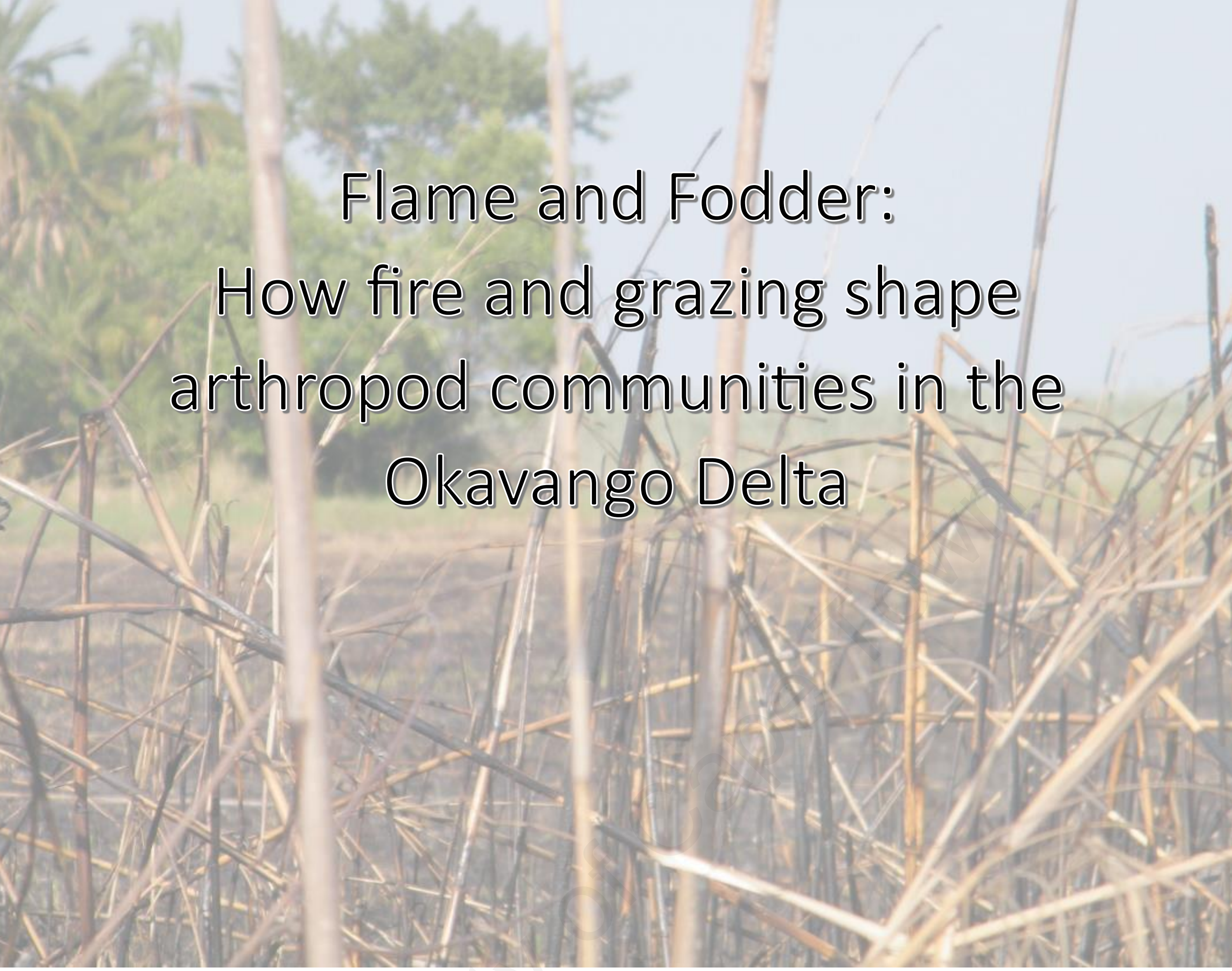

Flame and Fodder:
How fire and grazing shape arthropod communities in the Okavango Delta

University of Cape Town

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Abstract

The documentation of species presence and distribution is essential for the conservation of biodiversity worldwide. Invertebrates are relatively understudied compared to vertebrates, globally and within the southern African region. This is especially true for developing countries, due to accessibility, costs associated with remote fieldwork and lack of taxonomic expertise. Nevertheless, southern Africa is highly diverse in fauna and flora, and many species still are undescribed in many of the countries in this region. In Botswana, the Okavango Delta is an exceptionally unique biological system with a vast wetland in the middle of the Kalahari basin, acting as one of the only consistent water resources. The complexity of this flood-driven system is not only due to seasonal influxes from the catchment area in central Angola, but also due to the slow drop in elevation, which causes complex channels, streams, bogs and other aquatic habitats to form as the delta fans out towards the Makgadikgadi pans. At the core of this critical hydrological system lie aquatic and terrestrial systems and processes that ensure its continued functioning and overall health, with many of these services underpinned by invertebrates, arthropods in particular. Although the aquatic invertebrates are relatively well-studied, the terrestrial arthropods have received less attention, while undoubtedly also providing critical regulatory services on the islands within the Delta, and along the edges. As a World Heritage Site, the Okavango Delta should be prioritised for research related to ecosystem processes and monitoring of the smaller faunistic “cogs” that ensure the collective functioning of the overall system, especially due to the threats it faces. Anthropogenic disturbances have become more common and regular along the edges and within the Okavango Delta over the last few decades, and as such, human-induced fire and livestock grazing has increased the pressure on the natural systems in which it occurs. Given the fragmented knowledge of terrestrial arthropods within Botswana, and the Okavango Delta specifically, this study aimed to compare arthropod communities between ongoing disturbance regimes, using a multi-taxon approach. Specifically, this study aimed to: 1) compare the diversity and abundance of four terrestrial arthropod groups (ants, wasps, springtails and spiders) in burnt and grazed sites, 2) investigate whether burning or grazing have impacts on arthropod diversity, in terms of species richness and abundance, 3) provide a starting point dataset to monitor the impact of disturbances on arthropod communities in the Okavango Delta into the future, 4) generate starting point species inventories for these four taxa in this region, and 5) compile an updated species list of the spiders (Araneae) of Botswana. Using pitfall traps and litter extractions across two seasons, the abundance of the four groups was only fractionally higher in the wet season for the pitfall traps, but litter extractions had large increases in ants, springtails and wasps in the wet season. Ants had the most species and the highest diversity in the grazed sites compared to burnt sites, while Collembola and Araneae communities were more even in the burnt sites than in the grazed sites. Species richness, evenness and diversity varied between trapping methods and between groups studied, illustrating the varied responses of arthropod communities to disturbances. Ants and Collembola varied significantly between seasons, but not between disturbance types, while wasps and spiders differed significantly between both season and disturbance types. This study created the first starting point dataset for comparing the impacts that disturbances have on arthropod community shape and composition. An up-to-date species list for spiders of the Okavango Delta was compiled, adding 37 new records to the existing species list. From pitfall traps and litter extractions a total of 20 families and 51 genera were sampled, with 40 species identified. From active collections, a total of 18 families, 55 genera and 70 species were collected. The updated species list of spiders in the Okavango Delta contains 33 families, 141 genera and 220 species. This will serve as the basis for further species inventories and diversity studies in the region. It is recommended that terrestrial arthropod research be continued within this World Heritage Site to ensure the documentation of the diversity of species present here, but also to utilize these species as indicators for ecosystem changes to ensure the continued survival of this wetland and the species that depend on it.

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Chapter 1: Literature review

Introduction

Current estimates suggest that more than 80% of all species described globally are invertebrates, of which coleopterans make up nearly 25% (Cardoso *et al.,* 2011), with more than 392 000 beetle species described (Eggleton, 2020). Stork (2018) suggested there are more than 5.5 million species of insects worldwide, of which only an estimated 20% have been described, making the identification of critical species to conserve challenging. The scientific community is currently unable to confidently suggest the minimum number of species required to maintain ecosystem function, but the general consensus is that reduced species richness and diversity can inhibit many critical ecosystem services (Naeem *et al.,* 2016) and thus directly negatively impact humans, and other spheres of diversity. Although the order Coleoptera contains the most species identified, ants and termites make up a disproportionate percentage of total estimated global insect biomass, accounting for up to 120 million tons of the 200 million tonnes of all insect biomass estimated globally (Tuma *et al.,* 2020). Assuming that ants and termites comprise between 30 000 – 40 000 species (Ward, 2007; Engel *et al.,* 2009) of the total 5.5 million estimated insect species (Stork, 2018), they would represent more than 50% of total global insect biomass, while accounting for less than 1% of species.

Throughout history, insects were predominantly known as agricultural pests (Bebber 2014a, 2014b; Stejskal, 2015), disease vectors (Lounibos, 2002) and as a general 'nuisance' (cockroaches and flies). However, changes in the perceptions of insects within the scientific community had only started to shift in the 1980s, mostly because of an ignorance of the beneficial roles of insects in almost all ecosystems globally (Eggleton, 2020). Due to their proliferation and global abundance, arthropods are intricately involved in critical ecological processes, regulating ecosystem function and various ecosystem services (Noriega *et al*., 2018). The Millennium Ecosystem Assessment (MEA, 2005; Reid *et al.,* 2005) recognised four broad types of ecosystem services provided by their constituent species. Particularly for insects these include: 1) Provisioning services: The multitude of products and chemicals that are derived from invertebrates, from honey produced by the honey bee, *Apis mellifera,* to colourants and dyes (carmine) attained from Cochineal scale insect (*Dactylopius coccus*). 2) Regulatory services: Positive regulatory processes facilitated by insects including pollination (majority of wild plants being dependant on insects for pollination (Ollerton *et al.,* 2011), trophic level control (pest control of parasitic wasps (Tumlinson *et al.,* 1993)) and decomposition of leaf litter and other organic material in forest ecosystems in particular (Crossley, 1977). 3) Cultural services: non-material value and benefits generated by insects includes the use of certain species as model organisms for studying general biology (for example the use of *Drosophila* for genetic studies). These may also include the use of a range of insect species that may act as indicators of environmental changes within ecosystems (Gerlach *et al.*, 2013; Andersen and Majer, 2004) to a much finer scale than when using other taxa (Cardoso *et al.,* 2011). 4) Supportive services: These services are critical for all other ecosystem services. Some supportive services provided by insects include ecosystem engineering. For example, island formation by termites in the Okavango Delta (Dangerfield *et al*., 1998; McCarthy and Ellery, 1998), nutrient cycling (burying of dung by dung beetles (Cardoso *et al*., 2011)), and availability as a crucial food source to other taxa (60% of birds utilise insects as their main food source (Morse, 1971). Termites in tropical regions can also play similar roles to earthworms in the rest of the world (Jouquet *et al.,* 2011). These soil-nesting insects are invaluable for soil health, through transforming soil (Stork, 1992) and assisting in the process of nutrient cycling (Schuurman, 2005; Ulyshen and Wagner, 2013).

Losey and Vaughan (2006) estimated the value of ecosystem services provided by insects in the USA at $57 billion annually, while Klein *et al*. (2007) found 70% of the primary crops used for direct human consumption (87 out of 124) are pollinator-dependent, estimating the value of pollination services at €153 billion. Variances in these calculations are evident as Hanley *et al.* (2015) and An and Chen (2011) estimated pollination value at $379 million and €10.6 billion, respectively. Although these are only a few of the vast array of ecosystem services that insects offer, it is clear that insect-based ecosystem services are disproportionately critical for natural ecosystem and agricultural system productivity compared to those provided by vertebrates (Cardoso *et al.*, 2011). Although invertebrates, particularly arthropods, have exceptional diversity and deliver critical ecosystem services, they have mostly been excluded from global policies and conservation management efforts (Zamin *et al.,* 2010).

Messages from arthropods: Indicators of change

As invertebrates fill critical ecological roles within almost all known ecosystems, they are more vulnerable to similar threats as other biodiversity units (McGeoch *et al.,* 2011). Thus, changes of their communities through space and time can be used representatively for various ecosystem health parameters (Gerlach *et al*., 2013). Bioindicator systems, such as the use of multiple groups of insects, acting as environmental, ecological and biodiversity indicators (McGeoch, 1998), can provide more accurate insights into the health or state of a system (van Straalen and Krivolutsky, 1996). It has been suggested that invertebrates may represent trends in community composition more accurately than vertebrate species, due to their higher diversity, abundance and reproduction rate (Bisvac and Majer, 1999; Kremen *et al*., 1993). The impact of shifted invertebrate diversity impacts various trophic levels, like bats and birds, and may lead to pest emergence (Kambrekar *et al.,* 2015), population booms

(Nelson *et al.,* 2004) and increased disease transmission (Lehane *et al.,* 2005). As biodiversity is known to vary in both space and time (Rosenzweig, 1995), and broad patterns tend to emerge at various spatial and temporal scales, it remains important to be critical of the scale of assessment used when utilising arthropods as indicators of change. Some limiting factors that should be considered include: 1) more species will be recorded with increasing area sampled (Rosenzweig, 1995); 2) latitudinal gradients show a decrease in species as one moves further away from the equator (Willig *et al*., 2003); 3) increased habitat variation often delivers higher species richness; 4) diversity will peak across intermediate disturbance levels (Grime, 1973; Connell, 1978), and 5) diversity patterns are strongly influenced by the spatial scale at which observations are conducted, and community patterns representing local communities may differ from patterns observed on a landscape and regional scale, but local patterns are rarely independent of diversity patterns on a regional scale (Crist *et al*., 2003).

As bioindicator systems rely on underlying biodiversity patterns to make assessments meaningful, it is also important to consider that the overall pattern of higher diversity in the tropics may be attributed to environmental factors, such as habitat productivity, stability of ambient energy available in a system, the increased evolutionary speed of speciation at lower latitudes, and increased biotic filtering due to higher predator and pathogen pressures (Eggleton, 2020). These factors may influence the conclusions reached when using arthropods as bioindicator systems. Above-and below-ground arthropods are often used to monitor post-fire impacts and habitat recovery. These may include larger macrofauna such as insects and arachnids (Pryke and Samways, 2012) to smaller soil-dwelling arthropods such as Collembola (Janion-Scheepers *et al*., 2016). Arthropods are excellent indicators of ecosystem recovery, as they are very responsive to change and relatively quick and affordable to collect and identify (Samways, 1994). Also, importantly, these groups are the main food resources for vertebrates such as birds, reptiles, amphibians, and mammals such as bats, thus having the potential to indicate whole-ecosystem impacts (Losey and Vaughan, 2006; Salvarina *et al*., 2018). Based on these well-established diversity patterns and the link between local and regional diversity and richness, observations of invertebrate species and communities may provide valuable insights into the threats and associated changes that a system may experience, and how they may be mitigated or prevented completely.

Global arthropod declines

The current rate of biodiversity loss globally, and the increasing probability of species extinctions, are unprecedented (Barnosky *et al.,* 2011). As insects make up more than 60% of all terrestrial species, declines in their abundance and geographical range may be the first steps towards extinction (Diamond, 1989). Although the conservation practices for arthropods have only gained attention over the last 100 years (Kim, 1993), it is only in recent years that their declines have received increased attention from the scientific community, although less so from the general public (Eggleton, 2020). It is therefore even more challenging to estimate rates of historical decline of arthropods in areas where humans have inflicted changes in the environment for hundreds of years and where limited data is available (Eggleton, 2020). Hallmann *et al*. (2017) also found an astonishing decline in airborne insect biomass, between 76% and 82%, in protected areas of Germany over 27 years, which is worse than initially estimated by Shortall *et al.* (2009). These declines were not just limited to rare species, of which declines have been relatively well known, but also generalist species, suggesting that declines are due to commonly shared traits between insects, rather than specific habitat types as discussed by Gaston and Fuller (2007).

The term “Insect Armageddon” has become a heated topic within the scientific community in recent years, due to an alarming study by Leather (2018). With insect-related declines turning out to surpass those of plants and birds across a similar spatial scale (Thomas *et al*., 2004), these biodiversity losses will certainly have significant impacts on a wide range of ecosystem health parameters and associated or dependent species across the globe. Lister and Garcia (2018) found 78%-98% reductions in the biomass of ground-foraging and canopy-dwelling arthropods the rainforests of Puerto Rico within the 36-year study period, leading to congruent reductions in reptiles and birds in the study area due to a reduction in insects as a food source. Sanchez-Bayo and Whyckhuys (2019) corroborated findings by Dirzo *et al*. (2014), estimating current insect species is declining at 41% (twice the number of vertebrate species in decline) and the rate of local extinction of species are 10% of species per year, which is eight times higher than the respective rate of extinction for vertebrates.

The studies by Hallman *et al*. (2017) and Lister and Garcia (2018) received extensive criticism regarding the research approach and methodology used, most probably arriving at over-estimates for insect decline. Despite these concerns, the emphasis on the impacts of insect decline has become clearer through subsequent studies (for example: Sanchez-Bayo and Whyckhuys, 2019). Although the latter study was also criticized for using only specific species to represent groups (biases towards pollinators for the Hymenoptera and dung beetles for the Coleoptera), the review highlighted that most long-term available data contain insect groups that are well studied due to their perceived ecological value for humans (Eggleton, 2020). Outhwaite *et al*. (2020) provides the most insightful results regarding arthropod declines based on the variable responses of various groups of invertebrates. Although assessing up to 5000 species of UK invertebrates for 45 years, the responses of various groups differed dramatically from each other and from previous similar studies discussed above (Outhwaite *et al.,* 2020). Only non-insect terrestrial invertebrates showed a general decline, and the terrestrial insect results suggested range expansions or little response at all (Outhwaite *et al.,* 2020). Furthermore, results also showed that it may be likely that individual species abundances are declining. Seibold *et al.* (2019) assessed biomass, abundance and estimates of species loss in Germany, addressing some of the critiques raised against preceding insect decline research. Their results showed declines of 67% in biomass, 78% decline in abundance and 34% declines in species diversity in grasslands (Seibold *et al*., 2019). In forests, a 41% decline in biomass and 36% decline in species number was found, with rare species being most intensively affected, but general species also experiencing significant declines (Seibold *et al.,* 2019).

Despite warnings to interpret these studies with caution, this general trend of arthropod decline globally is undeniable. The study of arthropod declines is gaining momentum, although more intensive research will reveal more relevant local and global patterns. Some questions remain critical to the exploration of this phenomenon, such as whether the rate of arthropod decline is increasing, or have these declines been a slow and constant process that has gone unnoticed due to lack of research and/or baseline data (Eggleton, 2020)? The anthropogenic impacts of humans on natural habitats are undeniable, but the question remains whether these declines have only recently occurred at a very fast pace (or simply gone unnoticed), or whether we may have reached a tipping point, overriding the limits of ecological resilience, due to the loss of vast natural areas and their associated species and ecosystem services (Dobson, 2006; Valiente-Banuet, 2015).

Although general arthropod decline estimates can indicate global trends, and information on well-studied species like the Honey bee are more readily available, many specific groups of insects and their respective population dynamics, including Formicidae, Hymenoptera as a group and Hymenopteran parasitoids, are completely unknown (Sanchez-Bayo and Whyckhuys, 2019). Recent studies on the rarer Chrysididae parasitic wasps delivered concerning results, with 23% of the 48 species in Finland and their host species in sharp declines (Paukkunen *et al*., 2018). Limited population trend studies exist for Formicidae (Sanchez-Bayo and Whyckhuys, 2019) and spiders (Rix *et al.*, 2017). Clearly, invertebrates show a much higher risk of extinction, documented extinction rates and proportion of threatened species than those of better-studied taxa (Stork and Lyal, 1993; Thomas and Morris, 1994; MacKinney, 1999; Moir *et al.,* 2010; Cardoso *et al*., 2011).

Besides the impediments to insect conservation (see Cardoso *et al*., 2011), main threats to arthropods include (Fox *et al*. 2014): Land-use changes (in the form of habitat loss (Tsiafouli *et al.,* 2015) and intensive agriculture (Karp *et al*., 2012)), pollution (both general and specifically by pesticides (Schreinemachers and Tipraqsa, 2012), and climate change (increasing as the impacts of climate change are exacerbated (Bale *et al.,* 2002)). Thomas *et al.* (2019) proposed that insects may simply be too diverse to assume that any generalisation is possible. Additionally, entomological research is underfunded compared to vertebrate groups, based on their diversity and global contribution to functioning ecosystems, and this alone is a massive obstacle to large-scale and long-term arthropod population studies (Eggleton, 2020). The necessary research is also complex in nature, with an extensive list of variables to consider and account for (temperature, disturbances, seasonal and annual population trends), and requires exceptional coordination and interdisciplinary contributions from taxonomists, ecologists and other specialists in all related fields.

There are numerous problems with the available literature regarding global arthropod declines, mostly regarding the methodologies used, groups assessed, and most importantly, the limitations of current research in the extent of time and space assessed (Eggleton, 2020). Eggleton (2020) shared a valuable perspective; that local declines/extinction in countries where most of these studies have been completed does not necessarily imply global declines/extinction. Trends are emerging that suggest declines in various arthropod groups in specific points in space and time, and these should not be dismissed, but these results do not yet provide clear indications of how serious the global decline of arthropods are since we have only assessed a fraction of the complete picture (Eggleton, 2020). As the majority of the current literature is based on studies in the Northern Hemisphere, it is hard to envision how these trends may be applicable to the African context, and whether patterns in decline will be similar at all. As is made clear by the long list of impediments to successful invertebrate conservation, the threats this group faces, and the associated continuous decline of species, it will only be possible to protect species, described and undescribed, through the larger scale protection of regional ecosystems and their unique processes, function and structure (Samways, 1993).

As arthropod declines are of concern to the global scientific community and the general public, based on the expected impacts discussed above, and patterns of decline have proven to be differential. It may seem that continued exploration of this phenomenon is extremely important to generate a clearer understanding of how it is unfolding across various ecosystems and continents. Highly diverse areas, such as the Okavango Delta, will require even more attention than other well-studied systems, to ensure that these systems retain their functionality. Therefore, the implementation of baseline studies in these areas of highly concentrated biodiversity is exceptionally important to prevent the loss of ecological wealth and associated ecosystem services.

Arthropods and climate change

Historic and continued habitat fragmentation, habitat loss and isolation (driven by anthropogenic land use changes) are some of the major current threats to arthropods that will increasingly intensify the impacts of climate change through limiting range expansions, especially in landscape with highly variable elevation (Samways *et al*., 2020; Yadav *et al*., 2018, 2021). Limited studies have investigated the impacts of climate change on insect population dynamics and individual fitness (Deutsch *et al*., 2008; García-Robledo and Baer, 2021), although work by Parmesan (2006) reviewed patterns of impacts of climate change on various taxa, finding population range shifts in butterflies and that asynchrony in butterflies and their hosts have directly caused population crashes. The challenge in these investigations is that arthropod responses to changing climatic conditions can vary significantly between species, insect communities and geography (Ficetola *et al.,* 2021).

In the face of mounting evidence of the negative effects of increased temperature on arthropods (Parmesan, 2006; Forrest, 2016; Jain *et al*., 2022), these conditions may also benefit certain species (Tougeron and Abraham, 2017; Marshall *et al*., 2020), especially invasive species. In addition, species may shift ranges to enter new habitats and find new resources (Hickling *et al.*, 2005). These positive impacts are most likely to only be temporary, as increasing temperature and climate extremes will undoubtedly cause more deleterious pressure on arthropod populations in the short term (Harvey, 2020). Continued increasing temperatures may cause many species to be pushed beyond their optimum temperatures for survival and reproduction (Buckley and Kingsolver, 2021). Changes in annual weather patterns may also cause arthropods to fall into developmental traps, where a lack of cold temperatures during winter may cause delayed or accelerated developmental activity (Forrest, 2016). Pollinator interactions with host plants will also be negatively affected in some species (Tylianakis *et al*., 2008), while alterations in regional precipitation patterns have already affected the duration, extent and seasonality of large-scale fire regimes (Jain *et al*., 2022; Nimmo *et al.,* 2021). Due to their short life cycles that are heavily affected by ambient temperature, the phenology of arthropods are expected to alter in response to climate change, sometimes in unexpected ways (Forrest, 2016). Tropical areas are expected to be more affected (Roque *et al.,* 2018), as arthropods there already operate closer to their thermal maximum than in other parts of the world at lower latitudes (Eggleton, 2020). These impacts, varied and widespread, will undoubtedly have a negative effect on already strained ecosystem services and service providers (Dale and Polasky, 2007).

Climate change may continue to impact various ecosystems across the planet in varied ways, but wetlands may be particularly at risk. Changes in hydrology and increased temperatures may cause changes in the biogeochemistry of wetland systems (Stewart *et al*., 2013), and as climate change impacts increase, they may cease to act as carbon sinks (Laiho, 2006). Wetlands may lose their ability to purify water, due to a reduction in rainfall, and may lead to eutrophication of water bodies due to the release of organic carbon (Corman *et al*., 2018). It remains unclear how different wetlands across the world will respond to climate change (Salimi *et al.,* 2021), but clear impacts are inevitable for these temperature-and rainfall-dependent systems and their associated arthropod diversity, which contributes to its continued functionality. As climate change impacts both the system and its occupants, it is expected that these impacts may be compounding and negative overall.

The Okavango Delta: A critical wetland ecosystem for southern Africa

The Okavango River basin is one of the largest undeveloped, unexplored river basins in the world (Huntley and Matos, 1994; Figueiredo *et al*., 2009). Although the Delta is designated as a UNESCO world heritage site, the intricate system of rivers, swamps, peat bogs, Miombo woodlands and grasslands that feed and support it, are vastly understudied (NGOWP, 2018). The Angolan Planalto Central in central-Angola is considered to be the water tower for one of the world's largest conservation areas, the Kavango-Zambezi Trans Frontier Conservation Area (KAZA-TFCA) whereby innumerable small rivers, streams, seepage bogs and wetlands accumulate and disperse water from the Bié Plateau (NGOWP 2018).

After water accumulates within the river basins in the midlands of Angola in November (up to 1200mm, Ringrose *et al*. 1999), it makes its way towards the Caprivi strip in Namibia, ultimately entering Northern Botswana through the Upper-Delta in February/March and moving slowly across the Delta, reaching the furthest parts during July (Ramberg *et al*., 2006b), ultimately terminating in the Makgadikgadi pans (Mendolsohn and El Obeid, 2004). This typical flood-pulsed system has another distinct wet period, during December-March, when the local rains arrive (Ramberg *et al.,* 2006a). The annual variation in rainfall is exceptionally large (Nicholson, 2000), adding strong temporal fluctuations to the strong hydrological gradient that exists in the various streams, swamps, peat bogs and other biotopes (Ramberg *et al.,* 2006a). A variety of vegetation communities occur on the terrestrial islands, and their size can vary substantially (Ellery and Tacheba, 2003). Island formation ad growth in the Delta occurs through a combination of processes (Humphries *et al.* 2014). Channel bed aggradation (gradual accumulation of sediment), channel avulsion (channel migration) and peat oxidation (burning), individually and in combination, are critical processes in the formation of the now-almost 150 000 islands in the Delta (Gumbricht *et al*., 2004; Humphries *et al.* 2014). Interestingly, some of these islands were suspected to have initially started as termite mounds (McCarthy and Ellery, 1998) and these arthropods still contribute to this process. Soil and groundwater chemistry varies due to altering transpiration rates of various habitats within the system, with densely wooded island fringes attributed the highest transpiration rates (Ellery and Tacheba, 2003). As soluble compounds are pulled into the root zone from the aquatic habitats by plants, but are not absorbed, an increase in concentration of solutes is found in the soils of the islands as one moves to the centre, clearly defining vegetation zones (Ellery and Tacheba, 2003). The terrestrial islands follow a typical vegetation zonation, where fringes are generally dominated by broadleaved evergreen trees and deciduous trees along with well represented shrubs and herbs within the understory (Ramberg *et al.,* 2006a). Towards the centre of the islands, grasses are more dominant (Ellery and Tacheba, 2003) and community compositions shifts towards a more open habitat, allowing the presence of fire and other ecosystem drivers to play critical, yet understudied, roles in maintaining these communities. The spatial heterogeneity of habitats within the delta are exceptional with 46 habitats identified (Ramberg *et al.,* 2006a). Ellery and Tacheba (2003) documented 1299 species and sub-species of plants while estimating the true total to be closer to 1400 within the Delta. Even though this swamp only covers 4% of Botswana, it hosts 65% of Botswana's plant species (Ramberg *et al*., 2006a).

Various types of dry woodlands border the Delta on all sides (Mendelsohn and El Obeid, 2004). Most of these areas have never flooded, or have dried out due to shifts in flood dynamics (Robbel and Child, 1976). Due to the drying out of these historic floodplains, along with related changes in fire frequency and intensity, vegetation has become dominated by mature woody species, unable to survive regular flooding (Tang and Kozlowski, 1989). This exceptionally species-rich region is thus expected to harbour diverse groups of invertebrates within its great diversity of vegetation and habitat types.

Human impact in the Okavango Delta

Fire

Influences of anthropogenic disturbances vary across landscapes and habitats. Fire is a known ecosystem driver, not only globally, but also in the catchment and southern reaches of the Delta (Archibald *et al.,* 2010). Wetlands and grasslands in Africa have been burnt by local inhabitants for more than 55 000 years (Heinl *et al.,* 2007). These early "landscape managers" utilised fire to promote grazing quality for their livestock, attract game, or to prepare areas for farming after the flooding had subsided (Bernard and Moetapele, 2005; Heinl *et al*., 2007).

The Okavango Delta is a tropical wetland interspersed with drylands, with studies finding a higher fire frequency present in floodplains than on drylands, due to the higher fuel load and increased biomass production (Heinl *et al.,* 2006). In flood-pulsed systems like the Delta, the lack of flooding, rather than a flooding event, can also be seen as a disturbance (Bayley, 1995). Although strict policies have been developed to reduce the prevalence of human-initiated fires, these are extremely difficult to enforce and there are still fires burning across the Delta (Heinl *et al*., 2006. Cassidy *et al*., 2022). Fires within the dryland woodlands are limited more by the relative fuel load available (Heinl *et al.,* 2007), where increased canopy cover tends to reduce the fuel available to a fire (Frost, 1996). Generally, the available fuel loads in the Delta are low, due to sandy soils, high levels of herbaceous cover (which burns quickly and with low intensity) and intense herbivory (Heinl *et al.,* 2007), and when fires do occur, they tend to be low intensity and remain surface fires. Fires in the woodlands and their frequency are influenced by annual rainfall and relative distance to floodplains, which provide access to water and increase biomass as a result (Heinl *et al.,* 2006). The interlaced patches of burnt and unburnt aquatic and terrestrial vegetation create interesting interactions that influence vegetation dynamics (Heinl *et al*., 2006*,* 2008).

Two main ignition sources are prevalent for fires within the Delta, namely lightning strikes or fires caused by humans. During the thunderstorms that occur before the rainy season in November, the limited but dried-out fuel load can easily be ignited by the lightning strikes hitting the ground, due to the lack of rain that normally accompanies these storms (Heinl *et al.,* 2007). On the other hand, people may intentionally start fires to improve grazing capacity of grasslands, to open up vegetation plots for agricultural expansion or to attract wild game for hunting, while unintentional fires may occur due to campfires, certain cooking methods or during honey harvesting (Cassidy, 2003). High rains and leached, sandy soils (Pröpper *et al.,* 2015) leave little land available for commercial or even subsistence agriculture for the local communities, outside of the fertile floodplains. As a result, communities practice slash-and-burn forest clearing techniques to open fertile soil under woodlands, thereby slowly fragmenting, shrinking or potentially depleting the woodlands (NGOWP, 2017). Cassidy (2003) also highlighted concerns from local organizations that altered fire regimes have led to larger areas being burnt more frequently in recent years, driven by the increase in population densities in these areas along with the use of fire-prone clearing techniques. The latest assessments found that annual fire frequencies are significantly higher than what would be expected without human-induced fires, with extensive areas of fire hotspots being burnt for more than 14 of the 20 years being assessed (Cassidy *et al*., 2022).

The extensive impacts of fire on biodiversity can be both positive and negative (Whelan, 1995) and are relatively well described. These include, but are not limited to: reduction in competition between surviving species (Rodgers *et al.,* 1973), colonisation by new species (Barratt *et al*., 2009), increase in soil fertility (Schoch and Binkley, 1986), control of soil pH, pests and parasites (Wan *et al.,* 2001), and direct killing or wounding of individuals. In addition, most studies have focussed on vertebrates and plants. Few studies in Africa have assessed invertebrate responses to fire using multiple taxa (Pryke and Samways, 2012a), finding variable responses between taxa, and large knowledge gaps exists in this regard within the Okavango Delta. Heinl *et al.* (2004) showed that the habitats within the Delta have significantly varied and even contradictory responses to fire. Only a few landscape-scale fire regimes have been studied intensively across the savannas and flooded grasslands of Africa (for example van Wilgen *et al.,* 2007, Archibald *et al*., 2010; Smith *et al*., 2016). More recently, Russell-Smith *et al*. (2021) explored the opportunities and challenges associated with incentivising emissions reduction in fire-prone, southern African savannas, although the understanding of the influences of altered fire regimes on biodiversity remains patchy across this region. Research conducted in neighbouring countries provide insights into the possible impacts fire may have on arthropods in Botswana and specifically the Delta. Joubert *et al.* (2016) assessed the impacts of burning on grasshopper community composition in grasslands in South Africa, and found that fire frequency significantly affected grasshopper species composition, but not species richness. The majority of grasshopper species favoured grasslands that were recently burnt or grazed, but some showed preference to low levels of disturbance, or none at all (Joubert *et al.*, 2016). Similarly, Mavasa *et al*. (2023) studied the response of ants, beetles and spiders to disturbance in the South African savanna biome, and found greater species richness of ants and beetles in disturbed areas than in pristine savanna. Nonetheless, results showed that anthropogenic disturbances cause significant changes in the species composition of surface arthropods, specifically in available leaf litter (Mavasa *et al.*, 2023).

Disturbances and disturbance regimes will inevitably impact all levels of biological organization within a specific system and these regimes play important roles in the ecological interactions related to vegetation (Crews and Neuenschwander, 2007). As many of the fires along the fringes of the Delta are cause by anthropogenic activities, like burning to increase grazing capacity (Cassidy, 2003), it is valuable to acknowledge and investigate the impacts that these practices, among others, have on terrestrial arthropod communities.

Livestock grazing

Globally, livestock grazing has been found to have profound impacts on wetlands (Epele and Miserendino, 2015) and other associated ecosystems, from soil degradation and compaction (Greenwood and McKenzie, 2004) to declines in spider (Horvath *et al.,* 2009) and reptile species (Brown *et al.,* 2011). It has been suggested that even when grazing pressure is low, livestock may still have a significant impact on wetland functioning through nutrient deposition (faeces and urine) and consumption of riparian vegetation (Schmutzer *et al.,* 2008), among others. Livestock, being significantly water-dependent, need additional sources of water in the arid regions of Africa, albeit natural or man-made. As livestock remains one of the most prominent sources of income and wealth in the remote areas of Africa, cattle (specifically *Bos taurus*) numbers are steadily increasing (Thornton *et al.,* 2010), playing a critical role as commodity both socially and economically (Weise and Fynn, 2019). As a result, livestock has also become a valuable conservation tool for landscape managers, not by choice, but by necessity (Spooner *et al.,* 2002).

The spatial scale in which livestock foraging occurs has a definitive impact on large herbivore-arthropod interactions, as these herbivores influence the vegetation in three distinct levels; i.e., The feeding station scale (small scale), the vegetation patch scale (medium scale) and the landscape scale (large scale) (Dennis, 2003). Observed impacts of herbivores on arthropod communities are altered by the scale at which impacts are assessed, due partly to the fact that herbivores do not graze evenly across the patch/landscape (Clarke *et al.,* 1995) and partly to the variability in responses of plant communities to grazing (Oom *et al.,* 2002) as a result of variations in climatic, hydrological and geological attributes of a specific system. Historically, both domestic and wild herbivore populations in Africa migrated seasonally to accommodate for fluctuations in feed quality and availability. During the wet season, livestock grazed on higher quality forage available in woodlands and saline grasslands, while, in the dry season, they grazed on the only available green forage found in the floodplain systems, especially zones where deeper flooding occurs (Fynn *et al.,* 2015). Savanna habitats characterised by lower rainfall are unable to sustain reliable forage availability during the dry season (Illius and O'Connor, 1999; Owen-Smith, 2008) but offer higher forage quality than wetland or higher rainfall systems with higher productivity (Hopcraft *et al.,* 2010). Forage quality and availability are not the only restricting factors regulating livestock grazing decisions. Predation risk (landscape of fear) (Creel and Winnie, 2005) and intensifying fragmentation of ecosystems through anthropogenic disturbances (Fynn and Bonyongo, 2011; Harris *et al.,* 2009) both contribute significantly to livestock grazing decisions.

It is well documented that grazing can be important for maintaining insect diversity in grasslands (Smith, 1940; Zhu *et al.*, 2012), and research suggests that grasshopper diversity shows minimal changes between areas of livestock- and wild ungulate grazing (Samways & Kreuzinger, 2001). This suggests that livestock may fill the role of wild large herbivores in stimulating arthropod diversity through moderate disturbance (Wilkerson *et al.*, 2013; Pryke *et al.*, 2016). It is important to note that for other arthropod groups, like butterflies, the presence and intensity of grazing may affect species differentially, depending on the landscape management approach (Bussan, 2022). Although, in South Africa, Joubert *et al.* (2016) found that grasshopper abundances benefited from grazing, Klink *et al.* (2014) concluded that an increase in arthropod diversity by large herbivore presence is limited by the increase in biotic/abiotic heterogeneity that results, and is in turn dependent on whether the increase in habitat heterogeneity can compensate for the reduction in resources and direct mortality.

Losing biological wealth along with critical invertebrate-associated ecosystem services within this wetland system could lead to the loss of characteristic faunal/floral species as a result of a potential breakdown of complex trophic interaction. This chain of events would prove extremely detrimental for the local ecosystems, the local communities, the tourism industry and eventually the Okavango Delta as a critical hydrological system within sub-Saharan Africa. Investigating the impacts of livestock grazing on a broader range of arthropod communities could prevent extensive degradation and potential loss of one of the key functional groups within the Delta wetland system.

Invertebrate research in Botswana

Pinhey (1968, 1971, 1974, 1976) did exceptional work in documenting some 115 species of butterflies in Botswana (Lepidoptera: Nymphalidae and Lycaenidae) and found at-risk ecological interactions of the myrmecophilous lycaenids (larvae requiring both the host ant species and the specific host plant). However, the majority of invertebrate studies in Botswana have focused on aquatic species, while terrestrial species studied have been mainly limited to cosmopolitan species (for example butterflies Pinhey, 1976) and economically important pests like mosquitos and tsetse flies (Cornel *et al.,* 2018; Kgori *et al.,* 2006; Lyczkowski, 2006). Other examples of aquatic studies include work by Brown *et al.* (1992) working on gastropods in the lower Okavango River, Kipping (2011) producing an annotated checklist of dragonflies and damselflies of Botswana, and Dallas and Mosepele (2007; 2020) studied spatial variations in aquatic invertebrates, among many others (Appleton *et al.,* 2003). The extensive AquaRAP of the Okavango Delta (Alonso and Nordin, 2003) provided one of the most extensive assessments of the aquatic macro-invertebrate diversity of the Delta across four focal areas and 37 sites, providing novel detailed lists of the macro-invertebrates found. The National Geographic Okavango Wilderness Project conducted the first recorded large-scale survey of invertebrates in the Angolan headwaters, feeding the Delta in Botswana (NGOWP, 2017) and collected multiple new aquatic invertebrate species while finding higher abundance and diversity of terrestrial invertebrates in unburnt areas than in burnt areas.

Araneae, on the other hand, has been well-documented in southern-Africa through projects like the South African National Survey of Arachnida and the African Arachnid Database (Dippenaar-Schoeman *et al.,* 2015). The first survey of spiders in Botswana was by Russell-Smith (1981) who sampled using pitfall trapping 87 species from grassland and 84 species from Woodland in the Okavango Delta. It was followed by the Spider Fauna of Botswana Project by Eagle (1984) who collected spiders for a week at Xaxaba in the Okavango Delta. Dippenaar-Schoeman & Kassimatis (2002) participated in the Environmental monitoring of Tsetse aerial spraying in 2001 at the Harry Oppenheimer Okavango Research Centre. The Okavango Delta was also visited by several universities and museum personnel and the spiders collected are included in taxonomic revisions. More recently, Haddad & Mavrusik (2019) revised the distribution information on some of the first spiders collected in Botswana by Leonhard Schultze during his expedition from 1903-1905. This study also highlighted the necessity of correct distribution information when compiling national faunistic lists. Due to spiders colonising almost all habitats, (from sub-soil to mountains and even intertidal zones), it is likely that this adaptability will result in high levels of species diversity in wetlands (Marc *et al*. 1999) like the Delta. With specific species information available, the possibility of utilising spiders as indicators increases, and improving the knowledge pertaining to the diversity in the Okavango Delta will inevitably assist larger-scale understanding of patterns of diversity (Platnick, 1991).

Another popular topic for arthropod-related research in Botswana is related to entomophagy, highlighted through works by Moreki *et al*. (2012), Obopile & Seeletso (2013) and Moreki (2014), showcasing a decline in entomophagy in younger generations of Botswana's citizens. These studies, although identifying high numbers of edible species (27 edible species by Obopile & Seeletso (2013)), mostly focused on lepidopteran caterpillars and other large insects. Recently Mazebedi & Hesselberg (2020) described the diversity and distribution of terrestrial macro-invertebrates of Gcwihaba cave in northwest Botswana. Masunga *et al.* (2006) assessed the impacts of fungi and arthropods on elephant dung decomposition and Moeng *et al.* (2018) assessed the diversity and distribution of stem-borers of the order Lepidoptera, finding a number of new observations for stemborers in Botswana and as well as nine previously undescribed species. In addition, Boyes & Perrin (2009) explored the feeding ecology of Meyer's Parrot (*Poicephalus meyeri*) and found four arthropods that had previously been unknown within the diets of these parrots.

A study on the impacts of tsetse fly spraying on a range of aquatic and terrestrial invertebrates in the Okavango Delta using six sampling methods assessed the changes in invertebrate communities over the 2002 spray cycles of deltamethrin (Perkins and Ramberg, 2004). Working on a substantial number of taxa (26 higher taxa, but focusing on six. namely beetles, flies, ants, hemipterans, wasps and spiders), the study sampled over 100,000 individual invertebrate specimens. During their assessment, they identified 35 ant morphospecies, 23 morphospecies of spiders, 117 morphospecies of flies, and 59 morphospecies of hemipterans. Results showed clear negative impacts of tsetse fly spraying on both aquatic and terrestrial communities, with terrestrial invertebrate abundance being reduced by 60-70% (Perkins & Ramberg, 2004). Although worrying, the authors suggested that overall abundance is expected to return to natural levels shortly after spraying. This study remains one of the most comprehensive studies completed on terrestrial invertebrate communities to date in the Okavango Delta, and once again highlights the exceptional diversity of terrestrial invertebrates within this wetland.

Dangerfield (1997) also found significant results regarding the seasonality and abundance of soil fauna in woodland habitats in Botswana, finding more than double the abundance of soil fauna in the wet season than in the dry season. It is important to note that the variability in abundance and species composition is suggested to be driven by a combination of various biotic and abiotic factors, and that is difficult to determine which factors are most influential (Dangerfield, 1997). Most critically, Dangerfield (1997) established that diversity of soil fauna can vary significantly between location, habitat, season and the spatial component of these variations.

Literature regarding the wasps of Botswana, and specifically the Okavango Delta, are scarce. The cave-based study of Mazebedi and Hesselberg (2020) saw limited insight into the ecology of the cave wasps (Sphecidae) studied. Besides species checklists compiled by museums and research institutes, as well as observations made of wasp species during unrelated studies, the absence of wasp-focused literature within the Okavango Delta is concerning.

Ants have received some attention as part of larger studies. Moreki (2014) mentioned ants as one of the groups being consumed by citizens of Botswana, while McCarthy and Ellery (1998) noticed several species of ant colonies occupying islands in the Delta, while studying the role of biota in the initiation and growth of islands. Dalerum *et al.* (2019) explored the impact of distance to perennial water on ant communities in the Mopane woodlands of northern Botswana and found higher ant abundance richness and diversity during the wet season, with strong seasonal influences on the effects of distance to water. Their results suggest that small-scale environmental variations that are not linked to water access, also have a strong effect on abundance, richness and diversity.

No dedicated studies have focussed on Collembola within the Okavango Delta, and although some single species that have been described, little is known about their true diversity in the country. Russel-Smith (1981) assessed the seasonal activity of ground-living spiders in woodlands and grasslands of the Delta. Eighty-four spider species were collected in the woodland habitat, and 87 in the grassland habitat. This included a lower overall number of spiders trapped in the woodland habitat (33% fewer than grasslands), but with the communities in this habitat type being more consistent throughout the year than those of grasslands (Russel-Smith, 1981). Gnaphosidae, Lycosidae and Salticidae were most abundant in the woodlands, accounting for 84.1% of all specimens caught (Russel-Smith, 1981). Although total species richness was similar between the two habitat types, species composition was significantly different (Russel-Smith, 1981).

From the limited available literature on arthropods of the Okavango Delta, it is clear that ants, springtails and wasps are underrepresented in the process of understanding the complex systems and array of habitats that make up the Okavango Delta, while spiders have received much more attention as a group. This highlights the need for dedicated research on a wider range of invertebrate groups, to document the species present, and enable long-term monitoring of the effects of anthropogenic disturbances to ensure adequate protection and management of the invertebrate species and their associated ecosystem services within this world heritage site.

Aims and objectives

Given the fragmented knowledge of terrestrial arthropods within Botswana, and the Okavango Delta specifically, the study aimed to compare arthropod communities within and between ongoing disturbance regimes, using a multi-taxon approach. Specifically, through the exploration of these communities, this study aimed to:

1. Compare the diversity and abundance of four terrestrial arthropod groups (ants, wasps, springtails and spiders) between burnt and grazed sites.
2. Investigate whether burning or grazing has differential impacts on arthropod communities and whether identified impacts can be classified as positive or negative.
3. Provide a starting-point dataset that can be used to monitor the impact of disturbances on arthropod communities in the Okavango Delta comparatively into the future.
4. Generate starting-point species inventories for four taxa (ants, wasps, springtails and spiders) in this region
5. Compile an updated species list of spiders (Araneae) of the Okavango Delta, Botswana.

Through these objectives, this study aimed to provide starting point data for continued research of terrestrial arthropod species diversity within the Okavango Delta and to improve understanding of their community dynamics, as well as their association with critical ecosystem services in a World Heritage Site.

References

Alonso, L.E., Nordin, L.A. eds., 2004. *A rapid biological assessment of the aquatic ecosystems of the Okavango Delta, Botswana: high water survey*. Conservation International. Washington DC.

An, J., Chen, W., 2011. Economic value of insect pollination for fruits and vegetables in China. *Acta Entomologica Sinica* 54, 443–450.

Andersen, A.N., Majer, J.D., 2004. Ants show the way down under: invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment* 2, 291–298.

Appleton, C.C., Curtis, B.A., Alonso, L.E., Kipping, J., 2003. Freshwater invertebrates of the Okavango Delta, Botswana. *RAP* 27, 58–69.

Archibald, S., Scholes, R.J., Roy, D.P., Roberts, G., Boschetti, L., 2010. Southern African fire regimes as revealed by remote sensing. *International Journal of Wildland Fire* 19, 861–878.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51–57.

Barratt, B.I.P., Ferguson, C.M., Barton, D.M., Johnstone, P.D., 2009. Impact of fire on tussock grassland invertebrate populations. *Science for Conservation* 291, 75.

Bayley, P.B., 1995. Understanding large river: floodplain ecosystems. *BioScience* 45, 153–158.

Bebber, D.P., Holmes, T., Gurr, S.J., 2014a. The global spread of crop pests and pathogens. *Global Ecology and Biogeography* 23, 1398–1407.

Bebber, D.P., Holmes, T., Smith, D., Gurr, S.J., 2014b. Economic and physical determinants of the global distributions of crop pests and pathogens. *New Phytologist* 202, 901–910.

Bernard, T., Moetapele, N., 2005. Desiccation of the Gomoti River: Biophysical process and indigenous resource management in Northern Botswana. *Journal of Arid Environments* 63, 256–283.

Bisby, F.A., Roskov, Y., Orrell, T.M., Nicolson, D., Paglinawan, L.E., Bailly, N., Kirk, P.M., Bourgoin, T., Baillargeon, G., Ouvrard, D., 2010. Species 2000 and ITIS Catalogue of Life. *Annual Checklist.* Digital resource at http://www. catalogueoflife. org/annu al-checklist/2010.

Bisevac, L., Majer, J.D., 1999. Comparative study of ant communities of rehabilitated mineral sand mines and heathland, Western Australia*. Restoration Ecology* 7, 117–126.

Boyes, R.S., Perrin, M.R., 2009. The feeding ecology of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana. *Ostrich* 80, 153–164.

Brown, D.S., Curtis, B.A., Bethune, S., Appleton, C.C., 1992. Freshwater snails of East Caprivi and the lower Okavango River basin in Namibia and Botswana. *Hydrobiologia* 246, 9–40.

Brown, G.W., Dorrough, J.W., Ramsey, D.S., 2011. Landscape and local influences on patterns of reptile occurrence in grazed temperate woodlands of southern Australia. *Landscape and Urban Planning* 103, 277–288.

Buckley, L.B., Kingsolver, J.G., 2021. Evolution of thermal sensitivity in changing and variable climates. *Annual Review of Ecology, Evolution, and Systematics* 52, 563–586.

Bussan, S.K., 2022. Can cattle grazing benefit grassland butterflies? *Journal of Insect Conservation* 26, 359–-374.

Buxton, M., Lebani, K., Nyamukondiwa, C., Wasserman, R.J., 2019. First record of *Aedes* (*Stegomyia*) *aegypti* (Linnaeus, 1762) (Diptera: Culicidae) in Botswana. *Bioinvasions Records* 8, 551–557.

Cardoso, P., Erwin, T.L., Borges, P.A.V., New, T.R., 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* 144, 2647–2655.

Cassidy, L., 2007. Mapping the annual area burned in the wetlands of the Okavango panhandle using a hierarchical classification approach. *Wetlands Ecology and Management* 15, 253–268.

Cassidy, L., 2003. Anthropogenic burning in the Okavango panhandle of Botswana: livelihoods and spatial dimensions (PhD Thesis). University of Florida Gainesville, Florida, USA.

Cassidy, L., Perkins, J., Bradley, J., 2022. Too much, too late: fires and reactive wildfire management in northern Botswana’s forests and woodland savannas. *African Journal of Range and Forage Science* 39, 160–174.

Clarke, J.L., Welch, D., Gordon, I.J., 1995. The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep. I. The location of animals on grass/heather mosaics. *Journal of Applied Ecology* 166–176.

Compton, S.G., Van Noort, S., 1992. Southern African fig wasps (Hymenoptera: Chalcidoidea): resource utilization and host relationships. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 95, 423–435.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.

Corman, J.R., Bertolet, B.L., Casson, N.J., Sebestyen, S.D., Kolka, R.K., Stanley, E.H., 2018. Nitrogen and phosphorus loads to temperate seepage lakes associated with allochthonous dissolved organic carbon loads. *Geophysical Research Letters* 45, 5481–5490.

Creel, S., Winnie Jr, J.A., 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour* 69, 1181–1189.

Crews, K., Neuenschwander, A., 2007. Remote Sensing Time Series Analysis of Coupled Impacts of Disturbance and Management on Landscape Carbon Storage in the Okavango Delta, Botswana, in: AGU Fall Meeting Abstracts. pp. B23C-1492.

Crist, T.O., Veech, J.A., Gering, J.C., Summerville, K.S., 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity. *The American Naturalist* 162, 734–743.

Crossley, D.A., 1977. The roles of terrestrial saprophagous arthropods in forest soils: current status of concepts. In: Stork, N.E., Adis, J., Didham, R.K. (Eds.), *The Role of Arthropods in Forest Ecosystems*, pp. 49–56. Springer, Berlin Heidelberg.

Dale, V.H., Polasky, S., 2007. Measures of the effects of agricultural practices on ecosystem services. *Ecological Economics* 64, 286–296.

Dalerum, F., Retief, T.A., Havemann, C.P., Chimimba, C.T., Janse van Rensburg, B., 2019. The influence of distance to perennial surface water on ant communities in Mopane woodlands, northern Botswana. *Ecology and Evolution* 9, 154–165.

Dallas, H., Mosepele, B., 2020. Spatial variability of aquatic macroinvertebrate assemblages in the Okavango Delta, Botswana: considerations for developing a rapid bioassessment tool. *African Journal of Aquatic Science* 45, 350–363.

Dallas, H.F., Mosepele, B., 2007. A preliminary survey and analysis of the spatial distribution of aquatic invertebrates in the Okavango Delta, Botswana. *African Journal of Aquatic Science* 32, 1–11.

Dangerfield, J.M., 1997. Abundance and diversity of soil macrofauna in northern Botswana. *Journal of Tropical Ecology* 13, 527–538.

Dangerfield, J.M., McCarthy, T.S., Ellery, W.N., 1998. The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology* 14, 507–520.

de Oliveira Roque, F., Menezes, J.F., Northfield, T., Ochoa-Quintero, J.M., Campbell, M.J., Laurance, W.F., 2018. Warning signals of biodiversity collapse across gradients of tropical forest loss. *Scientific Reports* 8, 1–7.

Dennis, P., 2003. Sensitivity of upland arthropod diversity to livestock grazing, vegetation structure and landform. *Food, Agriculture and Environment* 1, 301–307.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* 105, 6668–6672.

Dippenaar-Schoeman, A.S., Kassimatis, E., 2002. In: Environmental monitoring of Tsetse aerial spraying 2001. Perkins, J and Ramberg, L. (ed). Harry Oppenheimer Okavango Research Centre, University of Botswana, Maun. *Arachnida: Araneae*, 113-131.

Dippenaar-Schoeman, A.S., Lyle, R., Marais, P., Haddad, C.R., Foord, S.H. Lotz, L.N., 2015. South African National Survey of Arachnida (SANSA): review of current knowledge, constraints and future needs for documenting spider diversity (Arachnida: Araneae). *Transactions of the Royal Society of South Africa*, *70*(3), 245–275.

Eggleton, P., 2020. The state of the world's insects. *Annual Review of Environmental Resources*, 45, 61–82.

Ellery, W.N., Tacheba, B., 2003. Floristic diversity of the Okavango Delta, Botswana. A Rapid Biological Assessment of the Aquatic Ecosystems of the Okavango Delta, Botswana: High Water Survey. *RAP-Bulletin of Biological Assessment* 25, 69–96.

Engel, M.S., Grimaldi, D.A., Krishna, K., 2009. Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. *American Museum Novitates*, 3650, 1–27.

Epele, L.B., Miserendino, M.L., 2015. Environmental quality and aquatic invertebrate metrics relationships at Patagonian wetlands subjected to livestock grazing pressures. *PLoS One* 10, e0137873.

Ficetola, G.F., Marta, S., Guerrieri, A., Gobbi, M., Ambrosini, R., Fontaneto, D., Zerboni, A., Poulenard, J., Caccianiga, M., Thuiller, W., 2021. Dynamics of ecological communities following current retreat of glaciers. *Annual Review of Ecology, Evolution, and Systematics* 52, 405–426.

Figueiredo, E., Smith, G.F., César, J., 2009. The flora of Angola: first record of diversity and endemism. *Taxon* 58, 233–236.

Forrest, J.R., 2016. Complex responses of insect phenology to climate change*. Current Opinion in Insect Science* 17, 49–54.

Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D., Roy, D.B., 2014. Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology* 51, 949–957.

Frost, P., 1996. The ecology of miombo woodlands. In: Campbell, B. (Ed.), *The miombo in transition: woodlands and welfare in Africa*, pp. 11–57. Centre for International Forestry Research: Bogor, Indonesia.

Fynn, R.W., Bonyongo, M.C., 2011. Functional conservation areas and the future of Africa's wildlife. *African Journal of Ecology 49*, 175–188.

Fynn, R.W.S., Murray-Hudson, M., Dhliwayo, M., Scholte, P., 2015. African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology Management* 23, 559–581.

García-Robledo, C., Baer, C.S., 2021. Positive genetic covariance and limited thermal tolerance constrain tropical insect responses to global warming. *Journal of Evolutionary Biology* 34, 1432–1446.

Gerlach, J., Samways, M., Pryke, J., 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation* 17, 831–850.

Gumbricht, T., McCarthy, J., McCarthy, T.S., 2004. Channels, wetlands and islands in the Okavango Delta, Botswana, and their relation to hydrological and sedimentological processes. Earth Surface Processes and Landforms: *The Journal of the British Geomorphological Research Group* 29, 15–29.

Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242, 344-247.

Haddad, C.R., Mavrusik, Y.M., 2019. Clarifying the taxonomic status and distributions of the spider species collected during the Leonhard Schultze expeditions in western and central southern Africa (Arachnida: Araneae). *Zootaxa* 4608, 451–483.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T.,Goulson, D., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE 12*: e0185809.

Hanley, N., Breeze, T.D., Ellis, C., Goulson, D., 2015. Measuring the economic value of pollination services: Principles, evidence and knowledge gaps. *Ecosystem Services* 14, 124–132.

Harris, G., Thirgood, S., Hopcraft, J.G.C., Cromsigt, J.P., Berger, J., 2009. Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research* 7, 55–76.

Harvey, J.A., Heinen, R., Gols, R., Thakur, M.P., 2020. Climate change-mediated temperature extremes and insects: From outbreaks to breakdowns. *Global Change Biology* 26, 6685–6701.

Heinl, M., Frost, P., Vanderpost, C., Sliva, J., 2007. Fire activity on drylands and floodplains in the southern Okavango Delta, Botswana. *Journal of Arid Environments* 68, 77–87.

Heinl, M., Neuenschwander, A., Sliva, J., Vanderpost, C., 2006. Interactions between fire and flooding in a southern African floodplain system (Okavango Delta, Botswana). *Landscape Ecology* 21, 699–709.

Heinl, M., Sliva, J., Tacheba, B., Bredenkamp, G.J., 2004. Vegetation changes after single fire-events in the Okavango Delta wetland, Botswana. *South African Journal of Botany* 70, 695–704.

Heinl, M., Sliva, J., Tacheba, B., Murray-Hudson, M., 2008. The relevance of fire frequency for the floodplain vegetation of the Okavango Delta, Botswana. *African Journal of Ecology* 46, 350–358.

Hickling, R., Roy, D.B., Hill, J.K., Thomas, C.D., 2005. A northward shift of range margins in British Odonata. *Global Change Biology* 11, 502–506.

Hopcraft, J.G.C., Olff, H., Sinclair, A.R., 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology and Evolution* 25, 119–128.

Horvath, R., Magura, T., Szinetar, C., Tothmeresz, B., 2009. Spiders are not less diverse in small and isolated grasslands, but less diverse in overgrazed grasslands: A field study (East Hungary, Nyírség). *Agriculture, Ecosystems and Environment* 130, 16–22.

Humphries, M.S., McCarthy, T.S., Cooper, G.R.J., Stewart, R.A., Stewart, R.D., 2014. The role of airborne dust in the growth of tree islands in the Okavango Delta, Botswana. *Geomorphology* 206, 307-317.

Huntley, B.J., Matos, E.M., 1994. Botanical diversity and its conservation in Angola. *Strelitzia* 1, 53–74.

Illius, A.W., O'Connor, T.G., 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications*, 9, 798–813.

Jain, P., Castellanos-Acuna, D., Coogan, S.C.P., Abatzoglou, J.T., Flannigan, M.D., 2022. Observed increases in extreme fire weather driven by atmospheric humidity and temperature. *Nature Climate Change* 12, 63– 70

Janion-Scheepers, C., Bengtsson, J., Leinaas, H.P., Deharveng, L., Chown, S.L., 2016. The response of springtails to fire in the fynbos of the Western Cape, South Africa. *Applied Soil Ecology* 108, 165–175.

Joubert, L., Pryke, J.S. and Samways, M.J., 2016. Positive effects of burning and cattle grazing on grasshopper diversity. *Insect Conservation and Diversity* 9, 290-301.

Jouquet, P., Traoré, S., Choosai, C., Hartmann, C., Bignell, D., 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology* 47, 215–222.

Kgori, P.M., Modo, S., Torr, S.J., 2006. The use of aerial spraying to eliminate tsetse from the Okavango Delta of Botswana. *Acta Tropica* 99, 184–199.

Kipping, J., 2011. The dragonflies and damselflies of Botswana: an annotated checklist with notes on distribution, phenology, habitats and Red List status of the species (Insecta: Odonata). *International Journal of Odonatology*, 14, 335–359.

Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* 274, 303–313.

Klink, R., Plas, F., Noordwijk, C., WallisDeVries, M., & Olff, H., 2014. Effects of large herbivores on grassland arthropod diversity. *Biological Reviews of the Cambridge Philosophical Society* 90, 347–366.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F., Sanjayan, M.A., 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology*, 7, 796–808.

Laiho, R., 2006. Decomposition in peatlands: Reconciling seemingly contrasting results on the impacts of lowered water levels. *Soil Biology and Biochemistry* 38, 2011–2024.

Lehane, M.J., Lehane, M.M., Lehane, M.J., 2005. *The biology of blood-sucking in insects*. Cambridge University Press, Cambridge.

Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. *Bioscience* 56, 311–323.

Lounibos, L.P. 2002. Invasions by insect vectors of human disease. Annual Review of Entomology 47, 233–266.

Lyczkowski, E., 2006. The effects of the 2006 spraying of Deltamethrin for tsetse control on aquatic macro-invertebrates in the Kwando/Linyanti river system, Botswana. *Independent Study Project (ISP) Collection*. [accessed 8 February 2023].

Marshall, K.E., Gotthard, K., Williams, C.M., 2020. Evolutionary impacts of winter climate change on insects. *Current Opinion in Insect Science* 41, 54–62.

Mavasa, R., Yekwayo, I., Mwabvu, T., Tsvuura, Z., 2023. Response of ants, beetles and spiders to disturbance varies among taxa in a South African savannah biome. *African Entomology 31*, 1-11.

Masunga, G.S., Andresen, Ø., Taylor, J.E., Dhillion, S.S., 2006. Elephant dung decomposition and coprophilous fungi in two habitats of semi-arid Botswana. *Mycological Research* 110, 1214–1226.

Mazebedi, R., Hesselberg, T., 2020. A preliminary survey of the abundance, diversity and distribution of terrestrial macroinvertebrates of Gcwihaba cave, northwest Botswana. *Subterranean Biology* 35, 49– 63.

McCarthy, T.S., Ellery, W.N., 1998. The Okavango delta. *Transactions of the Royal Society of South Africa* 53, 157–182.

McGeoch, M.A., 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews*, *73*, 181-201.

McGeoch, M.A., Sithole, H., Samways, M.J., Simaika, J.P., Pryke, J.S., Picker, M., Uys, C., Armstrong, A.J., Dippenaar-Schoeman, A.S., Engelbrecht, I.A. and Braschler, B., 2011. Conservation and monitoring of invertebrates in terrestrial protected areas. *Koedoe* 53, 131–143.

Mendelsohn, J., El Obeid, S., 2004. *Okavango River: The flow of a lifeline*. Struik, Cape Town.

Moeng, E., Mutamiswa, R., Conlong, D.E., Assefa, Y., Le Ru, B.P., Goftishu, M., Nyamukondiwa, C., 2018. Diversity and distribution of lepidopteran stemborer species and their host plants in Botswana. *Arthropod-Plant Interactions* 12, 733–749.

Moir, M.L., Vesk, P.A., Brennan, K.E.C., Keith, D.A., Hughes, L., McCarthy, M.A 2010, 'Restricciones actuales y directrices futuras en la estimación de la coextinción' (*Current Constraints and*

Future Directions in Estimating Coextinction), *Conservation Biology*, 24, 682-690.

Moreki, J., 2014. A study of entomophagy in Mogonono in Kweneng District, Botswana. *Online International Interdisciplinary Research Journal* 4: 70-79.

Moreki, J.C., Tiroesele, B., Chiripasi, S.C., 2012. Prospects of utilizing insects as alternative sources of protein in poultry diets in Botswana: a review. *Journal of Animal Science Advances* 2, 649–658.

Morse, D.H., 1971. The insectivorous bird as an adaptive strategy. *Annual Review of Ecology and Systematics 2,* 177–200.

Naeem, S., Chazdon, R., Duffy, J.E., Prager, C., Worm, B., 2016. Biodiversity and human well-being: an essential link for sustainable development. *Proceedings of the Royal Society B: Biological Sciences* 283, 20162091

National Geographic Okavango Wilderness Project, 2017. *Initial Findings from Exploration of the Upper Catchments of the Cuito, Cuanavale, and Cuando Rivers*, May 2015 to December 2016

Nelson, E.H., Matthews, C.E., Rosenheim, J.A., 2004. Predators reduce prey population growth by inducing changes in prey behavior. *Ecology*, 85, 1853–1858.

Nicholson, S.E., 2000. The nature of rainfall variability over Africa on time scales of decades to millenia. *Global and Planetary Change* 26, 137–158.

Nimmo, D.G., Carthey, A.J., Jolly, C.J., Blumstein, D.T., 2021. Welcome to the Pyrocene: Animal survival in the age of megafire. *Global Change Biology* 27, 5684–5693.

Noriega, J.A., Hortal, J., Azcárate, F.M., Berg, M.P., Bonada, N., Briones, M.J., Del Toro, I., Goulson, D., Ibanez, S., Landis, D.A., 2018. Research trends in ecosystem services provided by insects. *Basic and Applied Ecology* 26, 8–23.

Obopile, M., Seeletso, T.G., 2013. Eat or not eat: an analysis of the status of entomophagy in Botswana. *Food Security* 5, 817–824.

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326.

Oom, S.P., Hester, A.J., Elston, D.A., Legg, C.J., 2002. Spatial interaction models: from human geography to plant-herhivore interactions. *Oikos* 98, 65–74.

Owen-Smith, N., 2008. Effects of Temporal Variability in Resources on Foraging Behaviour, in: Prins, H.H.T., Van Langevelde, F. (Eds.), *Resource Ecology*, Wageningen UR Frontis Series. Springer Netherlands, Dordrecht, 159–181.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37, 637–669.

Perkins, J.S., Ramberg, L., 2004. *Environmental Monitoring of Tsetse Fly Spraying Impacts in the*

Okavango Delta-2002. Harry Oppenheimer Okavango Research Centre, University of Botswana.

Pinhey, E., 1968. Check List of the Butterflies (Lepidoptera Rhapalocera) of Botswana: Part 1. *Botswana Notes and Records* 1, 85–92.

Pinhey, E., 1971. Check List of the Butterflies (Lepidoptera Rhopalocera) of Botswana; Part 2. *Botswana Notes and Records* 3, 148–152.

Pinhey, E., 1974. Check list of the Butterflies (Lepidoptera Rhopalocera) of Botswana: Part 3 (with illustrations). *Botswana Notes and Records* 6, 197–214.

Pinhey, E., 1976. Checklist of the Butterflies (Lepidoptera Rhopalocera). *Botswana Notes and Records* 8, 269–288.

Platnick, N.I., 1991. Patterns of biodiversity: tropical vs temperate. *Journal of Natural History*, 25, 1083-1088.

Pröpper, M., Gröngröft, A., Finckh, M., Stirn, S., De Cauwer, V. eds., 2015. *The Future Okavango: Findings, Scenarios and Recommendations for Action: Research Project Final Synthesis Report 2010-2015*. University of Hamburg-Biocentre Klein Flottbek.

Pryke, J.S., Samways, M.J., 2012a. Differential resilience of invertebrates to fire. *Austral Ecology* 37, 460–469.

Pryke, J.S., Samways, M.J., 2012b. Importance of using many taxa and having adequate controls for monitoring impacts of fire for arthropod conservation. *Journal of Insect Conservation* 16, 177–185.

Pryke J.S., Roets F., Samways M.J., 2016. Wild herbivore grazing enhances insect diversity over livestock grazing in an African Grassland system*. PLoS ONE 11, e0164198*

Ramberg, L., Hancock, P., Lindholm, M., Meyer, T., Ringrose, S., Sliva, J., Van As, J., Vander Post, C., 2006a. Species diversity of the Okavango delta, Botswana. *Aquatic Sciences* 68, 310–337.

Ramberg, L., Wolski, P., Krah, M., 2006b. Water balance and infiltration in a seasonal floodplain in the Okavango Delta, Botswana. *Wetlands* 26, 677–690.

Reid, W., Mooney, H., Cropper, A., Capistrano, D., Carpenter, S., Chopra, K., Dasgupta, P., Dietz, T., Duraiappah, A., Hassan, R., Kasperson, R., Leemans, R., May, R., McMichael, A., Pingali, P., Samper, C., Scholes, R., Watson, T.R., Zakri, A.H., and Zurek, M., 2005. *Millennium Ecosystem Assessment Synthesis Report*. Island Press, Washington, DC.

Ringrose, S., Lesolle, D., Boshoma, T., Gopolang, B., Vanderpost, C., Matheson, W., 1999. An analysis of vegetation cover components in relation to climatic trends along the Botswana Kalahari Transect. *Botswana Notes and Records* 31, 33-52

Robbel, H.W., Child, G., 1976. *Notes on the ecology of the Moremi Wildlife Reserve*. Department of Wildlife, National Parks and Tourism.

Rodgers, W., 1973. The effect of fire and elephant on the ecology of *Terminalia spinosa* Engl. Combretaceae). *Miombo Research Centre* 1, 20.

Rosenzweig, M.L., 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge.

Russell-Smith, A., 1981. Seasonal activity and diversity of ground-living spiders in two African savanna habitats. *Bulletin of the British Arachnological Society* 5, 145–154.

Salimi, S., Almuktar, S.A.A.A.N., Scholz, M., 2021. Impact of climate change on wetland ecosystems: A critical review of experimental wetlands. *Journal of Environmental Management* 286, 112160.

Salvarina, I., Gravier, D., Rothhaupt, K.-O., 2018. Seasonal bat activity related to insect emergence at three temperate lakes. *Ecology and Evolution* 8, 3738–3750.

Samways, M.J., 1994. Insect Conservation Biology. *Conservation Biology*. Springer Science and Business Media.

Samways M.J., Kreuzinger K., 2001. Vegetation, ungulate and grasshopper interactions inside vs. outside an African savanna game park. *Biodiversity Conservation* 10, 1963–1981.

Samways, M.J., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., 2020. Solutions for humanity on how to conserve insects. *Biological Conservation* 242, 108427.

Schmutzer, A.C., Gray, M.J., Burton, E.C., Miller, D.L., 2008. Impacts of cattle on amphibian larvae and the aquatic environment. *Freshwater Biology* 53, 2613–2625.

Schoch, P., Binkley, D., 1986. Prescribed burning increased nitrogen availability in a mature loblolly pine stand. *Forest Ecology and Management* 14, 13–22.

Schuurman, G., 2005. Decomposition rates and termite assemblage composition in semiarid Africa. *Ecology* 86, 1236–1249.

Schreinemachers, P., Tipraqsa, P., 2012. Agricultural pesticides and land use intensification in high-, middle- and low-income countries. *Food Policy* 37, 616-626.

Sharrow, S.H., 2007. Soil compaction by grazing livestock in silvopastures as evidenced by changes in soil physical properties. *Agroforestry Systems* 71, 215–223.

Smith C.C., 1940. The effect of overgrazing and erosion upon the biota of the mixed-grass prairie of Oklahoma. *Ecology* 21, 381–397.

Smith, M.D., Knapp, A.K., Collins, S.L., Burkepile, D.E., Kirkman, K.P., Koerner, S.E., Thompson, D.I., Blair, J.M., Burns, C.E., Eby, S., 2016. Shared drivers but divergent ecological responses: Insights from long-term experiments in mesic savanna grasslands. *Bioscience* 66, 666–682.

Spooner, P., Lunt, I., Robinson, W., 2002. Is fencing enough? The short-term effects of stock exclusion in remnant grassy woodlands in southern NSW. *Ecological Management and Restoration* 3, 117–126.

Stejskal, V., Hubert, J., Aulicky, R., Kucerova, Z., 2015. Overview of present and past and pest-associated risks in stored food and feed products: European perspective. *Journal of Stored Products Research* 64, 122–132.

Stewart, R.I.A., Dossena, M., Bohan, D.A., Jeppesen, E., Kordas, R.L., Ledger, M.E., Meerhoff, M., Moss, B., Mulder, C., Shurin, J.B., Suttle, B., Thompson, R., Trimmer, M., Woodward, G., 2013. *Chapter Two - Mesocosm Experiments as a Tool for Ecological Climate-Change Research*, in: Woodward, G., O'Gorman, E.J. (Eds.), Advances in Ecological Research, Global Change in Multispecies Systems: Part 3. Academic Press, 71–181

Stork, N.E., 2018. How many species of insects and other terrestrial arthropods are there on Earth. *Annual Review of Entomology* 63, 31–45.

Stork, N.E., Eggleton, P., 1992. Invertebrates as determinants and indicators of soil quality. *American Journal of Alternative Agriculture*, *7*, 38-47.

Tang, Z.C., Kozlowski, T.T., 1982. Some physiological and growth responses of *Betula papyrifera* seedlings to flooding. *Physiologia Plantarum* 55, 415–420.

Thornton, P.K., 2010. Livestock production: recent trends, future prospects. *Philosophical Transactions of the Royal Society*: *Biological Sciences* 365, 2853–2867.

Tougeron, K., Abram, P.K., 2017. An ecological perspective on sleep disruption. *The American Naturalist* 190, E55–E66.

Tuma, J., Eggleton, P., Fayle, T.M., 2020. Ant-termite interactions: an important but under-explored ecological linkage. *Biological Reviews* 95, 555–572.

Tumlinson, J.H., Lewis, W.J., Vet, L.E., 1993. How parasitic wasps find their hosts. *Scientific American* 268, 100–106.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11, 1351–1363.

Ulyshen, M.D., Wagner, T.L., 2013. Quantifying arthropod contributions to wood decay. *Methods in Ecology and Evolution* 4, 345–352.

van Straalen, N.M., Krivolutsky, D.A., 1996. Bioindicator systems for soil pollution. *Springe*r Science and Business Media, Berlin.

Van Wilgen, B.W., Govender, N., Biggs, H.C., 2007. The contribution of fire research to fire management: a critical review of a long-term experiment in the Kruger National Park, South Africa. *International Journal of Wildland Fire* 16, 519–530.

Wan, S., Hui, D., Luo, Y., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecological Applications* 11, 1349–1365.

Wang, Z., Zeng, J., Meng, W., Lohman, D.J., Pierce, N.E., 2021. Out of sight, out of mind: public and research interest in insects is negatively correlated with their conservation status. *Insect Conservation and Diversity* 14, 700–708.

Ward, P.S., 2007. Phylogeny, classification, and species-level taxonomy of ants (Hymenoptera: Formicidae). *Zootaxa* 1668, 549–563.

Weise, F.J., Fynn, R.W.S., Stein, A.B., Tomeletso, M., Somers, M.J., Périquet, S., 2019. Seasonal selection of key resources by cattle in a mixed savannah-wetland ecosystem increases the potential for conflict with lions. *Biological Conservation* 237, 253–266.

Whelan, R.J., 1995. *The ecology of fire.* Cambridge University Press, Cambridge.

Wilkerson M.L., Roche L.M., Young T.P., 2013. Indirect effects of domestic and wild herbivores on butterflies in an African savanna. *Ecology and Evolution* 3, 3672–3682.

Willig, M.R., Kaufman, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology*, *Evolution, and Systematics* 34, 273-309.

Yadav, S., Stow, A.J., Dudaniec, R.Y., 2021. Microgeographical adaptation corresponds to elevational distributions of congeneric montane grasshoppers. *Molecular Ecology* 30, 481–498.

Yadav, S., Stow, A.J., Harris, R.M., Dudaniec, R.Y., 2018. Morphological variation tracks environmental gradients in an agricultural pest, Phaulacridium vittatum (Orthoptera: Acrididae). *Journal of Insect Science* 18, 13.

Zamin, T.J., Baillie, J.E., Miller, R.M., Rodríguez, J.P., Ardid, A.N.A., Collen, B.E.N., 2010. National red listing beyond the 2010 target. *Conservation Biology* 24, 1012–1020.

Zhu H, Wang D, Wang L, Bai Y, Fang J, Liu J., 2012. The effects of large herbivore grazing on meadow steppe plant and insect diversity. *Journal of Applied Ecology* 49, 1075–1083.

Chapter 2: Flame and Fodder: How fire and grazing shape arthropod communities in the Okavango Delta.

Abstract

Invertebrates are relatively understudied compared to their vertebrate counterparts, globally and within the southern African region. This is especially true for developing countries, due to accessibility, costs associated with remote fieldwork and lack of taxonomic expertise. Nevertheless, southern Africa is highly diverse in fauna and flora, and many species still are undescribed in many of the countries in this region. In Botswana, the Okavango Delta is an exceptional biological system. At the core of this critical hydrological system lie aquatic and terrestrial systems and processes that ensure its continued functioning and overall health, with many of these services underpinned by invertebrates, arthropods in particular. Although the aquatic invertebrates are relatively well-studied, the terrestrial arthropods have received limited attention, while undoubtedly also serving some critical regulatory service on the islands within the Delta, and along the edges. Anthropogenic disturbances have become more common and regular along the edges and within the Okavango Delta over the last few decades, and as such, human-induced fire and livestock grazing have increased the pressure on the natural systems in which they occurs. The impacts and effects of these disturbances, varying in their severity and periodicity, are mostly unknown within this specific region, and for this specific habitat. Given the fragmented knowledge of terrestrial arthropods within Botswana, and the Okavango Delta specifically (Araneae excluded; great work has been completed on this group), this study aimed to compare arthropod communities between ongoing disturbance regimes, using a multi-taxon approach. Specifically, this study aimed to: 1) Compare the diversity and abundance of four terrestrial arthropod groups (ants (Formicidae), wasps (Hymenoptera), springtails (Collembola) and spiders (Araneae)) in burnt and grazed sites. 2) Investigate whether burning or grazing have differential impacts on arthropod communities and whether the identified impacts can be classified as positive or negative. 3) Provide a starting point dataset to monitor the impact of disturbances on arthropod communities in the Okavango Delta into the future. 4) Generate starting point species inventories for four taxa (ants, wasps, springtails and spiders) in this region. Using pitfall traps and litter extractions for five-day trapping intervals across two seasons, this study collected 10 169 ants, 525 wasps, 9762 springtails and 523 spiders, totalling 20 979 specimens. The abundance of the four groups was found to be only fractionally higher in the wet season for the pitfall traps, but litter extractions showed large increases in ants, springtails and wasps in the wet season. Twenty-two species of ants were collected using pitfall traps, and 13 species using litter extractions. Twelve and ten species of springtails were collected from pitfall traps and litter extractions respectively. Fifty and 19 species of wasps were collected from pitfalls and litter extractions respectively. Sixty-nine and 32 species of spiders were collected from pitfalls and litter extractions respectively. Ants had the most species and the highest diversity in the grazed sites, while springtail and spider communities were more even in the burnt sites. Each group varied between trapping methods in species richness, evenness and diversity, illustrating the varied responses of arthropod communities to disturbances. Ants and springtails varied significantly between seasons, but not between disturbance types, while wasps and spiders differed significantly between both season and disturbance types. This study created a starting point dataset for arthropod communities and the impact that disturbances have on their community shape and composition. It is recommended that terrestrial arthropod research continue within this World Heritage Site not only to ensure the documentation of the vast diversity of species present here, but also to utilize these species as indicators for ecosystem changes to ensure the continued survival of this wetland and the species that depend on it.

Introduction

Invertebrates constitute a significant portion of global biodiversity, with estimates suggesting that over 70% of all described animal species are invertebrates (IUCN, 2022), and approximately 48% of these are insects (Ower and Roskov *et al.,* 2019; Roskov *et al*., 2019). Insects alone comprise more than 5.5 million species, although only a fraction of them have been described (Stork, 2018). Invertebrates, including arthropods, play vital roles in ecosystem services (Noriega *et al*., 2018), and their reduced species richness can hinder these essential services (Naeem *et al.,* 2016). In particular, insect-based ecosystem services are crucial for natural and agricultural productivity (Klein *et al*., 2007) but, despite their ecological importance, arthropods have been overlooked in global policies and conservation management efforts. Understanding biodiversity patterns in space and time is crucial, as habitat variation and intermediate disturbance levels often contribute to higher species richness (Rosenzweig, 1995). Invertebrates fill critical ecological roles in various ecosystems, making changes in their community's representative of ecosystem health parameters (van Straalen and Krivolutsky, 1996; Gerlach *et al*., 2013;). For example, monitoring arthropods above-and below-ground can effectively assess post-fire impacts and habitat recovery (for example Pryke and Samways, 2012; Janion-Scheepers *et al*., 2016), as they are responsive to environmental changes and cost-effective to study (Samways, 1994; Jumbam *et al.,* 2008).

Several recent studies have highlighted concerning insect declines (Shortall *et al.*, 2009; Hallmann *et al*., 2017; Leather, 2018; Lister and Garcia, 2018; Sanchez-Bayo and Whyckhuys, 2019; Seibold *et al*., 2019), although criticisms regarding methodology and timescales have been raised (Thomas and Hartley, 2019; Eggleton 2020; Outhwaite *et al*., 2020). More specialized research is needed to detect patterns at finer taxonomic levels. Population dynamics of many specific insect groups, such as wasps (Sanchez-Bayo and Whyckhuys, 2019), remain largely unknown and limited population trend studies exist for ants (Sanchez-Bayo and Whyckhuys, 2019) and spiders (Rix *et al.*, 2017). Invertebrates face higher risks of extinction and have documented higher extinction rates and proportions of threatened species compared to other taxa (Stork and Lyal, 1993; Thomas and Morris, 1994; Moir *et al.,* 2010; Cardoso *et al*., 2011). Although emerging trends suggest declines in specific insect groups, the complete picture of global insect decline is yet to be fully understood (Eggleton, 2020), especially considering the limited geographical scope of existing literature, which predominantly focuses on the Northern Hemisphere.

Given the relative scarcity of research on invertebrates in the African context, it is essential to investigate whether similar patterns of decline and their severity occur in this region, and how disturbance shape these communities. This study aims to contribute to filling this knowledge gap and understanding the dynamics of invertebrate populations, specifically focusing on arthropods, in the context of conservation and ecosystem disturbances.

The Okavango Delta, Botswana

Designated as a UNESCO World Heritage site, the Okavango Delta comprises a unique combination of wetland and dryland ecosystems (Gumbricht *et al.*, 2004). The annual rainfall in the region exhibits significant variation, contributing to the hydrological diversity of the aquatic habitats within the wetland system (Ramberg *et al.,* 2006). A variety of vegetation communities occur on the terrestrial islands, and their size can vary substantially (Ellery and Tacheba, 2003). Island formation and growth in the Delta occurs through a combination of processes (Humphries *et al.,* 2014). Channel bed aggradation (gradual accumulation of sediment), channel avulsion (channel migration) and peat oxidation (burning), individually and in combination, are critical processes in the formation of the now-almost 150 000 islands in the Delta (Gumbricht *et al.,* 2004; Humphries *et al.* 2014). The Delta boasts exceptional spatial heterogeneity and the botanical richness of the region is remarkable, with Ellery and Tacheba (2003) having documented over 1,300 plant species, accounting for approximately 65% of Botswana's plant species (Ramberg *et al*., 2006). The Delta is surrounded by various types of dry woodlands, some of which have not experienced flooding historically or have been affected by shifts in flood dynamics (Robbel and Child, 1976). These changes, along with other disturbances, have led to the dominance of mature woody species incapable of withstanding regular flooding (Tang and Kozlowski, 1989).

Despite occupying a relatively small area, the Okavango Delta harbours a diverse array of habitats, high plant species richness, and an abundance of water in the midst of the arid Kalahari Desert, making it an ideal habitat for a wide range of arthropods. However, this biodiversity hotspot faces significant threats from destructive human activities, which are impacting its ecological integrity.

Anthropogenic disturbances

Fire

Anthropogenic disturbances exert diverse effects on landscapes and habitats. Fire is a well-known driver of ecosystem dynamics, both globally and within the Okavango Delta's catchment and southern regions (Archibald *et al.,* 2010). Local communities in Africa have historically used fire for various purposes, including improving grazing quality (Heinl *et al.,* 2007), attracting game, and preparing areas for farming after floods recede (Bernard and Moetapele, 2005; Heinl *et al*., 2007). Despite policy-based efforts to curtail human-initiated fires, fires continue to burn across the Delta (Heinl *et al*., 2006), and policies remain difficult to enforce. Fire occurrence in dryland woodlands is primarily influenced by available fuel load (Heinl *et al.,* 2007), which is reduced by increased canopy cover. The Delta's sandy soils, high herbaceous cover, and intense herbivory result in low fuel loads, leading to predominantly low-intensity surface fires when they do occur (Heinl *et al.,* 2007). Fire frequency in woodlands is also influenced by annual rainfall and proximity to floodplains, which provide water and increases biomass (Heinl *et al.,* 2006). The interplay between burnt and unburnt patches of aquatic and terrestrial vegetation contributes to complex vegetation dynamics (Heinl *et al*., 2006*,* 2008). In addition to natural fires triggered by thunderstorms before the rainy season (Heinl *et al.,* 2007), deliberate fires are ignited by people to enhance grazing capacity, clear vegetation for agricultural expansion, or attract wild game for hunting. Recent assessments have indicated significantly higher annual fire frequencies due to human-induced fires, with extensive fire hotspots burning for a substantial portion of the assessed period (Cassidy *et al*., 2022).

The impacts of fire on biodiversity can vary (Whelan, 1995), with some understanding of these effects documented but impacts remain very species-specific. Few studies in Africa have assessed invertebrate responses to fire using multiple taxa (Pryke and Samways, 2012), and large knowledge gaps exists in this regard within the Okavango Delta. Heinl *et al.* (2004) showed that habitats within the Delta exhibit diverse and sometimes contradictory responses to fire. Landscape-scale fire regimes have been studied intensively in African savannas (for example van Wilgen *et al.,* 2007, Archibald *et al*., 2010; Smith *et al*., 2016), but understanding the influence of altered fire regimes on biodiversity remains incomplete across the region. Research conducted in neighbouring countries provide insights into the possible impact that fire may have on arthropods in Botswana and the Delta, specifically. Joubert *et al.* (2016) assessed the impacts of burning on grasshopper community composition in grasslands in South Africa, and found that fire frequency significantly affected grasshopper species composition, but not species richness. The majority of grasshopper species favoured grasslands that were recently burnt or grazed, but some showed preference to low levels of disturbance, or none at all (Joubert *et al.*, 2016). Similarly, Mavasa *et al.* (2023) studied the response of ants, beetles and spiders to disturbance in the South African savanna biome, and found greater species richness of ants and beetles in disturbed areas than in pristine savanna. Nonetheless, results showed that anthropogenic disturbances cause significant changes in the species composition of surface arthropods, specifically in available leaf litter (Mavasa *et al.,* 2023).

Given that many fires along the Delta's fringes are anthropogenic, understanding the impacts of these practices on terrestrial arthropod communities, is essential.

Livestock grazing

Globally, livestock grazing has been found to have profound impacts on wetlands (Epele and Miserendino, 2015) and other associated ecosystems, from soil degradation and compaction (Sharrow, 2004) to declines in spider (Horvath *et al.,* 2009) and reptile species (Brown *et al.,* 2011). Intensive agriculture has shown to have profound negative effects on soil biodiversity (Tsiafouli *et al.,* 2015). As livestock remains one of the most prominent sources of income and wealth in the remote areas of Africa, cattle numbers are steadily increasing (Thornton, 2010), playing a critical role as commodity both socially and economically (Weise *et al*., 2019). As a result, livestock has also become a valuable conservation tool for landscape managers (Spooner *et al.,* 2002).

Observed impacts of herbivores on arthropod communities are altered by the scale at which impacts are assessed, due partly to the fact that herbivores do not graze evenly across the patch/landscape (Clarke *et al.,* 1995) and partly to the variability in responses of plant communities to grazing (Oom *et al.,* 2002) as a result of variations in climatic, hydrological and geological attributes of a specific system. It is well documented that grazing can be important for maintaining insect diversity in grasslands (Smith, 1940; Zhu *et al.*, 2012), and research suggests that grasshopper diversity shows minimal changes between areas of livestock- and wild ungulate grazing (Samways and Kreuzinger, 2001). This suggests that livestock may fill the role of wild large herbivores in stimulating arthropod diversity through moderate disturbance (Wilkerson *et al.,* 2013; Pryke *et al.,* 2016). Importantly, for other arthropod groups like butterflies, the presence and intensity of grazing may affect species differentially, depending on the landscape management approach (Bussan, 2022). In certain cases arthropods may benefit from grazing, such as grasshoppers increasing in abundance under grazing (Joubert *et al.*, 2016). However, Klink *et al.* (2014) concluded that an increase in arthropod diversity by large herbivore presence is limited by the increase in biotic/abiotic heterogeneity that results, and is in turn dependent on, whether the increase in habitat heterogeneity can compensate for the reduction in resources and direct mortality.

Losing biological wealth, along with critical invertebrate-associated ecosystem services within this wetland system, could lead to potential breakdown of complex trophic interactions (Ebenman and Johnsson, 2005; Frank and Sudarshan, 2023). This chain of events would prove extremely detrimental for the local ecosystems, the local communities and the tourism industry.

The state of invertebrate research in the Okavango Delta

Invertebrate research in the Okavango Delta has primarily focused on aquatic species, charismatic terrestrial species (for example butterflies, Pinhey, 1976), and economically important pests like mosquitoes and tsetse flies (Kgori *et al.,* 2006, Lyczkowski, 2006; Cornel *et al.,* 2018). The AquaRAP of the Okavango Delta (Alonso and Nordin, 2004), provided one of the most extensive assessments of the aquatic macro-invertebrate diversity of the Delta. A critical study assessing the impacts of tsetse fly spraying on aquatic and terrestrial invertebrates in the Okavango Delta investigated 26 higher taxa, but focused analysis on six of these, with results showing clear negative impacts of tsetse fly spraying in aquatic communities, and terrestrial invertebrate abundance being reduced by 60-70% (Perkins and Ramberg, 2004). Insights into the seasonality and abundance of soil-fauna in woodland habitats were provided by Dangerfield (1997), who discovered higher abundance in the wet season compared to the dry season (almost double), but noted that the variability in abundance and species composition was most likely attributed to a combination of biotic and abiotic factors. Most critically, Dangerfield (1997) established that diversity of soil fauna can vary significantly between location, habitat and season and the assessment of the spatial component of these variations could provide valuable insights into the impacts of various factors on soil-bound communities.

Literature regarding Hymenoptera of Botswana, and specifically the Okavango Delta, are fragmented. The cave-based study of Mazebedi and Hesselberg (2020) found limited insight into the ecology of the cave wasps (Sphecidae), and the absence of wasp-focused literature within the Okavango Delta is concerning. Ants have received some attention as part of larger studies (McCarthy and Ellery, 1998; Moreki, 2014). Dalerum *et al.* (2019) explored the impact of distance to perennial water on ant communities in the Mopane woodlands of northern Botswana and found higher ant abundance richness and diversity during the wet season, with strong seasonal influences on the effects of distance to water. Their results suggest that small-scale environmental variations that are not linked to water access, also have a strong effect on abundance, richness and diversity.

Russel-Smith (1981) assessed the seasonal activity of ground-living spiders in woodlands and grasslands of the Delta and found 84 spider species collected in the woodland habitat, and 87 collected in the grassland habitat. This included a lower overall number of spiders trapped in the woodland habitat (33% fewer than grasslands), but with the communities in this habitat type being more consistent throughout the year than those of grasslands (Russel-Smith, 1981). Gnaphosidae, Lycosidae and Salticidae were most abundant in the woodlands and although total species number was similar between the two habitat types, species composition was significantly different (Russel-Smith, 1981).

From the limited available literature on arthropods of the Okavango Delta, it is clear that ants, soil fauna such as springtails, and wasps are underrepresented in the process of understanding the complex systems and array of habitats that make up the Okavango Delta, while spiders have received more attention as a group. A deeper understanding of the ecological dynamics of invertebrates in the context of habitat variability, human activities, and climate change is essential for effective conservation and sustainable management of the Okavango Delta's biodiversity. Thus, this study aimed to generate novel starting point datasets for four terrestrial invertebrate taxa and to investigate how fire and grazing may shape these communities.

Aims and hypotheses

Given the fragmented knowledge of terrestrial arthropods within the study area, the study aimed to compare arthropod communities within and between ongoing disturbance regimes, using a multi-taxon approach. Specifically, this study aimed to:

1. Compare the diversity and abundance of four terrestrial arthropod groups (ants, wasps, springtails and spiders) between burnt and grazed sites.
2. Investigate whether burning or grazing has differential impacts on arthropod communities.
3. Provide a novel starting-point dataset that can be used to monitor the impact of disturbances on arthropod communities in the Okavango Delta comparatively into the future.

Through these aims, this study aimed to provide novel starting point dataset for continued research of terrestrial arthropod species diversity within the Okavango Delta and to improve understanding of how disturbance shape these community dynamics. A total of four hypotheses were tested to guide the study’s context and goals:

1. **Hypothesis 1:** There is a significant difference in the species richness and abundance of terrestrial arthropod communities between burnt and grazed sites in the Okavango Delta.
2. **Hypothesis 2:** There is a significant difference in the species richness and abundance of terrestrial arthropod communities between seasons in the Okavango Delta.
3. **Hypothesis 3**: Grazed sites have higher arthropod species richness and abundance due to stimulated disturbance at moderate levels by livestock grazing, filling the historic role of wild ungulates.
4. **Hypothesis 4:** Pitfall traps contribute a significantly higher proportion of specimens collected than litter extractions for ants, wasp and spiders.

Materials and Methods

Study area

Field collection was conducted in the surrounds of the Mopiri research station (-19.08451°, 22.37136°), run by the Botswana Wild Bird Trust in the north-western section of the Okavango Delta, along the western edge of the lower panhandle (Fig. 1). The research station is located approximately 6kms

South-East of the from the village of Etsha 13, and approximately 4km North-East from the village of Etsha 6. The station is located within the NG/24 Okavango Jakotsha Community Trust, a nature reserve managed by a registered Community Based Organization, the Jakotsha community council, representing the interest of the villages of Etsha1-16, Jao and Ikoga in the managing of NG24 and the associated natural heritage contained therein.

Figure 1: Map showing location of study area.

Dry woodland and savannah vegetation classes have not been studied in adequate detail, or to a large enough extent in vegetation classification studies in the past, although they form part of the important transitional zone between the Kalahari Desert and the swamps of the Okavango Delta (Tedder *et al.,* 2013). Most vegetation assessment and classifications available for Botswana, and the Okavango Delta specifically, focused primarily in the southern and eastern reaches of the Delta (Ringrose *et al.,* 2003; McCarthy, *et al.*, 2005; Tedder *et al.,* 2013). These studies exhibit a large variation in the number of vegetation classes described in each, exemplifying how they are much more diverse in species and plant communities than the generalized "*Acacia*- or *Mopane*-dominated" classifications often used (Tedder *et al.,* 2013). Only recently have more dedicated research improved our understanding of the woodland species composition (Neelo *et al*., 2013; Tsheboeng *et al.*, 2016a) and how it changes with increasing distance from water (Tsheboeng *et al.,* 2016b).

The most recent, fine-scale map available, was the "Vegetation map of the Okavango Basin" (GeoTerra Image 2019: 20m resolution vegetation map produced for National Geographic Okavango Wilderness Project) and this map was used to broadly classify vegetation for the various sampling sites. The vegetation of the study area was a complex mix of Riparian woodland, *Acacia* woodland and *Mopane*-dominated woodland. Constant transitions between dense woodlands and sparsely-wooded grassland were evident, with mixed-woodlands creating dense stands on the channel edge. Interspersed between the woodland patches increasing as one moves away from the swamps, sparsely-wooded grassland and open grasslands dominated the majority of the landscape.

Wh'ere Island, utilised as the "burnt" treatment, could be classified as mixed-Riparian woodland, dominated by species such as *Croton megalobotrys, Syzygium cordatum* and *Gymnosporia senegalensis,* with *Colophospermum mopane* more prominent in the middle of the island. The island had small grasslands pockets, along with a section of Riparian Forest and the tip of the island.

The grazed sites were dense, woodland patches that persisted in areas where floodwaters reached seasonal channels in the recent past (less than 10 years ago), but no longer do. These patches were also dominated by a similar mix of species as W'here island, including *Senegalia nigrescens, Vachelia erioloba and Colophospermum mopane*, accompanied by a rich understory bordering old channels that, in recent history (over the last 20 years), transitioned to open grasslands.

Site selection

Villages line the Western edge of this section of the Delta, leading to a variety of anthropogenic disturbances in this area. These disturbances include regular burning of vegetation such as *Cyperus papyrus* and *Phragmites australis* to stimulate re-growth, and widespread grazing by livestock within the woodlands and historically seasonal floodplains, situated between the village complex and the edge of the permanently inundated Delta. As this study aimed to conduct a survey of multiple taxa of terrestrial arthropods and compare the impact of different disturbance types on these communities, two treatments were selected based on the most prevalent anthropogenic disturbances in the area: Human-induced fires and livestock grazing. Within the two disturbance types (grazed and burnt), three replicate sites were selected (Appendix B, Fig. B1). A total of six replicate sites were sampled during each sampling season. No "pristine" or "control" sites were accessible within reasonable distance from the main sampling area, limiting the comparisons that can be made between the grazed and burnt sites to less impacted communities. Second, although grazing occurs at relatively low intensities in the research area, it is unknown what pristine communities may look like in the Okavango Delta compared to grazed and burnt communities.

Table 1: Location details of all sampling sites (grazed and burnt).

Site	Latitude	Longitude
Grazed A	19°05'16.9" S	22°21'08.7" E
Grazed B	19°05'09.3" S	22°21'28.5" E
Grazed C	19° 05' 41,8" S	22° 22'16.2" E
Burnt A	19°° 4'17.56" S	22°23'15.31" E
Burnt B	19° 4'17.43" S	22°23'9.97" E
Burnt C	19° 4'12.60" S	22°22'57.36" E

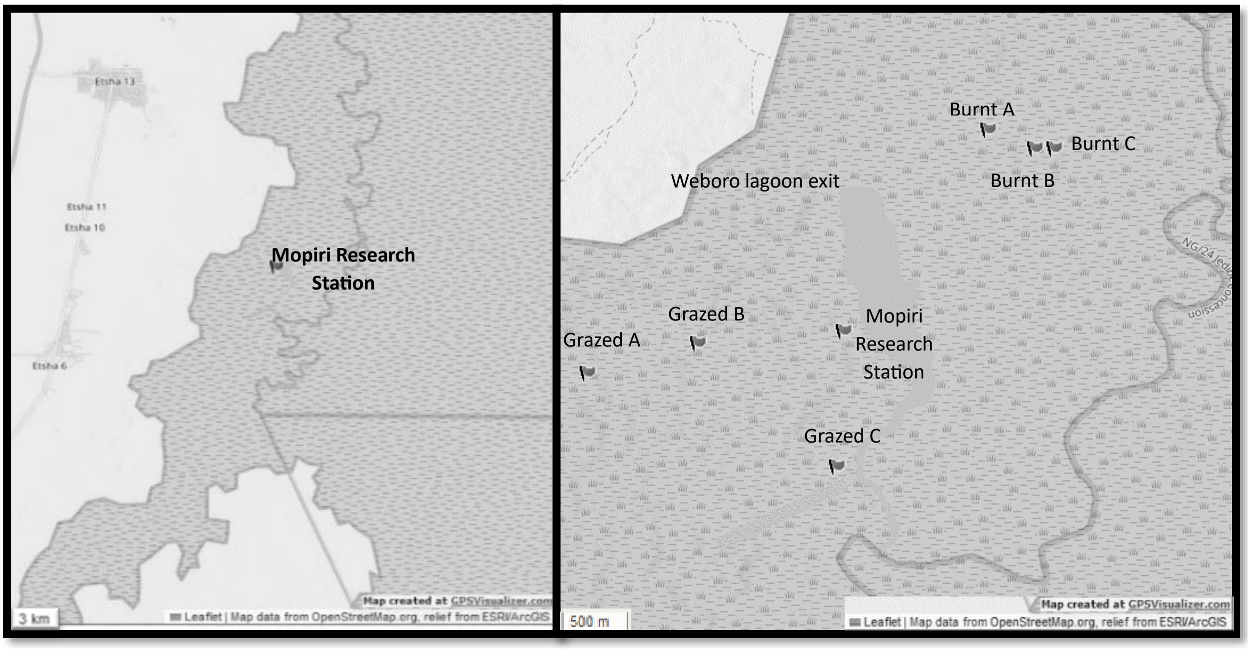

Figure 2: Map showing Mopiri research station in relation to the Etsha village complex and the study sites (grazed and burnt) where sampling occurred. Note Burnt sites on Whe're island.

Grazed sites

The grazed sites were selected based on the presence of livestock (predominantly cattle), or signs thereof, in and around the sites, as well as the absence of fire in the preceding one year before sampling (2020). The Etsha village complex's inhabitants utilize the section of natural vegetation between the villages and the edge of the Delta as permanent grazing for their cattle, consisting of herds of 20 – 80 cattle on average (personal observation). A multitude of cattle posts, both in-use and abandoned, are visible on the drive from the villages to the research station. These herds of cattle graze the grasses in the historically seasonally flooded channels (which had not flooded for at least five years prior to when sampling occurred), as well as the islands of woodland and savanna, that are scattered across the landscape.

Sampling occurred within the mixed woodland islands that are interspersed with grasslands. Three mixed woodland islands were selected based on evidence of livestock presence (direct observation or fresh dung, tracks and pathways) and the absence of any signs of recent fires. Generally, these islands are more resilient to fire and less prone to burning than the adjacent grasslands due to the larger trees and shrubs that constitute its vegetation and the associated increased moisture within the habitat. Low intensity fires characteristic of grasslands would seldom have a significant impact on these islands. The soil on these islands is typical of the region, being sandy, well drained, and nutrient poor, with most islands most likely being formed by termitaria over the last 1000 years (McCarthy and Ellery, 1998).

Burnt Sites

Burnt sites were selected based on absence of cattle or other livestock signs and the occurrence of burning shortly before the initial sampling season in November 2021. The only viable mixed woodland island within reasonable distance from the research station was Wh'ere island, accessed via the channel at the Weboro Lagoon exit 1 (Table 1, Fig. 2). Deep channels on the Western and Southern side of the island prevented cattle and other livestock from accessing the island, while the Northern and Eastern sides bordered the more permanently inundated parts of the Delta. The oldest part of the island (northern tip characterized by trees much larger than the remainder of the island) is a small section of riparian forest that most likely established in the termitaria that preceded the islands establishment. This section was not affected by burning. Most of the island consisted of mixed woodland, with a series of small patches of grassland pockets along the central line of the island, with the pockets ranging from 5-8m in diameter. Besides these grassland pockets, the island also hosts a palm grove in the south-western tip, with mixed-open woodland characterizing the overall vegetation of the entire island.

A fire had been set by local villagers near the island to stimulate reed growth about three weeks before the first sampling session (November 2021). This fire burnt an estimated 75% of the island, with the island fringes receiving the most damage, along with the palm grove and the grasslands interspersed within the open woodland. A second fire occurred between the two sampling sessions (December 2021), where the reeds and grasses on the eastern floodplain of the island were burnt, but this fire did not impact the island itself. During the second sampling season (February 2022), the island had recovered quickly with very few signs of the first fire. The only remnant of the fire was ash heaps scattered across the island and a few charred palm stems that protruded beneath new shrub growth.

Three sites were selected across the island to represent the "Burnt" treatment, and due to spatial limits, were relatively close together (about 200m apart) (Fig. 2). The island nonetheless showed extreme variation in vegetation communities, and the impact of fire was clearly visible within majority of these vegetation communities.

Sampling and identification

Sampling was conducted over two seasons, namely the dry season in November 2021, and the wet (rainy) season in February 2022, respectively. In order to gain accurate and usable insights into the arthropod communities and how disturbances shape them, a multi-taxon approach was used by selecting four groups of arthropods to include in the study. These groups were selected based on the varying roles that they have in ecosystems (from predators to soil fauna), and relevant access to taxonomists and experts on these groups: ants (Formicidae), wasps (Hymenoptera), springtails (Collembola) and spiders (Araneae).

A combination of two systematic sampling techniques was employed to collect specimens from the four selected groups (Appenidx B, Fig. B2). Pitfall traps were used to target above-ground invertebrates (Woodcock, 2005; Skvarla *et al.*, 2014) and litter samples and subsequent Berlese-Tullgren funnel extractions were used to target soil-dwelling invertebrates (Edwards, 1991; Bano and Roy, 2016). Samples were collected over the course of three weeks due to limitations of litter extraction equipment. Each treatment and their three replicate sites were sampled during the same period. Within each of the six replicate sites (three burnt and three grazed), 10 pitfall traps were deployed in a single line, 3m apart. The pitfall traps were half-filled with 100% propylene glycol and left in-field for five days. A total of 120 pitfall traps were collected over the two sampling seasons (60 per season). Upon collection, the pitfall traps were marked, sealed and packaged for transport back to South Africa to be sorted and specimens identified.

In addition, 10 litter samples were taken at each of the replicate sites. Each litter sample was collected in a 500ml plastic container and placed into plastic zip-lock bags. Upon returning to the research station, the litter was transferred into the Tullgren-funnel extraction set-up and left to extract into 100% propylene glycol for five days. A total of 120 litter extractions were completed over the two sampling seasons (60 per season). The extracted contents were then marked, sealed and packaged for transport to South Africa for further analysis.

All samples and individual specimens were packaged and transported to the University of Cape Town, Cape Town, South Africa. Pitfall traps and litter extractions were transferred into 96% ethanol. Each sample was sorted to morphospecies level (Beattie and Oliver, 1996) based on similar morphological characteristics (called species from hereon). Specimens were counted, while each species was photographed. Specimens were identified with assistance from taxonomic experts, where possible (ants: A. Ndaba[1], spiders: A.S Dippenaar-Schoeman[2], springtails: C. Janion-Scheepers[3], wasps: A. Naghizadehmollayousefi[4] and S. van Noort[5]). All ants, springtails and wasps will be deposited at the Entomology Collection, Iziko South African Museum, Cape Town, South Africa, while the spiders will be deposited at the National Collection of Arachnida, Agricultural Research Council (ARC), Pretoria, South Africa.

Statistical analysis

Species accumulation curves were constructed using Primer V.7 (Clarke and Gorley, 2015) to assess whether sampling was done to completion. To compare different sites, diversity indices were calculated using the DIVERSE function in Primer V.7, providing the Simpson's diversity index (1-D), Shannon-Wiener Diversity Index (H'), and Piellou's Evenness (J') for each site, treatment (grazed and burnt) and season (dry and wet). Data for all four taxa were transformed by calculating the square root of the averages of each morphospecies within each site. Transformations were done to mitigate outliers in the data and to attempt to stabilize the variance for PERMANOVA analysis, increasing the result validity. Multivariate analysis was undertaken using Primer V 7.0 to assess to overall changes within each taxon between seasons and between burnt and grazed sites. After transformation, a Bray-Curtis similarity index was used to assess the difference in assemblage structure between seasons and disturbance type for each taxon. Using the Bray-Curtis similarity index, a non-Metric Multi-Dimensional Scaling ordination was performed and overlayed with the results from the Hierarchical Cluster analysis (using group averages) to visualize the pattern of grouping between seasons and disturbance type for each taxon. Non-parametric Analysis of Similarity (ANOSIM with 999 permutations) was used to test for any significant differences in assemblage composition between seasons (wet and dry) and disturbance types (grazed and burnt). The Global R-value obtained from the ANOSIM assisted in comparing similarity of assemblages between sites and between seasons, where an R-value close to 1 indicates more differentiation between groups, and R-values closer to 0 indicate higher similarity between groups (Parr *et al.*, 2004). Where significant differences were found, the Permutational Multivariate Analysis of Variance (PERMANOVA) was used to assess where differences in assemblages occur (between seasons or between disturbance types).

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Results

A total of 20,979 specimens were collected over the two seasons between all four groups. Pitfall traps collected four times the total number of ants collected through litter extractions, while also collecting nearly double the number of springtails collected using litter extractions. Litter extractions collected just over 10% of the number of wasps collected by pitfall traps, while litter extractions collected roughly only one quarter of the total number of spiders collected by pitfall traps (Table 2). Overall, pitfall traps were more successful in terms of total specimens collected than litter extractions.

Rarefaction curves indicated that sampling was done to completion (Appendix A, Figures A1-A8). All but one accumulation curve appears to approach an asymptote, showing that sampling was done to completion using most trapping methods. The Chao 1 estimator generated for wasps collected by litter extractions in Fig. A6 continue to increase past the asymptote reached by the other estimators.

During the first sampling period (i.e., dry season), a total of 8,881 specimens were collected from pitfall traps and 171 specimens from litter extractions. During the second sampling season (i.e., wet season), 6,307 specimens were collected from pitfall traps and 5,620 specimens from litter extractions (Table 2). A total of 23 species of ants were collected from all trapping methods, 16 species of springtails and 76 species of spiders. Wasps were assigned unique morphospecies IDs, but not identified to any taxonomic level, with 54 wasp morphospecies found across all trapping methods. Photos of representatives of all four groups can be found in Appendix B (Figs B3-B10).

Table 2: Total abundances for each studied taxa across all seasons, disturbance types and trapping methods.

Group	Dry Season		Wet Season		Grazed Sites		Burnt Site		Trap Type	
	Pitfall	Litter	Pitfall	Litter	Pitfall	Litter	Pitfall	Litter	Pitfall	Litter
Ants	3909	89	4345	1826	4090	961	4164	954	8254	1915
Springtails	4632	18	1417	3695	4309	1939	1740	1774	6049	3713
Wasps	198	4	286	37	209	21	275	20	484	41
Spiders	142	60	259	62	162	54	239	68	401	122
Total abundance	8881	171	6307	5620	8770	2975	6418	2816	15188	5791
	9052		11927		11745		9234		20979	

Springtails, followed by ants, were the two most abundant taxa in the pitfall traps and litter extractions during the dry season (Table 2). In contrast, during the wet season ants, followed by springtails, were most abundant in pitfall traps, while springtails were significantly more abundant in the litter extractions than the ants overall (Table 2). Only four wasp specimens were collected through litter extraction during the dry season, while 525 wasp specimens were collected during the wet season litter extractions. Almost double the number of spiders were collected with pitfall traps in the wet season than in the dry season and the number of springtails collected by litter extraction increased drastically from the dry season to the wet season (Table 2). Pitfall traps in grazed and burnt sites collected more arthropods than litter extractions, while grazed sites had a higher total arthropod abundance than burnt sites (11,745 and 9,234, respectively).

Ants

Pitfall traps

A total of 22 species of ants were collected using pitfall traps, comprising 15 genera. In the grazed sites, 19 species of ants were collected during both the dry and wet season and in the burnt sites, 13 species were collected in the dry season and 12 in the wet season (Table 3). The dry season had 3,909 specimens while the wet season had 4,345. Over both seasons, grazed sites had 21 species, while burnt sites had 14 species. Grazed sites had 4,090 specimens, and burnt sites 4,764 over both seasons (Table 3). Overall, burnt and grazed sites shared 13 species, with eight species unique to the grazed sites and one species unique to the burnt sites.

Table 3: Descriptive statistics and diversity indices for ants collected by pitfall traps in grazed and burnt sites in both seasons. S = total species, N = total abundance, d = estimate of proportional species richness at full sampling effort, J' = Piellou's evenness, H' = Shannon's diversity estimate (log^{e}) and 1-D = Simpson's diversity estimate.

Taxa	Site	Season	S	N	d	J'	H' (loge)	1-D
Formicidae	Grazed	Dry	19	2110	2.352	0.5346	1.574	0.6937
	Burnt	Dry	13	1799	1.601	0.4416	1.133	0.4816
	Grazed	Wet	19	1980	2.371	0.3303	0.9726	0.4086
	Burnt	Wet	12	2365	1.416	0.317	0.7877	0.3314
	Grazed combined		21	4090	2.405	0.446	1.358	0.5846
	Burnt combined		14	4164	1.56	0.3854	1.017	0.4033

Pheidole sp.1 had the highest abundance in the grazed and burnt sites in the dry season (n=1001 and n=1273 respectively), as well as both grazed and burnt sites in the wet season (n=1503 and n=1920 respectively) (Table 4). *Pheidole* sp.1 accounted for 47% and 70% of the total abundance in the grazed and burnt sites in the dry season respectively, and 75% and 81% of the total abundance of the grazed and burnt sites in the wet season respectively. In the grazed sites in the dry season, *Monomorium* sp.1 had the second highest abundance (n=509), while *Ocymyrmex* sp.2 had the lowest abundance, with only one individual (Table 4). In the burnt site during the dry season, *Plagiolepis* sp.2 and *Monomorium* sp.1 had similar abundances (n=142 and n=140, respectively) and *Camponotus* sp.3 had the lowest abundance with only one specimen. In the wet season, the second most abundant species in the grazed site was *Myrmicaria* sp.1 (n=201), while *Ocymyrmex* sp.1, *Tetramorium* sp.1 and *Aenictus* sp.1 delivered only single specimens (n=1) (Table 4). In the burnt site during the wet season, *Dorylus* sp.1 had the second highest abundance (n=195) while *Camponotus* sp.2 had the lowest abundance (n=1). Overall, *Pheidole* sp.1 dominated both grazed and burnt sites by a large margin (Table 4). With this species excluded, two other species (*Monomorium* sp.1 and *Myrmicaria* sp.1) were dominant in the grazed sites, while four species (*Plagiolepis* sp.2*, Dorylus* sp.1, *Cardiocondyla* sp.1 and *Monomorium* sp.1) were dominant in the burnt sites.

Table 4: Total abundances of ants collected using pitfall traps showing site totals, season totals and disturbance totals.

	Site Totals				**Season Totals (Grazed+Burnt)**		**Disturbance Totals (Dry+Wet)**		**Total Abundance**
Species	**Grazed Dry**	**Burnt Dry**	**Grazed Wet**	**Burnt Wet**	**Dry**	**Wet**	**Grazed**	**Burnt**	
Aenictus sp1	0	0	5	0	0	5	5	0	**5**
Camponotus sp1	24	12	12	6	36	18	36	18	**54**
Camponotus sp2	3	2	0	1	5	1	3	3	**6**
Camponotus sp3	2	1	2	2	3	4	4	3	**7**
Cardiocondyla sp1	78	125	15	108	203	123	93	233	**326**
Dorylus sp1	0	0	0	195	0	195	0	195	**195**
Lepisiota sp1	21	42	10	9	63	19	31	51	**82**
Linepithema sp1	4	9	3	0	13	3	7	9	**16**
Monomorium sp1	509	140	128	0	649	128	637	140	**777**
Myrmicaria sp1	304	0	201	0	304	201	505	0	**505**
Ocymyrmex sp1	8	0	1	0	8	1	9	0	**9**
Ocymyrmex sp2	1	0	0	0	1	0	1	0	**1**
Odontomachus sp1	3	0	42	0	3	42	45	0	**45**
Pheidole sp1	1001	1273	1503	1920	2274	3423	2504	3193	**5697**
Plagiolepis sp1	28	16	2	45	44	47	30	61	**91**
Plagiolepis sp2	39	142	10	33	181	43	49	175	**224**
Plectroctena sp1	0	0	2	0	0	2	2	0	**2**
Polyrhachis sp1	6	0	3	0	6	3	9	0	**9**
Tetramorium sp1	14	12	1	10	26	11	15	22	**37**
Tetramorium sp2	24	0	1	0	24	1	25	0	**25**
Tetramorium sp3	7	10	35	33	17	68	42	43	**85**
Tetramorium sp4	34	15	4	3	49	7	38	18	**56**
Total abundance	2110	1799	1980	2365	3909	4345	4090	4164	8254

In the dry season, the species richness in the grazed sites was higher than the burnt sites, while grazed sites also had a higher evenness than burnt sites (Table 3). Grazed sites showed a higher species diversity than burnt sites. In the wet season, the species richness in grazed sites was higher than that of burnt sites, while grazed sites had a higher evenness than burnt sites (Table 3). Grazed sites showed slightly higher species diversity than burnt sites. Overall, species richness was higher in the grazed sites than the burnt sites, while grazed sites had higher evenness than burnt sites overall (Table 3). Grazed sites had higher species diversity than burnt sites overall.

The Analysis of Similarity (ANOSIM) test between grazed and burnt sites across all seasons indicated a non-significant, weak separation between grazed and burnt sites across all seasons for ants. The same analysis between the dry and wet seasons across all disturbance types (grazed and burnt) indicated a significant weak separation between the dry and wet seasons across all disturbance types (R=0.315 at 4%). Results from the Permutational Multivariate Analysis of Variance (PERMANOVA) indicated that disturbance type had significant effects (p=0.044). The non-Metric Multi-Dimensional Scaling (nMDS) indicated relatively high levels of similarity between all the sites (Fig. 3).

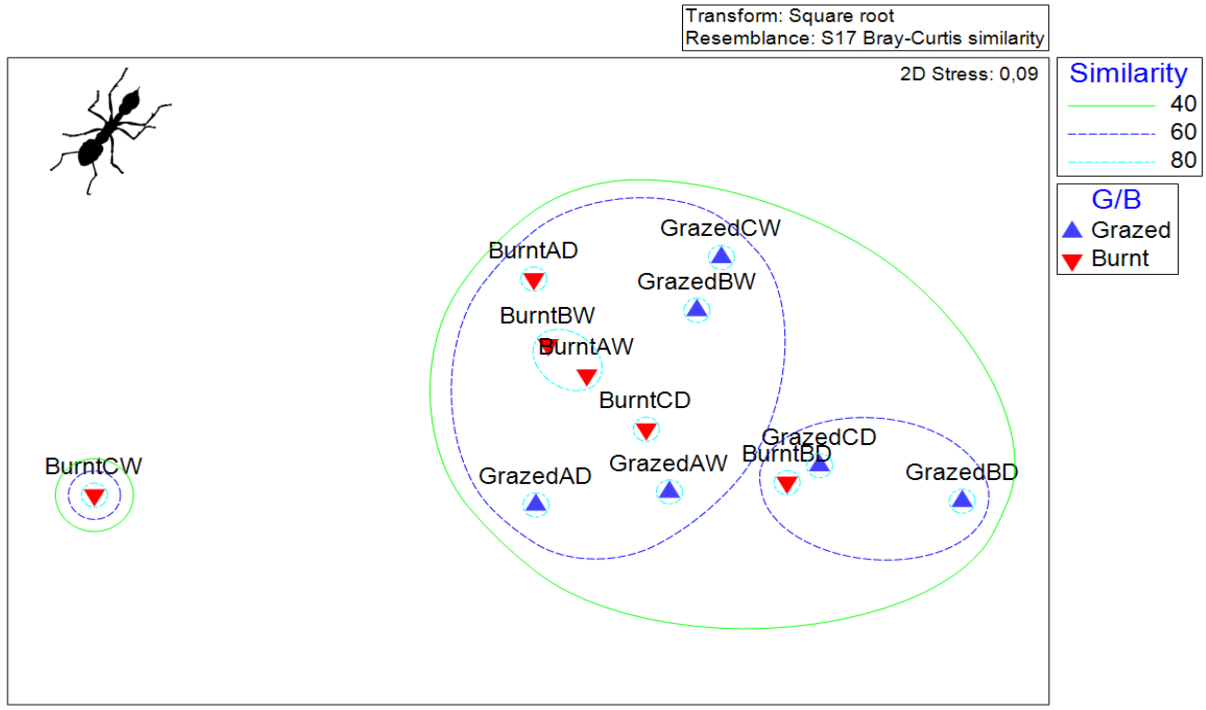

Figure 3: A non-metric Multi-Dimensional Scaling (nMDS) of ants collected using pitfall traps in grazed and burnt sites with both seasons combined. D = dry season, W = wet season.

Litter extraction

In total 13 species were collected using litter extractions, comprising 13 genera. In the grazed sites, nine species of ants were collected during the dry and wet season, while in the burnt sites, two species were collected in the dry season and seven in the wet season (Table 5). In the dry season, 89 specimens were collected while 1826 specimens were collected in the wet. Both grazed and burnt sites showed a higher abundance of ants in the wet season (n=901 and n=925 respectively) than in the dry season (n=60 and n=29 respectively). Overall, grazed sites had 12 species present, and burnt sites seven species. Grazed and burnt sites had similar abundances overall (Table 5). In both seasons combined, grazed and burnt sites shared six species, with six species unique to the grazed sites and one species unique to the burnt sites.

Table 5: Descriptive statistics and diversity indices for ants collected by pitfall traps in grazed and burnt sites in both seasons. S = total species, N = total abundance, d = estimate of proportional species richness at full sampling effort, J' = Piellou's evenness, H' = Shannon's diversity estimate (log^{e}) and 1-D = Simpson's diversity estimate.

Taxa	**Site**	**Season**	**S**	**N**	**d**	**J'**	**H' (loge)**	**1-lambda'**
Formicidae	Grazed	Dry	9	60	1.954	0.5274	1.159	0.5305
	Burnt	Dry	2	29	0.297	0.7973	0.5527	0.3793
	Grazed	Wet	9	901	1.176	0.3442	0.7563	0.4352
	Burnt	Wet	7	925	0.8785	0.4224	0.8220	0.3993
	Grazed combined		12	961	1.602	0.3327	0.8267	0.467
	Burnt combined		7	954	0.8746	0.421	0.8192	0.399

During the dry season, the grazed site was dominated by *Pheidole* sp.1 (n=40; 67% of total abundance), while seven out of nine species were singletons. The burnt site was also dominated by *Pheidole* sp.1 (n=22; 75% of total abundance), while *Plagiolepis* sp.1 had the lowest abundance (n=14) (Table 6). These were the only two species collected from this site. During the wet season, *Plagiolepis* sp.1 dominated the grazed site (n=633; 70% of total abundance) with *Pheidole* sp.1 having the second highest abundance (n=241) (Table 6). Three out of nine species were singletons (n=1) in the grazed sites. In the burnt sites, *Pheidole* sp.1 dominated (n=705; 76% of total abundance), with *Plagiolepis* sp.1 having the second highest abundance (n= 103). *Plectroctena* sp.1 and *Cardiocondyla* sp.1 were singletons. Overall, *Plagiolepis* sp.1 dominated the grazed sites, having a much higher abundance than the other species present (Table 6).

Table 6: Total abundances of ants collected using litter extractions showing site totals, season totals and disturbance totals.

Species	Site Totals				Season Totals (Grazed+Burnt)		Disturbance Totals (Dry+Wet)		Total Abundance
	Grazed Dry	**Burnt Dry**	**Grazed Wet**	**Burnt Wet**	**Dry**	**Wet**	**Grazed**	**Burnt**	
Anoplolepis sp1	0	0	0	4	0	4	0	4	4
Camponotus sp3	1	0	0	0	1	0	1	0	1
Cardiocondyla sp1	1	0	6	1	1	7	7	1	8
Linepithema sp1	1	0	1	0	1	1	2	0	2
Monomorium sp1	4	0	7	72	4	79	11	72	83
Myrmicaria sp1	1	0	0	0	1	0	1	0	1
Odontomachus sp1	1	0	0	0	1	0	1	0	1
Pheidole sp1	40	22	241	705	62	946	281	727	1008
Plagiolepis sp1	10	7	633	103	17	736	643	110	753
Plagiolepis sp2	1	0	7	39	1	46	8	39	47
Plectroctena sp1	0	0	1	1	0	2	1	1	2
Tetramorium sp1	0	0	1	0	0	1	1	0	1
Tetramorium sp3	0	0	4	0	0	4	4	0	4
Totals abundance	60	29	901	925	89	1826	961	954	1915

In the dry season, the species richness in the grazed sites was higher than that of the burnt sites, while burnt sites had a higher evenness than grazed sites (Table 5). Grazed sites showed higher species diversity than the burnt sites. In the wet season, the species richness in the grazed sites was higher than that of the burnt sites, while burnt sites had a higher evenness than grazed sites (Table 5). Burnt sites showed higher species diversity according to the Shannon index but burnt sites showed lower species diversity than grazed sites according to the Simpsons index. In both seasons combined, grazed sites showed higher species richness than burnt sites, while burnt sites had a higher evenness than grazed sites (Table 5). Grazed sites had higher species diversity than burnt sites.

The ANOSIM-test between grazed and burnt sites across all seasons indicated non-significant, weak separation between grazed and burnt sites across all seasons. The same analysis between the dry and wet season across all disturbance types (grazed and burnt) indicated a significant, strong separation between the two seasons (R=0.655 at 1%). Results from the PERMANOVA indicated that only the season had a significant effect (p=0.003). The nMDS showed some groupings (Fig. 4). Grazed and burnt sites from the wet season grouped together, with the grazed and burnt sites from the dry season forming two distinct, separate groupings.

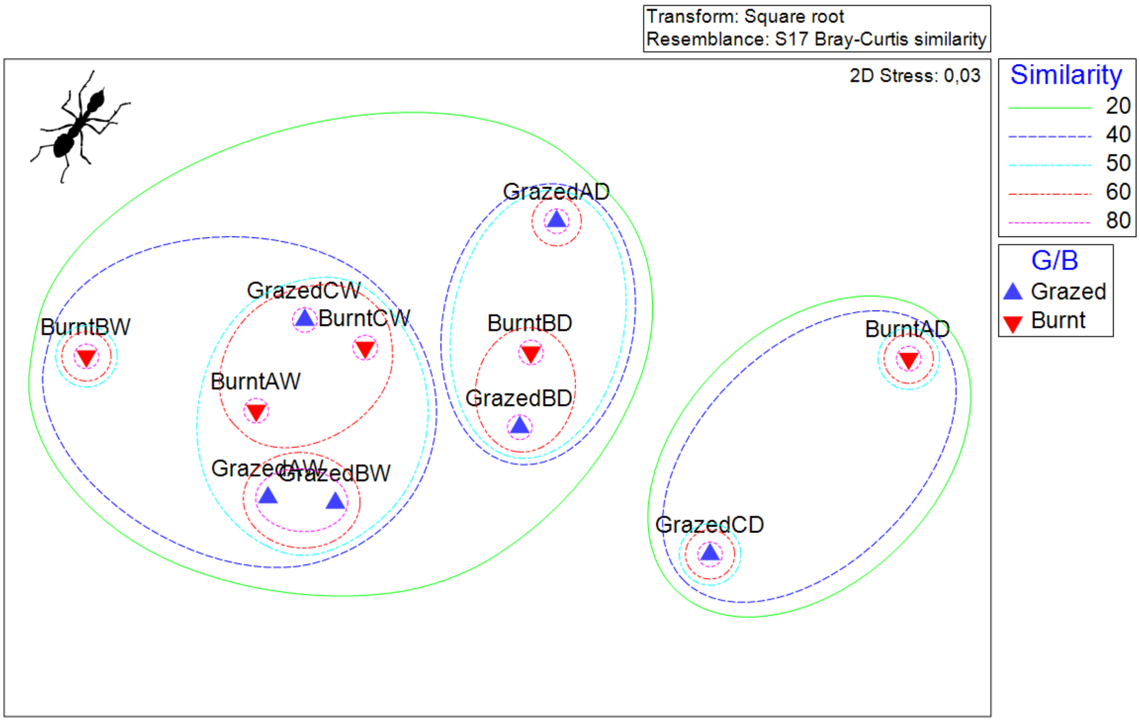

Figure 4: A non-metric Multi-Dimensional Scaling (nMDS) of ants collected using litter extraction in grazed and burnt sites with both seasons combined; D = dry season, W = wet season.

Springtails

Pitfall traps

A total of 12 species of springtails (Collembola) were collected using pitfall traps, comprising five families, with only two genera positively identified. In the grazed sites, eight species of springtails were collected during the dry season, while only three were collected during the wet season. In the burnt sites, four species were collected in the dry season and eight in the wet season. In the dry season more specimens were collected than in the wet season. Across both seasons, grazed sites contained eight species consisting of 4309 specimens, and burnt sites contained nine species consisting of 1,740 specimens (Table 7). Overall, grazed and burnt sites shared five species, with three species unique to the grazed sites and four species unique to the burnt sites.

Table 7: Descriptive statistics and diversity indices for springtails collected by pitfall traps in grazed and burnt sites in both seasons. S = total species, N = total abundance, d = estimate of proportional species richness at full sampling effort, J' = Piellou's evenness, H' = Shannon's diversity estimate ($\log^{e}$) and 1-D = Simpson's diversity estimate.

Taxa	Site	Season	S	N	d	J'	H' (loge)	1-lambda'
Collembola	Grazed	Dry	8	3697	0.8521	0.2119	0.4407	0.1784
	Burnt	Dry	4	935	0.4386	0.3517	0.4876	0.2416
	Grazed	Wet	3	612	0.3117	0.6647	0.7302	0.4756
	Burnt	Wet	8	805	1.046	0.6891	1.433	0.6939
	Grazed combined		8	4309	0.8365	0.32	0.6655	0.9075
	Burnt combined		9	1740	1.072	0.5184	1.139	0.5222

In the dry season*,* *Seira* sp.2 (Entomobryidae) was most abundant (n=3345; 90% of the total abundance) in the grazed sites, followed by Sminthuridae sp.1 (n=161) (Table 8). In the burnt sites, *Seira* sp.2 (Entomobryidae) also showed the highest abundance (n=808; 86% of total abundance), Sminthuridae sp.1 the second highest (n=100), and *Seira* sp.3 (Entomobryidae) and Entomobryidae sp.2 the lowest (n=13 and n=14, respectively) (Table 8). In the wet season, *Seira* sp.3 (Entomobryidae) dominated the grazed sites (n=391; 63% of total abundance), followed by *Seira* sp.2 (Entomobryidae) (n=209), with Sminthuridae sp.1 (Sminthuridae) showing the lowest abundance (n=12) (Table 8). In the burnt sites, *Seira* sp.2 (Entomobryidae) had the highest abundance (n=357; 44% of total abundance), followed by *Lepidocyrtus* sp.1 (Entomobryidae) (n=247) and with *Cryptopygus* sp.1 (Isotomidae) having the lowest abundance (n=1). Overall, *Seira* sp.2 (Entomobryidae) was most abundant in both grazed and burnt sites (Table 8). *Lepidocyrtus* sp.1 (Entomobryidae) and Sminthuridae sp.1 (Sminthuridae) were the second most abundant in the burnt sites, while *Seira* sp.3 (Entomobryidae) was second most abundant in the grazed sites.

Table 3: Total abundances of springtails collected using pitfall traps showing site totals, season totals and disturbance totals.

	Site Totals				**Season Totals (Grazed+Burnt)**		**Disturbance Totals (Dry+Wet)**		**Total Abundance**
Species	**Grazed Dry**	**Burnt Dry**	**Grazed Wet**	**Burnt Wet**	**Dry**	**Wet**	**Grazed**	**Burnt**	
Cryptopygus sp1	0	0	0	1	0	1	0	1	1
Entomobryidae sp2	112	13	0	0	125	0	112	13	125
Hypogastruridae sp1	8	0	0	0	8	0	8	0	8
Lepidocyrtus sp1	0	0	0	247	0	247	0	247	247
Pseudosinella sp1	6	0	0	0	6	0	6	0	6
Seira sp1	25	0	0	59	25	59	25	59	84
Seira sp2	3345	808	209	357	4153	566	3554	1165	4719
Seira sp3	39	14	391	70	53	461	430	84	514
Seira sp4	0	0	0	32	0	32	0	32	32
Sinella sp1	0	0	0	7	0	7	0	7	7
Sminthurididae sp1	161	100	12	32	261	44	173	132	305
Unknown	1	0	0	0	1	0	1	0	1
Total abundance	3697	935	612	805	4632	1417	4309	1740	6049

In the dry season, the species richness in the grazed sites was higher than that of the burnt sites, while grazed sites also had a slightly lower evenness than burnt sites (Table 7). Grazed sites showed a higher species diversity than burnt sites. In the wet season, the species richness in burnt sites was higher than that of grazed sites while grazed sites had a slightly lower evenness than burnt sites (Table 7). Burnt sites showed higher species diversity than grazed sites in the wet season. Combined, burnt sites showed higher species richness than grazed sites, and a higher evenness than grazed sites (Table 7). According to the Shannon index, burnt sites were more species diverse than grazed sites, but according to the Simpson’s index, grazed sites had higher diversity than burnt sites.

The ANOSIM test between grazed and burnt sites across all seasons indicated non-significant, weak separation between grazed and burnt sites across all seasons. The same analysis between the dry and wet season across all disturbance types (grazed and burnt) indicated a significant, strong separation between dry and wet seasons across all disturbance types (R=0.759, significance level of 1%). The PERMANOVA indicated that season and the interaction between disturbance type and season had significant effects (p=0.002 and p=0.008, respectively). The nMDS showed some sites in the wet season clustering separately from the other sites, which had high similarity (Fig. 5).

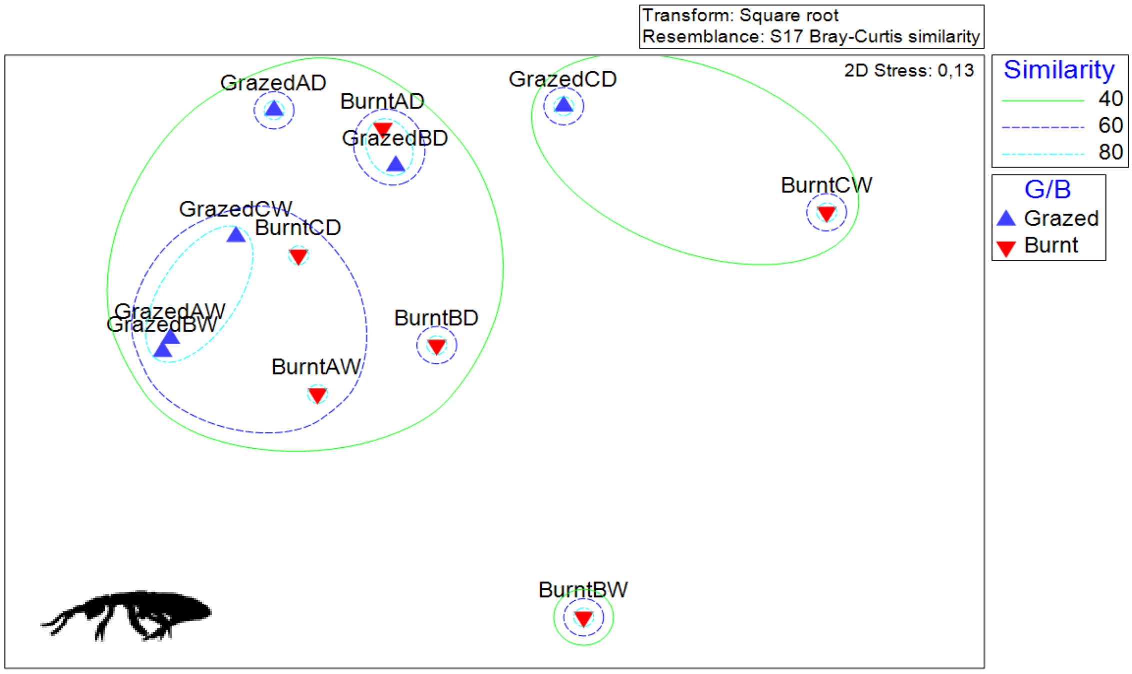

Figure 5: A non-metric Multi-Dimensional Scaling (nMDS) of springtails collected using pitfall traps in grazed and burnt sites with both seasons combined. D = dry season, W = wet season.

Litter extractions

A total of 10 species of springtails were collected using litter extractions. In the grazed sites, only two species of springtails were collected during the dry season while nine were collected during the wet season (Table 9). In the burnt sites, four species were collected in the dry season and six in the wet season. In the dry season, 18 specimens were collected, while 3,695 were collected in the wet season. Overall, grazed and burnt sites both had nine species present, with 1,939 specimens collected in the grazed sites, and 1,774 in the burnt sites (Table 9). In both seasons combined, grazed and burnt sites shared eight species, with one species each unique to the grazed and the burnt sites.

Table 9: Descriptive statistics and diversity indices for springtails collected by litter in grazed and burnt sites in both seasons. S = total species, N = total abundance, d = estimate of proportional species richness at full sampling effort, J’ = Piellou’s evenness, H’ = Shannon’s diversity estimate (log^{e}) and 1-D = Simpson’s diversity estimate.

Tax	Site	Season	S	N	d	J’	H’ (loge)	1-lambda’
Collembola	Grazed	Dry	2	7	0.5139	0.5917	0.4101	0.2857
	Burnt	Dry	4	11	1.251	0.8086	1.121	0.6727
	Grazed	Wet	9	1932	1.057	0.0996	0.2189	0.07092
	Burnt	Wet	6	1763	0.6689	0.1209	0.2166	0.08041
	Grazed combined		9	1939	1.057	0.1097	0.241	0.0776
	Burnt combined		9	1774	0.069	0.1178	0.2589	0.09177

During the dry season, *Seira* sp.2 (Entomobryidae) had the highest abundance in both grazed and burnt sites (n=6; 85% and 54% of total abundance respectively), while Entomobryidae sp.2 (Entomobryidae) had the lowest abundance in both (n=1) (Table 10). In the wet season, *Lepidocyrtus* sp.1 (Entomobryidae) dominated the grazed and burnt sites (n=1862; 96% of total abundance and n=1690; 95% of total abundance, respectively). *Seira* sp.2 (Entomobryidae) was least abundant in the grazed sites (n=1), while *Seira* sp.3 (Entomobryidae) was least abundant in the burnt sites (n=2) (Table 10). Overall, *Lepidocyrtus* sp.1 (Entomobryidae) dominated the grazed and burnt sites, with only small differences in abundances of other species between the grazed and burnt sites (Table 10). *Sinella* sp.1 (Entomobryidae) and *Cryptopygus* sp.1 (Isotomidae) had the second and third highest abundances in the burnt sites, while *Seira* sp.3 (Entomobryidae) and *Cryptopygus* sp.1 (Isotomidae) had the second and third highest abundances in the grazed sites (Table 10).

Table 10: Total abundances of springtails collected using litter extractions showing site totals, season totals and disturbance totals.

Species	Site Totals				Season Totals (Grazed+Burnt)		Disturbance Totals (Dry+Wet)		Total Abundance
	Grazed Dry	**Burnt Dry**	**Grazed Wet**	**Burnt Wet**	**Dry**	**Wet**	**Grazed**	**Burnt**	
Brachystomella sp1	0	0	2	3	0	5	2	3	5
Cryptopygus sp1	0	0	20	42	0	62	20	42	62
Ectonura sp1	0	0	0	4	0	4	0	4	4
Entomobryidae sp2	1	1	2	0	2	2	3	1	4
Entomobryidae sp3	0	0	6	0	0	6	6	0	6
Lepidocyrtus sp1	0	0	1862	1690	0	3552	1862	1690	3552
Seira sp2	6	6	1	0	12	1	7	6	13
Seira sp3	0	1	19	2	1	21	19	3	22
Sinella sp1	0	0	11	22	0	33	11	22	33
Sminthurididae sp1	0	3	9	0	3	9	9	3	12
Total abundance	7	11	1932	1763	18	3695	1939	1774	3713

In the dry season, the species richness in the burnt sites was higher than that of the grazed sites, while burnt sites also had a higher evenness than grazed sites (Table 9). Burnt sites showed a higher species diversity than grazed sites. In the wet season, the species richness in burnt sites was higher than that of grazed sites, while grazed sites had a slightly lower evenness than burnt sites (Table 9). Grazed and burnt sites showed similar species diversity. In both seasons combined, grazed sites had higher species richness than burnt sites, while burnt sites had a higher evenness than grazed sites (Table 9). Burnt sites had a higher species diversity than grazed sites.

The ANOSIM test between grazed and burnt sites across all seasons indicated a weak, non-significant separation between the grazed and burnt sites across all seasons. The same test between the dry and wet season across all disturbance types (grazed and burnt) indicated a very strong, significant separation between the two seasons (R=1 with a significance level of 1%). Results from the PERMANOVA indicated that only the season had a significant effect (p=0.006). The nMDS showed very clear grouping (Fig. 6). All six grazed and burnt sites from the wet season grouped together, while all six grazed and burnt sites from the dry season grouped together, showing clear distinction between the seasons.

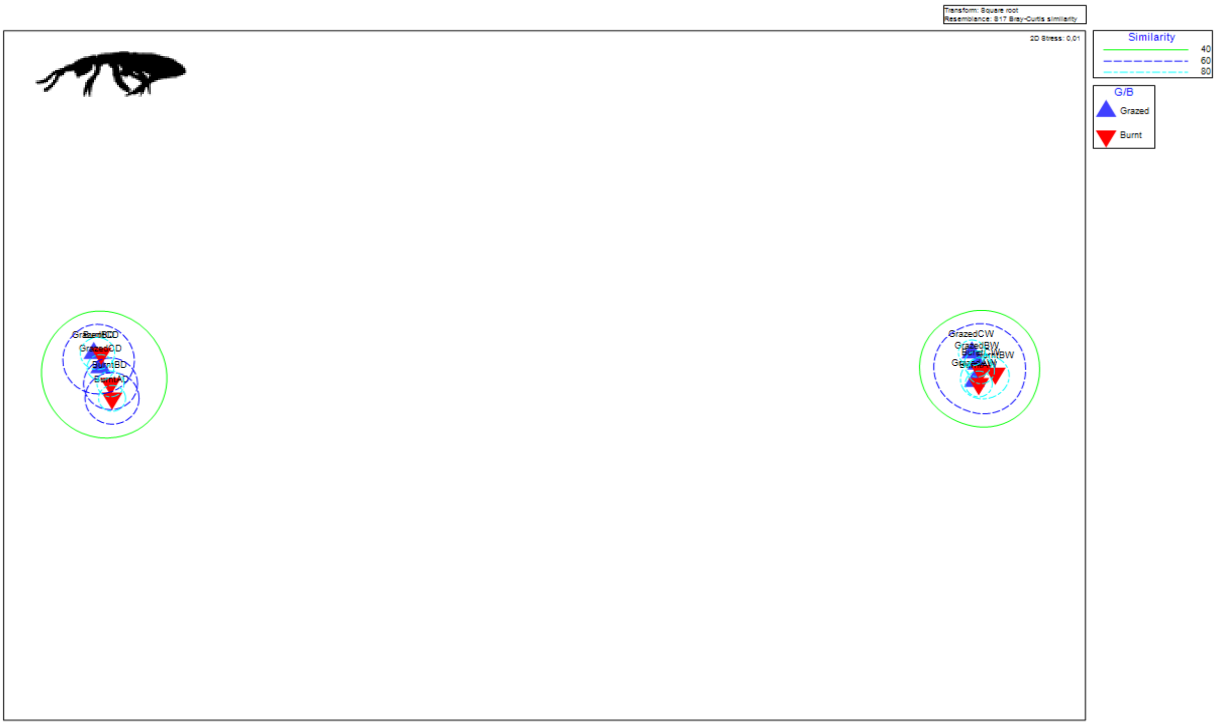

Figure 6: A non-metric Multi-Dimensional Scaling (nMDS) of springtails collected using litter extractions in grazed and burnt sites with both seasons combined, D = dry season, W = wet season.

Wasps

Pitfall traps

A total of 49 species of wasps were collected using pitfall traps (Table 11). In the grazed sites, 13 species of wasps were collected during dry season and 16 were collected during the wet season. In the burnt sites, 23 species were collected in the dry season and 32 in the wet season. The wet season was more successful in collecting wasps (Table 11). Overall, grazed sites had 28 species present, while burnt sites had 40. Grazed and burnt sites had similar abundances (Table 11). In both seasons combined, grazed and burnt sites shared 19 species, with 9 species unique to the grazed sites, and 21 species unique to the burnt sites.

Table 11: Descriptive statistics and diversity indices for wasps collected by pitfall traps in grazed and burnt sites in both seasons. S = total species, N = total abundance, d = estimate of proportional species richness at full sampling effort, J’ = Piellou’s evenness, H’ = Shannon’s diversity estimate (log^{e}) and 1-D = Simpson’s diversity estimate.

Taxa	**Site**	**Season**	**S**	**N**	**d**	**J’**	**H’ (loge)**	**1-lambda’**
Wasps	Grazed	Dry	14	124	2.692	0.7457	1.968	0.821
	Burnt	Dry	16	73	3.496	0.8575	2.377	0.8862
	Grazed	Wet	23	84	4.965	0.8145	2.554	0.8847
	Burnt	Wet	32	202	5.84	0.7851	2.721	0.8957
	Grazed combined		29	208	5.241	0.7239	2.438	0.8609
	Burnt combined		40	275	6.943	0.7939	2.929	0.9118

In the dry season, Scelionidae sp. 10 had the highest abundance in the grazed sites (n=38; 30% of total abundance), followed by Ceraphronidae sp. 7 (n=29) (Table 12). Three out of 12 species were singletons. In the burnt site, Ceraphronidae sp. 7 had the highest abundance (n=17; 23% of total abundance), followed by Scelionidae sp. 10 (n=15). Five species out of nine were singletons. In the wet season, Ceraphronidae sp. 7 had the highest abundance in the grazed sites (n=24; 28% of total abundance), followed by Scelionidae sp. 10 (n=11) (Table 12). Eleven species out of 23 were singletons. In the burnt sites, Scelionidae sp. 10 had the highest abundance (n=48; 23% of total abundance), followed by Scelionidae sp. 6 (n=35) (Table 12). Eleven species were singletons. Overall, Scelionidae sp. 10 and Ceraphronidae sp. 7 had the highest abundance in the grazed sites, while Scelionidae sp. 10 and Scelionidae sp. 6 were most abundant in the burnt sites (Table 12). The majority of other wasp species showed higher abundance in the burnt sites than in the grazed sites (Table 12).

In the dry season, the species richness in the burnt sites was higher than that of the grazed sites, while grazed sites had a slightly lower evenness than burnt sites (Table 11). Burnt sites showed higher species diversity than grazed sites. In the wet season, the species richness in burnt sites was higher than that of grazed sites, while grazed sites had a higher evenness than burnt sites (Table 11). Burnt sites showed higher species diversity than grazed sites. In both seasons combined, burnt sites showed higher species richness than grazed sites, while also showing a higher evenness than grazed sites (Table 11). Burnt sites showed a higher species diversity than grazed sites.

Table 12: Total abundance of Hymenoptera (wasps) collected using pitfall traps showing site totals, season totals and disturbance totals.

	Site Totals				Season Totals (Grazed+Burnt)		Disturbance Totals (Dry+Wet)		Total Abundance
Species	Grazed Dry	Burnt Dry	Grazed Wet	Burnt Wet	Dry	Wet	Grazed	Burnt	
Bethylidae sp. 1	5	3	2	1	8	3	7	4	11
Bethylidae sp. 2	0	0	0	2	0	2	0	2	2
Braconidae sp. 1	1	0	0	1	1	1	1	1	2
Braconidae sp. 2	0	0	0	2	0	2	0	2	2
Ceraphronidae sp. 1	0	0	0	1	0	1	0	1	1
Ceraphronidae sp. 2	0	0	0	9	0	9	0	9	9
Ceraphronidae sp. 3	0	0	0	1	0	1	0	1	1
Ceraphronidae sp. 4	0	4	0	0	4	0	0	4	4
Ceraphronidae sp. 5	0	3	2	2	3	4	2	5	7
Ceraphronidae sp. 6	0	0	3	0	0	3	3	0	3
Ceraphronidae sp. 7	29	17	24	4	46	28	53	21	74
Diapriidae sp. 1	0	3	8	11	3	19	8	14	22
Diapriidae sp. 2	0	0	2	0	0	2	2	0	2
Encyrtidae sp. 1	1	4	0	2	5	2	1	6	7
Encyrtidae sp. 2	0	1	0	0	1	0	0	1	1
Encyrtidae sp. 3	0	1	0	0	1	0	0	1	1
Eulophidae sp. 3	0	0	4	0	0	4	4	0	4
Evaniidae sp.	1	0	0	0	1	0	1	0	1
Figitidae sp. 1	0	0	1	0	0	1	1	0	1
Hymenoptera sp. 1	2	1	0	0	3	0	2	1	3
Hymenoptera sp. 2	0	1	0	0	1	0	0	1	1
Hymenoptera sp. 3	0	0	0	1	0	1	0	1	1
Hymenoptera sp. 4	0	0	0	1	0	1	0	1	1
Hymenoptera sp. 5	0	0	0	1	0	1	0	1	1
Hymenoptera sp. 6	0	0	0	1	0	1	0	1	1
Ichneumonidae sp. 1	0	0	1	0	0	1	1	0	1
Ichneumonidae sp. 2	0	0	1	2	0	3	1	2	3
Mutilidae sp. 1	7	0	6	2	7	8	13	2	15
Mutillidae sp. 2	0	0	1	0	0	1	1	0	1
Mymaridae sp. 1	0	0	0	5	0	5	0	5	5
Mymaridae sp. 2	0	0	0	11	0	11	0	11	11
Mymaridae sp. 3	0	0	0	12	0	12	0	12	12
Platygastridae sp. 1	1	4	5	11	5	16	6	15	21
Platygastridae sp. 2	0	0	1	0	0	1	1	0	1
Pompilidae sp. 1	0	0	0	3	0	3	0	3	3
Pompilidae sp. 2	0	0	1	0	0	1	1	0	1
Pteromalidae sp. 1	0	0	0	1	0	1	0	1	1
Pteromalidae sp. 2	0	1	1	0	1	1	1	1	2
Scelionidae sp. 1	0	0	0	11	0	11	0	11	11
Scelionidae sp. 2	0	0	0	2	0	2	0	2	2
Scelionidae sp. 3	0	0	0	1	0	1	0	1	1
Scelionidae sp. 4	1	0	1	1	1	2	2	1	3
Scelionidae sp. 5	7	6	0	0	13	0	7	6	13
Scelionidae sp. 6	0	0	1	35	0	36	1	35	36
Scelionidae sp. 7	0	0	3	3	0	6	3	3	6
Scelionidae sp. 8	0	0	1	8	0	9	1	8	9
Scelionidae sp. 9	15	5	1	0	20	1	16	5	21
Scelionidae sp. 10	38	15	11	48	53	59	49	63	112
Scelionidae sp. 11	16	4	3	6	20	9	19	10	29
Total abundance	124	73	84	202	197	286	208	275	483

The ANOSIM test between grazed and burnt sites across all seasons indicated a strong, significant separation between grazed and burnt sites (R=0.833, significance level of 1%). The same test between the dry and wet season across disturbance types (grazed and burnt) indicated a strong, significant separation between the two seasons as well (R=0.778, significance level of 1%). Results from the PERMANOVA indicated that that disturbance type, season and their interaction had significant effects (p=0.003, p=0.001 and p=0.014, respectively). The nMDS showed clear grouping (Fig. 7). Grazed sites in the dry season grouped with burnt sites in the dry season, showing similarity between these two groups, while also grouping with some grazed sites from the wet season. The burnt sites in the wet season grouped independently.

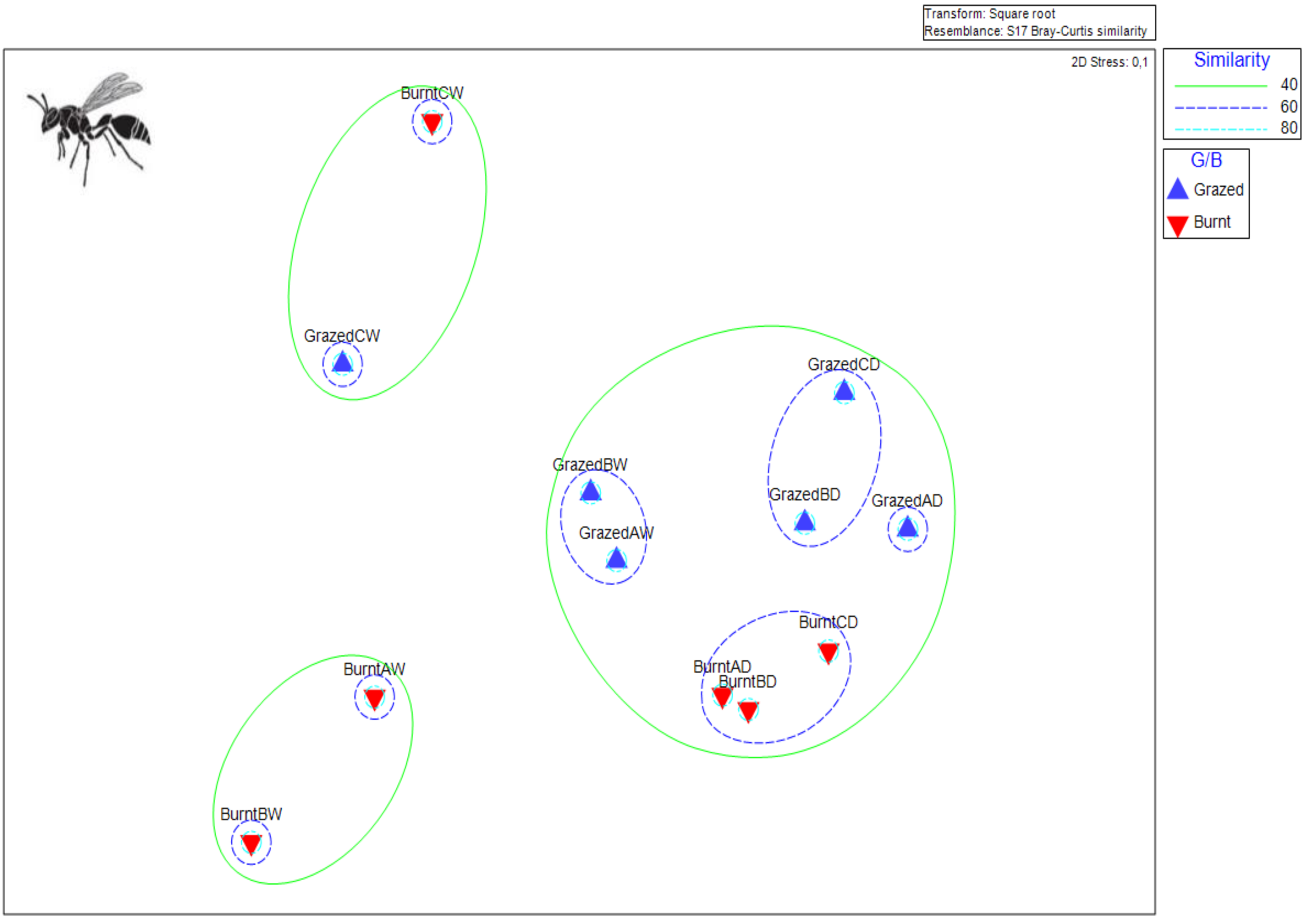

Figure 7: An nMDS of wasps collected using pitfall traps in grazed and burnt sites with both seasons combined, D = dry season, W = wet season.

Litter extractions

A total of 19 species of wasp were collected using litter extractions. In the grazed sites, only one species of wasp was collected during the dry season, while 12 were collected during the wet season (Table 13). In the burnt sites, three species were collected in the dry season and eight in the wet season. Four specimens of wasps were collected in the dry season while 37 specimens were collected in the wet season. Grazed and burnt sites had very low abundances in both seasons (Table 13). Overall, grazed sites had 13 species present and burnt sites had 10. A total of 21 specimens of wasps were collected in the grazed sites, while 20 specimens were collected in the burnt sites. In both seasons combined, grazed and burnt sites shared four species, with nine species unique to the grazed sites and six species unique to the burnt sites.

Table 13: Descriptive statistics and diversity indices for wasps collected by pitfall traps in grazed and burnt sites in both seasons. S = total species, N = total abundance, d = estimate of proportional species richness at full sampling effort, J' = Piellou's evenness, H' = Shannon's diversity estimate (log^{e}) and 1-D = Simpson's diversity estimate.

Taxa	Site	Season	S	N	d	J'	H' (loge)	1-lambda'
Wasps	Grazed	Dry	1	1	***	***	0	***
	Burnt	Dry	3	3	1.82	1	1.099	1
	Grazed	Wet	12	20	3.672	0.9042	2.247	0.9105
	Burnt	Wet	8	17	2.471	0.8919	1.855	0.8676
	Grazed combined		13	21	3.942	0.9089	2.331	0.919
	Burnt combined		10	20	3.004	0.8855	2.039	0.8842

In the dry season, only one specimen of *Agaonidae* sp.was collected in the grazed sites (Table 14). No other species were present. In the burnt sites, all of the species present were singletons (n=1). In the wet season, *Ceraphronidae* sp. 7 was most abundant (n=5; 25% of total abundance) in the grazed sites, followed by *Scelionidae* sp. 11 (n=4) (Fig. 14). Nine out of 12 species were singletons. In the burnt sites, *Ceraphronidae* sp. 7, *Scelionidae* sp. 1 and *Scelionidae* sp. 11 all had the highest abundances of n=4 (each being 23% of total abundance), while five out of eight species were singletons (n=1) (Table 14). Overall, wasp *Ceraphronidae* sp. 7 and *Scelionidae* sp. 1 were most abundant in the grazed sites, while *Ceraphronidae* sp. 7, *Scelionidae* sp. 1, and *Scelionidae* sp. 11 had the highest abundances in the burnt sites (Table 14). Most of the species present in both sites were singletons.

In the dry season, the species richness in the burnt sites was higher than that of the grazed sites (Table 13). Consequently, the burnt sites were more diverse and had higher evenness. In the wet season, the species richness in grazed sites was higher than that of burnt sites, while grazed sites had a slightly higher evenness than burnt sites (Table 13). Overall, grazed sites showed higher species richness than burnt sites, while also showing higher evenness than brunt sites (Table 13). Grazed sites had higher species diversity than burnt sites overall.

Table 14: Total abundance of Hymenoptera (wasps) collected using litter extractions showing site totals, season totals and disturbance totals.

	Site Totals				Season Totals (Grazed+Burnt)		Disturbance Totals (Dry+Wet)		Total Abundance
Species	**Grazed Dry**	**Burnt Dry**	**Grazed Wet**	**Burnt Wet**	**Dry**	**Wet**	**Grazed**	**Burnt**	
Agaonidae sp.	1	0	0	0	1	0	1	0	1
Bethylidae sp. 1	0	1	0	0	1	0	0	1	1
Braconidae sp. 1	0	0	0	1	0	1	0	1	1
Ceraphronidae sp. 1	0	0	0	1	0	1	0	1	1
Ceraphronidae sp. 2	0	0	0	1	0	1	0	1	1
Ceraphronidae sp. 4	0	0	1	0	0	1	1	0	1
Ceraphronidae sp. 6	0	0	1	0	0	1	1	0	1
Ceraphronidae sp. 7	0	1	5	4	1	9	5	5	10
Eulophidae sp. 1	0	0	1	0	0	1	1	0	1
Eulophidae sp. 2	0	0	1	0	0	1	1	0	1
Eulophidae sp. 3	0	0	1	0	0	1	1	0	1
Mymaridae sp. 1	0	0	1	0	0	1	1	0	1
Platygastridae sp. 1	0	0	1	1	0	2	1	1	2
Scelionidae sp. 1	0	0	0	4	0	4	0	4	4
Scelionidae sp. 6	0	1	2	0	1	2	2	1	3
Scelionidae sp. 7	0	0	0	1	0	1	0	1	1
Scelionidae sp. 9	0	0	1	0	0	1	1	0	1
Scelionidae sp. 10	0	0	1	0	0	1	1	0	1
Scelionidae sp. 11	0	0	4	4	0	8	4	4	8
Total abundance	0	3	15	13	3	28	15	16	31

The ANOSIM test between grazed and burnt sites across all seasons indicated a very weak, non-significant difference between grazed and burnt sites across all seasons. The same test between the dry and wet season across all disturbance types (grazed and burnt) indicated a weak, non-significant separation between the two seasons. The nMDS showed no grouping (Fig. 8). Although groupings may appear evident based on the nMDS ordination, the distances between the seemingly grouped sites only appear so due to the large distance between the two dry season grazed sites and one dry season burnt site, and the remaining sites. Consequently, the large proportion of singletons will make it very difficult to recognize any clear patterns. Even when the three outliers were removed (BurntCD, GrazedAD and Grazed BD), the remaining sites grouped together with no discernible pattern.

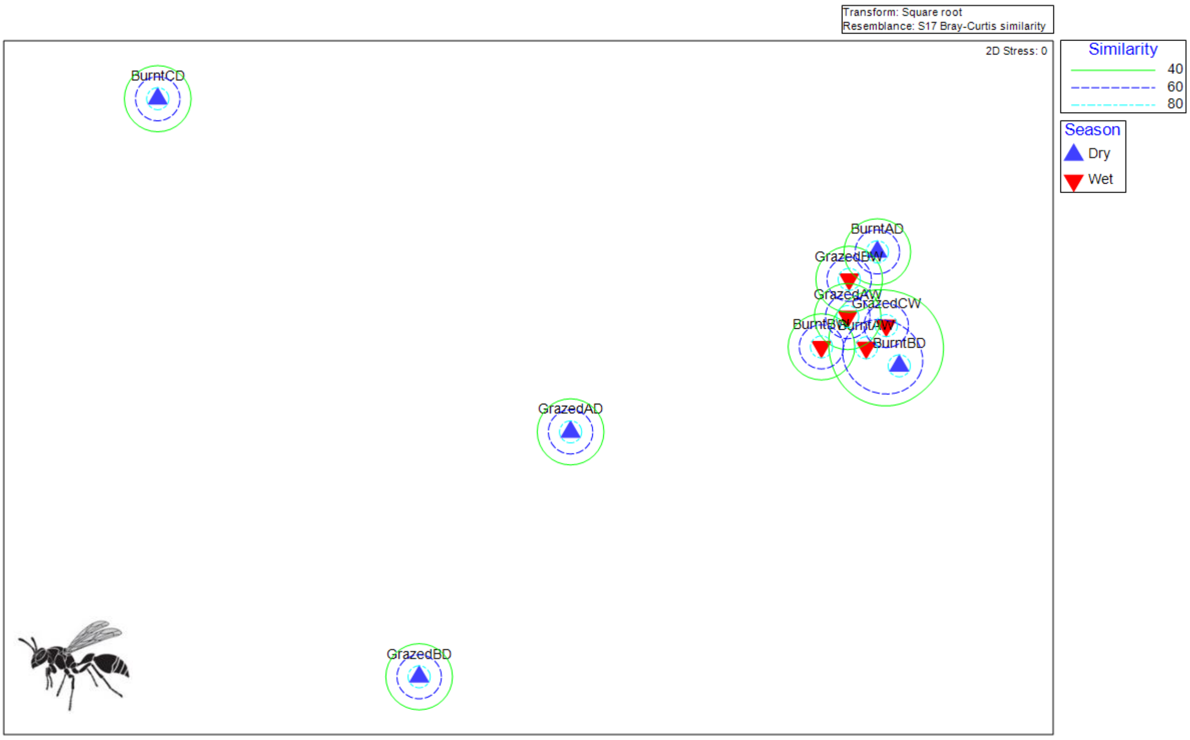

Figure 8*:* A non-metric Multi-Dimensional Scaling *(*nMDS) of wasps collected using litter extractions in grazed and burnt sites with both seasons combined, D = dry season, W = wet season.

Spiders

Pitfall traps

A total of 69 spider species were collected using pitfall traps, comprising 19 families and 45 genera. In the grazed sites, 27 species of spiders were collected during dry season, while 33 were collected during the wet season (Table 15). In the burnt sites, 21 species were collected in the dry season and 19 in the wet season. In the dry season, fewer specimens were collected than in the wet season (Table 15). Both grazed and burnt sites showed a higher abundance of spiders in the wet season (n=105 and n=154, respectively) than in the dry season (n=57 and n=85, respectively) (Table 15). Overall, grazed sites had 47 species present, with burnt sites having 35 species. A total of 162 specimens were collected in grazed sites, and 239 in burnt sites (Table 15). In both seasons combined, grazed and burnt sites shared 16 species, with 31 species unique to the grazed sites and 19 species unique to the burnt sites.

Table 15: Descriptive statistics and diversity indices for spiders collected by pitfall traps in grazed and burnt sites in both seasons. S = total species, N = total abundance, d = estimate of proportional species richness at full sampling effort, J’ = Piellou’s evenness, H’ = Shannon’s diversity estimate (log^{e}) and 1-D = Simpson’s diversity estimate.

Taxa	Site	Season	S	N	d	J’	H’ (loge)	1-lambda’
Araneae	Grazed	Dry	27	57	6.431	0.8465	2.79	0.8941
	Burnt	Dry	21	85	4.502	0.776	2.363	0.8471
	Grazed	Wet	33	105	6.876	0.7242	2.532	0.8128
	Burnt	Wet	19	154	3.574	0.5176	1.524	0.5724
	Grazed combined		47	162	9.042	0.8054	3.101	0.9061
	Burnt combined		35	239	6.208	0.6786	2.413	0.8026

During the dry season, *Proevippa wanlessi* (Lycosidae) was most abundant in both grazed and burnt sites (n=18 and n=30; 31.5% and 35% of total abundance, respectively), with 15 out of 27 species being singletons in the grazed site, and 11 out of 33 species being singletons in the burnt sites (Table 16). During the wet season, *Hippasa australis* (Lycosidae) was most abundant in the grazed sites (n=44; 41% of total abundance), while 19 out of 21 species were singletons. In the burnt sites, *Hippasa funerea* (Lycosidae) was most abundant (n=99; 64% of total abundance) with six out of 19 species were singletons (Table 16). Overall, *P. wanlessi* and *H. australis* were most abundant in the grazed sites, while *P. wanlessi* and *H. funerea* were most abundant in the burnt sites (Table 16). Grazed and burnt communities had a higher number of unique species than shared species.

In the dry season, the species richness in the grazed sites was higher than that of the burnt sites, while grazed sites also had a slightly higher evenness than burnt sites (Table 15). Grazed sites showed higher species diversity than the burnt sites. In the wet season, the species richness in the grazed sites was higher than that of the burnt sites, while grazed sites also had a higher evenness than burnt sites (Table 15). Grazed sites showed higher species diversity than the burnt sites in the wet season. In both seasons combined, grazed sites showed higher species richness than burnt sites while also showing a higher evenness than burnt sites. Grazed sites had higher species diversity than burnt sites (Table 15).

The ANOSIM test between grazed and burnt sites across all seasons indicated a strong, significant separation between grazed and burnt sites across all seasons (R=0.667, significance level of 2%). The same test between the dry and wet seasons across all disturbance types (grazed and burnt) indicated a very strong, significant separation between the two seasons as well (R=0.981, significance level of 1%). Results from the PERMANOVA indicated that that disturbance type, season and their interaction had significant effects (p=0.002, p=0.003 and p=0.002, respectively). The nMDS showed clear grouping

(Fig. 9). All grazed and burnt sites in the dry season grouped together, suggesting higher similarity between these sites. All three grazed sites from the wet season grouped together, while all three burnt sites in the wet season grouped together, independently. Clear separation can be seen between the grazed and burnt sites during the wet season (Table 15).

Table 16*:* Total abundance of spiders collected using pitfall traps showing site totals, season totals and disturbance totals.

	Site Totals				Season Totals (Grazed+Burnt)		Disturbance Totals (Dry+Wet)		Total Abundance
Species	**Grazed Dry**	**Burnt Dry**	**Grazed Wet**	**Burnt Wet**	**Dry**	**Wet**	**Grazed**	**Burnt**	
Allocosa exserta	0	5	0	0	5	0	0	5	5
Allocosa faberrima	1	1	1	1	2	2	2	2	4
Allocosa lawrencei	0	1	0	0	1	0	0	1	1
Allocosa tuberculipalpa	2	7	0	0	9	0	2	7	9
Allocosa umtalica	1	0	0	0	1	0	1	0	1
Amusia cataracta	0	0	9	0	0	9	9	0	9
Apochinomma formicaeforme	0	0	0	1	0	1	0	1	1
Asemesthes lineatus	1	0	0	0	1	0	1	0	1
Benoitia sp.1	0	0	1	0	0	1	1	0	1
Camillina sp.1	0	1	3	2	1	5	3	3	6
Camillina sp.2	0	0	0	3	0	3	0	3	3
Ceratinopsis idanrensis	0	0	1	0	0	1	1	0	1
Ceratinopsis sp.1	2	0	2	2	2	4	4	2	6
Clubiona sp.1	0	3	0	0	3	0	0	3	3
Copa flavoplumosa	0	0	2	0	0	2	2	0	2
Copa sp.2	0	0	3	0	0	3	3	0	3
Diores russelli	0	2	0	0	2	0	0	2	2
Diores sp.2	1	6	1	2	7	3	2	8	10
Drassodes sp.1	0	0	0	5	0	5	0	5	5
Echemus erutus	1	10	0	0	11	0	1	10	11
Eleleis limpopo	0	1	0	0	1	0	0	1	1
Evarcha ignea	0	0	0	1	0	1	0	1	1
Evarcha sp.2	1	0	0	0	1	0	1	0	1
Fuchiba aquilonia	1	0	0	0	1	0	1	0	1
Gamasomorpha sp.1	0	1	0	0	1	0	0	1	1
Helsdingenia extensa	2	0	2	0	2	2	4	0	4
Helsdingenia sp.2	0	0	1	0	0	1	1	0	1
Heriaeus crassispinus	0	0	1	4	0	5	1	4	5
Hippasa australis	0	0	44	0	0	44	44	0	44
Hippasa funerea	0	0	0	99	0	99	0	99	99
Hyllus dotatus	1	0	2	0	1	2	3	0	3
Langona bethae	0	0	1	0	0	1	1	0	1
Langona warchalowskii	2	5	1	3	7	4	3	8	11
Limoneta sp.1	0	0	0	2	0	2	0	2	2
Loxosceles simillima	0	0	1	0	0	1	1	0	1
Lycosa praestans	1	1	0	0	2	0	1	1	2
Manzuma botswana	1	0	0	0	1	0	1	0	1
Mermessus sp.1	0	1	1	0	1	1	1	1	2
Metaleptyphantes sp.1	2	0	1	0	2	1	3	0	3
Micaria sp.1	0	1	0	0	1	0	0	1	1
Nigorella hirsuta	1	0	3	0	1	3	4	0	4
Nomisia sp.2	0	0	1	0	0	1	1	0	1
Nomisia varia	2	0	2	0	2	2	4	0	4
Ostearius molanopygius	2	0	2	0	2	2	4	0	4
Oxyopes jacksoni	2	0	0	0	2	0	2	0	2
Oxyopes longispinosus	0	0	7	0	0	7	7	0	7
Oxyopes vogelsangeri	0	3	0	0	3	0	0	3	3
Palpimanus sp.1	1	1	0	0	2	0	1	1	2
Pardosa crassipalpis	0	0	1	0	0	1	1	0	1
Pardosa sp.1	2	1	1	0	3	1	3	1	4
Pellenes sp.1	0	0	0	1	0	1	0	1	1
Proevippa sp.2	1	0	0	0	1	0	1	0	1
Proevippa wanlessi	18	30	0	0	48	0	18	30	48
Rastellus africanus	0	0	0	4	0	4	0	4	4
Rhaeboctesis denotatus	1	0	0	0	1	0	1	0	1
Scytodes maritima	0	0	1	0	0	1	1	0	1
Thyenula sp.1	0	3	3	0	3	3	3	3	6
Trabea heteroculata	1	0	1	0	1	1	2	0	2
Trichothyse sp.1	0	0	2	0	0	2	2	0	2
Voraptus sp.1	0	0	0	1	0	1	0	1	1
Xysticus natalensis	0	0	1	18	0	19	1	18	19
Xysticus sp.2	0	0	1	0	0	1	1	0	1
Zelotes caldarius	2	0	0	0	2	0	2	0	2
Zelotes corrugatus	4	1	1	1	5	2	5	2	7
Zelotes sp.3	0	0	0	2	0	2	0	2	2
Zelotes sp.4	0	0	0	2	0	2	0	2	2
Total abundance	57	85	105	154	142	259	162	239	401

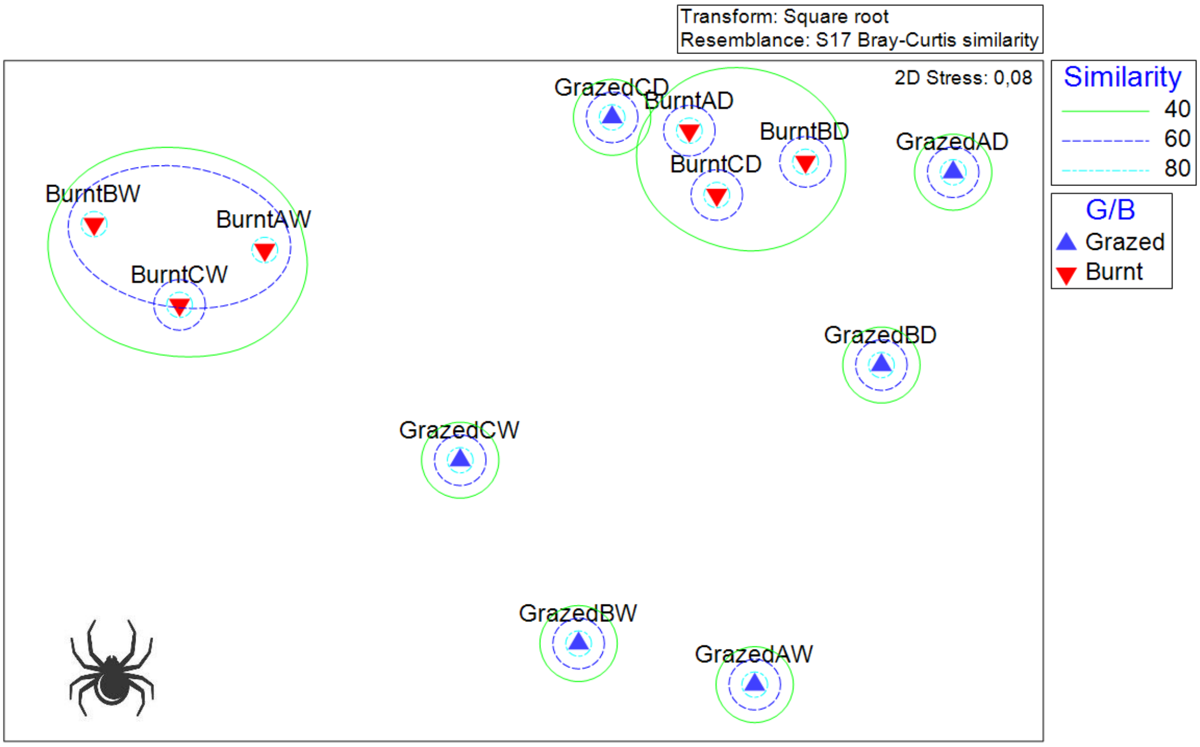

Figure 9: A non-metric Multi-Dimensional Scaling (nMDS*)* for spiders collected using pitfall traps in grazed and burnt sites with both seasons combined. D = dry season, W = wet season.

Litter extractions

A total of 32 species of spiders were collected using litter extractions, comprising 12 families and 23 genera. In the grazed sites, nine species of spiders were collected in both the dry and wet season, while in the burnt sites, 14 species were collected in the dry season and nine in the wet season (Table 17). A total of 62 specimens were collected in the dry season, while 86 specimens were collected in the wet season. Overall, grazed sites had 14 species present, and burnt sites 20. A total of 54 specimens were collected in the grazed sites, while 68 specimens were collected in the burnt sites (Table 17). In both seasons combined, grazed and burnt sites shared five species, with nine species unique to the grazed sites and 15 species unique to the burnt sites.

Table 17: Descriptive statistics and diversity indices for spiders collected by pitfall traps in grazed and burnt sites in both seasons. S = total species, N = total abundance, d = estimate of proportional species richness at full sampling effort, J' = Piellou's evenness, H' = Shannon's diversity estimate (log^{e}) and 1-D = Simpson's diversity estimate.

Taxa	Site	Season	S	N	d	J'	H' (loge)	1-lambda'
Araneae	Grazed	Dry	9	26	2.455	0.8638	1.898	0.8462
	Burnt	Dry	14	34	3.687	0.8608	2.272	0.8877
	Grazed	Wet	9	28	2.401	0.7718	1.696	0.7593
	Burnt	Wet	9	34	2.269	0.7006	1.539	0.6756
	Grazed combined		14	54	3.259	0.7836	2.068	0.8176
	Burnt combined		20	68	4.503	0.7316	2.192	0.8042

In the dry season, *Camillina* sp.1 was most abundant in both grazed and burnt sites (n=8; 30% of total abundance and n=9; 26% of total abundance, respectively) (Table 18). Grazed sites had four out of 10 species as singletons, while burnt sites had nine out of 15 species as singletons. In the wet season, *Camillina* sp.1 was most abundant in both grazed and burnt sites (n=13; 46% of total abundance and n=19; 56% of total abundance, respectively) (Table 18). Grazed sites had five out of 10 species as singletons, while burnt sites had four out of 10 species as singletons. Overall, *Camillina* sp.1 dominated the grazed sites, with *Ceratinopsis idanrensis* and *Rastellus* sp.1 having the second highest abundances (Table 18). *Camillina* sp.1 dominated the burnt sites while *Rastellus africanus* had the second highest abundance (Table 18).

In the dry season, the species richness in the burnt sites was higher than that of the grazed sites, while grazed and burnt sites had almost identical evenness (Table 17). Burnt sites showed a higher species diversity than grazed sites, although only slightly. In the wet season, the species richness in grazed sites was higher than burnt sites, while grazed sites had a higher evenness than burnt sites (Table 17). Grazed sites showed higher species diversity than burnt sites. In both seasons combined, burnt sites showed higher species richness than grazed sites, but grazed sites had higher evenness than burnt sites (Table 17). According to Shannon's index, burnt sites had a higher species diversity than grazed sites, while Simpson's index indicated the opposite, with grazed sites having a higher species diversity than burnt sites, although the difference is small.

Table 18: Total abundance of spiders collected using litter extractions showing site totals, season totals and disturbance totals.

Species	Site Totals				Season Totals (Grazed+Burnt)		Disturbance Totals (Dry+Wet)		Total Abundance
	Grazed Dry	**Burnt Dry**	**Grazed Wet**	**Burnt Wet**	**Dry**	**Wet**	**Grazed**	**Burnt**	
Camillina sp.1	8	9	13	19	17	32	21	28	49
Allocosa faberrima	0	0	0	1	0	1	0	1	1
Allocosa sp.4	0	0	0	1	0	1	0	1	1
Camillina sp.2	2	0	1	0	2	1	3	0	3
Ceratinopsis sp.1	6	0	0	0	6	0	6	0	6
Diores sp.2	0	3	0	2	3	2	0	5	5
Drassodes sp.1	0	0	0	3	0	3	0	3	3
Dresserus sp.1	0	0	0	1	0	1	0	1	1
Gamasomorpha sp.	0	0	1	0	0	1	1	0	1
Heliophanus sp.1	0	1	0	0	1	0	0	1	1
Helsdingenia sp.2	1	0	0	0	1	0	1	0	1
Heriaeus crassispinus	0	4	0	0	4	0	0	4	4
Heriaeus sp.2	0	1	0	0	1	0	0	1	1
Hogna sp.1	0	1	0	0	1	0	0	1	1
Limoneta sp.1	0	0	4	0	0	4	4	0	4
Linyphiidae sp.1	0	0	1	1	0	2	1	1	2
Linyphiidae sp.2	0	0	0	2	0	2	0	2	2
Mermessus sp.1	1	0	2	0	1	2	3	0	3
Nomisia sp.2	3	0	0	0	3	0	3	0	3
Palpimanus sp.1	0	1	0	0	1	0	0	1	1
Pellenes sp.1	0	1	1	0	1	1	1	1	2
Rastellus africanus	0	6	0	4	6	4	0	10	10
Rastellus sp.1	3	0	4	0	3	4	7	0	7
Spermophora sp.1	1	0	0	0	1	0	1	0	1
Theuma sp.1	0	1	0	0	1	0	0	1	1
Xysticus sp.2	1	3	0	0	4	0	1	3	4
Zelotes caldarius	0	1	0	0	1	0	0	1	1
Zelotes corrugatus	0	1	0	0	1	0	0	1	1
Zelotes sp.4	0	1	1	0	1	1	1	1	2
Total abundance	26	34	28	34	60	62	54	68	122

The ANOSIM test between grazed and burnt sites across all seasons indicated a relatively strong, significant separation between grazed and burnt sites across all seasons (R=0.509, significance level of 2%). The same test between the dry and wet seasons across all disturbance types (grazed and burnt) indicated a weak, non-significant separation between the two seasons. Results from the PERMANOVA indicated that the disturbance type and the season had a significant interaction (p=0.014 and p=0.013, respectively). Then nMDS showed some distinct groupings (Fig. 10). Grazed sites in the wet season grouped together, with burnt sites from both seasons grouping together separately. Three burnt sites had no similarity to any other sites, while all three grazed sites from the dry season also showed no similarity (Fig. 10).

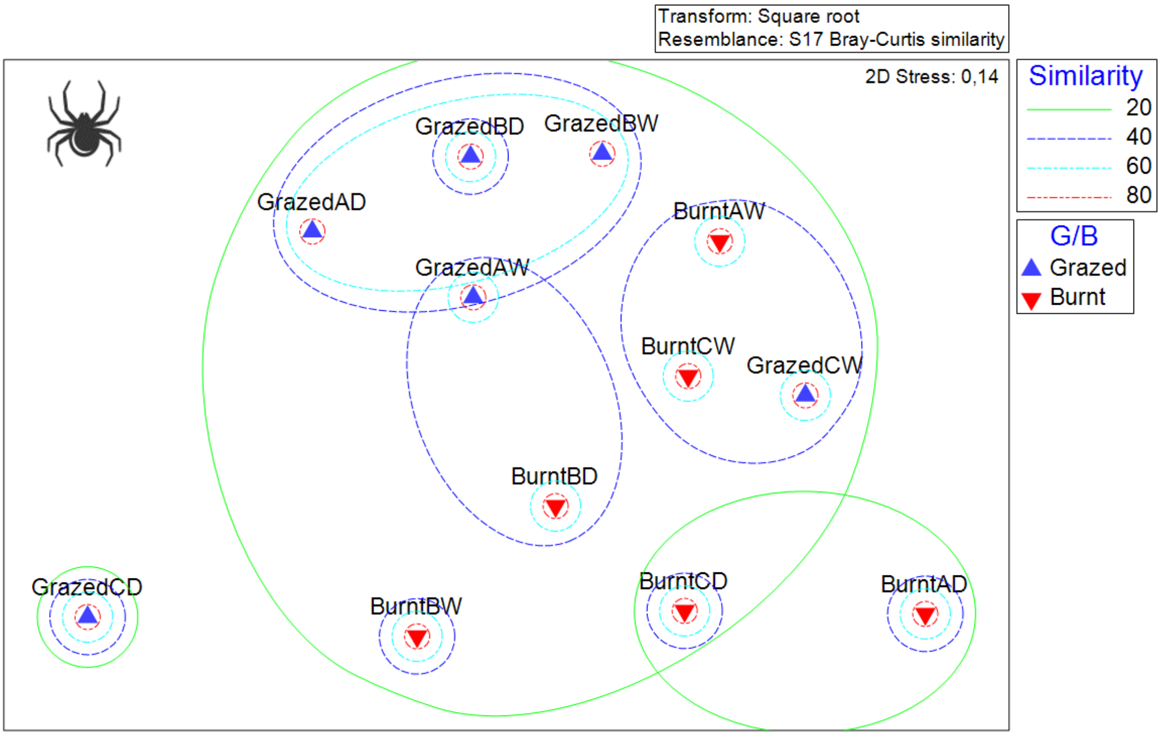

Figure 10: A non-metric Multi-Dimensional Scaling (nMDS) of spiders collected using litter extractions in grazed and burnt sites with both seasons combined. D = dry season, W = wet season.

Discussion

This study aimed to assess how different anthropogenic disturbances shape terrestrial arthropod communities in the Lower-panhandle of the Okavango Delta, Botswana. While assessing four focal taxa, namely ants (Formicidae), springtails (Collembola), wasps (Hymenoptera) and spiders (Araneae), results varied between taxa and between trapping methods. This was not unexpected, as it is well established that arthropods, insects in particular, have variable responses to disturbances, especially fire (Pryke and Samways, 2012), and that trapping methods may target or exclude species to varying degrees.

Ant and springtail communities were found to be strongly affected by seasonality, but not by disturbance types, although differences in community composition between grazed and burnt sites were evident. Ants are known to be more resilient to disturbances (Pryke and Samways, 2012), as they can retreat into below-ground refugia, and this may explain the similar abundances collected across both sites using both trapping methods. Similarly, certain groups of springtails are resilient to fire, especially during dry periods when they are inactive (Janion-Scheepers *et al*., 2016). Wasp and spider communities were found to be strongly affected by both seasonality and disturbance type, which could be due to some groups migrating vertically in the surface layer and on vegetation due to difference in available moisture between seasons (Hassall *et al*., 1986) as well as alterations in behaviour to exploit resources available on the surface (Telford and Dangerfield, 1993). Most wasps are also able to fly, which means they may be more likely to escape fires and grazing activity than ground-living arthropods, and may recolonize heavily disturbed sites more easily. The uncertainty regarding seasonal behaviour of these two groups and differences in life history stages during sampling severely limits the inferences that can be made from these results. It is likely that the factors mentioned, along with a myriad of others (for example habitat structure, water availability, competition and other biotic factors) interact to influence the abundances of species in these communities in more complex and nuanced ways (Lawton and McGarvin, 1986). Over intermediate time-scales, the effects of burning are varied (Swengel, 2001), with some taxa persisting at lower abundances, some resembling control sites and others increasing in abundance post-burn.

The wet season showed an overall higher species richness and abundance of taxa under investigation, suggesting that it may be more effective to sample during the wet season when assessing arthropod diversity in the Okavango Delta. These results are congruent to results found by Pryke and Samways (2012) with studied taxa being more resilient to fire in terms of their species richness than in terms of their abundance. Pitfall traps proved to be generally much more effective at collecting large numbers of specimens and species, although litter extractions did collect some species that were not collected using pitfall traps. This demonstrates the benefit of using multiple trapping methods during baseline surveys or general biodiversity monitoring. Unexpectedly, pitfall trapping and litter extractions produced a large number of wasp species and proved to be very effective in collecting soil-living wasps.

Ants

Pheidole sp.1 dominated both grazed and burnt sites, having exceptionally high abundances compared to other species present. After *Pheidole* sp.1, *Myrmicaria* sp.1 and *Monomorium* sp.1 had the highest abundances in the grazed sites, with all of the other species showing abundances of less than 100. In burnt sites, more species comprised larger proportions of the total abundance, but eight species that were present in the grazed site were absent in the burnt sites, while only one species was present in the burnt site and absent in the grazed sites. This suggests that as the burnt sites recover post-fire, more species will have a chance to re-colonise and increase the species richness and diversity to levels more similar to grazed sites. These burnt sites seem to be in the process of recolonisation, with Majer (1985) having found increases in ant species diversity during post-mining recovery, before the sites were dominated by *Pheidole megacephala*, after which diversity decreased. The same phenomenon may be underway in the burnt sites of the Delta, where other *Pheidole* species have become dominant, suggesting that these sites are in the late stages of this observed succession.

From litter extractions, grazed sites had 12 species present, while burnt sites had only seven. Ant abundances were also very similar between grazed and burnt sites, while grazed sites showed higher species richness and species diversity, and lower evenness than burnt sites. *Pheidole* sp. 1 was most abundant in the burnt sites while having the second highest abundance in the grazed sites. *Plagiolepis* sp.1 was the most abundant ant species in the grazed sites, having the second highest abundance in the burnt sites, suggesting that its populations were still recovering from the impact of the fire and that *Pheidole* sp.1 populations may be more dominant under high disturbance. The latter may become less dominant under lower levels of disturbance (grazing in this case), or it was able to escape the impacts of the latest fire more effectively than *Plagiolepis* sp.1. This trend may also be due to *Pheidole* sp.1 being more resilient to fire.

Pryke and Samways (2012) observed no difference in species richness between burnt and control sites, but did confirm higher abundance of ants in the burnt sites, as reflected in the results of this study. This suggests that although ants are known to be resilient to fire (Parr *et al*., 2004; Pryke and Samways, 2012), the similarity in abundances in both pitfall traps and litter extractions, along with grazed sites being more species rich and diverse, may imply that fire has a more detrimental effect on ant communities' composition and diversity than on abundance, contradicting findings by McGeoch *et al*., (2011) that species richness is less impacted than abundance. Grazing under low-intensity has shown to not affect ant species richness, diversity or abundance in a variety of grazed systems (Whitford *et al*. 1999), while Dennis *et al*. (1998) highlighted the value of higher habitat heterogeneity in less-intensive grazed systems. Although ants may be able to survive fire-based disturbances relatively well, the loss of rarer species may have a more prominent effect on community composition and diversity in burnt sites than in grazed sites. Gerlach and Samways (2013) note that pitfall trapping, although effective for trapping ants, may only record a subset of this group, and other techniques should be used in conjunction. This group remains valuable during assessments of various aspects of an ecosystem, even if they are poor indicators of species richness of other taxa (Gerlach and Samways 2013).

Springtails

From pitfall trap results, springtail abundances were almost three times higher in grazed sites than in burnt sites, but burnt sites had higher species richness, evenness and diversity. Grazed sites had higher abundances of springtails in the dry season, with a significant reduction in abundance in the wet season. *Seira* sp.2 (Entomobryidae) was most abundant in both grazed and burnt sites, with this species' abundance being more than three times higher in grazed sites than in burnt sites. This may imply that *Seira* sp.2 (Entomobryidae) may be more adapted to the dry season and associated desiccation, which seems to be a characteristic of this genus (Liu *et al*., 2021). Burnt sites also showed a reduction in springtail abundance from the dry season to the wet season, suggesting this community may also be dominated by more desiccation-tolerant species of springtail, with their abundance decreasing as the burnt sites recover, with more vegetation and higher moisture levels (Liu *et al*., 2021).

Pitfall data may suggest that although grazed sites had a higher abundance, springtail communities in the burnt sites were more species rich, even and diverse, possibly due to diversity peaking over moderate disturbance levels (Rosenzweig, 1995). However, litter extractions suggested otherwise. With similar abundances in both disturbance types, burnt sites having higher evenness and species diversity, and grazed sites having a higher species richness, results somewhat corroborate findings by Janion-Scheepers *et al*. (2016), where many species appeared to be resistant or recover very quickly after fire. These authors also found variable responses from free-living, soil-dwelling and surface-dwelling species, with soil-dwelling communities undergoing very little change during fires, mainly due to their ability to retreat into the soil (Janion-Scheepers *et al*., 2016). The changes in abundances between the dry and the wet season may suggest that certain highly abundant species are more abundant during drier conditions, with species being adapted for those conditions, and that their abundances decline during the wet season, while this observation may also be due to excess of available refugia due to suspected low fire intensity, allowing species to escape and avoid the fire on Wh'ere Island. This could also be due to these species utilising different habitats or niches within a habitat, or that these communities may shift seasonally in unknown ways. Springtails are known to be sensitive to both litter depth and type (Hopkin, 1997) and as such, the sampling methods employed may not have accounted for these variations.

Based on the significant effects of season on the differences observed, it was observed that springtail communities between grazed and burnt sites do not differ significantly, but do show differences in richness, diversity and evenness. These results, varying between different sampling methods, may serve as another example why it is important to utilise various trapping methods in conjunction when investigating differences in arthropod communities.

Wasps

Pitfall trap results found burnt sites to have a higher abundance of wasps than grazed sites, while litter extractions found both disturbance types to have similar abundances. Grazed sites had marginally more species present than burnt sites in the pitfalls, yet burnt sites had higher species richness, evenness and diversity. From litter extractions, grazed sites were found to have higher species richness, evenness and diversity, contrasting the results from pitfall traps. In pitfall traps, 19 species were shared between disturbance types, grazed sites had 10 unique species, while burnt sites had 21 unique species. In the litter extractions, four species were shared between the disturbance types, with nine species unique to the grazed sites and six species unique to the burnt sites, indicating that these burnt communities each have more unique species than those shared, or unique to grazed sites. A large proportion of wasps collected in pitfall and litter extractions were singletons, potentially due to high levels of rarity or the fact that pitfall traps are not conventionally used to target Hymenoptera other than Formicidae, and thus misrepresenting the true community. This is also concerning, as specialist species can be more subject to local extinction due to their low abundances (Clemente *et al*., 2019)

Two different species were found to be dominant in the grazed and burnt sites, Ceraphronidae sp. 7 in the grazed and Scelionidae sp. 10 in the burnt sites. Burnt sites had a higher proportion of other species contributing more to the total abundance, while grazed sites had only two species that contributed the largest portion of the total abundance. To add to the contradictory results obtained on this taxon, strong separation was found between both disturbance type and season in pitfall traps, while no separation was found at all between groups in the litter extractions. From pitfall traps, burnt sites were found to have higher species richness and diversity and contained more unique species, suggesting that wasp communities in the two disturbance types are unique, and that the disturbance types have differential impacts on these wasp communities, leading to different community compositions. The absence of most of the singletons or “rare” species in the grazed sites may be cause for concern, as an indicator of the potential for grazing to be more impactful on the wasp community than burning. The parasitic wasps are an exceptionally large group, although they are not the only insect parasitoids (Shaw, 2006) and most likely made out a large proportion of the wasps sampled during this study. Parasitic wasps operate at a high trophic level, tend to be very specialised and is dependent on host populations, and their food plants, potentially negatively impacted by grazing, burning and climate change (Giron *et al*., 2002; Shaw, 2006). The abundance of each species may well be strongly associated with how the host populations responds to various disturbances and the resulting availability of host foodplants. Host availability is a key factor to consider when assessing parasitic wasp communities, but other untested factors like host density also may have a strong influence on wasp abundances, along with a range of environmental factors not considered in this study.

This may again be a case of diversity peaking over moderate disturbance levels (Rosenzweig, 1995), as the intensity and severity of the fire that burnt the burnt sites could not be determined and so may have been more moderate than initially suspected. Many insect species globally are known to be attracted to fire or smoke, and some wasp species may oviposit in freshly burnt wood (Frost, 1984). Additionally, the impact of disturbance in grazed sites may have been limited, while moderate disturbance in the form of fire may have been beneficial to wasp communities observed here, as fire is known to have both positive and negative impacts on all arthropod communities (Whelan, 1994). It is important to note that there may be a large number of abiotic and biotic factors that may have an additive and multiplicative affect to the results shown here and it notoriously difficult to assess which one these is most impactful (Dangerfield 1997), especially for flying taxa like wasps.

Spiders

From pitfall traps, burnt sites had a higher abundance of spiders overall than grazed sites, although grazed sites were much more species rich, diverse, and had a higher number of species present. From litter extraction, results found burnt sites to have a higher abundance and more species present as well as higher species richness, but less even than grazed sites. The incongruence between pitfall trap and litter extraction results may be due to the sampling technique employed, as litter extraction targets smaller individuals and burnt sites have notably less litter available post-burn.

Proevippa wanlessi was second most abundant in pitfall traps in both sites, with *Hippasa australis* most abundant in the grazed sites and *Hippasa funerea* most abundant in the burnt sites. Corroborating the findings of Alonso and Nordin (2003), van den Berg and Dippenaar-Schoeman (1991) and Dippenaar-Schoeman *et al*. (1989), spiders were dominated by Gnaphosidae and Lycosidae in both grazed and burnt sites. In the current study, Gnaphosidae was represented by 17 species, while Lycosidae was represented by 14 species, across both seasons and disturbance types. This reflects similar findings by Russel-Smith (1981) that Gnaphosidae was the most diverse family found on the study sites involved. Sixteen spider species were shared between disturbance types in the pitfall traps, with 31 unique to the grazed sites, and 19 unique to the burnt sites. Litter extractions shared five species, with grazed sites having nine unique species and burnt sites 15. The 76 species found during this study was found to be higher than previous findings of 55 species (van den Berg and Dippenaar-Schoeman, 1991), although this study was conducted in a heavily urbanised area, but similar to records from Russel-Smith (1981) of 84 species collected, potentially owing to longer sampling periods, variations in sampling techniques employed or sampling during more productive times of the year. Clear differences in these communities are evident with strong separations occurring between seasons and disturbance types in pitfall traps, yet only separations between seasons occurring in litter extractions. As spiders are often found on the ground and within vegetation, they may be more susceptible to fire, it is possible that this disturbance may not necessarily impact species abundance as such, but may have a more impactful negative result on species richness. The absence of Theridiidae (web-spinners) attests to the fact that pitfall traps and litter extraction do not target these species, and so additional trapping methods are required to assess the impact of fire and grazing on this group. Due to complex life history stages, habitat utilisation, seasonal variations in behaviour and activity, among others, it remains difficult to make any assumption about the impacts of these two disturbance types on spider communities in the Delta.

Effect of disturbances

Fire is known to reduce available habitat, destroying organisms and reproductive structures in the process, and can increase competition for available resources. Grazing can also have similar effects through removal of plant matter, destruction of flowers and habitat heterogeneity and compaction of soil (Sharrow, 2007). These two disturbance types may be congruent in their impact on arthropod assemblages in the Okavango Delta, as can be seen from the results found in this study, where no consistent differences were found across all taxa studied. This could be due to the low intensity grazing and low intensity fires that may have a much less detrimental effect on arthropod assemblages in the study area, or that there are enough refugia within the wetland to accommodate the spatial movement of groups driven by fire and increase grazing intensity. It is also important to acknowledge that most responses to disturbances could be species-specific, complicating the conclusions that can made from studying taxa on higher taxonomic levels. The presence of a undisturbed control sites would have allowed more insightful analysis of the observed patterns, and would be highly recommended for future research in the Okavango Delta. It is also recommended that more attention be placed on assessing the impacts of varying degrees of disturbances, and their associated impacts on these groups.

On different trapping techniques

Based on the differences in total species collected by pitfall traps and litter extractions and the species composition of those communities, it is recommended that the communities sampled with these techniques be considered to be independent and should be assessed separately. The arthropod litter communities (more commonly found during litter extractions) and those that are more susceptible to pitfall trapping, should be treated as completely different spheres of the same habitat, and require nuanced approaches for analysis. In the rarefaction curves, the Chao 1 estimator generated for wasps collected by litter extractions in Fig. A6 continue to increase past the asymptote reached by the other estimators This may be a result of a few compounding factors that include, but is not limited to: inadequate sampling effort, high diversity of target species or rare/hard-to-detect species. The trapping method (litter extraction) could have caused this pattern, suggesting that this group was indeed under-sampled by this trapping method due to the nature of the collection method.

Subsequently, a more effective trapping method should be used for assessing wasp species diversity if this group is the focus of sampling effort.

Caveats

Some limitations should be clarified within this research project to ensure responsible interpretation of the data and conclusions reached. Firstly, the field data collection occurred over two months, with five trap days within each month per site. Although often used in ecological studies, this time frame limits the comprehensiveness of the conclusions that can be drawn from data collected. Only a small number of sites were sampled across a relatively small area, which may not represent landscape-scale community patterns accurately at such a fine scale. No “pristine” or “control” sites were accessible within reasonable distance from the main sampling area, limiting the comparisons that can be made between the grazed and burnt sites to less impacted communities. Second, although grazing occurs at relatively low intensities in the research area, it is unknown what pristine communities may look like in the Okavango Delta compared to grazed and burnt communities. More research is required in assessing pristine sites to allow direct comparisons of pristine and disturbed areas. It is also difficult to assess in what stage of recovery these communities are in the burnt and grazed sites, as the level of impact was not quantified. Lastly, limitations in available species lists and documented species for Botswana also increases the difficulty of assessing the impacts of disturbances on specific species. More knowledge is needed regarding highly sensitive species in order to accurately assess species loss in order to utilise arthropods as indicators of ecosystem health in the Okavango Delta. Despite these caveats, this is the first comprehensive systematic sampling in this region, and can be used as a baseline for future monitoring.

Future research

Although this study did not find conclusive evidence across all study taxa that fire or grazing has severe negative impacts on communities, there have been concerns regarding fire intensity and frequency and how this may affect invertebrate assemblages (Coleman and Rieske, 2006; Moretti *et al.*, 2006). This study did not account for fire intensity and frequency or grazing intensity, and it is recommended that these factors be included in future research in the Okavango Delta. From the results collected in this study, it is clear that the terrestrial ecosystems of the Okavango Delta harbour high levels of diversity and that the disturbance types present do in fact shape these communities in synergistic and compounding ways. Research is needed to assess landscape-scale impacts of these disturbances on arthropod communities, and over longer timescales to accurately assess recovery and community changes over time. Much work is needed in documenting the large number of species present within the Okavango Delta, and their respective roles in ensuring the effective functioning of this system. It is recommended that more attention be brought to constructing species checklists for as many arthropod groups as possible in the Delta, so further research may find it easier to assess impacts of disturbances on these communities by having access to species-specific data. This would also allow the identification of key indicator groups and species, which may ease the sampling and identification burden associated with under-documented ecosystems. It may very well be the case that as most naturally-occurring herbivores are now absent in the study region, that grazing by cattle is in some way beneficial in mimicking grazing by natural herbivores and maintaining vegetation dynamics critical in the functioning of these terrestrial communities. However, the Okavango Delta remains understudied in terms of certain terrestrial arthropod taxa, and being a World heritage site, this is concerning for the ongoing functioning of this system. Grazing and fire are by no means the only factors influencing invertebrate communities in the Delta, but understanding how these disturbances shape and influence communities, will undoubtedly assist in management decisions aimed at preserving this iconic African wetland.

Conclusion

The differential response of arthropods to disturbances found in this study is characteristic. Ant and springtails abundance and diversity proved to be strongly influenced by season, while wasp and spider diversity and abundance was found to be affected by both season and disturbance types. The varied results from different trapping techniques increases the difficulty of recognizing clear patterns, if any were present, but ensures that larger parts of the communities studied are accounted for. In addition, the results show that disturbances in the Okavango Delta synergistically shape and influence terrestrial arthropod communities in nuanced and complex ways, and much more research is needed to establish the direct mechanisms most impactful on the variations observed. The absence of country-specific data on arthropods highlights the difficulty in identifying key indicator species, and species may be lost without ever being recorded in the region. It is clear that the Okavango Delta is in need of extensive and continued research to ensure these disturbances are managed adequately and that their impacts are reduced. This region undoubtedly holds a myriad of interesting species and interactions that are waiting to be documented, several new species to be described, and possibly improve the scientific community’s understanding of disturbance impacts in wetland systems in Africa.

References

Alonso, L.E., Nordin, L.A. eds., 2004. *A rapid biological assessment of the aquatic ecosystems of the Okavango Delta, Botswana: high water survey*. Conservation International, Washington, D.C.

Archibald, S., Scholes, R.J., Roy, D.P., Roberts, G., Boschetti, L., 2010. Southern African fire regimes as revealed by remote sensing. *International Journal of Wildland Fire* 19, 861–878.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D., Whittaker, J.B., 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores: Rising temperature and insect herbivores. *Global Change Biology* 8, 1–16.

Bano, R.,Roy, S., 2016. Extraction of Soil Microarthropods: A low-cost Berlese-Tullgren funnels extractor. *International Journal of Fauna and Biological Studies 2*, 14-17.

Beattie, A. J., Oliver, I., 1996. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology 10*, 99–109.

Bernard, T., Moetapele, N., 2005. Desiccation of the Gomoti River: Biophysical process and indigenous resource management in Northern Botswana. *Journal of Arid Environments* 63, 256–283.

Brown, G.W., Dorrough, J.W., Ramsey, D.S., 2011. Landscape and local influences on patterns of reptile occurrence in grazed temperate woodlands of southern Australia. *Landscape and Urban Planning* 103, 277–288.

Cardoso, P., Erwin, T.L., Borges, P.A.V., New, T.R., 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* 144, 2647–2655.

Cassidy, L., 2003. Anthropogenic burning in the Okavango panhandle of Botswana: livelihoods and spatial dimensions (PhD Thesis). University of Florida Gainesville, Florida, USA.

Cassidy, L., Perkins, J., Bradley, J., 2022. Too much, too late: fires and reactive wildfire management in northern Botswana's forests and woodland savannas. *African Journal of Range and Forage Science* 39, 160–174.

Clarke, K.R., Gorley, R.N., 2015. Getting started with PRIMER v7. *PRIMER-E: Plymouth, Plymouth Marine Laboratory*.

Clement, S., 2019. Culture, conservation, and the Anthropocene. *Biodiversity Revisited is an initiative of the Luc Hoffmann Institute, in collaboration with WWF, Future Earth, ETH Zürich Department of Environmental Systems Science, University of Cambridge Conservation*

Research Institute, and the Centre for Biodiversity and Environment Research at University College London., p.58.

Coleman T.W., Rieske L.K., 2006. Arthropod response to prescription burning at the soil-litter interface in oak-pine forests. *Forest Ecology Management* 233**,** 52–60.

Cornel, A.J., Lee, Y., Almeida, A.P.G., Johnson, T., Mouatcho, J., Venter, M., De Jager, C., Braack, L., 2018. Mosquito community composition in South Africa and some neighboring countries. *Parasites and Vectors*, *11*, 1-12.

Crews, K., Neuenschwander, A., 2007. Remote Sensing Time Series Analysis of Coupled Impacts of Disturbance and Management on Landscape Carbon Storage in the Okavango Delta, Botswana, in: AGU Fall Meeting Abstracts, B23C-1492.

Crist, T.O., Veech, J.A., Gering, J.C., Summerville, K.S., 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity. *The American Naturalist* 162, 734–743.

Dalerum, F., Retief, T.A., Havemann, C.P., Chimimba, C.T., Janse van Rensburg, B., 2019. The influence of distance to perennial surface water on ant communities in Mopane woodlands, northern Botswana. *Ecology and Evolution* 9, 154–165.

Dangerfield, J.M., 1997. Abundance and diversity of soil macrofauna in northern Botswana. *Journal of Tropical Ecology* 13, 527–538.

Dennis, P., Young, M.R., Gordon, I.J., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology* 23, 253-264.

Eagle, V., 1985. A survey of the spider fauna of Botswana project report June 1984. *Botswana Notes and Records 17*, 131-139.

Ebenman, B., Jonsson, T., 2005. Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology and Evolution* 20, 568-575.

Edwards, C.A., 1991. The assessment of populations of soil-inhabiting invertebrates. *Agriculture, Ecosystems and Environment* 34, 145-176.

Eggleton, P., 2020. The state of the world's insects. *Annual Review of Environmental Resources* 45, 61–82.

Ellery, W.N., Tacheba, B., 2003. Floristic diversity of the Okavango Delta, Botswana. A Rapid Biological Assessment of the Aquatic Ecosystems of the Okavango Delta, Botswana: High Water Survey. *RAP-Bulletin of Biological Assessment* 25, 69–96.

Epele, L.B., Miserendino, M.L., 2015. Environmental quality and aquatic invertebrate metrics relationships at Patagonian wetlands subjected to livestock grazing pressures. *PLoS One* 10, e0137873.

Figueiredo, E., Smith, G.F., César, J., 2009. The flora of Angola: first record of diversity and endemism. *Taxon* 58, 233–236.

Frank, E., Sudarshan, A., 2023. The Social Costs of Keystone Species Collapse: Evidence from The Decline of Vultures in India. *University of Chicago, Becker Friedman Institute for Economics Working Paper*, (2022-165).

Frost, P.G.H., 1984. The responses and survival of organisms in fire-prone environments. In: Goldammer, J.G., de Ronde, C. (Eds.), *Ecological effects of fire in South African ecosystems*. Springer, Berlin, Heidelberg, 273–309.

Frost, P., 1996. *The ecology of miombo woodlands*. In: Campbell, B. (Ed.), *The miombo in transition: Woodlands and Welfare in Africa*. Center for International Forestry Research, Bogor, Indonesia, 11–57.

Fynn, R.W.S., Murray-Hudson, M., Dhliwayo, M., Scholte, P., 2015. African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management* 23, 559–581.

Gerlach, J., Samways, M., Pryke, J., 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation* 17, 831–850.

Giron, D., Rivero, A., Mandon, N., Darrouzet, E. and Casas, J., 2002. The physiology of host feeding in parasitic wasps: implications for survival. *Functional Ecology* 16, 750–757.

Gumbricht, T., McCarthy, J., McCarthy, T.S., 2004. Channels, wetlands and islands in the Okavango Delta, Botswana, and their relation to hydrological and sedimentological processes. Earth Surface Processes and Landforms. *The Journal of the British Geomorphological Research Group* 29, 15–29.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., de Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE 12*: e0185809.

Hassall, M., Visser, S., Parkinson, D., 1986. Vertical migration of *Onychiurus subtenuis* (Collembola) in relation to rainfall and microbial activity. *Pedobiologia* 29, 175–182.

Heinl, M., Frost, P., Vanderpost, C., Sliva, J., 2007. Fire activity on drylands and floodplains in the southern Okavango Delta, Botswana. *Journal of Arid Environments* 68, 77–87.

Heinl, M., Neuenschwander, A., Sliva, J., Vanderpost, C., 2006. Interactions between fire and flooding in a southern African floodplain system (Okavango Delta, Botswana). *Landscape Ecology* 21, 699–709.

Heinl, M., Sliva, J., Tacheba, B., Bredenkamp, G.J., 2004. Vegetation changes after single fire-events in the Okavango Delta wetland, Botswana. *South African Journal of Botany* 70, 695–704.

Heinl, M., Sliva, J., Tacheba, B., Murray-Hudson, M., 2008. The relevance of fire frequency for the floodplain vegetation of the Okavango Delta, Botswana. *African Journal of Ecology* 46, 350–358.

Hopkin, S.P., 1997. Biology of the springtails: (Insecta: Collembola). Oxford University Press, Oxford.

Horvath, R., Magura, T., Szinetar, C., Tothmeresz, B., 2009. Spiders are not less diverse in small and isolated grasslands, but less diverse in overgrazed grasslands: A field study (East Hungary, Nyírség). *Agriculture, Ecosystems and Environment* 130, 16–22.

Humphries, M.S., McCarthy, T.S., Cooper, G.R.J., Stewart, R.A. and Stewart, R.D., 2014. The role of airborne dust in the growth of tree islands in the Okavango Delta, Botswana. *Geomorphology* 206, 307-317.

Huntley, B.J., Matos, E.M., 1994. Botanical diversity and its conservation in Angola. *Strelitzia* 1, 53–74.

IUCN. 2022. *The IUCN Red List of Threatened Species. Version 2022-2*. https://www.iucnredlist.org. Accessed on 10 December 2022.

Janion-Scheepers, C., Bengtsson, J., Leinaas, H.P., Deharveng, L., Chown, S.L., 2016. The response of springtails to fire in the fynbos of the Western Cape, South Africa. *Applied Soil Ecology* 108, 165–175.

Jumbam, K.R., Jackson, S., Terblanche, J.S., McGeoch, M.A., Chown, S.L., 2008. Acclimation effects on critical and lethal thermal limits of workers of the Argentine ant, *Linepithema humile*. *Journal of Insect Physiology 54*, 1008–1014.

Kgori, P.M., Modo, S., Torr, S.J., 2006. The use of aerial spraying to eliminate tsetse from the Okavango Delta of Botswana. *Acta Tropica* 99, 184–199.

Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society: *Biological Sciences* 274, 303–313.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F., and Sanjayan, M.A., 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7, 796–808.

Lawton, J. H. and McGarvin, M. 1986. The organization of herbivore communities. In Kikkawa, J. and Anderson, D. J. (eds), *Community ecology: pattern and process*, 163–186. Blackwell Scientific Publications, Oxford.

Leather, S.R., 2018. “Ecological Armageddon” - more evidence for the drastic decline in insect numbers: Insect declines. *Applied Biology* 172, 1–3.

Lister, B.C., Garcia, A., 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences*, 115, E10397-E10406.

Liu, W.A., Phillips, L.M., Terblanche, J.S., Janion-Scheepers, C., Chown, S.L., 2021. An unusually diverse genus of Collembola in the Cape Floristic Region characterised by substantial desiccation tolerance. *Oecologia* 195, 873–885.

Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. *Bioscience* 56, 311–323.

Lyczkowski, E., 2006. The effects of the 2006 spraying of Deltamethrin for tsetse control on aquatic macro-invertebrates in the Kwando/Linyanti river system, Botswana. *Independent Study Project (ISP) Collection*. 268. https://digitalcollections.sit.edu/isp_collection/268

Mazebedi, R., Hesselberg, T., 2020. A preliminary survey of the abundance, diversity and distribution of terrestrial macroinvertebrates of Gcwihaba cave, northwest Botswana. *Subterranean Biology* 35, 49-63.

Majer, J.D., 1985. Recolonization by ants of rehabilitated mineral sand mines on North Stradbroke Island, Queensland, with particular reference to seed removal. *Australian Journal of Ecology 10*, 31–48.

McCarthy, T.S., Ellery, W.N., 1998. The Okavango Delta. *Transactions of the Royal Society of South Africa* 53, 157–182.

McCarthy, J., Gumbricht, T. & McCarthy, T., 2005. Ecoregion classification in the Okavango Delta, Botswana from multitemporal remote sensing, *International Journal of Remote Sensing* 26, 4339–4357.

McGeoch, M.A., Sithole, H., Samways, M.J., Simaika, J.P., Pryke, J.S., Picker, M., Uys, C., Armstrong, A.J., Dippenaar-Schoeman, A.S., Engelbrecht, I.A. and Braschler, B., 2011. Conservation and monitoring of invertebrates in terrestrial protected areas. *Koedoe 53*, 131–143.

Mendelsohn, J., El Obeid, S., 2004. Okavango River: The flow of a lifeline. *Struik*, Cape Town.

Moir, M.L., Vesk, P.A., Brennan, K.E.C., Keith, D.A., Hughes, L., McCarthy, M.A., 2010. Current constraints and future directions in estimating coextinction: coextinction: constraints and directions. *Conservation Biology* 24, 682–690.

Moreki, J.C., 2014. A study of entomophagy in Mogonono in Kweneng District, Botswana. *Online International Interdisciplinary Research Journal* 4, 70-79.

Moretti, M., Duelli, P., Obrist, M.K., 2006. Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. *Oecologia* 149**,** 312–27.

Naeem, S., Chazdon, R., Duffy, J.E., Prager, C., Worm, B., 2016. Biodiversity and human well-being: an essential link for sustainable development. *Proceedings of the Royal Society B: Biological Sciences* 283, 20162091.

National Geographic Okavango Wilderness Project (NGOWP), 2017: Initial Findings from Exploration of the Upper Catchments of the Cuito, Cuanavale, and Cuando Rivers, May 2015 to December 2016.

Neelo, J., Teketay, D., Masamba, W., Kashe, K., 2013. Diversity, population structure and regeneration status of woody species in dry woodlands adjacent to molapo in Northern Botswana. *Open Journal of Forestry* 3, 138–151.

Nicholson, S.E., 2000. The nature of rainfall variability over Africa on time scales of decades to millennia. *Global and Planetary Change* 26, 137–158.

Noriega, J.A., Hortal, J., Azcárate, F.M., Berg, M.P., Bonada, N., Briones, M.J., Del Toro, I., Goulson, D., Ibanez, S., Landis, D.A., 2018. Research trends in ecosystem services provided by insects. *Basic and Applied Ecology* 26, 8–23.

Outhwaite, C.L., Gregory, R.D., Chandler, R.E., Collen, B., Isaac, N.J., 2020. Complex long-term biodiversity change among invertebrates, bryophytes and lichens. *Nature Ecology and Evolution* 4, 384-392.

Ower, G. and Roskov, Y., 2019. The catalogue of life: Assembling data into a global taxonomic checklist. *Biodiversity Information Science and Standards* 3: e37221.

Parr, C.L., Robertson, H.G., Biggs, H.C., Chown, S.L., 2004. Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology* 41, 630-642.

Perkins, J.S., Ramberg, L., 2004. Environmental Monitoring of Tsetse Fly Spraying Impacts in the Okavango Delta-2002. Harry Oppenheimer Okavango Research Centre, University of Botswana.

Pinhey, E., 1976. Checklist of the Butterflies (Lepidoptera Rhopalocera). *Botswana Notes and Records* 8, 269–288.

Pryke, J.S., Samways, M.J., 2012. Differential resilience of invertebrates to fire. *Austral Ecology* 37, 460–469.

Ramberg, L., Wolski, P., Krah, M., 2006. Water balance and infiltration in a seasonal floodplain in the Okavango Delta, Botswana*.* *Wetlands* 26, 677–690.

Ringrose, S., Van Der Post, C. & Matheson, W., 2003. Mapping ecological conditions in the Okavango delta, Botswana using fine and coarse resolution systems including simulated SPOT vegetation imagery'. *International Journal of Remote Sensing* 24, 1029–1052.

Rix, M.G., Huey, J.A., Main, B.Y., Waldock, J.M., Harrison, S.E., Comer, S., Austin, A.D., Harvey, M.S., 2017. Where have all the spiders gone? The decline of a poorly known invertebrate fauna in the agricultural and arid zones of southern Australia: Spider declines in southern Australia. *Austral Entomology* 56, 14–22.

Robbel, H.W., Child, G., 1976. Notes on the ecology of the Moremi Wildlife Reserve. Department of Wildlife, National Parks and Tourism. Gaborone.

Röder, A., Pröpper, M., Stellmes, M., Schneibel, A., Hill, J., 2015. Assessing urban growth and rural land use transformations in a cross-border situation in Northern Namibia and Southern Angola. *Land Use Policy 42*, 340–354.

Roskov Y., Ower G., Orrell T., Nicolson D., Bailly N., Kirk P.M., Bourgoin T., DeWalt R.E., Decock W., Nieukerken E. van, Zarucchi J., Penev L., eds. (2019). Species 2000 and ITIS Catalogue of Life, 2019 Annual Checklist. Digital resource at www.catalogueoflife.org/annual-checklist/2019. *Species 2000: Naturalis, Leiden, the Netherlands*.

Rosenzweig, M.L., 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge.

Russell-Smith, A., 1981. Seasonal activity and diversity of ground-living spiders in two African savanna habitats. *Bulletin of the British Arachnological Society* 5, 145–154.

Salvarina, I., Gravier, D., Rothhaupt, K.O., 2018. Seasonal bat activity related to insect emergence at three temperate lakes. *Ecology and Evolution* 8, 3738–3750.

Samways, M.J., 1994. Insect Conservation Biology. *Bulletin of Entomological Research* 84, 589–590.

Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation* 232, 8–27.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574, 671–674.

Sharrow, S.H., 2007. Soil compaction by grazing livestock in silvo-pastures as evidenced by changes in soil physical properties. *Agroforestry Systems* 71, 215–223.

Shaw, M.R., 2006. Habitat considerations for parasitic wasps (Hymenoptera). *Journal of Insect Conservation* 10, 117-127.

Shortall, C.R., Moore, A., Smith, E., Hall, M.J., Woiwod, I.P., Harrington, R., 2009. Long-term changes in the abundance of flying insects. *Insect Conservation and Diversity* 2, 251–260.

Skvarla, M.J., Larson, J.L. and Dowling, A.P.G., 2014. Pitfalls and preservatives: a review. *The Journal of the Entomological Society of Ontario* 145*,* 1–10*.*

Smith, M.D., Knapp, A.K., Collins, S.L., Burkepile, D.E., Kirkman, K.P., Koerner, S.E., Thompson, D.I., Blair, J.M., Burns, C.E., Eby, S., 2016. Shared drivers but divergent ecological responses: Insights from long-term experiments in mesic savanna grasslands. *Bioscience* 66, 666–682.

Spooner, P., Lunt, I., Robinson, W., 2002. Is fencing enough? The short-term effects of stock exclusion in remnant grassy woodlands in southern NSW. *Ecological Management and Restoration* 3, 117–126.

Stork, N.E., 2018. How many species of insects and other terrestrial arthropods are there on Earth. *Annual Review of Entomology* 63, 31–45.

Stork, N.E., Lyal, C.H.C., 1993. Extinction or "co-extinction" rates? *Nature* 366, 307–307.

Swengel, A.B., 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation* 10, 1141–1169.

Tang, Z.C., Kozlowski, T.T., 1982. Some physiological and growth responses of *Betula papyrifera* seedlings to flooding. *Physiologia Plantarum* 55, 415–420.

Telford, SR, Dangerfield, J., 1993. Mating behaviour and mate choice experiments in some tropical millipedes (Diplopoda: Spirostreptidae). *African Zoology*, *28*, 155–160.

Tedder, M.J., Kirkman, K.P., Morris, C.D., Trollope, W.S.W. & Bonyongo, M.C., 2013. Classification and mapping of the composition and structure of dry woodland and savanna in the eastern Okavango Delta, *Koedoe* 55, Art. #1100

Thomas, C., Jones, T.H., Hartley, S.E., 2019. "Insectageddon": A call for more robust data and rigorous analyses. *Global Change Biology* 25, 91–92.

Thomas J. A., Morris M. G., 1994. Patterns, mechanisms and rates of extinction among invertebrates in the United Kingdom *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 344, 47–54.

Thornton, P.K., 2010. Livestock production: recent trends, future prospects. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365, 2853–2867.

Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H., Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund, L., Jørgensen, H.B., Christensen, S., Hertefeldt, T.D., Hotes, S., Gera Hol, W. h., Frouz, J., Liiri, M., Mortimer, S.R., Setälä, H., Tzanopoulos, J., Uteseny, K., Pižl, V., Stary, J., Wolters, V., Hedlund, K., 2015. Intensive agriculture reduces soil biodiversity across Europe. *Global Change Biology* 21, 973–985.

Tsheboeng, G., Murray-Hudson M., and Kashe, K., 2016a. A baseline classification of riparian woodland plant communities in the Okavango Delta, Botswana. *Southern Forests: Journal of Forest Science* 78, 1–8.

Tsheboeng, G., Murray-Hudson, M., and Kashe, K., 2016b. Response of riparian plant community composition to distance from surface water in the Okavango Delta, Botswana. *Journal of African Ecology* 55, 402-410.

van den Berg, A. and Dippenaar-Schoeman, A.S., 1991. Ground-living spiders from an area where the harvester termite *Hodotermes mossambicus* occurs in South Africa. *Phytophylactica*, *24*, 247-

254.

Dippenaar-Schoeman, A.S., van den Berg, A.M., van den Berg, A., 1989. Species composition and relative seasonal abundance of spiders from the field and tree layers of the Roodeplaat Dam Nature Reserve. *Koedoe* 32*,* 25–38.

van Straalen, N.M., Krivolutsky, D.A (eds)., 1996. Bioindicator systems for soil pollution. *Springer.* Kluwer, Dordrecht.

Van Wilgen, B.W., Govender, N., Biggs, H.C., 2007. The contribution of fire research to fire management: a critical review of a long-term experiment in the Kruger National Park, South Africa. *International Journal of Wildland Fire* 16, 519–530.

Weise, F.J., Fynn, R.W.S., Stein, A.B., Tomeletso, M., Somers, M.J., Périquet, S., 2019. Seasonal selection of key resources by cattle in a mixed savannah-wetland ecosystem increases the potential for conflict with lions. *Biological Conservation* 237, 253–266.

Whelan, R.J., 1995. The ecology of fire. *Cambridge University Press*, Cambridge, UK

Whitford, W.G. and Kay, F.R., 1999. Biopedturbation by mammals in deserts: a review. *Journal of Arid Environments* 41, 203-230.

Woodcock, B.A., 2005. Pitfall trapping in ecological studies. In: *Insect Sampling in Forest Ecosystems,* S.R. Leather (Ed.) 5, 37-57.

Zamin, T.J., Baillie, J.E., Miller, R.M., Rodríguez, J.P., Ardid, A.N.A., Collen, B.E.N., 2010. National red listing beyond the 2010 target. *Conservation Biology* 24, 1012–1020.

Chapter 3: An updated checklist of the spiders (Arachnida: Araneae) of the Okavango Delta, Botswana.

Abstract

Spiders have been well-documented in Africa, through large-scale projects like the African Arachnid Database and the South African National Survey of Arachnida. Although this group has received adequate attention in some countries, this does not prove true for all African countries.

In Botswana, the Okavango Delta is an exceptionally unique biological system. The complexity of this flood-driven system is not only due to seasonal influxes from the catchment area in central-Angola, but also due to the slow drop in elevation, which causes complex channels, streams, bogs and other aquatic habitats to form as the delta fans out towards the Makgadikgadi pans. At the core of this critical hydrological system lies aquatic and terrestrial systems and processes that ensure its continued functioning and overall health, with many of these services underpinned by invertebrates, arthropods in particular, with groups like spiders (Araneae) fulfilling crucial predatory roles. Although the aquatic invertebrates are relatively well-studied, the terrestrial arthropods have received limited attention, while undoubtedly also serving some critical regulatory service on the islands within the Delta, and along the edges. Although spiders in particular have seen only three studies within the Okavango Delta, research has shown this group to be highly diverse. As a World Heritage Site, the Okavango Delta should be prioritised for research related to ecosystem processes and monitoring of the smaller faunistic elements that ensure the collective functioning of the overall system, especially due to the threats it faces. Anthropogenic disturbances have become more common and regular along the edges and within the Okavango Delta over the last few decades, and as such, human-induced fire and livestock grazing has increased the pressure on the natural systems in which it occurs. Given the fragmented knowledge of terrestrial spiders within Botswana, and the Okavango Delta specifically, this study aimed to compile an updated species list of spiders (Araneae) of the Okavango Delta, Botswana. Using data from 120 pitfall traps, 120 litter extractions and active collecting, expanding on work by other research groups in gathering information about spiders in the Delta, this study was able to construct an updated species list for the spiders of the Okavango Delta, adding 39 new species to existing records for the Okavango Delta. A total of 183 species were found in the literature, consisting of 31 families and 119 genera. The updated species list contains 220 species, from 33 families and 141 genera. This is the most up-to-date species list of spiders of the Okavango Delta and will serve as the basis for further species inventories and diversity studies in the region. It is highly recommended that terrestrial arthropod research continues within this World Heritage Site to ensure the documentation

of the diversity of species present here, but also to utilize these species as indicators for ecosystem changes to ensure the continued survival of this unique wetland.

Introduction

The World Spider Catalog (2023), at the time of writing, contained 132 families, 4303 genera and 51 153 species, showcasing this diversity within the mega-diverse group. Spider taxonomy received attention from the scientific community as early as the 1750s, with Clerck (1757) and Linnaeus (1758) publishing limited records of spiders, serving as the starting point for modern spider taxonomy (Platnick and Raven, 2013). Interestingly, the 10 most productive authors regarding spider taxonomy have been jointly responsible for describing almost one third of all described species up until the mid-2010s (Platnick and Raven, 2013). Work continues to revise historic description of species (Coddington, 2005). Spider taxonomy has seen great advances in the last few decades, and the scientific community is consistently improving their understanding of arachnid phylogeny. Spiders are well-known as predators within all natural- and agroecosystems (Dippenaar-Schoeman *et al.,* 2013), even in aquatic and intertidal habitats (Nyffeler and Pusey, 2014). All spiders are predators, with one species; *Bagheera kiplingi* (Meehan *et al*., 2009) supplementing its diet by also feeding on plants. As a collective, spiders can consume large numbers of prey, and may prove to be an effective method for insect bio-control (Michalko *et al*., 2018) within the agricultural systems (Dippenaar-Schoeman *et al.,* 2013). Terrestrial spiders, although all capable of producing silk, do not all use silk as their main methods of prey capture. A large number are free-living wanderers and have abandoned webs. Although other animals also utilise silk, none come close to the diversity of uses and structures employed by spiders (Craig, 2003). Alternative prey capture methods used by the free-living spiders include ambush, stalking and active hunting (Wise, 1995), and the main prey includes insects and other arachnids, for example mites and other spiders (Nyffeler, 1999; Dippenaar-Schoeman *et al.,* 2013; Nyffeler and Birkhofer, 2017), whilst eggs and larvae are also consumed (Young and Edwards, 1990). Due to their high abundance compared to other groups, and the fact that insects and plant-feeding mites are their main prey, spiders play a critical role in shaping and maintaining arthropod populations (Nyffeler *et al.,* 1994a, b; Wise, 1995). Spiders are considered good indicators for environmental changes as they are sensitive to vegetation structure and habitat changes (Magura *et al.,* 2010; Reynolds, 2014), while also acting as ecological accumulators that indicate environmental toxin levels (Haughton *et al*., 2003) and serve as food source for many birds (Gunnarson, 2007), reptiles (Avery, 1966) and mammals (Gibb *et al.,* 2021). Spiders are thus ideal for biodiversity inventories and have been widely used across various habitats in diversity studies (Robertson et al., 2011; Dippenaar-Schoeman *et al.,* 2013, 2015) due to numerous factors making them ideal for such inclusion. These include: 1) spiders are exceptionally diverse (Coddington and Levi, 1991), generalist predators that have an ecologically important impact as a group, on the invertebrate population (Bishop and

Reichert, 1990); 2) spiders are highly abundant and may be collected using various trapping methods (Green, 1999); and 3) amateurs are easily trained to utilise morphospecies sorting techniques very efficiently (Oliver and Beattie, 1993). Spiders also contribute to significant medical advances, where spider toxins are utilised as therapeutics (Saez and Herzig, 2019), and in the growing field of Integrated Pest Management (IPM), where spider toxins are also being explored for novel pest control mechanisms (King and Hardy, 2013). Spider silk is also at the forefront of biomimicry studies, where researcher aims to create synthetic structures that may imitate the strength and durability of spider silk (Harmer *et al.,* 2011, Ko and Wan, 2018) or monitor air quality (Stojanowska *et al.,* 2023). Spider bites remain medically significant, although treatments have improved substantially over the last few decades (Isbister and White, 2004; Vetter and Isbister, 2008; Isboster and Fan, 2011).

Even with all the positive impact that spiders may have within a system, the general public has remained caught in an outdated, negative perception of spiders, although some exceptions exist (Mammola *et al.*, 2022). As such, this group has faced many of the impediments to invertebrate conservation outlined by Cardoso *et al.* (2011). Most spider species do not have enough data to be adequately assessed (Seppala *et al.,* 2018) although Foord *et al.* (2022) did excellent work in compiling a National Red List of spiders for South Africa, showcasing the value and necessity of this type of research. Their main threats as identified by Branco and Cardoso (2020), includes current agricultural practices, livestock and associated impacts, forestry, climate change and urbanisation, among others.

Spiders in Africa

The southern Africa subregion is extremely diverse in ecosystem and habitat type, contributing to the high diversity of spider species found in the region. Published data was used to compile the African Arachnida Database (AFRAD) that are housed at the ARC in Pretoria. It is a comprehensive collection of data pertaining to Arachnida on the continent, including distribution data, identification keys, checklists, and literature on Afrotropical arachnids, all within a single project, available online (Agricultural Research Council, until 2014). Similar to other invertebrates, tropical spider species tend to be less well-described and, much remains to do in collating current knowledge (Cardoso *et al*., 2019). It may seem that a slight variation of the accepted latitudinal patterns of species diversity may become apparent as spider species richness increases towards the middle and southern latitudes, most likely peaking in southern Africa (Platnick, 1991). This highlights the value and necessity of the ongoing documentation of African spider species for larger landscape and continental ecological understanding. Unfortunately, the case may be that collections remain biased towards larger specimen found in more accessible localities (Coddington and Levi, 1991). Additionally, almost half of spiders collected in tropical habitats are single specimens owing due to rarity, which may either be due to the true rarity of adult spiders in general or the fact that spiders may occupy habitats inaccessible to humans (Coddington *et al*., 1991). This complicates the accuracy with which species richness can be estimated globally, and locally. In South Africa, arachnologists have managed to make strides forward through collaboration. The South African National Survey of Arachnida (SANSA), was launched as a national umbrella project supported by experts and researcher to record and collate all available data on spiders in South Africa (Dippenaar-Schoeman *et al*., 2013; 2015). This project has seen large scale documentation of spider diversity data for the country, acting as an example of how effective and necessary collaborative efforts are in the process of documenting such a diverse group of arthropods. This consistent research being conducted in South Africa, with review publications already available for multiple habitat types (Dippenaar-Schoeman *et al.,* 2015), will enable more efficient research within the rest of southern Africa, and the continent as a whole, and continue the already established work of documenting the spider diversity of Africa. Dippenaar-Schoemann and Jocqué (1997) reported 71 families, 893 genera, and over 5000 spider species from Sub-Saharan Africa and, over the years, many more species descriptions from the region have been published (African Arachnida Database). But only a few African countries have published lists of spiders: Botswana (Eagle 1985), Kenya (Kioko *et al.* 2021), Namibia (Griffin and Dippenaar-Schoemann 1991), South Africa (Dippenaar-Schoeman *et al.* 2010), Sudan (Siyam & Dunlop 2014), Tanzania (Russell-Smith 2020) and Zimbabwe (FitzPatrick, 2001).

The Okavango Delta is a World Heritage Site situated in the North-Western district of Botswana, Ngamiland West, where high levels of habitat variability along with large quantities of water in seasonal and permanent rivers, would allude to biodiversity hotspot within the region (Darkoh and Mbaiwa, 2014). The aquatic habitats are relatively well-studied compared to the terrestrial habitats, but the Okavango Delta remains understudied when it comes to terrestrial invertebrates, with the exclusion of spiders (Russel-Smith, 1981; Eagle, 1985; Dippenaar-Schoeman and Kassimatis, 2002). From as early as the 1880s, researchers visiting Botswana have been describing new species at a steady rate (Eagle, 1985). In Botswana, spider taxonomy has slowly gained attention over the last 40 years. Russel-Smith (1981) was the first to compile a checklist of spiders for the Okavango Delta by comparing the seasonal activity and diversity of ground-living spiders in two African savanna habitats, documenting 36 species at the time of publication. Gradually, new species were added or revised (Eagle, 1985; Kuntner and Hormiga, 2002; Logunov, 2009; Wesolowska, 2011; Azarkina and Foord, 2015; Haddad and Mavrusik, 2019). A two-week survey conducted by Dippenaar-Schoeman and

Kassimatis (2002) and further work brought the checklist up to 27 families, 78 genera and 177 species for the Okavango Delta.

An updated species list provides a much-needed framework for continued research (Dippenaar-Schoeman, 2015) and thus any large-scale documentation of spiders would be beneficial to the ongoing cataloguing of spider inventories in African countries, through contributions to AFRAD. This updated species list of the spiders of the Okavango Delta is intended to serve as a launching point for further investigation and to continue the exploration of the spider diversity of this World Heritage site.

Materials and methods

Sampling took place over two months (end of dry and wet season) in November 2021 and February 2022. Collection was completed close to Mopiri Research Station, Okavango Delta, Ngamiland, Botswana (Fig. 1). For detailed collection methodology for spiders by pitfall traps and litter extractions, please refer to *Chapter 2: Materials and methods*. Additional to the spiders collected from pitfall traps and litter extractions, active sampling was used to collect spiders opportunistically whenever possible around the research station, as well as at various study sites. This also involved two hours per day spent (after mid-day) actively walking around the research station, and around the grazed and burnt sites selected. This equated to roughly 14 hours a week spent actively searching for spiders, throughout the two-month period spent on the research station over November 2021 and February 2022. Specimens collected through opportunistic active sampling were placed in plastic containers and frozen for two days. After being completely frozen, specimens were transferred to marked plastic vials and stored in 95% ethanol in preparation for transport and storage back to South Africa. All specimens collected through passive and active sampling methods were safely transported to the University of Cape Town and sorted to morphospecies. Basic photos were taken of each morphospecies. After basic morphospecies sorting, specimens were sent to A.S. Dippenaar-Schoeman for identification. All specimens were stored in 70% ethanol.

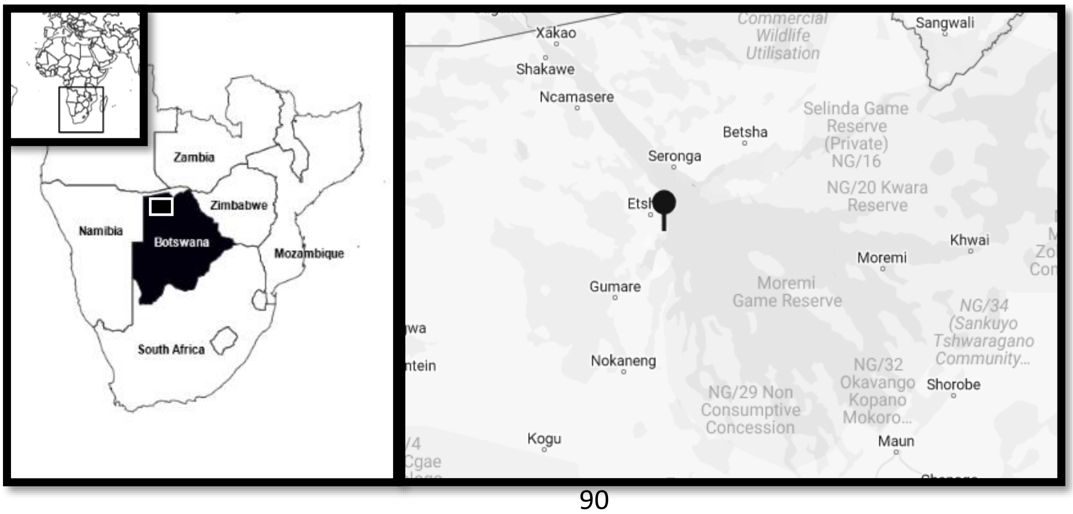

Figure 1: Map of collection site at Mopiri research station, Okavango Delta, Botswana.

Assessing historical literature

Dippenaar-Schoeman *et al*. (in prep) had compiled a preliminary spider checklist for the species of the Okavango Delta but has remained unpublished. Expanding on extensive work already completed, new observations of species collected during the two fieldwork seasons of this study were added to the framework species list (Dippenaar-Schoeman *et al*., unpublished), along with relevant collection details. The data was obtained from the African Arachnida Database (AFRAD) containing records of species sampled in the area. Most of the records came from primary data collected with specimens sampled (Russel-Smith, 1981; Eagle, 1985; Dippenaar-Schoeman and Kassimatis, 2002), as well as all the species from taxonomic revisions, as only six dedicated spider inventories were completed in the Okavango Delta. Limited additional sources within the literature provided additional species observations for the Okavango Delta (for example: Lawrence, 1936; Platnick and Murphy, 1987; Platnick and Griffin, 1990; Lotz, 2007). Species names were provided, but many specimens could not be identified to species level as many of the sampled material were immature or the taxonomy of the relevant genus are still unresolved. Exact localities of where species were sampled are provided where possible, but due to the scattered nature of spider records in historic literature and taxonomic revisions, localities were not available for all species. Where no exact locality is given, the location information available only confirmed that these species were collected in the Okavango Delta. The updated species list includes only those specimens that could be identified to species level.

Results

From the available published and unpublished literature, and the specimens collected in this study, a total of 33 families were found to have been recorded in the Okavango Delta, represented by 141 genera and 220 species. From pitfall traps and litter extractions a total of 20 families and 51 genera were sampled, with 40 species identified (Table 1). From active collections, a total of 18 families, 55 genera and 70 species were collected (Table 1). Many specimens were immature, making identification difficult, only allowing genus-level identifications. These specimens, along with published record only identified to genus-level, were not included in the final species list. From this study, 37 new records of species were documented for the Okavango Delta from the field collections based at Mopiri Research Camp in 2021/2022, consisting of two newly recorded families and 22 newly recorded genera.

Table 1: Summary of specimens collected during the 2021/2022 sampling seasons, along with historical records, in the Okavango Delta.

Sources	Number of families	Number of genera	Number of species
Passive (pitfall traps and litter extractions)	20	51	40
Active collection	18	55	70
Historic literature	31	119	183
Update species list	**33**	**141**	**220**

The Salticidae (43 species), Gnaphosidae (29 species), Thomisidae (27 species), Araneidae (27 species) and Lycosidae (20 species) were most species rich (Table 2). Seventeen families contained only a single genus. Two new families, Liocranidae and Pisauridae, were recorded for the first time in the Okavango Delta, with Liocranidae represented by *Rhaeboctesis denotatus*, while Pisauridae was represented by *Nilus margaritatus* and *Perenethis simoni* (Table 2). Additionally, two families, Oonopidae and Ulboridae were recorded for the first time in the Okavango Delta, but no species level identifications were possible with juvenile specimens representing these families.

Table 2: Summary of the spider families in the Okavango Delta, along with the number of genera and species collected in each.

Family	Number of Genera	Number of Species
Agelenidae	2	2
Araneidae	20	27
Caponiidae	1	1
Cheiracanthiidae	1	3
Clubionidae	1	2
Corinnidae	7	8
Ctenidae	1	1
Gnaphosidae	17	29
Hersiliidae	1	1
Ischinothelidae	1	1
Linyphiidae	4	4
Liocranidae	1	1
Lycosidae	11	20
Migidae	1	1
Oecobiidae	1	1
Oxyopidae	3	9

Palpimanidae	1	1
Philodromidae	1	3
Pholcidae	1	1
Pisauridae	2	2
Prodidomidae	2	2
Salticidae	26	43
Scytodidae	1	1
Selenopidae	1	2
Sicariidae	1	1
Sparassidae	3	5
Tetragnathidae	2	7
Theraphosidae	1	1
Theridiidae	2	2
Thomisidae	15	27
Trachelidae	4	4
Trochanteriidae	1	1
Zodariidae	4	6

Table 3: Checklist of spiders of the Okavango Delta, 2023. Species collected during this study for the first time are indicated with an asterisk (*).

Family	Genus and species	Records in Okavango Delta
Agelenidae		
	Benoitia deserticola (Simon, 1910)	Pom-Pom
	Olorunia punctata Lehtinen, 1967	Pom-Pom
Araneidae		
	Araneus apricus Karsch, 1884	Pom-Pom, Mopiri
	Araneus strupifer (Simon, 1886)	Pom-Pom
	Argiope trifasciata (Forsskål, 1775)	Pom-Pom
	Cyclosa insulana (Costa, 1834)	Pom-Pom, Xaxaba
	Cyphalonotus larvatus (Simon, 1881)	Pom-Pom
	Cyrtophora citricola (Forsskål, 1775)	Xaxaba
	**Eriovixia excelsa* (Simon, 1889)	Mopiri
	Gasteracantha sanguinolenta Koch, 1844	Pom-Pom
	Gea infuscata Tullgren, 1910	Pom-Pom
	Hypsosinga lithyphantoides Caporiacco, 1947	
	Kilima decens (Blackwall, 1866)	Pom-Pom
	Larinia bifida Tullgren, 1910	Pom-Pom
	Lipocrea longissima (Simon, 1881)	Pom-Pom
	**Nemoscolus cotti Lessert*, 1933	Mopiri
	Nemoscolus tubicola (Simon, 1887)	
	Neoscona blondeli (Simon, 1886)	Pom-Pom
	Neoscona hirta (C. L. Koch, 1844)	Boro River; Mopiri
	Neoscona moreli (Vinson, 1863)	Maun; Tsotsoronga Pan; Mopiri

	Neoscona rapta (Thorell, 1899)	Pom-Pom
	Neoscona subfusca (C.L. Koch, 1837)	Mopiri
	Neoscona triangula (Keyserling, 1864)	Xugana
	Nephilingis cruentata (Fabricius, 1775)	Xaxaba
	Pararaneus cyrtoscapus (Pocock, 1898)	Pom-Pom
	**Prasonica seriata* Simon, 1895	Mopiri
	Singa lawrencei (Lessert, 1930)	Pom-Pom
	Singafrotypa mandela Kuntner and Hormiga, 2002	Xugana Lagoon
	**Trichonephila senegalensis annulata* (Thorell, 1859)	Mopiri
Caponiidae		
	Caponia natalensis (Cambridge, 1874)	Pom-pom
Cheiracanthiidae		
	Cheiracanthium africanum Lessert, 1921	Pom-Pom
	**Cheiracanthium furculatum* Karsch, 1879	Mopiri
	Cheiracanthium vansoni Lawrence, 1936	Boro River
Clubionidae		
	Clubiona subtrivialis Simon, 1906	Pom-Pom, Mopiri
	Clubiona annuligera Lessert, 1923	Pom-pom
Corinnidae	*Apochinomma formicaeforme* Pavesi, 1881	Maun, Maxwee, Maphaneng Pan
	Cambalida dippenaarae Haddad, 2012	Lesideng Res. Camp
	Cambalida fulvipes (Simon, 1896)	Pom-Pom camp
	Copa flavoplumosa Simon, 1885	Maun, Maphaneng Pan, Mopiri
	Copuetta lacustris (Strand, 1916)	Shakawe Fishing camp
	Graptartia granulosa Simon, 1896	Maxwee
	Medmassa semiaurantiaca Simon, 1910	Lesideng Res. camp
	Messapus tigris Haddad and Mbo, 2015	Near Shakawe
Ctenidae		
	Afroneutria velox (Blackwall, 1865)	Ngotsha in Chobe and Xaxaba
Gnaphosidae		
	Ammoxenus psammodromus Simon, 1910	Maxwee
	Aphantaulax inornata Tucker, 1923	Pom-Pom
	Amusia cataracta Tucker, 1923	Pom-Pom, Mopiri
	**Asemesthes lineatus* Purcell, 1908	Mopiri
	Asemesthes windhukensis Tucker, 1923	
	Camillina cordifera (Tullgren, 1910)	Maxwee
	Camillina maun Platnick and Murphy, 1987	Maxwee, Mopiri
	**Echemus erutus* Tucker, 1923	Mopiri
	Ibala robinsoni Fitzpatrick, 2009	Boro River
	Leptopilos butleri Haddad and Booysen, 2022	Shakawe
	Megamyrmaekion caudatum Reuss, 1834	Maxwee, Mopiri
	**Nomisia varia* (Tucker, 1923)	Mopiri
	Pterotricha auris (Tucker, 1923)	Maxwee
	Rastellus africanus Platnick and Griffin, 1990	Smiti; Mopiri; Maxwee
	Rastellus struthio Platnick and Griffin, 1990	Smiti
	Setaphis browni (Tucker, 1923)	Maxwee; Smiti

	Setaphis subtilis (Simon, 1897)	Shorobe, Maxwee
	Trephopoda parvipalpa (Tucker, 1923)	Maxwee
	Xerophaeus robustus Lawrence, 1936	Gomodimo pan
	**Zelotes caldarius* (Purcell, 1907)	Mopiri
	Zelotes chinguli FitzPatrick, 2007	Maxwee
	**Zelotes corrugatus* (Purcell, 1907)	Mopiri
	Zelotes gooldi (Purcell, 1907)	Maxwee
	Zelotes frenchi Tucker, 1923	Maxwee
	Zelotes fuligineus (Purcell 1907)	Maxwee
	Zelotes nyathii Fitzpatrick, 2007	Boro River
	Zelotes mosioatunya FitzPatrick, 2007	Maxwee
	Zelotes otavi FitzPatrick, 2007	Maxwee
	Zelotes radiatus Lawrence, 1928	Maun
	Zelotes scrutatus (O. P.-Cambridge, 1872)	Maxwee
Hersiliidae		
	Hersilia occidentalis Simon, 1907	Xabaxaba Camp
Ischinothelidae		
	Thelechoris striatipes (Simon, 1889)	Xabaxaba
Linyphiidae		
	Ceratinopsis idanrensis Locket and Russel-Smith, 1980	Maxwee, Mopiri
	**Helsdingenia extensa* (Locket, 1968)	Mopiri
	Metaleptyphantes perexiguus (Simon and Fage, 1922)	Maxwee
	**Ostearius malanopygius* (O. Pickard-Cambridge, 1880)	Mopiri
Liocranidae		
	**Rhaeboctesis denotatus* Lawrence, 1928	Mopiri
Lycosidae		
	**Allocosa exserta* Roewer, 1959	Mopiri
	**Allocosa faberrima* (Simon, 1910)	Mopiri
	**Allocosa lawrencei* (Roewer, 1951)	
	Allocosa mafensis (Lawrence, 1927)	
	**Allocosa tuberculipalpa* (Caporiacco, 1940)	Mopiri
	**Allocosa umtalica* (Purcell, 1903)	Mopiri
	Amblyothele albocincta Simon, 1910	Maxwee
	Evippomma squamulatum (Simon, 1898)	Xaxaba
	Foveosa foveolata (Purcell, 1903)	Shorobe Lagoon, Maxwee
	Hippasa funerea Lessert, 1925	Mopiri
	Hogna bimaculata (Purcell, 1903)	Pom-Pom
	**Lycosa praestans* Roewer, 1960	Mopiri
	Ocyale guttata (Karsch, 1878)	Maun
	Pardosa crassipalpis Purcell, 1903	Pom-Pom
	Pardosa foveolata (Purcell, 1903)	Maxwee
	Pardosa injucunda (Cambridge 1876)	Mboma Island
	Pardosa lusingana Roewer, 1959	Maxwee
	Pardosa kavango Alderweireldt and Jocque, 1992	Moremi
	**Proevippa wanlessi* (Russel-Smith, 1981)	Mopiri
	**Trabea heteroculata* Strand, 1913	Mopiri

Migidae		
	Moggridgea whytei Pocock, 1897	Xugana Island,
Oecobiidae		
	Paroecobius wilmotae Lamoral, 1981	Xugana Island
Oxyopidae		
	Hamataliwa kulczynskii (Lessert, 1915)	Okavango Delta
	Oxyopes falconeri Lessert, 1915	Okavango Delta
	Oxyopes longispinosus Lawrence, 1938	Lesideng Res. Camp, Mopiri
	Oxyopes pallidecoloratus Strand, 1906	Okavango Delta
	Oxyopes schenkeli Lessert, 1927	Okavango Delta
	**Oxyopes vogelsangeri* Lessert, 1946	Mopiri
	Peucetia striata Karsch, 1878	Nxai-Pan, Nagamiland
	Peucetia transvaalica Simon, 1896	Xugana Lagoon. Gibbereca
	Peucetia viridis (Blackwall, 1858)	Xharagha, Xaxaba Camp, Boro River
Palpimanidae		
	Diaphorocellus helveolus (Simon, 1910)	Pom Pom
Philodromidae		
	Tibellus armatus Lessert, 1928	Xugana lagoon
	Tibellus gerhardi Van den Berg and Dippenaar-Schoeman, 1994	Gibbereca
	Tibellus minor Lessert, 1919	Xugana island
Pholcidae		
	Smeringopus sambesicus Kraus, 1957	Xaxaba
Pisauridae		
	**Nilus margaritatus* (Pocock, 1898)	Mopiri
	**Perenethis simoni* (Lessert, 1916)	Mopiri
Prodidomidae		
	**Eleleis limpopo* Rodrigues and Rheims, 2020	Mopiri
	Theuma fusca Purcell, 1907	Maxwee
Salticidae		
	Afraflacilla altera (Wesolowska, 2000)	
	Asemonea cuprea Wesolowska, 2009	
	Bianor albobimaculatus (Lucas, 1846)	Pom-Pom
	Evarcha bihastata Wesolowska and Russell-Smith, 2000	
	Evarcha ignea Wesolowska and Cumming, 2008	
	Festucula leroyae Azarkina and Foord, 2014	Pom-Pom
	Heliophanus debilis Simon, 1901	
	Heliophanus demonstrativus Wesolowska, 1986	
	Heliophanus gloriosus Wesolowska, 1986	Kwando River; Pom-Pom
	Heliophanus trepidus Simon, 1910	
	Holcolaetis albobarbata Simon, 1910	
	Holcolaetis vellerea Simon, 1909	Shakawe Fishing camp, Okavango swamps
	Hispo georgius (Peckham and Peckham, 1892)	Maxwee
	**Hyllus argyrotoxus* Simon, 1902	Mopiri

	Hyllus brevitarsis Simon, 1902	Maxwee
	Hyllus dotatus (Peckham and Peckham, 1903)	
	Hyllus argyrotoxus Simon, 1902	
	Hyllus brevitarsis Simon, 1902	Maxwee
	Hyllus plexippoides Simon*,* 1906	Maxwee
	Hyllus treleaveni (Peckham and Peckham, 1902)	
	Icius steeleae Logunov, 2004	
	Langona bethae Wesolowska and Cumming, 2011	Lesideng Res. camp; Pom-Pom
	**Langona warchalowskii* Wesolowska, 2007	Mopiri
	Manzuma botswana Azarkina, 2020	Maxwee
	**Mexcala elegans* Peckham and Peckham, 1903	Mopiri
	Microheros termitophagus (Wesołowska and Cumming, 1999)	
	**Natta horizontalis* Karsch, 1879	Mopiri
	**Nigorella hirsuta* Wesołowska, 2009	Mopiri
	Parajotus refulgens Wesolowska, 2000	
	Paramodunda thyenioides (Lessert, 1925)	Maxwee
	**Pellenes bulawayoensis* Wesolowska, 2000	Mopiri
	Pellenes rufoclypeatus Peckham and Peckham, 1903	Maxwee
	Phlegra imperiosa Peckham and Peckham, 1903	Maxwee
	Phintella aequipes (Peckham and Peckham, 1903)	
	Portia schultzi Karsch, 1878	Shakawe Fishing camp, Okavango swamps, Mopiri
	Thyene coccineovittata (Simon, 1886)	
	Thyene inflata (Gerstaecker, 1873)	Pom-Pom; Maxwee
	Thyene natalii. Peckham and Peckham, 1903	Pom-Pom
	**Thyene ogdeni* Peckham and Peckham, 1903	Mopiri
	Tusitala barbata Peckham and Peckham, 1902	Pom-Pom, Mopiri
	Tusitala hirsuta Peckham and Peckham, 1902	Pom-Pom
	Velloa bianoriformis (Strand, 1907)	Ramotswa; Maun; Xaxaba
	Vicirionessa mustela (Simon, 1902)	
Scytodidae		
	Scytodes fusca Walckenaer, 1837	Pom-Pom camp, Xaxaba
Selenopidae		
	Selenops kruegeri Lawrence, 1940	
	Selenops ovambicus Lawrence, 1940	
Sicariidae		
	Loxosceles simillima Lawrence, 1927	
Sparassidae		
	Olios correvoni Lessert, 1921	
	Olios darlingi (Pocock, 1901)	
	Olios sjostedti Lessert, 1921	Shakawe Fishing camp
	Palystes johnstoni Pocock, 1896	4-rivers camp; Maxwee
	Pseudomicrommata longipes (Bösenberg and Lenz, 1895),	Maxwee; Palapaya
Tetragnathidae		

	Leucauge decorata (Blackwall, 1864)	Pom-Pom
	**Leucauge medjensis* Lessert, 1930	Mopiri
	Leucauge thomeensis Kraus, 1960	Pom-Pom
	Tetragnatha bogotensis Keyserling, 1865	Crocodile Camp, Xaxaba
	Tetragnatha isidis (Simon, 1880)	Pom-Pom
	Tetragnatha keyserlingi Simon, 1890	Crocodile Camp
	Tetragnatha vermiformis Emerton, 1884	Santandadibe River
Theraphosidae		
	Ceratogyrus brachycephalus Hewitt, 1919	Pom-Pom
Theridiidae		
	Latrodectus geometricus C. L. Koch, 1841	Pom-Pom
	**Steatoda capensis* Hann, 1990	Mopiri
Thomisidae		
	Diaea puncta Karsch, 1884	Lesideng Residence Camp
	Geraesta congoensis (Lessert, 1943)	Shakawe Fishing Camp
	Firmicus lentiginosus (Simon, 1886)	Pom-Pom camp
	**Heriaeus crassispinus* Lawrence, 1942	Mopiri
	Hewittia gracilis Lessert, 1928	Pom-Pom camp
	Misumenops rubrodecoratus Millot, 1942	Pom-Pom camp
	Monaeses austrinus Simon, 1910	Pom-Pom camp
	Monaeses quadrituberculatus Lawrence, 1927	Pom-Pom camp, Mopiri
	Oxytate argenteooculata (Simon, 1886)	Pom-Pom camp
	Runcinia aethiops (Simon, 1901)	Xugana Lagoon
	Runcinia insecta (L. Koch, 1875)	Pom-Pom camp
	Runcinia carae Dippenaar-Schoeman, 1983	Xugana Lagoon, Xaxaba
	**Runcinia depressa* Simon, 1906	Mopiri
	Runcinia erythrina Jézéquel, 1964	Pom-Pom camp
	Runcinia flavida (Simon, 1881)	Pom-Pom camp
	Runcinia grammica (C. L. Koch, 1837)	Pom-Pom camp
	Simorcus cummingae van Niekerk and Dippenaar-Schoeman, 2010	Lesideng Research Camp
	Simorcus okavango van Niekerk and Dippenaar-Schoeman, 2010	Lechwe Camp
	Sylligma ndumi Lewis and Dippenaar-Schoeman, 2011	Shakawe Fishing camp,
	Thomisops senegalensis Millot, 1941	Xugana lagoon
	Thomisus citrinellus Simon, 1875	Pom-Pom
	Thomisus granulatus Karsch, 1880	Pom-Pom, Mopiri
	Thomisus kalaharinus Lawrence, 1936	Tsotsoroga Pan
	Thomisus scrupeus (Simon, 1886)	Pom-Pom
	Tmarus berlandi Lessert, 1928	
	Tmarus cameliformis Millot, 1942	Pom-Pom
	**Xysticus natalensis* Lawrence, 1938	Mopiri
Trachelidae		
	**Fuchiba aquilonia* Haddad and Lyle, 2008	Mopiri

	Orthobula radiata Simon, 1897	Maun, Maxwee
	Jocquestus schenkeli (Lessert, 1923)	Pom-Pom camp
	Trachelas chubby Lessert, 1921	
Trochanteriidae		
	Platyoides alpha Lawrence, 1928	
Zodariidae		
	Akyttara homunculus Jocqué, 1991	Boro River
	Capheris oncka Lawrence, 1927	Manxunyane
	Diores delicatulus Lawrence, 1936	Tsotsoroga Pan
	Diores russelli Jocqué, 1990	Boro River, Mopiri
	Diores salisburyensis Tucker, 1920	Pom-Pom camp
	Ranops caprivi Jocqué, 1991	Pom-Pom camp

Discussion

Results from this study are similar to results obtained through previous work in the Okavango Delta (Russel-Smith, 1981; Dippenaar-Schoeman and Kassimatis, 2002), yet showcase the high spider diversity of the region by adding a substantial number of newly recorded species. It is expected that subsequent sampling may continue to deliver new species, in the different seasons and varying habitats of the Okavango Delta. Although the spiders of southern Africa have received more attention than spider in other parts of Africa, much remains unknown about the population dynamics on the species level, and it would be valuable to improve the state of knowledge in this regard to better interpret trends in abundance and diversity data.

This study contributed 37 new records to the latest unpublished species checklist of the Okavango Delta, Botswana. This is the most up-to-date species list of the spider fauna of the Okavango Delta and should form the basis of continued effort into doing a complete inventory of the spider species of this unique region. Further large-scale ongoing projects (SANSA, AFRAD) will continue to contribute to the existing wealth of diversity data available for species within southern Africa, and every novel survey will contribute valuable new data towards the global knowledge of spider species distribution. Any additions to this list will prove valuable for conservation and landscape management planning within Botswana, and may improve the ability to monitor impacts of anthropogenic pressure on this World Heritage Site using arachnids as indicator taxa. The Okavango Delta's terrestrial spider diversity is well documented and future research will prove valuable if it is able to continue the necessary work of mapping the spider diversity occurring there. Although threats remain and may become more severe in the near future, there are a number of routes to follow to encourage the protection of this unique habitat, from land protection and adequate management practice to public education and supporting appropriate laws and policies (Prieto-Benítez and Mendez, 2011). There remains a multitude of ways that average citizens may be complicit in maintaining this natural heritage and the biodiversity that thrives within it.

References

Alonso, L.E., Nordin, L.A. eds., 2004. *A rapid biological assessment of the aquatic ecosystems of the Okavango Delta, Botswana: high water survey*. Conservation International. Washington DC.

Avery, R.A., 1966. Food and feeding habits of the common lizard (*Lacerta vivipara*) in the west of England. *Journal of Zoology* 149, 115-121.

Azarkina, G.N., Foord, S.H., 2015. A review of three *Tusitala* (Araneae: Salticidae) species from Southern Africa, with a new synonymy and description of a new species from Botswana. *African Invertebrates 56*, 285–307.

Bishop, L., Riechert, S.E., 1990. Spider colonization of agroecosystems: mode and source. *Environmental Entomology 19*, 1738–1745.

Cardoso, P., Erwin, T.L., Borges, P.A.V., New, T.R., 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* 144, 2647–2655.

Cardoso, P., Shirey, V., Seppälä, S., Henriques, S., Draney, M.L., Foord, S., Gibbons, A.T., Gomez, L.A., Kariko, S., Malumbres-Olarte, J., Milne, M., 2019. Globally distributed occurrences utilised in 200 spider species conservation profiles (Arachnida, Araneae). *Biodiversity Data Journal* 7, 1-15.

Clerck, C., 1757. Svenska spindlar, uti sina hufvud-slågter indelte samt under några och sextio särskildte arter beskrefneoch med illuminerade figurer uplyste. [Swedish spiders, classified into their main genera and described with illustrations of over sixty distinct species]. Stockholm, 154.

Coddington, J.A., Levi, H.W., 1991. Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics 22*, 565–592.

Coddington, J.A., 2005. Phylogeny and classification of spiders. In: Ubick, D., Paquin, P., Cushing, P.E., Roth, V. (Eds.), *Spiders of North America: An Identification Manual*, 18-24. American Arachnological Society.

Coddington, J.A., Griswold, C.E., Silva Dávila, D., Peñaranda, E., Larcher, S.F., 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. In: Dudley E.C. (Ed.), *The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology*, Dioscorides Press, Portland, Oregon, U.S.A.

Craig, C.L., 2003. *Spiderwebs and silk: tracing evolution from molecules to genes to phenotypes*. Oxford University Press, Oxford.

Darkoh, M.B., Mbaiwa, J.E., 2014. Okavango delta- A Kalahari oasis under environmental threats. *Journal of Biodiversity and Endangered Species 2*, 123–-130.

Dippenaar-Schoeman, A. S., Jocqué, R. 2014. *African Arachnida Database (AFRAD)*, Agricultural Research Council.

Dippenaar-Schoeman, A.S., Jocqué, R., 1997. African Spiders: An Identification Manual. *Plant Protection Research Institute Handbook* 9, 392 pages.

Dippenaar-Schoeman, A.S., Kassimatis, E., 2002. Environmental monitoring of Tsetse aerial spraying 2001. In: Perkins, J and Ramberg, L. (eds.), Harry Oppenheimer Okavango Research Centre, University of Botswana, Maun, Arachnida: Araneae, 113-131.

Dippenaar-Schoeman, A.S., Haddad, C.R., Foord, S.H., Lyle, R., Helberg, L., Mathebula, S., Van den Berg, A.M., Van Niekerk, E. and Jocqué, R. 2010. *First Atlas of the Spiders of South Africa*, South African National Survey of Arachnida Technical Report Version 1. Agricultural Research Council, Pretoria.

Dippenaar-Schoeman, A.S., Lyle, R., Marais, P., Haddad, C.R., Foord, S.H., Lotz, L.N., 2015. South African National Survey of Arachnida (SANSA): review of current knowledge, constraints and future needs for documenting spider diversity (Arachnida: Araneae). *Transactions of the Royal Society of South Africa* 70, 245–275.

Dippenaar-Schoeman, A.S., Van den Berg, A.M., Lyle, R. and Haddad, C.R., 2013. Current knowledge of spiders in South African agroecosystems (Arachnida, Araneae). *Transactions of the Royal Society of South Africa* 68, 57–74.

Eagle, V., 1985. A survey of the spider fauna of Botswana project report June 1984. *Botswana Notes and Records* 17, 131–139.

FitzPatrick, M.J., 2001. The spider fauna of Zimbabwe (Arachnida: Araneae). *Arnoldia Zimbabwe* 10, 177-188.

Gibb, H., Silvey, C.J., Robinson, C., L'Hotellier, F.A., Eldridge, D.J., 2021. Experimental evidence for ecological cascades following threatened mammal reintroduction. *Ecology* 102, 3191.

Green, J., 1999. Sampling method and time determines composition of spider collections. *Journal of Arachnology*,27, 176–182.

Griffin, E., Dippenaar-Schoeman, A.S., 1991. A checklist of, and references to, the Namibian spider fauna (Arachnida, Araneae). *Cimbebasia* 13*,* 155-181.

Gunnarsson, B., 2007. Bird predation on spiders: ecological mechanisms and evolutionary consequences. *The Journal of Arachnology 35*, 509–529.

Haddad, C.R., Mavrusik, Y.M., 2019. Clarifying the taxonomic status and distributions of the spider species collected during the Leonhard Schultze expeditions in western and central southern Africa (Arachnida: Araneae). *Zootaxa* 4608, 451–483.

Harmer, A.M., Blackledge, T.A., Madin, J.S., Herberstein, M.E., 2011. High-performance spider webs: integrating biomechanics, ecology and behaviour. *Journal of the Royal Society Interface* 8, 457-471.

Haughton, A.J., Champion, G.T., Hawes, C., Heard, M.S., Brooks, D.R., Bohan, D.A., Clark, S.J., Dewar, A.M., Firbank, L.G., Osborne, J.L., 2003. Invertebrate responses to the management of genetically modified herbicide–tolerant and conventional spring crops. ii. within-field epigeal and aerial arthropods. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 358*, 1863–1877.

Isbister, G.K., Fan, H.W., 2011. Spider bite. *The Lancet 378*, 2039-2047.

Isbister, G.K., White, J., 2004. Clinical consequences of spider bites: recent advances in our understanding. *Toxicon* 43, 477-492.

Jocqué R., Alderweireldt M., Dippenaar-Schoeman, A.S., 2013. *Biodiversity.* In: Penney D (Ed.) *An African perspective: spider research in the 21st Century: trends & perspectives*. Siri Scientific Press, Manchester, 18–57.

Kioko, G.M., Mavrusik, Y.M., Li, S., Kioko, E.N., Ji, L., 2021. Checklist of the spiders (Araneae) of Kenya. *African Invertebrates* 62, 47-229.

King, G.F., Hardy, M.C., 2013. Spider-venom peptides: structure, pharmacology, and potential for control of insect pests. *Annual Review of Entomology 58*, 475–496.

Ko, F.K., Wan, L.Y., 2018. Engineering properties of spider silk. *Handbook of Properties of Textile and Technical Fibres* 1, 185–220.

Kuntner, M., Hormiga, G., 2002. The African spider genus *Singafrotypa* (Araneae, Araneidae). *The Journal of Arachnology 30*, 129–139.

Lawrence, R.F., 1936. Scientific results of the Verney-Lang Kalahari Expedition, March to September, 1930. Spiders (Ctenizidae excepted). *Annals of the Transvaal Museum 17*, 145–158.

Linnaeus, C., 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus differentiis, synonymis, locis [System of nature through the three kingdoms of nature, according to classes, orders, genera, species, with distinguishing characters, synonyms, places]. *Editio decima, reformata*. Stockholm, 821.

Logunov, D., 2009. Further notes on the Harmochireae of Africa (Araneae, Salticidae, Pelleninae). *ZooKeys* 16, 265–272.

Lotz, L.N., 2007. The genus Cheiracanthium (Araneae: Miturgidae) in the Afrotropical Region: 2: description of new species: systematics. *Navorsinge van die Nasionale Museum: Researches of the National Museum* 23, 148-180.

Magura, T., Horváth, R., Tóthmérész, B., 2010. Effects of urbanization on ground-dwelling spiders in forest patches, in Hungary. *Landscape Ecology 25*, 621–629.

Mammola, S., Malumbres-Olarte, J., Arabesky, V., Barrales-Alcalá, D.A., Barrion-Dupo, A.L., Benamú, M.A., Bird, T.L., Bogomolova, M., Cardoso, P., Chatzaki, M., Cheng, R.C., Chu, T.A., Classen-Rodríguez, L.M., Čupić, I., Dhiya'ulhaq, N.U., Drapeau Picard, A.P., El-Hennawy, H.K., Elverici, M., Fukushima, C.S., Ganem, Z., Gavish-Regev, E., Gonnye, N.T., Hacala, A., Haddad, C.R., Hesselberg, T., Ho, T.A.T., Into, T., Isaia, M., Jayaraman, D., Karuaera, N., Khalap, R., Khalap, K., Kim, D., Korhonen, T., Kralj-Fišer, S., Land, H., Lin, S.W., Loboda, S., Lowe, E., Lubin, Y., Martínez, A., Mbo, Z., Miličić, M., Kioko, G.M., Nanni, V., Norma-Rashid, Y., Nwankwo, D., Painting, C.J., Pang, A., Pantini, P., Pavlek, M., Pearce, R., Petcharad, B., Pétillon, J., Raberahona, O.C., Russo, P., Saarinen, J.A., Segura-Hernández, L., Sentenská, L., Uhl, G., Walker, L., Warui, C.M., Wiśniewski, K., Zamani, A., Chuang, A., Scott, C., 2022. The global spread of misinformation on spiders. *Current Biology* 32, 871-873.

Meehan, C.J., Olson, E.J., Reudink, M.W., Kyser, T.K., Curry, R.L., 2009. Herbivory in a spider through exploitation of an ant–plant mutualism. *Current Biology* 19, 892–893.

Michalko, R., Pekar, S., Entling, M.H., 2018. An updated perspective on spiders as generalist predators in biological control. *Oecologia* 189, 21–36.

Nyffeler, M., Pusey, B.J., 2014. Fish predation by semi-aquatic spiders: a global pattern. *PloS one* 9, 99459.

Nyffeler, M., 1999. Prey selection of spiders in the field. *Journal of Arachnology* 27, 317–324.

Nyffeler, M., Sterling, W. L., Dean, D.A., 1994a: How spiders make a living. *Environmental Entomology* 23, 1357–1367.

Nyffeler, M., Sterling, W.L., Dean, D.A., 1994b. Insectivorous activities of spiders in United States field crops. *Journal of Applied Entomology* 118, 113–128.

Nyffeler, M., Birkhofer, K., 2017. An estimated 400–800 million tons of prey are annually killed by the global spider community. *The Science of Nature* 104, 1–12.

Oliver, I., Beattie, A.J., 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology 7*, 562–568.

Platnick, N.I., Griffin, E., 1990. On *Rastellus*, a new genus of the spider family Ammoxenidae (Araneae, Gnaphosoidea). *American Museum novitates* 2995, 1–11.

Platnick, N.I., Murphy, J.A., 1987. Studies on Malagasy spiders. 3, The zelotine Gnaphosidae (Araneae, Gnaphosoidea), with a review of the genus Camillina. *American Museum novitates* 2874, 1–33.

Platnick, N.I., 1991. Patterns of biodiversity: tropical vs temperate. *Journal of Natural History* 25, 1083–1088.

Platnick, N.I., Raven, R.J., 2013. Spider systematics: past and future. *Zootaxa* 3683, 595–600.

Prieto-Benítez, S., Méndez, M., 2011. Effects of land management on the abundance and richness of spiders (Araneae): A meta-analysis. *Biological Conservation* 144, 683-691.

Reynolds, B.N., 2014. *The effects of long-term burning regimes on savanna spider assemblages*. PhD thesis, (unpublished) University of Pretoria.

Robertson, M.P., Harris, K.R., Coetzee, J.A., Foxcroft, L.C., Dippenaar-Schoeman, A.S., Van Rensburg, B.J., 2011. Assessing local scale impacts of *Opuntia stricta* (Cactaceae) invasion on beetle and spider diversity in Kruger National Park, South Africa. *African Zoology* 46, 205–223.

Russell-Smith, A., 1981. Seasonal activity and diversity of ground-living spiders in two African savanna habitats. *Bulletin of the British Arachnological Society* 5, 145–154.

Russell-Smith, A., 2020. A checklist of the spiders of Tanzania. *Journal of East African Natural History* 109, 1–41.

Saez, N.J., Herzig, V., 2019. Versatile spider venom peptides and their medical and agricultural applications. *Toxicon* 158, 109–126.

Seppälä, S., Henriques, S., Draney, M.L., Foord, S., Gibbons, A.T., Gomez, L.A., Kariko, S., Malumbres-Olarte, J., Milne, M., Vink, C.J., Cardoso, P., 2018. Species conservation profiles of a random sample of world spiders I: Agelenidae to Filistatidae. *Biodiversity data journal* 6, e26203.

Siyam, M., Dunlop, J.A., El-Hennawy, H.K., 2014. New spider records from the Republic of the Sudan. *Arachnology* 16, 264-272.

Stojanowska, A., Zeynalli, F., Wróbel, M., Rybak, J., 2023. The use of spider webs in the monitoring of air quality—A review. *Integrated Environmental Assessment and Management* 19, 32–44.

Vetter, R.S., Isbister, G.K., 2008. Medical aspects of spider bites. *Annual Review of Entomology 53*, 409-429.

Wesolowska, W., 2011. New species and new records of jumping spiders from Botswana, Namibia and Zimbabwe (Araneae: Salticidae). *Genus. International Journal of Invertebrate Taxonomy 22*, 307–346.

Wise, D.H., 1995. *Spiders in ecological webs*. Cambridge University Press. Cambridge

World Spider Catalog. 2023. World Spider Catalog. Version 24. Natural History Museum Bern, online at http://wsc.nmbe.ch, accessed on 15 January 2023.

Young, O.P., Edwards, G.B., 1990. Spiders in United States field crops and their potential effect on crop pests. *Journal of Arachnology* 18, 1–27.

Chapter 4: Summary and conclusions

Arthropods are well-known to provide valuable ecosystem services and drive unseen processes in terrestrial ecosystems, ranging from forests to wetlands. Their diversity and abundance can often be used representatively to estimate, with caution, the trends of the larger community and also as indicators, relating to impacts of changes in ecosystem states through assessing the presence and absence of certain species (Gerlach *et al.,* 2013). Globally, arthropods and other invertebrates are relatively understudied, with vertebrate research regularly receiving more resources, both intellectual and financial (Titley *et al.,* 2017). The fragmented knowledge on these ecologically important groups is concerning when acknowledging the value of the ecosystem services provided, including many unknown services yet to be quantified. The loss of these yet unknown services may impact humans and other species of fauna and flora. Thus, arthropods are vital for the healthy functioning of global systems and the species that depend on them, including humans.

In regional biodiversity hotspots, like the Okavango Delta, vertebrates are well documented (McCarthy and Ellery, 1998), but their invertebrate counterparts less so. The inaccessibility and remoteness of these areas tend to exclude many researchers, and so remain understudied unless dedicated research is undertaken with specific aims focused in these remote areas (Cooper *et al.,* 2012). This World Heritage Site acts as the foundation of a thriving tourism industry that not only supports the region, but the country of Botswana as a whole (Mbaiwa and Stronza, 2010). Thus, it would be beneficial to improve the knowledge available regarding invertebrate communities in the Okavango Delta, not only to gain insight into the species present here, but also to understand how these species may underpin some of the ecological processes that maintain this valuable natural system. The terrestrial invertebrate fauna of Botswana has been sparsely documented, with the exception of aquatic species and spiders (Russel-Smith, 1981; Dangerfield, 1997; Dippenaar-Schoeman, 2002; Alonso and Nordin, 2004; Ramberg *et al*., 2006), thus knowledge gaps exist. This study continued the much-needed work in documenting some of the vast number of species that remain undocumented in the Okavango Delta. Along with the lack of ongoing research on terrestrial invertebrates of Botswana, human-induced disturbances also influence biological communities in various ways, positively and negatively, variably across time. In order to understand how to improve management recommendations and associated practices, the understanding of the communities present in this system is needed.

The first aim of this study was to compare the abundance and diversity of four terrestrial arthropod groups in grazed and burnt sites. Abundance of the four groups was only fractionally higher in the wet season for the pitfall traps, but litter extractions had large increases in Formicidae, Collembola and Hymenoptera (wasps) in the wet season. This may support the proposition of increasing sampling efficiency by only sampling in the wet season, reducing time in-field, although the current study also found vastly different communities in the wet and dry season in all of the groups. Formicidae was the most abundant, which could be partly due to their resilience towards disturbance, being surface-active, and the collection method (pitfall traps). It may seem efficient to sample Araneae in the wet season when using pitfall traps, but litter extractions may be equally efficient in both.

The second aim of this study was to assess whether burning or grazing had differential impacts on arthropod communities. The results from this study showed some influence on patterns in abundance and diversity of the arthropod communities. Comparable pristine sites would be required to gain insight into the positive or negative nature of the impacts. Ants had the most species and the highest diversity in the grazed sites, while Collembola and spider communities were more even in the burnt sites (Chapter 2). These were the only clear results across both trapping methods and seasons. Besides these, each group varied between trapping methods in species richness, evenness and diversity, illustrating the varied responses of arthropod communities to disturbances, as well as the value of using a multi-taxon approach paired with multiple trapping methods (Chapter 2). Ants and Collembola varied significantly between seasons, but not between disturbance types, while wasps and spiders differed significantly between both season and disturbance types. Trends may become more apparent if subsequent research employs longer sampling periods, across multiple years, and accounts for disturbance intensity and severity. These variables may all have played a role in the variable responses seen in this study. Nonetheless, it remains apparent that the responses of various arthropod groups may vary between groups, across disturbance types and across seasons (Pryke and Samways, 2012), and should be accounted for in future research.

The third aim was to create a starting point to monitor the impact of disturbances on arthropod communities in the Okavango Delta into the future. The current study has now created this dataset and provided an updated point of comparison between arthropod communities and the impact that disturbances have on their community shape and composition. Many specimens are yet to be identified and these identifications may lead to discovery of new location records for species or even novel species. Lastly, this study was able to construct an updated species list for Spiders of the Okavango Delta (Chapter 3), adding 39 new geographical observations for spider species in the Delta. This will serve as the basis for further species inventories and diversity studies in the region.

From this study, it is recommended that larger scale inventories need to be done and species lists be constructed for as many arthropod groups as possible in the next 5-10 years. The involvement of more specialists, including molecular ecologists, to focus on the terrestrial arthropods and attempt species-level identifications is crucial to ensure these species are documented before they are lost to climate change or anthropogenic disturbances. It may seem that most of the groups included in this study are resilient to disturbances to some degree, although this study did not account for disturbance intensity, and so it would be interesting to see how arthropod communities compare between sites within the Delta, and sites on the edges. As mentioned, this study could not locate a pristine site within the area accessible from the Mopiri Research Station, and so was unable to compare disturbed and pristine sites. It would be ideal to compare the data generated in this study with data collected on pristine terrestrial islands, with minimal influence from disturbance to assess how these communities differ. Longer sampling periods may also clarify trends or indicate annual changes in communities where trends may be localized to islands or having larger, regional scale influences.

Through this study, the state of knowledge of four arthropod groups in the Okavango Delta has been improved, ‘baseline’ data have been generated and will be made available for future research, and critical research within a world heritage site has continued. The Okavango Delta and its arthropod community dynamics remain somewhat of a mystery to the scientific world, and will slowly reveal the secrets of its species and their unique roles, if we persist in the quest to document and describe all living species in Africa, and on planet Earth.

References

Alonso, L.E. and L. Nordin (editors)., 2003. A rapid biological assessment of the aquatic ecosystems of the Okavango Delta, Botswana: High Water Survey. *RAP Bulletin of Biological Assessment* 27. Conservation International, Washington, DC.

Cooper, C.B., Hochachka, W.M., and Dhondt, A.A., 2012. The opportunities and challenges of citizen science as a tool for ecological research. In: Dickinson, J.L., Bonney, R., and S. Kelling (eds.), *Citizen science: public participation in environmental research* 99-117.

Dippenaar-Schoeman, A.S., Kassimatis, E., 2002. Environmental monitoring of Tsetse aerial spraying 2001. In: Perkins, J and Ramberg, L. (eds.), Harry Oppenheimer Okavango Research Centre, University of Botswana, Maun, *Arachnida*: *Araneae*, 113-131.

Dangerfield, J.M., 1997. Abundance and diversity of soil macrofauna in northern Botswana. *Journal of Tropical Ecology* 13, 527–538.

Gerlach, J., Samways, M., Pryke, J., 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation* 17, 831–850.

Mbaiwa, J.E. and Stronza, A.L., 2010. The effects of tourism development on rural livelihoods in the Okavango Delta, Botswana. *Journal of sustainable tourism* 18, 635-656.

McCarthy, T.S., Ellery, W.N., 1998. The Okavango delta. *Transactions of the Royal Society of South Africa* 53, 157–182.

Pryke, J.S., Samways, M.J., 2012. Differential resilience of invertebrates to fire. *Austral Ecology* 37, 460–469.

Ramberg, L., Wolski, P., Krah, M., 2006. Water balance and infiltration in a seasonal floodplain in the Okavango Delta, Botswana. *Wetlands* 26, 677–690.

Russell-Smith, A., 1981. Seasonal activity and diversity of ground-living spiders in two African savanna habitats. *Bulletin of the British Arachnological Society* 5, 145–154.

Titley, M.A., Snaddon, J.L., Turner, E.C., 2017. Scientific research on animal biodiversity is systematically biased towards vertebrates and temperate regions. *PloS one*, *12*, e0189577.

Appendix A

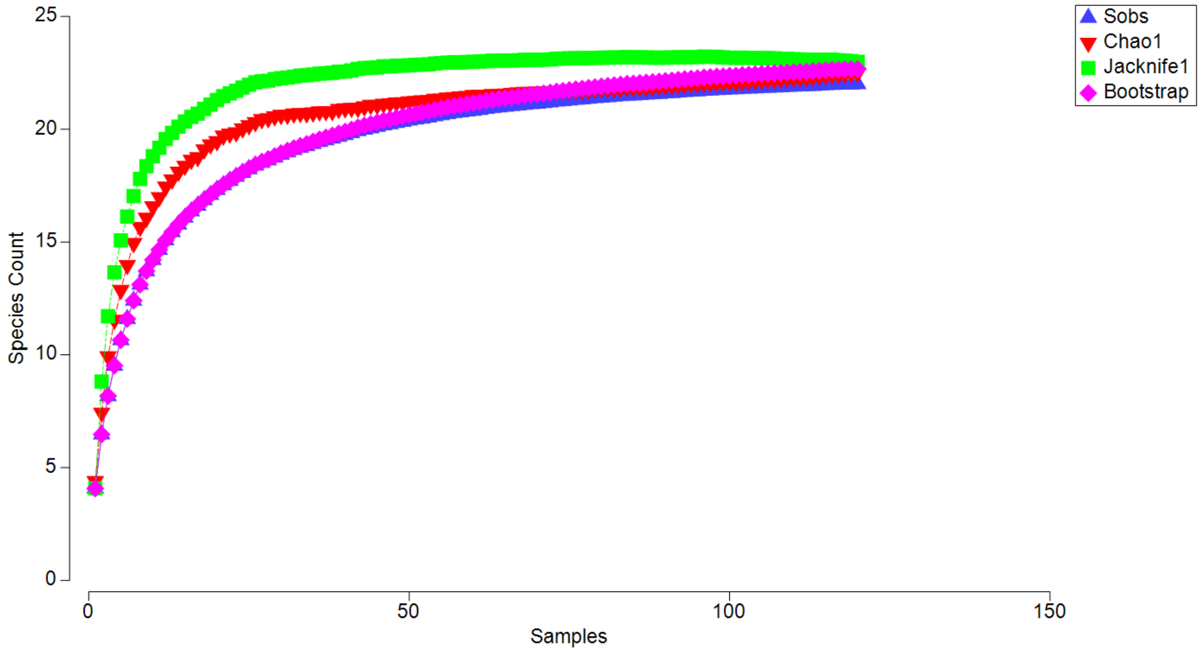

Figure A1: Species accumulation curves of ants sampled by pitfall traps showing number of observations (Sobs), Chao 1, Jacknife 1 and Bootstrap average.

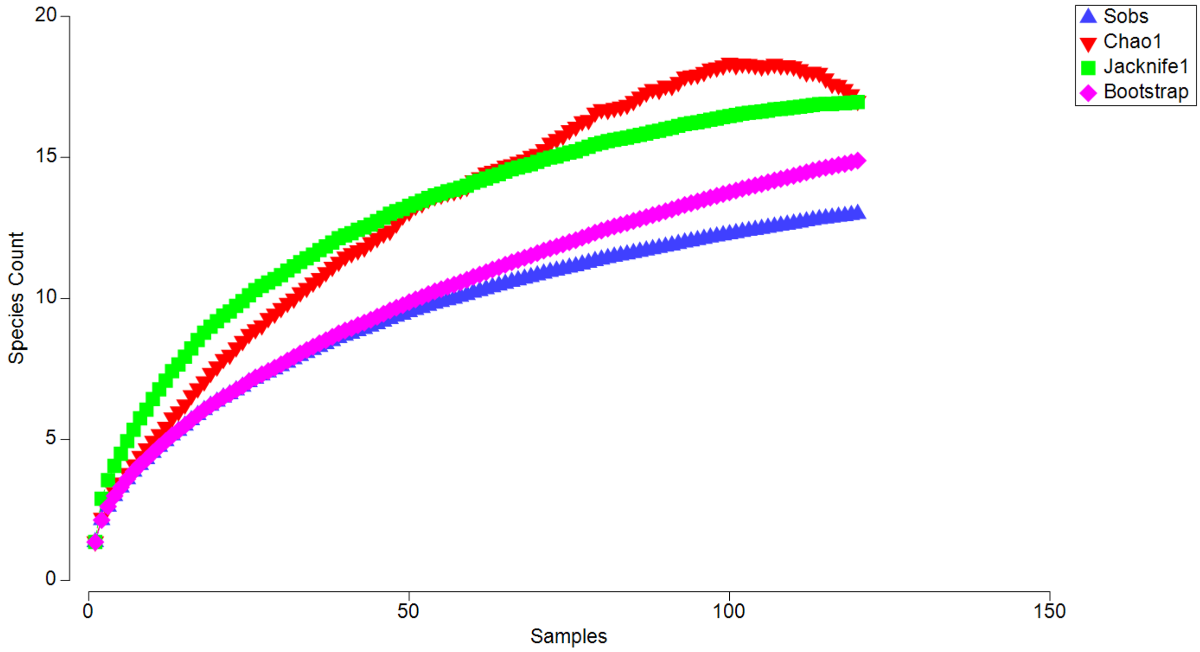

Figure A2: Species accumulation curves of ants sampled by litter extractions showing number of observations (Sobs), Chao 1, Jacknife 1 and Bootstrap average.

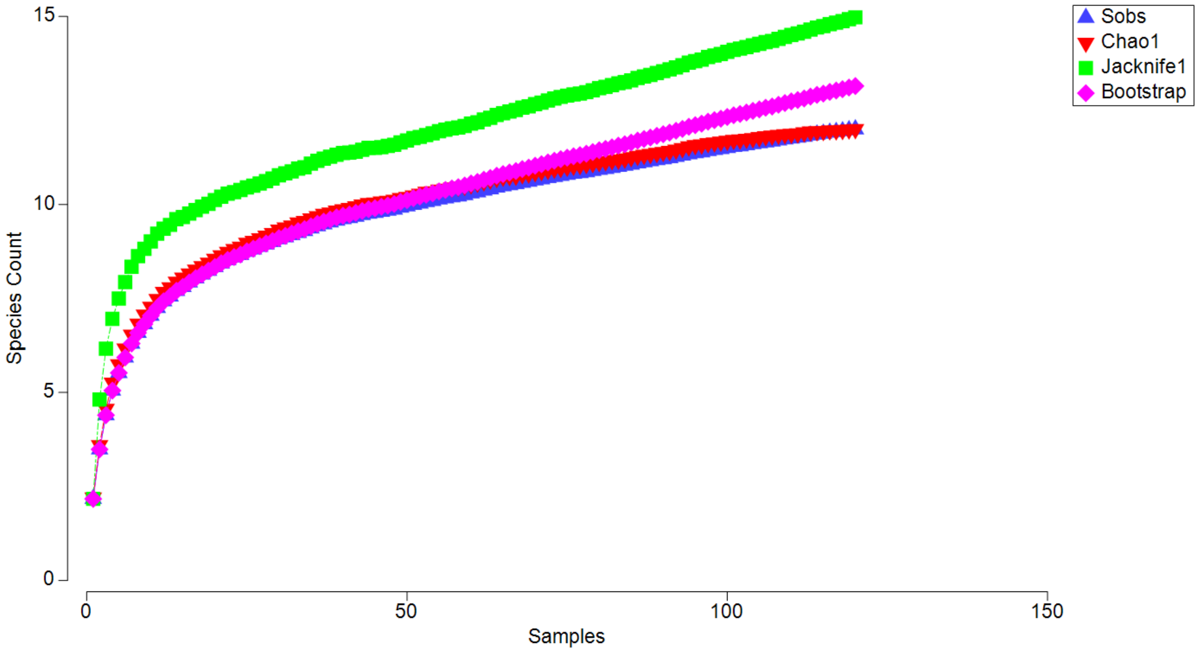

Figure A3: Species accumulation curves of Collembola sampled by pitfall traps showing number of observations (Sobs), Chao 1, Jacknife 1 and Bootstrap average.

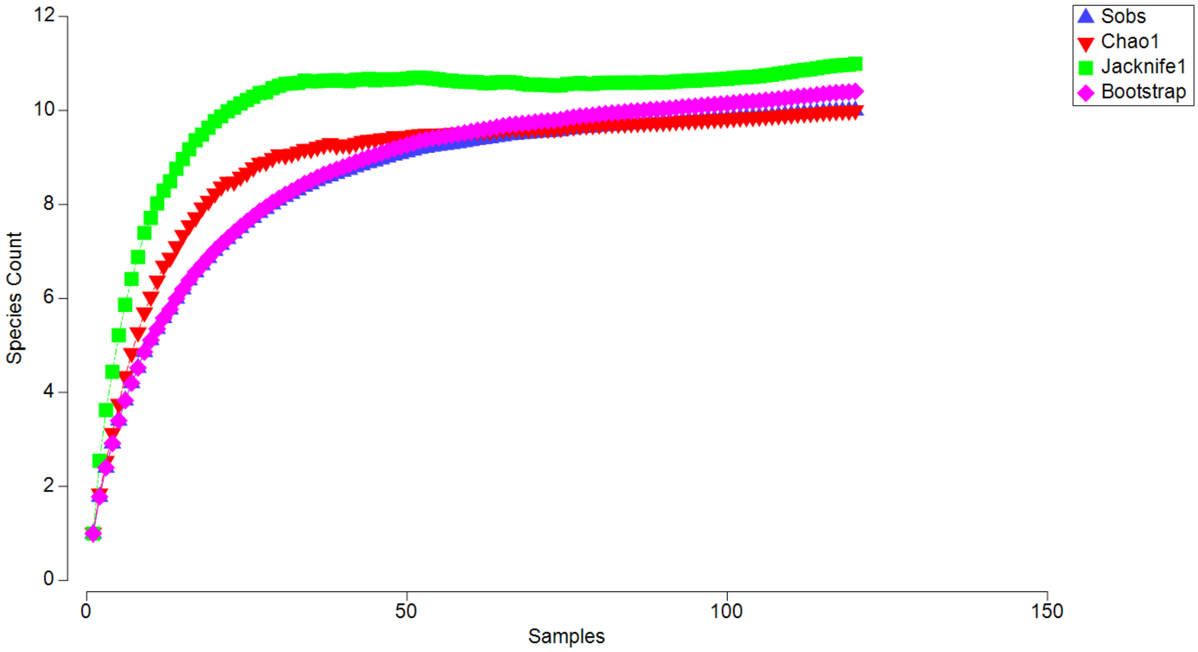

Figure A4: Species accumulation curves of Collembola sampled by litter extractions showing number of observations (Sobs), Chao 1, Jacknife 1 and Bootstrap average.

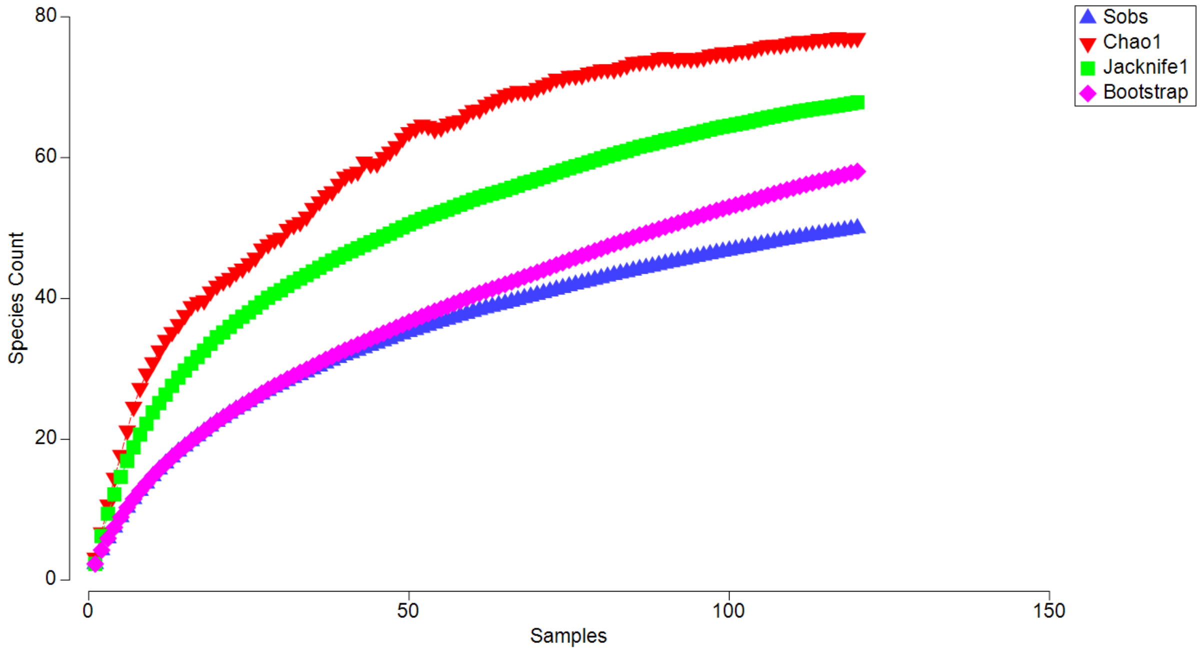

Figure A5: Species accumulation curves of wasps sampled by pitfall traps showing number of observations (Sobs), Chao 1, Jacknife 1 and Bootstrap average.

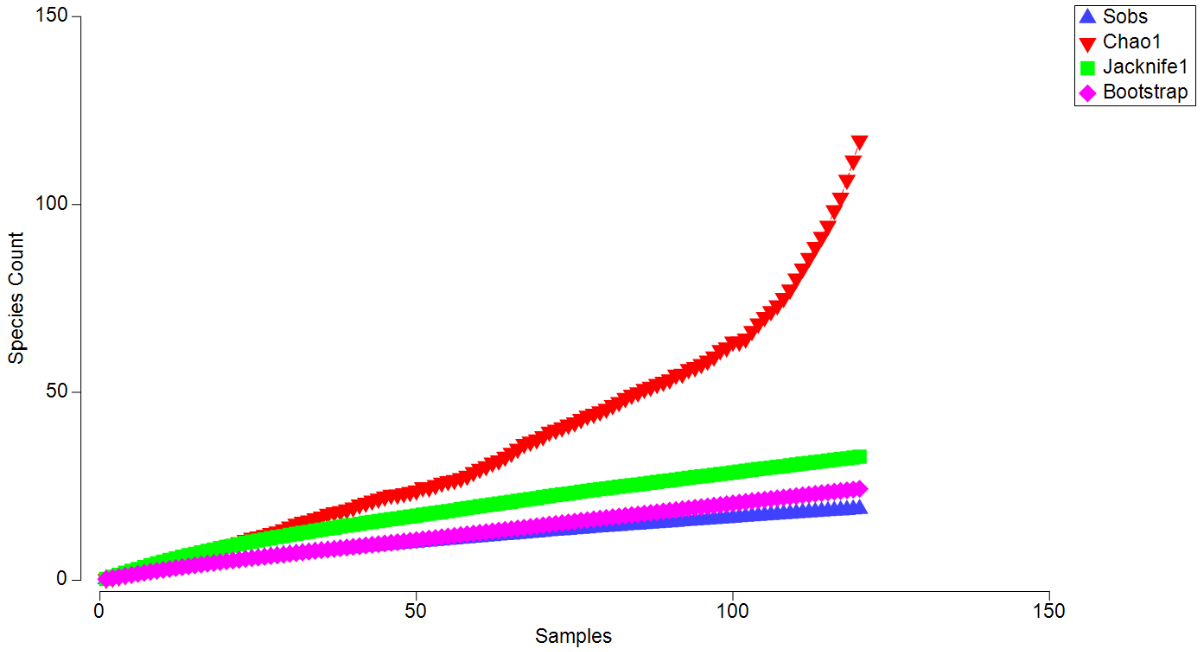

Figure A6: Species accumulation curves of wasps sampled by litter extractions showing number of observations (Sobs), Chao 1, Jacknife 1 and Bootstrap average.

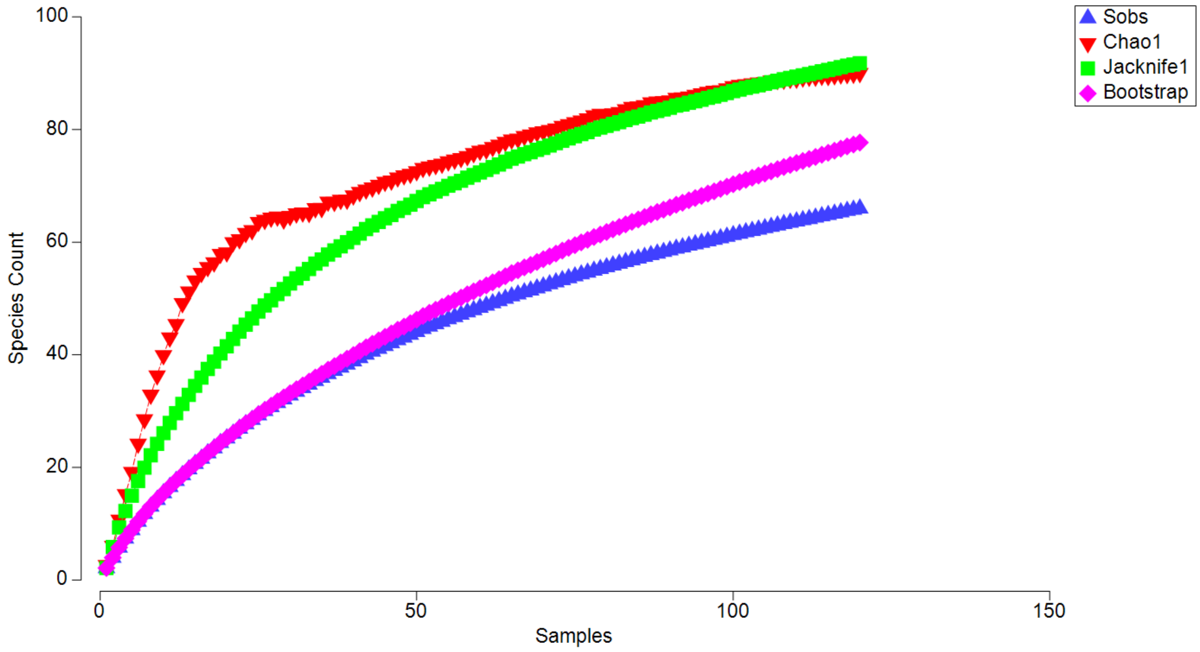

Figure A7: Species accumulation curves of spiders sampled by pitfall traps showing number of observations (Sobs), Chao 1, Jacknife 1 and Bootstrap average.

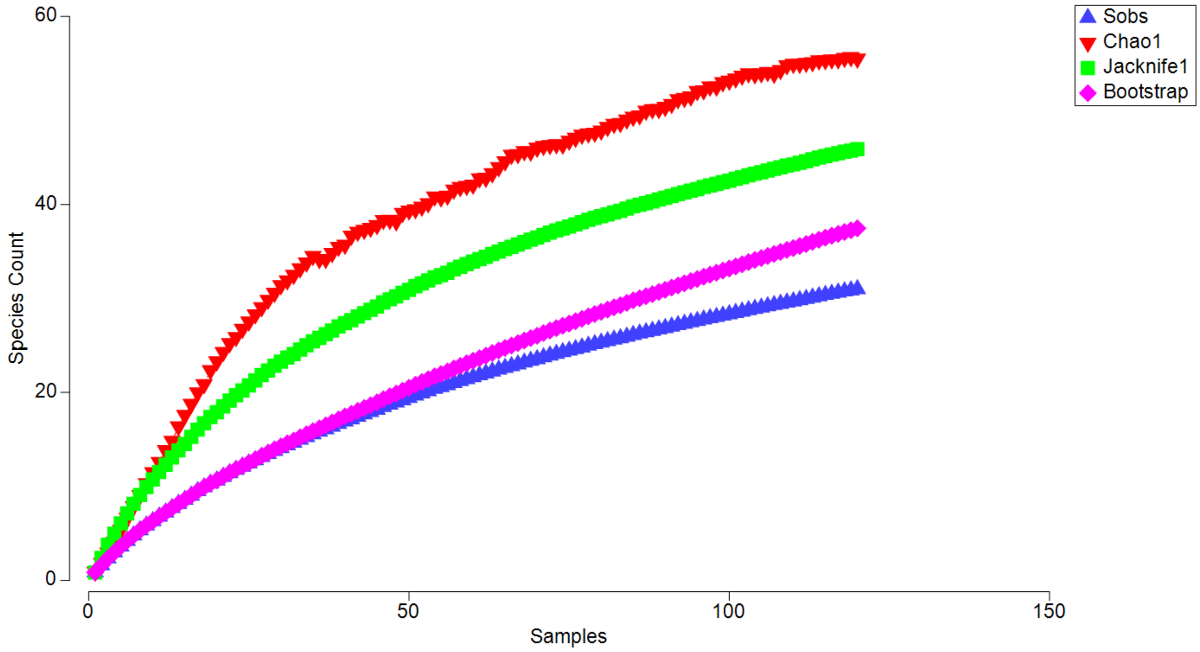

Figure 4: Species accumulation curves of spiders sampled by litter extractions showing number of observations (Sobs), Chao 1, Jacknife 1 and Bootstrap average.

Appendix B

Site photos

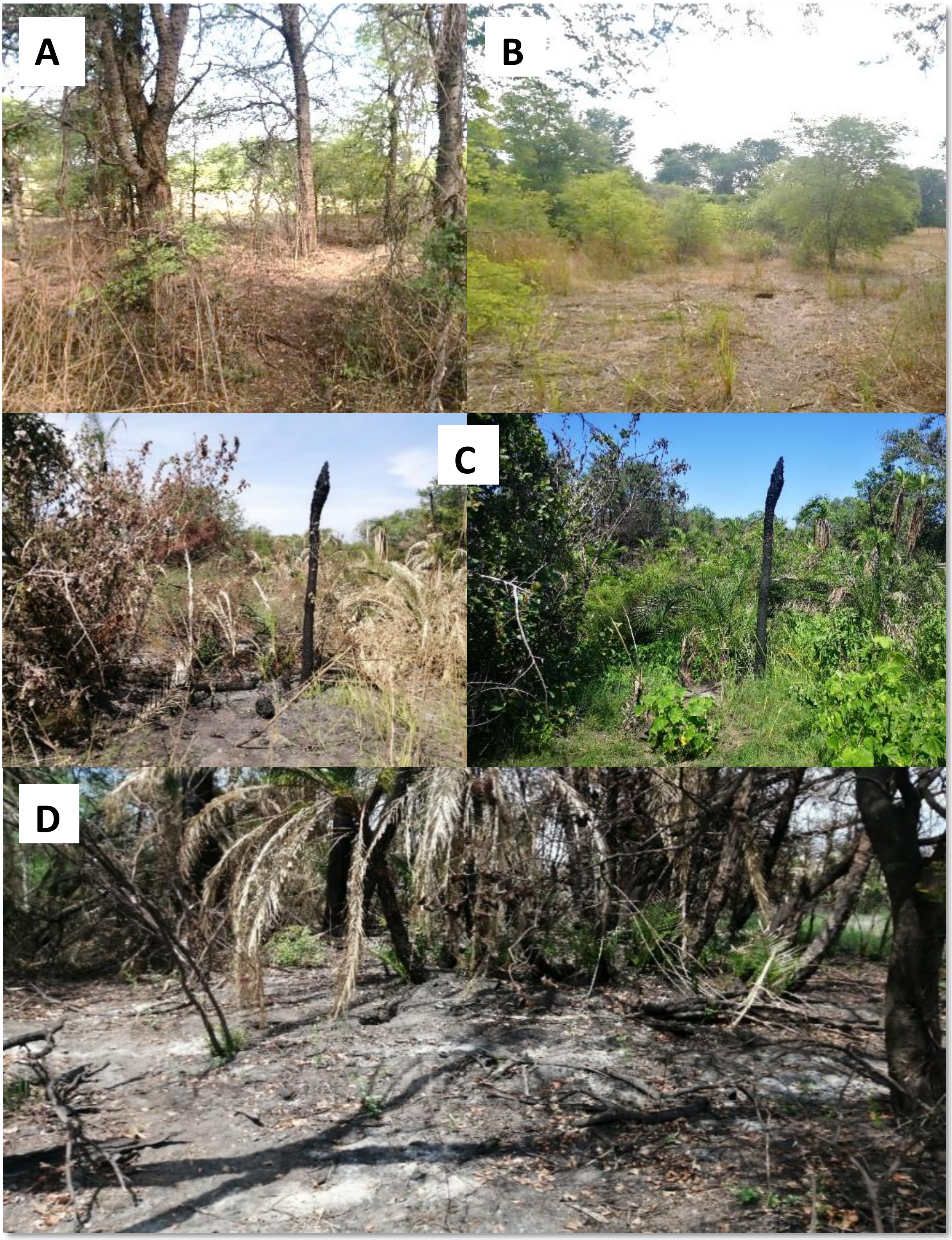

Figure B1: Site photos: **A)** Grazed woodland site, **B)** Grazed woodland site, **C)** Side-by-side of a burnt palm a few weeks after the fire in 2021 (left) and 3-months post-fire (right), **D)** Burnt undergrowth on Whe're island.

Trapping and extraction methods

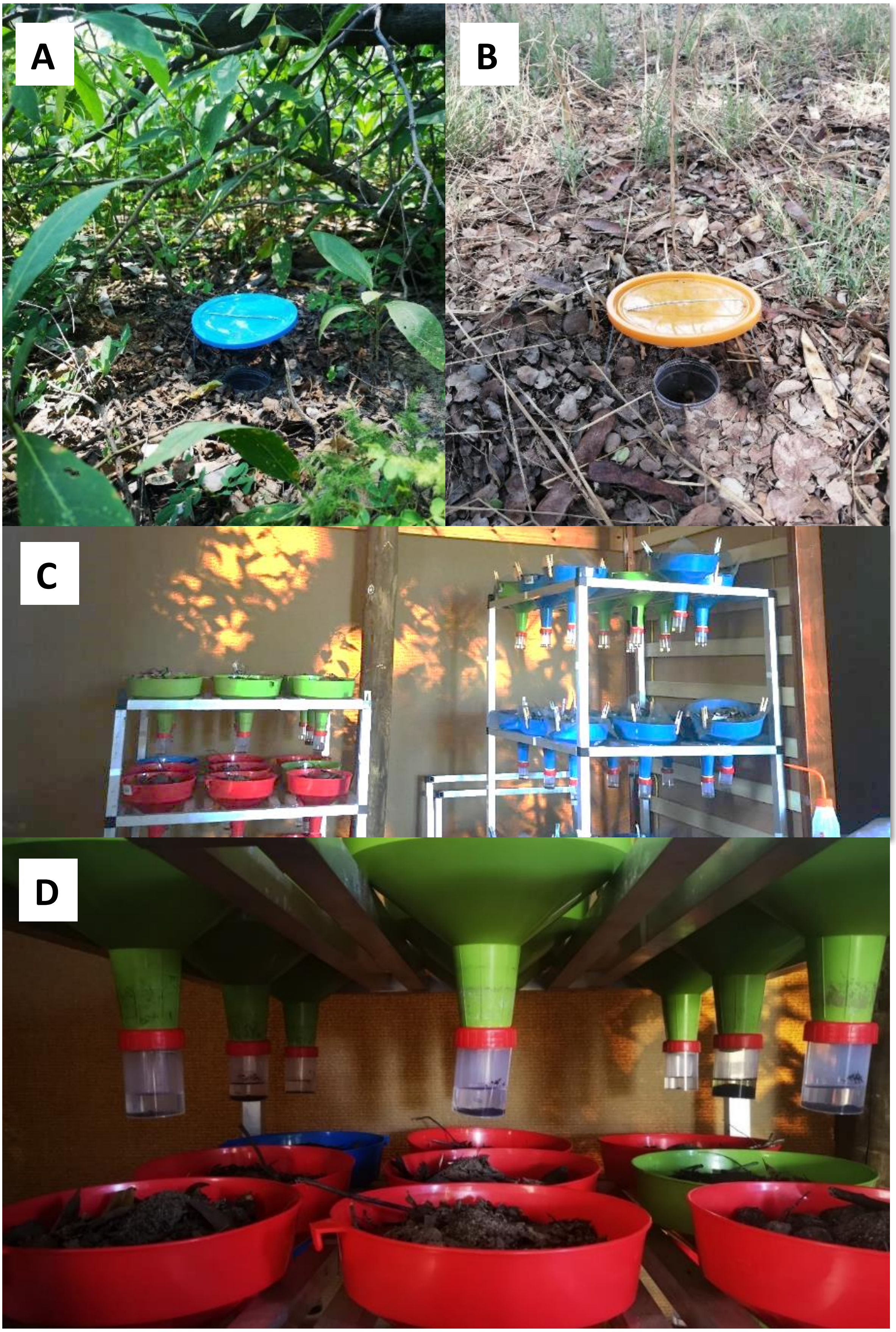

Figure B2: Trapping and extraction methods: **A)** and **B)** Active pitfall trap **C) and D)** Litter extraction using Berlese-Tullgren funnel design.

Examples of species collected during this study

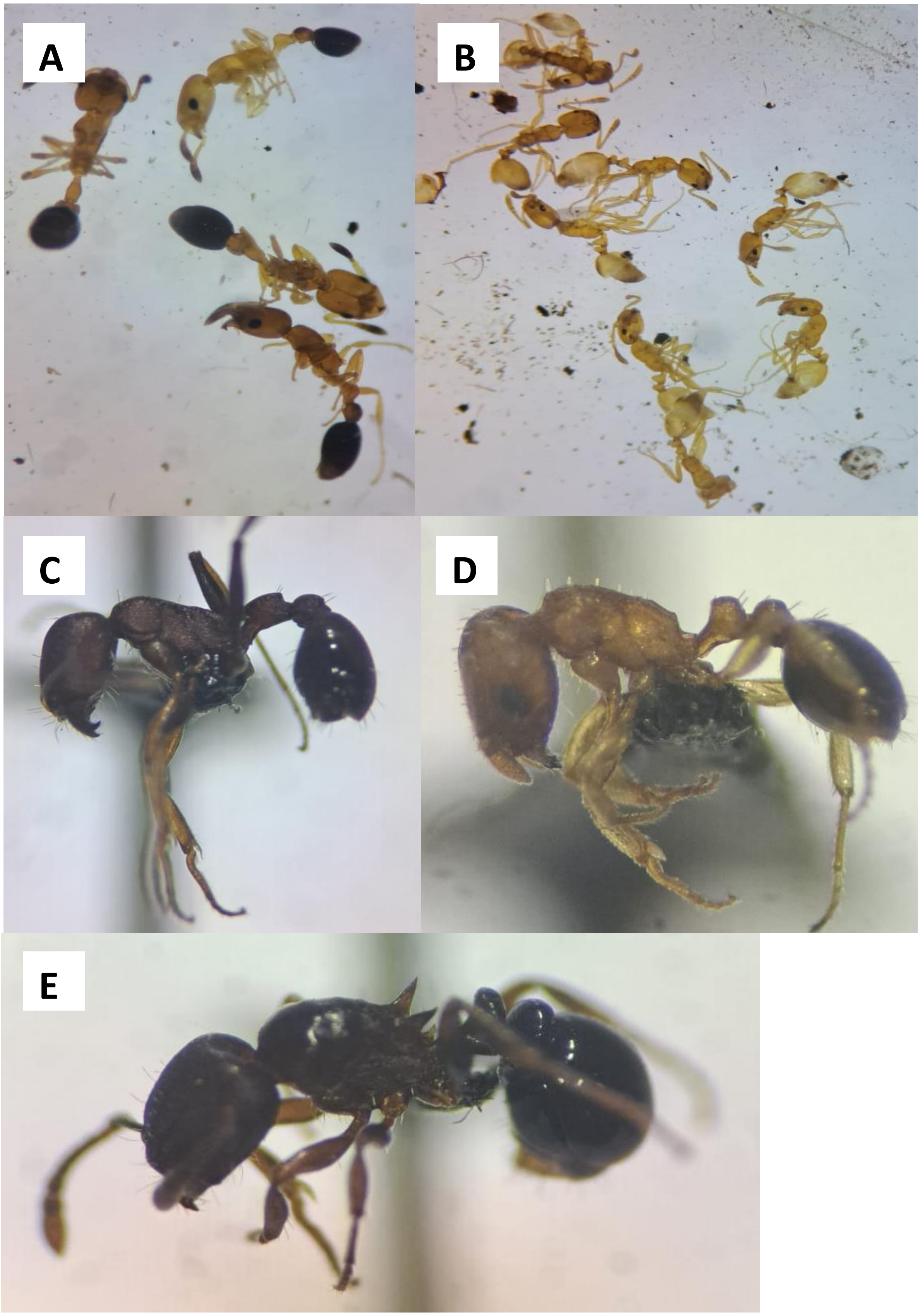

Figure B3: Examples of ants collected in the Okavango Delta: **A)** *Cardiocondyla* sp.1, **B)** *Monomorium* sp.1, **C)** *Tetramorium* sp.1. **D)** *Tetramorium* sp.4, **E)** *Tetramorium* sp.3.

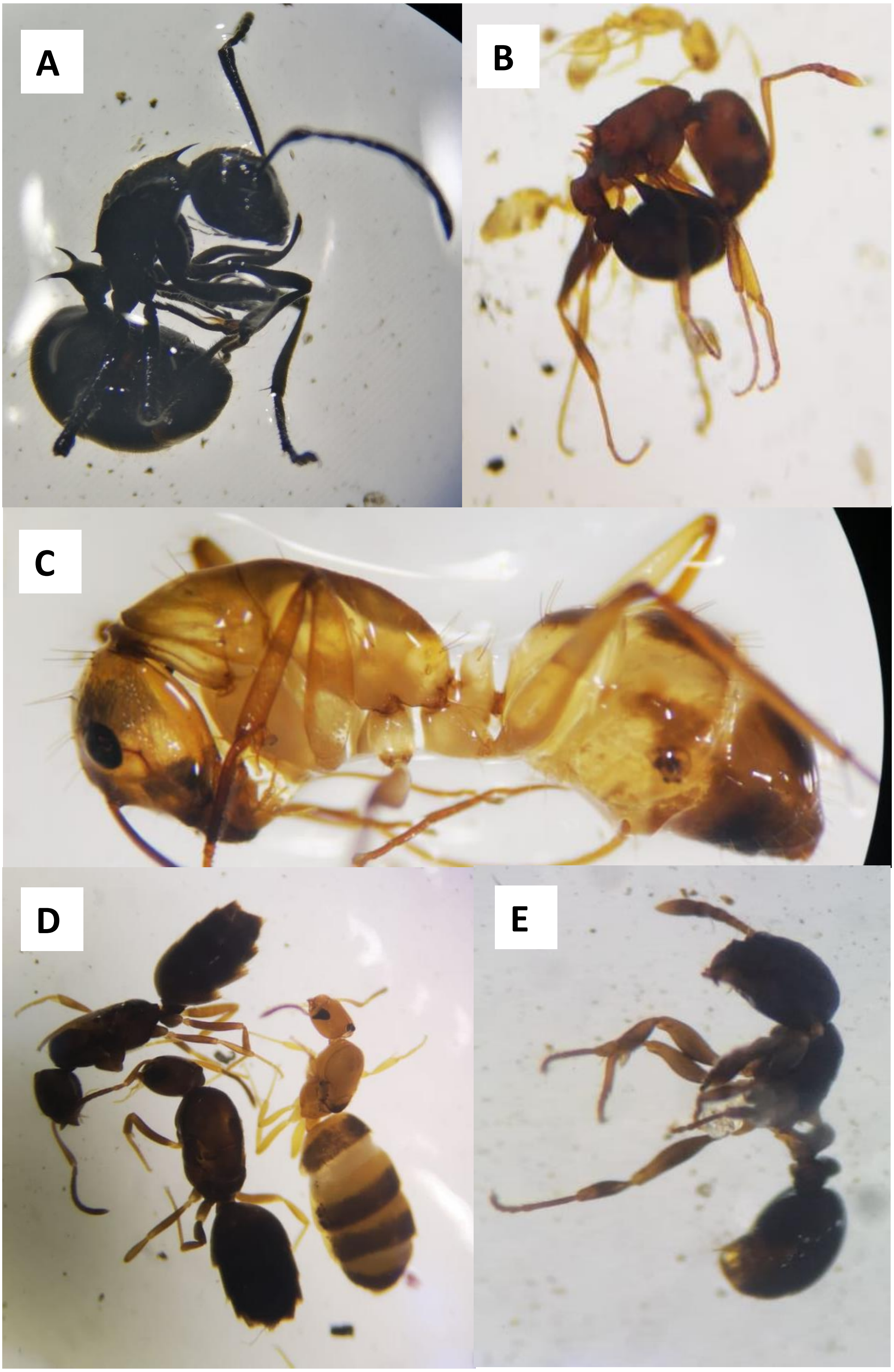

Figure B4: Examples of ants collected in the Okavango Delta: **A)** *Polyrhachis* sp.1, **B)** *Tetramorium* sp.1, **C)** *Camponotus* sp.3, **D)** *Anoplolepis* sp.1, **E)** *Tetramorium* sp.3.

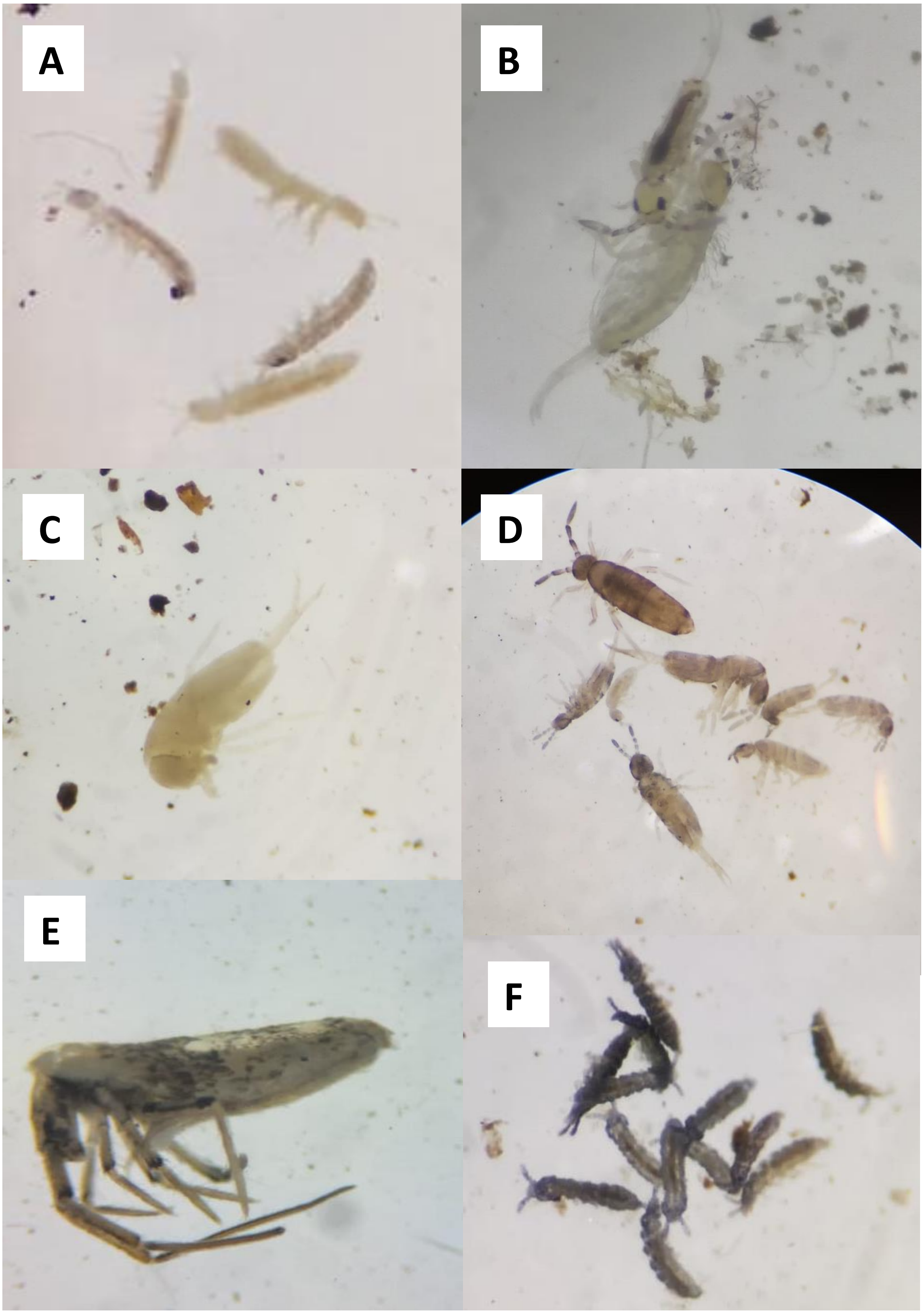

Figure B5: Examples of springtails collected in the Okavango Delta: **A)** *Cryptopygus* sp.1, **B)** *Seira* sp.2, **C)** *Sinella* sp.1, **D)** *Lepidocyrtus* sp.1, **E)** *Seira* sp.4, **F)** *Brachystomella* sp.1.

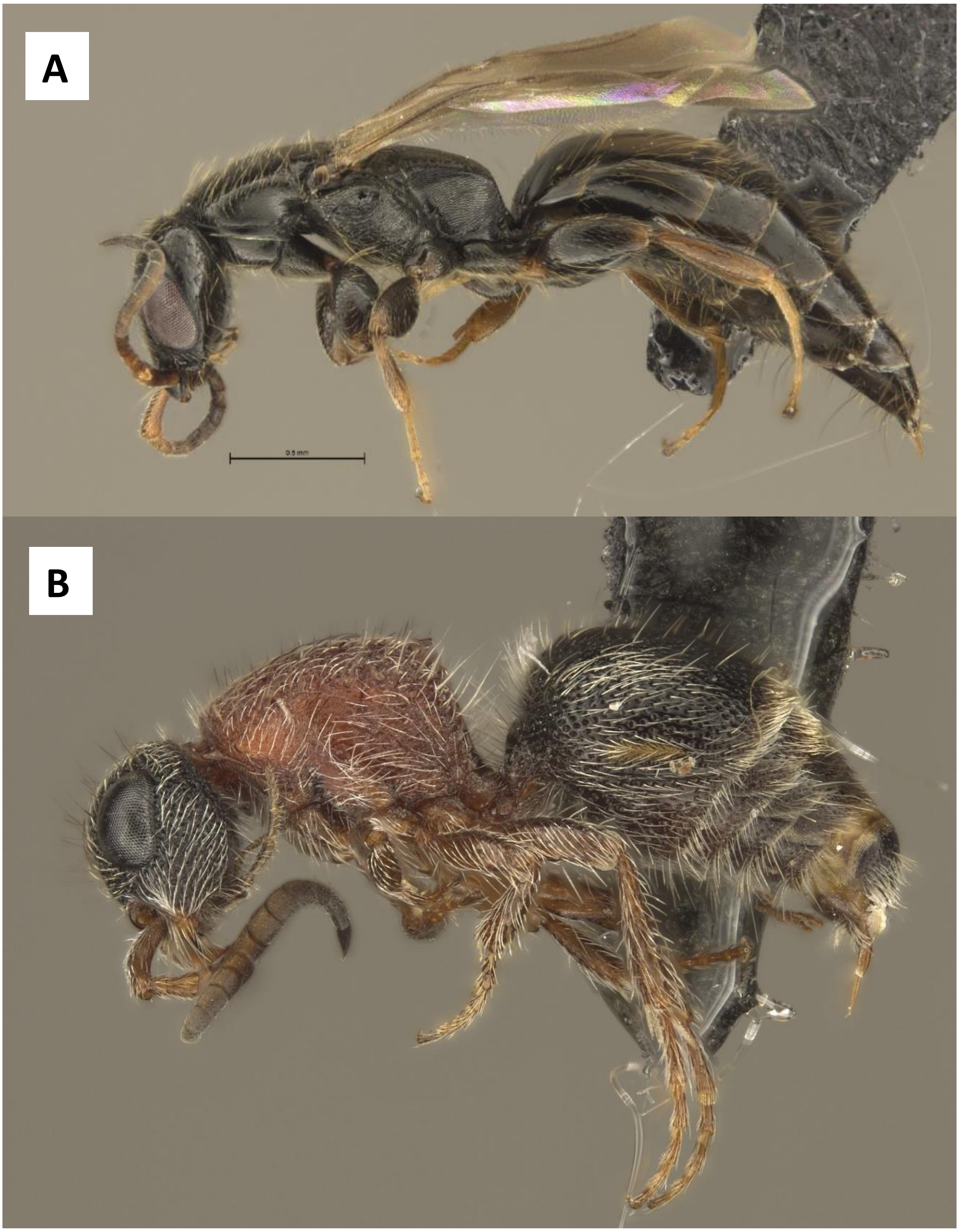

Figure B6: Examples of wasps collected in the Okavango Delta: **A)** Bethylidae sp. 1, **B)** Mutillidae sp. 1 Photos courtesy of A. Naghizadehmollayousefi.

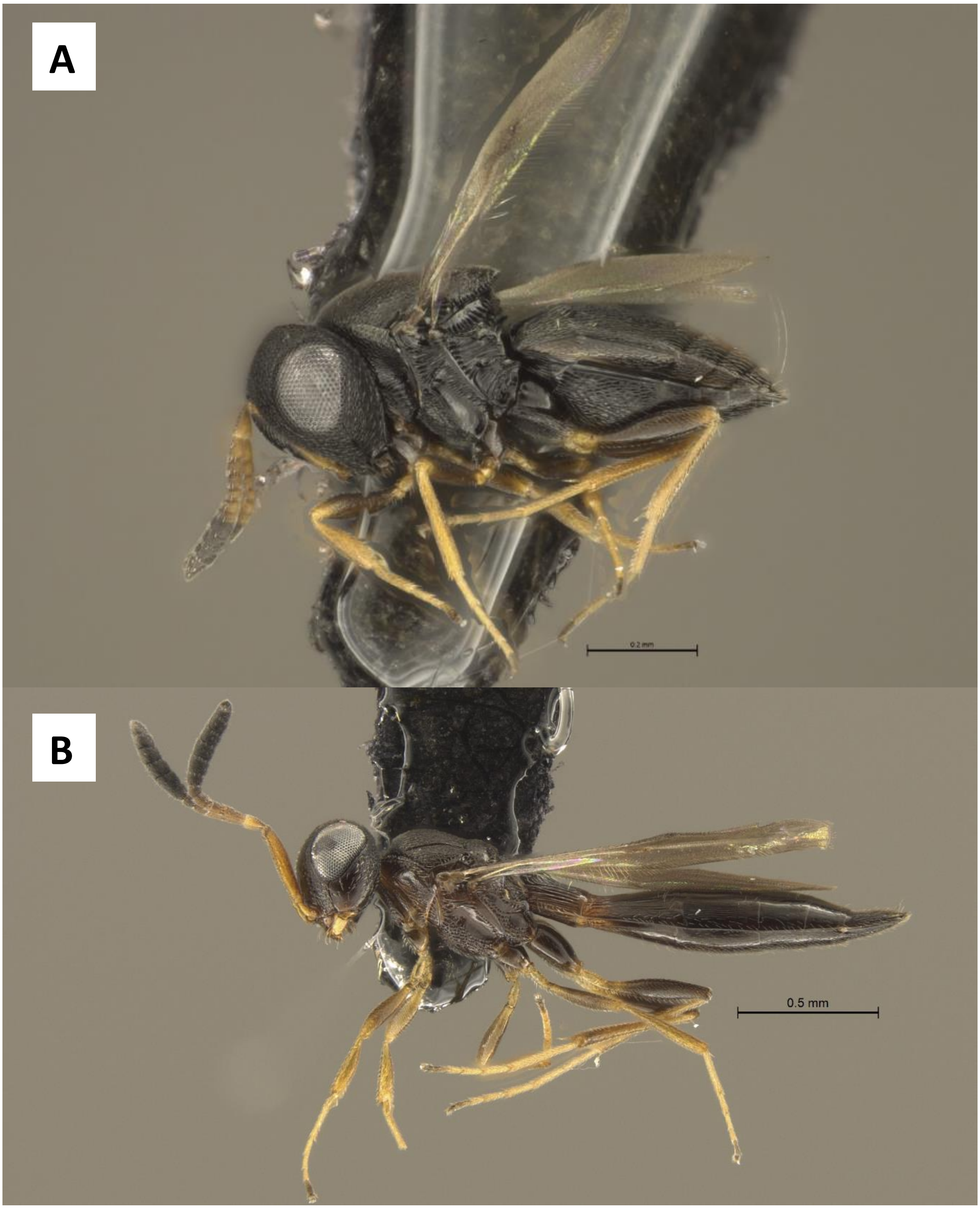

Figure B7: Examples of wasps collected in the Okavango Delta: A) Scelionidae sp. 9) Scelionidae sp. 10).

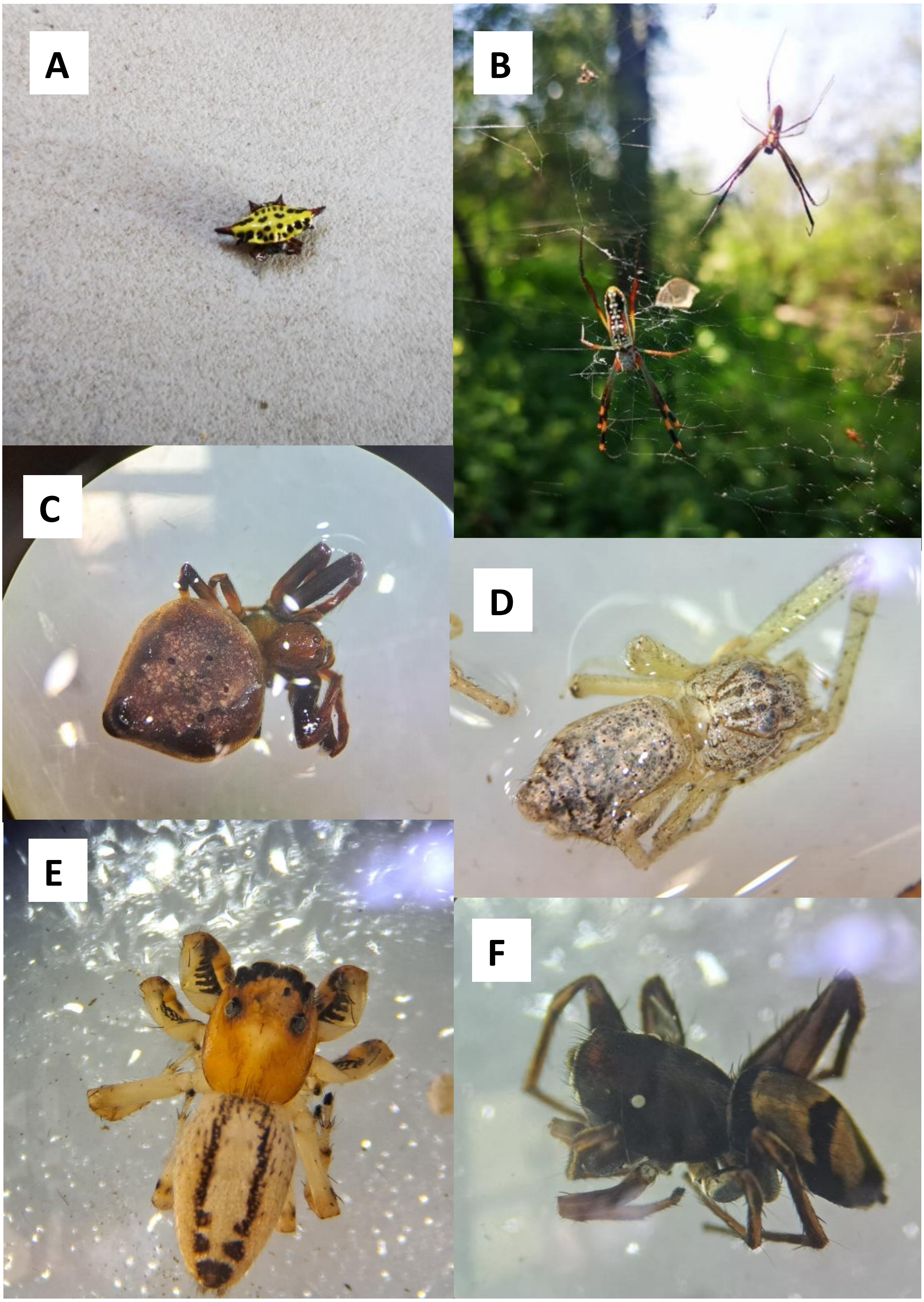

Figure B8: Examples of spiders collected in the Okavango Delta: **A)** *Gasteracantha sanguinolenta* (Araneidae), **B)** *Trichonephila senegalensis annulata (*Araneidae), **C)** *Eriovixia excelsa* (Araneidae), **D)** *Tmarus cameliformis* (Thomisidae), **E)** *Thyene ogdeni* (Salticidae), **F)** *Mexcala elegans* (Salticidae).

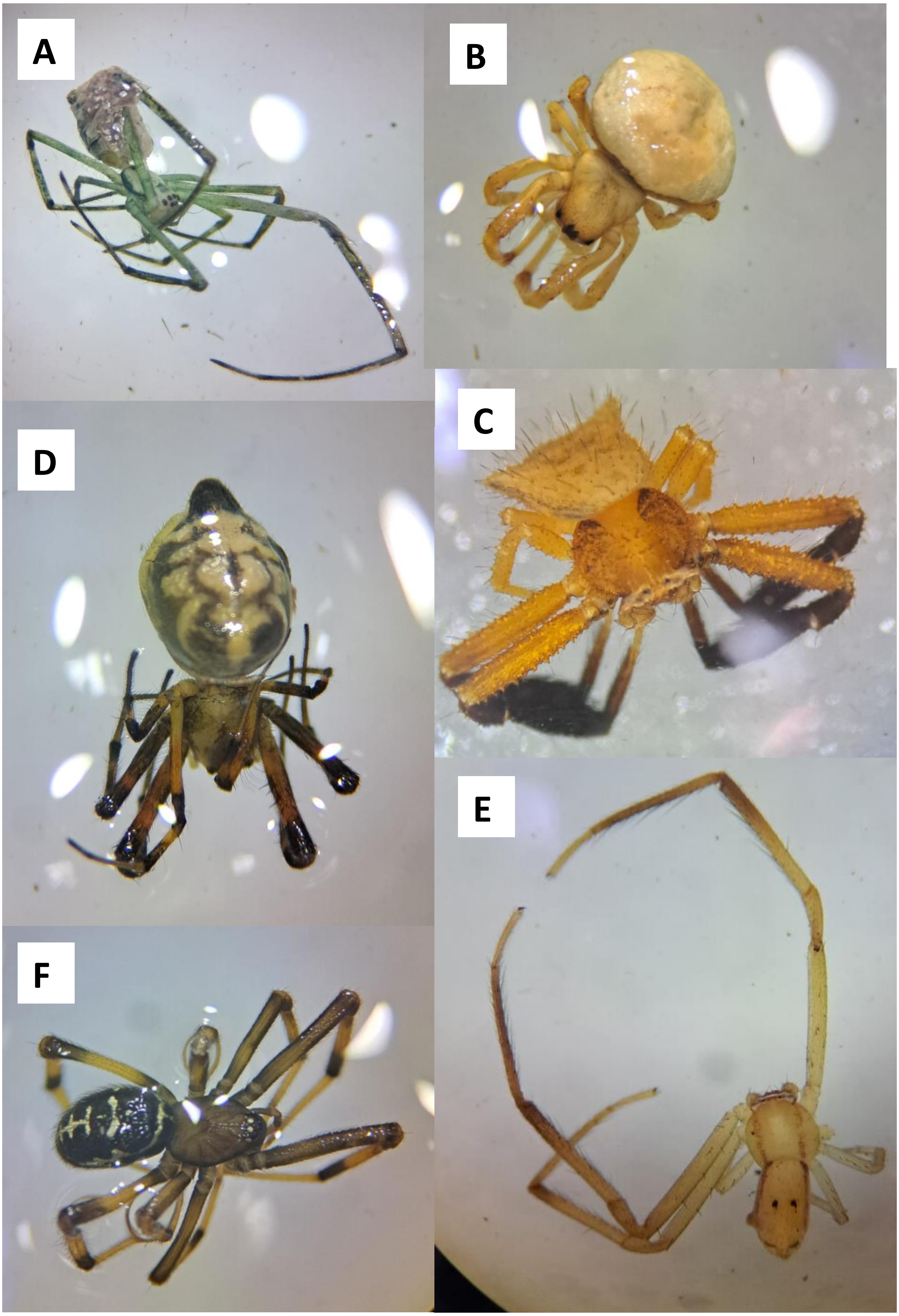

Figure B9: Examples of spiders collected in the Okavango Delta: **A)** *Leucauge sp* (Tetragnathidae)**, B)** *Araneus apricus* (Araneidae)**, C)** *Thomisus granulatus* (Thomisidae)**, D)** *Leucauge medjensis* (Tetragnathidae)**, E)** *Runcinia depressa* (Thomisidae)**, F)** *Steatoda capensis* (Theridiidae).

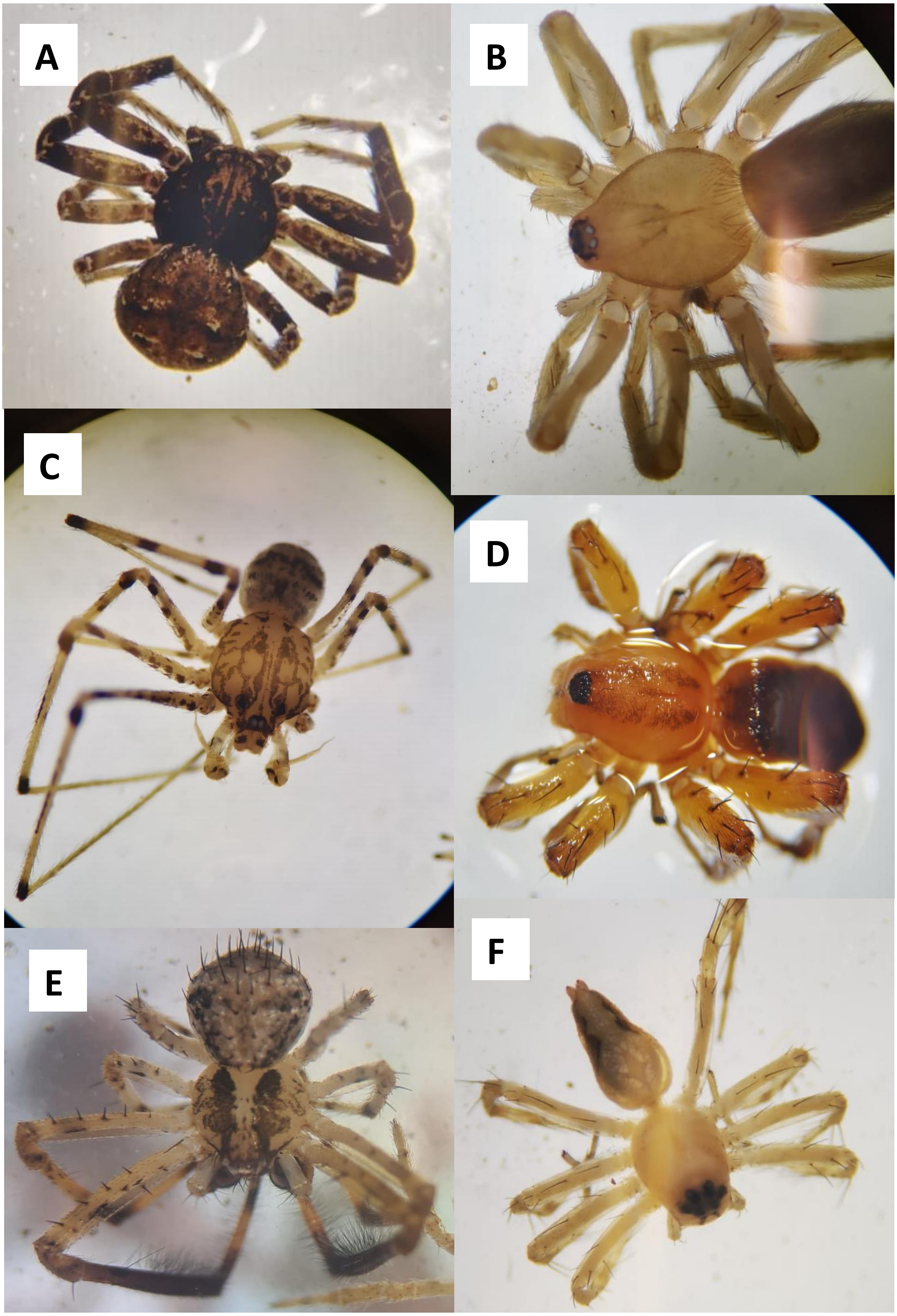

Figure B10: Examples of spiders collected in the Okavango Delta: **A)** *Xysticus natalensis* (Thomisidae)**, B)** *Camillina maun* (Gnaphosidae)**, C)** *Scytodes fusca* (Scytodidae)**, D)** *Copa flavoplumosa* (Corinnidae)**, E)** *Heriaeus crassispinus* (Thomisidae)**, F)** *Oxyopes vogelsangeri* (Oxyopidae).