster analysis for a) plants as pollen equivalents and b) pollen data. Vegetation types are indicated for each cluster. Sites are named according to locality (o=Otjikoto (green), g=Grootfontein (black), w=Waterberg (blue), k=Kuzikus (red)) and grazing intensity (decreasing from 11 to 1, where highest grazing intensity is closest to the watering point (11)).

The PEq diagram (Fig. 2-3) reflects changes in vegetation composition along the precipitation gradient. The semi-arid sites (Grootfontein, *AI*=0.26 and Otjikoto, *AI*=0.24) show dominance of *Dichrostachys cinerea* and broad-leaved taxa such as Combretaceae, *Croton*, and *Spirostachys africana*. The abundances of *Acacia* and *Grewia* increase at the arid sites (Waterberg, *AI*=0.17; Kuzikus, *AI*=0.11), but Poaceae especially becomes dominant.

The projection of clusters on the first PCA axis, which captures 23.5% of the variance in the PEq data (Fig. 2-4a), displays changes in the grasses/woody vegetation ratio, which in turn are related to precipitation. While clusters 3 and 4 are dominated by woody taxa and cluster 1 has no grasses, the abundance of Poaceae in cluster 2 is high, particularly in the plots from Kuzikus. From the RDA results, Poaceae dominance correlates negatively with precipitation (Fig. 2-4b).

The distribution of clusters along the second PCA axis, which captures 18% of the variance, reflects changes in taxa composition according to soil type and precipitation. Taxa from mixed woodland and plots where cambisols are dominant (clusters 1, 3) are seen on one side of the axis, while taxa from *Acacia* shrubland and plots with sandy soils (cluster 4) are seen on the other side. The taxa turnover from *Dichrostachys cinerea* and Combretaceae to *Acacia* is related to precipitation (Fig. 2-4b).

According to the RDA results, the influence of precipitation on vegetation composition is highly significant ($p=0.001$) despite the low $r^2_{\text{adjusted}} = 0.062$ (Table 2-4a).

Figure 2-3. Abundance diagram of selected plant taxa as pollen-equivalents (PEq). Arrangement of taxa follows their occurrence along the precipitation gradient. Sites are arranged according to mean annual precipitation (MAP). Absolute mean vegetation cover and mean woody cover relative to vegetation cover are indicated for each site.

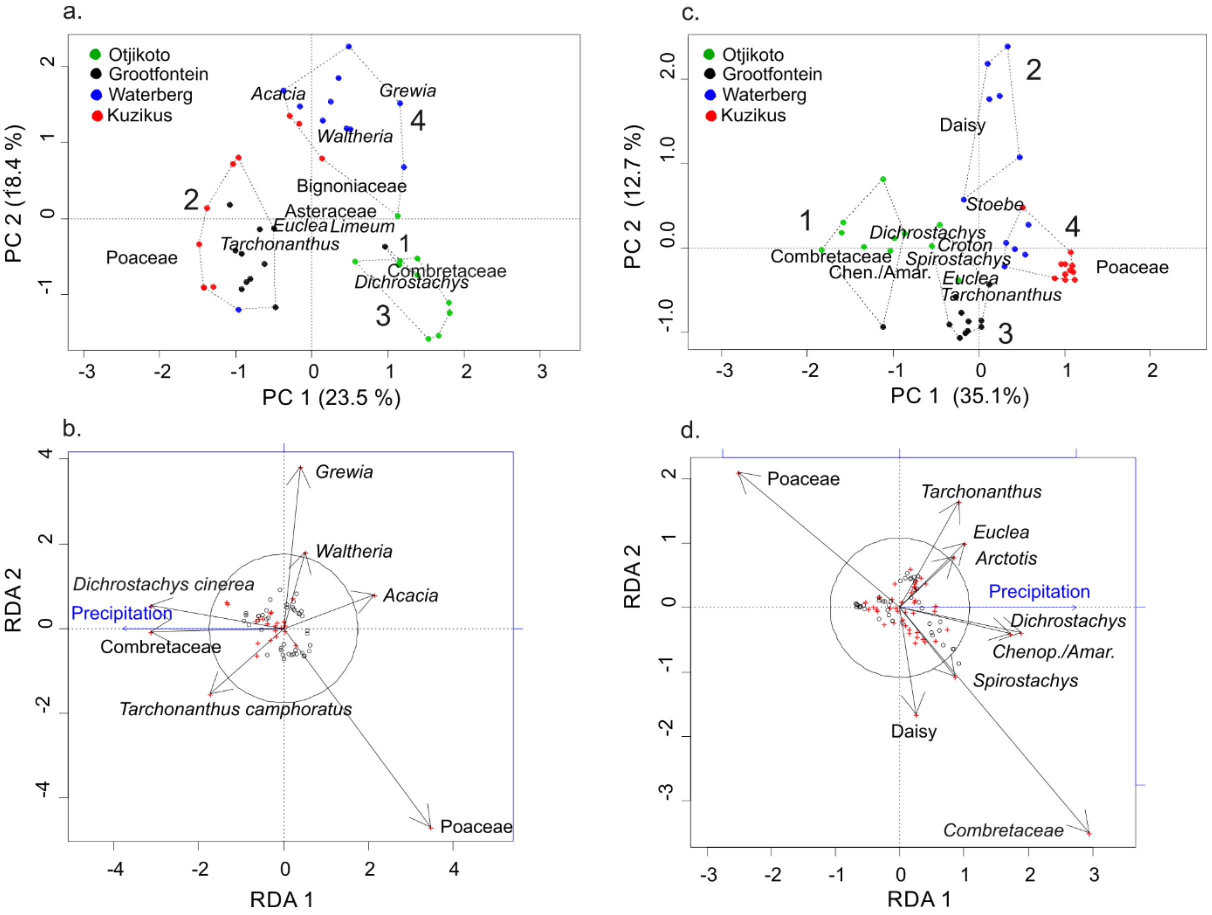

Figure 2-4. Principal components analysis (a, c) and redundancy analysis (b, d) of plants as pollen-equivalents (a, b) and pollen (c, d). Polygons correspond to clusters derived from cluster analysis. Vectors of taxa that cross the margins of the equilibrium circle contribute significantly in the ordination. Red crosses indicate taxa, black circles indicate plots.

We identified a total of 100 pollen taxa (Table 2-3). Removing rare taxa resulted in a dataset of 46 taxa for multivariate statistical analysis.

Cluster analysis of the pollen data identified four vegetation types as described above (Fig. 2-2). Clusters 1 and 3 comprise all plots from the semi-arid sites, which are characterised by mixed woodland. Cluster 3b contains plots dominated by grazing-tolerant taxa. Clusters 2 and 4b comprise plots from Acacia shrubland dominated by Poaceae, Asteraceae (Daisy, *Stoebe*), and *Grewia*. The open Acacia woodland is incorporated into cluster 4a.

The projection of clusters on the first PCA axis, which captures 35.1% of the variance in the pollen data (Fig. 2-4c), displays the transition from mixed woodland to open savanna along the precipitation gradient. This pattern is consistent with the PEq results and supported by the RDA results (Fig. 2-4d). The second PCA axis displays the dominance of shrub pollen (cluster 3, Grootfontein plots) and Asteraceae pollen (cluster 2) at the ends of the axis. According to the RDA results, the influence of precipitation on taxa composition is highly significant (Fig. 2-4d, $r^2_{\text{adjusted}} = 0.214$, p=0.001).

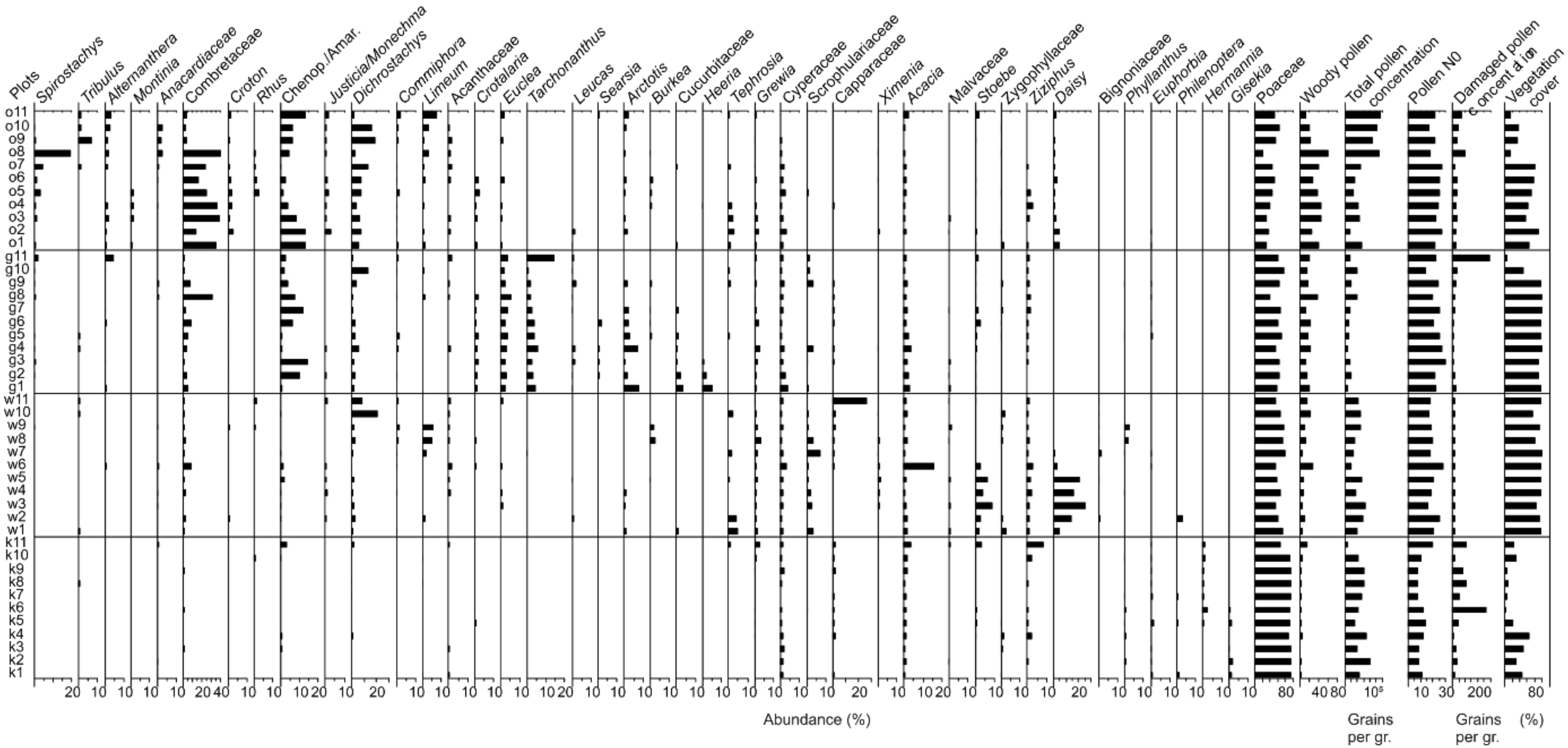

Figure 2-5. Percentage abundance diagram of selected pollen taxa. Arrangement of taxa follows their occurrence along the precipitation gradient. Concentrations of damaged pollen and total pollen are indicated, as well as pollen richness (N0) values and mean abundance percentages of woody pollen for each site.

2.3.2 Richness and diversity patterns of vegetation and pollen data along the precipitation gradient

Species richness (N0) values decrease after translating vegetation survey taxa into PEq data. However, both datasets show the same richness pattern along the precipitation gradient (Fig. 2-6e). Taxonomical loss for each study site is as follows: Kuzikus 36%, Waterberg 42%, Grootfontein 38%, and Otjikoto 35%.

Generally, the pollen N0 values are higher than those of PEq except at Waterberg (Fig. 2-6e). While we find no clear relationship between taxa richness (N0) and precipitation, the effective numbers of common (N1) and dominant pollen taxa (N2) increase from dry to more humid conditions. However, this relationship is not observed for the vegetation survey or PEq. Further, N1 and N2 patterns differ among the datasets according to the magnitude of taxonomical loss after translation. For example, Waterberg has higher taxonomical loss and a stronger decrease in N1 and N2 values for the PEq data, whereas the contrary is observed for Otjikoto. Nevertheless, N1 and N2 values are closer for PEq and pollen data than the N0 values. Diversity values are consistent in all datasets for Otjikoto and Kuzikus.

2.3.3 Vegetation-pollen relationships along local grazing gradients in terms of composition, taxa richness, and diversity

Otjikoto (MAP = 456 mm)

In total, we recorded 26 taxa (N0) and a mean vegetation cover of 61% at the most humid site. Otjikoto is the most encroached site with the lowest grass cover (5%) of all study sites. Woody vegetation represents 74% of the local vegetation, encompassing encroachment species such as *Dichrostachys cinerea* and *Terminalia prunioides*. Broad-leaved savanna taxa such as *Spirostachys africana, Croton,* and *Montinia caryophyllacea* are also recorded.

Vegetation composition is significantly affected by grazing in the PEq (r^2_{adjusted}=0.263, p=0.001) and pollen data (r^2_{adjusted}=0.169, p=0.014). Cluster analyses of both datasets clearly differentiate plots with high grazing intensity, as reflected by cluster 1 (PEq) and cluster 3b (pollen) (Fig. 2-2). Taxa such as *Alternanthera pungens* and *Tribulus* are more frequent on plots 11 to 8 in both datasets. The pollen signals of *Limeum* and *Dichrostachys*, pollen concentration, and the amount of damaged pollen (Fig. 2-5) are also high on these plots. The dominance of Combretaceae, *Croton,* and *Acacia* increases at medium to low grazing intensity in both datasets. Further, there is a high abundance of *Dichrostachys cinerea* in the vegetation and a low signal of Poaceae pollen.

Species richness and diversity follow similar patterns along the grazing gradient in all datasets except at high grazing intensity (Fig. 2-6a).

We recorded the highest number of pollen taxa (N0=30) at Otjikoto. Highest N0 values are recorded for plots with low pollen concentration (Fig. 2-5). Comparing the N1 values in relation to N0, Otjikoto has the highest proportion of common taxa in the local taxa pool of all datasets.

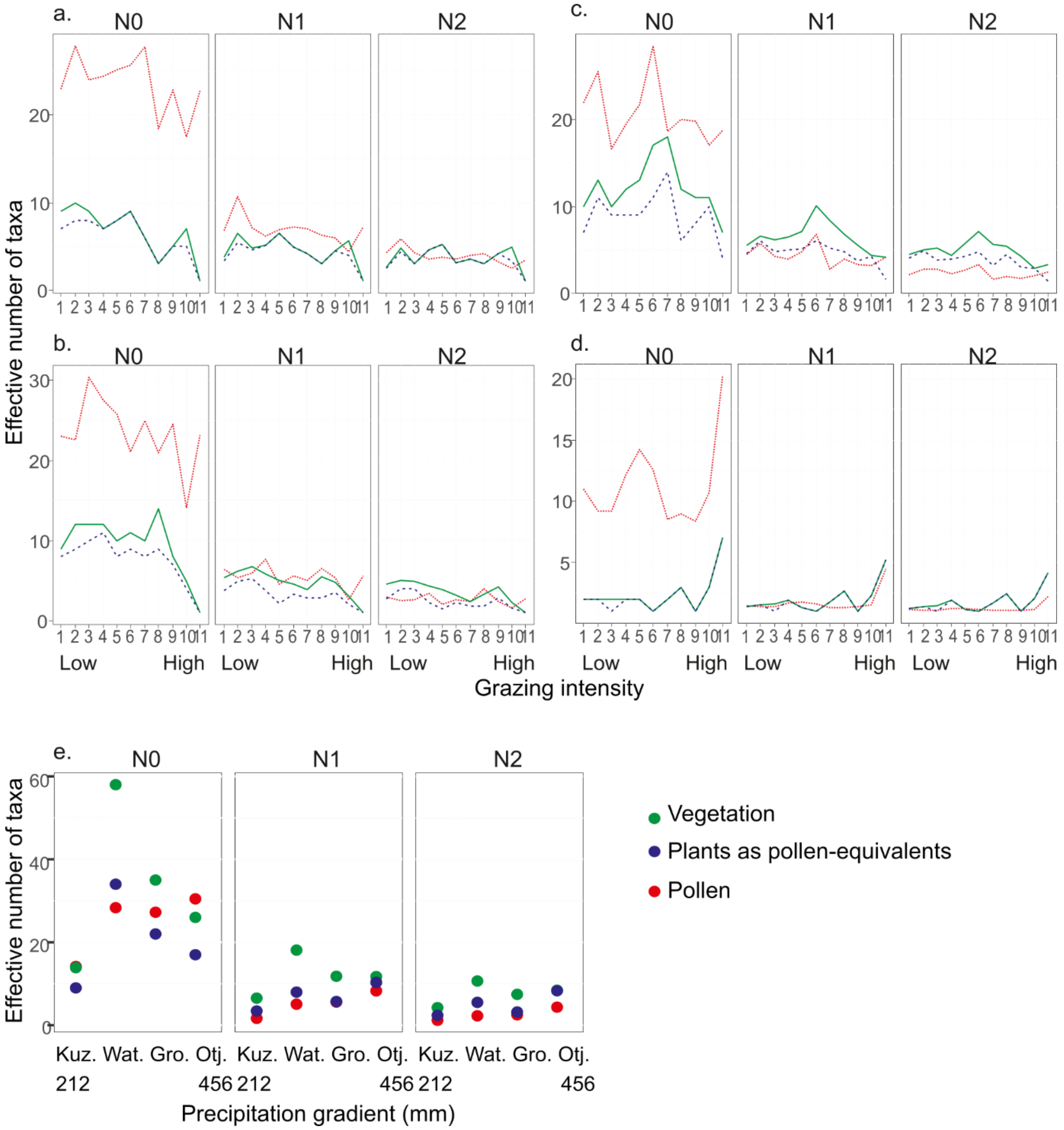

Figure 2-6. Taxa richness and diversity patterns for vegetation (green, solid line), plants as pollen-equivalents (violet, dashed line), and pollen (red, dotted line) along local grazing gradients: a) Otjikoto, b) Grootfontein, c) Waterberg, and d) Kuzikus, and the precipitation gradient (e). Effective numbers of all taxa (N0), common taxa (N1), and dominant taxa (N2) are indicated.

Grootfontein (MAP = 455 mm)

The landscape is characterised by a mix of open grasslands and encroached areas. Mean vegetation cover is 87% and species richness N0=35. Dominant trees are *Acacia mellifera*, *Combretum hereroense*, and *Terminalia prunioides*, and dominant shrubs *Tarchonanthus camphoratus*, *Euclea*, *Ziziphus mucronata*, *Searsia*, and *Ozoroa*.

We find a significant relationship between vegetation composition and grazing impact in both PEq (r^2_{adjusted}=0.119, p=0.008) and pollen data (r^2_{adjusted}=0.078, p=0.022).

Lamiaceae (*Leucas* type) and *Dichrostachys* are common on plots 11 to 8 in both datasets. However, taxa composition differs at highest grazing intensity. While the PEq data show dominance of *Limeum* and *Solanum* at the watering point (Fig. 2-3), the pollen data show dominance of *Alternanthera* and *Tarchonanthus* (Fig. 2-5). In this plot the pollen concentration is low and the concentration of damaged pollen is at highest. Scrophulariaceae (*Aptosimum*), *Tarchonanthus,* and *Acacia* are common at low grazing intensity in both datasets. We also observe an increase of *Arctotis* and *Heeria* pollen at lowest grazing pressure (plots 1 and 2).

As observed at Otjikoto, species richness and diversity follow similar patterns in all datasets except at highest grazing intensity (Fig. 2-6b). N0, N1, and N2 values increase gradually from highest to medium grazing intensity in both the vegetation survey and PEq records, but not in the pollen data, where high N0 values are observed in plots with low pollen concentrations.

Waterberg (MAP = 342 mm)

The highest mean vegetation cover (92%) and species richness (N0=58) of all study sites are recorded at Waterberg. We observe changes in vegetation composition related to landscape structure. For example, in the first five plots, which are located on the sandveld and affected by encroachment, the dominant taxa are *Acacia ataxacantha*, *A. erioloba, Grewia flava*, *G. flavescens, Dichrostachys cinerea*, and *Rhigozum*, but in plot six, which is located in a depression shaped by an ephemeral rill, *Acacia hebeclada*, *Terminalia sericea,* and *Aptosimum* become more frequent. Beyond this point the landscape turns to valley and the abundances of Poaceae, *Acacia mellifera, Solanum,* and forbs such as *Sida ovata* and *Waltheria indica* increase.

The distribution of the taxa is consistent for the vegetation survey and PEq results and does not show a relationship to grazing (Table 2-4b). In contrast, the pollen assemblage is significantly affected by grazing impact (r^2_{adjusted}=0.235, p=0.006). The pollen signals of Capparaceae (*Cleome*) and *Dichrostachys cinerea* reach high values on plots 11 to 8, and there are frequent records of *Limeum* and *Phyllanthus* on these plots (Fig. 2-5). *Stoebe* and Daisy-type are more frequent at medium to low grazing intensity. Waterberg has the lowest percentages of damaged pollen from all study sites.

With regard to richness and diversity, all three datasets reflect a negative impact of high grazing intensity (Fig. 2-6c). However, at the highest grazing pressure, the pollen data show high N0, N1, and N2 values, which are inconsistent with the vegetation and PEq patterns. Further, the highest pollen N0 value (N0=28) corresponds to the plot with the lowest pollen concentration (Fig. 2-5).

Kuzikus (MAP = 212 mm)

We find the lowest mean vegetation cover (28%) and species richness (N0=14) at Kuzikus. Vegetation forms a patchy pattern. In the herbaceous layer, ground cover is 23% (Table 2-1) and the dominant taxon is Poaceae, which forms 65% of the total vegetation. In the shrub and tree layer, the dominant woody taxa are *Grewia flavescens, Acacia hebeclada,* and *A. erioloba*.

Species richness and diversity follow a similar pattern along the grazing gradient in all datasets (Fig. 2-6d). Highest N0, N1, and N2 values are recorded where grazing intensity is highest. The N2/N1 ratio indicates that the pool of common taxa is mostly composed of dominant taxa. As found in the other study sites, high pollen N0 values are recorded in plots with low pollen concentration.

In contrast, the relationship between vegetation composition and grazing intensity varies between PEq and pollen records. While we find no relationship between PEq and grazing (Table 2-4b), the pollen assemblage appears significantly affected by grazing ($r^2_{\mathrm{adjusted}}=0.172$, p=0.006). The pollen signals of *Hermannia*, *Ziziphus*, and *Acacia* are high at high grazing intensity and for *Gisekia* and *Philenoptera* at low grazing intensity (Fig. 2-5).

2.3.4 Vegetation–pollen relationships

Procrustes rotation analysis and Protest permutation tests show that vegetation and pollen follow similar compositional gradients (Fig. 2-7). The Procrustes analyses yield a significant fit between PCA-scores of the first four axes of PEq and the pollen data, both with respect to comparison of plots ($m^2=0.65$, p=0.001) and taxa ($m^2=0.67$, p=0.001). High agreement is found for *Tribulus*, Scrophulariaceae, and *Acacia*, and high residuals for *Solanum* and *Spirostachys*. Plots from Kuzikus show the best fit, while most of the plots with high residuals originate from Otjikoto.

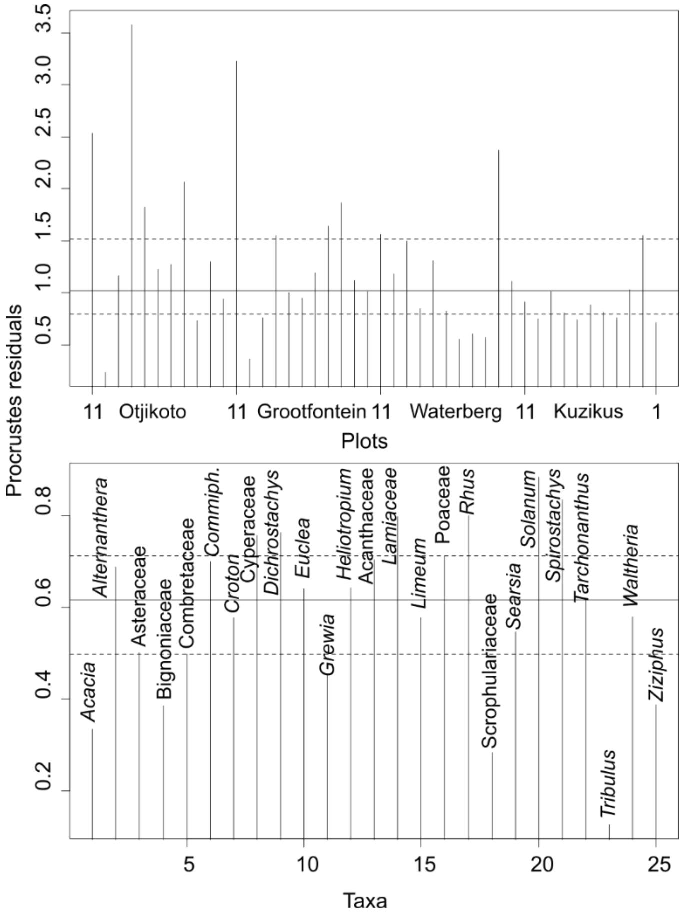

Figure 2-7. Procrustes residual values for paired plots and taxa. Plots are arranged along the grazing intensity gradients from 11 to 1 for each study site, where 11 corresponds to the watering point. Residual values closer to 0 indicate a closer agreement between corresponding plants as pollen equivalents and pollen data points. The length of the vertical lines indicates the degree of dissimilarity. Dotted and solid horizontal lines correspond to the first three quartiles.

2.4 Discussion

2.4.1 Vegetation–pollen relationships along a precipitation gradient

Our results show a high correspondence between vegetation, plants as pollen-equivalents (PEq), and pollen data. Our approach allowed us to identify from pollen records the transition from mixed woodland to open *Acacia* woodland along a north–south precipitation gradient in central and northern Namibia. These results contrast with studies from African tropical forests (Lézine et al., 2009; Vincens et al., 2006), as well as from temperate vegetation zones dominated by anemophilous woody taxa (Felde et al., 2014).

Vincens et al. (2006) and Lezine et al. (2009) show that the underrepresentation of entomophilous and zoophilous taxa in the pollen record makes it difficult to distinguish forest types and stages, particularly when vegetation is affected by anthropogenic impact. In our study, the underrepresentation of entomophilous taxa at disturbed sites, such as Fabaceae at Otjikoto and Kuzikus, does not constrain the differentiation of savanna landscapes on the basis of pollen assemblages as reflected by cluster analysis. Furthermore, we find a high correspondence between pollen and vegetation data for some entomophilous taxa such as *Acacia* (Fig. 2-7). This is because savanna environments have a lower species turnover (Scholes, 1997) and higher evenness of pollination modes (Ramírez, 2004) when compared to tropical forests. For these reasons, the effects of pollen production and dispersal derived from changes in vegetation structure are less important in the pollen record.

With respect to temperate vegetation zones, Felde et al. (2014) show that in open areas the pollen-source area and the proportion of long-distance dispersal pollen are high, thus leading to an overlap of pollen assemblages from different vegetation zones. The background pollen load of anemophilous tree taxa, particularly in treeless areas, constrains the potential of pollen to identify treelines. In our study, long-distance dispersal pollen of woody taxa is rare in the pollen record, even in very open areas such as Kuzikus. Taking into account the dominance of entomophilous and zoophilous pollination modes among tree and forb taxa, we assume that the background pollen component of tree taxa originates from the local surrounding vegetation and the extra-local source area (sensu Jacobson & Bradshaw 1981). These results show the potential of modern pollen to track woody vegetation in arid and semi-arid environments.

Our results confirm the observation of Schüler et al. (2014) that even taxa identified to only family or genus level, as is common in palynology, is sufficient to distinguish different savanna landscapes.

In our study, the transition from mixed woodland to open *Acacia* woodland is clearly related to changes in the woody taxa/grasses ratio. The usefulness of the arboreal/non-arboreal pollen (AP/NAP) ratio to differentiate vegetation types has also been confirmed for tropical rainforests (Bonnefille, 2011), as well the usefulness of Poaceae pollen to differentiate savanna landscapes (Vincens et al., 2000; Julier et al., 2017). However, we agree with Julier et al. (2017) that other taxa should be considered along with Poaceae, because of biases related to high pollen productivity, influx, and redeposition.

Although precipitation significantly explains the compositional change in vegetation and pollen spectra, the proportion of explained variance is low (Table 2-4). PCA results suggest that besides precipitation, soil characteristics also determine changes in taxa composition. In particular, the distribution of clusters along the second PCA axis in the PEq data implies there is compositional change according to soil type: PCA clearly separates mixed woodland and cambisols from *Acacia* shrubland and sandy soils. In addition, the distribution of pollen taxa along the second PCA axis suggests a moisture gradient by placing forbs and shrubs at opposite ends of the axis. These results confirm previous studies that have demonstrated the interplay of different factors such as precipitation regime, fire, and soil properties on determining the composition of savanna biomes (Azihou et al., 2013; Elenga et al., 2000; Okitsu, 2010).

2.4.2 Vegetation–pollen relationships in terms of compositional change along grazing intensity gradients

Our results show that pollen records reflect better the impact of grazing on vegetation composition in arid and semi-arid environments than vegetation data (Table 2-4). This result is in contrast to studies performed on temperate pasture landscapes (Dietre et al., 2012; Ejarque et al., 2011). Ejarque et al. (2011) and Dietre et al. (2012) show that the indicative value of key pollen taxa at a local scale is hampered by the overrepresentation of these taxa in the extra-local vegetation. For this reason, low pollen percentages of traditional anthropogenic pollen indicators reflect long-distance transport rather than local grazing pressure. To improve the interpretation of pollen records, Ejarque et al. (2011) and Dietre et al. (2012) suggest analysing pollen and spores contained in dung pellets.

In our study, the pollen assemblages display a rather local signal. Surprisingly, they reflect a significant impact of grazing on vegetation composition, which is not seen in the vegetation data of Waterberg and Kuzikus. Our results suggest that the mismatch between pollen and vegetation data at Waterberg can be explained by landscape heterogeneity and various soil characteristics, which strongly determine vegetation composition at this site. Indeed, in savannas, the distribution of woody taxa has been shown to be determined more by soil type than by grazing pressure (Dahlberg, 2000). Regarding Kuzikus, we interpret the patchy distribution of vegetation as a consequence of the spatial distribution of soil nutrients and water rather than of grazing pressure.

We also identified pollen taxa as indicators of grazing pressure for the Namibian savanna. High pollen signals of ephemeral and unpalatable taxa such as *Limeum, Alternanthera,* and *Tribulus* indicate the strongest local grazing pressure. These taxa were mainly recorded in plots 11 to 8 suggesting a threshold at 150m away from the watering point. This distance corresponds to the “sacrifice area” defined by previous studies (Graetz and Ludwig, 1976; Perkins and Thomas, 1993). Procrustes analysis highlights a high correspondence between vegetation and pollen data for *Tribulus* (Fig. 2-7), which reinforces its usefulness as a local indicator of grazing (Tolsma et al., 1987). Furthermore, pollen of *Hermannia* provides evidence of local and extra-local disturbance, and the simultaneous occurrence of *Phyllanthus, Crotalaria,* and *Dichrostachys* indicates encroachment. The replacement in the pollen record of *Dichrostachys* by *Acacia* indicates a decrease in the intensity of the grazing pressure (Fig. 2-5). *Dichrostachys cinerea* is a pioneer woody taxa and has often been described as an indicator of overgrazing (Dahlberg, 2000). These results are consistent with previous botanical studies performed on southern Africa savannas (Mukaru, 2009; Scholes et al., 2002; Todd, 2006).

We confirm the relationship between grazing pressure and landscape openness, as well as between Poaceae pollen and landscape openness in grazed landscapes (Dietre et al., 2012; Ejarque et al., 2011). In our study, woody cover and woody pollen increase away from the watering points showing that at high grazing pressure the landscape becomes open (Fig. 2-3 and 2-5). In contrast, Poaceae cover and Poaceae pollen show no common trend along the grazing gradient. This mismatch between grasses and their pollen signal is also captured in the Procrustes analysis (Fig. 2-7). At watering points, the Poaceae signal is high despite the absence of grasses. Given that Poaceae is a principal taxon of savanna vegetation, we consider that the grass pollen in our plots is from the surrounding vegetation and the extra-local source area, brought in by wind and grazing animals. We also see high quantities of Poaceae pollen in encroached plots, for example at Otjikoto. This suggests an increase in local grass pollen production in response to a release from grazing pressure (Groenman-van Waateringe, 1993; Mazier et al., 2006). Grasses growing between shrubs profit from the difficulty of access for grazers, and thus have a chance to flower. Nevertheless, Poaceae pollen percentages remain lower than woody pollen percentages in such encroached plots, maintaining the usefulness of Poaceae pollen as an indicator of landscape openness.

Moreover, we found a relationship between damaged pollen and vegetation cover. The amount of damaged pollen increases when vegetation cover decreases, as observed in plots with high grazing intensity (Fig. 2-5). This can be explained as a consequence of weathering and oxidation at exposed sites (Havinga, 1967), but particularly as an effect of post-depositional processes. According to O'Rourke (1990), damaged pollen can be re-entrained in the atmospheric pollen load at arid environments because of low moisture in the air and soils to ground the pollen. The high amounts of damaged pollen at Kuzikus can be interpreted as having been blown out of sandy soils and redeposited on the vegetation-free surface. This observation highlights the usefulness of damaged pollen to identify overgrazed landscapes.

Our results help fill a knowledge gap about the pollen signals of grazing regimes in savanna environments. Despite their local applicability, our results highlight the suitability of modern pollen as an indicator of grazing impact in arid and semi-arid environments.

2.4.3 Taxa richness and diversity along the precipitation gradient

Our results indicate that the richness of vegetation and PEq is more affected by landscape structure than by landscape openness and precipitation. These results contrast with studies performed in the temperate northern vegetation zone (Meltsov et al., 2013). According to Meltsov et al. (2013), landscape openness has more influence on vegetation richness than landscape structure: they find a positive linear correspondence between vegetation richness and landscape openness from closed forest to semi-open vegetation and assume the relationship would be unimodal if more open sites were taken into account.

In our study, high N0 values from Waterberg can only be explained by the site-specific landscape heterogeneity rather than precipitation alone. Further, Waterberg has the highest woody cover of all study sites (Fig. 2-3), which implies that landscape openness cannot be considered as a determinant of species richness at this site.

We agree with Meltsov et al. (2013) that local pollen richness is affected by land openness. At open and semi-open sites the pollen records have higher N0 values than the PEq data (Fig. 2-6) because of the pollen load from the surrounding vegetation and from the extra-local source area. The opposite is observed at Waterberg, which has dense vegetation that limits the background pollen input. The low amount of damaged pollen observed at this study site supports our inference of low redeposition of pollen. Studies performed in dense tropical forests show that a dense canopy leads to a very local pollen signal (Gosling et al., 2018) and can constrain pollen richness to a plot scale (Elenga et al., 2000).

From these observations we confirm that modern pollen can give reliable estimates of vegetation richness within a floristic region despite differences in taxonomical resolution, but that caution must be taken when comparing sites from different floristic regions because of various factors determining the richness of pollen records (Gosling et al., 2017; Birks et al., 2016; Felde et al., 2015; Meltsov et al., 2013).

Using modern pollen and vegetation data, our results are a first attempt to show that the effective numbers of common taxa (N1) and dominant taxa (N2) are reliable indicators of plant-diversity change in savanna ecosystems despite limitations derived from taxonomical resolution (Gosling et al., 2018). Previous studies performed in temperate vegetation zones (Felde et al., 2016) demonstrated their potential. The ecological meaningfulness of Hill's diversity measures is highlighted when considering the ratio of N1 to N0 (Hill, 1973) and N2 to N1 (Sheldon, 1969). In our Otjikoto dataset, the N1/N0 ratio reflects the high dominance of common taxa in the local taxa pool, which in turn is consistent with the encroached status of this site. Further, the N2/N1 ratio at Kuzikus shows the high evenness in the taxa composition at this site, which is strongly dominated by Poaceae.

2.4.4 Taxa richness and diversity along grazing gradients

Our study is the first attempt to analyse pollen richness and diversity along grazing gradients in savanna environments. A few studies, performed mostly in temperate mesic and humid landscapes (Dietre et al., 2012; Ejarque et al., 2011; Mazier et al., 2006) or in arid montane environments (Kar et al., 2015), show how pollen can reflect the impact of grazing on vegetation composition, but they have not analysed the suitability of pollen to reflect changes in vegetation richness and diversity according to changing grazing pressure.

At our Namibian sites, vegetation and pollen have similar richness patterns along the grazing gradient except at highest grazing intensity (Fig. 2-6). In these watering-point plots, pollen richness is high whereas richness of the vegetation and plants as pollen-equivalents is low. Pollen richness is higher than plant richness because samples collected around watering points contain pollen of ephemeral taxa not recorded during the vegetation survey, as well as background pollen from the surrounding vegetation and pollen and spores contained in animal dung. The latter are presumed to reflect the grazing animal's preferences and to display well the local vegetation composition (Carrión, 2002; Dietre et al., 2012). Furthermore, the abundance of rare pollen taxa is expected to be high in overgrazed areas because of the overall lower pollen production, which in turn leads to low pollen concentrations in the samples and therefore to a broader counting of pollen grains enhancing the chance of rare taxa being recorded (Baker, 2012; Felde et al., 2016). Although the pollen concentration is not always low at the watering points from our study sites because of pollen influx and redeposition (e.g. Otjikoto), we confirm that plots with low pollen concentrations have high N0 values.

Regarding vegetation and plants as pollen-equivalents, we observe a negative impact of heavy grazing on species richness. In our study, heavy grazing reduces vegetation cover (Fig. 2-3) and is associated with the dominance of a reduced pool of grazing-tolerant taxa. These results are in line with botanical studies performed in other arid grazed environments (Carmona et al., 2012; Hanke et al., 2014; Rutherford and Powrie, 2013). An exception is observed at Kuzikus, where vegetation and plants as pollen-equivalents display high richness and diversity values at the highest grazing intensity. Taking into account the overgrazed stand and the patchy vegetation pattern at this locality, the occurrence of a high number of vegetation taxa at the watering point may be explained by fine-scale spatial heterogeneity derived from water availability, nutrient deposition, erosion, and disturbance at this point (Hanke et al., 2014).

Our study shows that the effective numbers of common taxa (N1) and dominant taxa (N2) are suitable indices of diversity patterns along a grazing gradient.

2.5 Conclusions

- Modern pollen records reflect the vegetation composition of arid and semi-arid environments in northern and central Namibia along a precipitation gradient.
- Modern pollen records can reflect the impact of grazing on local vegetation.
- Although precipitation and grazing significantly explain changes in vegetation composition, they only explain a low proportion of the compositional change suggesting that other factors should be taken into account as well.
- Pollen–vegetation correspondence in terms of species richness (N0) is limited because pollen taxa richness is affected by the background pollen loading in open areas and by pollen concentration, while plant taxa richness is influenced by landscape structure, which makes it difficult to compare different regions.
- The effective numbers of common taxa (N1) and dominant taxa (N2) are reliable indicators of plant diversity change along precipitation and grazing gradients.

Our results indicate that despite discussed limitations, modern pollen assemblages can reflect changes in vegetation composition, richness, and diversity patterns along precipitation and grazing gradients. These results demonstrate that pollen analysis could be used to reconstruct vegetation in the Namibian savanna thus allowing the interpretation of past vegetation composition on the basis of fossil pollen.

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3 Manuscript 2

Vegetation state-changes in the course of shrub encroachment in an African savanna since about 1850 CE and their potential drivers

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Summary

1. Shrub encroachment has far-reaching ecological and economic consequences in many ecosystems worldwide. Yet compositional changes associated with shrub encroachment are often overlooked despite having important effects on ecosystem functioning.

2. We document the compositional change and potential drivers for a northern Namibian *Combretum* woodland transitioning into a *Terminalia* shrubland. We use a multiproxy record (pollen, sedimentary ancient DNA, biomarkers, compound-specific carbon ($\delta^{13}C$) and deuterium (δD) isotopes, bulk carbon isotopes ($\delta^{13}Corg$), grain size, geochemical properties) from Lake Otjikoto at high taxonomical and temporal resolution.

3. We provide evidence that state-changes in semi-arid environments may occur on a scale of one century, and that transitions between stable states can span around 80 years and are characterized by a unique vegetation composition. We demonstrate that the current grass/woody ratio is exceptional for the last 170 yrs, as supported by *n*-alkane distributions and the $\delta^{13}C$ and $\delta^{13}Corg$ records. Comparing vegetation records to environmental proxy-data and census data we infer a complex network of global and local drivers of vegetation change. While our δD record suggests physiological adaptations of woody species to higher atmospheric pCO_2 concentration and drought, our vegetation records reflect the impact of broad-scale logging for

the mining industry, and the macrocharcoal record suggests a decrease in fire activity associated with the intensification of farming. Impact of selective grazing is reflected by changes in abundance and taxonomical composition of grasses and by an increase of non-palatable and trampling-resistant taxa. In addition, grain-size and spore records suggest changes in the erodibility of soils because of reduced grass cover.

4. *Synthesis.* We conclude that transitions to an encroached savanna state are supported by gradual environmental changes induced by management strategies, which affected the resilience of savanna ecosystems. In addition, feedback mechanisms that reflect the interplay between management legacies and climate change maintain the encroached state.

3.1 Introduction

Shrub encroachment is affecting savannas worldwide (Saha, Scanlon, & D'Odorico, 2015; Stevens, Lehmann, Murphy, & Durigan, 2017; Tian, Brandt, Liu, Rasmussen, & Fensholt, 2017). This process is assumed to indicate a savanna state-change from open woodlands and grasslands, characterized by dominance of C_4 grasses, to a bush-thickened savanna (Joubert et al., 2008; Meyer et al., 2007). Southern Africa is a hotspot of studies reporting shrub encroachment (O'Connor, Puttick, & Hoffman, 2014; Roques, O'Connor, & Watkinson, 2001; Wigley, Bond, & Hoffman, 2009). This is not only because shrub encroachment is a widespread phenomenon, but also because the area is traditionally used as grazing grounds and encroachment reduces the land-carrying capacity, threatening local economies (De Klerk, 2004; Moyo et al., 1993).

Shrub encroachment has been described as an alternative stable state occurring several times during the last two millennia in African savannas (Gil-Romera et al., 2010). There is also some indication that African savannas are characterized by grassland/woodland phases occurring with a periodicity of 250–600 years (Gil-Romera et al., 2010; Gillson, 2004). Such woodland phases were not always led by the spread of encroaching species (Gil-Romera et al., 2010; Scott et al., 1991), which suggests that a mere increase in woody cover, as reported by several studies since the 20th century (Hoffman et al., 2019; van Rooyen et al., 2018; Wiegand et al., 2005), does not necessarily mean shrub encroachment. Accordingly, identification of encroached states should be related to the increasing cover of encroacher species and the suppression of perennial grasses (Gil-Romera et al., 2010). However, the low taxonomic resolution of pollen records, particularly regarding Poaceae, constrains the identification of these phases on a long timescale.

It is assumed that resilience of savanna ecosystems is scale dependent. For example, savanna seems to be resilient to changes at a centennial timescale, as the vegetation fluctuates between two stable states of grassland and woodland (Gil-Romera et al., 2010; Gillson, 2004). Conversely, savanna seems to be less resilient at a decadal scale, as encroachment may occur within a century and without regression to a grassy state even at a patch scale (Rohde and Hoffman, 2012). Similarly, African landscapes are predicted to shift to woodland states, with abrupt transitions at the local scale, but smoother at the continental scale (Higgins and Scheiter, 2012). Transitions have been described as the unstable equilibrium between the `basins of attraction' of stable states (Holling, 1973; Scheffer et al., 2001), but surprisingly little is known about the duration of such transitions (Higgins and Scheiter, 2012; Joubert et al., 2008) or the compositional changes they entail (Joubert et al., 2008; Liao et al., 2018).

Different opinions exist as to the causes of shrub encroachment in savannas (Devine et al., 2017; Venter et al., 2018; Ward, 2005). Amongst others, changes in precipitation, atmospheric $p\mathrm{CO}_2$, vegetation fires, and land use are considered to be triggers and/or drivers (Aleman et al., 2016; Berry and Kulmatiski, 2017; Buitenwerf et al., 2012; Case and Staver, 2017), which likely interplay at different timescales. For example, while climate shifts are considered the main driver of changes in the grass/woody vegetation ratio on a long timescale (Gil-Romera et al., 2010; Scott et al., 1991), changes in grazing pressure and fire, besides stochastic variations in rainfall, are thought to drive decadal-scale variability (Gillson, 2004; van Rooyen et al., 2018). Interestingly, different studies have shown that precipitation, fire and herbivory may have different effects on encroacher species, and thus a different effect on savanna stability (Joubert et al., 2013, 2012, 2008). Hence, disentangling triggers that induce changes of state, as well as understanding stabilizing feedbacks, requires long time-series with adequate taxonomic resolution.

In addition, gradual change in environmental conditions are assumed to have little effect on the feedbacks that support a stable state but still alter its resilience (Scheffer et al., 2001). For example, management legacies are assumed to affect the properties of temperate woodland responses to current environmental change up to 200 years after disturbance (Perring et al., 2018). Similarly, shrub encroachment of Namibian savannas has been related to management strategies during colonial administration (Moyo et al., 1993; Rohde and Hoffman, 2012; Verlinden and Kruger, 2007). However, it remains unclear to what extent management may have affected species composition and thus savanna stability in Namibia.

Lake sediments represent unique environmental archives. Traditionally they are mostly used to resolve millennial-scale environmental changes in savannas (Metwally et al., 2014; Quick et al., 2018). Vegetation reconstruction using pollen deposited in lakes has been demonstrated to be a powerful method to track structural and compositional changes in savannas despite the low pollen taxonomic resolution (Miller & Gosling, 2014; Neumann, Scott, Bousman, & van As, 2010). Recently, sedimentary ancient DNA (*sed*aDNA) using the g-h universal primers (Taberlet et al., 2007) was established as a further proxy. This technique enables the reconstruction of tropical plant diversity at high taxonomic resolution (Boessenkool et al., 2014; Bremond et al., 2017). Further, fire dynamics and its impact on savanna vegetation can be reconstructed from sedimentary charcoal (Colombaroli et al., 2018; Gillson and Ekblom, 2009), while carbon (δ^{13}C) and deuterium (δD) isotope compositions of plant-wax *n*-alkanes can be used to reconstruct vegetation structure and hydrological variability (Garcin et al., 2018; Miller et al., 2019; Walther & Neumann, 2011). In addition, grain-size analyses of lake sediments are useful to reconstruct sediment mobility in savanna landscapes and to identify soil erosion (Walther and Neumann, 2011). However, high-resolution multiproxy approaches that include the use of *seda*DNA, and that track vegetation and environmental changes in semi-arid savannas at a decadal scale, are still missing.

Lakes are rare in southern Africa. Lake Otjikoto, a sinkhole lake located in the Karstveld area in northern Namibia (Fig. 3-1), represents a unique environmental archive (Scott et al., 1991). Applying a multiproxy approach to lake sediments from Otjikoto including the analyses of pollen, *sed*aDNA, biomarkers, geochemical proxies, grain size, and macrocharcoal analyses, this study provides the first decadal-scale record of the turnover of open savanna woodlands to shrublands from northern Namibia in the period between about 1850 and the present-day. This enables the discussion of savanna state-changes and, in combination with climate and land-use data, the investigation of potential triggers and drivers and related feedbacks of the vegetation.

3.2 Materials and methods

3.2.1 Site

The lake basin is formed from a groundwater cave, which developed from soluble dolomite of the Tsumeb subgroup of the Damara sequence (Kamona and Günzel, 2007). Water depth is ~71 m; diameter is ~102 m. Water pH measurements vary between 7.0 and 8.7 (Marchant, 1980). The potential natural vegetation in the vicinity of the lake comprises *Terminalia prunioides-Combretum apiculatum* woodlands (Mendelsohn, El Obeid, & Roberts, 2000). Accordingly, a low grass layer and dominance of trees characterize this vegetation type, which is common on shallow sandy-loamy soils. *Terminalia prunioides, Combretum apiculatum, C. imberbe, Commiphora glandulosa, Vachellia reficiens, V. hebeclada,* and *Senegalia mellifera* are the most common taxa. The shrub layer comprises *Grewia* sp., *Gymnosporia senegalensis, Dichrostachys cinerea,* and *Croton gratissimus.* However, a dense shrubland characterizes the current local vegetation, which is mainly composed of *Terminalia prunioides, Senegalia mellifera, Dichrostachays cinerea, Ziziphus mucronata,* and *Grewia* sp. Shore vegetation is sparse, with *Sclerocarya birrea* and *Ficus* growing on the steep rock walls surrounding the lake. Crop fields are close to the lake. Mean annual precipitation is 456 mm, falling mainly in the summer months (November–March); mean monthly temperature in summer is 27°C and in winter 15°C (Tsumeb climate station; Harris et al., 2014). Cattle farming is the dominant land use.

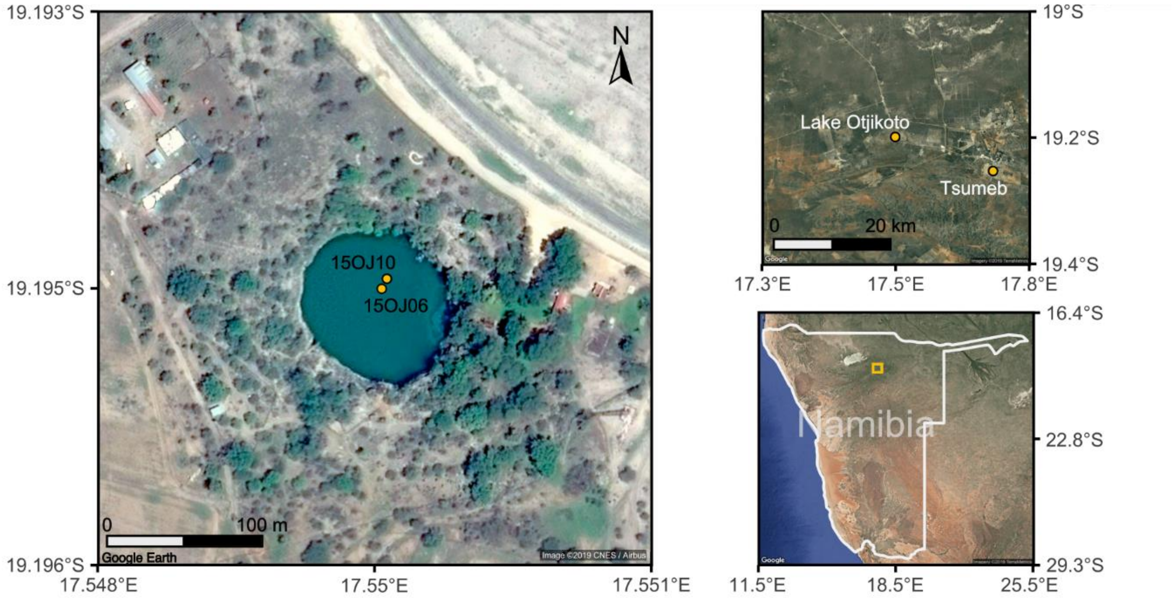

Figure 3-1. Map of the study site in Namibia.

3.2.2 Materials

Two cores - 15OJ10 (length 31 cm, Ø = 6 cm) and 15OJ06 (length 30 cm, Ø = 6 cm) - were collected in March 2015 using UWITEC coring equipment at a water depth of 50 m (19.19467°S, 17.54980°E). The core extraction was carried out with a pulley and without motor support. Divers from Dantica diving club Windhoek assisted with the core extraction from the lake bed. Core 15OJ10 was sampled at a 0.5 cm resolution in the field. We obtained 61 samples for pollen analysis; 30 subsamples were used for sedimentological, geochemical, *n*-alkane, and isotope analyses. Core 15OJ06 was sampled at a 1.5 cm resolution at the Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research. We obtained 21 samples for *seda*DNA and charcoal analysis. All samples were stored at 4°C.

3.2.3 Dating

Sixteen subsamples from core 15OJ10 and 21 from core 15OJ06 were analysed for ^{210}Pb, ^{226}Ra, and ^{137}Cs by direct gamma assay at the Liverpool University Environmental Radioactivity Laboratory. Measures were obtained using an Ortec HPGe-GWL well-type coaxial low background intrinsic germanium detector (Appleby et al., 1986). ^{210}Pb dates were calculated using the CRS dating model (Appleby and Oldfield, 1978). Corrections were made using the ^{137}Cs date 1964 as a reference point (Appleby, 2001).

3.2.4 Pollen and non-pollen palynomorph (NPP) analysis

Pollen extraction was performed using standard procedures (10%HCl, KOH, 40%HF – including 4 hours boiling – and acetolysis; Faegri and Iversen, 1989; Moore et al., 1991). We added one tablet of *Lycopodium* spores (batch 1031) to each sample to calculate pollen concentrations (Stockmarr, 1971).

At least 400 pollen grains were counted per sample using a microscope of x400 magnification. Critical identification was made by x1000 magnification based on standard literature (Bonnefille and Riollet, 1980; Gosling et al., 2013; Leźine, 2005; Schüler and Hemp, 2016; Scott, 1982), taxonomical studies (Banks and Lewis, 2018; Poston and Nowicke, 1993), and online pollen catalogues (Bremond, 2011). We differentiate the *Acacia*-type into *Vachellia* and *Senegalia* by means of columella identification (Kyalangalilwa et al., 2013). Spores identification follows Gelorini et al. (2011). Pollen percentages were calculated based on the total terrestrial pollen sum per sample. Shore taxa (*Ficus*, Cyperaceae) and aquatic taxa were not included in the pollen sum.

3.2.5 Sedimentary ancient DNA (sedaDNA) analysis

The sampling of core 15OJ06 for *seda*DNA was carried out at +10°C in a climate chamber that was previously cleaned (DNA-ExitusPlusTM - AppliChem, Germany, deionized water and ethanol 100%) to prevent contamination. Extraction and polymerase chain reaction (PCR) followed the same procedures as described in Zimmermann et al. (2017). For each sample (n=21) and extraction negative control (n=3) we performed 6 PCR replicates to ensure the accurate detection of taxa (Ficetola et al., 2015). For each PCR we used two negative controls and different primer tag combinations leading to a total of 126 PCR-products and 30 negative controls. All PCR products were purified using the MinElute PCR Purification Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. DNA concentrations were measured with the dsDNA BR Assay Kit (Life Technologies, USA) using 1 µL of the purified amplifications with the Qubit 2.0 fluorometer (Invitrogen, Carlsbad, CA, USA). Purified samples were pooled in equal concentrations and sent to the Fasteris SA sequencing service (Geneva, Switzerland) for library preparation following the MetaFast protocol. Sequencing was realized on an Illumina HiSeq 2500 platform (2 × 125 bp) (Illumina Inc., San Diego, CA, USA) using 1/10 of a flow cell lane. Obtained data were processed and assigned their taxonomic name using the software package OBITools (Boyer et al., 2016) following the descriptions in Zimmermann et al. (2017). Sequences selected for further analyses needed at least 95% best identity with respect to an entry in the reference database and at least 10 sequence counts in at least 2 samples in the dataset. Taxa percentages were calculated based on the sum of sequence counts per sample. After sequencing, two replicate batches were excluded from the analysis because they lacked sequencing depth, probably due to errors in the allocation of tags.

3.2.6 Biomarker analysis

For the analysis of *n*-alkanes, 30 freeze-dried sediment samples were extracted using dichloromethane containing 1% methanol. Further procedures used for the analysis of *n*-alkanes follow those described by Vogts et al. (2009) and Badewien et al. (2015).

The carbon ($\delta^{13}C$) and deuterium (δD) isotopic compositions of saturated hydrocarbons were measured using gas chromatography isotope ratio mass spectrometry (GC-IRMS) consisting of a GC-Unit (7890N, Agilent Technology, USA) connected to GC-Isolink and coupled to a Delta V Plus mass spectrometer (ThermoFisher Scientific, Germany). We used a combustion interface for $\delta^{13}C$, and a pyrolysis furnace for δD (Supplement S1A; Chapter 6.2). Isotope measurements were controlled based on *n*-alkane standards with known isotopic composition (Campro Scientific, Germany and Arndt Schimmelmann, Indiana University, USA).

Isotope measurements of bulk organic carbon (δ^{13}Corg) were made on decarbonized samples using an elemental analyser (1108 from Carlo Erba) coupled to a MAT 252 isotope ratio mass spectrometer from Thermo Fisher Scientific (Supplement S1B; Chapter 6.2). All subsamples were analysed in duplicate.

3.2.7 Charcoal analysis

Charcoal was extracted from 1 cm^3 subsamples following Mooney and Tinner (2011). Samples were bleached (24 hours) and washed through a sieve (125 µm) to separate macrocharcoal particles. All charcoal particles (>125 µm) were counted for each sample using a binocular microscope at x15 magnification and a Bogorov counting chamber.

3.2.8 Geochemical analysis

Total carbon (TC) and total nitrogen (TN) content were analysed for 30 freeze-dried subsamples (core 15OJ10) using an Elementar vario EL III (CNS) analyser. An Elementar vario MAX C was used to quantify total organic carbon (TOC). Total inorganic carbon (TIC) was calculated by deducting TOC from TC values.

3.2.9 Grain-size and end-member modelling analysis (EMMA)

Samples were pre-treated with CH_3COOH (10% for 24 hours) to remove carbonates, and with H_2O_2 (initial 0.3%, with addition of 10 ml (35%) every second day for up to six weeks) to remove the organic sediment fraction. Grain-size analysis was performed using a Coulter LS 200 Laser Diffraction Particle 30 Analyser.

Robust grain size end-members (EMs) have been modelled from all grain-size distributions using the EMMA algorithm of Dietze et al. (2012). We used the compact protocol in the R package EMMAgeo (Dietze and Dietze, 2019). Definition of the robust EMs considered the main mode classes that were modelled most frequently (see kernel density estimate in Fig. S2a), when the number of end-members and weight transformation limit were varied between a minimum and maximum value (Dietze et al., 2012; Dietze and Dietze, 2019). EM loadings (Fig. S2b) represent scaled grain size class-wise EM contributions, and scores (Fig. S2c) represent the contribution of EMs in the samples.

3.3 Results

3.3.1 Chronology

The core 15OJ10 covers the period from 1886 to 2015. The results suggest a relatively steady accumulation since the late 1980s with a mean sedimentation rate of 0.34 cm y^{-1}. Sedimentation rates in the 1930s were around 0.21 cm y^{-1}, increasing to around 0.31 cm y^{-1} by the early 1980s (Fig. S3a). Low ^{210}Pb concentrations in the pre-1930 samples made accurate dating problematic. However, ^{210}Pb dates suggest even lower sedimentation rates in the late 19th and early 20th century with a mean value of 0.15 cm y^{-1}. We applied linear interpolation to obtain the chronology of segments between dated samples.

The core 15OJ06 covers the period from 1849 to 2015. Since the ^{210}Pb concentrations reach the limit of detection at a depth of 23.25 cm (dated to 1907), we calculated ages for samples below 23 cm by linear extrapolation. The sedimentation rate since the early 1980s has a mean accumulation value of 0.30 cm y^{-1} (Fig. S3b). The results show lower sedimentation rates increasing from 0.14 cm y^{-1} during the first few decades of the 20th century to 0.20 cm y^{-1} during the period from 1940 to the 1970s.

3.3.2 Pollen and non-pollen palynomorph records

We identified 116 pollen and spore taxa (Table S4). The most dominant taxa are Poaceae, Anacardiaceae, and Combretaceae. The pollen diagram captures a signal of grasses decreasing up the core, with values dropping below 60% in the 1970s and from the turn of this century, while the pollen signal of woody vegetation increases (Fig. 3-2).

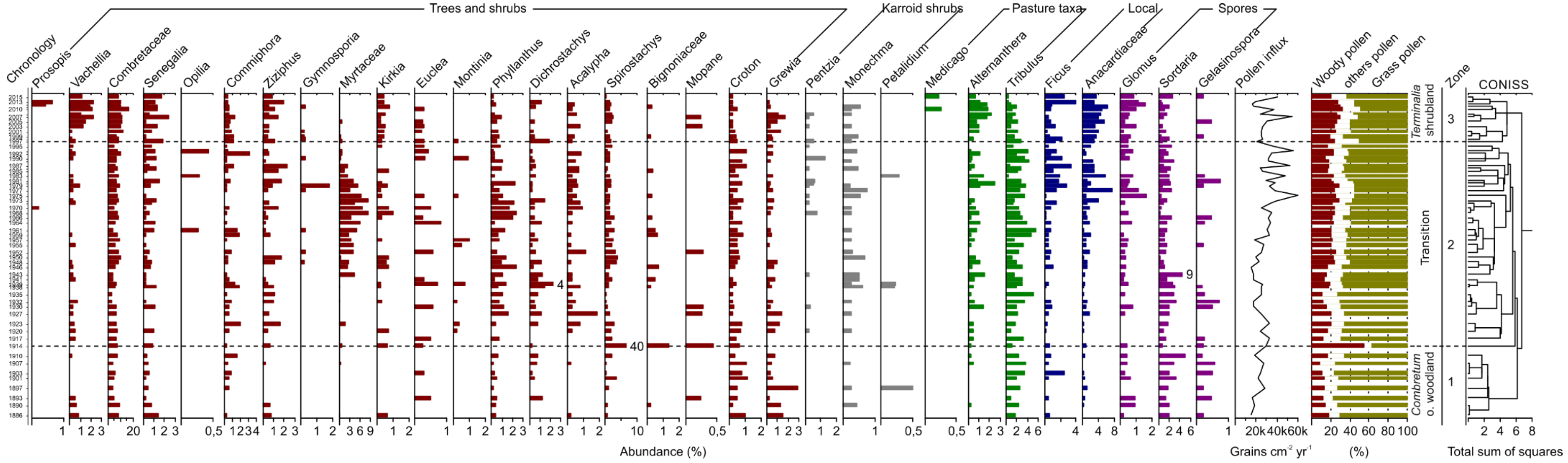

Figure 3-2. Percentage abundance diagram of selected pollen and spore taxa. Arrangement of taxa follows their dominance in the pollen zones (separated by dotted lines). Taxa are displayed in subgroups: trees and shrubs (brown), Karroid shrubs (grey), taxa associated with pastures (green), local shore taxa (blue), and spores (purple). Pollen influx, as well as mean abundance percentages of woody, grass, and other pollen taxa are displayed. Truncated values are indicated on the bars.

Based on a visual inspection of all proxies of both cores and guided by the results of the cluster analysis of the pollen record we defined three zones. The taxa association in zone 1 (1886-1910) comprises Combretaceae, *Dichrostachys, Croton, Grewia, Euclea, Senegalia,* and *Petalidium*. Bignoniaceae, *Spirostachys*, and *Colophospermum mopane* yield high percentages at the border to zone 2. The pollen signals of *Dichrostachys* and *Ziziphus* are high in zone 2 (1914-1997), while *Grewia* is lower compared with zone 1. Furthermore, zone 2 is characterized by high abundance of *Myrtaceae*, as well of *Alternanthera, Tribulus, Pentzia, Monechma, Opilia, Montinia, Gymnosporia,* and Euphorbiaceae taxa. Zone 3 (1998-2015) is characterized by high values in *Vachellia, Senegalia, Grewia,* and *Ziziphus*. This goes together with an increased signal of *Alternanthera* and low values for *Euclea*. The signal of *Prosopis* increases towards the top.

NPP results show a gradual decrease of *Gelasinospora* and *Sordaria* towards the top of the core. *Glomus* reaches highest values in zone 3.

3.3.3 Sedimentary ancient DNA records

We obtained 4,211,287 sequence counts (sqc) from Illumina sequencing for 21 samples with 4 replicates. After bioinformatic filtering 1,840,462 sqc were assigned to 177 taxa (Table S5). Of these, 37 could be identified to family level (905,299 sqc), 58 to genus level (323,335 sqc), and 64 to species level (239,924 sqc). Most dominant taxa are *Moraceae, Combretum,* and Anacardiaceae. Overall, the *sed*aDNA record reflects a turnover from taxa characteristic of open savanna woodlands in zone 1 to shrubland taxa in zone 3 (Fig. 3-3).

Zone 1 (1849-1907) is characterized by dominance of *Dichrostachys, Combretum,* Ebenaceae, and *Catophractes alexandri* and the occurrence of *Gossypium*. A mixed grass layer consisting of perennial grasses such as *Fingerhutia africana, Schmidtia,* and *Cenchrus* and annual grasses such as *Brachiaria deflexa, Aristida,* and *Tragus* characterizes zones 1 and 2, as well as the occurrence of Karroid shrubs. Zone 2 (1919-1991) is distinguished by a high abundance of taxa associated with pastures such as *Antigonon leptopus, Mentzelia,* Tribuloideae, *Alternanthera pungens, Geigeria,* and *Acanthospermum,* as well as of shrub taxa from the Euphorbiaceae, Celastraceae, and Opiliaceae families. In zone 2 the signals of Myrtoideae are high. Zone 3 (1996-2015) is characterized by high signals of *Terminalia, Vachellia,* and *Senegalia,* as well as *Grewia,* Rhamnaceae, and *Medicago*. The perennial grasses *Hyperthelia dissoluta, Panicum,* and *Heteropogon contortus* characterize zone 3. Furthermore, the relative abundance of Moraceae increases in the upper part of the core.

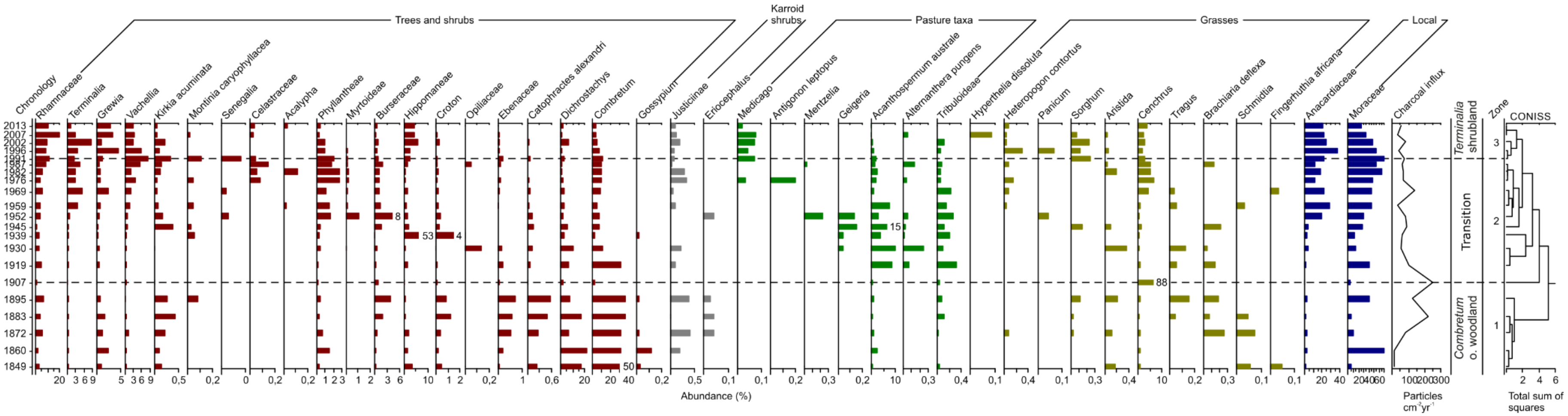

Figure 3-3. Diagram of selected *seda*DNA taxa. Arrangement of taxa follows their dominance in the *seda*DNA zones (separated by dotted lines). Taxa are displayed in subgroups: trees and shrubs (brown), Karroid shrubs (grey), taxa associated with pastures (green), grasses (yellow), and local shore taxa (blue). Macrocharcoal influx is also displayed.

3.3.4 Biogeochemical and macrocharcoal analysis

Concentration of organic and inorganic carbon (TOC, TIC) is highest in zones 1 (5.1%) and 3 (4.9%), respectively (Fig. 3-4). The average chain length (ACL; Poynter, 1989) values for *n*-alkanes with an odd number of carbon atoms (C_{27}-C_{33}) range from 31.1 to 30.3 and increase with depth. The carbon preference indices (CPI_{25-35}; Marzi et al., 1993) range from 13.6 to 3.4 with an average of 8.4. The C/N ratios range from 18.05 to 13.4 with an average of 16.04. The carbon isotopic compositions of organic matter (δ^{13}Corg) range from -19.9 to -27.3 with an average of -24.0‰ and with the more ^{13}C-depleted values in zone 3. Similarly, the weighted mean δ^{13}C values of *n*-alkanes with an odd number of carbon atoms ($\delta^{13}C_{WMA27-33}$) range from -24.6‰ to -32.3‰ and have the more ^{13}C-depleted values in zone 3. We also find the more depleted weighted mean δD values ($\delta D_{WMA27-33;}$ range: -135.7‰ to -159.6‰) in this zone. In addition, macrocharcoal flux is highest in zones 1 and 2 and decreases upwards in the core (Fig. 3-3).

3.3.5 Grain-size end-members

We obtained five rEM (robust grain-size end-members) after calculating similarly–likely EM models (Fig S2). The mean rEMs explain 77% of the mean total variance of the original grain-size dataset. The rEM1 (23% explained variance) has a primary mode between 0.2 and 14.5 µm with a maximum at 1.8 µm, covering the clay and very fine silt fraction. The rEM2 (13% explained variance) has a broad primary mode between 3 and 66 µm covering the whole silt fraction, with a maximum at 18.7µm, which corresponds to medium silt. The rEM3 (14% explained variance) has a mean mode between 16 and 144µm, and a maximum at 51µm (medium silt to fine sand fraction). The rEM4 (23% explained variance) has a very robust mode in the very fine to fine sand between 51 and 310 µm, with a maximum at 127 µm. The coarsest component rEM5 (26% explained variance) has a robust mode in the fine to medium sand between 86 and 454 µm, and a maximum at 211 µm.

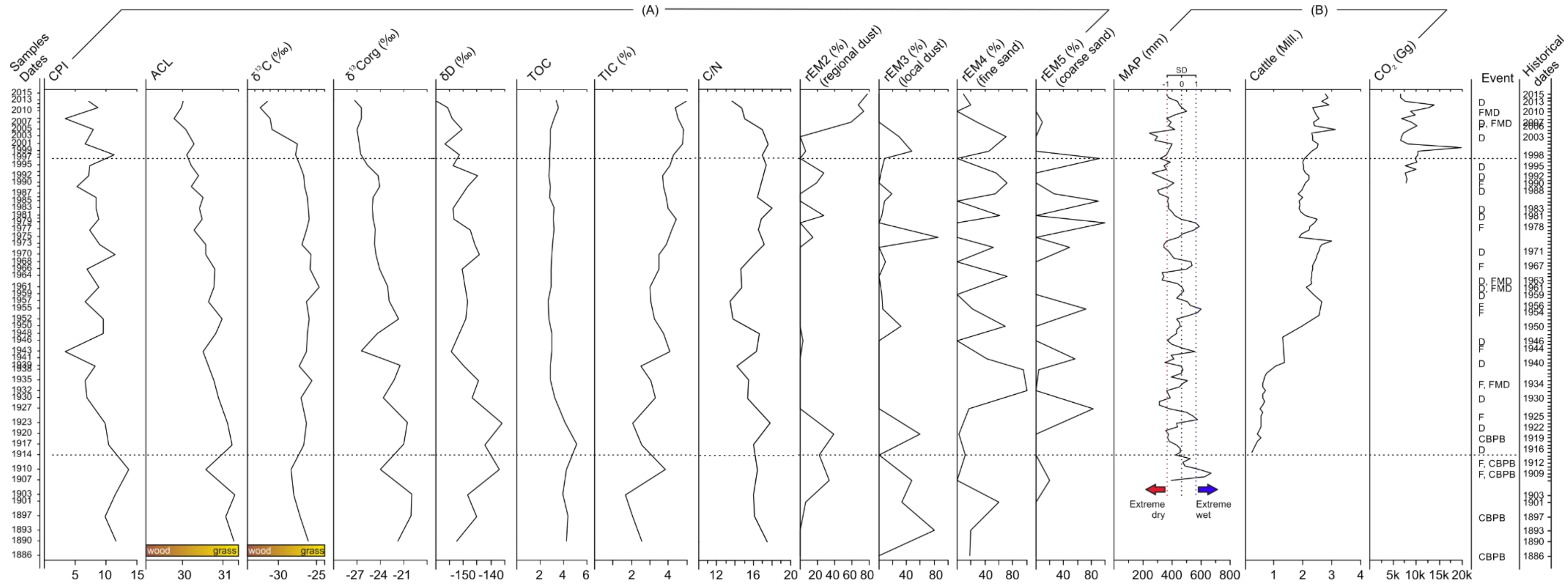

Figure 3-4. A) Biogeochemical and sedimentological proxies from core 15OJ10: Carbon preference indices (CPI_{25-35}); average chain length of *n*-alkanes with an odd number of carbon atoms (ACL_{27-33}); weighted mean of carbon isotopic compositions of *n*-alkanes ($\delta^{13}C_{WMA27-33}$); carbon isotopic composition of organic matter (δ^{13}Corg); weighted mean of deuterium isotopic compositions of *n*-alkanes ($\delta D_{WMA27-33}$); total organic carbon (TOC) content; total inorganic carbon (TIC) content; total organic carbon to nitrogen ratio (C/N); scores from robust end-member loadings (rEM). Dotted lines indicate pollen zones. B) Historical records: mean annual precipitation (3-year running mean - MAP) calculated from climate data (meteorological station Tsumeb), vertical black dotted line corresponds to the long-term MAP, red and blue dotted lines correspond to the standard deviation (SD); livestock numbers Namibia (data 1915-1959 (Lange et al., 1998); data 1961-2015 (FAO, 2018a)); CO_2 emissions Namibia (FAO, 2018b); documented events (D: drought; F: flood; FMD: foot & mouth disease; CBPP: contagious bovine pleuropneumonia (Directorate of Planning, 2011, 2005; Nicholson and Selato, 2000; Schneider, 2012; Sweet, 1998)).

3.4 Discussion

3.4.1 Source of the lake sediments

We consider terrestrial plants to be a major source of organic matter in the sediments of Lake Otjikoto due to their high CPI_{25-35} and C/N values (Meyers, 1997). Although higher TOC values (>4 %) below 25 cm depth, and the oscillating variation of $\delta^{13}C_{org}$ content below 18 cm, suggest a bacterial and algal contribution to the sediments (cf. Kristen et al. (2007)), corresponding C/N values (>16) indicate a higher proportion of allochthonous input relative to the autochthonous component of the organic matter (Meyers, 1997).

3.4.2 Savanna state-change: from open woodland to dense shrubland

Multidecadal shift in the grass/woody ratio

Our multiproxy approach indicates a shift in the dominance among grasses and woody vegetation. In particular, our results show an increase in woody vegetation since about 1915 in the Tsumeb region with a particularly strong increase after about 1998. These results validate vegetation models that suggest an increase in woody cover at low rates since 1850 in Africa, and an accelerated rate between 1990 and 2010 (Higgins and Scheiter, 2012). Our findings also support results from remote-sensing analyses of sub-Saharan savannas, which have observed an increase in woody vegetation cover over the last three decades (Mitchard and Flintrop, 2013; Venter et al., 2018).

The ratio of Poaceae/woody pollen (Fig. 3-2) indicates that the current grass/woody ratio is exceptional for the last 170 years and is similar to the ratio found by Scott et al. (1991) in a previous palynological study from Lake Otjikoto. Scott et al (1991) identified two earlier woodland phases with woody pollen abundances up to 33% and Poaceae pollen below 60% (Fig. S6). In our study, we estimate grass pollen abundances to decrease to below 60% in the 1970s and in the 21st century, while woody pollen percentages increase up to 32% suggesting a woodland phase in zone 3. These results are consistent with a modern pollen-vegetation study conducted in the vicinity of the lake, which found a mean woody pollen abundance of 33% by a mean woody cover of 74% at the study site (Tabares et al., 2018).

Biogeochemical results also support our pollen findings. The relatively constant $\delta^{13}C_{WMA27-33}$ values throughout zones 1 and 2 indicate mixed C_3/C_4 vegetation with the C_4 proportion generally above 50% (Badewien et al., 2015b). Only in the very recent past (zone 3) does $\delta^{13}C_{WMA27-33}$ shift towards more ^{13}C-depleted values providing evidence for an increase of the C_3 proportion up to around 80%, which is also supported by $\delta^{13}C_{org}$ values around -27‰ (Meyers, 1997). It has been reported that southern African savanna trees show significant variations in their ACL values, which, for example, are higher for *Combretum apiculatum* and *Colophospermum mopane* than for *Terminalia prunioides* and *Ziziphus* sp. (Kristen et al., 2010; Vogts et al., 2009; for Australian trees see: Hoffmann, Kahmen, Cernusak, Arndt, & Sachse, 2013). Assuming a significant contribution of trees to the sedimentary *n*-alkanes, the overall shift of ACL towards lower values throughout the profile is thus in agreement with the vegetation shifts inferred from pollen analyses and *seda*DNA as discussed in detail below.

In addition, grain-size distribution lets us infer changes in landscape openness via the type of sediment transport reflected in the grain size rEM (Dietze et al., 2014). The two types of sand deposits represented by rEM4 and rEM5 indicate short-term, high energetic sediment input from run-off during rain events or sand storms in an open landscape with reduced grass cover

(Dietze et al., 2014; Walther & Neumann, 2011). In particular, within the error of the age model, rEM5 can be associated with the main flood events documented in the region from the 1920s until 2000 (Fig. 3-4). We assume that an increased woody cover (as observed from the 21st century) favours the development of soil crusts on bare patches by constraining trampling (Thomas and Dougill, 2007). Although soil crusts reduce infiltration and promote run-off and erosion, they also increase soil roughness limiting the detachment of soil particles (Bullard et al., 2018; Rodríguez-Caballero et al., 2012; Valentin, 1993). Accordingly, soil crusts may retain the coarser sand fractions, which would explain the low percentages of rEM4 and rEM5 in zone 3. However, prolonged drought (as observed in the 1990s), followed by heavy rains, can damage the crust surfaces (Kidron et al., 2017; Thomas and Dougill, 2007), causing the loss of fine sand-sized particles (100-200µm), which require less energy to be detached compared to coarser and finer-sized particles (Bullard et al., 2018; Salles et al., 2000). This would explain why only fine sand (rEM4) mobilized during La Niña flood in 2006 (Fig. 3-4).

An increased woody cover would also retain the local dust sedimentation (rEM3), by reducing the near-surface wind energies. Hence, the associated importance of more remote dust (rEM2) from several hundred kilometres away within the detrital sediment fraction is seen during the last decade.

Compositional turnover in the course of shrub encroachment

Our pollen and *sed*aDNA results indicate a savanna state-change from open *Combretum* woodland to *Terminalia* shrubland during the 20th century at local (i.e. the vicinity of Otjikoto) and probably regional (i.e. the wider Tsumeb area) scales. These results are the first time-series with sufficient taxonomic resolution to show compositional change in the course of shrub encroachment in a semi-arid savanna at a multidecadal scale. They confirm theoretical assumptions (Joubert et al., 2008; Li, 2002) which were based on compositional observations of only a few decades or on the analyses of spatial gradients (Strohbach, 2001; van Rooyen et al., 2018).

According to our proxies, an open *Combretum* woodland dominated the landscape around Lake Otjikoto until the turn of the 19th to 20th century (i.e. zone 1 in our record). A high grass cover and the dominance of *Combretum* species in the tree layer are characteristic of this vegetation type (Mendelsohn et al., 2000), which is represented by high Poaceae pollen values and up to 50% *Combretum* in the *sed*aDNA records. Our results also show that *Grewia, Dichrostachys cinerea*, *Croton, Kirkia acuminata*, *Catophractes alexandri* (Bignoniaceae), and Ebenaceae (likely *Euclea sp.*) were common taxa in the tree and shrub layer of this vegetation type. This aligns well with modern observations of this vegetation type preserved on flat areas between dolomite hills (Giess, 1971), particularly on moderately deep soils (Mendelsohn et al., 2000). In addition, our results reflect botanical observations from the early 20th century of the existence of woodlands and lime steppes in the Tsumeb region (Dinter, 1918). A high pollen signal of *Petalidium* (likely *P. eurychlamys*) in the late 19th century and the *sed*aDNA record of *Gossypium* reflect early observations regarding both taxa as local indicators of open broad-leaved savanna vegetation (Dinter, 1922; Mildbraed, 1941). We assume that open *Combretum* woodlands represent the potential natural vegetation of the region and a stable savanna state. These results confirm a previous low-resolution pollen record from Lake Otjikoto (Scott et al., 1991) that revealed the presence of open Combretaceae-*Spirostachys* woodlands in the region during the late Holocene.

Our results allow us to infer a transition phase that ranges from 1920 to about 1997 (zone 2 in our record) and provide empirical evidence to previous studies, which assume a transition period of several decades between alternative stable grassland/woodland states (Higgins and Scheiter, 2012; Joubert et al., 2008).

The transition is marked by a high turnover in the vegetation proxy composition. While Poaceae are still abundant during this period some shrub taxa are also common (*Ziziphus* (Rhamnaceae), *Grewia, Phyllanthus/*Phyllantheae) particularly during the second half of the 20th century. Furthermore, this transition phase is characterized by unique taxa, particularly those associated with disturbance (e.g. common pasture taxa such as *Antigonon* and *Mentzelia* (López-Olmedo et al., 2007), and non-palatable weeds such as *Alternanthera pungens, Tribulus/*Tribuloideae, and *Geigeria* (Tabares et al., 2018)). This transition is also distinguished by the propagation of dwarf shrubs (*Monechma/*Justiciinae, *Pentzia*), annual grasses (*Tragus, Brachiaria deflexa, Aristida*), and the increase of shrub taxa (*Croton, Euphorbia, Gymnosporia* (Celastraceae), *Montinia caryophyllacea*, *Opilia*). We assume that our inferred transition phase corresponds to the unstable state described by Joubert et al. (2008), which is distinguished by the above-mentioned characteristics and by the spread of encroacher seedlings (e.g. *Senegalia mellifera*) in a mixed grass sward. The increase of *Senegalia* pollen in zone 3 may therefore indicate the maturity of *Senegalia mellifera* trees established in zone 2.

The vegetation at the local and regional scale around Lake Otjikoto after 1997 (zone 3 in our record) can be characterized as a *Terminalia prunioides* shrubland (*Terminalia prunioides* association in Hüttich et al., 2009; Mendelsohn et al., 2000; *Acacia-Terminalia prunioides* in Strohbach, 2014). This represents a stable encroached savanna state (Joubert et al., 2008) and is supported by the finding that the compositional change within zone 3 is rather small compared to zone 2. The vegetation is characterized by high abundances of *Vachellia, Senegalia,* and *Terminalia* and the decline of *Combretum* (Fig. 3-3) in our sedimentary vegetation proxy records, which likely indicates the spread of local encroacher species such as *Vachellia reficiens*, *Senegalia mellifera,* and *Terminalia prunioides* in the region (De Klerk, 2004; Strohbach, 2001). The transition toward *Terminalia prunioides* vegetation type is also reflected by the changes in the shrub layer: the abundances of *Grewia* and *Ziziphus* (Rhamnaceae) increase, while *Catophractes alexandri* (Bignoniaceae) and *Euclea* (Ebenaceae) decrease. Furthermore, a state-change towards encroached savanna is indicated by the decline in Poaceae pollen signals suggesting a reduction in grass cover, which is characteristic of *Terminalia prunioides* shrubland (Strohbach, 2014). Interestingly, the increase of Fabaceae (e.g. *Vachellia, Senegalia* in pollen and *sed*aDNA values) in zone 3 corresponds with more depleted $\delta^{13}C$ values of organic matter. This matches modern studies along spatial gradients that likewise found depleted $\delta^{13}C$ values in Fabaceae C_3 plant matter (Badewien et al., 2015b; Vogts et al., 2009).

We hypothesize that the current *Terminalia* encroached state may have occurred earlier in the region, as suggested by the compositional changes reflected in an early pollen record of Lake Otjikoto (Scott et al., 1991). In particular, the early woodland phase (zone O1), which is dominated by Combretaceae, may correspond to a phase of *Terminalia* encroachment, since the abundance of *Spirostachys* is low, while *Grewia* and *Acacia* have high pollen signals (Fig. S6). Interestingly, this phase is preceded by high abundances of *Tribulus*, which suggests a transition phase.

Given the changes in species composition and in the grass/woody ratio observed in our study, our results provide empirical evidence to support the hypothesis of Rohde and Hoffman (2012) that transitions from an open woodland into an encroached state in savannas from northern Namibia may occur on a scale of one century and without reversals to a grassy state.

3.4.3 Triggers and drivers

It is likely that a complex network of global, regional, and local triggers and drivers including land management (forestry, husbandry/cultivation), precipitation, and atmospheric $p\mathrm{CO}_2$ caused the observed vegetation turnover in the Tsumeb area (Fig. 3-5). However, limited data availability prevents us from doing straightforward multivariate statistical analyses such as decomposition of explained variances to statistically relate driver changes to changes in vegetation (Tian, Herzschuh, Mischke, & Schlütz, 2014); instead only trends can be compared.

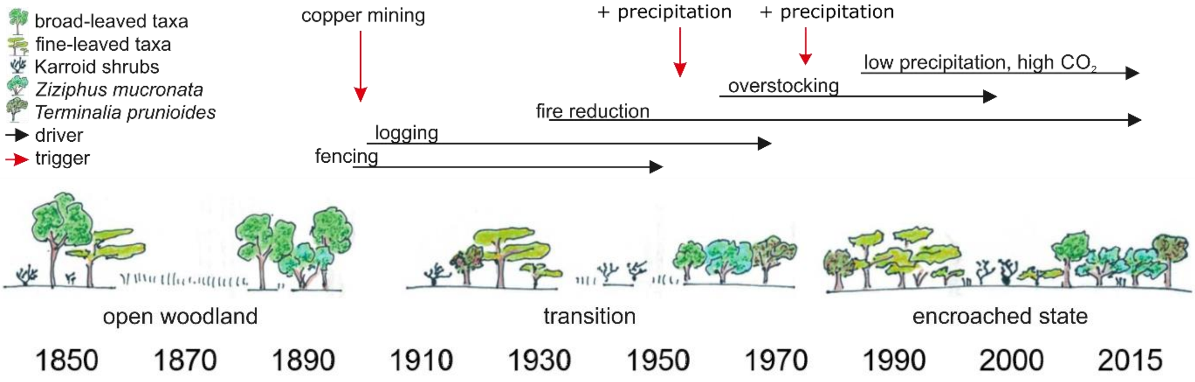

Figure 3-5. Network of triggers and drivers of savanna vegetation change.

Forestry in the context of mining

Our results support previous studies that assign the emergence of shrubland in northern Namibia to forest management (Strohbach, 2001). In particular, the expansion of thickets in the Tsumeb region, as indicated in forest reports from the 1950s, has been assigned to selective and broad-scale logging in the course of mining in the early 20th century (Erkkilä, 2001; Lau and Reiner, 1993). *Combretum*, *Spirostachys africana*, and *Colophospermum mopane* were cut for props and fuel for the Tsumeb mine (Erkkilä and Siiskonen, 1992) and this is reflected in the decline of these taxa in the Otjikoto pollen record. After logging, it is likely that dense thickets of *Spirostachys africana* formed because of its ability to form stump shoots and root suckers (Gandiwa et al., 2012; Moyo et al., 1993). The *Spirostachys/*Hippomaneae peaks in the pollen and *sed*aDNA records may indicate resprouting events during the Depression and the Second World War, times in which the mine production came to standstill (Lau and Reiner, 1993). In contrast, other local taxa became reduced because of their low growth rates (e.g. *Colophospermum mopane*, Cunningham, 1996) or their weak coppicing ability (e.g. *Combretum*, Strohbach, 2001). In order to supply the mines, *Eucalyptus* was planted in the Tsumeb region from the beginning of the 20th century (Dinter, 1918, 1909) and from 1949 at Lake Otjikoto (Lau and Reiner, 1993), which is reflected in our proxy records (Myrtaceae/Myrtoideae). Later on, gradual environmental changes, such as changes in the tree species composition and the reduction of soil moisture as a consequence of deforestation (Moyo et al., 1993), may have favoured the spread of *Vachellia*, *Senegalia*, and *Terminalia prunioides*, which are better adapted to drier conditions.

Husbandry

Land-use records from this study and census information (FAO, 2018a; Lange et al., 1998) indicate that the intensity of husbandry increased throughout the 20th century, which likely affected grass species composition and productivity.

The signal of *Sordaria*, an obligate coprophilous fungus spore associated with dung deposits of wild/domestic herbivores (Dietre et al., 2012; van Geel et al., 2011; van Geel and Aptroot, 2006), suggests the continuous presence of herbivores in the vicinity of the lake. The high values of *Sordaria* in the first half of the 20th century could be the result of herding of cattle at watering points and on productive pastures close to the lake, particularly during drought episodes (as suggested by the fungal peak at about 1946 (Fig. 3-2 and 3-4)). Surprisingly, the signal of *Sordaria* decreases in the second half of the 20th century although grazing intensity was likely highest during this period – census information on cattle in Namibia indicates an increase from ~700k animals before 1930 to ~2500k after 1950 (FAO, 2018a; Lange et al., 1998).

The decrease in the *Sordaria* signal could be related to a decline of transhumance pastoralism (as similarly observed by Gelorini et al. (2012) at lakes in Uganda), which is associated with changes in land tenure and management in the region. During the first half of the 20th century, most of the Otjikoto region became freehold land (Mendelsohn, Jarvis, Roberts, & Robertson, 2009), which resulted in the construction of fences, concentration of livestock, and eventually the restriction of traditional transhumance in the surroundings of the lake. From the 1960s, movement of cattle was further restricted because of the outbreak of foot-and-mouth disease (Schneider, 2012). The increase of cattle in the mid-20th century likely originated from the intensification of farming from the 1950s (Lau and Reiner, 1993). Additionally, the introduction of subsidies for feed and water-hole exploration in response to the prolonged drought in the early 1960s (Fig. 3-4), allowed ranchers to increase their stocks in years with good rain, and to maintain them in the drought years (Schneider, 2012; Sweet, 1998).

As reflected in the *sed*aDNA record, these practices led to the decrease of highly palatable grasses such as *Schmidtia* (likely *S. papophoroides*), *Brachiaria deflexa*, and *Fingerhutia africana*. They were, if at all, replaced by less palatable grasses such as *Hyperthelia dissoluta* and *Heteropogon contortus* which are characteristic of overgrazed areas (Kgosikoma et al., 2015). High grazing pressure on pastures during the mid-20th century is also indicated by above-average signals of non-palatable taxa such as *Geigeria* (Strohbach & Kutuahuripa, 2014) and *Acanthospermum* (Tolsma et al., 1987), as well as by trampling-resistant taxa such as *Alternanthera* and *Tribulus/*Tribuloideae (Tabares et al., 2018). High grazing pressure alongside poor grazing resources would also explain the cultivation of *Medicago* to complement livestock fodder from the 1990s around Lake Otjikoto as indicated in the *sed*aDNA record (Fig. 3-3).

The persistent high grazing pressure on pasture with already low grass density may have lowered the seed production of grasses to such an extent that potential niches could not be (re)invaded (O'Connor & Pickett, 1992; Tessema, de Boer, & Prins, 2016). This might explain why our *sed*aDNA record lacks *Fingerhutia africana* and *Schmidtia* (likely *S. papophoroides*) towards the present-day. According to the state-transition models, the lack of both species may also reflect the vegetation's response to overgrazing when disturbance passed a threshold.

Fire management

Our results show that there were changes in fire management related to husbandry and cultivation near Lake Otjikoto, which further altered the resilience of *Combretum* woodlands and supported shrub establishment in the long-term.

High macrocharcoal flux and high *Gelasinospora* values (a fungus growing preferentially on burned wood (Revelles and van Geel, 2016)) in sediments of the early 20th century point to local forest fires within a radius of about 5 km from the lake (Clark, 1988; Duffin et al., 2008). The emergence of cleared areas is reflected in the *sed*aDNA signals of pioneer grasses such as *Brachiaria deflexa* and *Tragus*. During the early 20th century, these areas were likely burned prior to crop cultivation as indicated by records of *Sorghum* (Lau and Reiner, 1993). Landscape opening is also reflected by the aeolian input of well-sorted coarse silt (rEM3), which was probably blown in from burned fields (Ravi et al., 2009).

During the mid-20th century the coincidence of lower charcoal flux and a decrease in *Sorghum sed*aDNA suggest that fire was used to manage livestock grazing by fostering the establishment of palatable grasses (Lau and Reiner, 1993; Sweet, 1998). This would explain the rise in *sed*aDNA signals of *Cenchrus* (likely *C. ciliaris* (Gilo and Kelkay, 2017)) and *Panicum* (likely *P. maximum*) in the second half of the 20th century. Both these highly palatable perennial grasses are common in the *Terminalia prunioides* shrubland (Strohbach, 2014) and are usually planted for hay and pasture (Sweet and Burke, 2006; van Oudtshoorn, 2016). The expansion of monoculture farming in the Tsumeb region, particularly from the 1980s (Lau and Reiner, 1993), is also suggested by decreases in charcoal flux and *Gelasinospora* signals (Fig. 3-3 and 3-2) towards zone 3, which in turn suggest the suppression of wildfire and/or the reduction of controlled fires to conserve pastures for livestock (Joubert et al., 2012).

An initially reduced grass cover in combination with artificial fire suppression may have affected the grass/shrub competition by reducing mortality of woody seedlings and saplings (Case and Staver, 2017; Joubert et al., 2012). The remaining grass tussocks may have improved the survival of seedlings of encroaching Fabaceae taxa such as *Crotalaria* and *Prosopis*, as the tussocks provide soil moisture and protection against heat stress (De Dios et al., 2014; Wagner et al., 2018), triggering a vegetation change into an encroached state.

Precipitation and atmospheric CO_2 changes

Comparing the pollen and *sed*aDNA records of *Vachellia* and *Senegalia* with the mean annual precipitation curve (Fig. 3-4) it seems plausible that drought years from 1980 onwards contributed to the spread of these drought-tolerant taxa. Previous periods with consecutive rainy summers (particularly 1976-1979 and 1954-1956) and reduced grass cover also favoured the germination and establishment of their seeds and saplings. These results are in line with several studies, which identified a positive relationship between rainfall, seed production, and seedling survival of encroacher species (Joubert et al., 2013, 2008; Wagner et al., 2018).

Our records show a die-back of *Senegalia* in the 21st century. This may be related to persistent drought stress, as reported from Botswana in 2013 (Joubert et al., 2013). Persistent drought can also inhibit the recovery of *Cenchrus ciliaris, Combretum apiculatum,* and *Dichrostachys cinerea* (O'Connor, 1998), which explains the low *sed*aDNA signals of related taxa from the mid-1990s (i.e. zone 3).

Interestingly, the *Vachellia* pollen and *sed*aDNA signals in zone 3 are high when compared with *Senegalia*, which probably reflects differences in drought sensitivity. As observed by Joubert et al. (2013), *S. mellifera* has a lower tolerance for prolonged periods of moisture stress than *Vachellia* species such as *V. reficiens*, *V. erubescens*, and *V. erioloba*. According to the authors, *S. mellifera* mostly relies on an extensive shallow-root system, while *V. reficiens* and *V. erioloba* rely on a deeper tap-root system, which enables water uptake from deep soil layers.

The observed depletion of δD values of plant-derived *n*-alkanes since around 1992 (Fig. 3-4) may also reflect the water uptake of deep-rooted trees from deep soil layers. In arid and semi-arid environments, soil water has higher δD values than precipitation because of strong evaporation (Da Silveira Lobo Sternberg, 1988). Consequently, water from soil surface layers is more enriched in D compared to soil water from deep layers (De Deurwaerder et al., 2018; Ehleringer and Dawson, 1992). Therefore, under dry conditions, xylem water from grasses is expected to have higher δD values compared to trees with a deep root system. Field studies performed in Namibian savannas show that xylem water from deep-rooted species such as *V. erioloba*, *V. hebeclada*, and *Prosopis juliflora* comes from D-depleted deep soil layers (Kanyama, 2017). Our pollen and *sed*aDNA results indicate an increase of *Vachellia* and *Prosopis* in zone 3. However, it is unclear to what extent the isotope composition of xylem water is reflected by leaf lipids. While greenhouse experiments found a correlation between leaf wax and soil water δD composition (Hou et al., 2008), field studies show that the leaf wax δD signature depends mostly on evaporative enrichment of leaf water during photosynthesis (Feakins and Sessions, 2010).

Considering the influence of photosynthesis on δD values, depletion in zone 3, particularly since the beginning of the 21st century, may also reflect an increase in the water-use efficiency of woody vegetation, which in turn is enhanced through, for example, reduced stomatal conductance and stomata density due to an increasing atmospheric $p\mathrm{CO_2}$ concentration (Fig. 3-4). Studies conducted in tropical environments have shown that trees increase their water-use efficiency at higher CO_2 concentrations, despite high transpiration rates (Brienen et al., 2011; van der Sleen et al., 2014). In contrast, trees in arid and semi-arid environments, and under higher CO_2 concentrations, reduce their stomata opening while carbon assimilation increases (Evans et al., 2000; Krishnamurthy and Machavaram, 2000). This improved ratio of carbon assimilation-to-conductance results in an increase of transpiration efficiency (Evans et al., 2000), which in turn leads to ^{1}H enrichment in leaves and thus a decrease in δD values. Such higher atmospheric CO_2 concentrations may have favoured the propagation of *Vachellia* and *Senegalia* towards the present-day, because Fabaceae species are expected to benefit from such conditions in nutrient-limited savanna environments (Wagner et al., 2018; Ward et al., 2014). As observed by Evans et al. (2000), *Acacia* species increase their nitrogen content per unit foliage area when growing under a higher CO_2 concentration. Consequently, the photosynthetic capacity of leaves increases (Evans, 1989), which can then improve the competitiveness of *Acacia* species against grasses.

The interpretation of the leaf wax δD is complicated further as the signature of the water source of plants may have changed as well. The high δD values around 1916 (i.e. in the transition between zones 1 and 2) probably reflect an enrichment of source water. Such an interpretation is supported by the high concentration of inorganic carbon (TIC) and an increase of *Ficus* pollen that inhabits the walls of the sinkhole. A low lake level may result from low rainfall between 1916 and 1922 (Fig. 3-4). The decrease of δD values from the mid-1990s (i.e. at the transition to zone 3) despite high TIC and *Ficus* pollen signals and low precipitation, however, contradicts the interpretation of the leaf wax δD as primarily representing a precipitation signal (Niedermeyer et al., 2016; Sachse et al., 2012) but rather supports our interpretation of changes in the plant water source.

Our results suggest that environmental changes derived from management (i.e. reduced soil moisture, reduced grass cover, changes in species composition and competitiveness, reduced fire intensity) may have affected the resilience of *Combretum* woodlands, making them more susceptible to change into an encroached state by stochastic events such as consecutive years of precipitation and drought, and by high $p\mathrm{CO}_2$ concentrations. These results are in line with state-transition models, which predict gradual changes in environmental conditions to alter the resilience of stable states, thus enhancing the likelihood of a state-change (Scheffer et al., 2001).

3.4.4 State stabilizing feedbacks

Comparing our multiproxy record with historical climate and land-use data allows us to infer the feedback mechanisms that support the stable states observed in our study. This allows us to interpret the observed vegetation changes in the context of state-transition models (Hirota et al., 2011; Scheffer et al., 2001).

Open Combretum woodland

Transhumance and intense fires, as reflected by our spore and charcoal records, may have stabilized an open woodland phase. A high grass cover, as observed in phase 1, may produce enough fuel for intense fires, which increase seedling and sapling mortality (Beckett and Bond, 2019; Case and Staver, 2017; Hirota et al., 2011; Staver et al., 2011). Since tree seedlings are not as fire-resistant as adult trees and some of them are very palatable (e.g., *Dichrostachys*), a combination of fire and browsing may also have prevented tree seedlings from being recruited to mature age classes (Gillson, 2004; Joubert et al., 2012; Scheffer et al., 2001).

In addition, wetter conditions may have favoured competitiveness of *Combretum* and *Spirostachys* against drought-tolerant taxa. An early *Combretum-Spirostachys* woodland phase at Otjikoto was linked to wetter climatic conditions (Scott et al., 1991). Although vegetation models predict a woody state in savannas with increased precipitation (Hirota et al., 2011), our results allow us to infer that under such climatic conditions open *Combretum* woodland is possible, but also *Terminalia* shrubland, as the latter profits from wet years followed by persistent drought.

Terminalia shrubland

Several feedback mechanisms may stabilize the encroached state and inhibit the reverse transition towards an open woodland state:

First, open patches in degraded pastures may have supported the formation of trampling-resistant soil crusts (Dougill and Thomas, 2004) containing nitrogen-fixing cyanobacteria. These soil crusts, in turn, may have favoured the establishment of nitrogen-fixing shrubby Fabaceae, which eventually inhibit grass growth under their canopy (Maron and Connors, 1996). Such a feedback mechanism would explain the decrease in the C/N ratio (Fig. 3-4) in the uppermost sedimentary record due to the allochthonous input of nitrogen-enriched soil materials (Talbot, 2005) in Lake Otjikoto. The latter is also supported by the predominance of fine-sized sediments in zone 3 (rEM1, rEM2), which may also depress the C/N values by uptake of inorganic N, since higher proportions of clay can absorb ammonia well (Meyers, 1997).

Second, the reduction of grass cover towards the present day in Tsumeb coincides with soil erosion, as suggested by *Glomus*, a spore of an arbuscular mycorrhizal fungus associated with eroded soils (Revelles and van Geel, 2016; van Geel et al., 2011) (Fig. 3-2). On bare soil patches with soil crusts, run-off increases and water infiltration decreases, which further reduces the establishment of grass seedlings (Strohbach, 2001). In addition, climate- and/or human-induced damage to soil crusts can lead to soil losses (as suggested by rEM4 in zone 3), which in turn promote rill formation thus reducing the surface run-off and limiting the run-on input to vegetation (i.e. limiting the formation of temporary ponds and soils with water tables (Rodríguez-Caballero et al., 2012; Valentin, 1993)). Our study supports previous studies that find soil erosion in the course of bush encroachment since the second half of the 20th century (De Klerk, 2004; Strohbach, 2001).

Third, the practice of bush removal (indicated for Lake Otjikoto by a slight decrease of shrub pollen in the uppermost core section and observed in the locality of Otjiguinas Farm during fieldwork) enables the establishment of fast-growing species such as *Hyperthelia dissoluta* (recorded in the uppermost section). This perennial grass spreads across disturbed fields forming dense tall swards, which inhibit the growth of other grasses (Cech et al., 2010; Jordaan, 2017).

Fourth, once established, woody vegetation with a mixed rooting system such as *Senegalia mellifera* and *Prosopis* sp., can suppress grass production (Smit, 2003), as they can effectively take-up soil moisture from the upper soil layer after rain events with their lateral roots and survive dry phases due to water uptake by deep roots (Ansley et al., 2014; Brown and Archer, 1999). A reduced grass cover in turn reduces the intensity of fire, resulting in the self-propagation of a woody state (Higgins and Scheiter, 2012; Hirota et al., 2011; Scheffer et al., 2001).

Fifth, climate change (i.e. higher atmospheric $p\mathrm{CO}_2$ concentration and changes in precipitation variability) may induce physiological adaptations (as suggested by our δD record) enhancing the competitiveness of trees over grasses. Although persistent drought constrains the CO_2-related photosynthetic advantages for savanna trees (Nackley et al., 2018), the assimilation rates are still higher for C_3 plants compared to C_4 grasses under such conditions (Bellasio et al., 2018). This is because C_4 grasses under water restriction experience metabolic inhibitions that have a greater effect on leaf assimilation compared to the limited stomatal conductance of savanna trees (Bellasio et al., 2018). Furthermore, under restored watering conditions, photosynthetic rates recover faster when inhibited by stomatal than by metabolic factors, which in turn affects the competitiveness of C_4 grasses under optimal conditions (Bellasio et al., 2018). Such a feedback mechanism implies that at higher atmospheric $p\mathrm{CO}_2$ concentration, an increase in the frequency of droughts and heavy rains may favour the expansion of C_3 vegetation (Zhang et al., 2019).

These feedback mechanisms explain the ongoing encroachment processes observed at our study site up to the present, even though management intensity may have adjusted to the local carrying capacity (e.g. decline of cattle numbers from the 1970s (Lange et al., 1998) and a levelling off of cattle populations since 2000) or decreased (e.g. regulation of timber production since 1968 (Erkkilä and Siiskonen, 1992)). The current vegetation may thus represent a management legacy from the first half of the 20th century, as well as the impact of climate change.

3.5 Conclusions

We have shown that the expansion of shrubs is a multidecadal trend characterized by the turnover from stable open woodland to a stable encroached state. Our results indicate that such a state-change may occur on a scale of a century and without short-term reversions to a grassy state, but with an unstable transition phase, which covers about 80 years and is characterized by a steady turnover of taxa, some of which are restricted to the transition phase.

We demonstrate that the current grass/woody ratio is exceptional for the last 170 years, and that such a process is related to gradual changes in soil moisture, erodibility, and species composition and competitiveness. Our inferences largely support prior theoretical considerations about shrub encroachment dynamics in southern African savannas that were mostly based on space-for-time approaches or studies with low taxonomic and temporal resolution.

Our study shows, for the first time, the potential of *seda*DNA analysis to track vegetation changes in savanna environments, as well as to infer related local and global triggers and drivers. In particular, detailed taxonomical information enabled us to confirm and complement our pollen findings, and thus to reconstruct the turnover from broad-leaved to fine-leaved tree taxa and *Terminalia.*

Taking into account an earlier pollen record of Lake Otjikoto (Scott et al., 1991), we suggest that shrub encroachment is not a new phenomenon, and that it possibly occurred in the past in the Tsumeb region, as suggested by changes in taxonomic composition and the grass/woody ratio observed in the previous record. In this sense, the encroached state observed in our study can be interpreted as a successive phase in a context of state-transitions, and is in line with previous studies that define encroachment as an alternative stable state (Gil-Romera et al., 2010).

Comparing our vegetation proxies to environmental proxies and historical data we inferred the impact of logging, as well as physiological adaptations related to changes in precipitation regime and high atmospheric $p\mathrm{CO}_2$ concentrations. Furthermore, detailed information of grass taxonomical composition (which is restricted in the pollen record) made it possible to infer changes in land use, such as crop cultivation, selective grazing, and overgrazing. Combined with our macrocharcoal record, we deduce changes in fire management associated with the intensification of farming.

Our study helps fill a knowledge gap about the feedback mechanisms supporting shrub encroachment. Such mechanisms reflect the interplay between historical land use and climate change (Perring et al., 2018), enabling us to confirm the far-reaching effects of management legacies on vegetation in savanna ecosystems.

Overall, this study highlights the suitability of multiple lake sedimentary proxies (particularly *sed*aDNA) to resolve complex compositional change and related environmental conditions in semi-arid savannas on at least decadal and centennial timescales.

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4 Manuscript 3

Relative pollen productivity estimates of savanna taxa from southern Africa and their application to reconstruct shrub encroachment during the last century

The Holocene, 2020, submitted.

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Abstract

To understand the resilience of African savannas to global change, quantitative information on the long-term dynamics of vegetation is required. Past dynamics can be reconstructed with the REVEALS model, which requires pollen productivity estimates (PPE), which are calibrated using surface pollen and vegetation data. Here we calculated PPE values for five savanna taxa using the extended R-value (ERV) model and two pollen dispersal options: the Gaussian plume model (GPM) and the Lagrangian stochastic model (LSM). We used Combretaceae as the reference taxon – values obtained with Poaceae as the reference taxon are presented in the supplement. Our results indicate that Combretaceae is the taxon with the highest pollen productivity and *Grewia* the taxon with the lowest productivity. *Acacia* and *Dichrostachy*s are intermediate pollen producers. The ERV calculations failed to produce a reliable PPE for Poaceae. We find no clear indication of whether the GPM PPEs or the LSM PPEs are more realistic, but the differences between these values confirmed that the pollen fall speed has a greater effect in the modelling of GPM than in the LSM. We also applied REVEALS to the pollen record of Lake Otjikoto (northern Namibia) and obtained the first quantitative reconstruction of the last 130 years of vegetation history in the region. Cover estimates for Poaceae indicate the predominance of a semi-open landscape throughout the 20th century, while cover values below 50% since the 21st century correspond to a thick savanna. This change in grass cover is associated with the spread of *Vachellia*, *Senegalia* and *Grewia* reflecting an encroached state.

4.1 Introduction

Quantitative information on long-term vegetation dynamics in southern African savannas is necessary to characterize shrub encroachment (Hoffman et al., 2019; Stevens et al., 2016). Several studies have used compositional changes of fossil pollen records (Miller and Gosling, 2014; Neumann et al., 2010) or woodland/grassland pollen taxa ratios (Gil-Romera et al., 2010; Gillson, 2004) to track vegetation change in savannas qualitatively or semi-quantitatively. Quantitative reconstructions of past vegetation cover based on fossil pollen records remain a challenge due to the non-linearity of pollen-vegetation relationships (Prentice and Webb, 2009). Although some calibration efforts have been made using modern pollen analogues of savanna taxa (Duffin and Bunting, 2008; Julier et al., 2018; Schüler et al., 2014), calibration of fossil pollen records from southern African savannas are still lacking, even though such gained knowledge may have implications for land management.

Pollen deposition in the savanna is characterized by over-representation of wind-pollinated grasses and under-representation of the insect-pollinated shrubs and trees that dominate the vegetation (Duffin and Bunting, 2008; Mariani et al., 2016). Furthermore, it is known that assumptions on dispersal and productivity of the individual taxa eventually impact the reconstructed vegetation composition (Prentice, 1985). Whether and how such effects also apply for savanna taxa in southern Africa, is currently unknown. Duffin and Bunting (2008) applied the extended R-value model (ERV; Parsons and Prentice, 1981) to calculate relative pollen productivity estimates (PPEs; Sugita, 1994) of savanna taxa by using the Prentice-Sugita model for pollen dispersal (Prentice, 1988, 1985; Sugita, 1993). This model is based on Sutton’s equations of small particle dispersal and deposition (Sutton, 1947), which is a particular form of the Gaussian plume model (GPM; Jackson and Lyford, 1999). However, studies about dispersal of insect-pollinated taxa (Mariani et al., 2016) argue that mechanistic dispersal models, such as the Lagrangian stochastic model (LSM; Kuparinen et al., 2007) better display transport, particularly of large pollen grains, whose contribution is assumed to be anisotropic and to take place under unstable atmospheric conditions (Pérez et al., 2018). To date, the LSM has not been tested for modelling pollen dispersal of southern African savanna taxa.

In this study, we aim 1) to calculate fall-speed values and PPEs of the five main taxa of savanna vegetation in northern Namibia, and 2) to reconstruct past vegetation cover based on PPEs and fossil pollen data from Lake Otjikoto in north-central Namibia. Here we apply, for the first time in southern Africa, the LSM dispersal model (Kuparinen et al., 2007) and the REVEALS (Regional Estimates of Vegetation Abundance from Large Sites; Sugita, 2007; Theuerkauf et al., 2016) model to quantify landscape cover changes in semi-arid savanna environments.

4.2 Methods

4.2.1 Study sites

We investigated 10 sites in north-central Namibia (Fig. 4-1). The distance between sites is at minimum 2 km to avoid spatial autocorrelation (Bunting et al., 2013) and the distance between the northernmost and the southernmost sites is approx. 200 km. The mean annual rainfall in the study area ranges from 306 to 460 mm falling mainly in the summer months (October – March; Harris et al., 2014; Table 4-1).

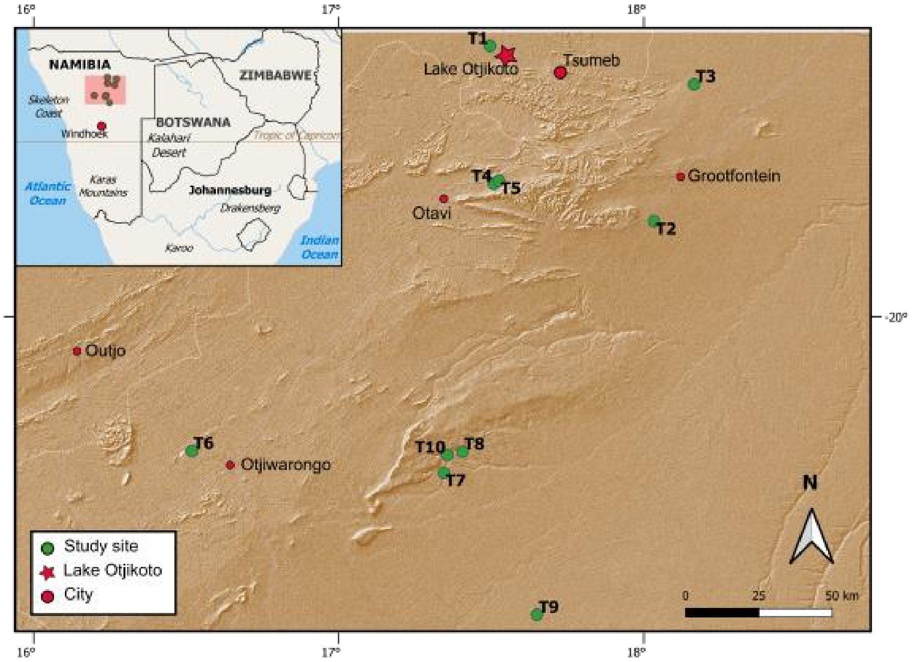

Figure 4-1. Map of the study sites.

The five northern sites (T1–T5) are located in Karstveld. This landscape is characterized by dominance of soluble dolomite and limestone in the substrate; cambisols and chromic luvisols are the main top soils (Mendelsohn et al., 2000). The vegetation consists of mixed woodland dominated by broad-leaved taxa such as *Colophospermum mopane*, *Combretum imberbe*, *C. apiculatum* and *Terminalia prunioides* (Mendelsohn et al., 2000).

Table 4-1. Overview of the study sites including GPS coordinates of the sample point in each transect. Mean annual precipitation (MAP) was estimated from climate cell gridded data (CRU TS v. 4.03; Harris et al., 2014), vegetation structure and landscape according to Mendelsohn et al. (2009).

Site_ID	Latitude	Longitude	Elevation (m)	MAP (mm)	Landscape	Vegetation structure
T1	-19.16366	17.4961	1212	406	Karstveld	Mixed woodland, broad-leaved taxa
T2	-19.70513	18.03364	1426	397	Karstveld	Mixed woodland, broad-leaved taxa
T3	-19.28155	18.16444	1297	425	Karstveld	Mixed woodland, broad-leaved taxa
T4	-19.58974	17.508012	1508	460	Karstveld	Mixed woodland, broad-leaved taxa
T5	-19.57997	17.52529	1513	460	Karstveld	Mixed woodland, broad-leaved taxa
T6	-20.41182	16.51911	1382	378	Thornbusch savanna	Mixed woodland
T7	-20.47968	17.34482	1403	342	Thornbusch savanna	Mixed woodland
T8	-20.41427	17.40593	1398	342	Thornbusch savanna	Mixed woodland
T9	-20.91421	17.65009	1341	306	Thornbusch savanna	Acacia shrubland
T10	-20.42483	17.35616	1438	342	Thornbusch savanna	Mixed woodland

The sites T6 to T10 are found in the thornbush shrubland, except for the southernmost site (T9), which is in the central Kalahari. The local substrate at the southern sites consist of Kalahari sands and sands of the Etjo formation. The main top soils are ferralic and clay rich arenosols (Mendelsohn et al., 2010). Common vegetation types are mixed woodland and *Acacia* shrubland, which are characterized by *Terminalia sericea*, *Burkea africana*, *Baiquiaea plurijuga*, *Vachellia erioloba* and *Senegalia mellifera* (Mendelsohn et al., 2010).

All study sites are situated on farms and used for cattle herding and reflect the main vegetation composition of their corresponding landscape (Table 4-1). Dominant encroacher species are *T. prunioides* and *Dichrostachys cinerea* in the Karstveld, and *S. mellifera* in the thornbush sites (De Klerk, 2004).

4.2.2 Vegetation data

Vegetation composition was analysed within 7 km^2 from each study site using plot releves as well as satellite imagery (Fig. 4-2a). The releves were used to identify plant species composition within a radius of 250m from pollen sampling point, while satellite imagery was used to map the spatial pattern of major vegetation types within a radius of 1.5km.

The releves were performed during field work on 11 plots of 5x5m at each study site. The plots were spaced 50 m apart along a 500 m long transect (Fig. 4-2b). Transects were defined according to the homogeneity of the vegetation and avoiding the presence of buildings in the studied area.

The plot located in the middle of the transect at each study site was chosen to take pollen samples (Fig. 4-2b). For each of the central plots, surface soil samples (approx. 60 g) were collected from six subplots and pooled for subsequent pollen analysis.

Plant abundances in each plot were estimated using the Braun-Blanquet method (1964). We assigned scores to infer the relative percentage of plant cover in the ground and tree layers as described in Tabares et al. (2018).

At each study site, the releves data from the corresponding 11 plots were combined into average cover values for each taxon. To match the pollen types Combretaceae, *Acacia*, *Grewia* and Poaceae, we merged the average cover of the corresponding woody species at the genus level, while grass cover was aggregated at the family level.

Satellite imagery was used to estimate plant abundances within a radius of 1.5 km at each study site (satellite images courtesy of the DigitalGlobe Foundation: www.digitalglobefoundation.org). We used multispectral GeoEye-1 and WorldView-2 satellite images at 0.4 m resolution. All scenes were pan-sharpened and ortho-corrected. For each scene, training samples were manually defined for three land-cover classes (bare soil, woody vegetation, grasses). The training samples were then used to automatically classify each scene using all available spectral bands and the respective models using the RStoolbox package (Leutner et al., 2019; R Core Team, 2018). The decision for a respective classification model was based on a visual inspection of the results and accuracy metrics.

To enable distance weighting (Broström et al., 2004; Calcote, 1995), plant abundances were estimated in fifteen 100 m wide concentric rings around each pollen sampling point (Fig 4-2a). The area of each land cover class derived from the satellite data was then calculated for each ring using R.

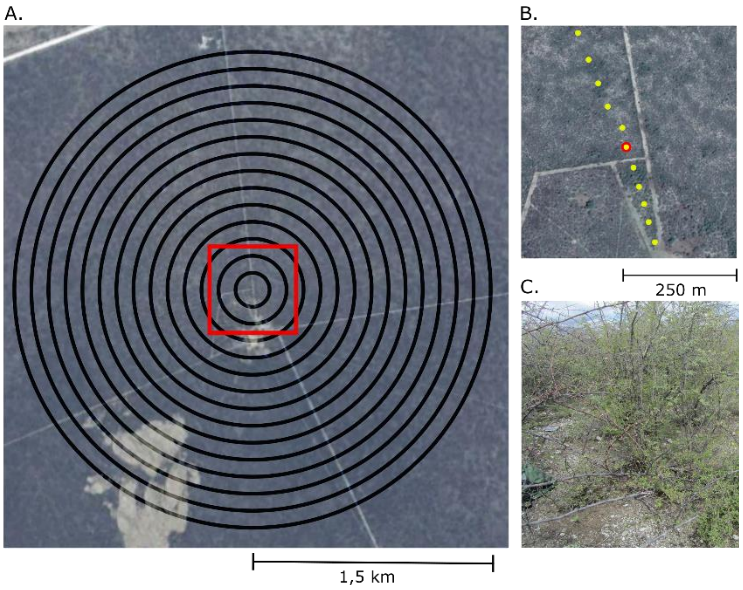

Figure 4-2. Vegetation sampling design. A) Area of vegetation classified with satellite images using concentric rings. The red frame indicates the area surveyed on the field; B) Vegetation plots along a transect in the field, where the central plot (red) is the sampling point; C) Vegetation in the plot at site T1 (image by X. Tabares).

The woody vegetation cover for each ring was transformed into taxa-specific cover, multiplying first by the added cover of the selected woody taxa obtained in the field survey for each site, and then multiplying by the abundance averages of the individual taxa.

4.2.3 Modern pollen analysis

Pollen samples were prepared for pollen analysis following standard procedures (10%HCl, KOH, 40%HF – including 4 hours boiling – and acetolysis; Faegri and Iversen, 1989; Moore et al., 1991). A minimum of 400 pollen grains were counted per sample using a microscope of x400 magnification. Taxonomical identification was based on standard literature (Bonnefille and Riollet, 1980; Gosling et al., 2013; Leźine, 2005; Reille, 1995; Scott, 1982). Pollen percentages were calculated relative to the total terrestrial pollen sum.

We selected five pollen taxa according to their dominance in the regional vegetation and in the modern pollen spectra (Duffin and Bunting, 2008): *Acacia* (incl. *Vachellia* sp. and *Senegalia* sp.), *Dichrostachys cinerea*, Combretaceae (incl. *Combretum* sp. and *Terminalia* sp.), *Grewia* (*Grewia* sp.) and Poaceae.

We estimated pollen fall speeds using Stoke's Law (Gregory, 1945), which predicts the settling velocity of spherical smooth particles smaller than 70 µm diameter. Although pollen grains have different structures and shapes, empirical studies have demonstrated that Stoke's Law is a reasonable theoretical predictor of pollen settling velocity (Borrell, 2012; Di-Giovanni et al., 1995; Gregory, 1973). Pollen size measurements were taken for at least 30 pollen grains of each selected taxon. Pollen grains were chosen at random from the slides of the surface samples from our study sites.

4.2.4 Pollen productivity estimates analysis

Pollen productivity estimates (PPEs) are calculated as pollen productivity ratios between two taxa (Broström et al., 2008; Bunting et al., 2013). In this study, we chose Combretaceae as the reference taxon (PPE=1) because its pollen type is well represented in the pollen record, and because the corresponding species are common in the regional vegetation (i.e. *Combretum* sp. and *Terminalia* sp.). Furthermore, this allows for comparability of our results with a previous PPE study in African savannas by Duffin and Bunting (2008).

Although Poaceae is one of the main components of savanna vegetation, its use as a reference taxon in calibration studies is problematic because the pollen type is produced by many species, which produce pollen in varying amounts and hence the resulting pollen signal can be highly variable (Baker et al., 2016; Li et al., 2015; Mariani et al., 2016). For comparison, we show a set of PPEs calculated with Poaceae as a reference taxon (Table S1). We interpreted the taxa as low, medium or high pollen producers according to Kuneš et al. (2019).

For the calibration of pollen-vegetation relationships we applied the ERVinR function (Theuerkauf et al, in preparation), which is based on the ERV sub-model 3 (Sugita, 1994, 1993). This model describes the pollen-vegetation relationships as follow:

$$yik = dwpaik*Pi + \omega i \tag{1}$$

where,

yik = pollen loading of species i at site k

$dwpaik$ = distance weighted plant abundance of species i at site k

Pi = pollen productivity of species i

ωi = background pollen loading for species i

As a slight adaption, the ERVinR function assumes a uniform regional vegetation composition at all sites (Theuerkauf et al, in preparation):

$$yik = dwpaik*Pi + dwpair*Pi \tag{2}$$

where dwpair corresponds to the distance weighted regional plant abundance of species i. The ERVinR model aims to find best matching PPEs and regional abundance for each taxon with the given local distance weighted plant abundances and observed pollen deposition. For validation, the resulting regional abundances can be compared against observed abundances.

To obtain the most reliable set of PPEs for this study, we proceeded as follows: first, we applied the ERVinR function comparing the GPM with the LSM as dispersal models for simulation of pollen flow for the five selected taxa. Second, we tested the ERV-model performance at a region size (RegionCutOff) of 3, 10 and 50 km radius and repeated calculations 20 times to derive error estimates. Third, we repeated the analysis without Poaceae to identify the influence of this taxon on the model performance. Fourth, we selected the results obtained with the RegionCutOff and the number of taxa that yielded the best values and repeated calculations 100 times to derive PPE errors. The PPEs corresponding to the selected results were used in the REVEALS reconstruction. To assess the goodness of fit between the modelled pollen and the empirical pollen counts, we also calculated Pearson product-moment correlation analysis for each taxon.

4.2.5 Vegetation cover reconstruction

For the reconstruction of past vegetation cover we applied the REVEALS model (Sugita, 2007; Theuerkauf et al., 2016) to a fossil pollen record from Lake Otjikoto in Namibia (Tabares et al., 2020). The REVEALS model was applied using the PPE values obtained in our study (Table 4-2). For Poaceae we used the PPE calculated with Combretaceae as the reference taxon and available in the literature for savanna environments (PPE = 2.02; Duffin and Bunting, 2008). Due to the poor model fit obtained for Poaceae in our study (Fig. S4 and S5), we decided not to use the corresponding PPE value (Table S3).

Model runs were performed using GPM for neutral atmospheric conditions and LSM for unstable conditions. Due to the lack of vegetation survey data from around the lake, we validated the REVEALS results against regional vegetation data. Since our satellite images were taken in the period 2012–2015, we calculated the mean cover estimates of the REVEALS results from the same period and compared them with the corresponding mean cover values of the northern sites (T1-T5), which belong to the same landscape (Karstveld).

All analyses were performed in R software (R Core Team, 2018) with the package DISQOVER (http://disqover.botanik.uni-greifswald.de).

4.3 Results

4.3.1 Pollen and vegetation

We identified a total of 54 pollen types and 139 plant taxa (Table S2). The total vegetation cover in the surveyed plots varies from 56–97%. The taxa selected for ERV analysis represented 56–82% of the total vegetation cover (Fig. 4-3). In the pollen record, the selected taxa represented between 62% and 81% of the total pollen sum.

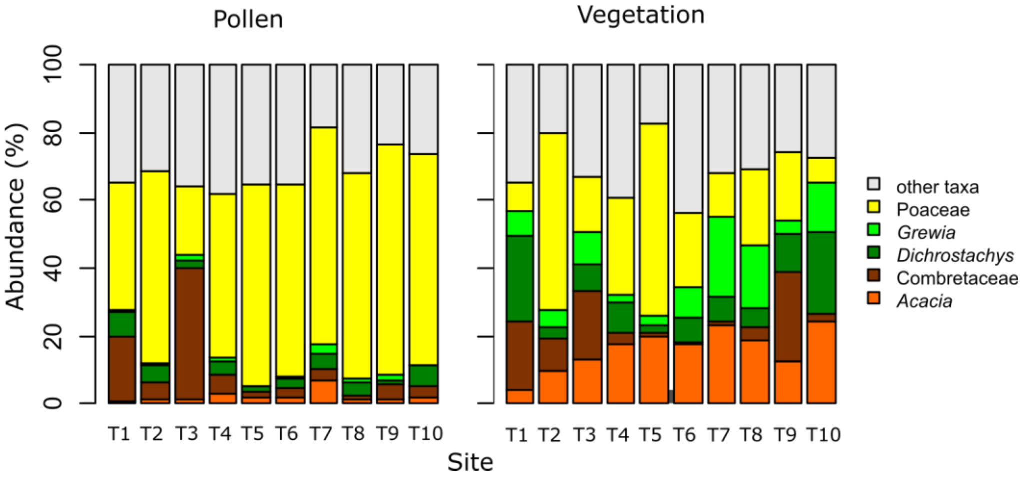

Figure 4-3. Pollen percentages and total vegetation abundances at the study sites.

Poaceae is the dominant pollen taxon at all sites, with the exception of T3, where Combretaceae pollen reaches high values (38%). Combretaceae also shows the greatest variation in the pollen (1.1–38%) and vegetation data (0.7–26%).

Acacia is rare in the pollen record (0.6–6.7%) although more abundant in the vegetation (4.2–24%). *Dichrostachys* and *Grewia* are also under-represented, reaching 25% and 23% in the vegetation but only 7.3% and 2.5% in the pollen record, respectively.

4.3.2 Pollen fall speeds and PPEs

Pollen fall speeds range between 0.014 m/s^{-1} for Combretaceae as the smallest pollen type and 0.067 m/s^{-1} for *Grewia* as the largest pollen type (Table 4-2).

Table 4-2. Mean pollen grain size, fall speed estimates and calculated pollen productivity estimates (PPEs) for selected taxa. RegionCutOff was set to 10 km. GPM: Gaussian plume model; LSM: Lagrangian stochastic model; SE: standard error. PPEs calculated with Poaceae as the reference taxon are presented in Table S1.

Taxa	Mean axis (µm)	Fall speed (m s^{-1})	PPE GPM	SE	PPE LSM	SE
Acacia	46.25	0.065	0.420	0.015	0.235	0.009
Dichrostachys	27.5	0.023	0.290	0.013	0.430	0.018
Grewia	47.13	0.067	0.230	0.010	0.090	0.004
Combretaceae	22.18	0.015	1.000	0.000	1.000	0.000
Poaceae	31.76	0.031	-	-	-	-

The resulting PPEs differ in response to the chosen dispersal model and the selected size of the region (RegionCutOff; Table S3). All calculations indicate higher pollen productivity in Combretaceae than in *Acacia*, *Dichrostachys* and *Grewia*. The PPE values of Poaceae (PPE range: 2.8–4.9) indicate the highest pollen productivity using both dispersal models (Table S3A). Furthermore, we find that for the taxa with high pollen fall speeds – *Acacia* and *Grewia* – PPEs obtained with GPM are higher than PPEs obtained with LSM. For *Dichrostachys,* a taxon with a low pollen fall speed, PPEs obtained with GPM are lower than PPEs obtained with LSM.

Changing the size of the region (3, 10 or 50 km radius) has some influence on the resulting PPEs; they are mostly larger with a larger radius (Table S3). Poaceae PPE values are higher for LSM within a radius of 50 km compared to GPM. In addition, after excluding Poaceae from the calculations, PPE values increased and model performance improved (Fig. S4). Both dispersal models achieved the best fit at 10 and 50 km. We selected the results obtained in the 10 km radius for further calculations, because these showed smaller standard errors than for the 50 km radius (Table S3). Final PPE and SE results (obtained after 100 iterations) are presented in Table 4-2.

Comparing the selected results from both dispersal models, the GPM has slightly lower optimization scores than the LSM (Fig. 4-4b). The standard errors of the PPE values are small for both models, however LSM results show lower SE values for *Acacia* and *Grewia* than GPM (Table 4-2). According to both models, *Grewia* is a low pollen producer (PPE <0.5). *Acacia* is a low to medium pollen producer (PPE: 0.4-1) according to the GPM, as is *Dichrostachys* according to the LSM.

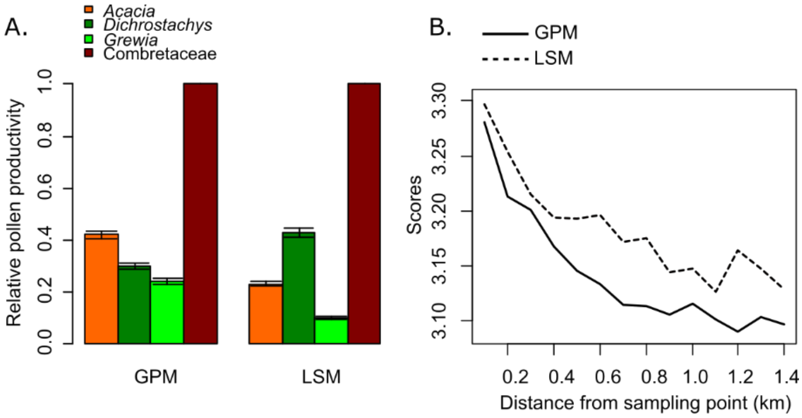

Figure 4-4. A) Pollen productivity estimates (PPEs) with standard error, and B) model performance obtained with the Gaussian plume model (GPM) and Lagrangian stochastic model (LSM) at 10 km radius without Poaceae.

The scatter plots of empirical pollen deposition against modelled pollen deposition show a close match for *Acacia* and Combretaceae and for both dispersal models (Fig. 4-5). In particular, the GPM results show high correspondence for both taxa (*Acacia*: R=0.88, p=0.00081; Combretaceae: R=0.78, p=0.0084; Fig. 4-5a). Empirical and modelled pollen deposition match less well for *Grewia* and *Dichrostachys*. For *Grewia*, we observe one clear outlier with high empirical pollen values yet low modelled pollen values. The low modelled values reflect the low abundance of *Grewia* in the vegetation at site T9. We found no correspondence between empirical and modelled pollen deposition for Poaceae (Fig. S5).

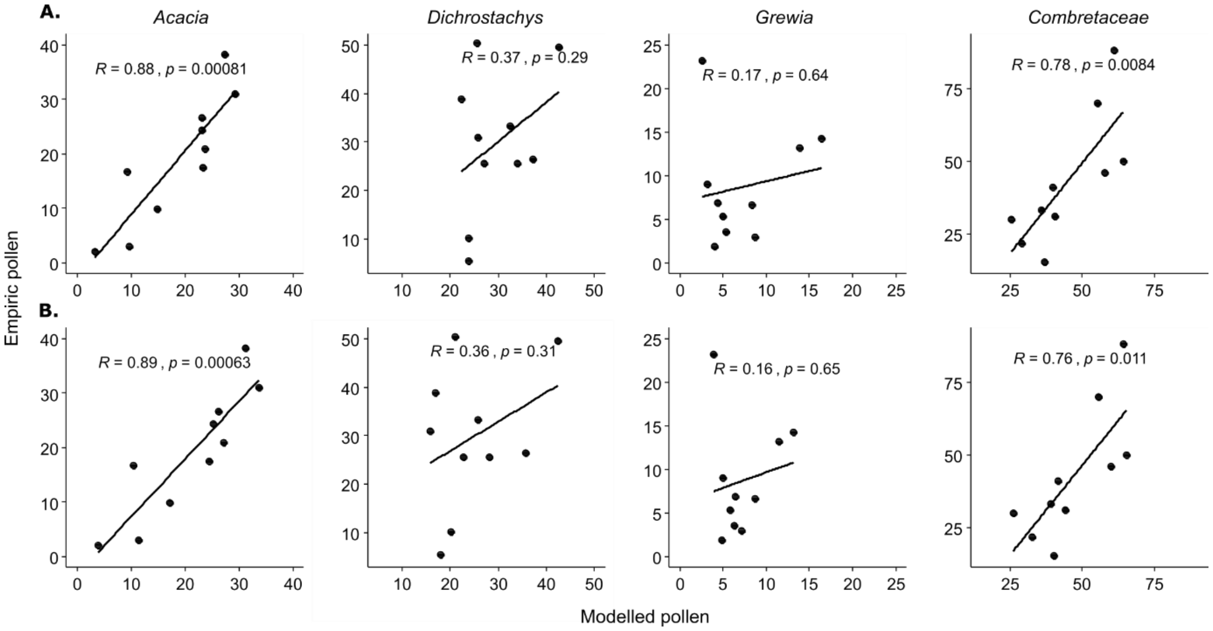

Figure 4-5. Scatterplots of empirical pollen deposition against modelled pollen deposition using (A) Guassian plume model (GPM) and (B) Lagrangian stochastic model (LSM) of dispersal at 10 km radius. The scatterplots obtained including Poaceae in the analysis are presented in Fig. S5.

4.3.3 Vegetation reconstruction

The REVEALS model gives similar results when using either the GPM or the LSM dispersal option and the corresponding PPE values. Both variants show a mean Poaceae cover of >60% in zone 1 (Fig. 4-6), which slightly increases in zone 2 (GPM: 67%; LSM: 69%). Zone 3 is characterized by a sharp decrease of the Poaceae cover (mean cover GPM: 47%; LSM: 53%) and a corresponding increase in the cover of woody taxa (from zone 2 to zone 3: GPM: 32–52%; LSM: 30–46 %). *Vachellia* and *Senegalia* (both corresponding to the *Acacia* pollen type) reach their highest cover values (*Vachellia* GPM: 25%, LSM: 17%; *Senegalia* GPM: 22%, LSM: 15%) in the 21st century.

In addition, GPM estimates of taxa with higher pollen fall speeds (*Vachellia, Senegalia, Grewia*) are generally higher compared to LSM, while the opposite is observed for Poaceae and Combretaceae.

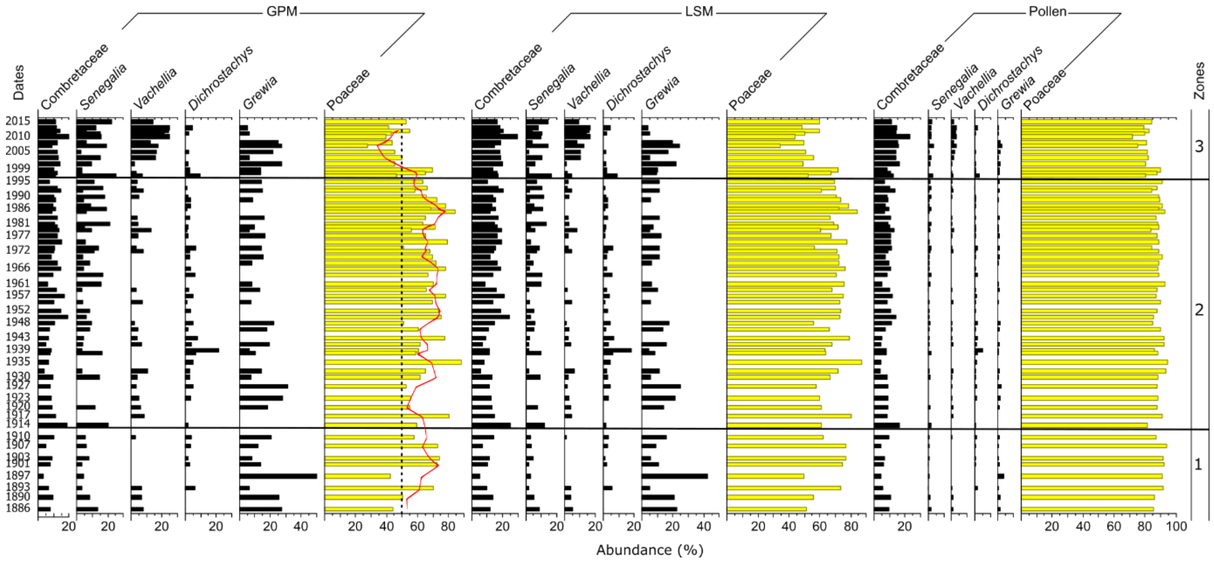

Figure 4-6. Quantitative vegetation reconstruction based on pollen data from Lake Otjikoto. REVEALS model using the Gaussian plume model (GPM) (left) and the Lagrangian stochastic model (LSM) (centre) of dispersal. Original pollen percentages are also presented (right). The red line denotes the grass cover running mean (calculated from 3 time points); the vertical black dotted line is the 50% abundance. Pollen zones according to Tabares et al. (2020).

Cover differences between regional vegetation and vegetation estimates are largest for *Acacia* and *Dichrostachys* (Fig. 4-7a): the *Acacia* cover is overestimated in the GPM results (15%), while the opposite is observed for *Dichrostachys* by quite similar values (9.3%) in both models. Cover differences for the other taxa are smaller than 7.5%.

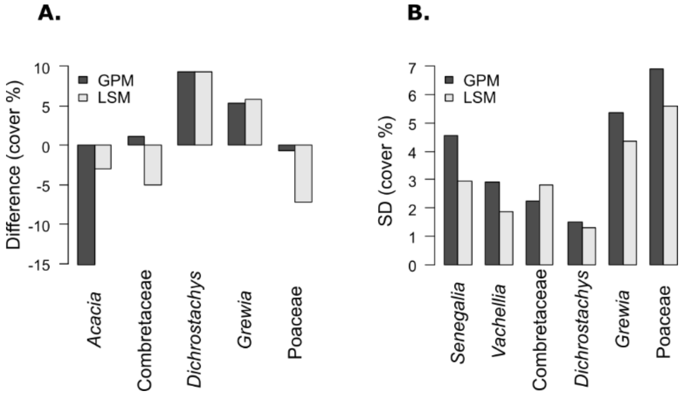

Figure 4-7. REVEALS statistics for the Gaussian plume model (GPM) and Lagrangian stochastic model (LSM) of dispersal. A) Cover differences between regional vegetation data and estimated abundances. B) Average standard deviation (SD) from cover estimates of single taxa.

The GPM cover estimates show slightly higher SD values compared to LSM for all taxa, except for *Combretaceae* (Fig. 4-7b).

4.4 Discussion

4.4.1 PPEs and dispersal model

PPEs are a key parameter for reconstructing past landcover from pollen data. Following on from Duffin and Bunting (2008), we here present the second study on PPEs for major savanna plant taxa of southern Africa. We present PPEs for *Grewia* and *Dichrostachys* for the first time, as well as PPEs for *Acacia* and Combretaceae using Poaceae as the reference taxon (Table S1).

High pollen values and mostly much lower cover values of Poaceae (Fig. 4-3) indicate that grasses are the highest pollen producers in the study region. However, our calculations failed to produce a close match between modelled and empirical pollen values (Fig. S5), so uncertainty in the resulting PPE is high. There may be at least two reasons for this weak link between plant abundances and pollen deposition of grasses. First, the Poaceae pollen type is produced by many grass species, which probably differ in their pollen productivity (Prieto-Baena et al., 2003). So, the actual pollen deposition at each site is not only determined by the overall cover of grasses but also by the actual grass species composition at each site. Furthermore, the cover and pollen production of grasses is much affected by grazing animals and weather conditions, resulting in high seasonal and annual variations (de Morton et al., 2011; Groenman-van Waateringe, 1993; Tabares et al., 2018). The pollen in our top-soil samples likely originate from previous seasons as well as the current one, during which the cover of grasses may have been substantially different than during the time of our vegetation survey.

For the other taxa we find reasonably good correspondence between empirical and modelled pollen data (Fig. 4-5), indicating successful ERV application. Independent of dispersal model selection, we find that Combretaceae is the taxon with the highest and *Grewia* the taxon with the lowest pollen productivity (Fig. 4-4a). *Acacia* and *Dichrostachys* are intermediate pollen producers. Overall, the present study confirms the ranking of pollen productivity observed by Duffin and Bunting (2008), with decreasing productivity from Poaceae to Combretaceae and finally *Acacia*. As Duffin and Bunting (2008) did, we find that, when calculated with the GPM dispersal, the PPE of *Acacia* is about half as high as that of Combretaceae.

Our comparison of PPEs produced with the two dispersal options have similar correlation coefficients for modelled and empirical pollen values (Fig. 4-5). With respect to regional vegetation composition, calculations with the LSM produce better estimates for *Acacia* while calculations with the GPM produce better estimates for Combretaceae and Poaceae (Fig. 4-7a). Hence, there is no clear indication that either dispersal option is more suitable. Still, the PPEs calculated with the LSM and GPM option differ substantially. The effects are obviously related to the fall speed of pollen. For the taxa with a high fall speed of pollen, such as *Acacia* and *Grewia*, GPM PPEs are about twice as high as LSM PPEs (Table 4-2). For *Dichrostachys,* a taxon with a low fall speed of pollen, LSM PPEs are higher than GPM PPEs. This interaction between dispersal model and fall speed of pollen is because pollen fall speed has a large influence in the GPM but not in the LSM (Kuparinen et al., 2007; Theuerkauf et al., 2016, 2013). Therefore, the GPM predicts much shorter dispersal distances for taxa with high fall speeds (*Acacia*, *Grewia*) than for taxa with low fall speeds (*Dichrostachys*). PPE calculations with the GPM thus tend to arrive at higher PPEs for taxa with high fall speeds to compensate for the lower predicted dispersal.

As mentioned above, our results do not clearly decide whether the GPM PPEs or the LSM PPEs are more realistic. In general, calculations with the most realistic dispersal model will produce the most realistic PPEs. Limitations of the simple Gaussian plume model in describing dispersal particles are well known. Most notably, this class of models underestimates the contribution of pollen from distances greater than 10 km (Mariani et al., 2016; Theuerkauf et al., 2013). This is because the GPM is based on the existence of an isotropic field of winds and neutral atmospheric conditions (Pérez et al., 2018; Prentice, 1985), while the transport and contribution of pollen from distances greater than 10 km imply transient atmospheric states characteristic of unstable atmospheric conditions (Pérez et al., 2018).

The far more complex Lagrangian stochastic dispersal models are much better suited to describe the contribution of long-distance pollen under unstable atmospheric conditions

(Kuparinen et al., 2007), as well as the dispersal of pollen grains with high fall speeds (Kuneš et al., 2019). Hence, this class of models is state-of-the-art in all kinds of research related to atmospheric diffusion (Kuparinen, 2006; Lin et al., 2012). However, whether the general advantages of LSMs also apply to the present study is unknown. Both the GPM and the LSM dispersal option were applied using atmospheric parameters estimated for central and northern Europe. Whether these parameters are suitable for applications in southern Africa still needs to be validated. For comparability with the study of Duffin and Bunting (2008), we have used the GPM option with parameters for neutral atmospheric conditions. However, unstable atmospheric conditions prevail during the day and in the summer months in southern Africa, while stable atmospheric conditions are dominant throughout the rest of the year (Luhunga and Mutayoba, 2013; Swart, 2017). Stable conditions inhibit vertical movement in the atmospheric boundary layer, resulting in low mixing height and low wind speed, and consequently low dispersion and high concentration of airborne particles (Luhunga and Mutayoba, 2013; Stull, 1988; Swart, 2017). Under stable conditions, a low proportion of long-distance pollen can then be expected in the pollen record. We hypothesize that these conditions may partly explain the small source area of pollen observed for savanna species (Duffin and Bunting, 2008), as well as the local character of the pollen signal observed in Namibian savannas (Tabares et al., 2018). Also, and probably because of this, the GPM achieves a slightly better fit compared to the LSM (Fig. 4-4b). Due to the importance of atmospheric conditions for the proper application of the dispersal model, we emphasize the need for further studies.

In the present study we have used pollen data from top-soil samples collected within semi-open vegetation. Pollen deposited at such sites not only arrives through atmospheric processes, but a significant amount of pollen may also arrive via flowers growing at the site, from soil material deposited by trampling animals or passing vehicles or via dung – all processes that are not represented in atmospheric dispersal models. Hence, even complex dispersal models may be limitedly suited to describe pollen deposition at such sites, and hence limitedly suited to calculate robust PPEs from such datasets. Future studies should therefore attempt to include pollen data from sites clearly dominated by atmospheric pollen deposition, such as from pollen traps in the absence of suitable lakes. Although the studied taxa are characterized by insect and animal pollination, pollen grains of *Acacia*, *Grewia*, Combretaceae and *Dichrostachys* have usually been recorded in aerial pollen counts (Ezike et al., 2016; Julier et al., 2018; Kenrick, 2003; Zietsman, 1991).

4.4.2 Fall speed of pollen grains

We obtained pollen fall-speed values for *Grewia* and Combretaceae very similar to those calculated by Duffin and Bunting (2008) in South Africa (Fig. 4-8a). However, the taxonomical composition of the pollen types likely constrains the regional applicability of fall-speed values. In our study, the pollen types of Poaceae and *Acacia* comprise different species with a wide range of sizes in pollen grains, such as *Aristida* sp. and *Heteropogon contortus* within the Poaceae type (mean axis range: 22–43 µm; Fig. 4-8b), and *Senegalia mellifera* and *Vachellia reficiens* within the Acacia type (mean axis range: 37–55 µm). This could explain the differences in the fall-speed values obtained by Duffin and Bunting (2008) for both taxa.

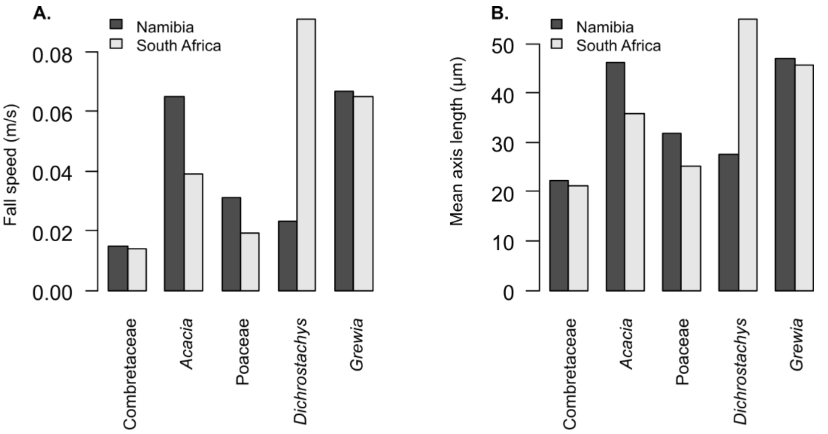

Figure 4-8. Pollen fall speed (A) and mean axis length (B) values of pollen grains from selected savanna taxa from Namibia (Table 4-2) and South Africa (Duffin and Bunting, 2008).

The discrepancy observed in the fall-speed values of *D. cinerea* between both studies probably results from methodological differences (i.e. it is not clear whether the cited authors measured single pollen monads or polyads, as they merged *D. cinerea*, *Albizia* sp. and *Acacia* sp. under the *Acacia* pollen type for ERV calculations). Differences in size measurements may also be related to variance in pollen preparation and sample storage.

Pollen size measurements may also depend on taphonomic processes, as we measured pollen grains taken from soil samples, while Duffin and Bunting (2008) measured pollen from lake sediments. Surface samples from lake sediments are commonly used for modern pollen analyses, while the use of surface soil samples has been questioned due to bias derived from poor pollen preservation (Han et al., 2017). However, pollen from surface soil samples are known to reflect well the vegetation composition in savanna and arid environments (Carrión, 2002; Tabares et al., 2018). In addition, the similarity between the mean axis values (Fig. 4-8b) obtained for *Grewia* and Combretaceae and those obtained by Duffin and Bunting (2008) do not suggest shrinkage or deterioration of pollen grains in the two collection environments.

4.4.3 Quantitative vegetation reconstruction from around Lake Otjikoto

We quantified the change in landscape openness in a semi-arid savanna based on fossil pollen for the first time in southern Africa. The validation of our results with regional vegetation data (Fig. 4-7) confirms the suitability of REVEALS to be applied in savanna environments (Mariani et al., 2016). These results also help quantify past vegetation changes related to encroachment, since the *Acacia*, Combretaceae and *Dichrostachys* pollen taxa comprise the main encroacher species in the Karstveld region (i.e., *Senegalia mellifera*, *Terminalia prunioides*, *Dichrostachys cinerea*).

Application of REVEALS with both dispersal models (GPM, LSM) unanimously indicates a predominance of the semi-open landscape throughout the 20th century and a sharp decrease (16–20%) in grass cover since 1990 linked to an increase in the cover of woody vegetation (Fig. 4-6). The latter reflects the encroachment process in north-central Namibia and confirms previous studies (De Klerk, 2004; Tabares et al., 2020; Wessels et al., 2019).

Our results allowed us to quantify changes in the cover of grasses and woody taxa, which are associated with changes in land use and management during the last 130 years. In particular, the low percentages of grass cover in zone 1 may reflect large-scale fires related to field clearing as a management practice (Tabares et al., 2020). Transhumance pastoralism and cropping took place in the vicinity of the lake at the turn of the 20th century. Interestingly, the low mean cover of tree taxa (~19% compared to 60–65% grass cover) may reflect the effect of combining fire and browsing, which has been assumed to prevent the establishment of tree seedlings (Gillson, 2004; Joubert et al., 2012). However, transhumance pastoralism may also have favoured the spread of *Grewia* through seed dispersal (Tews et al., 2004), which would explain its high abundance in zone 1.

During the first half of the twentieth century, changes in land tenure led to the construction of fences and the restriction of transhumance (Lau and Reiner, 1993; Mendelsohn et al., 2010). The concentration of livestock in turn led to changes in fire management, particularly the suppression of wildfires and/or the reduction of controlled fires to preserve pastures for livestock (Joubert et al., 2012). This is reflected in a 4–7% increase in the mean grass cover in zone 2. It is assumed that fire suppression affects grass/tree competition by reducing the mortality of seedlings and saplings (Case and Staver, 2017; Joubert et al., 2012), which would explain the spread of tree taxa (mean cover ~24%), particularly from the 1960s.

The decrease of grass cover since the 1990s, and particularly in the 21st century (average grass cover <50%), has been associated with overgrazing and prolonged droughts (Tabares et al., 2020). In particular, several studies have shown that high grazing pressure in pastures with low grass density reduces seed production and limits the potential of grasses to (re)invade niches (O'Connor and Pickett, 1992; Tessema et al., 2016). In addition, the effects of intensive grazing on the resilience of grasses are assumed to be greater under drought conditions (Souther et al., 2020).

A reduced grass cover in zone 3 (with lowest cover values of 27–34%) is related to an increase in woody cover (mean cover 46–52%), reflecting an encroached vegetation state. These findings support results from remote-sensing analyses, which have observed an increase in woody vegetation in north-central Namibia in the 21st century (Wessels et al., 2019).

The reduction of grass cover below 50% corresponds to a change from semi-open to thick savanna, while cover values below 30% reflect closed vegetation (Fisher et al., 2014; Gil-Romera et al., 2010). The spread of local encroachers *Vachellia* (likely *V. reficiens*), *Senegalia* (likely *S. mellifera*) and *Grewia* (likely *G. flava*), demonstrate that changes in land openness in zone 3 correspond to changes in vegetation composition characteristic of an encroached vegetation state (Tabares et al., 2020).

Interestingly, such a change in woody vegetation cover can also affect local atmospheric conditions and pollen dispersal. Unlike temperate regions, where woody vegetation is expected to absorb more solar energy than grasses thus increasing air convection (Baldocchi and Ma, 2013), studies conducted in semi-arid environments have shown that woody vegetation experiences lower surface temperatures than grassy areas due to effective convection heat loss and evaporative cooling (Rotenberg and Yakir, 2010). Therefore, the heat transfer to the atmospheric boundary layer decreases, as does the movement of convective air (Stull, 1988). Consequently, shrub encroachment can favour the prevalence of stable atmospheric conditions in the Namibian savannas, which can limit the long-distance contribution of pollen to the Lake Otjikoto record.

4.5 Conclusions

Our results extend the contribution of Duffin and Bunting (2008) and present new PPE values for *Grewia* and *Dichrostachys*, as well as PPE values for *Acacia* and Combretaceae using Poaceae as the reference taxon.

The ERV model failed to produce a close match with the empirical pollen values for Poaceae. This is probably because this pollen taxon covers many species with different pollen productivities. Furthermore, grass productivity is affected by grazing and climatic conditions in savanna environments. ERV modelling was successful for the other taxa. PPE results indicate that Combretaceae is the taxon with the highest productivity and *Grewia* the taxon with the lowest pollen productivity. *Acacia* and *Dichrostachys* are intermediate pollen producers.

We also compared the PPEs produced with the GPM and LSM dispersal model. However, our results do not allow us to draw a conclusion on whether GPM PPEs or LSM PPEs are more realistic. Although PPE values calculated with both models differ markedly, these differences are related to the pollen fall speed, which has a strong influence on the GPM but not on the LSM.

We considered at least two limitations with the dispersal models in our study. First, both the GPM and LSM dispersal options have been applied using atmospheric parameters estimated for central and northern Europe. Whether these parameters are suitable for applications in southern Africa needs to be validated. Furthermore, the deposition of pollen in soil samples, such as those collected in this study, occurs through processes that are not represented in atmospheric dispersal models. This suggests the need for pollen trap studies in the absence of suitable lakes in Namibia.

We also considered that the applicability of pollen fall speeds on a regional scale may be limited by the taxonomic composition of pollen types, as well as by differences in measurements resulting from methodology, pollen preparation and sample storage.

We obtained the first quantitative vegetation reconstruction for southern African savannas. Applying REVEALS with both models to the pollen record of Lake Otjikoto allowed us to quantify changes in the cover of grasses and woody taxa associated with changes in land use and management during the last 130 years in north-central Namibia. Our results indicate a marked reduction in grass cover in the 21st century, as well as an increase in the cover of shrub species. Both changes reflect the encroachment trend observed by remote-sensing based studies in the region and seen in the vegetation composition. Validation of the REVEALS results with regional vegetation data confirms its suitability to be applied to fossil pollen records and to reconstruct vegetation history in savanna environments.

Acknowledgements

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5 Synthesis

The overall objective of this research is to improve our understanding of the dynamics of past vegetation in savannas, particularly in relation to shrub encroachment. For this, it was first necessary to evaluate pollen suitability to reconstruct vegetation composition in changing environmental conditions. Therefore, modern pollen vegetation relationships were analysed along grazing and precipitation gradients. The findings were relevant to the interpretation of the fossil pollen record from Lake Otjikoto. The sedimentary record was analysed using a multiproxy approach that allowed us to reconstruct the compositional changes that have occurred in the last 170 years in north-central Namibia, as well as to infer the triggers and drivers of encroachment, and its stabilizing feedback mechanisms. These findings were validated by performing a quantitative reconstruction of the land cover for the last 130 years in the region, using newly determined pollen productivity estimates (PPEs).

5.1 Modern pollen-vegetation relationships in Namibian savannas

Modern pollen assemblages reflect changes in vegetation composition along precipitation and grazing intensity gradients (Chapter 2). Further, the pollen types of *Alternanthera* and *Tribulus* are reliable indicators of high grazing pressure on vegetation (Chapter 2). These findings are important, as precipitation and grazing impacts are assumed to be drivers/triggers of shrub encroachment in Namibian savannas (Joubert et al., 2013, 2008). However, although precipitation and grazing significantly explain changes in vegetation composition, they only explain a low proportion of the compositional change (Chapter 2). This suggests that a more complex interaction among different factors (soil properties, fire, competition) should be considered when analysing vegetation dynamics in savannas.

The suitability of modern pollen to reflect savanna vegetation is confirmed by Procrustes analysis (Chapter 2). The results showed a high correspondence between modern pollen and vegetation data for disturbance indicators such as *Tribulus*, and especially for some entomophilous woody taxa such as *Acacia*, *Grewia*, *Ziziphus* and Combretaceae. Stable atmospheric conditions, which limit long-distance pollen dispersal of woody taxa even in very open areas (Chapter 4), make it easier to infer a background pollen component of tree taxa that originates from the surrounding local vegetation and the extra-local source area (sensu Jacobson and Bradshaw, 1981; Duffin and Bunting, 2008).

Modern pollen can also reflect changes in landscape opening. In the pollen-vegetation records, the transition from mixed woodland to open *Acacia* woodland is clearly related to changes in the woody/grass pollen ratio (Chapter 2). This makes pollen useful for identifying woodland phases in the past.

Regarding diversity patterns, pollen–vegetation correspondence in terms of species richness (N0) is limited. This is because pollen N0 is affected by the background pollen loading in open areas and by pollen concentration, while plant N0 is influenced by landscape structure, which makes it difficult to compare different regions. In contrast, the effective numbers of common taxa (N1) and dominant taxa (N2) are reliable indicators of plant diversity change along precipitation and grazing gradients.

5.2 Past vegetation dynamics at Lake Otjikoto: from open woodland to encroached shrubland

The multiproxy analysis of the sediment record from Lake Otjikoto shows that the expansion of shrubs is a multidecadal trend characterized by the turnover from stable open woodland to a stable encroached state (Chapter 3). Such a state-change may occur on a scale of a century and without short-term reversions to a grassy state, but with an unstable transition phase lasting about 80 years characterized by a steady turnover of taxa, some of which are restricted to the transition phase.

The Combretaceae open woodlands (Mendelsohn et al., 2000) dominated the landscape around Lake Otjikoto until the turn of the 19th to 20th century. This stable state is characterized by the dominance of *Combretum* species and by a high grass cover that includes highly palatable grasses such as *Schmidtia* (probably *S. papophoroides*), *Brachiaria deflexa* and *Fingerhutia africana*. The woodland state was likely stabilized by transhumance and intense fires, as suggested by spore and charcoal records. High-intensity fires (due to the high grass cover favoured by non-intensive grazing) and sapling browsing, likely increased the mortality of woody vegetation over the rate of grass establishment, generating a negative feedback that maintained the open woodland state (D’Odorico et al., 2012). Furthermore, wetter conditions may have favoured the competitiveness of broad-leaved taxa such as *Combretum* and *Spirostachys* against drought-tolerant taxa. This is in line with an early *Combretum*-*Spirostachys* woodland phase at Otjikoto, which is related to wetter climatic conditions during the late Holocene (Scott et al., 1991), suggesting that this vegetation is the potential natural vegetation of the region.

The transition phase spans from 1920 to approximately 1997. During this period, the impact of management (especially logging and farming) and related changes in land use affected control variables such as grazing, fire and species composition. These changes in turn affected grass production, soil water availability and fuel accumulation, favouring the establishment of threshold conditions. The main vegetation changes are associated with a decline in the abundance of *Combretum*, as a consequence of selective logging (Erkkilä and Siiskonen, 1992), while shrubby taxa such as *Ziziphus*, *Grewia* and *Phyllanthus* spread in the second half of the 20th century. These changes in vegetation composition were likely enhanced by positive feedbacks that involved a decrease in soil moisture, limiting the re-establishment of *Combretum* and *Spirostachys*.

There were also changes in grass composition driven by changes in land use. The decrease in the *Sorghum seda*DNA signal and charcoal flux in the mid-20th century, for example, suggest that fire was not used to clear fields for cultivation but to control livestock grazing by promoting the establishment of perennial and palatable grasses, such as *Cenchru*s (likely *C. ciliaris*) and *Panicum* (likely *P. maximum*). High grazing pressure in pastures in the mid-20th century is indicated by an increase in unpalatable taxa such as *Geigeria* and *Acanthospermum*, as well as by trampling-resistant taxa such as *Alternanthera* and *Tribulus* (Chapter 2). High grazing pressure alongside poor grazing resources would also explain the cultivation of *Medicago* to supplement cattle forage from the 1990s, and the reduction of fires to conserve pasture for livestock (Joubert et al., 2012), as suggested by charcoal and spore records.

Threshold conditions may also have been driven by climate change (i.e. higher atmospheric $p\mathrm{CO}_2$ concentration and changes in precipitation variability) by inducing physiological adaptations (as suggested by the δD record) that could improve the competitiveness of trees over grasses (Bellasio et al., 2018). This implies that at higher atmospheric $p\mathrm{CO}_2$ concentration, an increase in the frequency of droughts and heavy rains may favour the expansion of C_3 vegetation (Zhang et al., 2019).

The vegetation after 1997 can be characterized as a *Terminalia prunioides* shrubland (Hüttich et al., 2009; Mendelsohn et al., 2000; Strohbach, 2014), which represents a stable encroached savanna state (Joubert et al., 2008) and differs from previous woodland states due to changes in the composition of woody and grass taxa. The vegetation proxies show high abundances of *Vachellia, Senegalia*, and *Terminalia*, which probably indicates the spread of local encroacher species such as *Vachellia reficiens*, *Senegalia mellifera*, and *Terminalia prunioides* in the region (De Klerk, 2004; Strohbach, 2001). In the grass layer, highly palatable grasses are replaced by less palatable grasses, such as *Hyperthelia dissoluta* and *Heteropogon contortus*, which are characteristic of overgrazed areas (Cech et al., 2010; Jordaan, 2017).

The encroached state is stabilized by negative feedback mechanisms that support the establishment and competitiveness of woody encroacher taxa. In particular, a low grass cover can support tramp-resistant soil crusts (Dougill and Thomas, 2004), which contain nitrogen-fixing cyanobacteria (as suggested by geochemical and rEM records). These soil crusts may favour the establishment of nitrogen-fixing shrubby Fabaceae such as *Senegalia mellifera*, which in turn inhibit grass growth under their canopy (Maron and Connors, 1996; Smit, 2003). A reduced grass cover then reduces the intensity of fire (as suggested by the charcoal record), resulting in the self-propagation of a woody state (Higgins and Scheiter, 2012; Hirota et al., 2011; Scheffer et al., 2001).

Establishment of certain grasses can, however, also be constrained by shrub removal and damage to soil crusts. In woody patches, the removal of shrubs allows the establishment of fast-growing species such as *Hyperthelia dissoluta*, which inhibits the growth of other grasses (Jordaan, 2017). In bare soil patches, damage to soil crusts results in soil losses (as suggested by rEM records), which in turn reduce runoff by limiting the formation of temporary ponds and water tables (Rodríguez-Caballero et al., 2012; Valentin, 1993), thus reducing the availability of water for grasses.

The results suggest that environmental changes derived from management (i.e. reduced soil moisture, reduced grass cover, changes in species composition and competitiveness, reduced fire intensity) may have affected the resilience of *Combretum* open woodlands, making them more susceptible to becoming an encroached state by stochastic events such as consecutive years of precipitation and drought and by high $p\mathrm{CO}_2$ concentrations. These results are in line with state-transition models, which predict gradual changes in environmental conditions to alter the resilience of stable states, thus enhancing the likelihood of a state-change (Scheffer et al., 2001).

5.3 Quantitative reconstruction of past land cover at Lake Otjikoto

The application of REVEALS (Sugita, 2007; Theuerkauf et al., 2016) to the fossil pollen record of Lake Otjikoto allowed us to quantify the changes in grass cover and woody taxa associated with changes in land use and management during the last 130 years in north-central Namibia (Chapter 4). Cover estimates for Poaceae indicate the predominance of a semi-open landscape throughout the 20th century, with a sharp decrease (16–20%) since 1990 linked to an increase in woody vegetation cover. In particular, Poaceae cover estimates below 50% since the 21st century correspond to thick savanna (Gil-Romera et al., 2010), and values less than 30% to closed vegetation (Fisher et al., 2014). The grass cover estimates were also validated with regional vegetation data achieving cover differences of less than 7.5%, which suggests a close match with the vegetation data, as well as the accuracy of the Poaceae PPE (2.02; Duffin and Bunting, 2008) used in this study.

The REVEALS results also confirm that the changes in the woody/grass ratio in the fossil pollen record reflect well the change in landscape openness in the region from open woodland to encroached shrubland, which is also confirmed by biogeochemical results (Chapter 3). These findings are in line with remote sensing-based studies (Wessels et al., 2019), which have observed an increase in woody vegetation in north-central Namibia in the 21st century.

The reduction of grass cover is associated with an increase in the cover of *Vachellia* (probably *V. reficiens*), *Senegalia* (probably *S. mellifera*) and *Grewia* (probably *G. flava*), reflecting the increasing dominance of taxa characteristic of an encroached state (Chapter 3). According to the validation results, the cover estimates for *Acacia* are over-represented (+ 3–15%), the opposite occurs for *Dichrostachys* and *Grewia* (- 5–9.3%), while the difference for Combretaceae is less than 5%. These results suggest a close match between cover estimates and regional vegetation, which allows us to infer the magnitude of the shrub encroachment in the region, although the interpretation of the *Acacia* cover must be taken with care. Overall, the results of this study confirm the suitability of REVEALS to be applied to fossil pollen records and to reconstruct the vegetation history of savanna environments.

5.3.1 Pollen productivity estimates for savanna taxa

The pollen productivity estimates (PPE; Chapter 4) required for the pollen-based quantitative reconstruction of the vegetation were calculated using the extended R-value model (ERV; Parsons and Prentice, 1981) and two pollen dispersal options: the Gaussian Plume Model (GPM; Jackson and Lyford, 1999) and the Lagrangian Stochastic Model (LSM; Kuparinen et al., 2007). The results indicate that Combretaceae is the taxon with the highest productivity and *Grewia* the taxon with the lowest pollen productivity. *Acacia* and *Dichrostachys* are intermediate pollen producers.

The ERV model failed to produce a reliable PPE for Poaceae, probably because this pollen taxon covers many species with different pollen productivities (Prieto-Baena et al., 2003), which in turn are affected by grazing and weather conditions (de Morton et al., 2011; Chapter 2). In this research, for example, no common trend was observed between Poaceae pollen and grass vegetation along grazing gradients (Chapter 2), which makes it difficult to make PPEs in overgrazed farmland (Chapter 4). In contrast, Duffin and Bunting (2008) carried out their study in a national park, which probably allows a better correspondence between grass pollen and vegetation and, therefore, a more accurate Poaceae PPE, as demonstrated by its application in REVEALS (Chapter 4).

Although the results do not allow us to conclude whether the GPM PPEs or the LSM PPEs are more realistic, the differences between these values confirmed that the pollen fall speed has a greater effect in the modelling of GPM than in the LSM (Kuparinen et al., 2007; Theuerkauf et al., 2016, 2013). The estimations with both dispersal models in this study are probably limited by the differences between the atmospheric parameters of the models and those prevailing in the study area (Luhunga and Mutayoba, 2013; Swart, 2017), as well as the processes related to the deposition of pollen in soil samples, which are not considered in the models.

5.4 Conclusions

Is pollen analysis a suitable tool to reflect the vegetation change associated with shrub encroachment in savanna environments?

Yes, but with limitations. The results show that modern pollen assemblages reflect changes in vegetation composition related to precipitation, as well as the impact of grazing on vegetation, which are supposed to be triggers/drivers of shrub encroachment. Furthermore, the pollen and vegetation taxa showed a high correspondence for some grazing indicators and encroacher woody taxa, and the woody/grasses pollen ratio is suitable to reflect changes in landscape openness and, therefore, to identify woodland phases.

However, to differentiate mere woodland phases from encroached phases, it is important not only to identify changes in the composition of woody taxa, but also in the composition of grasses. Unfortunately, the low resolution of the Poaceae pollen type limits this possibility. Therefore, this study recommends use of multiple proxies (particularly *sed*aDNA) to identify shrub encroachment.

Does the current encroached landscape correspond to an alternative stable state of savanna vegetation?

Probably yes. This study hypothesizes that the *Terminalia* shrubland corresponds to an encroached state and that it is not a new phenomenon, since it possibly occurred previously in the region, as suggested by changes in taxonomic composition and the grass/woody ratio observed in an earlier pollen record from Lake Otjikoto (Scott et al., 1991). In particular, the early woodland phase (zone O1; Fig. S6, Chapter 6.2), which is dominated by Combretaceae, may correspond to a phase of *Terminalia* encroachment, since the abundance of *Spirostachys* is low, while *Grewia* and *Acacia* have high pollen signals. Interestingly, this phase is preceded by high abundances of *Tribulus*, which suggests a transition phase.

In this sense, the encroached state observed in this study can be interpreted as a successive phase in a context of state transitions, and is in line with previous studies that define encroached savanna landscapes as alternative stable states (Gil-Romera et al., 2010). However, a multiproxy analysis of a sediment record covering a longer time period is necessary to confirm this hypothesis.

To what extent does the quantitative reconstruction of the vegetation based on fossil pollen records reflect the past vegetation cover of the savannas?

Validation of REVEALS cover estimates with regional vegetation data generally shows a close match for all taxa, suggesting that REVEALS is suitable for reconstructing plant cover from fossil pollen data in savannas. In particular, Poaceae cover estimates reflect well the changes in the landscape openness that occurred in the last 130 years in the region and allow us to infer the magnitude of the encroachment process since the 21st century, which is supported by several studies (De Klerk, 2004; Strohbach, 2001; Wessels et al., 2019). However, an improvement in the PPEs could lead to more accurate cover estimates. In particular, for the Poaceae PPE it would be advisable to carry out studies in areas not affected by overgrazing and use pollen traps.

5.5 Outlook

The present study contributes to our understanding of the dynamics of past vegetation in the Namibian savannas, and to the methodological discussion on the usefulness of pollen in paleoecological studies in arid and semi-arid environments. The results of this work, however, raise questions and reveal limitations that may well be the starting point for future studies.

First, since grass identification beyond the Poaceae pollen type is limited, it would be of great value to investigate the morphological characteristics of pollen grains of local grass species from the study sites. This would allow an assessment of whether the different species could be separated by their pollen grain size or by other morphological characteristics. Similar studies carried out in other grassland ecosystems were able to differentiate between polyploid and diploid grasses, as well as identifying different grassland landscapes (Jan et al., 2015; Schüler and Behling, 2011). Such knowledge applied to fossil pollen would improve the reconstruction of past vegetation dynamics in the Namibian savanna.

Second, to corroborate the hypothesis about the occurrence of a previous encroached state in the Namibian savanna, it would be necessary to analyse a sedimentary record that covers a longer period of time than the one studied. For this, a multi-proxy approach would be advisable so as to obtain detailed knowledge about the compositional change, its triggers and drivers, and feedback mechanisms. The advantages of such an approach were demonstrated in this study. A reconstruction of plant diversity in the past and its changes over time would be of great value.

Finally, the PPE of Poaceae needs refining and requires more studies using pollen traps in areas without overgrazing. This would allow more precise estimates to be made and, therefore, more precise cover estimates. It would also allow a comparison with the study by Duffin and Bunting (2008). Generating PPEs for other savanna taxa such as *Spirostachys, Colophospermum mopane* or *Burkea* would also allow a more detailed reconstruction of the vegetation and associated environmental changes. In addition, studies on the atmospheric conditions in Namibia are required, since these parameters are indispensable for the application of pollen dispersal models, and therefore, for PPEs.

6 Appendix

6.1 Supplementary information for Manuscript 1

S1. Detrended Correspondence Analysis (DCA) and Constrained Correspondence Analysis (CCA).

Method

Pollen data and plants as pollen-equivalents (PEq) data were square-root transformed prior to analyses. First, we performed detrended correspondence analysis (DCA) to estimate the compositional change in the PEq and pollen data. Second, we performed a constrained correspondence analysis (CCA) using mean annual precipitation (MAP) and an aridity index (*AI*) as constraining variables. The aridity index (*AI*) was calculated as the ratio of annual precipitation (*P*) to potential evapotranspiration (PET) (UNEP, 1997).

$AI = P/\mathrm{PET}$

Due to a lack of local PET records for Namibia, we obtained the data from the CGIAR-CSI Global-Aridity and Global-PET Database (Zomer et al., 2008). All analyses were implemented using the R package vegan (Oksanen et al., 2016).

Results

The first DCA axis of the PEq ordination has a length of 5.9 SD and stretches between the watering points from Otijoto and Grootfontein (Fig. S1a). These two plots differ in species composition and dominance: *Alternanthera pungens* dominates at Otjikotos watering point, *Limeum* and *Solanum* dominate at Grootfontein (Fig. S1c). Removing these outliers, the average standard deviation of species turnover decreases to 2.5 SD.

The length of the second DCA axis is 2.6 SD. Cluster 3 and a subcluster of cluster 4 are placed at either end of the axis. Cluster 3 comprises taxa such as *Croton,* Combretaceae, *Dichrostachys,* and Acanthaceae (Fig. S1a,c). The subcluster includes four sites from Waterberg (w2, w4, w8, w9), which are characterised by the occurrence of Bignoniaceae, *Waltheria, Heliotropium,* and *Acacia*.

The amount of compositional change in the pollen dataset is 1.9 SD (Table S1). Cluster order on the first DCA axis follows the precipitation gradient (Fig. S1b). Cluster 3 stretches along the second DCA axis separating the Grootfontein and Otjikoto sites. Plot g1 and plots o9 and o10 are placed at the corresponding ends of the axis. While plot g1 is characterised by lowest grazing intensity and dominance of *Heeria* and Cucurbitacea, plots from Otjikoto are characterised by high grazing intensity and dominance of *Tribulus* and Anacardiaceae (Fig. S1d).

According to the CCA results, the influence of precipitation and aridity on taxa composition is highly significant in both datasets (Table S1). However, the explained variance remains low when compared to the RDA results (Table 4 and S1). *AI* explains slightly more variance than precipitation suggesting the influence of seasonality on compositional change of vegetation. Calculated *AI* values for the study sites are as follows: Otjikoto 0.24, Grootfontein 0.26, Waterberg 0.17 and Kuzikus 0.11.

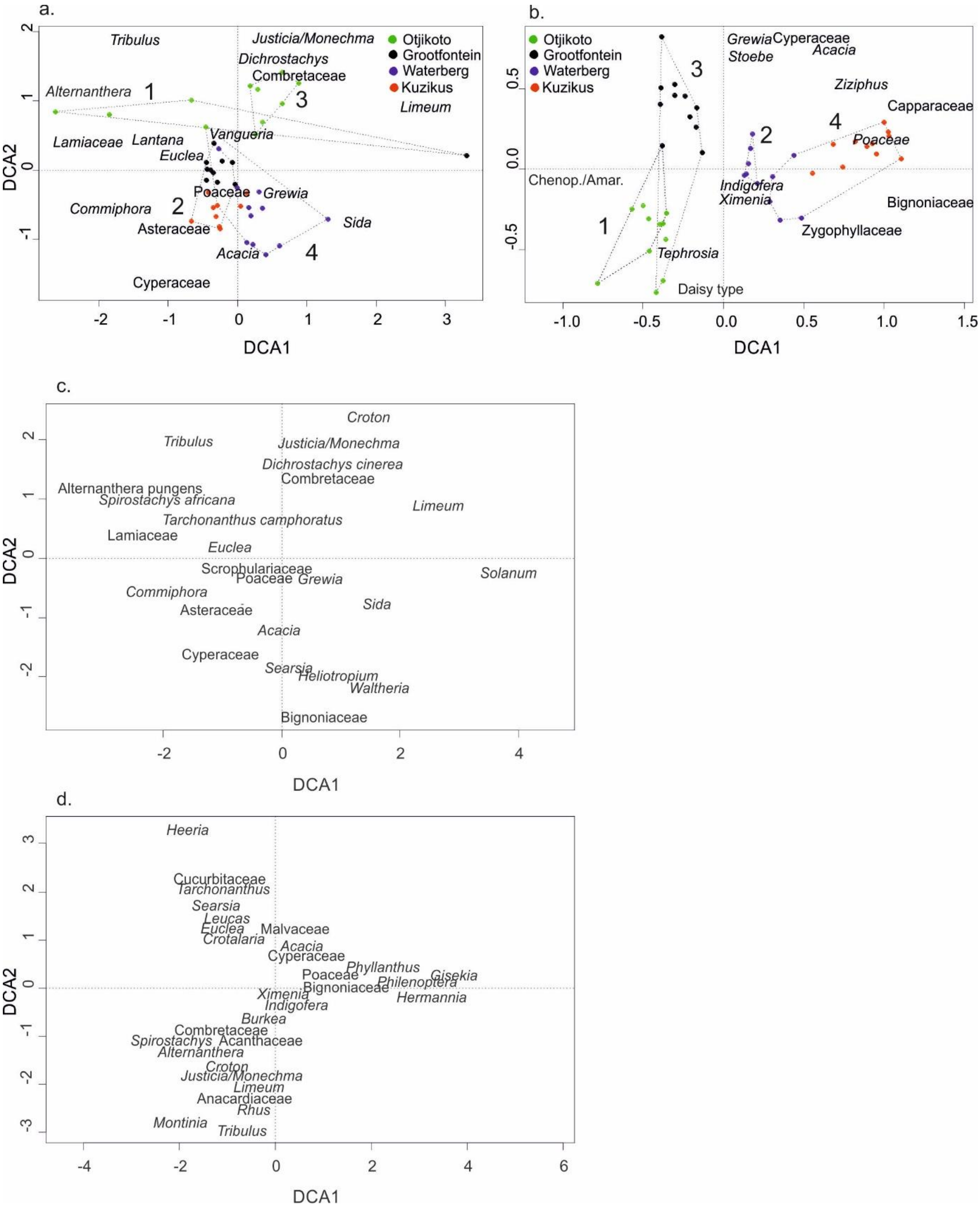


Figure S1. Detrended correspondence analysis (DCA) for plants as pollen equivalents (a, c) and pollen data (b, d – selected taxa). Polygons correspond to clusters derived from partitional clustering. The axes are measured in standard deviation (SD) units.

Discussion

The first DCA axis in the plants as pollen-equivalents (PEq) dataset shows the effect of the two outliers, which in turn determine the amount of compositional turnover in the data. Removing these two plots suggests a homogeneous dataset (2.5 SD) and supports the appropriate use of linear-based ordination methods for this study (Legendre and Birks, 2012). Moreover, results of direct gradient analysis explained more variance in both datasets when applying linear-based methods (RDA) than unimodal ones (CCA).

A comparison of the DCA and PCA results shows that both ordination methods have similar trends. Clusters of PEq data on the second DCA and PCA axes reflect changes in vegetation composition according to soil type (see section 4.1 in the main Discussion). The distribution of pollen taxa on the first PCA and DCA axes reflect the influence of MAP. The first DCA axis also differentiates between semi-arid and arid sites according to *AI* values (UNEP, 1997).

Table S1. Detrended Correspondence Analysis (DCA) and direct gradient analysis (RDA, CCA) of plants as pollen-equivalents (PEq) and pollen: length of the first DCA axis in standard deviation (SD) units (a); explained variance (adjusted (Adj.) r^2) and significance coefficient (p) for RDA (b) and CCA (c, d) using precipitation (c) and aridity index (*AI*) (b, d) as constraining variables.

	a. Axis length	**b. RDA - *AI***		**c. CCA - Precipitation**		**d. CCA - *AI***	
	SD	**Adj. r^2**	**p**	**Adj. r^2**	**p**	**Adj. r^2**	**p**
PEq	5.93	0.075	0.1537	0.048	0.001	0.044	0.001
Pollen	1.90	0.232	0.1241	0.143	0.001	0.139	0.001

We also observe differences between the two methods. The second PCA axis suggests the influence of soil moisture in the pollen data by setting forbs and shrubs at opposite ends of the axis. In contrast, DCA clearly differentiates along the grazing intensity gradient with Otjikoto and Grootfontein sites reflecting changes in taxa composition related to grazing.

In conclusion, our results suggest that the use of linear-based methods is appropriate for our study. Decision criteria are not only the length of the first DCA axis, but the kind of information needed according to the research question. While PCA distributes taxa according to the magnitude of change in their abundance, DCA associates taxa according to their similarity (occurrence). In our study, the use of a Euclidean metric seems to be more appropriate to preserve the usefulness of Poaceae as an indicator of landscape openness (Ejarque et al., 2011). Poaceae abundance has also been used to differentiate among vegetation types (Vincens et al., 2000; Julier et al., 2017). In our study, the transition from mixed woodland to open *Acacia* savanna is also differentiated by changes in Poaceae abundance. However, we agree with Julier et al. (2017) that other taxa should be used along with Poaceae, because of biases related to high pollen productivity, influx, and redeposition. Our results show that unconstrained cluster analysis as well as DCA are helpful in identifying such taxa associations.

6.2 Supplementary information for Manuscript 2

S1. Stable isotope analyses - methodological details.

A. Compound specific carbon ($\delta^{13}C$) and deuterium (δD) isotope analysis

The carbon and deuterium isotopic compositions of saturated hydrocarbons were measured by GC-IRMS, which is composed of a GC unit (7890N, Agilent Technology, USA) connected to a GC-Isolink coupled via open split to a Delta V Plus mass spectrometer (ThermoFisher Scientific, Germany). For carbon isotope analysis, the organic substances of the GC effluent stream were oxidised to CO_2 in the combustion furnace held at 940°C on a CuO/Ni/Pt catalyst, whereas the organic compounds were pyrolysed at 1450°C to obtain ^{2}H for deuterium isotope analysis. We injected 3 µl of saturated fraction to the programmable temperature vaporisation inlet (PTV, Agilent Technology, USA) with a septumless head, working in split/splitless mode. The injector was held at a split ratio of 1:2 and a constant temperature of 300°C. The saturated fractions were separated on a fused silica capillary column (HP Ultra 1, 50 m x 0.2 mm ID, 0.33 µm FT, Agilent Technology, Germany). The temperature programme started at 80°C, held for 2 minutes and was then increased at a rate of 5°C min^{-1} to 325°C, held for 15 minutes. Helium, set to a flow rate of 1.3 ml min^{-1}, was used as a carrier gas. All saturated hydrocarbon fractions were measured in triplicate for carbon and deuterium isotope analysis and the standard deviation was ≤0.5‰ for most of the compounds and samples for $\delta^{13}C$ and ≤3‰ for δD. The quality of the isotope measurements was checked regularly by measuring different *n*-alkane standards with known isotopic composition (provided by Campro Scientific, Germany and Arndt Schimmelmann, Indiana University, USA).

B. Bulk carbon ($\delta^{13}C_{org}$) isotope analysis

For analyses of carbon isotope ratios of sedimentary organic matter ($\delta^{13}C$org), samples were decarbonized with HCL (7%) at 80°C. Samples were weighed into tin capsules and measured using an elemental analyser (1108 from Carlo Erba) coupled to a MAT 252 isotope ratio mass spectrometer from Thermo Fisher Scientific. All samples were analysed in duplicate. The calibration was performed using a certified isotope standard (IAEA CH-6 with a $\delta^{13}C$ value of -10.45‰). Instrument performance was checked using a sediment reference sample with a $\delta^{13}C$org value of -26.07‰ (IVA). The reproducibility for replicate analyses was 0.5‰.

S2. Grain size end-member modelling

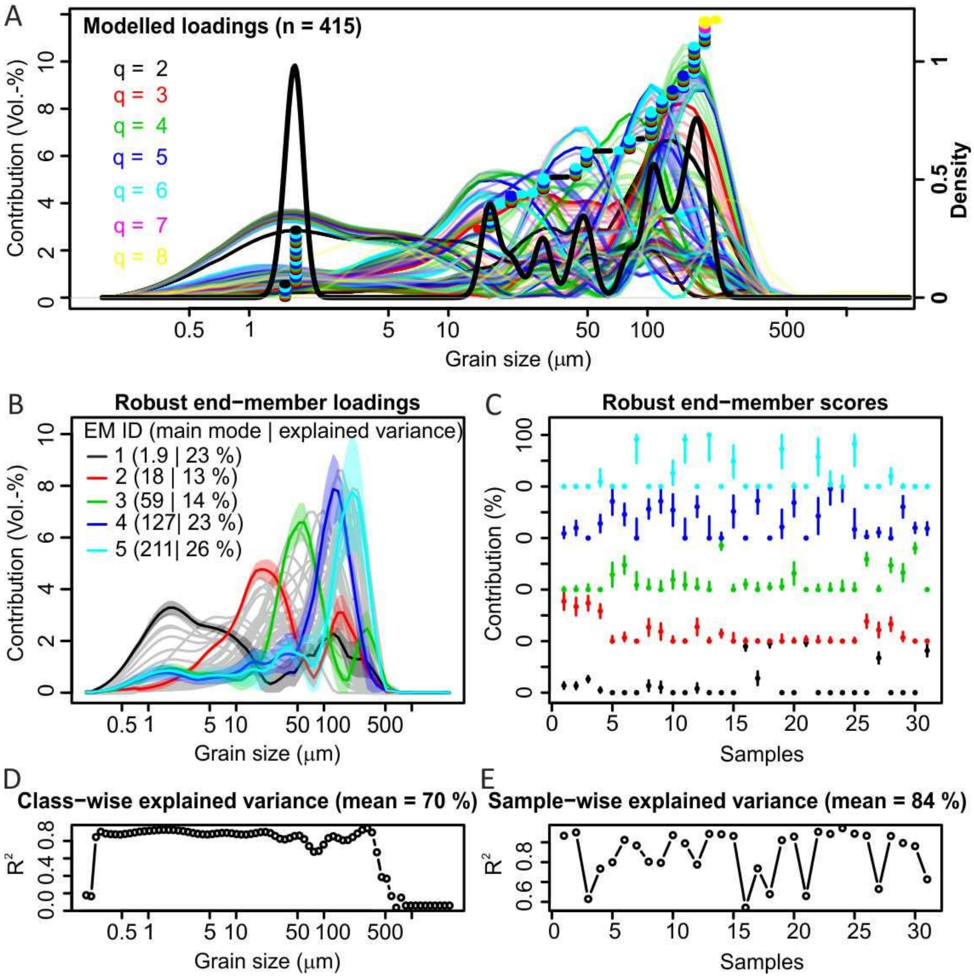
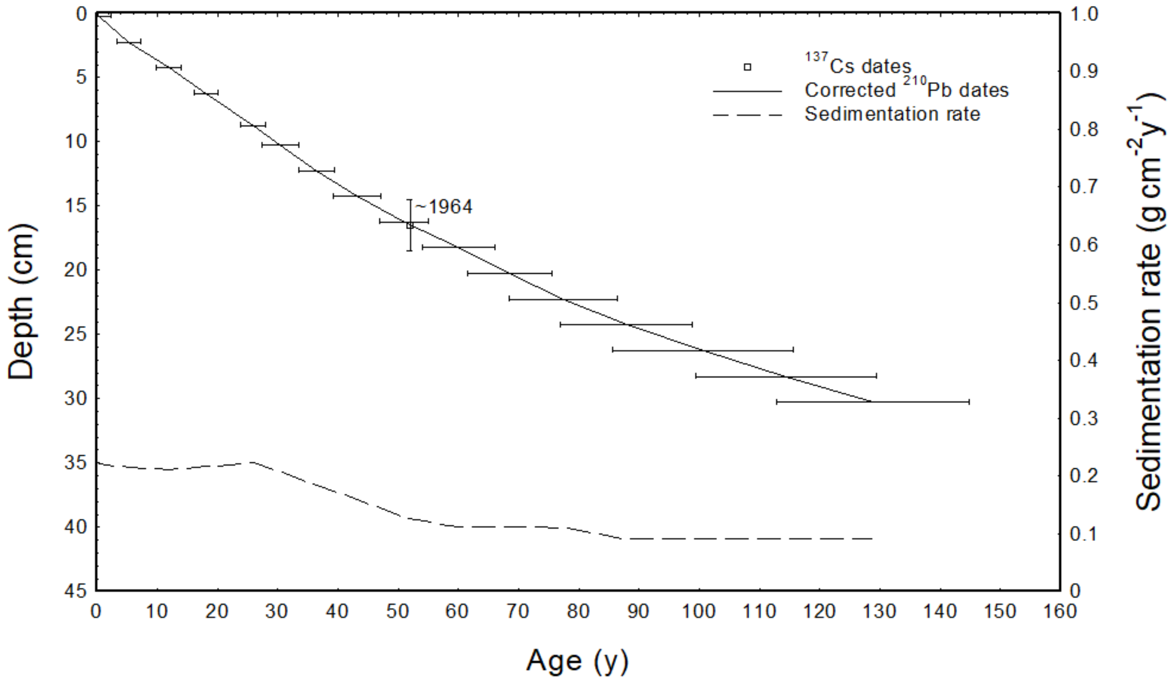


Figure S2. Grain size end-member modelling of 15OJ10 sediment core. A) All modelled end-member loadings that are similarly likely for different numbers of end-members (coloured) for a model parameter space between a minimum and maximum number of end-members and weight transformation value (Dietze and Dietze, 2019). Dots mark respective main modes. Thick black line is a kernel density estimate that shows robust end-members, i.e. high density at loading with similar main modes. B) Robust end-member loadings, class-wise end-member contributions, defined after the five highest mode positions in A. C) Robust end-member scores (mean and one standard deviation) are the relative contributions of an end-member to each sample. D) and E) show the class- and sample-wise explained variance of the mean robust end-member model.

S3. Radiometric chronology of the Lake Otjikoto

A.



B.

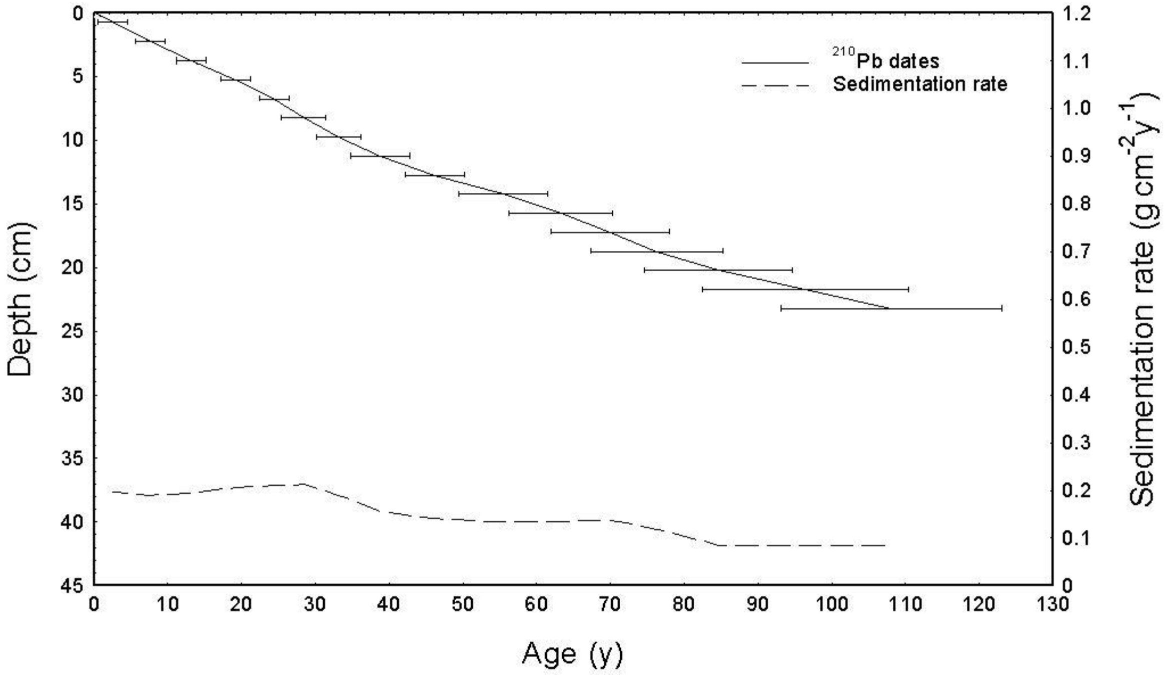


Figure S3. Radiometric chronology of Lake Otjikoto showing the corrected CRS model ^{210}Pb dates and sedimentation rates for A) core 15OJ10 and B) core 15OJ06.

S4. Pollen and spores

Table S4. List of identified pollen and spore taxa.

Pollen and spores

Abutilon
Acalypha
Acanthaceae
Adenium
Afzelia
Aizoaceae
Alchornea
Aloe
Alternanthera
Anacardiaceae
Apiaceae
Aquatics
Arctotis
Bauhinia
Bignoniaceae
Blepharis
Brassicaceae
Burkea
Capparaceae
Chamaecrista
Chen./Amara.
Cichorioideae
Combretaceae
Commelina
Commiphora
Convolvulaceae
Cordia
Corymbium
Crassulaceae
Crotalaria
Croton
Cucurbitaceae
Cyperaceae
Dichrostachys
Diptychandra
Dodonea
Ecbolium
Ehretia
Euclea
Euphorbia type
Euphorbiaceae undeff
Ficus
Gazania type
Grewia
Grubbia
Gymnosporia
Heeria
Heliotropium
Hyphaene
Hypoestes
Justicia
Kalanchoe
Kirkia
Kohautia
Lamiaceae
Limeum
Logania type
Lythraceae
Malvaceae
Medicago
Melhania
Meliaceae
Monsonia
Montinia
Mopane
Myrtaceae
Nuxia type
Nyctagynaceae
Ocimum
Opilia
Opuntia
Orobanchaceae
Parkinsonia
Pedaliaceae
Pentzia
Petalidium
Philenoptera
Phyllanthus
Poaceae
Podocarpus
Polygonaceae
Portulacaceae
Prosopis
Proteaceae
Pterospermum
Rhus
Rhynchosia
Rubiaceae
Ruellia
Scrophulariaceae
Senecio
Senegalia
Sida
Solanum
Spirostachys
Talinum
Tapinanthus
Tarchonanthus
Tephrosia
Tragia
Triaspis
Tribulus
Vachellia
Verbenacea
Waltheria
Xanthium type
Ximenia
Ziziphus
Acrodyctis
Cercophora
Curvularia
Gelasinospora
Glomus
Neurospora
Sordaria
Spegazzinia

S5. *seda*DNA taxa

Table S5. List of identified *seda*DNA taxa.

***seda*DNA taxa**

Family

Acanthaceae
Amaranthaceae
Anacardiaceae
Apocynaceae
Asparagaceae
Asteraceae
Bignoniaceae
Brassicaceae
Burseraceae
Capparaceae
Chenopodiaceae
Convolvulaceae
Cucurbitaceae
Cupressaceae
Ebenaceae
Ehretiaceae
Euphorbiaceae
Fabaceae
Heliotropiaceae
Hyacinthaceae
Lamiaceae
Loranthaceae
Lythraceae
Meliaceae
Moraceae
Musaceae
Myrtaceae
Opiliaceae
Pedaliaceae
Ranunculaceae
Rhamnaceae
Sapindaceae
Scrophulariaceae
Solanaceae
Typhaceae
Verbenaceae
Vitaceae

Genus

Acalypha
Aristida
Arthraxon
Astrantia
Bougainvillea
Calostephane
Capsicum
Celastraceae
Cenchrus
Combretum
Commelina
Corchorus
Cordia
Croton
Cyphostemma
Dichrostachys
Duranta
Ehretia
Eriocephalus
Euphorbia
Geigeria
Gossypium
Grewia
Heliotropium
Hibiscus
Hypoestes
Lepidium
Leucaena
Lycopersicon
Maprounea
Medicago
Mentzelia
Mirabilis
Monsonia
Muhlenbergia
Oxygonum
Panicum
Persea
Phaseolus
Phylica
Pisum
Poaceae
Polygonum
Pyrus
Quercus
Schmidtia
Senegalia
Sida
Solanum
Sorghum
Stuckenia
Tagetes
Terminalia
Themeda
Thunbergia
Tragus
Vachellia
Zaleya

Species

Abutilon mauritianum
Acanthospermum australe
Aegopodium podagraria
Aloe grandidentata
Alternanthera pungens
Antigonon leptopus
Aucoumea klaineana
Baratranthus axanthus
Bellida graminea
Beta vulgaris
Blepharis maderaspatensis
Brachiaria deflexa
Cassinopsis ilicifolia
Castilleja vadosa
Catophractes alexandri
Dodonaea viscosa
Euphorbia hypericifoliae
Fingerhuthia africana
Garnotia tenella
Glyphochloa talbotii
Grubbia rosmarinifolia
Haematoxylum dinteri
Helinus integrifolius
Heteropogon contortus
Hyperthelia dissoluta
Ipomoea cairica
Kirkia acuminata
Lactuca sativa
Leucosphaera bainesii
Malosma laurina
Parkinsonia anacantha
Paspalum notatum
Philenoptera cyanescens
Phyllanthus
Pithecellobium sp. DS14533
Portulaca oleracea
Psidium guajava
Pterospermum heterophyl.
Saccharum spontaneum
Schistocarpaea johnsonii
Senegalia senegal
Senna gardneri
Spermacoce princeae
Stemodiopsis buchananii
Stilbe rupestris

***seda*DNA taxa**				
Citronella smythii		*Mecomischus halimifolius*		*Tribulus terrestris*
Combretum coccineum		*Melhania ovata*		*Vachellia hebeclada*
Commicarpus pedunculosus		*Meum athamanticum*		*Veronica anagalloides*
Conocarpus erectus		*Montinia caryophyllacea*		*Vicia faba*
Cucurbita pepo		*Nama demissa*		*Waltheria indica*
Cyperus congestus		*Neyraudia reynaudiana*		
Diptychandra aurantiaca		*Pachira quinata*		
Subfamily	**Subtribe**	**Tribe**		**No rank**
Apioideae	Justiciinae	Acacieae	Lantaneae	PACMAD clade
Asclepiadoideae		Andropogoneae	Phyllantheae	
Malvoideae		Caesalpinieae	Pomaderreae	
Mimosoideae		Hippomaneae	Ruellieae	
Papilionoideae		Indigofereae		
Tribuloideae		Ipomoeeae		

S6. State-changes at Lake Otjikoto

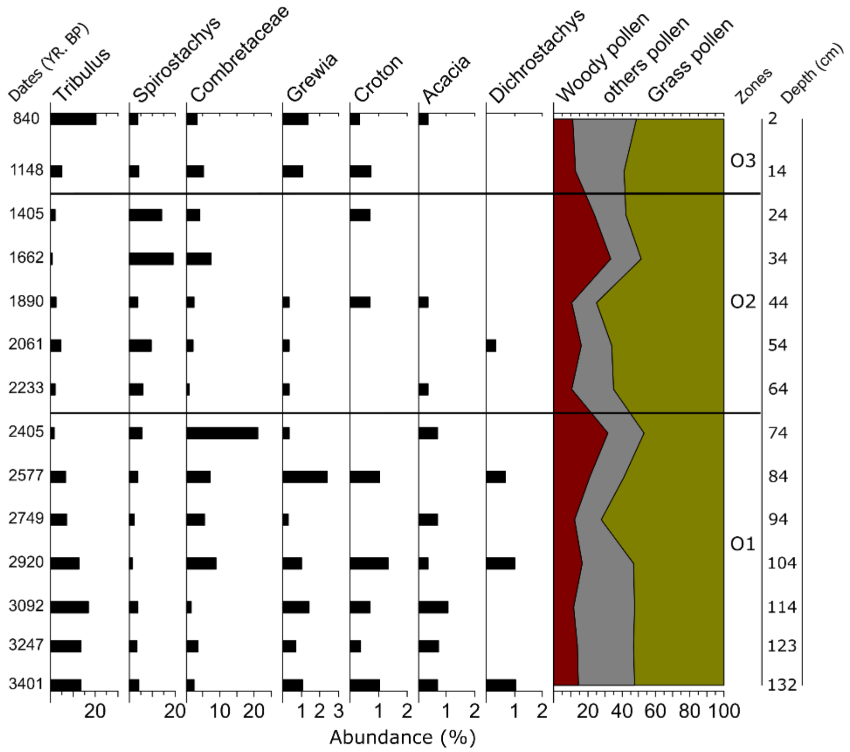


Figure S6. Percentage abundance diagram of selected pollen taxa from Lake Otjikoto (Leźine, 2005; Scott et al., 1991). The O1 and O2 phases correspond to woodland phases dominated by Combretaceae and *Spirostachys*, respectively. The woodland phases are separated by periods of open vegetation, as observed in phase O3. Mean abundance percentages of woody, grass, and other pollen taxa are also displayed.

6.3 Supplementary information for Manuscript 3

S1. Pollen productivity estimates with Poaceae as reference taxon

Table S1. Pollen productivity estimates (PPE) calculated with a Gaussian plume model (GPM) and a Lagrangian stochastic model (LSM) of dispersal at 3, 10 and 50 km radius, and with Poaceae as reference taxa. Standard errors (SE) derived from 20 repetitions.

	GPM 3km	**SE**	**GPM 10km**	**SE**	**GPM 50km**	**SE**	**LSM 3km**	**SE**	**LSM 10km**	**SE**	**LSM 50km**	**SE**
Acacia	0.151	0.004	0.161	0.007	0.197	0.009	0.064	0.002	0.067	0.002	0.079	0.007
Dichrostachys	0.152	0.007	0.140	0.005	0.137	0.006	0.190	0.006	0.178	0.008	0.152	0.012
Grewia	0.064	0.002	0.075	0.004	0.104	0.007	0.026	0.001	0.032	0.002	0.045	0.005
Poaceae	1	0	1	0	1	0	1	0	1	0	1	0
Combretaceae	0.258	0.01	0.217	0.014	0.239	0.02	0.430	0.05	0.270	0.021	0.257	0.020

S2. Pollen and vegetation taxa

Table S2. Pollen and vegetation taxa.

Pollen	Vegetation		
Acacia	*Vachellia ataxacantha*	*Eragrostis alsinoides*	*Pterodiscus aurantiacus*
Acanthaceae	*Vachellia erioloba*	*Eragrostis echinochloidea*	*Ptycholobium biflorum*
Aizoaceae	*Senegalia cinerea*	*Eragrostis pallens*	*Pupalia lappacea*
Aloe	*Vachellia haematoxylon*	*Eriocephalus* sp.	*Rhigozum brevispinosum*
Alternanthera	*Vchellia hebeclada*	*Euclea divinorum*	*Rhynchosia minima*
Amaranthaceae	*Senegalia hereroensis*	*Euclea* sp.	*Rhynchosia venulosa*
Anacardiaceae	*Vachellia karroo*	*Evolvulus alsinoides*	*Schmidtia* sp.
Arctotis	*Senegalia mellifera*	*Ficus* sp.	*Sclerocarya birrea*
Bauhinia	*Vachellia nilotica*	*Forsskaolea* sp.	*Searsia* sp.
Bignoniaceae	*Vachellia reficiens*	*Geigeria* sp.	*Setaria verticillata*
Burkea	Acanthaceae indet.	*Grewia bicolor*	*Sida cordifolia*
Capparaceae	*Achyranthes* sp.	*Grewia* sp.	*Sida ovata*
Cichorioideae	*Acrotome* sp.	*Grewia flava*	*Solanum* sp.
Combretaceae	*Albizia* sp.	*Grewia flavescens*	*Spirostachys africana*
Commelina	*Aloe* sp.	*Grewia villosa*	*Sporobolus panicoides*
Commiphora	*Alternanthera pungens*	*Gymnosporia* sp.	*Stipagrostis uniplumis*
Crassulaceae	Amaranthaceae indet.	*Helicrysum*	*Talinum caffrum*
Crotalaria	Anacardiaceae indet.	*Helinus integrifolius*	*Tarchonanthus camphoratus*
Croton	*Anthospermum*	*Heliotropium* sp.	*Tephrosia purpurea*
Chrozophora	Apocinaceae indet.	*Hermannia* sp.	*Terminalia prunoides*
Cucurbitaceae	*Aptosimum* sp.	*Heteropogon* sp.	*Terminalia sericea*
Cyperaceae	*Aristida congesta*	*Hibiscus* sp.	*Tribulus* sp.
Dichrostachys	*Asparagus* sp.	*Hirpicium* sp.	*Urochloa* sp.
Euclea	*Barleria lanceolata*	*Hyparrhenia* sp.	*Vangueria* sp.
Euphorbia	*Basananthe heterophylla*	*Indigofera* sp.	*Vernonia fastigiata*
Evolvulus	*Bauhinia petersiana*	*Ipomoea palmata*	*Waltheria indica*
Ficus	*Berchemia discolor*	Juncaceae indet	*Ximenia americana*
Flacourtiaceae	*Bidens biternata*	*Justicia betonica*	*Ximenia caffra*
Gisekia	*Bidens shimperi*	*Kyphocarpa angustifolia*	*Ziziphus mucronata*
Grewia	*Blepharis* sp.	Lamiaceae indet.	
Indigofera	Boraginaceae indet.	*Lantana* sp.	
Kirkia	*Boscia albitrunca*	*Leucas pechuelii*	
Kohautia	*Brachiaria* sp.	*Leucosphaera bainesii*	
Lamiaceae	Brassicaceae indet.	*Limeum*	
Malvaceae	*Catophractes alexandri*	*Marsdenia* sp.	
Maytenus	*Cenchrus ciliaris*	*Melinis repens*	
Peltophorum	*Chloris virgata*	*Monechma* sp.	
Philenoptera	*Cleome gynandra*	*Montinia caryophyllacea*	
Phyllanthus	*Cleome monophylla*	*Mundulea sericea*	
Poaceae	*Coccinia sessilifolia*	*Neorautanenia* sp.	
Polygonaceae	*Combretum hereroense*	*Nidorella resedifolia*	
Portulacaceae	*Combretum imberbe*	*Ocimum americanum*	

Pollen	**Vegetation**	
Prosopis	*Combretum apiculatum*	*Oxigonum alatum*
Rhynchosia	*Commelina* sp.	*Ozoroa* sp.
Sapindaceae	*Commiphora africana*	*Panicum* sp.
Schrophulariaceae	*Commiphora angolensis*	*Pavonia senegalensis*
Senecio type	*Commiphora glandulosa*	*Pavonia burchellii*
Spirostachys	*Crotalaria*	*Peltophorum africanum*
Tephrosia	*Croton gratissimus*	*Pergularia daemia*
Tribulus	*Cucumis* sp.	*Philenoptera nelsii*
Urticaceae	Cyperaceae	*Poa indet*
Verbenaceae	*Dichrostachys cinerea*	*Pogonarthria squarrosa*
Ximenia	*Dicoma* sp.	*Pollichia campestris*
Ziziphus	*Diospyros* sp.	Polygonaceae indet
Zygophyllaceae	*Enneapogon* sp.	

S3. Pollen productivity estimates at 3, 10 and 50 km radius

Table S3. Pollen productivity estimates (PPE) calculated with a Gaussian plume model (GPM) and a Lagrangian stochastic model (LSM) of dispersal at 3, 10 and 50 km radius. Standard errors (SE) derived from 20 repetitions. A) PPE values and SE calculated for the five selected taxa; B) PPE values and SE calculated after excluding Poaceae from dataset.

A)	**GPM 3km**	**SE**	**GPM 10km**	**SE**	**GPM 50km**	**SE**	**LSM 3km**	**SE**	**LSM 10km**	**SE**	**LSM 50km**	**SE**
Acacia	0.605	0.025	0.790	0.050	0.877	0.054	0.179	0.017	0.279	0.024	0.387	0.064
Dichrostachys	0.614	0.037	0.695	0.048	0.629	0.053	0.545	0.054	0.738	0.060	0.693	0.094
Grewia	0.258	0.015	0.374	0.030	0.456	0.029	0.075	0.008	0.131	0.010	0.198	0.026
Poaceae	4.024	0.161	4.937	0.276	4.571	0.303	2.873	0.285	4.134	0.285	4.660	0.518
Combretaceae	1	0	1	0	1	0	1	0	1	0	1	0
B)												
Acacia	0.340	0.021	0.429	0.0319	0.695	0.107	0.137	0.005	0.235	0.023	0.420	0.069
Dichrostachys	0.313	0.015	0.282	0.0227	0.372	0.060	0.366	0.014	0.480	0.046	0.502	0.059
Grewia	0.195	0.015	0.216	0.0142	0.379	0.063	0.067	0.003	0.116	0.013	0.159	0.032
Combretaceae	1	0	1	0	1	0	1	0	1	0	1	0

S4. Model performance at 3, 10 and 50 km radius

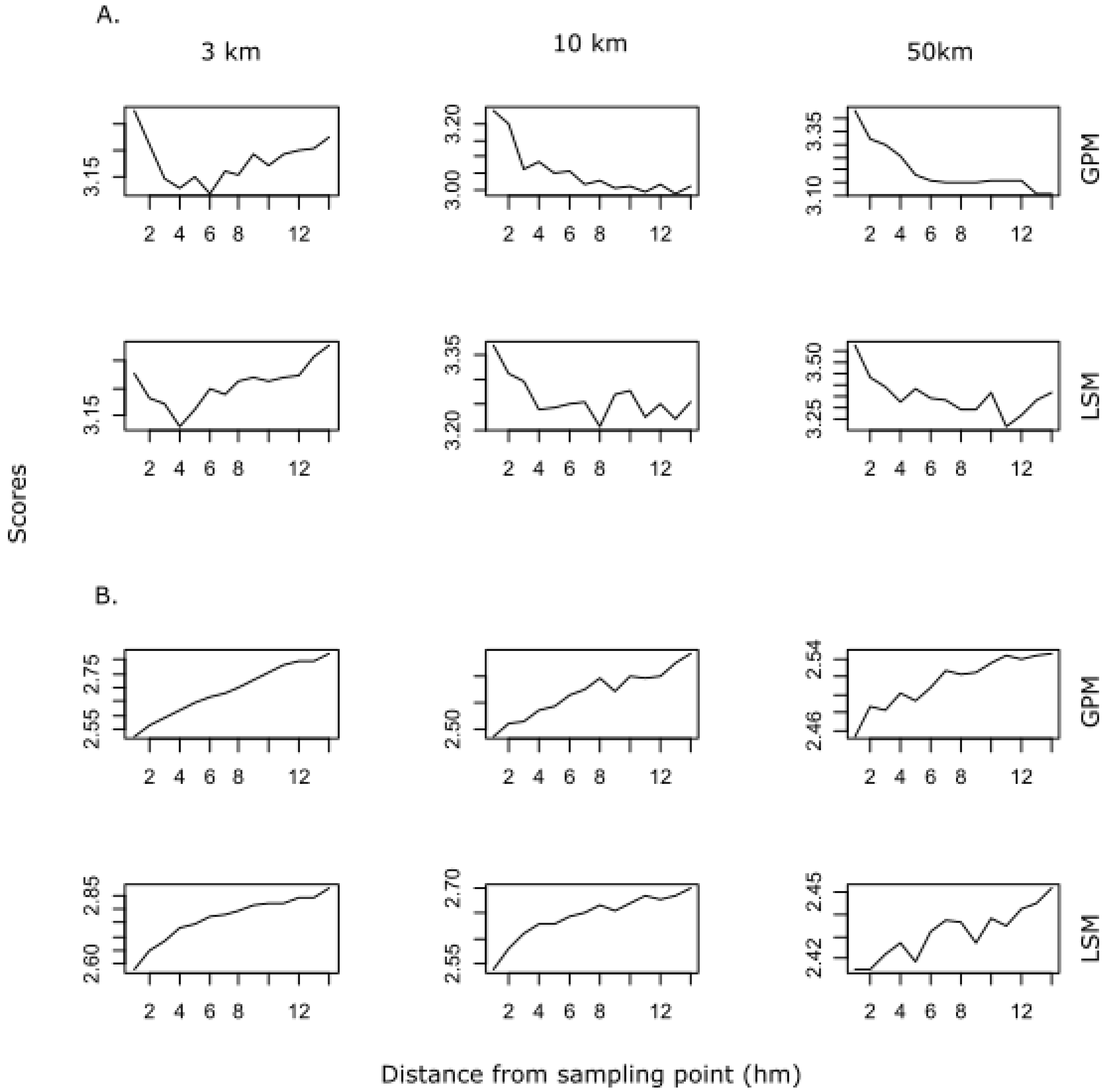


Figure S4. Model performance obtained with a Gaussian plume model (GPM) and a Lagrangian stochastic model (LSM) at 3, 10 and 50 km radius. Scores derived from 20 iterations. A) Dataset without Poaceae; B) Dataset including Poaceae.

S5. Empirical vs. modelled pollen deposition including Poaceae

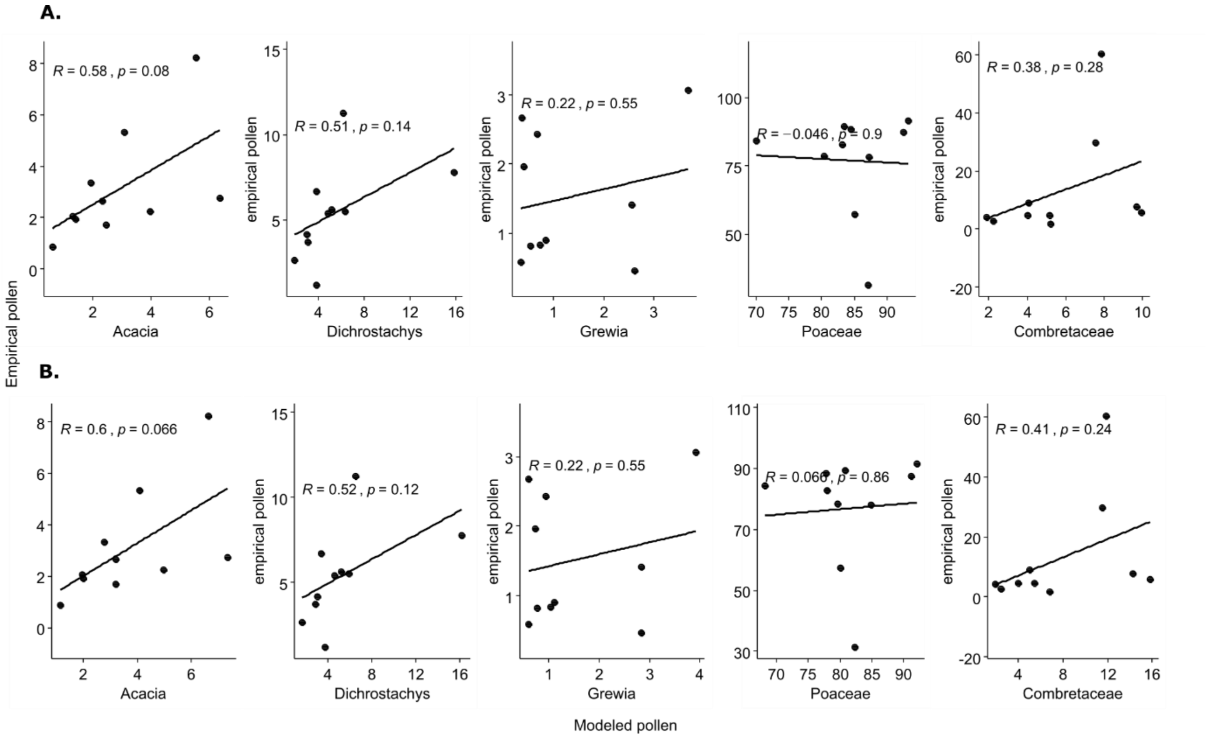


Figure S5. Scatterplots of empirical pollen deposition against modelled pollen deposition using (A) Gaussian plume model (GPM) and (B) Lagrangian stochastic model (LSM) of dispersal at 10 km radius. Calculations made including Poaceae in the dataset (cf. Fig. 4-5 in the main text).

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Eidesstattliche Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit mit dem Titel „A palaeoecological approach to savanna dynamics and shrub encroachment in Namibia" selbstständig und unter Verwendung der angegebenen Literatur und Hilfsmittel angefertigt habe. Wörtlich oder sinngemäß übernommenes Gedankengut habe ich als solches kenntlich gemacht. Diese Dissertation wurde in dieser oder ähnlicher Form noch nicht anderweitig als Promotionsleistung vorgelegt und wird erstmalig an der Universität Potsdam eingereicht, dem Verfahren zu Grunde liegende Promotionsordnung ist mir bekannt.

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Potsdam, 15.5.2020

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