The costs and benefits of hosting colonial sociable weaver nests for arid zone savanna trees

Timothy Khan Aikins

Thesis presented for the degree of

Doctor of Philosophy

FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence,

Department of Biological Sciences, Faculty of Science, University of Cape Town

February 2023

Supervised by: Assoc. Prof. Robert L. Thomson and Prof. Michael D. Cramer

Abstract

The savanna ecosystem is water and, in some instances, nutrient-limited, creating competition among species. Species, however, coexist in this ecosystem through processing like facilitation acting together with competition. Facilitation is an ecological interaction in which one species enhances the habitat of another species. Research on facilitative interactions between birds and plants has mainly focused on pollination and seed dispersal, but many birds interact closely with plants at the nesting site during breeding or even year round for nesting and roosting. These interactions are not always reciprocally beneficial, but with costs and benefits that change in spatio-temporal contexts, especially in resource-constrained arid zone environments. The overall impacts of bird nesting, especially colonial species, on the growth and reproduction of host trees can be large, with these interactions potentially being crucial components of ecosystems. Overall, understanding the nature of the interactions between host trees and nesting birds may provide key information on understanding the life history of species and their communities. I, therefore, test the hypothesis that the interactions between animals and plants in the savanna ecosystem enhance the islands of fertility created by trees, which influences the growth and survival of vegetation in the environment. I used the interaction between sociable weavers (*Philetairus socius*) and their host trees (camelthorn *Vachellia erioloba* and shepherd *Boscia albitrunca*) to test this hypothesis. I predicted that trees that host the sociable weaver nest would have benefits and costs in the interaction, influencing the growth and reproduction of host trees differently from trees without a nest.

I found that soils under trees without nests were characterized by higher N (2.3-fold) and P (1.3-fold) compared to grassland areas. However, I found that soils under nest trees had even higher concentrations of N (3.5-fold) and P (4.1-fold) than soils under trees without nests. Therefore, nest trees and trees without nests create islands of fertility, but nests accentuate nutrient accumulation. Soil C and N increased with increasing tree size and colony size.

Seedling growth was significantly greater in the soils from islands of fertility that were accentuated by weaver nest presence. Seedlings grown in soils from bird islands of fertility showed more growth in shoots, while seedlings in grasslands showed more growth in roots, and lastly, tree islands of fertility were intermediate in both. There was significantly greater mean seedling height (1.4-fold) and the number of leaves (1.4-fold) in soils from bird islands of fertility than in both tree islands of fertility and grassland sites. The foliar nutrient stoichiometries of seedlings grown on nest-accentuated islands of fertility were similar to the stoichiometric ratios in soils from bird islands of fertility, showing that the faecal input of the sociable weaver accounts for the growth differences in these islands of fertility. The benefits for trees that host sociable weaver nests include higher foliar N, P, K, and Ca. Trees hosting nests did not show differences in seed weight, number of seeds per pod and pod weight. Seed nutrients did not vary substantially between trees with and without a nest. Seed germination and emergence did not differ between trees with and without a nest. There was, however, significantly shorter seed germination and emergence time in seeds infested with beetles than in seeds with no beetle infestation.

The costs of hosting a sociable weaver nest include lower soil water infiltration rates under nest trees with larger colony sizes, which limits seed germination, despite good seed banks and nutrient-rich soils. There was also an average of 30% reduction in the photosynthetic area of nest trees, significantly more and larger branch fall in nest trees, and a mean of 39% dead terminal nest branches. The rate of dieback in trees was higher (ca. 6-fold) for nest trees than for trees without a nest. Trees with nests have significantly greater damage from beetles to the seeds (50% infestation) than trees without nests (34% infestation). Beetle-infested seeds in nest trees had a significantly high percentage of seeds that failed to emerge after germination than beetle-infested seeds in control trees.

The ecological engineering activities of sociable weavers address the limitations of nutrients for the growth of the host tree in an arid zone savanna, but there is also a growth and reproductive cost for the host trees. The biotic interaction between sociable weavers and their host trees facilitates the survival of host trees in the resource-constrained arid zone savanna environment. In this interaction, there are growth costs to hosting the nest, but there were no substantial reproductive costs to host trees except for a high beetle infestation of host seeds. These combinations of feedback also establish the camelthorn and shepherd trees as powerful ecosystem engineers. The study also contributes to the literature on ecological engineering, showing how the association between the sociable weavers and savanna trees ameliorate conditions in N-limited desert soils which drives the growth of plants in this soil condition.

Acknowledgement

Thanks to the University of Cape Town for hosting me and funding this study and the South African Department of Science and Technology – National Research Foundation Centre of Excellence at the FitzPatrick Institute for providing funding to conduct my research. Thanks to the Dorothy Cameron Scholarship at the Department of Biological Sciences, University of Cape Town, and the International Students Scholarship at the University of Cape Town for extra funding. I thank the Oppenheimer family and the Tswalu Kalahari for permitting us to perform research on their property. I thank my home institution (University for Development Studies, Ghana) for giving me the permission to undertake this study.

I thank my supervisors; Robert L. Thomson and Michael D. Cramer (Professors), for giving me the opportunity to be part of their research labs and securing funding for the entire research and stipend for the whole 4 years of my study. I have learnt a lot from both of you, from R software and statistics to writing quality academic papers. Thank you for the extra academic opportunity you gave me by always opening your homes to my family and me, not forgetting Sandy and Nosipho.

I thank Dr. Dawood Hattas, Desmond Barnes (Department of Biological Sciences, UCT), Ian Newton and Patricia Groenewald (Department of Archaeometry, UCT), and Edward Chirwa for their laboratory assistance. I also appreciate the support of Olufemi Olubodun, Anthony Lowney, Dylan and Theresa Smith, Benjamin Murphy, Wendy Panaino, Thilo Beck, Paulo, Grace, Tilly, and Valerie, Christiaan Brink, and Billy Krochuk for their assistance at Tswalu Kalahari Reserve during my fieldwork. I would like to thank all my Fitz friends, Chima Nwaogu, Temitope Adelola, and Emmanuel Adekola for their support and advice. Thank you to all the support staff at the Fitz: Rob Little, Carmen Smith, Gonzalo Aguilar, Janine Dunlop, and Anthea Links. I am particularly thankful to Hilary Buchanan and Claire Khai for their administrative assistance during my time in South Africa.

To the family I met in Cape Town; Michael Nyarko, Miss Evelyn Nyarko, Mrs. Evelyn Nyarko, Bla Michael Kofi Nyarko, Derek Nkrumah, Jesse and Sharon Twum-Boafo, Yawlie, Ruth, Deborah, Afia Rich, and Levite, I say thank you.

I thank the management of my home University, University for Development Studies located in Tamale, Ghana for giving me the permission to undertake this study. I thank Prof. Felix Abagale, Prof. Elliot Alhassan, Prof. Samuel Cobbinah, Prof. Ziblim Imoro, Prof. Bernard Baatuuwie and Dr. Conrad Weobong for their support.

A huge thanks to my family and friends back home in Ghana, who have supported me from afar throughout my PhD and my travels. My mum (Mama Cecilia Kontoh), dad (Mr. Emmanuel Aikins Khan), my siblings (Israel and Lucy Aikins Khan) and in-laws (Mr. Isaac Annor and Mama Martha Yeboah) for taking care of my sons for the entire period I have been away. Thanks to the Asare, Osei, Appiah, and Amoako families in Tamale for all the motivation. To my wife Angela Achiaa Aikins, who at the same time was also studying towards a PhD in UCT, thank you for your love, care and support during this journey. Finally to my two sons "Prof." Fiifi Annor Aikins" and "Engineer" Nyameaye Nkum Aikins, thank you for being good boys throughout the years I have been away.

Funding and permits

This research was funded by Center of Excellence of the FitzPatrick Institute of African Ornithology, University of Cape Town provided by the National Research Foundation-Department of Science and Technology Center of Excellence of the FitzPatrick Institute of African Ornithology, University of Cape Town. Further funding was received from the University of Cape Town and the University of Cape Town Dorothy Cameron Scholarship. I had support from the Tswalu Foundation and the Kalahari Endangered Ecosystem Project (KEEP) sponsors, as this study is part of the KEEP project.

The study was carried out on a private reserve (Tswalu Kalahari Reserve) in the Northern Cape Province of South Africa with permission from the Oppenheimer Family.

Conferences and Seminar Presentations

1. **Timothy K. Aikins**, Michael D. Cramer, and Robert L. Thomson (2020). Islands of fertility Created by Sociable Weaver colonies and their host trees. *University of Cape Town, Department of Biological Science Research Day Conference*, 27 November 2020.
2. **Timothy K. Aikins**, Michael D. Cramer, and Robert L. Thomson (2021). Costs and benefits to iconic Kalahari trees hosting Sociable Weaver nests. *Somerset West Bird Club Seminar,* Cape Town, South Africa. 1 July 2021.
3. **Timothy K. Aikins**, Michael D. Cramer, and Robert L. Thomson (2021). Islands of fertility Created by Sociable Weaver colonies and their host trees. *The African Birdfair 2021 Conference,* South Africa, 30-31 July 2021.
4. **Timothy K. Aikins**, Robert L. Thomson, and Michael D. Cramer (2022). The costs and benefits of hosting a Sociable Weaver nest: mutualism or parasitism? 15th Pan African Ornithological Conference, Victoria Falls, Zimbabwe, 21-25 November 2022.
5. **Timothy K. Aikins**, Robert L. Thomson, and Michael D. Cramer (2022). Islands of fertility Created by Sociable Weaver colonies and their host trees. *University of Cape Town, Department of Biological Science Research Day Conference*, 29 November 2022.

Published Article

Aikins, T.K., Cramer, M.D. and Thomson R.L. (2023). Positive feedbacks between savanna tree size and the nutritional characteristics of “Islands of fertility” are amplified by sociable weaver colonies, *Journal of Arid Environments*, Volume 209, 104903, https://doi.org/10.1016/j.jaridenv.2022.104903

Aikins, T.K., Thomson, R.L. & Cramer, M.D. (2023). All savanna islands of fertility are not equal: colonial birds influence soil nutrient stoichiometries with consequences for tree seedling growth. *Plant Ecology* **224,** 685–696. https://doi.org/10.1007/s11258-023-01333-1

Declarations

I, Timothy Khan Aikins, hereby: (a) grant the University of Cape Town free license to reproduce the above thesis in whole or in part for research; (b) declare that: i) the above thesis is my unaided work, both in conception and execution, and that apart from the regular guidance of my supervisors, I have received no assistance; ii) neither the substance nor any part of the thesis has been submitted in the past, or is being, or is to be submitted for a degree at this University or at any other University, except as stated below; I am now presenting the thesis for the Degree of Doctor of Philosophy.

Timothy Khan Aikins, February 2023.

Table of Content

First image of the sociable weaver perched on a camelthorn tree drawn by Lieut. William Paterson (Source: Paterson 1789).

Chapter 1: General Introduction

About a fifth of the Earth's surface is made up of savannas and similar ecosystems (Huntley & Walker 2012; Wagner *et al.* 2018) and forms about 40% of southern Africa (Wagner *et al.* 2018). Savannas serve as habitat for animals and have great potential for tourism, conservation, and livestock farming (Safriel *et al.* 2005). Most of the savannas in southern Africa are semi-arid or arid rainfall less than 600 mm (Sankaran *et al.* 2005). The savanna vegetation comprise grasses and trees coexisting (Huntley & Walker 2012; Wagner *et al.* 2018) and the vegetation structure is regulated by competition between the grasses and trees (Bond 2008; Cramer *et al.* 2010). However, the co-existence between grasses and trees is possible due to ecological processes such as facilitation operating in addition to competition (den Boer 1986; Fargione & Tilman 2002; Callaway 2007).

Facilitation is an essential ecological process in which one organism ameliorates the habitat of another organism (Bronstein 2009). Entire communities are built on many habitat-modifying species, which Dayton (1975) referred to as "foundation species". Jones *et al.* (1997) coined this process as "ecosystem engineering" and the species that modify habitats as "bioengineers." Facilitative or positive interactions benefit at least one of the participants and harm neither, but facilitative interaction in which both species benefit is considered mutualism (Stachowicz 2001). Some well-studied facilitative interactions are those between animals and plants, like pollination and seed dispersal mutualism (Stachowicz 2001). Studies on mutualistic interactions have shown that these interactions are not always reciprocally beneficial, but the extent of costs and benefits will vary spatiotemporally (Bronstein 1994a). In mutualisms, there are costs and benefits to both participants, but it is only mutually beneficial if the benefits are more than the costs (Bronstein 2001a; Holland *et al.* 2004; Morris *et al.* 2010).

The benefits of mutualism can be diverse, ranging from the acquisition of nutrients, the movement of partners or their offspring, and protection from biotic and abiotic factors (Holland

2002). Other benefits of mutualism include habitat provisioning, increased growth, facilitated reproduction, and parasite grooming (Hale & Valdovinos 2021). About 1/3 of crop production is pollinated by animals (Klein *et al*. 2006). Reciprocal beneficial interactions could also result in a reproductive, energetic or survival cost to one of the participants. When one party in mutualism does not reciprocate, these can ultimately result in fitness cost to the other party (Bronstein 2001b). For instance, the mutualism between the ant defenders and aphids sometimes results in the ant defenders eating the aphids rather than protecting them from natural enemies (Offenberg 2001). When an animal does not transfer pollen after feeding on the plant's nectar, it could result in failure of the reproduction of the host plants (Bronstein 2001a) especially for plants that are widely dispersed from each other or with fewer population. Mutualistic interactions are therefore not considered exclusively beneficial but could result in a cost to host species. The interactions between birds and plants have mostly been mutualistic, where birds pollinate, eat and disperse plant propagules (García 2016). Another dimension of the interaction between birds and trees is where birds use the tree as nesting or roosting sites. Trees offer a platform for birds to nest, roost, and forage (Kaur & Kumar 2020). Even with aquatic birds that inhibit waterbodies for feeding prefer to nest on trees (Sandhu 1993). The nesting and roosting activities of birds on trees result in damage and, subsequently, contribute to death of host trees despite the high faecal deposit by these birds, which enriches the soil (Gilmore *et al*. 1984; Moore *et al*. 1995; Shieldcastle & Martin 1997; Natusch *et al*. 2017). In savanna ecosystem, large scattered trees can serve as keystone species due to their complex canopy structure and large trunk cavities, which serve as shelter for several animal species, including nesting birds (Díaz *et al*. 2013; Lindenmayer *et al*. 2013). In this ecosystem, birds can damage these keystone tree species, especially when combined with harsh environmental conditions (Fedriani *et al.* 2017). The potential costs and benefits of the nest-building behaviour of colonial birds on the growth and reproduction of host trees are less documented in the arid zone, unlike the forest ecosystem. The aggregation of birds in colonies in host trees for extended periods will have local consequences. These changes could be beneficial due to the input of faunal nutrients to improve soil fertility and productivity, or they could be detrimental to the host trees and other living organisms in the environment.

Faunal nutrient input has the potential to positively affect the growth of the host plant. There is evidence of significant amounts of nutrients supplied by colonial breeding birds at their roosting or nesting sites in the terrestrial ecosystem (e.g., Smith 1984; Ryan & Watkins 1989; Qin *et al.* 2014). For example, significant increases in leaf and soil N, P, and Zn levels in seabird interaction with island forest vegetation (Erskine *et al.* 1998; Anderson & Polis 1999; García *et al*. 2002). Birds that feed on arthropods may also decrease local arthropod densities in trees, reducing subsequent damage to leaves (van Bael *et al.* 2003). However, excessive faunal faecal deposition can cause soil damage, kill woody vegetation, and dramatically alter soil chemistry (Weseloh & Ewins 1994; Hebert *et al.* 2005). Physical vegetation damage through branch breaking, death of host plants, and deposit of excreta on leaves of host trees have also been reported for seabirds and forest birds (Mulder & Keall 2001; Ellis 2005; Havik *et al.* 2014; Otero *et al.* 2015; Natusch *et al.* 2017). Despite the ubiquitous nature of biotic interactions between birds and their host trees, much of our current knowledge of these positive interactions and their effects on communities and ecosystems is based on forest and marine ecosystems research (see Mulder & Keall 2001; Ellis 2005; Havik *et al.* 2014; Otero *et al.* 2015; Natusch *et al.* 2017). Whether and how colonial birds impact the performance and survival of host trees in the arid environment remains less explored. Increasing our knowledge of biotic interactions in the desert ecosystem will provide a better understanding of this phenomenon. I, therefore, test the hypothesis that the interactions between animals and plants in the savanna ecosystem enhances the islands of fertility created by trees which influences the growth and survival of vegetation in the environment.

I used the interaction between the sociable weaver and its host trees *Vachellia erioloba,* and *Boscia albitrunca* trees, to explore the costs and benefits of hosting colonial birds in an arid environment. The sociable weavers are passerine birds, about 14cm long, with light bluish-grey legs and bill (Figure 1.1D). They build a massive nest of about 1-5 m wide (Figures 1.1A and 1.1B). The nest has chambers (Figure 1.1C) for roosting or breeding by a pair with their offspring or other birds. A colony of sociable weavers consists of many conspecifics using the same nest (if there is only one nest per tree) or the same tree (if there are several nests per tree). The colony's size varies from 2 to 500 individuals per colony (Maclean 1973a). The sociable weaver is endemic to the dry Acacia savannas in the Kalahari ecosystem of Southern Africa (Spottiswoode 2005). The diet of the sociable weaver consists of approximately 80% animal material (mostly harvester termite *Hodotermes mossambica*), and the remaining are seeds of grasses and other plant products. However, the young eat mainly animal food. They usually feed within a 1.5 km range of their nest (Maclean 1973c). The sociable weavers are colonial and continue to use the same nest for generations. They defecate outside their nest, and their faeces form a massive pile under the nest mass (Figure 1.1E).

The camelthorn tree *Vachellia erioloba* is one of the most robust and large trees and the most preferred tree for sociable weavers in the Kalahari (Figure 1.1A). The camelthorn is a protected species under the National Forests Act, 1998 (Act No. 84), which prohibits the removal of dead or living trees (Seymour & Milton 2003). It is a leguminous tree and begins flowering from August to September, and in February, the pods reach full size and swell in March (Barnes 2001a). Insects and mammals consume the seeds and pods of camelthorn. Camelthorn trees perform ecological roles such as reduction in nutrient leaching, reduction of soil erosion on steeps, and increase nutrients under trees through nutrient cycling and concentration of livestock dung (Materechera and Materechera 2001; Barnes 2001b). The shepherd tree *Boscia albitrunca* (Figure 1.1B) is also a protected species under the National Forests Act, 1998 (Act

No. 84), which prohibits the removal of a dead or living tree or parts without permits. Shepherd trees are non-leguminous but contribute to the cycling of nutrients in mainly oligotrophic sands and perform other ecological services such as reducing nutrient leaching, mitigating soil degradation, preventing soil erosion, and replenishing organic matter (Alias & Milton 2003). Like camelthorns, the seeds of shepherd trees are endozoochorous (Dean *et al*. 1999; Leistner 1996; van der Walt & le Riche 1999), but unlike the camelthorn, shepherd tree seeds are non-dormant, with a short viability period (Briers 1988). The endozoochorous nature of the seeds makes them quickly establish under other large trees that provide shade for mammals like the camelthorn (Milton & Dean 1995; Dean *et al.* 1999; Leistner 1996). Since the recruitment of shepherd trees depends on large trees like the camelthorn, threats to camelthorn indirectly threaten shepherd trees (Alias & Milton 2003).

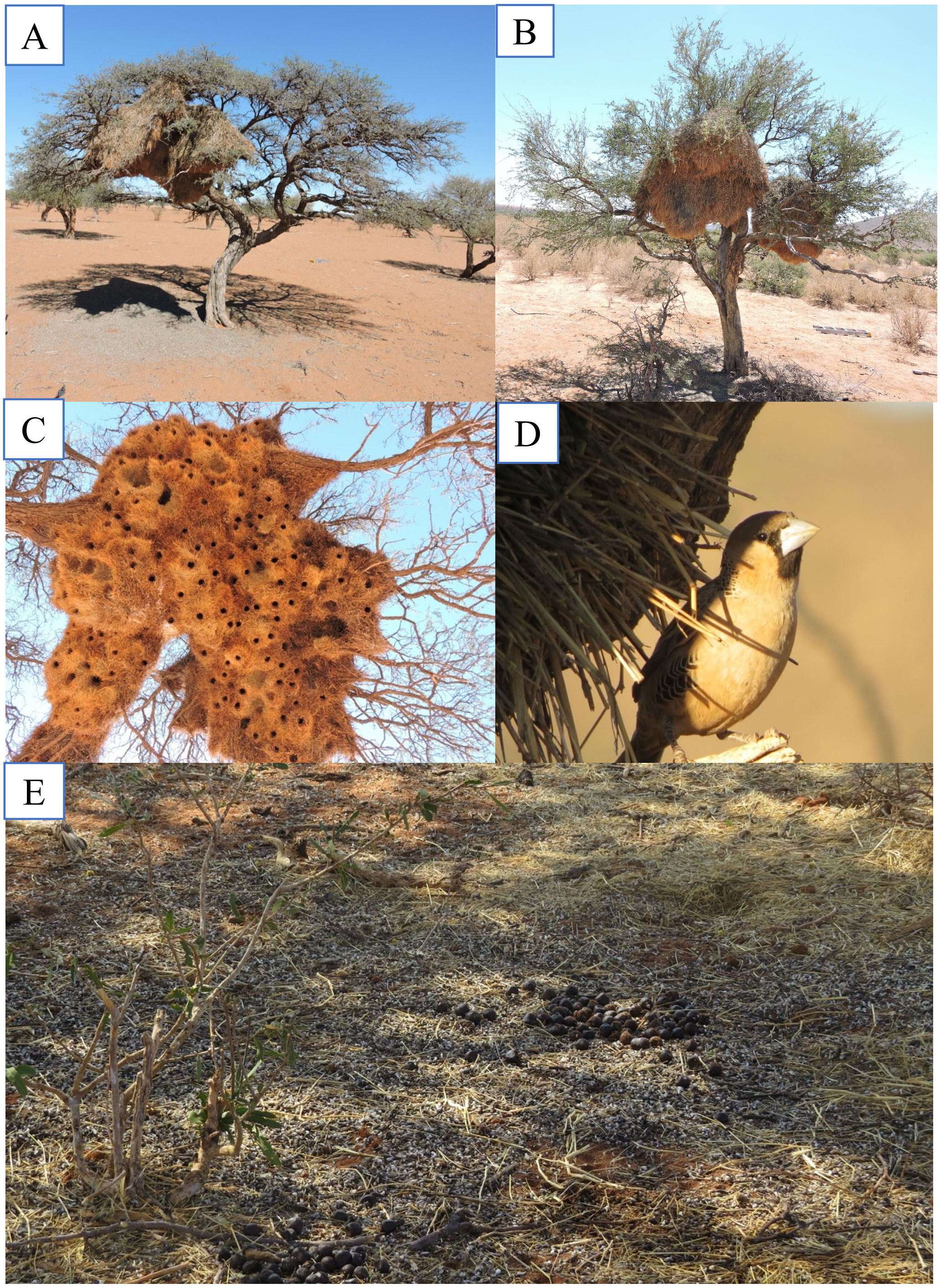

Figure 1.1: Camelthorn tree (A) and shepherd tree (B) with the sociable weaver nest. A view of the sociable weaver nest from below shows the entry holes into the chambers (C). A sociable weaver (D) waiting outside the nest before it enters its chamber. A pile of the sociable weaver and mammalian faecal matter with grass nest materials under the nest tree (E).

In the Kalahari of Southern Africa, the interactions between sociable weavers and their host trees have existed for many years (see the first description of the sociable weaver by Paterson 1789; where he drew the sociable weaver perched on camelthorn tree), but little is known about the potential benefits and costs of this interaction for the host trees. However, Prayag *et al*. (2020) showed how camelthorn host trees obtain nutrients from the faecal deposition of the sociable weaver. The colonial nature of sociable weavers and their continuous use of the same nest for generations make this interaction an excellent study system for studying the benefits and costs of hosting colonial birds in an arid environment. Other animals, including insects, birds and mammals, use this nest (Lowney & Thomson 2021) for foraging, shade, territorial behaviours, and roosting sites. This results in the deposition of faecal matter, nest materials, and carcasses in the vicinity of the host trees. In an otherwise nutrient-poor sandy desert environment, the flux of nutrients under these colonies could provide abundant nutrients to the host trees. It may stimulate further plant growth under trees. Ironically, the area below the nests is devoid of vegetation, creating a circular soil patch under the tree. Therefore, hosting colonial birds could have detrimental effects on host trees, such as nutrient toxicity, herbivory, branch breaking, reduced photosynthetic area, reduced leaf biomass, and reproductive limitations.

The nature of the interaction between the sociable weaver and its tree hosts is not thoroughly studied. Prayag *et al*. (2020) reported high soil nutrients under host trees, but we do not know whether the high nutrient input is influenced by the tree species and the size of the trees that host the nest. In addition, the influence of colony size on soil fertility is not established. Furthermore, understanding the effect of these high nutrients under the nest trees on the growth of host seedlings, host trees, and the accompanying reproductive consequences would give a broader understanding of this biotic interaction. Since both the sociable weaver (Lowney & Thomson 2021) and the host trees are considered ecosystem engineers (Dean et al. 1999: Seymour & Milton 2003), understanding their interactions is essential to know how they impact the rest of the Kalahari plant and animal communities. This research has significant applied and conservation value. The findings of this research will offer insights into the study of animal aggregations and biotic interactions between birds and trees. It will set the stage for more detailed investigations into the dynamics of other potentially crucial animal aggregation-host tree interactions.

To test the overarching hypothesis, I set out four data chapters with four specific hypotheses to establish the potential costs and benefits of hosting the colonial nest of the sociable weaver nest in an arid environment. The first data chapter (Chapter 2) explored the influence of sociable weavers on creating an island of fertility through their faecal deposition beneath the host trees. I hypothesised that the presence of trees and sociable weaver nests alters soil properties in a size-dependent fashion, creating islands of fertility that vary with tree species due to differences in nitrogen fixation ability and tree size. Furthermore, I hypothesise that the area devoid of vegetation under the nest trees results from physiological drought (a combination of high fertilisation level and low water infiltration rate), lack of viable seeds, and the inability of the nest soils to support plant growth due to nutrient toxicity.

In chapter 3, I explored the growth of host tree seedlings (camelthorns) in soils influenced by the faecal matter of the sociable weaver (bird islands of fertility), soil under trees without nest (tree islands of fertility) and grassland sites and how these influence foliar nutrient concentrations and stoichiometries. I hypothesised that the savanna grasslands, the tree islands of fertility, and the bird islands of fertility differ in both the concentrations and stoichiometries of soil nutrients due to the different sources of nutrients (mammalian and sociable weaver droppings), and this subsequently determines the growth and foliar nutrient concentrations and stoichiometries of plants that grow in these soils.

In Chapter 4, I explored the growth benefits of the presence of the sociable weaver nest through its faecal deposit on the host trees. I hypothesised that the presence of the sociable weaver nest on host trees and the deposition of faunal nutrients under the trees would result in positive feedback to host trees that vary with host tree species and negative feedback that also vary with host tree species and intensifies with nest area cover. I explored how the nest influences the foliar nutrient concentrations of host trees and leaf biomass. I also examined the growth costs for host trees by assessing branch health and tree mortality.

In Chapter 5, I explored the reproductive fitness of camelthorn host trees. I studied the benefits and costs of the sociable nest for host trees in terms of pods and seed quantity and quality, seed nutrients, germination and emergence. I hypothesised that the higher supply of nutrients to camelthorn trees that host sociable weaver nests would positively influence the quantity and quality of the pods and seeds produced and alter the germination and emergence of host seeds. I also hypothesise that the sociable weaver nest on camelthorn trees would attract more beetles since the nest serves as a refuge and, therefore, negatively influences the quality of the seeds produced and reduces the germination and emergence of host tree seeds.

Chapter 6 discusses the findings of the study in relation to the overarching hypothesis and discusses the possible implications of the cost and benefits of the sociable weaver nest for the host trees and the conservation implications for the Kalahari ecosystem. The limitations of the study and recommendations for future research are also discussed in this chapter.

Chapters 2-5 have been written in the form of a manuscript to facilitate their publication. Therefore, there might be repetition in the introductions and methods. Also to avoid repetition in referencing all literature cited, I compiled in a single list towards the end of the thesis. Supplemental materials for each of the main chapters (Chapters 2-5) are presented at the end of each chapter.

Chapter 2: Positive feedbacks between savanna tree size and the nutritional characteristics of “islands of fertility” are amplified by Sociable Weaver colonies

A modified version of this chapter has been published as:

Aikins, T.K., Cramer, M.D. and Thomson R.L. (2023). Positive feedbacks between savanna tree size and the nutritional characteristics of “Islands of fertility” are amplified by sociable weaver colonies, Journal of Arid Environments, Volume 209, 104903, https://doi.org/10.1016/j.jaridenv.2022.104903.

Abstract

In arid environments, areas of high soil nutrient concentrations are common under woody plants due to ecosystem functions, including faunal deposition. Sociable weavers (*Philetairus socius*) are birds that build nests on camelthorn (*Vachellia erioloba*) and shepherd (*Boscia albitrunca*) trees and their faeces enrich the soil. Nevertheless, the soil under the nests is devoid of vegetation. I evaluated the hypotheses that the presence of trees and weaver nests alters soil properties, which vary with tree species and size as well as nest size, but that the area devoid of vegetation under nest trees is due to physiological drought, lack of viable seeds or nutrient toxicity. I sampled and analysed soil properties under trees with and without a sociable weaver nest and the grassland between them. Soils under trees were characterized by higher N (2.3-fold) and P (1.3-fold) compared to grassland areas. Furthermore, soils under nest-trees had higher N (3.5-fold), and P (4.1-fold) concentrations than soils under trees without nests. Some soil properties also varied with increasing tree and colony size. Soil water infiltration rate decreased under nest-trees with increased colony size, limiting seed germination, despite good seed banks and nutrient-rich soils. This combination of feedbacks establishes these trees as powerful ecosystem engineers.

Introduction

"Islands of fertility" that represent biotically induced accumulations of nutrients are typical of arid environments (Schlesinger *et al.* 1996; Austin *et al.* 2004). In these ecosystems, soil fertility is commonly characterised by high spatiotemporal variability, with higher concentrations of nutrients under shrub canopies compared to bare ground interspaces between shrubs (Schlesinger *et al.* 1996; Austin *et al.* 2004; Zhao *et al.* 2020). The spatial variability in soil fertility in these arid areas is commonly the result of patchy plant distributions that are primarily driven by access to water. These vegetation patches may create areas of high organic matter deposition (e.g., seeds, leaf litter) and high nutrient uptake (Austin *et al.* 2004; Rotundo & Aguiar 2005). Nutrient input from animals can also substantially influence soil fertility (Dean *et al.* 1999; Cao *et al.* 2018). In these cases, the spatial clustering of the animal presence or activity would contribute to spatial heterogeneity in soil fertility (Dean *et al.* 1999; Cao *et al.* 2018). However, our understanding of how the input of faunal nutrients contributes to the spatial variability of soil fertility between areas receiving faunal nutrients and those not receiving faunal nutrients, especially in arid environments, has received less attention.

Woody plants can form islands of fertility without the participation of fauna. For example, Schlesinger *et al.* (1996) reported higher available N, P, and K under *Larrea tridentata* shrubs than in interspaces between shrubs in the Chihuahuan Desert. Leguminous trees and shrubs have been found to increase soil fertility through N fixation and rich biomass accumulation (Fernández *et al.* 2020). Higher N content was also reported in soils under leguminous *Robinia pseudoacacia* forests compared to other non-leguminous tree forest (Tölgyesi *et al.* 2020). Nevertheless, the provision of forage, shade, perches, cover and other resources (Yan *et al.* 2018) results in woody vegetation islands becoming preferred sites for animals that contribute to the formation of these fertile hotspots (Aguilera *et al.* 1999; Dean *et al.* 1999). The attraction of animal taxa should further contribute to the fertile vegetation island effect through faunal nutrient input, with the potential to influence soil fertility and the distribution of soil nutrients (Dean *et al*. 1999; Cao *et al*. 2018; Mashizi & Sharafatmandrad, 2020). The nature and outcomes of this interaction can be determined by the size and species of plants. For example, Mashizi and Sharafatmandrad (2020) found that some, but not all, shrub species in the arid dunes had higher plant and animal diversity associated with them compared to the interspace between shrubs. The size of the shrub also determined the diversity of plants and animals via their ability to provide habitat. Yet, how characteristics of the host vegetation influence the extent of the faunal nutrient input remains largely unexplored.

Birds move a diversity of nutrients from distances in ways that few other animals can (Fujita & Kameda 2016). The majority of the studies on the contribution of birds to the formation of islands of fertility have focused on sea birds and forest birds and mostly in the temperate regions (Otero *et al*. 2018; Natusch *et al*. 2017). The faecal nutrient inputs by seabirds have been reported to increase total P in organic soil in the Arctic (Zwolicki *et al*. 2013; Ziółek & Melke 2014). The nutrients deposited by metallic starlings (*Aplonis metallica*) significantly increased soil nutrients under host trees in the forest ecosystem (Natusch *et al*. 2017). Birds in arid environments also have the potential to significantly alter soil nutrient distribution and contribute to the island of fertility (Dean *et al*. 1999; Prayag *et al*. 2020).

In the Kalahari Desert, several faunal species take advantage of woody plants, gaining benefits through various mechanisms. Mammals depend on these woody plants for shade, while birds depend on them to build their nests and roost at night (Lowney & Thomson 2021). Sociable weavers (*Philetairus socius*) form a long-term relationship with host trees; mainly camelthorn trees (*Vachellia erioloba*) and shepherd trees (*Boscia albitrunca*) in the Kalahari Desert. They build huge colonial nests through generations by cooperative effort, with colonies that may have hundreds of individuals using the nests throughout the year (Maclean 1973a; Lowney *et al*. 2020). The sociable weavers act as ecological engineers by building this huge nest which attracts diverse animal species, including several other species of birds, reptiles, and insects (Lowney & Thomson 2022). Sociable weavers deposit their faeces at camelthorn trees that host the colonies resulting in significantly higher concentrations of soil N, P, and K compared to camelthorn trees without colonies (Prayag *et al*. 2020). This initial study focussed on the effect of large sociable weaver colonies and was limited to camelthorn trees; therefore, uncertainty remains about how generalisable these effects are across the range of tree and colony sizes and how this varies in other non-legume tree species. In nutrient-poor desert environments (Zhao *et al*. 2017), the nutrient flux under these trees with nest colonies may be expected to stimulate sub-canopy plant growth. However, paradoxically, the area beneath camelthorn and shepherd trees with nests is devoid of vegetation, creating a bare soil patch under the tree (Figure 2.1). The reasons for this patch of bare soil remain obscure, although Prayag *et al*. (2020) suggested that faunal modification of the soil results in a decrease in the water infiltration rate.

The extent to which the presence of the sociable weaver colony influences the creation of fertile islands is relevant to fully understanding how these ecosystem engineers impact the surrounding Kalahari ecosystem. I hypothesized that the presence of trees and weaver nests alters soil properties in a size-dependent fashion, creating relatively fertile islands that vary with tree species due to differences in nitrogen fixation ability. Furthermore, I hypothesize that the area devoid of vegetation under the nest-trees is the result of a physiological drought (combination of high fertilization level and low water infiltration rate), lack of viable seeds, and/or inability of the nest soils to support plant growth due to nutrient toxicity. I determined, for a range of nest colony sizes, whether soils below nests differed from those of matched neighbouring trees without nests and also from soils in the grassland between trees. I measured these soil properties based on the constituents of sociable weaver faecal matter (Prayag *et al*. 2020) and of importance to plants and for understanding ecosystem function (pH, N, C, C:N ratio, $\delta^{15}N$, $\delta^{13}C$, Ca, P, K, and Zn). For example, $\delta^{15}N$ and $\delta^{13}C$ indicate the sources of the soil

N and C and C:N ratios relate to soil microbial activities. I measured water infiltration rates, and viable seed loads below nest-trees and grew camelthorn seedlings in soils from nest-trees and trees without a nest to assess possible nutrient toxicity to this native species.

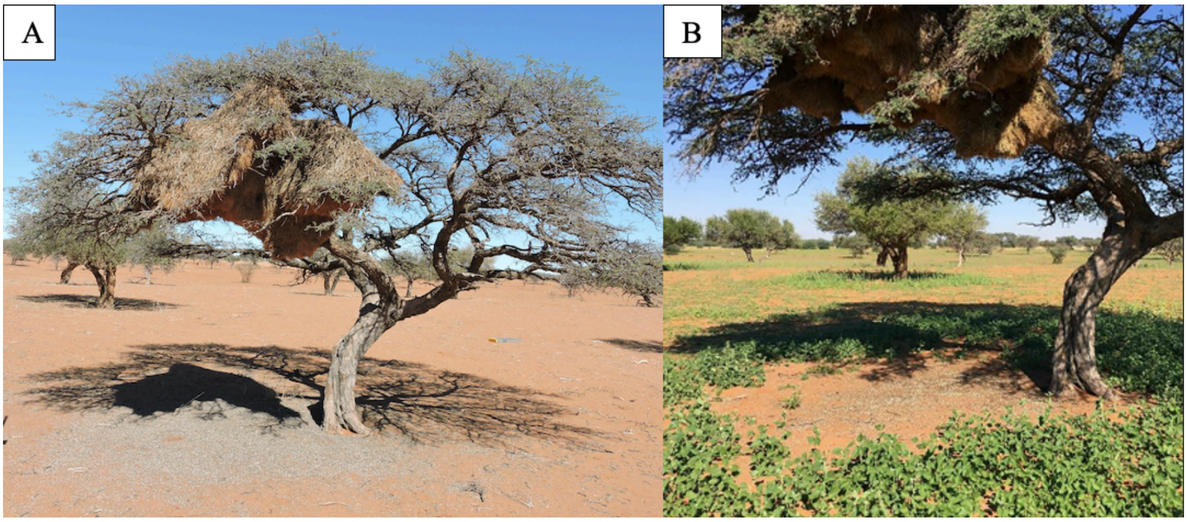

Figure 2.1: A) Camelthorn tree with a weaver nest and a pile of faecal matter beneath the nest in the dry season. B) The same tree during the rainy season with an area devoid of vegetation directly below the nest where the faecal matter accumulates.

Materials and Methods

Study Area

The study was undertaken in Tswalu Kalahari Reserve in the Northern Cape Province, South Africa (27° 22'S 22° 47' E). Tswalu Kalahari Reserve covers an area of about 1000 km^2. The climate is typically hot and arid, the long-term annual mean temperature is 20.3º C, with an annual mean maximum of 29.5º C and a minimum of 11.1º C (Cromhout 2006). Rainfall is highly variable and occurs mainly during summer (December-March), with a mean of 325 per year and ranging between 175 and 595 mm (van Rooyen & van Rooyen 2017). Tswalu Kalahari lies in the Desert biome of South Africa and has five different vegetation types (Mucina & Rutherford 2006). The trees selected for this study were within the Koranna-Langeberg Mountain Bushveld and the Olifantshoek Plains Thornveld. Permission was obtained from Tswalu Kalahari Reserve to collect all samples used in this research.

Study Design

I employed stratified random sampling to select camelthorn and shepherd trees that contained sociable weaver nests (hereafter nest-trees) out of about 360 nest-trees that have been mapped in the study area. The sampling involved randomly selecting ca. 50% of trees closer to the rocky mountain areas and the remaining 50% in the dunes (away from the mountain). For each selected nest-tree, I chose a tree without a nest of the same species that had a similar height and trunk diameter at breast height (DBH) as the paired nest-tree. Trees without nests were chosen near nest-trees (mean 78 m; range 16 m – 192 m) to account for spatial variation in the study area. Our sampling resulted in 33 camelthorn nest-trees, paired with 33 camelthorn trees without a weaver nest. Similarly, 28 shepherd nest-trees and 28 paired shepherd trees without a nest. The mid-point between each nest-tree and its paired tree without a nest was marked as a "grassland" site, as a reference for the potential soil nutrient enrichment driven by trees alone.

I measured circumference at breast height with a tape measure and then converted it to DBH by dividing the circumference by pi (3.14). I also measured the heights of all 122 trees using a hypsometer (Nikon Forestry Pro, Nikon Vision Co., Ltd, Tokyo, Japan) (Table 2.1). Sociable weaver nests exist as a mass of individual chambers; the number of individual nesting chambers per colony was counted (Table 2.1). The number of chambers gives a good proxy for the size of the colony and the number of individual sociable weavers in that colony (Leighton & Echeverri 2014).

Soil sampling

Soil samples were taken at each of the sites (nest-tree, tree, and grassland sites; i.e. 183 samples). Soil samples from nest-trees were collected directly under the nests and active chambers. Any accumulated faecal matter was removed from the soil surface and samples were taken with an auger (7 cm diameter) to a depth of 20 cm as the soil below the depth of 20cm did not clearly show the effect of the faecal input of the sociable weaver on soil nutrients (Prayag et al. 2020), although the trees were able to access the nutrients as shown by the significant effects of the sociable weaver faeces on the $\delta^{15}N$ values.

Soil samples taken from trees without a nest (and grassland sites) matched the distance between the trunk of the tree and the soil sampling point of the nest-trees. Soil samples were bagged in the field, air-dried for 48 h (soils were already dry at collection), and sieved through a 2 mm mesh.

Soil nutrient and pH analysis

The soils were coned and quartered (Gerlach *et al*. 2002) to sub-sample the soils for the various tests. The dry sub-sampled soils from each sampling point were milled to a fine powder using a mortar and pestle. The milled soil samples were placed in sample cups sealed with 4 µm Polypropylene film (Chemplex Industries Inc, Florida, USA) and subjected to analysis on an energy dispersive benchtop X-ray fluorescence analyser (Spectro Xepos spectrometer, Spectro, Amatek, Kleve, Germany). The analysis was controlled by data acquisition software (Spectro X-Lab Pro), which incorporates TurboQuant software for automatic correction of matrix effects. The instrument was calibrated using a certified standard GBW07312 (National Research Center for Certified Reference Materials, Beijing, China), for which elemental concentrations were obtained from the NOAA Technical Memorandum NOS ORCA 68 (1992). To correct our results for the presence of carbon, I used gravimetric loss on ignition (LOI). Air-dried soil samples were oven-dried at 105 ºC for 24 h and then weighed into crucibles (ca. 20 g). The samples were then subjected to 550 ºC for 3 h before being allowed to cool, kept in an oven at 105 ºC, and then reweighed (Hoogsteen *et al*. 2015).

C and N and their stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) were measured at the Department of Archaeology (University of Cape Town) using a mass spectrometer. Air-dried and sieved ground soil samples (40 mg) were weighed in tin capsules (Elemental Microanalysis Ltd, Devon, UK). These were then combusted in a Flash 2000 organic elemental analyzer (Thermo Scientific, Bremen, Germany), and the gases were passed to a Delta V Plus isotope ratio mass spectrometer (IRMS) via a Conflo IV gas control unit (Thermo Scientific, Bremen, Germany). Results were calibrated using two in-house standards and one IAEA standard. The in-house standards used were: Choc, Sucrose (Australian National University), Valine (from Sigma), Merck Gel (by Merck), and NH_4Cl. All in-house standards have been calibrated against IAEA (International Atomic Energy Agency) standards.

Soil pH was determined using the methods of McLean (1982). A 25 ml 1 M KCl solution was added to 10 g air-dried soil in plastic tubes with lids. Soil mixtures were shaken for 20 minutes. After settling for 1 hour, the sample pH was taken using a calibrated Edge multiparameter digital electrode meter (Hanna Instruments Ltd, Bedfordshire, UK).

Soil water infiltration rate

Soil water infiltration was measured using a single-ring flooding infiltrometer (10 cm in diameter and 13 cm in height) with a standard pressure bottle (McCarthy 1934). The ring was inserted into the soils to a depth of 3 cm at nest-trees directly under the nest-trees, and similar positions for the corresponding tree without a nest. The area enclosed by the ring was flooded with water and the time taken for 10 mm of water to infiltrate from the constant pressure bottle was recorded. Three consecutive measurements were taken at the same location and the average of the three records was used as millimetre per hour (mm h^{-1}).

Soil viable seed load and camelthorn seedling growth

To determine whether the bare soil patch under the nest-trees is the result of a lack of viable seeds, I measured seedlings germinating from soils from the nest-trees and trees without a nest. The soils were from a random sample of the collected soils (n = 48, 12 camelthorn pairs, and 12 shepherd pairs). Soil samples were transported to the University of Cape Town greenhouse where soils were placed in germination trays (25 x 15 cm). The temperature in the greenhouse was regulated at 25 °C. The soils were watered each day with an overhead water irrigation system for 3 minutes at 7 am and 2 pm. The number of seeds that germinated each week was counted. The cumulative number of seeds that germinated at the end of the 7th week was recorded as the soil viable seed load, as no further seed germination was observed.

The soil samples were transferred into growing pots and a single seed of camelthorn tree was planted in each pot. Seeds were obtained from a single camelthorn tree without a nest. Seeds were mechanically scarified using sandpaper and soaked in water for 24 h before being transferred to a Petri dish in a phytotron for germination. After, germination, the seeds were planted in growing pots at 2 cm depth. The heights of the plants were measured 10 weeks after planting.

Data Analysis

To explore the characteristics of our study system and check the effectiveness of our paired tree design, I explored the range, mean, and standard error (SE) of the DBH of the tree, the height of the tree, and the number of nest chambers. I compared the means of DBH and height between the site (nest-trees and trees) and tree species using linear models. I compared the means of the number of nest chambers between camelthorn and shepherd nest-trees using the Student's t-test.

Initial exploration of the data indicated heteroscedasticity and this was controlled for with appropriate variance functions; model = lme (Y ~ X, random=~1|S, data=df, weights=varIdent(form=~1|X), method = “REML”). I ran linear mixed models (LMM) in R (version 4.0.3) using the nlme package to test soil properties as the response variables (all were normally distributed) and added fixed effects of tree species (camelthorn, shepherd trees), site (nest-tree, grassland, or tree), DBH and number of chambers (a proxy for colony size). I used the “Anova()” function (in car package) to test whether the model terms explain a significant proportion of the variation of the data. Pairwise comparisons of the levels of fixed factors (site and species) were also considered if these terms proved to explain significant variation in the models using the emmeans. The p-values in the multiple pairwise comparisons were adjusted using the Tukey method.

First, I tested the assumption that trees alone create islands of fertility. I used site (grassland and trees without nest) and tree species as fixed factors, and their interaction in our models. In all models, the interaction terms were removed if not explaining significant variation ($p > 0.05$). Pair identity (trees without nest and grassland pairs) was included as a random effect. Secondly, I tested the hypothesis that the presence of sociable weaver, tree species and tree size influence the formation of relative fertile vegetation island. I included site (nest-trees and trees without nest), tree species, and DBH as fixed factors and the interaction of site and tree species. Pair identity (nest-tree/tree without nest pairs) was included as a random effect. Third, I investigated whether the size of the tree and the size of the colony could affect the properties of the soil. Here I used both the nest-tree and the tree without a nest for the tree size effect and only the nest-trees for the colony size effect (I did not include the tree size in the colony size model because the tree size and the colony size were colinear). Finally, I was interested in the area devoid of vegetation under the nest-tree and testing why these areas remain bare. I used the soil water infiltration rate, the viable soil seed load, and the initial growth of camelthorn seedlings (seedling height) as our response variables. I included sites (nest-trees and trees without nests) and tree species as factors. Pair identity (nest-tree/tree without nest pairs) was included as a random effect.

Results

Characteristics of the study system

Camelthorn nest-trees had a significantly greater mean DBH ($p < 0.001$) and height ($p < 0.001$) compared to camelthorn trees, shepherd nest-trees, and shepherd trees (Table 2.1). For shepherd trees, there were no differences in DBH between nest-trees and trees but they differed in height, nest-trees being taller than trees (Table 2.1). Nests in camelthorn trees were larger (more nest chambers) than shepherd nests ($t = 5.76$, $p < 0.001$) and also had more chambers per DBH (2.23 vs 1.29 per cm) and more chambers per height (16.4 vs 9.1 chambers per m). Since there are differences in DBH and height, I included tree characteristics in our analysis.

Table 2.1: Characteristics of trees with and without sociable weaver nests randomly selected for the study. The range, mean and standard error (SE) of diameter at breast height (DBH), height, and the number of nest chambers are provided. Different letters associated with mean values indicate significant differences ($P < 0.05$) as determined by the Tukey post-hoc test (DBH and height) and the Student's t-test (nest chambers).

Tree species	**DBH (cm)**		**Height (m)**		**Nest Chambers**	
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Camelthorn						
Nest-trees (n = 33)	42 ± 1.9^{b}	14–70	5.72 ± 0.23^{c}	2.8–8.6	94 ± 7^{b}	12–189
Trees (n = 33)	35 ± 1.3^{a}	22–50	4.96 ± 0.20^{b}	3.2–7.4		
Shepherd						
Nest-trees (n = 28)	34 ± 1.2a	23–52	4.81 ± 0.16b	4.0–7.0	44 ± 4a	7–93
Trees (n = 28)	31 ± 1.6a	21–56	4.26 ± 0.13a	3.0–6.0		

Do trees create islands of fertility?

The soil pH, δ^{13}C, and the C:N ratios of grasslands did not differ between the tree species (Figure 2.2, Table S2.1), but the soil N, δ^{15}N, and C in grasslands were lower in sites associated with shepherd than with camelthorn trees. There was higher soil pH under trees of both species than in grassland sites. Soil N was significantly higher under both leguminous camelthorn (2.3-fold) and shepherd trees (2.2-fold) relative to their respective grassland sites. Similarly, soil C was also higher under both camelthorn (2.4-fold) and shepherd trees (2.2-fold) compared to their grassland sites.

Soil $\delta^{15}N$ values under camelthorn trees were not different from those of adjacent grasslands, while those of shepherd trees were significantly higher than those of adjacent grasslands (Figure 2.3). Soil $\delta^{13}C$ values were significantly lower under both camelthorn and shepherd trees compared to the grasslands. The C:N ratios in the soil were lower under shepherd trees than in camelthorn trees, but this did not differ between sites for both tree species. The soil K, Ca, and Zn of the grasslands did not differ between the associated tree species (Figure 2.3) while the soil P was higher in the shepherd tree grasslands than in the camelthorn tree grasslands. There was a higher soil P under shepherd trees than under camelthorn trees. The soil P, K, Ca, and Zn under trees were higher than those of the grasslands of both tree species.

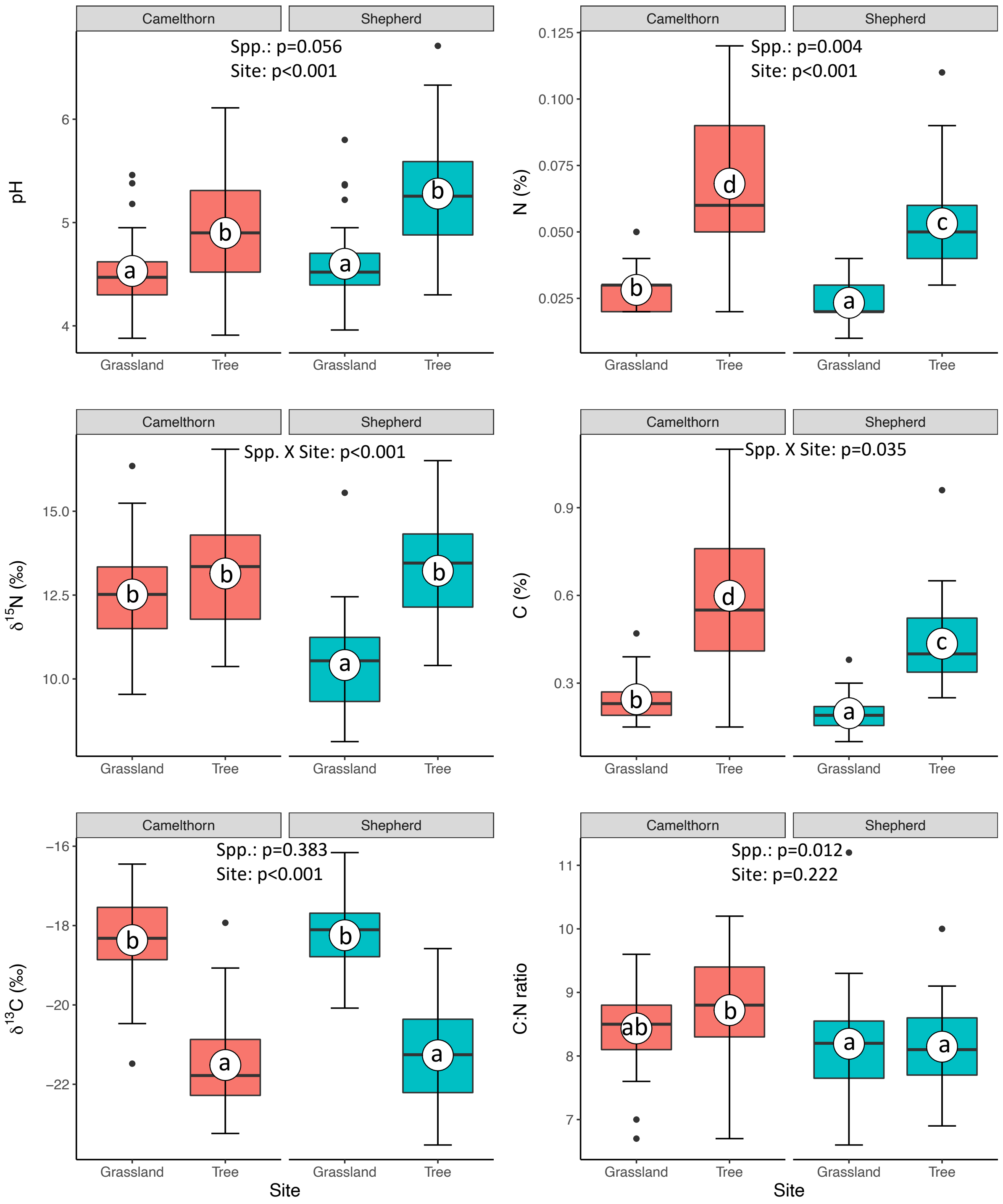

Figure 2.2: Soil properties measured under trees and in grasslands. The measured properties include soil pH, N, δ^{15}N, C, δ^{13}C, and C:N ratio. The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. The whiskers represent 1.5 × the interquartile range. Outliers above/below are shown as dark points. Circles represent the mean, and letters indicate a pairwise comparison between species and sites.

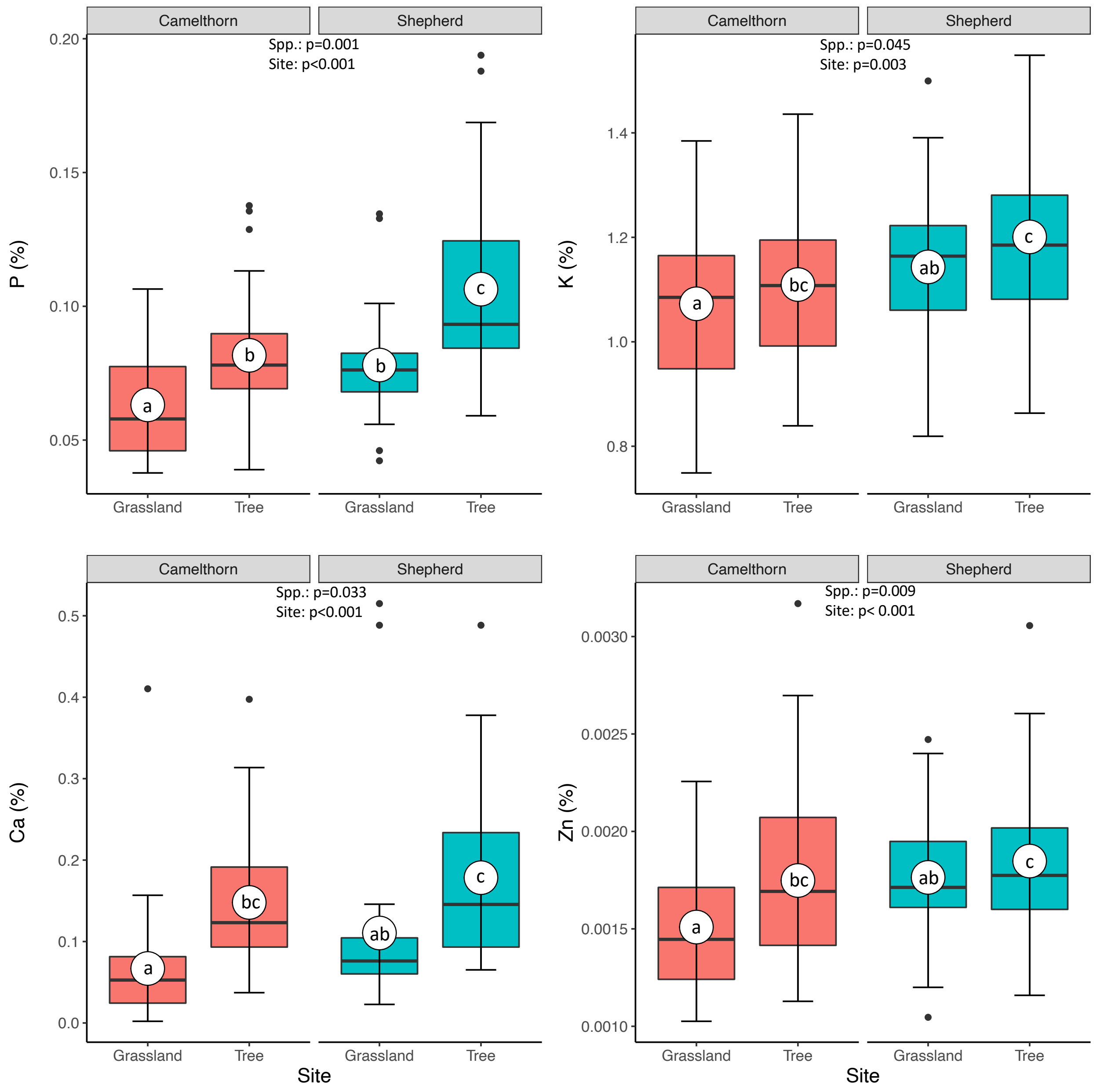

Figure 2.3: Plant-available soil minerals (P, K, Ca, and Zn) found in soils below trees and grasslands. The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. The whiskers represent 1.5 × the interquartile range. Outliers above/below are shown as dark points. The circles represent the mean.

Do sociable weaver nests enhance islands of fertility?

After accounting for tree size, soil N and C were significantly explained by the interaction between the sites (presence or absence of a sociable weaver nest) and tree species (Figure 2.4, Table S2.2). Both camelthorn and shepherd nest-trees showed significantly higher C and N compared to the trees without nests. Camelthorn nest-trees had a 5.0-fold increase in soil N and a 3.5-fold increase in soil C while shepherd nest-trees had a 3.5-fold increase in soil N and a 2.0-fold increase in soil C. The soil C:N ratio was significantly explained by both site and tree species (Figure 2.4, Table S2.2). The nest-trees of both species showed lower values (1.3-fold) than the trees without nests. Soil C:N ratio was significantly lower under shepherd nest-trees than in camelthorn nest-trees.

Our models also showed that the variation in $\delta^{15}N$ was explained by trees with and without nests (Figure 2.4, Table S2.2). The soil below the nest-trees of both species had significantly higher levels of $\delta^{15}N$ compared to trees without nests. The soil $\delta^{15}N$ did not, however, vary between camelthorn nest-trees and shepherd nest-trees. Soil $\delta^{13}C$ was significantly explained by the interaction between the site (that is, a tree or nest-tree) and the tree species. The camelthorn nest-tree soils had significantly higher $\delta^{13}C$ compared to camelthorn trees without a nest, a difference not found between shepherd trees with and without nests.

The variation in soil P, K, Ca, and Zn was explained by the presence or absence of nests (Figure 2.5, Table S2.2). The nest-trees of both species showed significantly higher levels of these nutrients in the soil compared to trees. The interaction between the site and the tree species was not significant and was removed from the model, indicating that the trends of these soil minerals between trees and the nest-trees were the same for both tree species. Tree species explained significant variation in soil P but not K, Ca, and Zn for nest-trees. The soil under the shepherd nest-trees showed higher levels of soil P than the camelthorn nest-trees.

Soil nutrient stoichiometry under the nest-trees differed significantly from the faecal matter of the sociable weaver. The N:P, Ca:P and Zn:P ratios (in mmoles) of the faecal matter of the sociable weaver (N:P = 12.4, Ca:P = 0.72 and Zn:P = 0.008) were higher compared to the soils of the nest-trees (N:P = 1.48, Ca:P = 0.6 and Zn:P = 0.000005). However, the K:P ratio was significantly higher in nest-tree soils (2.44) compared to the faecal matter of the sociable weaver (1.01).

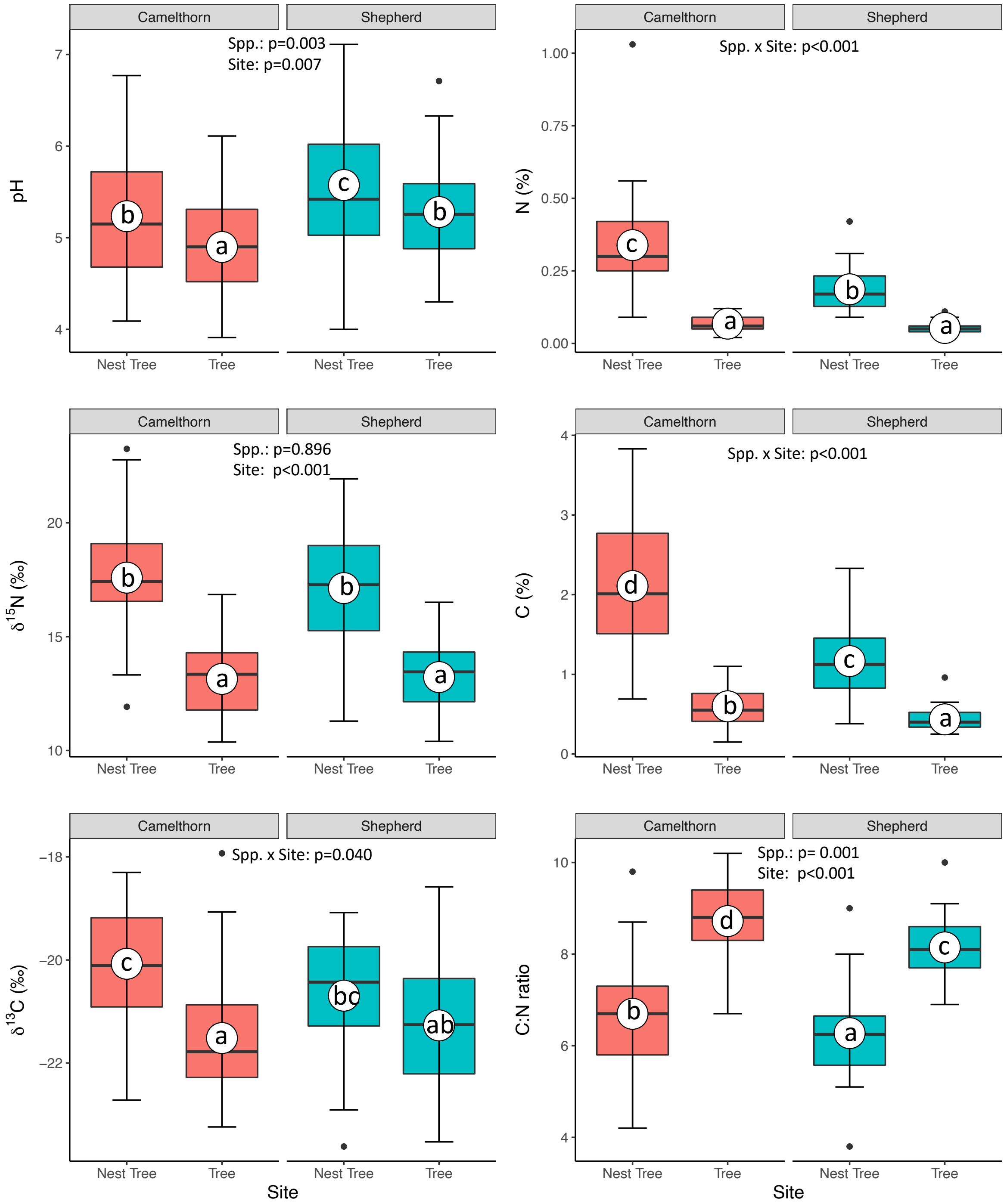

Figure 2.4: Soil properties (soil pH, N, δ^{15}N, C, δ^{13}C, and C: N ratio) measured under two tree species (camelthorn and shepherd trees) either with or without sociable weaver nests present. The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. The whiskers represent 1.5 × the interquartile range, and the outliers above/below are shown as dark points. Circles represent the mean, and letters indicate a pairwise comparison between species and sites.

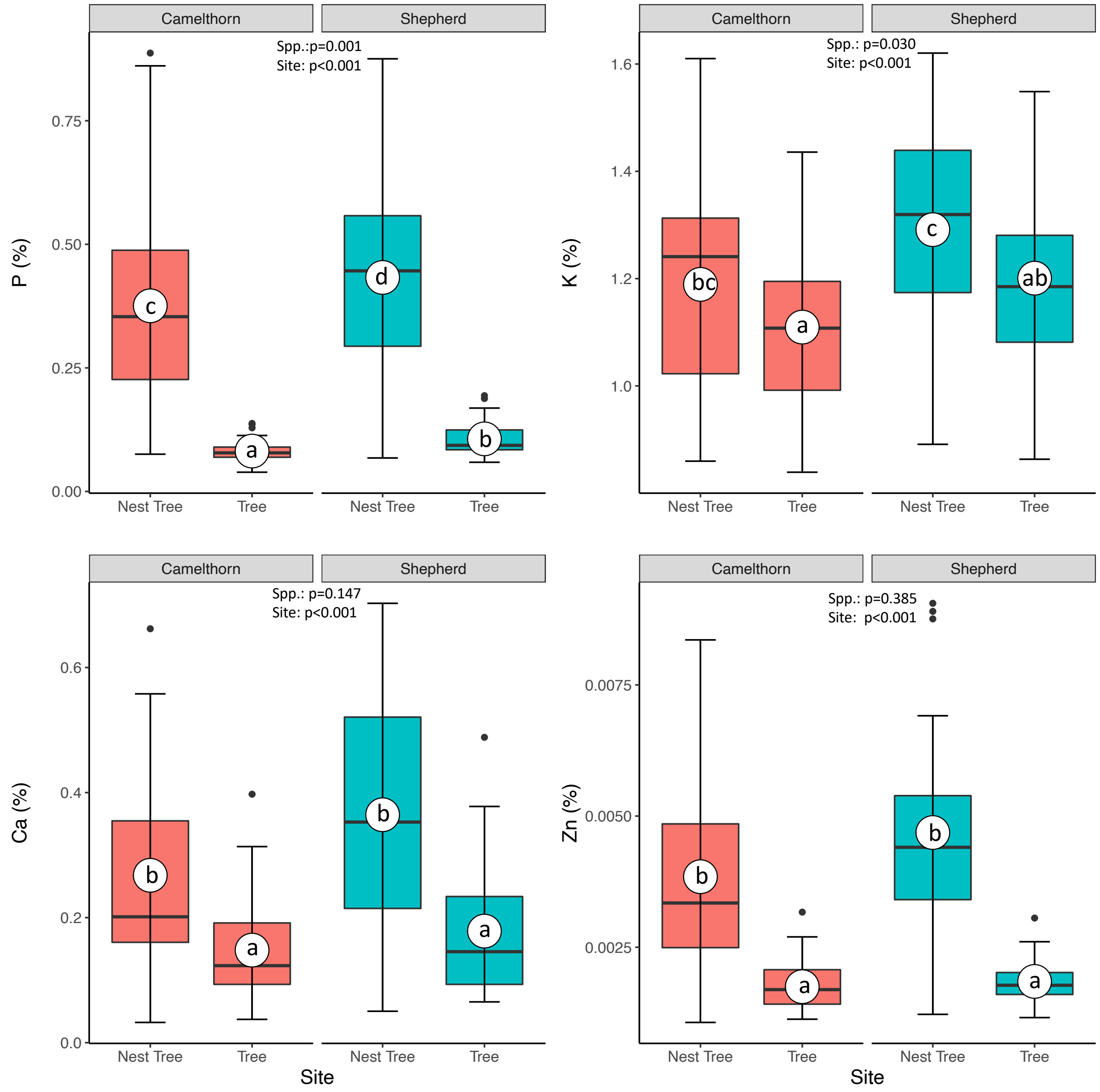

Figure 2.5: Plant-available soil minerals (P, K, Ca, and Zn) found in soils below two species of trees (camelthorn and shepherd trees) and site (nest-tree and tree). The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. The whiskers represent 1.5 × the interquartile range, and the outliers above/below are shown as dark points. Circles represent the mean, and letters indicate a pairwise comparison between species and sites.

Effects of tree size on the formation of the island of fertility

Our model shows that the interaction between site and DBH explained significant variation in soil C and N (Table S2.3). DBH did not explain all other soil properties investigated. Therefore, I tested the relationship between DBH and soil C, as well as soil N separately, for nest-trees and trees. For nest-trees, there was a positive increase of soil C and N with increasing DBH of shepherd trees, but this was not the case in camelthorn trees (Figures 2.6A and 2.6B). This indicates that nest-trees with larger DBH have higher soil C and N under shepherd trees. The coefficient of determination (R^2) of our regression model shows that the DBH of shepherd trees explains 34% of the variations in soil N and 31% of the variations in soil C. However, the size of the tree did not explain significant variations in the levels of soil C and N for tree sites.

Effects of colony size on the formation of the island of fertility

The variation in soil N, C, and Ca was explained by colony size, after accounting for tree species and tree size (Figures 2.6D, 2.6E, and 2.6F, Table S2.4). Increasing colony size was characterized by an increase in soil N and C. Our regression model showed that colony size explained 22% and 14% of the variation in soil C for camelthorn and shepherd nest-tree soils, respectively (Figure 2.6D). The size of the colony explained 17% of the variation in soil N under camelthorn nest-trees but this was not significant under shepherd nest-trees (Figure 2.6E). Colony size also significantly explained variation in soil Ca (15%) under camelthorn nest-trees but not under shepherd nest-trees (Figure 2.6F, Table S2.4), with increasing colony size leading to decreased soil Ca levels. However, colony size did not explain variation in soil pH, C:N ratio, $\delta^{15}N$, $\delta^{13}C$, P, K, and Zn (Table S2.4).

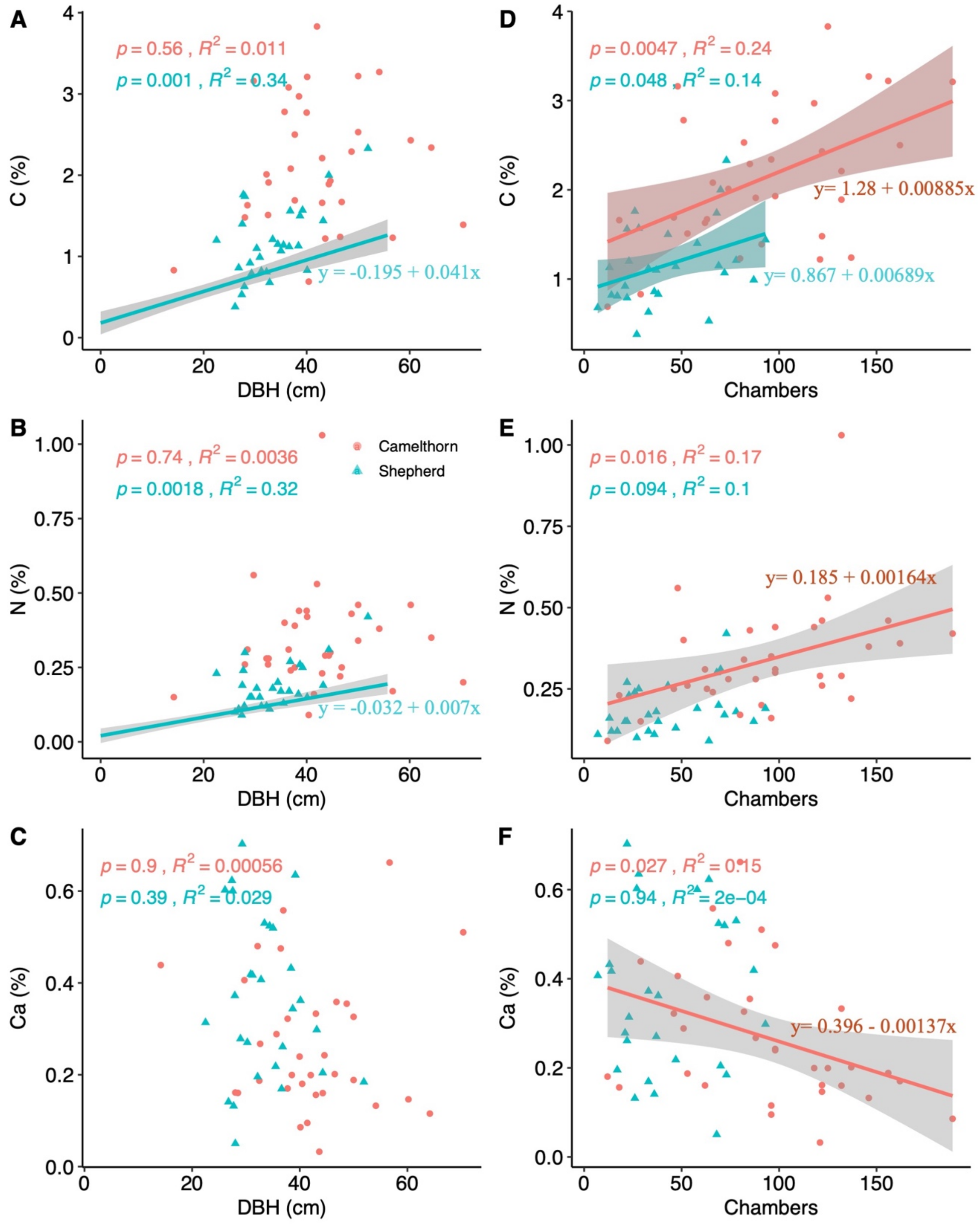

Figure 2.6: Regression showing the relationship between soil properties (C, N, and Ca) with tree size (DBH) and colony size (number of chambers) for camelthorn and shepherd nest-trees only. Lines represent linear fits (regression equations reported), and the grey bands are the 95% confidence intervals. P-values and R^2 are reported for each species.

Causes of the bare soil patch under the nest-trees

In the seed bank experiment, the number of seedlings that germinated was significantly explained by the interaction between tree species and site (i.e., tree or nest-tree) (Figure 2.7A, Table S2.5). The camelthorn tree soils had significantly higher seedling numbers compared to the camelthorn nest-tree soils, while there were no differences between the shepherd trees and the shepherd nest-trees (Figure 2.7A). The number of nest chambers did not explain the seedling numbers in the soils below nest-trees for either species (Figure S2.1). In the growth experiment, the height of camelthorn seedlings was significantly higher in nest-tree soils than in trees, but did not differ between soils of the two tree species (Figure 2.7B, Table S2.5).

Soil water infiltration rate was explained by the interaction between tree species and site (Figure 2.7C, Table S2.5). Soil water infiltration rate was higher under shepherd trees than under nest-trees, but there were no differences between camelthorn trees and nest-trees. The size of the sociable weaver colony (number of chambers) explained the variation in the soil water infiltration rate for both tree species; increasing colony size was correlated with a lower soil water infiltration rate (Figure 2.7D).

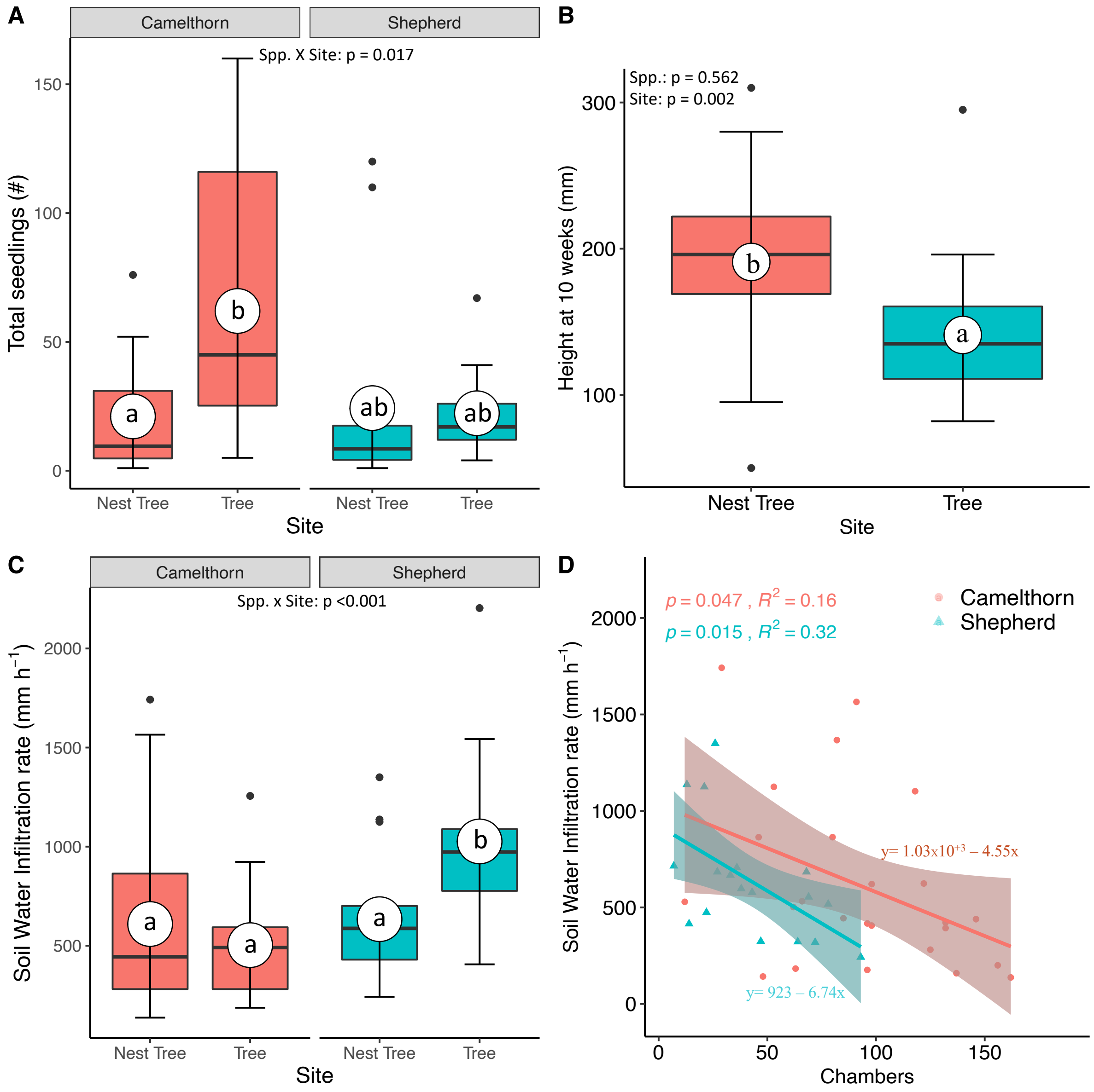

Figure 2.7: Number of germinated seedlings **(A)** observed below two tree species (camelthorn and shepherd trees) and two sites (tree and nest-tree). Camelthorn seedling height **(B)** from soils below two sites (nest-tree and tree). Soil water infiltration rate **(C)** observed below the two species of trees and the two sites. The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. The whiskers represent 1.5 × the interquartile range, and the outliers above/below are shown as dark points. Circles represent means, with letters indicating pairwise comparison between species and sites**.** **(D)** Relationship between soil water infiltration rate and colony size (number of chambers) for camelthorn and shepherd trees. The lines represent linear fits (regression equation reported), and the bands are the 95% confidence intervals. P-values and R^2 are reported for each species.

Discussion

The presence of trees alone leads to elevated soil fertility compared to surrounding grasslands. The soils at both camelthorn and shepherd tree sites showed significantly higher levels of soil pH, N, C, P, K, Ca, and Zn compared to grassland sites. This is consistent with trees concentrating essential nutrients for plant growth under their canopy, hence functioning as "islands of fertility" where N, P, and K accumulations are especially important (Schlesinger *et al*. 1996; Aguilera *et al*. 1999; Dean *et al*. 1999; Yan *et al*. 2018). Furthermore, I observed higher $\delta^{13}C$ values in grassland soil than in tree soils, which may indicate that soil C at these sites is more strongly influenced by C_4 grasses (Gillson 2015). The $\delta^{15}N$ values of the grasslands within which camelthorn and shepherd trees grow also varied. I found a significantly higher $\delta^{15}N$ in camelthorn grasslands compared to shepherd grasslands. This could be attributed to the increased activities of mammals in the camelthorn grasslands, leading to higher deposition of faecal matter. For example, this elevates the isotopic ratio ($\delta^{15}N$) from close to 0‰ in terrestrial systems that are not influenced by transfers between trophic levels (Högberg 1997). The differentiation between the tree islands of fertility and surrounding grassland, therefore, varies with environmental context.

Sociable weaver nests further improved the islands of fertility by increasing soil nutrients and altering other soil properties. The presence of a nest in trees increased soil N, $\delta^{15}N$, C, $\delta^{13}C$, C:N, P, K, Ca, and Zn relative to trees without a nest. The highly elevated N in the soil associated with nests in our study suggests that N may be a key nutrient contributed by weaver nests (see also Prayag *et al*. 2020). I observed strongly positive $\delta^{15}N$ values in both nest-tree and tree soils, but higher $\delta^{15}N$ values in nest-tree than in tree soils. These strongly positive $\delta^{15}N$ values are generally associated with arid ecosystems (Pataki *et al*. 2008), but the higher values found in nest-tree soils compared to the tree soils suggest greater faunal contributions. The higher $\delta^{15}N$ ratio in the soils under nest-trees could be attributed to NH_3 volatilization once the droppings of the sociable weavers are deposited, resulting in further fractionation of the N isotope increasing $\delta^{15}N$ values of the remaining N (Mulder *et al.* 2011; Nel *et al.* 2018; Prayag *et al.* 2020). Furthermore, N reutilisation in plants combined with organic matter microbial decomposition results in a steady increase in $\delta^{15}N$ over time (Nel *et al.* 2018), and this is especially likely under nest-trees. Although low C:N ratios are often associated with a high degree of microbial decomposition (Brust 2019), in nest-tree soils it may also indicate the input of faecal N.

Higher soil N and C under camelthorn nest-trees compared to shepherd nest-trees may be because camelthorn trees are leguminous and fix N_2 in the soil. Fixation of N_2 may be evident from the $\delta^{15}N$ values under camelthorn trees, as this was similar to the levels in adjacent grassland sites possibly due to fixation of N_2 that results in somewhat lower $\delta^{15}N$ values (Craine *et al.* 2015). It is common for leguminous trees and shrubs to improve soil fertility through N_2 fixation and biomass accumulation (Fernández *et al.* 2020). Cramer *et al.* (2007) also found that leguminous trees and shrubs fix nitrogen, especially when in competition with grasses. The higher soil N and C of camelthorn nest-trees as compared to the soil of shepherd nest-trees may also be due to the larger size of the camelthorns, resulting in more N and C from leaf litter. Changes in foliar nutrient concentrations in response to increased nutrient availability can result in positive feedback through increased litter quality and increased decomposition rates and therefore high nutrient availability (Hayes *et al.* 2013) resulting in large trees with deeper root systems.

For plants to benefit from nutrient input, these must be balanced to address the full nutrient requirements of plants. According to Liebig's law of the minimum, plant growth can only be increased to the limit set by the most limiting nutrient (Ågren *et al.* 2012). For plants to benefit from N in weaver faeces, the addition of other potentially limiting nutrients would be beneficial. High levels of P, K, Ca, and Zn under the nest-tree soils imply that plants can benefit from the abundant N under the nest-trees. Furthermore, the higher concentrations of P, K, Ca, and Zn that I found are consistent with other studies on soils associated with colonial birds (Hobara *et al.* 2005; Breuning-Madsen *et al.* 2010; Zwolicki *et al.* 2013; Irick *et al.* 2015; Otero *et al.* 2018). However, the stoichiometric ratios of constituent elements in the sociable weaver faecal matter have very different ratios to the soils below nest-trees. For example, the N:P ratios are much lower in the soil than in the weaver faeces. This indicates that either N is lost from the weaver faeces or that the weaver faeces are not the only inputs of P to the soil. Indeed, our δ^{15}N values indicate fractionation between weaver faeces and soil, and this has been associated with volatilisation of N (Prayag *et al.* 2020), indicating that there is loss of N through this pathway. Despite the arid climate, leaching of N is also possible (but likely limited), especially considering the water repellency of the soils below the nests.

There are, however, also other inputs to the soil below the nest-trees from various sources (e.g., mammalian urine and dung). For example, the levels of δ^{13}C at both the nest-tree and tree sites indicate that soil C at these sites is derived from a combination of grasses with the C_4 photosynthetic pathway and materials from trees with the C_3 photosynthetic pathway (Gillson 2015). The higher δ^{13}C values under the nest-trees compared to the trees show a more dominant contribution of C_4 vegetation materials (Hattersley 1982) which is associated with the seeds consumed by the weavers, the grasses used as nest-building material as well as mammalian inputs. For example, Maclean 1973c reported that sociable weavers feed predominantly on grass seeds and other plant products, but also insects seasonally, potentially contributing to the high δ^{13}C under the nest-trees. Furthermore, the high δ^{13}C under the nest-trees could also be attributed to the more decomposed organic carbon of the soil associated with nest soils (Boström *et al.* 2007). Thus, the composition of the soil below the nests is the product of a combination of inputs and losses, with weaver faeces being one of several inputs. Nevertheless, the presence of a weaver nest is a focus for all of these inputs and losses.

Soil N and C were positively influenced by the size of shepherd nest-trees, but not the size of camelthorn nest-trees. The positive association for shepherd nest-trees could be attributed to diverse factors associated with tree size. For example, bigger trees have access to nutrients deeper in the soil with deeper roots (Gherardi *et al*. 2013), increased interception of wet and dry deposition (Zhang *et al*. 2011; Yan *et al*. 2019) and greater faunal inputs to larger trees. The shepherd nest-trees were generally smaller than the camelthorn nest-trees, possibly suggesting that the lack of relationship between camelthorn tree size and soil properties is due to camelthorns exceeding a threshold in the size-soil enrichment relationship. However, the soil properties considered here are all "intensive" (e.g., concentrations), whereas the "extensive" properties should also be considered. It is difficult to measure the extent of the soil influence from a tree or a nest-tree, but the best proxies are likely to be the tree size (e.g., DBH) and the nest chamber number and nest size since the extent of the soil influence should scale with the size of the tree and nest.

Some of the intensive properties of the soils correlate with the size of the colony (number of nest chambers). For example, I found a significant positive relationship between colony size and soil N (under both camelthorn and shepherd trees) and C (only camelthorn). Similar to our findings, Ellis *et al*. (2006) reported a significant positive correlation between nest density and concentrations of NH_4^+ and NO_3^- in soils. Also, Mulder *et al*. (2011) reported a weak relationship between soil N content and seabird density while that for $\delta^{15}N$ and seabird density was consistently strong, mainly due to either leaching and NH_3 volatilisation (Mulder *et al*. 2011). Otero *et al*. (2018) reported that the amount of nutrients moved by birds into islands of fertility depends on the size of the population, the length of the association with the site, and the type of feeding. This implies that as the size of the colony increases and the length of the association between birds and host vegetation is prolonged, the higher the nutrients deposited by birds. This explains the increase in soil N and C with colony size for nest soils in our study system.

The soils under the nest-trees are rich in plant nutrients and therefore should support subcanopy plant growth, but these areas below the nest are generally devoid of vegetation. I found no evidence that the area devoid of vegetation under the nest-trees is the result of a lack of viable seeds or the inability of the nest soils to support plant growth due to nutrient toxicity. Our results show that both the nest-tree and the tree sites have similar seed bank sizes, and there was also no relationship between the number of nest chambers and the number of viable seeds. Camelthorn seedlings grew taller in nest-tree soils compared to trees without nests, showing that the area without vegetation beneath the nest-trees cannot be attributed to toxicity. The negative relationship between colony size and soil water infiltration rate, however, provides evidence to support the hypothesis that the area devoid of vegetation under the nest-trees is a result of physiological drought (combination of high fertilization and low soil water infiltration rate). Increasing colony size leads to increased deposition of faecal matter and nest material which breaks down to increase the amount of organic matter and fine particles in the soil, thus decreasing soil water infiltration (Luna *et al*. 2018). Therefore, the bare patch created under the nest-trees could be attributed to physiological drought under these trees. This bare patch may have beneficial consequences for the host tree. In savannas, it is common for trees and grasses to compete with each other for nutrients (Cramer *et al*. 2010). As a consequence, the bare patch may relieve the host trees of a source of competition. Furthermore, the lack of flammable grasses or shrubs below the very flammable weaver nest can reduce the severity of fires for both the weavers and the host trees (Dean *et al*. 1999).

Conclusions

The presence of trees alone creates an island of fertility as a result of diverse faunal activities (e.g., nesting, roosting, resting, and feeding), but the presence of the sociable weaver nests further enhanced the islands of fertility created by the trees through faecal deposition. These hotspots of nutrients result in heterogeneous distributions of nutrients in an otherwise relatively uniform grassland system and contribute to the formation of a savanna. The feedback between tree and nest size and the intensive and extensive properties of the island of fertility is accentuated by the fact that the nests alter the soil properties, discouraging plant growth beneath the nests. This combination of feedbacks establishes camelthorn and shepherd trees as powerful ecosystem engineers that exploit sociable weavers as nutrient harvesting agents. Nevertheless, the cost of hosting the weaver colony is not insubstantial resulting in loss of photosynthetic area, branch breakage, and potential susceptibility to fire, all of which need further investigation.

Supplementary Materials

Table S2.1: Linear mixed model analysis with soil properties as response variables and tree species (2 levels- camelthorn and shepherd) and site (2 levels- Tree and Grassland) as factors. We included pairs as a random effect. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis.

Response Variables	**Factors**	X^2	**df**	**P-value**
pH	Site	35.68	1	< 0.001
	Tree species	3.64	1	0.056
N	Site	137.62	1	< 0.001
	Tree species	8.35	1	0.004
C	Site	120.48	1	< 0.001
	Tree species	10.73	1	0.001
	Site*Tree species	4.43	1	0.035
C: N	Site	1.49		0.222
	Tree species	6.36		0.012
δ^{15}N	Site	63.63	1	< 0.001
	Tree species	10.22	1	0.003
	Site*Tree species	28.36	1	< 0.001
δ^{13}C	Site	242.45	1	< 0.001
	Tree species	0.76	1	0.383
Ca	Site	19.60	1	< 0.001
	Tree species	4.53	1	0.033
P	Site	46.35	1	< 0.001
	Tree species	10.42	1	0.001
K	Site	8.53	1	0.003
	Tree species	4.01	1	0.045
Zn	Site	13.38	1	< 0.001
	Tree species	6.90	1	0.009

Table S2.2: Linear mixed model analysis with soil properties as response variables and tree species (2 levels- camelthorn and shepherd) and site (2 levels- Tree and Nest-tree) as factors. We included pairs as a random effect. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis.

Response Variables	**Factors**	X^2	**df**	**P-value**
pH	Site	7.33	1	0.008
	Tree species	8.97	1	0.003
N	Site	158.60	1	< 0.001
	Tree species	6.48	1	0.011
	Site*Tree species	17.21	1	< 0.001
C	Site	216.15	1	< 0.001
	Tree species	9.11	1	0.003
	Site*Tree species	25.91	1	< 0.001
C: N ratio	Site	129.97		< 0.001
	Tree species	10.20		0.001
$\delta^{15}N$	Site	152.55	1	< 0.001
	Tree species	0.02	1	0.896
$\delta^{13}C$	Site	24.86	1	< 0.001
	Tree species	0.90	1	0.342
	Site*Tree species	4.23	1	0.040
Ca	Site	64.65	1	< 0.001
	Tree species	2.11	1	0.025
P	Site	181.55	1	< 0.001
	Tree species	10.31	1	0.147
K	Site	21.39	1	< 0.001
	Tree species	4.74	1	0.030
Zn	Site	106.95	1	< 0.001
	Tree species	0.75	1	0.385

Table S2.3: Linear mixed model analysis with soil properties as response variables and tree species (2 levels- camelthorn and shepherd), Site (2 levels- Tree and Nest-tree) and DBH (Tree size) as factors. We included pairs as a random effect. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis.

Response Variables	**Factors**	X^2	**df**	**P-value**
pH	Tree Species	6.43	1	0.011
	Site	7.51	1	0.006
	DBH	0.19	1	0.665
N	Tree Species	14.11	1	< 0.001
	Site	113	1	< 0.001
	DBH	3.31	1	0.069
	Site*DBH	4.41	1	0.036
C	Tree Species	21.16	1	< 0.001
	Site	138	1	< 0.001
	DBH	5.71	1	0.017
	Site*DBH	6.78	1	0.009
C: N ratio	Tree Species	7.76	1	0.005
	Site	123	1	< 0.001
	DBH	0.01	1	0.935
δ^{15}N	Tree Species	0.04	1	0.833
	Site	134	1	< 0.001
	DBH	0.537	1	0.464
δ^{13}C	Tree Species	0.51	1	0.474
	Site	22	1	< 0.001
	DBH	0.121	1	0.728
Ca	Tree Species	3.42	1	0.064
	Site	64	1	< 0.001
	DBH	1.13	1	0.289
P	Tree Species	3.03	1	0.082
	Site	164	1	< 0.001
	DBH	0.54	1	0.462
K	Tree Species	4.07	1	0.044
	Site	21	1	< 0.001
	DBH	0.57	1	0.450
Zn	Tree Species	1.57	1	0.211
	Site	108	1	< 0.001
	DBH	1.54	1	0.215

Table S2.4: Linear model analysis with soil properties as response variables and tree species (2 levels- camelthorn and shepherd) and chambers (colony size) as factors. F-value, degrees of freedom (df), and p-values are provided for each analysis.

Response Variables	**Factors**	***F-value***	**df**	**P-value**
pH	Tree Species	5.31	1	0.025
	Chambers	2.45	1	0.123
N	Tree Species	3.59	1	0.063
	Chambers	11.33	1	0.001
C	Tree Species	7.46	1	0.008
	Chambers	14.50	1	< 0.001
C: N ratio	Tree Species	1.05	1	0.311
	Chambers	0.11	1	0.744
δ^{15}N	Tree Species	0.16	1	0.690
	Chambers	2.89	1	0.095
δ^{13}C	Tree Species	1.21	1	0.276
	Chambers	1.12	1	0.294
Ca	Tree Species	0.778	1	0.382
	Chambers	3.055	1	0.086
P	Tree Species	0.013	1	0.910
	Chambers	1.852	1	0.179
K	Tree Species	0.473	1	0.494
	Chambers	2.204	1	0.143
Zn	Tree Species	0.289	1	0.593
	Chambers	1.898	1	0.174

Table S2.5: Linear mixed model analysis with soil viable seed load, soil water infiltration rate and camelthorn seedling height as response variables and tree species (2 levels- camelthorn and shepherd) and site (2 levels- Tree and Nest-tree) as factors. We included pairs as a random effect. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis.

Response Variables	**Factors**	χ^2	**df**	**P-value**
Soil Water Infiltration Rate	Species	15.24	1	< 0.001
	Site	2.15	1	0.143
	Tree species*Site	12.43	1	< 0.001
Total seedlings	Species	1.74	1	0.188
	Site	4.03	1	0.045
	Species*Site	5.68	1	0.017
Camelthorn Seedling Height	Tree Species	0.34	1	0.561
	Site	9.46	1	0.002

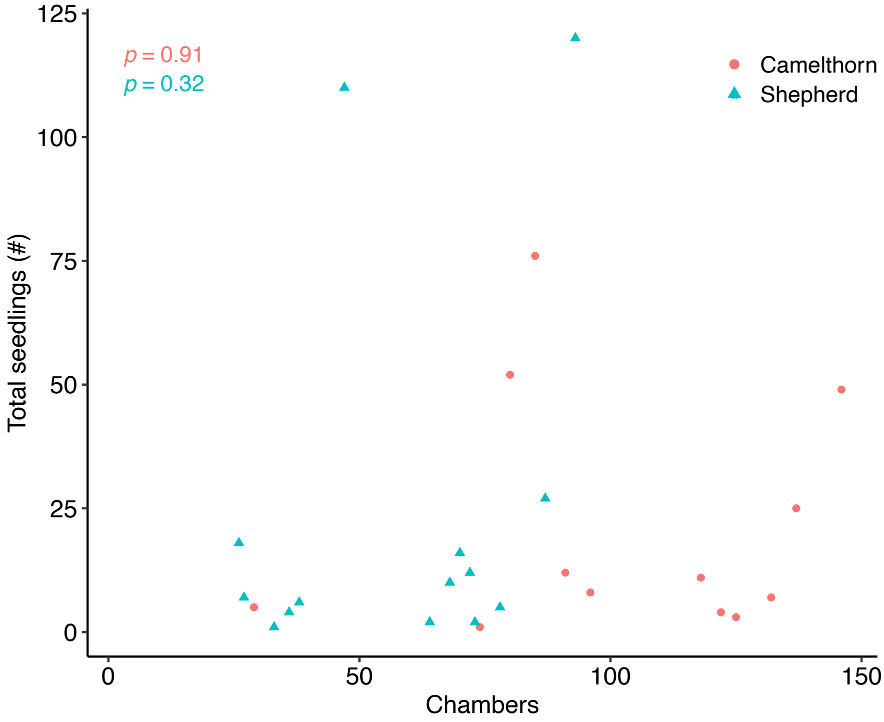

Figure S2.1: Scatter plots showing the relationship between total seed load in soils and colony size (chambers) for both camelthorn and shepherd trees. P-values are reported for each species.

Chapter 3: All savanna islands of fertility are not equal: colonial birds influence soil nutrient stoichiometries with consequences for tree seedling growth.

A modified version of this chapter has been published in Plant Ecology as:

Aikins, T.K., Thomson, R.L. & Cramer, M.D. (2023). All savanna islands of fertility are not equal: colonial birds influence soil nutrient stoichiometries with consequences for tree seedling growth. *Plant Ecology* **224,** 685–696. https://doi.org/10.1007/s11258-023-01333-1

Abstract

Islands of fertility associated with tree/shrub patches in arid grasslands create spatial heterogeneity of soil nutrients. Faunal activities under these trees/shrubs may contribute to diverse characteristics of these fertile patches of soil due to different faecal inputs. I hypothesized that grasslands, the tree islands of fertility (TIFs), and the bird islands of fertility (BIFs) differ in both the concentrations and stoichiometries of soil nutrients due to the sources of nutrients and that this subsequently determines the growth and foliar nutrient concentrations and stoichiometries of plants that grow on these soils. I used the islands of fertility created by camelthorn (*Vachellia erioloba*) and shepherd (*Boscia albitrunca*) trees (tree islands of fertility) that also host sociable weavers *Philetairus socius* (bird islands of fertility) in the Kalahari Desert for this study. I sampled and grew camelthorn seedlings in soils from BIFs, TIFs, and matrix grasslands. Despite the higher soil nutrients in TIFs than in grasslands, there were no significant differences in seedling growth. However, I observed significantly higher seedling growth in BIF soils compared to TIF soils. Seedlings grown in soils from BIFs and grasslands allocated more growth to shoots and roots, respectively, while TIFs were intermediate. The foliar nutrient stoichiometries of seedlings grown in BIF soils were similar

to the stoichiometric ratios in BIF soils and sociable weaver faecal matter. This shows that the faecal input of the sociable weaver accounts for the growth differences in these islands of fertility. The ecological engineering activities of the sociable weaver address nutrient limitations essential for camelthorn seedling growth, which TIF soils could not address despite the high faecal input of mammals.

Introduction

Woody plants accumulate soil nutrients beneath their canopy via various processes, resulting in hotspots of nutrients referred to as "islands of fertility" (Schlesinger *et al.* 1990; 1996). Plant roots forage for nutrients and transport them into the leaves of the plants, which later deposit these as leaf litter beneath the canopy enriching the soils (Schlesinger & Pilmanis 1998). Plants that shed their leaves annually (Abril *et al.* 2009) and those with dense canopies (Camara 2021) can deposit large quantities of nutrients below their canopies. For leguminous trees, high soil N concentrations are additionally due to their nitrogen-fixing capacity (Schlesinger & Pilmanis 1998; Tölgyesi *et al.* 2020). Tree canopies also trap aeolian dust, while low-stature plants and leaf litter may trap runoff containing nutrients (Parsons *et al.* 1992; Schlesinger *et al.* 1999). While islands of fertility may form due to the presence of trees alone, animals also contribute to the formation of islands of fertility through faecal deposition under these woody plants when they seek shade or roost (Dean *et al.* 1999; Mashizi & Sharafatmandrad 2020; Prayag *et al.* 2020). The nutrient stoichiometry of the different sources of nutrients in the island of fertility should determine the key enhanced nutrients with potential implications for the vegetation that grows in these soils.

Ecological stoichiometry indicates ecological processes that include nutrient limitations, energy flow between tropic levels, and material cycling across different ecosystems (Elser *et al.* 1996). According to Liebig's law of the minimum (Marschner 2012) nutrient availability and balance between multiple nutrients determine plant growth. Therefore, nutrient stoichiometry is a determinant of nutrient limitations in ecosystems (Güsewell 2004; Han *et al*. 2013; Mo *et al*. 2015; Sardans & Peñuelas 2015). The foliar nutrient stoichiometry of most plant species is somewhat plastic and influenced by the edaphic environment and several plant traits, including plant size, growth form, relative growth rate, leaf construction, and longevity (Elser *et al*. 2010; Sterner & Elser 2002; Güsewell 2004; Peñuelas & Sardans 2009). The strong links of foliar nutrient stoichiometric variations to soil fertility have been inferred to be adaptive; hence plant foliar nutrients vary with the prevailing environmental conditions (Reich & Oleksyn 2004; Han *et al*. 2005; Elser *et al*. 2010). Many species of plants, however, exhibit a degree of stoichiometric homeostasis through which they maintain their tissue stoichiometries relatively independently of the environment (Sterner and Elser 2002; Elser *et al*. 2010), resulting in nutrient concentrations and stoichiometries of plant tissues being less variable than those in the soils (Güsewell & Koerselman 2002; Neff *et al*. 2006). Plant nutrient stoichiometries have been reported to have stronger genotypic links than environmental links, with different taxa having evolved different nutrient stoichiometries (Neff *et al*. 2006; Verboom *et al*. 2017). Although soil nutrient content could influence plant nutrient levels, it is not clear that plant nutrient stoichiometry necessarily follows that of the soil. Investigating the extent to which the sources of nutrients (e.g., mammal and avian droppings) influence the soil and its subsequent influence on the foliar nutrient concentrations and stoichiometries of plants growing in these soils, at least within a species, may help to establish the drivers of growth responses of the plants to their edaphic environment.

Faunal nutrient input can be a significant source of soil nutrients in islands of fertility (Ellis 2005), resulting in localized changes in the physical and chemical properties of the soil under trees that attract animals (Schlesinger *et al*. 1996; Dean *et al*. 1999; Prayag *et al.* 2020). In terrestrial ecosystems, seabird faecal matter can increase available levels of N and P by

100- and 400-fold, respectively (Mulder *et al.* 2011). The increased availability of N and P, in turn, may increase the growth of plants in this ecosystem compared to other systems (Mulder & Keall 2001). However, high faunal nutrient input from colonial birds may not always lead to positive outcomes. For example, high guano input can result in high levels of NH_4^+ that may reach toxic levels (Anderson & Polis 1999; Kolb *et al.* 2010) and negatively affect the growth of mature woody plants (Dusi 1977; Haynes & Goh 1978). Since the stoichiometric composition of the animal's food, its body size, and body nutrients influence the nutrient stoichiometry (e.g., N:P ratios) in their faecal matter (Sitters *et al.* 2017; Sitters & Venterinka 2021; le Roux *et al.* 2020), mammals and birds will not have the same nutrient contributions at islands of fertility. Furthermore, the amounts of faeces/urine deposited, together with nutrient stoichiometry, determine how plants grow in response to the faunal input (le Roux *et al.* 2020). The principles of eco-stoichiometry explains nutrient regulation mechanism of plant-soil interaction and show the nutrient utilization strategy of different plants as influenced by their environmental factors (Tao *et al.* 2021). It may be expected that the nutrient stoichiometry of plants growing in islands of fertility that differ in their origins will vary based on the soil nutrient stoichiometry in these islands of fertility as influenced by the sources of faunal nutrients and also on the soil type (e.g., mammalian or avian sources).

Sociable weavers (*Philetairus socius*) are colonial birds endemic to southern Africa that make large nests in host trees that are used all year and attract numerous other animal associates (Maclean 1973a; Lowney & Thomson, 2021). Due to their large colonies that alter resources and ameliorate conditions in the harsh Kalahari environment, the sociable weaver acts as an ecosystem engineer (Lowney *et al.* 2020; Lowney & Thomson 2022). Sociable weavers defecate outside of their nests, accumulating guano under their host trees and increasing soil C, N, and P compared to grassland and tree soils (Prayag *et al.* 2020, Aikins *et al.* 2023), which can increase biomass yield and foliar nutrients in host trees and their seedlings. Trees with and without sociable weaver nests also receive mammalian faecal input under canopies. Prayag *et al*. (2020) used wheat (*Triticum aestivum*) as a phytometer and found higher shoot biomass in soils influenced by the nutrient input of the sociable weaver. The nutrient concentrations and stoichiometries of the faecal inputs (of mammalian and sociable weavers) and the soil may be relevant for explaining the growth and foliar nutrient concentrations and stoichiometries of plants that grow in these soils. Documenting the effect of these islands of fertility on the growth of camelthorns seedlings may provide insight into how the mature trees that grow in these islands of fertility benefit from the nutrient flux.

I hypothesized that the savanna grasslands, the tree islands of fertility (TIFs; Figure 3.1B), and the bird islands of fertility (BIFs; Figure 3.1A) differ in both the concentrations and stoichiometries of soil nutrients due to the sources of nutrients (mammalian and sociable weaver droppings) and that this subsequently determines the growth and foliar nutrient concentrations and stoichiometries of plants that grow on these soils. I tested this by sampling and analyzing mammalian and sociable weaver droppings and soil nutrients from BIFs, TIFs, and grasslands and subsequently grew camelthorn (*Vachelia erioloba*) seedlings in these soils. I predicted seedlings grown on soils from BIFs would have greater growth, higher biomass yield, and higher foliar nutrients than TIFs. I also predicted that the nutrient concentrations and stoichiometries in mammalian and sociable weaver droppings would be similar to the soils and seedling foliage from TIFs and BIFs, respectively.

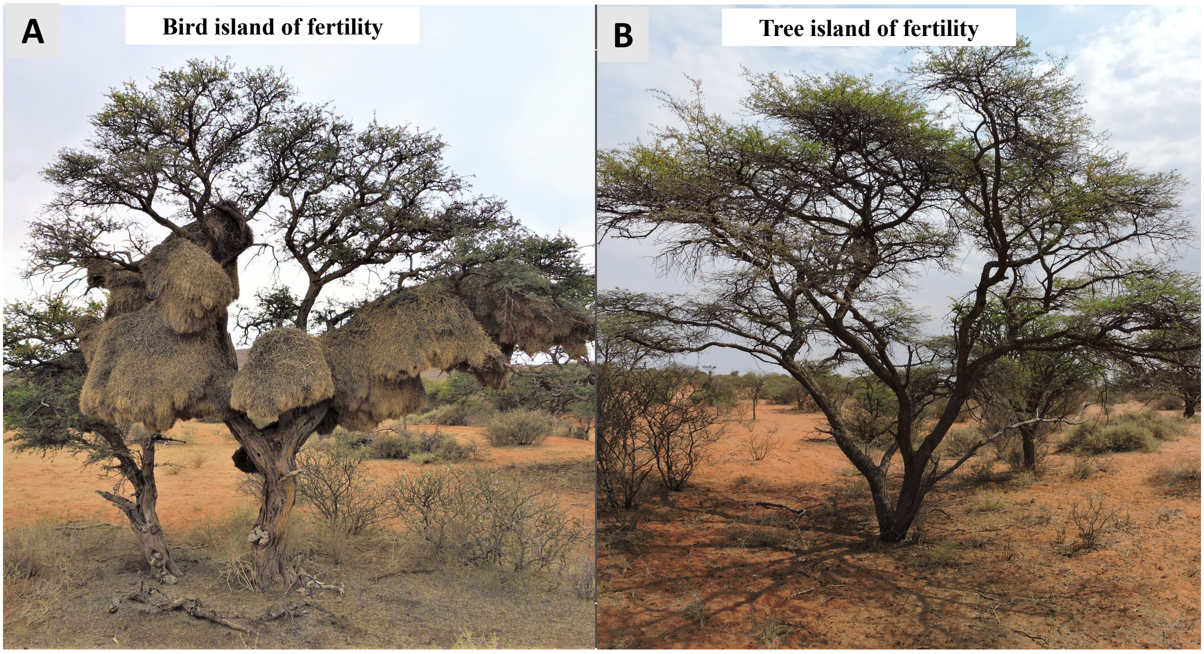

Figure 3.1: (A) Bird island of fertility showing the sociable weaver nest on a camelthorn tree with a pile of faecal matter and nest materials from the sociable weaver under the tree. (B) Tree island of fertility showing a camelthorn tree with no nest typically has mammalian faecal matter scattered under the tree.

Materials and Methods

Site description and experimental Setup

I collected the soils and seeds used in this study from Tswalu Kalahari, a reserve in the Northern Cape Province, South Africa (27.225 ° S 22.478 ° E). The climate is typically hot and arid; the long-term annual mean temperature is 20.3 ºC, with an annual mean maximum of 29.5 ºC and a minimum of 11.1 ºC (Cromhout 2006). Rainfall is highly variable, occurring mainly during summer (December-March), with a mean of 325 mm per year (range 175 – 595 mm; van Rooyen and van Rooyen 2017). The soils collected for this study were within the Koranna-Langeberg Mountain Bushveld and Olifantshoek Plains Thornveld vegetation types of the study area. The soils are red Kalahari sands, with the main component of the soil classified as fine sand (Prayag *et al*. 2020). I obtained permission from Tswalu Kalahari Reserve to collect all samples used in this study.

To measure the nutrient concentrations and stoichiometries of both mammalian and sociable weaver droppings, I collected fresh mammalian faecal matter under BIFs and TIFs. I used fresh faecal matter because I did not have an idea of how long the old faecal matter has been deposited and the changes that has taken place since it was deposited. Secondly, I used the fresh faecal matter of the sociable weavers, to avoid NH_3 volatilization once the droppings of the sociable weavers are deposited, resulting in further fractionation of the N isotope increasing $\delta^{15}N$ values of the remaining N (Mulder *et al.* 2011; Nel *et al.* 2018; Prayag *et al.* 2020). I randomly selected (from the list of nest-trees) 14 paired BIFs matched with TIFs of similar height and trunk DBH that had no nest. I removed all the old faecal matter under the canopies of these trees. After 10 days, I collected all fresh faecal matter under these trees, oven-dried it at 70°C to constant weight, and then milled it using a ball mill (MM200, Retsch, Germany). I obtained the data on the nutrient concentrations of the sociable weaver faecal matter from Prayag *et al.* (2020).

To sample soils for soil nutrient analysis and the growth of camelthorn seedlings, I randomly selected 12 camelthorn and 12 shepherd trees that contained a sociable weaver nest from a list of nest-trees documented in the study area. I matched each selected nest-tree with a tree (without a nest) of a similar height and trunk diameter at breast height (DBH) to that of the paired nest-tree. I selected the paired trees without nests near nest-trees (mean 78 m; range 16 m – 192 m) to control for spatial variability within the study area. I designated the midpoint between the nest-tree and the tree as the grassland site. This resulted in a total of 72 sites (12 triplet sites; nest-tree, tree, and grassland for each species, hereafter referred to as BIFs, TIFs, and grasslands sites, respectively). I collected soil samples from these sites for nutrient analysis and to grow camelthorn seedlings in the greenhouse to investigate the seedling growth response to nutrient concentrations and stoichiometries in the islands of fertility. Soil samples (approximately 1.5 kg each) were collected directly under the nests, and active chambers or from branches below that could have supported a nest in the control trees. I cleared the soil surface of the accumulated faecal matter and grass materials before taking samples using a soil auger (7 cm diameter) to a depth of 20 cm. In this study, I considered the effect of tree species because our previous study found that some soil nutrient concentrations varied depending on tree species (camelthorn vs. shepherd trees, Aikins *et al*. 2023).

I sieved the soils through a 1 mm sieve and then coned and quartered (Gerlach *et al*. 2002) to sub-sample the soils for the various tests. The dry sub-sampled soils from each sampling point were milled to a fine powder using a mortar and pestle. I determined soil pH by adding 25 ml 1 M KCl solution to 10 g air-dried soil, shaking for 20 mins using an orbital shaker at 20 rpm, and after settling for 1 h, I measured the pH. I separated the dried shoot biomass into leaves and stems. The leaves were crushed in a mortar and pestle and subsequently milled to powder using a ball mill (MM200, Retsch, Germany).

I conducted a growth experiment to determine how camelthorn seedlings perform under these soils as influenced by mammalian and sociable weaver faeces. I collected seeds from a single camelthorn tree without a nest (to limit genetic variability). The seed coat of camelthorn is tough and absorption of water to promote germination is slow. I therefore scarified the seeds with sandpaper to allow easy absorption of water (Mira *et al*. 2017). One hundred seeds were scarified using sandpaper and soaked in water for 24 h before being transferred to a Petri dish in a phytotron for germination. After germination, I randomly assigned the seedlings to 72 individual pots filled with each of the 72 soil samples at a depth of 2 cm (Figure 3.2). The seedlings grew in a greenhouse at the University of Cape Town with a temperature of 25 ^{o}C. Seedlings were watered twice daily (7 am and 2 pm) for 3 min each using an automatic overhead water irrigation system. I regularly changed each pot's position in the greenhouse to create uniform conditions for all plants. I immediately removed all weeds from the pots as they germinated during the experiment. I measured the initial growth parameters of each seedling two weeks after planting. Plant height, stem diameter, and the number of leaves were then measured once a week, every week until the 10th week, after which I harvested the plants. Roots were washed free of soil, and the number of nodules was counted. I separated the harvested plants into the shoot and root biomass and oven-dried at 70 °C for 48 h, and I weighed the dry samples to obtain their biomass.

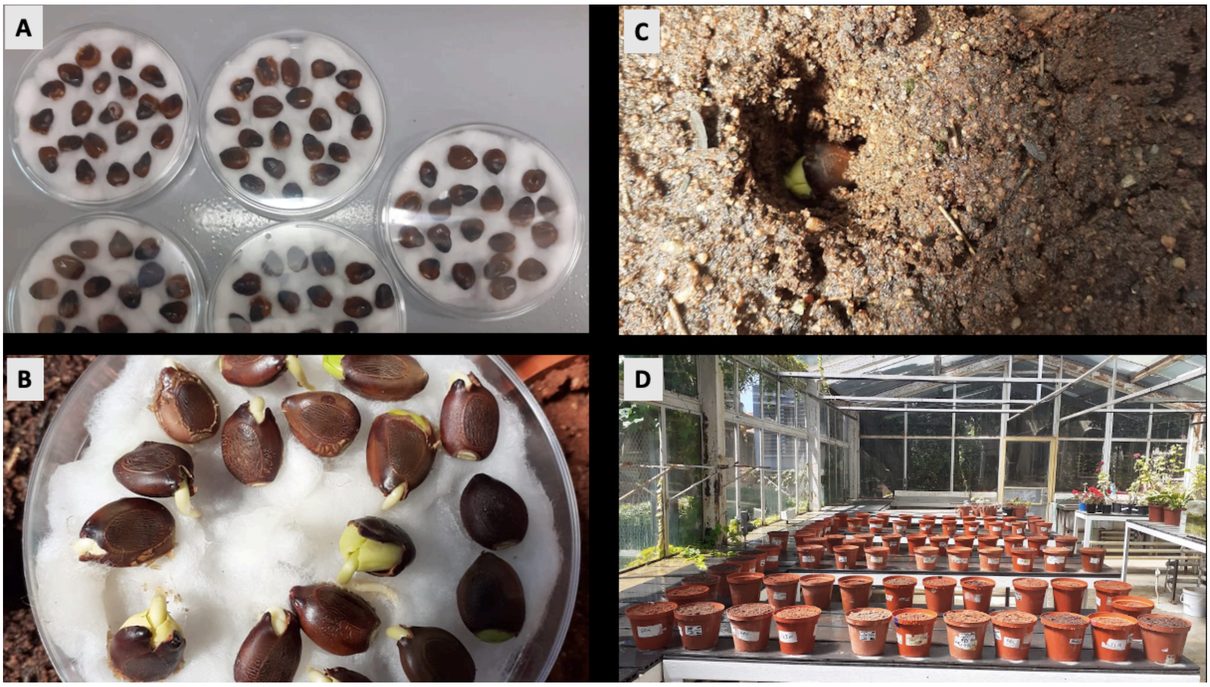

Figure 3.2: A: Soaked seeds transferred to a Petri dish for germination. B: Germinated seeds ready for planting in growing pots. C: Seed planted in the growing pot. D: Setup of the greenhouse with an automatic overhead water irrigation system.

Analysis of soil, faecal matter, and camelthorn seedling leaves

I placed the milled soil, faecal matter, and leaf samples in XRF sample cups sealed with a 4 μm Polypropylene thin film (Chemplex Industries Inc, Florida, USA) at the bottom and inserted into an Energy Dispersive benchtop X-Ray Fluorescence (ED-XRF) Spectro Xepos spectrometer (Spectro, Amatek materials analysis division, Kleve, Germany). I controlled the analysis using a computer data acquisition system using Spectro X-Lab Pro, which incorporates the TurboQuant software for automatic matrix effect correction. I calibrated the instrument using a certified standard GBW07312 (National Research Center for Certified Reference Materials, Beijing, China), for which elemental concentrations were obtained from the NOAA Technical Memorandum NOS ORCA 68 (1992). The focus elements for this study were P, K, Ca, and Zn, as these minerals were in higher proportions in the faecal matter of the sociable weaver and the soils under the selected trees, although I also considered other essential elements. XRF measures total P, which according to Vona *et al*. (2022), detects a higher concentration of P than other methods of detecting the concentration of P, such as ammonium lactate extraction, Mehlich 3 extraction, water extraction, and cobalt hexamine extraction. Therefore, I performed a regression analysis between soil XRF total P and citric acid extracted P for the same samples (data obtained from Prayag *et al*. 2020) to determine the relationship between the two measures of soil P. I used the equation of the line ($\text{Soil P}_{\text{(XRF)}} = 7.0991_{\text{citric acid extracted P}} + 0.0541$, $R^2 = 0.776$) to estimate the equivalent citric acid P of the soil from our XRF soil P values.

I performed the analyses of C, N, $\delta^{15}N$, and $\delta^{13}C$ using a mass spectrometer. I weighed the oven-dried and milled leaves of the camelthorn seedlings (ca. 2 mg), the mammalian faecal matter (ca. 2 mg), and the powdered soils (ca. 40 mg) into tin capsules (Elemental Microanalysis Ltd, Devon, UK). These were combusted in a Flash 2000 organic elemental analyzer (Thermo Scientific, Bremen, Germany), and the gases were passed to a Delta V Plus isotope ratio mass spectrometer (IRMS) via a Conflo IV gas control unit (Thermo Scientific, Bremen, Germany). Large quantity of soil was used because of the very little organic component in the Kalahari red sand. To combat this large sample, firstly, samples were well homogenised, but to maximize combustion of soils, I increased the oxygen injection timing for soils to 4 seconds. I also run soils at the beginning of a reactor column when the chemicals are brand new. I found that this increased combustion as the part of the reactor that collects the combusted samples is still empty and fresh. Also, to minimise carry over with these large samples, I run blank combustions in between soil samples. I calibrated the results using two in-house standards and one IAEA standard. I obtained the data on faecal nutrients of the sociable weaver from Prayag *et al*. (2020).

Data Analysis

I performed all statistical analyses with R (version 4.0.3). I explored the characteristics of the faecal nutrients between sources (sociable weaver, mammals under nest trees, mammals under trees) using a linear model. The faecal nutrient values were log-transformed before analysis. I tested the residuals of the models of the response variables (growth parameter, biomass, and foliar nutrients) for normality, and all were normally distributed. To address the issue of heteroscedasticity, I used the appropriate variance functions; model = lme (Y ~ X, random=~1|S, data=df, weights=varIdent(form=~1|X), method = "REML"). I ran linear-mixed effects models using the nlme package to test our response variables: soil nutrients, growth parameters (height, number of leaves, stem diameter, and shoot, root, and total biomass), and foliar nutrients, relative to explanatory variables: sites (3 levels: BIFs, TIFs, and grasslands) and species (2 levels: camelthorn and shepherd) with random effect of the triplet identity (unique identification number for each collection site; BIFs, TIFs, and grasslands). I used the 'Anova' function to test whether the model terms explain a significant proportion of the variation in our response variables. I then performed emmeans post-hoc pairwise comparisons to test differences between the levels when the main effect is significant. The p-values in the multiple pairwise comparisons were adjusted using the Tukey method. I calculated the average concentrations of mammalian faecal nutrients from the nutrient content per species.

I fitted a generalized additive model (GAM) using the mgcv package (Wood 2017) to seedling growth parameters to compare growth over weeks (k = 9) grouped by sites. I represented the GAM smooth term using penalized regression splines with smoothing parameters selected by REML. I used the negative binomial distribution in our model with 95% confidence bands. To test for factors that significantly predict the total biomass of the camelthorn seedlings, I used multiple linear regression analysis followed by a forward and backward stepwise simplification using the stepAIC function (MASS package; Venables & Ripley 2002). I used soil properties (pH, N, P, K, and Ca) as response variables (predictors) and used total biomass as our explanatory variables.

Results

Soil and faecal matter nutrient concentration and stoichiometries

Soil pH was significantly higher in the BIF soils of both tree species compared to their grassland soils. For both tree species, the soil pH of the BIFs and TIFs did not differ (Table 3.1). BIFs had significantly higher soil C, N, $\delta^{15}N$, P, K, and Ca for both tree species than TIFs and grassland sites. Grassland soils had higher soil $\delta^{13}C$ than both BIF and TIF soils, but soil $\delta^{13}C$ did not vary between BIFs and TIFs. The TIF soils of both tree species had higher C, N, and P than the grassland soils. There were, however, lower soil C:N, K:P, and Zn:P under BIFs than under TIFs and grasslands, but N:P was higher under TIFs than under grasslands (Table 3.2). There was a higher N concentration in the sociable weaver's than in the mammal faecal matter (Table S3.1). There were also higher levels of P, K, and Zn in the faecal matter of the sociable weaver than in the faecal matter of the mammals under TIFs. Also, due to the differences in mammal species that frequent the nest-trees and trees without nest, I found higher levels of P, K, and Zn in the faecal matter of mammals under the BIFs than TIFs. C:N and Ca:P ratios were higher in mammalian faecal matter from both BIFs and TIFs than in the sociable weaver faecal matter (Table 3.2). The faecal C:N and Ca:P ratios of the mammals were ca. 3.2- and 5.7-fold higher than the sociable weaver, respectively. N:P, K:P, and Zn:P ratios did not vary between faunal nutrient sources.

Table 3.1: Properties of soils used for the growth of seedlings in the greenhouse that came from sites related to camelthorn and shepherd trees. The mean and standard error (SE) of the soil pH, C, $\delta^{13}C$, N, $\delta^{15}N$, P, K, and Ca are provided ($n = 12$). Different letters on mean values in the same column across species and sites indicate significant differences ($P < 0.05$) as determined by Tukey's post-hoc pairwise comparisons of the different levels within the explanatory terms of the LMM.

Soil Sources	**Soil properties (mean ± SE)**								
	Soil pH	C (%)	$\delta^{13}C$ (‰)	N (%)	$\delta^{15}N$ (‰)	P (%)	Citric acid P (mg/kg)	K (%)	Ca (%)
Camelthorn tree									
Bird Islands of fertility	5.63 ± 0.22^{b}	1.95 ± 0.28^{c}	-20.42 ± 0.18^{a}	0.29 ± 0.04^{c}	17.76 ± 0.75^{c}	0.41 ± 0.08^{d}	500 ± 110^{d}	$1.23 \pm 0.05b^{cd}$	0.30 ± 0.05^{bc}
Tree Islands of fertility	4.90 ± 0.18^{ab}	0.47 ± 0.05^{b}	-21.37 ± 0.37^{a}	0.05 ± 0.01^{b}	13.04 ± 0.41^{b}	0.08 ± 0.01^{bc}	40 ± 10^{bc}	1.11 ± 0.05^{ab}	0.14 ± 0.02^{a}
Grassland	4.71 ± 0.13^{a}	0.25 ± 0.03^{a}	-18.87 ± 0.39^{b}	0.03 ± 0.003^{a}	12.66 ± 0.44^{b}	0.07 ± 0.01^{a}	20 ± 10^{a}	1.10 ± 0.04^{a}	0.06 ± 0.01^{a}
Shepherd tree									
Bird Islands of fertility	5.66 ± 0.23^{b}	1.20 ± 0.17^{c}	-20.91 ± 0.31^{a}	0.18 ± 0.03^{c}	16.74 ± 0.77^{c}	0.43 ± 0.04^{d}	530 ± 50^{d}	1.30 ± 0.05^{bd}	0.35 ± 0.05^{c}
Tree Islands of fertility	5.39 ± 0.15^{b}	0.42 ± 0.03^{b}	-21.46 ± 0.24^{a}	0.05 ± 0.003^{b}	12.83 ± 0.42^{b}	0.09 ± 0.01^{c}	60 ± 10^{c}	1.18 ± 0.04^{ac}	0.16 ± 0.04^{ab}
Grassland	4.44 ± 0.07^{a}	0.18 ± 0.02^{a}	-18.32 ± 0.22^{b}	0.02 ± 0.003^{a}	9.96 ± 0.35^{a}	0.07 ± 0.003^{ab}	30 ± 10^{ab}	1.13 ± 0.04^{ac}	0.12 ± 0.04^{a}

Table 3.2: Soil nutrient stoichiometry (w/w) of soils from bird islands of fertility, tree islands of fertility, and grassland sites. Nutrient stoichiometry of sociable weavers and mammalian faecal matter are also given (sociable weaver data was obtained from Prayag *et al*. 2020). The mean ± SE is reported for each soil and faecal nutrient source and the nutrient stoichiometries. The means of soil ratios with the same letters in columns did not significantly differ.

Soil Sources	**Nutrient stoichiometry (mean ± SE)**				
	C:N ratio	N:P ratio	K:P ratio	Ca:P ratio	Zn:P ratio
Bird islands of fertility (n= 24)	6.5 ± 0.24^{a}	0.86 ± 0.21^{ab}	3.9 ± 0.5^{a}	0.82 ± 0.07^{a}	0.012 ± 0.001^{a}
Tree islands of fertility (n= 24)	8.4 ± 0.19^{b}	0.67 ± 0.06^{b}	13.8 ± 0.64^{b}	1.57 ± 0.15^{b}	0.021 ± 0.002^{b}
Grassland (n= 24)	7.9 ± 0.37^{b}	0.42 ± 0.04^{a}	17.0 ± 0.7^{c}	1.51 ± 0.44^{ab}	0.029 ± 0.005^{b}
Faunal Nutrient Sources					
Sociable weaver	7.05 ± 0.53^{a}	5.89 ± 1.04^{a}	1.34 ± 0.04^{a}	1.22 ± 0.13^{a}	0.025 ± 0.003^{a}
Mammals (BIFs)	23.32 ± 2.98^{b}	4.42 ± 0.71^{a}	2.24 ± 0.45^{a}	7.80 ± 1.53^{b}	0.024 ± 0.004^{a}
Mammals (TIFs)	21.51 ± 1.98^{b}	10.29 ± 2.28^{a}	1.65 ± 0.36^{a}	6.09 ± 0.93^{b}	0.028 ± 0.004^{a}

Bird and tree islands of fertility effects on the growth of camelthorn seedlings

There was a slight variation in size (mean ± SE, 29.0 ± 0.11 mm) and mass (0.30 ± 0.01 g) of camelthorn seeds used for this study (Table S3.2; seed germination rate was 79%). There was generally poor nodulation in the roots of all the seedlings in this experiment; only two out of the 72 camelthorn seedlings formed root nodules (a seedling grown in soil from a TIF formed seven nodules, while a seedling grown in grassland soil formed 11). None of the seedlings grown in the soils from BIFs formed root nodules.

The identity of the tree species (camelthorn vs. shepherd) associated with the source soils for the study did not explain significant differences in the height of camelthorn seedlings, the number of leaves, stem diameter, shoot biomass, root biomass, root-to-shoot ratio, and total biomass (Table S3.3). The site term (BIFs, TIFs, and grasslands) explained significant variation in the height of the camelthorn seedlings and the number of leaves but not the stem diameters

(Figures 3.3, 3.4A, 3.4B, & 3.4C; Table S3.3). There was also a significantly greater mean seedling height (ca. 1.4-fold) and number of leaves (ca. 1.4-fold) in soils from BIFs than in both TIFs and grasslands sites. The interaction between the tree species and sites did not explain significant variation in our growth response variables. Time-course analysis of seedling growth showed that 'site' significantly influenced the weekly growth in height (Chi-square = 48.46, P < 0.001) and number of leaves (Chi-square = 83.31, p < 0.001; Figures 3.5A and 3.5B). Seedlings grown in soils from BIFs were taller and had more leaves than in TIF and grassland soils. The stem diameter, however, did not vary between sites (Figure 3.5C)

Seedling shoot biomass and total biomass varied significantly with 'site' (Figure 3.6A, Table S3.3). There were significantly higher mean shoot biomass and total biomass of plants grown on BIF soils compared to TIF and grassland soils. Still, there were no significant differences in the mean shoot biomass between the TIFs and grassland soils. The mean shoot biomass of seedlings grown in BIF soils was about 1.6-fold higher than those grown in soils from TIF, and 1.7-fold higher compared to the grassland soils. The mean total biomass of seedlings grown in soils from BIFs was approximately 1.5-fold higher than the TIFs soils and 1.5-fold higher than the grassland soils. Seedling root biomass did not vary significantly with the site, but the root-to-shoot ratio varied significantly with the site. Camelthorn seedlings grown in grassland and TIF soils increased biomass partitioning to the roots. There was a significantly higher root-to-shoot ratio in seedlings grown in grassland soils than in BIFs, but there was no significant difference between grassland soils and TIF soils. Furthermore, there were no significant differences in the root-to-shoot ratio in seedlings grown in soils from TIFs and BIFs (Figure 3.6B). The mean root-to-shoot biomass in seedlings grown in soils from grasslands was approximately 1.3-fold higher compared to the seedlings grown in soils from the BIFs.

The results also show that 25% of the variance in total seedling biomass can be explained by two predictors (i.e., soil N/P and K; $F_{(2, 69)} = 11.33$, $p<0.001$). I found Soil N and P to be collinear; hence our fitted regression model was: Total biomass = 0.03 + 2.28*(soil N/P) + 1.07*(soil K). Soil N/P ($\beta = 2.28$, $p<0.001$) and K ($\beta = 1.07$, $p = 0.021$) significantly predicted total biomass. Soil N and P was the most important soil property that predicted total biomass.

Figure 3.3: A typical example of the effect of soils from bird and tree islands of fertility and the grassland sites on the growth of camelthorn seedlings.

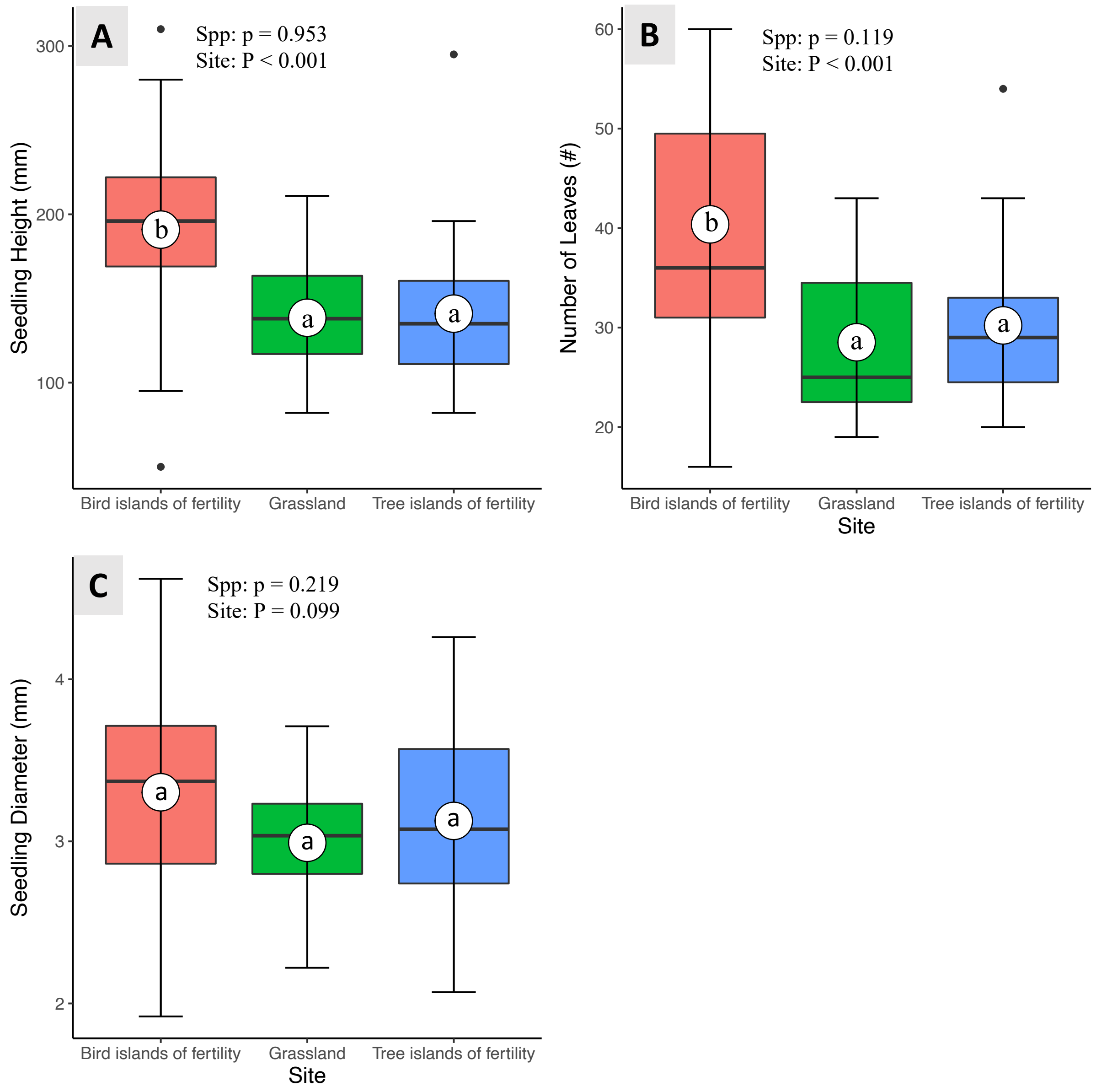

Figure 3.4: Final height of the seedlings, number of leaves, and diameter of the stem of camelthorn seedlings grown in soils from bird islands of fertility, tree islands of fertility, and grasslands. The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. Whiskers represent 1.5 × the interquartile range. Outliers above/below are shown as dark points. Circles represent the mean, and letters indicate a pairwise comparison between sites. The p-values of the linear mixed-effects model for species and site effects are present for each growth parameter (no interaction between species and sites).

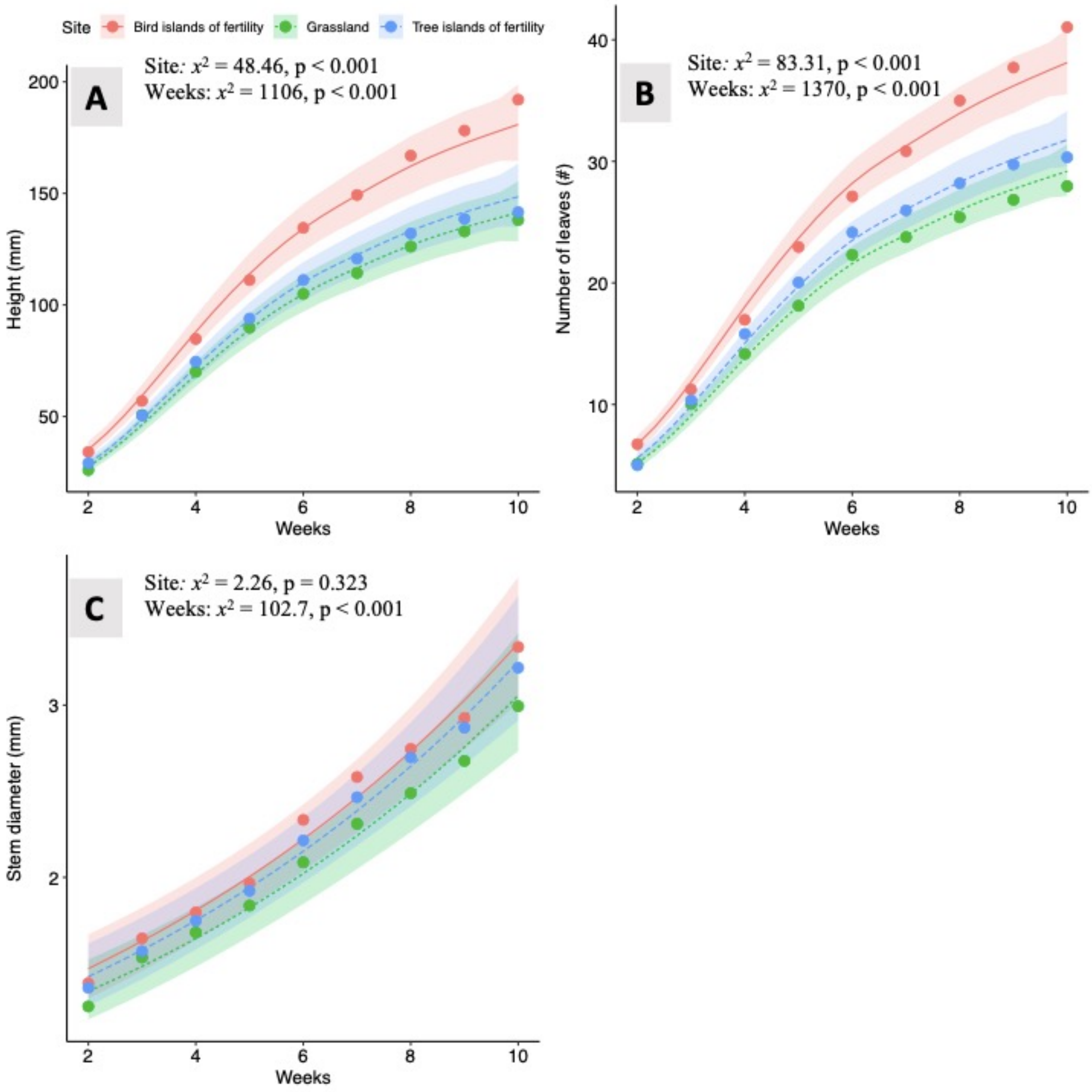

Figure 3.5: Time course analysis of the height (A), number of leaves (B), and stem diameter (C) of camelthorn seedlings grown in soils from the bird islands of fertility, tree islands of fertility, and grasslands. The bands represent the 95% confidence bands fitted with a generalized additive model (GAM) using a negative binomial distribution.

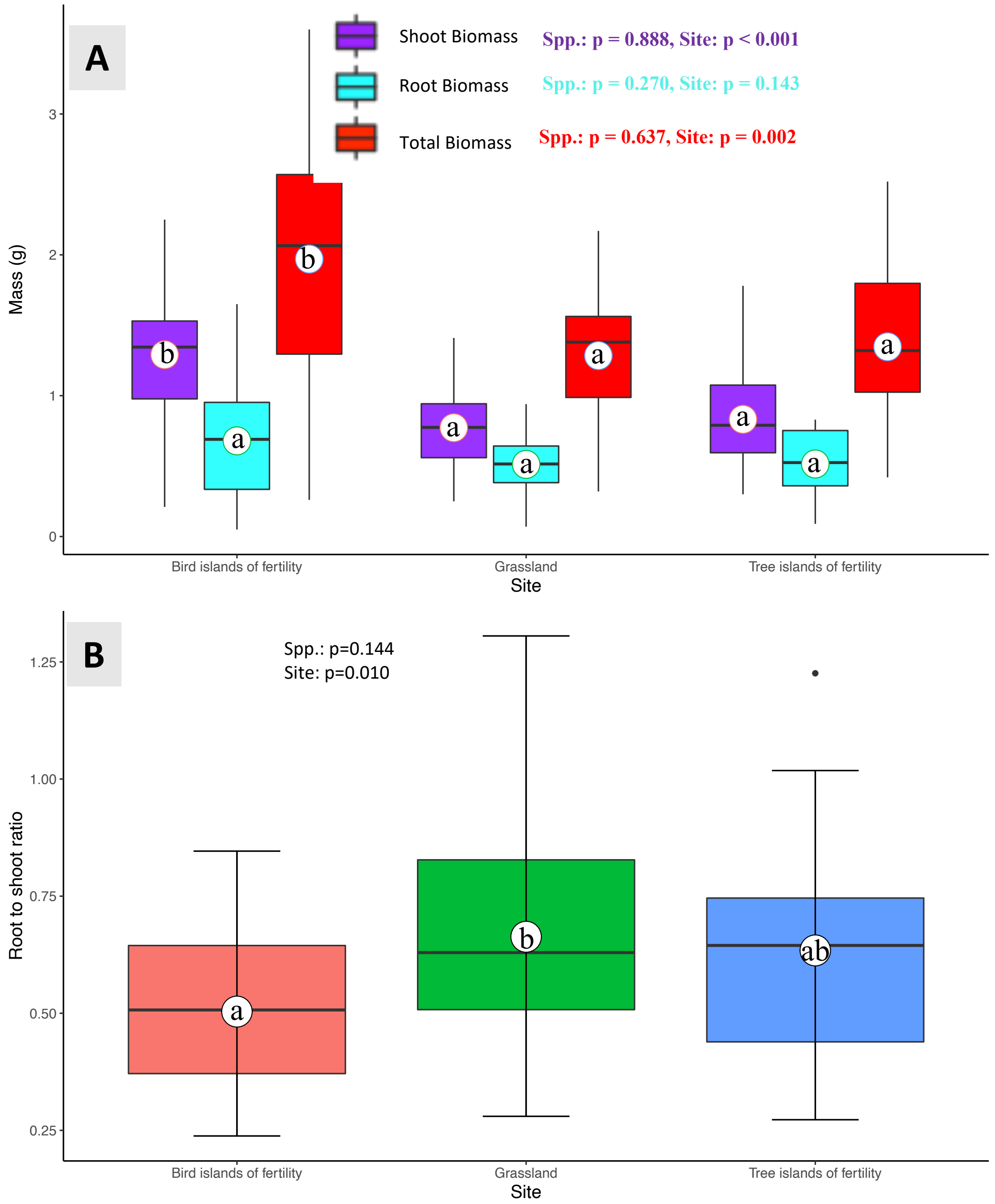

Figure 3.6: Final shoot biomass, root biomass, total biomass (A), and the root-to-shoot ratio between sites (B). The final biomass is dry and destructively measured at the end of the experiment (11 weeks after planting). The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. Whiskers represent 1.5 × the interquartile range, and outliers above/below are shown as dark points. The circles represent the mean, and the letters indicate a pairwise comparison between sites separately for each biomass measure. The p values of the linear mixed-effects model for species and site effects are presented for each biomass (no interaction between species and sites).

Bird and tree islands of fertility affect the foliar nutrients of camelthorn seedlings

The foliar N and $\delta^{15}N$ were significantly higher in the plants grown on soils from BIFs compared to TIFs and grasslands (Figures 3.7A and 3.7B, Table S3.4). There was a significant difference in $\delta^{15}N$ between the seedlings grown in TIF and grassland soils, but there was no significant difference in foliar N between BIF and grassland seedlings. There were also significant differences in foliar P between sites, but foliar K, Ca, and Zn did not vary (Figure 3.8, Table S3.4). There was significantly higher foliar P (ca. 1.8-fold) in seedlings grown in BIFs compared to the grassland soils but not different from the TIFs soils (Figure 7A). The foliar nutrients of the camelthorn seedlings did not vary between the tree species that were associated with the soils collected for the experiment (Table S3.4). There were also no significant interactions between the tree species and the sites.

The seedling foliar nutrient stoichiometry differed between sites for C:N, K:P, Ca:P, and Zn:P, but not for N:P ratios. Foliar C:N and Ca:P ratios decreased in the order of grassland = TIFs > BIFs (Table 3.3). Seedling foliar K:P and Zn:P ratios were higher in seedlings grown in grassland soils than in TIFs and BIFs. K:P was also higher in TIFs seedlings than BIFs seedlings but there was no difference between BIFs and TIFs for Zn:P ratios. There was, however, a significant positive correlation between foliar N and P concentrations of seedlings grown in the soil from BIFs but not for TIFs and grassland soils (Figure 3.9).

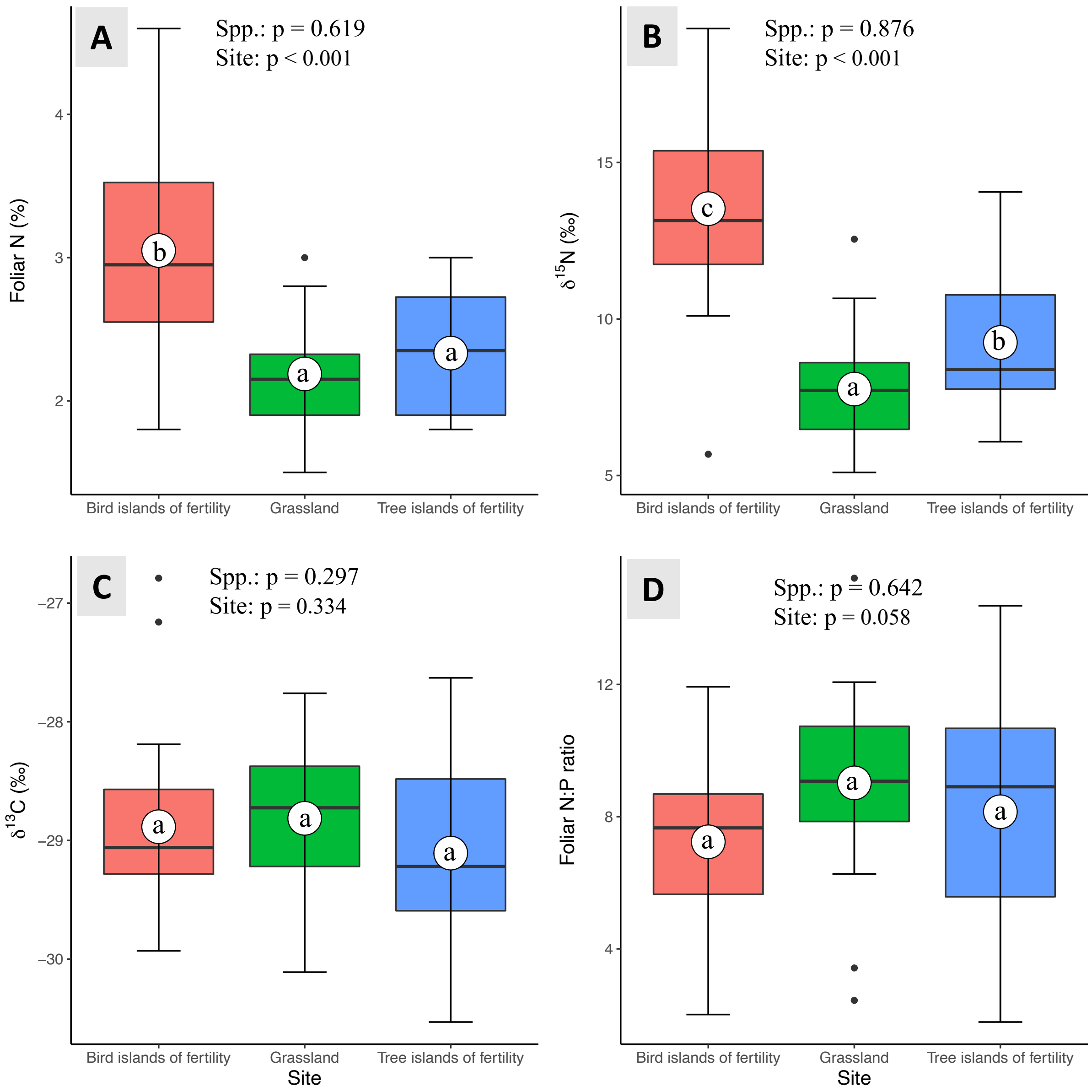

Figure 3.7: Foliar N, δ^{15}N, δ^{13}C, N:P ratio of camelthorn seedlings grown in soils from bird islands of fertility, tree islands of fertility, and grasslands (11 weeks after planting). The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. Whiskers represent 1.5 × the interquartile range, and outliers above/below are shown as dark points. Circles represent the mean and letters indicate a pairwise comparison between species and sites. The p values of the linear mixed-effects model for species and site effects are presented for each foliar nutrient (no interaction between species and sites).

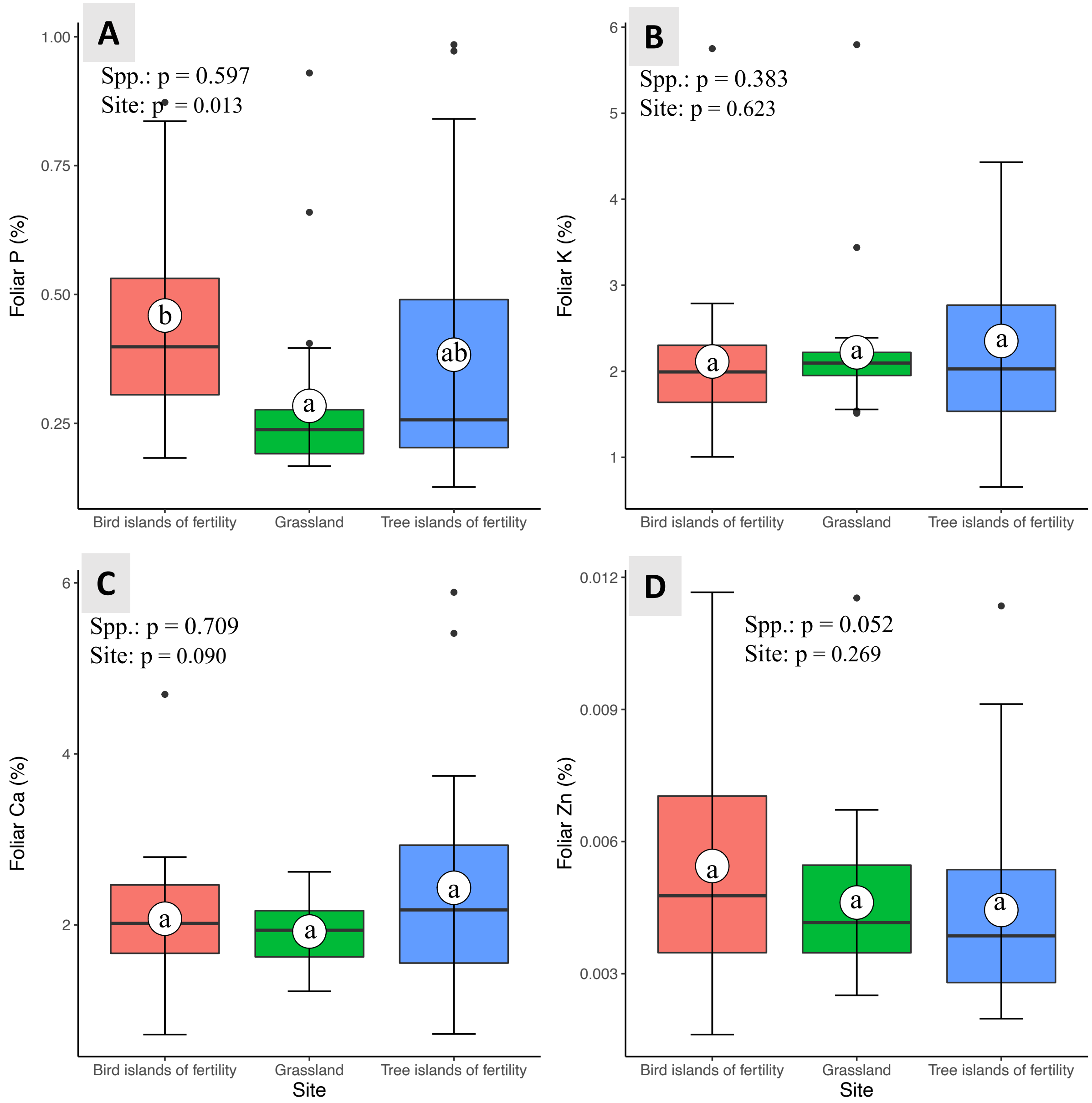

Figure 3.8: Foliar minerals of camelthorn seedlings grown in soils from bird islands of fertility, tree islands of fertility and grassland. Measured minerals include P, K, Ca, and Zn. Foliar minerals were measured 11 weeks after planting. The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. Whiskers represent 1.5 × the interquartile range, and outliers above/below are shown as dark points. Circles represent the mean, and letters indicate a pairwise comparison between species and sites. The p values of the linear mixed-effects model for species and site effects are presented for each foliar nutrient (no interaction between species and sites).

Table 3.3: Foliar nutrient stoichiometry (w/w) of camelthorn seedlings grown in soils from bird islands of fertility, tree islands of fertility, and grassland sites. The mean ±SE is reported for each soil source and the nutrient stoichiometries. Means with the same letters in columns did not significantly differ.

Soil Sources (n= 24)	**Foliar nutrients stoichiometry of camelthorn seedlings (mean ± SE)**				
	C:N ratio	N:P ratio	K:P ratio	Ca:P ratio	Zn:P ratio
Bird islands of fertility	16.5 ± 0.89^{a}	7.37 ± 0.43^{a}	5.06 ± 0.36^{a}	4.91 ± 0.42^{a}	0.012 ± 0.001^{a}
Tree islands of fertility	20.8 ± 0.80^{b}	8.24 ± 0.74^{a}	7.19 ± 0.49^{b}	8.22 ± 0.55^{b}	0.013 ± 0.001^{a}
Grassland	21.7 ± 0.61^{b}	9.02 ± 0.55^{a}	8.69 ± 0.47^{c}	8.33 ± 0.51^{b}	0.018 ± 0.001^{b}

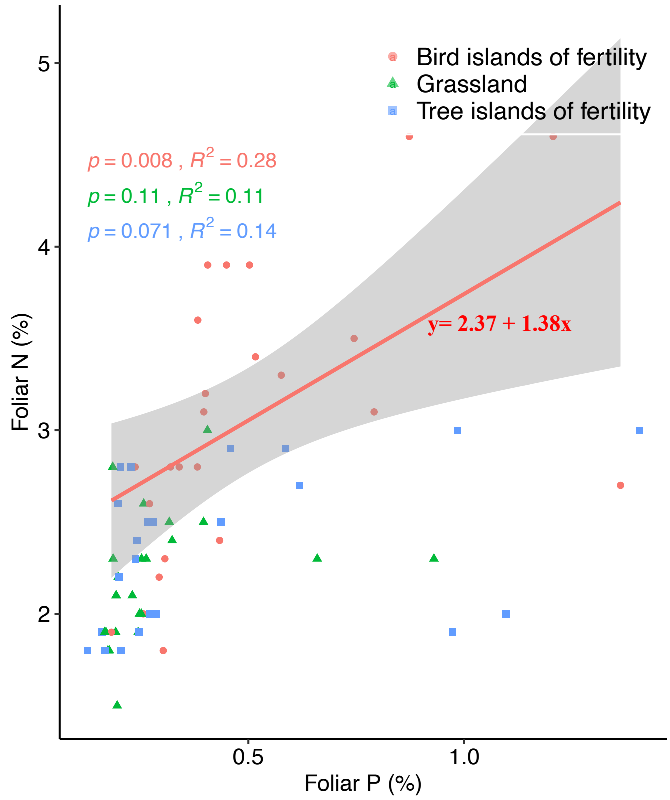

Figure 3.9: Regression showing the relationship between the foliar concentrations of N and P of camelthorn seedlings grown in soils from bird islands of fertility, tree islands of fertility, and grasslands. The red line represents linear fits for the BIFs site only (regression equation reported), and the grey bands are the 95% confidence intervals. P-values and R^2 are reported for each site.

Which nutrients drive the seedling growth in bird islands of fertility?

The foliar N, P, and Mg of the seedlings grown on BIF-soils were higher than those found in mature camelthorn tree leaves (Table S3.5) and other *Vachellia* species (Table S3.6). Similarly, I found that the soil N, P, K, and Ca in the BIFs were significantly higher than in the TIFs and the grassland soils (Table 3.1). Since only N and P were higher in both seedling foliage and soil, soil N and P could be the nutrients that drive increased seedling growth in BIF soils.

Discussion

The presence of the sociable weaver nests increased the growth of camelthorn seedlings grown on soils from those sites more than that in soils from below trees without nests. The greater height, number of leaves, and shoot biomass of seedlings grown in the BIF soils could be due to the soil nutrients derived from the faunal nutrient input of the sociable weaver. Although both the BIFs and the TIFs receive input of faunal nutrients, the differences in growth between the two are probably due to a combination of the amount/availability of faecal matter deposited and the nutrient stoichiometry in the faecal matter. This also suggests that the faunal input from the sociable weaver nests did not make the soils toxic and thus toxicity does not explain the fact that the soil below the nests is commonly barren (Prayag *et al*. 2020). It must, however, be noted that, in the green house experiment, there was lack of continued faecal input and nutrient leaching might have occurred to neutralize toxicity. The higher root biomass relative to shoot biomass at grassland sites than at BIFs could be explained by the fact that plants in these low soil nutrient conditions (characteristic of grassland soils) develop roots to enhance their ability to forage for more nutrients to facilitate growth (e.g., Kang and Van Iersel 2004; Kołodziejek 2019). We attribute the infrequent nodulation to the lack of competition between camelthorn seedlings and other plants in the pots (e.g. Cramer et al. 2007) since we immediately removed all other plants as soon as they germinated.

The higher concentrations of N in the foliar tissue of seedlings grown on BIF soils relative to TIF and grassland soils are a positive response to high concentrations of soil N from BIFs derived from the sociable weaver faeces. Indeed, the sociable weaver faeces had *ca*. 1.9–2.3 times more N than mammalian faeces (Table S3.1). The elevated $\delta^{15}N$ values in the leaves of seedlings grown on the BIFs compared to seedlings grown on the TIFs and the grassland sites suggest assimilation of faunal-derived N since the $\delta^{15}N$ in the BIF soils also had high $\delta^{15}N$ values (Table 3.1; Prayag et al. 2020; Aikins et al. 2023). This enrichment of soil $\delta^{15}N$ in BIFs relative to TIFs occurred despite sociable weaver and mammalian faeces having similar $\delta^{15}N$ values, indicating that the mammalian faeces do not contribute strongly to either the soil or foliar $\delta^{15}N$ in TIFs or BIFs. The availability of N from mammalian faeces is thus questionable.

Elevated foliar P of the seedlings grown in soils of BIFs relative to grasslands was consistent with the differences in soil P between BIFs and grasslands. This together with the intermediate concentration of foliar P in seedlings grown on TIF soils suggests that sociable weaver faeces also contribute P. The high soil P determined by XRF analysis in soils from this study compared to other savanna soils in Africa (Table 3.1; Table S3.7), is due to the XRF measuring total P. The calculated citric acid extractable P levels in grassland and TIF soils (Table 3.1) were, however, low relative to that of the BIFs in the aeolian sand at our study site. The P derived from sociable weaver faeces together with some contribution from mammalian faeces thus likely contributed to increased seedling growth on soil BIFs.

The similar growth and foliar nutrient concentration between TIFs and grasslands, despite some differences in these soils, could be attributed to the fact that the concentration of nutrients in the soils of TIFs did not address the real limitations that the seedlings had, while the BIF soils did to a greater extent. This was unexpected because we found an accumulation of mammalian faecal matter under the TIFs, and therefore expected it to influence the growth of the seedlings. Furthermore, the mammalian faecal matter had substantial concentrations of nutrients that could increase the growth of seedlings in soils from TIFs. The lack of difference in the growth between the TIFs and grassland seedlings could mean that nutrients in this faecal matter were not available in soils. Indeed, the faecal matter under these trees is dry and hard (field observation) in this relatively arid environment, and consequently may not readily decompose or be washed into the soil to supply nutrients, therefore microbial breakdown is important to consider. Additionally, according to Brust (2019), the C:N ratio of the organic substrate between 1 and 15 has rapid mineralization and release of N for the uptake of plants. However, a ratio of 20 to 30 results in an equilibrium state between mineralization and immobilization (Brust 2019). The C:N ratios of the mammalian faecal matter under TIFs and BIFs were 22 and 25, respectively, compared to 7.1 in the sociable weaver faecal matter. This implies that N in the faecal matter of the sociable weaver would be more readily released in BIF soils than N in the faecal matter of mammals in soils from TIFs and BIFs. Sociable weaver faecal matter is thus the primary source of nutrients under the BIFs and drives the growth of the seedlings as this N is readily mineralized and released, while N in the mammalian faecal matter under TIFs and BIFs may not be. A source of N that is unaccounted for in this analysis is mammalian urine which we were unable to analyse, although if this was co-deposited with the faecal material it also did not result in a distinct N concentration or δ^{15}N in TIF- relative to grassland-soils.

Foliar concentrations of individual nutrients are difficult to interpret since the concentration depends on both the availability in the soil and the demand for growth, where the demand may be determined by other nutrient limitations or non-nutrient limitations (e.g. water availability, root access, nutrient allocation). For example, the accumulation of P in the leaves of seedlings grown on BIF soils could result from “luxury” uptake (Wookey et al. 1995). The lack of differences between BIF, TIF and grassland soil grown seedlings in foliar N:P indicates, however, that these two elements were in balance. Lower values of foliar K:P and Ca:P in BIF than in TIF or grassland soil grown seedlings is consistent with the soil ratios of these elements.

This means, firstly, that camelthorn seedlings do not exhibit strong stoichiometric homeostasis for K and Ca, but rather their tissue nutrient stoichiometries partially depend on soil nutrient stoichiometries (e.g., Han et al. 2005; Elser et al. 2010). Secondly, the elevated availability of N and P from sociable weaver faeces is not matched by elevated K and Ca, possibly resulting in these elements limiting further responsiveness of seedling growth to the input of sociable weaver faeces. For example, Le Roux et al. (2020) have highlighted the importance of nutrient stoichiometry in mammalian faecal matter for plant growth. The lack of differences in foliar K, Ca, and Zn between sites, despite higher levels of these nutrients in the soils of BIFs, may be due to the higher soil P and N in these soils, enabling growth dilution of K, Ca, and Zn.

Conclusion

I found that savanna islands of fertility differ in terms of constituents and support for plant growth. I also found that sociable weavers as ecological engineers bring resources together under trees in these nutrient-poor arid sandy soils that ameliorate nutrient limitations for camelthorn seedling growth that soils from TIFs could not address despite the high mammalian faecal input. N and P in BIFs derived from sociable weavers are the main nutrients that apparently drive the growth of seedlings. My findings thus provide empirical evidence for colonial birds enhancing the growth of host tree seedlings, and by implication possibly mature plants with sociable weaver nest, in this savanna ecosystem.

Supplementary Materials

Table S3.1: Elemental composition (%, based on weight element per foliar dry weight), $\delta^{15}N$ and $\delta^{13}C$ of mammalian and sociable weaver faecal matter collected under the nest-trees and trees without nests. The nutrient concentration of the sociable weaver faecal matter is also given for comparison (data from Prayag *et al.* 2020). Mean ± SE is given for each faecal nutrient. Means with the same letters in the rows did not differ significantly.

Elements/ isotopes	Sociable Weavers	BIFs mammalian nutrient	TIFs mammalian nutrient
N (%)	4.81 ± 0.28^{b}	2.09 ± 0.42^{a}	2.54 ± 0.42^{a}
C (%)	32.91 ± 1.75^{a}	39.49 ± 3.03^{a}	39.21 ± 1.69^{a}
P (%)	0.85 ± 0.06^{b}	0.89 ± 0.47^{ab}	0.42 ± 0.15^{a}
K (%)	1.16 ± 0.10^{b}	0.88 ± 0.19^{ab}	0.55 ± 0.13^{a}
Ca (%)	1.06 ± 0.15^{a}	3.76 ± 0.95^{b}	2.28 ± 0.48^{ab}
Zn (%)	0.019 ± 0.002^{b}	0.012 ± 0.003^{ab}	0.009 ± 0.001^{a}
$\delta^{15}N$ (‰)	10.12 ± 0.22^{a}	9.29 ± 0.27^{a}	9.55 ± 0.33^{a}
$\delta^{13}C$ (‰)	-21.37 ± 0.52^{a}	-22.21 ± 1.37^{a}	-22.4 ± 0.82^{a}

Table S3.2: Characteristics of the seeds used for the experiment. Seeds are from a single camelthorn tree without a sociable weaver nest. Mean size and weight are given as well as mean pod weight and mean number of seeds per pod (n= 10 pods).

Seed Characteristics	**Mean ± SE**	**Range**
Seed size (mm)	8.29 ± 0.11	7.81 - 8.90
Seed weight (g)	0.30 ± 0.01	0.25 - 0.38
Pod weight (g)	18.71 ± 0.33	13.76 - 22.92
Seeds per pod (#)	17 ± 0.97	14-21

Table S3.3: Linear mixed model analysis with camelthorn seedlings growth parameters and biomass yield as response variables and site (3 levels- BIFs, TIFs and grassland) as a factor. We included triplets as a random effect. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis.

Response Variables	**Factors**	X^2	**df**	**P-value**
Height	Site	18.22	2	< 0.001
	Tree species	0.003	1	= 0.953
Number of leaves	Site	18.98	2	< 0.001
	Tree species	2.44	1	= 0.119
			1	
Stem diameter	Site	4.62	2	= 0.099
	Tree species	1.51	1	= 0.219
Shoot biomass	Site	18.05	2	< 0.001
	Tree species	0.02	1	= 0.888
Root biomass	Site	3.89	2	= 0.143
	Tree species	1.22	1	= 0.270
Root-to-shoot ratio	Site	9.30	2	= 0.010
	Tree species	2.13	1	= 0.144
Total Biomass	Site	12.36	2	= 0.002
	Tree species	0.22	1	= 0.637

Table S3.4: Linear mixed model analysis with camelthorn seedlings foliar nutrients as response variables and site (3 levels- BIFs, TIFs and grassland) as a factor. We included triplets as a random effect. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis.

Response Variables	**Factors**	X^2	**df**	**P-value**
Foliar N	Site	25.96	2	< 0.001
	Tree species	0.62	1	= 0.431
Foliar δ^{15}N	Site	74.94	2	< 0.001
	Tree species	0.02	1	= 0.876
Foliar δ^{13}C	Site	2.19	2	= 0.334
	Tree species	1.09	1	= 0.297
Foliar N:P	Site	5.70	2	= 0.058
	Tree species	0.22	1	= 0.642
Foliar P	Site	8.75	2	= 0.013
	Tree species	0.27	1	= 0.597
Foliar K	Site	0.95	2	= 0.623
	Tree species	0.76	1	= 0.383
Foliar Ca	Site	4.81	2	= 0.090
	Tree species	0.14	1	= 0.709
Foliar Zn	Site	2.62	2	= 0.269
	Tree species	3.78	1	= 0.052

Table S3.5: Foliar nutrients (mean ± SE) of camelthorn seedlings grown on BIFs, TIFs and grassland sites in this study compared with foliar nutrients of camelthorn trees reported by other authors. Means with the same letters in the rows did not differ significantly. All percentage values are based on the weight of the element per dry-weight plant tissue.

Nutrient (%, w/w)	**Current study**			**Aikins *et al.* 2023b (unpublished)**		**Mnisi and Mlambo 2016 (Livestock farm)**		**Ravhuhali *et al.* 2020**		**Ditlhogo *et al.* 2020**
	Bird islands of fertility	Tree islands of fertility	Grassland	Bird islands of fertility	Tree islands of fertility	Molelwane	Masuthle	Clay-loamy soil	Red-brown sand soil	Kgalagadi District, Botswana
N	3.05 ± 0.16^{b}	2.33 ± 0.09^{a}	2.19 ± 0.07^{a}	2.94 ± 0.1	2.78 ± 0.1	2.35	2.47	2.42	1.99	
P	0.50 ± 0.06^{b}	0.42 ± 0.07^{ab}	0.28 ± 0.04^{a}	0.23 ± 0.02	0.20 ± 0.02	0.04	0.05			0.07
K	2.11 ± 0.18^{a}	3.02 ± 0.49^{a}	2.39 ± 0.28^{a}	1.55 ± 0.11	1.42 ± 0.11					0.02
Ca	2.07 ± 0.16^{a}	3.22 ± 0.51^{b}	2.21 ± 0.25^{a}	1.13 ± 0.16	1.47 ± 0.23	6.78	3.15			0.09
Zn	0.0049 ± 0^{a}	0.0048 ± 0^{a}	0.0048 ± 0^{a}	0.003 ± 0.001	0.004 ± 0.001	7.56x10^{-4}	5.52x10^{-4}			
S	0.74 ± 0.16^{a}	1.01 ± 0.23^{a}	0.72 ± 0.11^{a}	0.58 ± 0.05	0.57 ± 0.06					
Mg	0.13 ± 0.03^{b}	0.05 ± 0.02^{a}	0.01 ± 0^{a}	0.06 ± 0.02	0.06 ± 0.02					
Si	0.51 ± 0.1^{a}	1.88 ± 0.78^{a}	0.52 ± 0.1^{a}	0.31 ± 0.02	0.36 ± 0.06					
Mn	0.05 ± 0.03^{a}	0.03 ± 0.01^{a}	0.06 ± 0.03^{a}	0.1 ± 0.06	0.06 ± 0.04					
Fe	1.36 ± 1.01^{a}	1.05 ± 0.46^{a}	1.68 ± 1.1^{a}	3.78 ± 2.47	2.04 ± 1.75					
Cl	0.56 ± 0.07^{b}	1.0 ± 0.21^{b}	0.67 ± 0.07^{ab}	0.18 ± 0.01	0.17 ± 0.01					
Mo	3.58 ± 0.53^{a}	4.58 ± 0.81^{a}	3.88 ± 0.67^{a}							
Co	1.88 ± 0.36^{a}	2.5 ± 0.52^{a}	2.5 ± 0.52^{a}							
Ni	0.08 ± 0.06^{a}	0.04 ± 0.03^{a}	0.1 ± 0.07^{a}	0.37 ± 0.25	0.19 ± 0.17					
Cu	0.00238 ± 0^{a}	0.00238 ± 0^{a}	0.00240 ± 0^{a}	0.007 ± 0.005	0.004 ± 0.003					

Table S3.6: Foliar nutrients (mean) of other *Vachellia* species reported by other authors. N was calculated from crude protein values using the conversion % N = % crude protein/6.25 (Jones 1931). All percentage values are based on the weight of the element per dry-weight plant tissue.

Author	**Plant Species**	**N (%)**	**P (%)**	**K (%)**	**Ca (%)**	**Zn (%)**
Marume, *et al.* (2012)	*Vachellia karroo*	3.71	0.08		2.3	
Brown *et al*. (2016)	*Vachellia karroo*	2.02	0.14	1.24	1.64	
Kahiya *et al*. (2003)	*Vachellia karroo*	1.96				
Mokoboki *et al.* (2005)	*Vachellia karroo*	1.73				
Aganga *et al*. (2000)	*Vachellia karroo*	2.02	0.13	0.97	1.73	0.007
Mapiye *et al*. (2009)	*Vachellia karroo*	2.37	0.008	0.187	0.377	0.002
Aganga *et al*. (2000)	*Vachellia tortilis*	2.27	0.18	1.05	1.47	0.006
Aganga *et al*. (2000)	*Vachellia nilotica*	2.90	0.14	1.37	0.93	0.007

Table S3.7: Soil total phosphorus of selected African savannas measured using an XRF element analyzer. Range of means is given for each site where the soils were collected. Percentage values are based on weight of elements per dry weight soil.

Country	**Description**	**Soil Total P (%)**	**Source**
South Africa	Kruger National Park	0.01-0.0124	Hartshorn *et al*. (2009)
Cameroon	Annual grass savanna (Eastern Cameroon)	0.0383	Sugihara *et al*. (2017)
Cameroon	Transition savanna, Mbam-Djerem National Park	0.0316-0.0997	Domingues *et al*. (2015)
Cote D'Ivoire/ Burkina Faso	Savanna soils	0.045-0.082	Baumann *et al*. (2021)
Burkina Faso	Sudan Savanna	0.032	Iwasaki (2022)

Chapter 4: Growth benefits and costs to trees hosting colonial birds that build large avian nests

Abstract

The interactions of organisms within communities are a vital component of functioning ecosystems. The benefits and costs of specific biotic interactions could fluctuate with the life stages of the species and environmental variability. We evaluated the benefits and costs of the biotic interactions between sociable weavers *Philetairus socius* and their host trees in the Kalahari. The presence of a sociable weaver nest may have nutritional benefits due to the faecal deposition below the nests, but the presence of the nest mass could exert a cost to the host trees through branch breaking and tree canopy cover. We hypothesised that the presence of sociable weaver nests on host trees would benefit host trees via the deposition of the faunal nutrients under the nest trees and costs to host trees due to the loss of photosynthetic area and physical damage. We assessed foliar nutrients, biomass growth, canopy area loss, branch fall, and tree mortality of host trees and control trees in the Tswalu reserve in South Africa. We found the benefits of hosting the sociable weaver nest to include higher foliar N, P, K, and Ca. The costs include an average 30% reduction in the photosynthetic area of nest trees, significantly more and larger branch fall in nest trees, and a mean of 39% dead terminal nest branches. We also found that the rate of dieback in trees was higher for nest trees than for trees without a nest. Together, these costs could form a significant proportion of the productivity of the trees. We found nutritional benefits and physical damage in this interaction, but a cost-benefit evaluation would require an analysis of the consequences of reproductive fitness for host trees.

Introduction

Interspecific biotic interactions determine the organisation and functioning of ecosystems through direct positive, neutral, or negative interactions within or between trophic levels (Traveset & Richardson 2014). The costs and benefits of a specific biotic interaction could fluctuate with species ontogeny and environmental variability, with costs outweighing the benefits or vice versa during certain times in the lifespan of the interacting individuals (Newman *et al*. 2022) or under particular conditions (Lang & Benbow 2013). Because the net fitness effects of the biotic interaction are the theoretical basis for considering the interaction mutualism, parasitism, or commensalism (Ewald 1987; Johnson *et al*. 1997), this may complicate categorising certain interactions, which could, for example, start as mutualistic but change to parasitic in nature with time in the relationship, age of the host, or environmental conditions (Ewald 1987; Johnson *et al*. 1997; Newman *et al*. 2022). Therefore, mutualism and parasitism are extremes of a dynamic continuum of species interactions called the "mutualism-parasitism continuum" (Ewald 1987; Johnson *et al*. 1997).

Positive interspecific interactions are common and are significant drivers of community species diversity (Bronstein 1994a; 1994b). Positive interactions between plants and animals can alter plant and animal communities, particularly in harsh environments, by improving environmental conditions to benefit the interacting species (Greenlee & Callaway 1996; Choler *et al*. 2001; Callaway *et al*. 2002; Olofsson 2004; Brooker *et al*. 2008). In mutualisms, heterospecific partners may obtain resources or services they cannot easily produce or acquire otherwise. For example, mutualists can help in the movement of organisms or their gametes, as is the case in pollination and seed dispersal (Schoonhoven *et al*. 2005; Barker & Bronstein 2016). They may also protect partners from natural enemies, such as defensive mutualisms of ants with plants (Rico-Gray &

Oliveira 2007) and provide essential nutrients, such as in the association between colonial birds and their host trees (e.g., Prayag *et al*. 2020; Aikins *et al*. 2023). Mutualisms do not only involve benefits but also costs to hosts, and several studies have measured these costs. For example, in the relationship between plants and mycorrhizae, it is estimated the plant uses about 20% of the total carbon production to support mycorrhizae (Johnson *et al.* 1997). The knowledge that mutualisms involve costs is not new, as cost and benefit analysis has been a standard method in studying the ecological dynamics of mutualism in various systems (Roughgarden 1975; Keeler 1985; Bronstein 2001a). Thus, there is a fine line between what might be considered mutualism versus parasitism.

Biotic interactions between nesting or roosting birds and their tree hosts can produce nutritional benefits for the host trees. For instance, seagull guano input under host plants significantly increased leaf N, P, Zn, and all K ratios of Salsola species on islands in Northern Africa (García *et al*. 2002). An increase in the number of vascular plant species and enlargement of the leaf surface has been observed in nitrophilous species in forests that host heronries in Poland (Żolkos & Meissner 2008). Despite the benefits that birds provide to their host trees, their association also results in costs. For instance, cormorant colonies collect twigs from host trees by stripping branches near their nests (Lemmon *et al*. 1994), resulting in the death of the trees (Koh *et al*. 2012; Traveset & Richardson 2014). These costs/benefits of bird-host tree interaction are well documented in seabird colonies on islands and some forest ecosystems but less so in desert ecosystems where oligotrophic soils predominate.

Desert ecosystems are characterised by low productivity, mainly due to water limitation (Laity 2009; Yahdjian *et al*. 2011) and nutrients, particularly in sandy deserts (Laity 2009; Yahdjian *et al*. 2011). Biotic interactions in desert ecosystems may play a crucial role in addressing the challenges of extreme conditions (Franklin *et al*. 2016). Biotic interactions can alleviate water stress (e.g. hydraulic redistribution, Bogie *et al*. 2018) and elevate soil nutrients by trapping runoff deposition (Tongway & Ludwig 1994; Throop & Belnap 2019). Faunal nutrients, especially from colonial birds, are an essential source of soil nutrients for terrestrial ecosystems in some hyperarid lands or deserts, where the amount of nutrients is naturally limiting (Laity 2009; Yahdjian *et al*. 2011; Aikins *et al*. 2023). The association between the sociable weaver (*Philetairus socius*) and its host trees (camelthorn tree *Vachellia erioloba* or shepherd tree *Boscia albitrunca*) is a useful system for investigating the potential benefits/costs of the presence of colonial birds on the growth of host trees in the desert ecosystem.

We investigated the costs and benefits of the association between colonial sociable weavers and their host trees. Sociable weavers build huge perennial nests in host trees that attract numerous other animal associates (Maclean 1973b; Lowney & Thomson 2021) and are ecosystem engineers (Lowney *et al*. 2020; Lowney & Thomson 2022). The sociable weaver faecal matter accumulation under the nest increases soil C, N, and P compared to grassland and tree soils (Prayag *et al*. 2020; Aikins *et al*. 2023) and may increase biomass yield and foliar nutrients in host trees and their seedlings. Trees with sociable weaver nests also receive more mammalian faecal input under their canopies (Aikins *et al*. 2023a, unpublished). Although the high faunal nutrient input could increase host tree growth, the presence of the nest mass on the trees could also hinder the growth of the host trees. We hypothesized that the presence of the sociable weaver nest on host trees and the deposition of the faunal nutrients under the trees would result in benefits and costs to host trees and intensifies with nest size. We predicted that host trees would have higher leaf nutrients, greater terminal shoot growth, and a higher leaf area index than trees without sociable weaver nests. We also predicted that trees with nests would have associated costs, including reduced photosynthetic area, higher branch fall, a higher number of dead main branches, a higher number of dead terminal branches, and higher mortality.

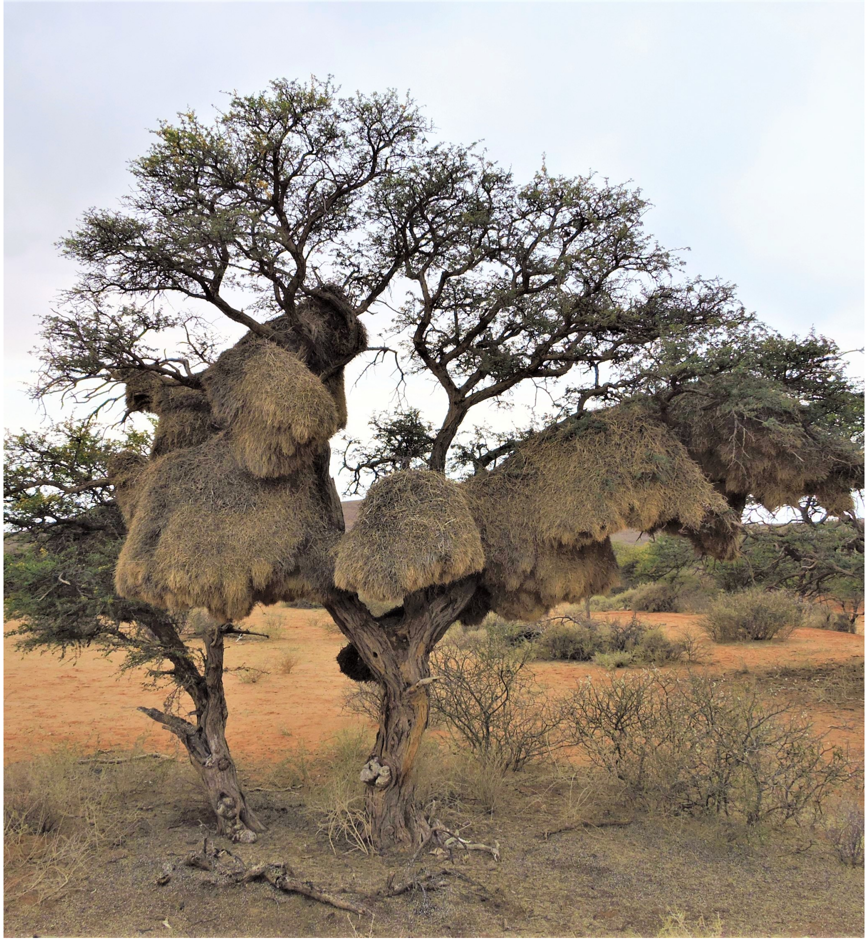

Figure 4.1: Camelthorn trees (7 m tall) host enormous sociable weaver nests, but at what cost?

Materials and Methods

Study area

This study was carried out in the Tswalu Kalahari Reserve in the Northern Cape Province of South Africa (27.225° S 22.478 ° E). The study site is arid, with an annual mean temperature of 20.3º C, an annual mean maximum of 29.5º C, and a minimum of 11.1º C (Cromhout 2006). It experiences highly variable summer rainfall (December-March) with a mean of 325 mm per year (range 175 - 595; van Rooyen & van Rooyen 2017). The reserve is in the desert biome (Mucina & Rutherford

2006) with grasses and herbs (primarily visible in the summer rainfall season) with sparsely distributed trees (mainly camelthorn *Vachellia erioloba* and shepherd tree *Boscia albitrunca*). Shrubs, including blackthorn (*Senegalia mellifera*) and three-thorn (*Rhigozum trichotomum*), are common and grow primarily in the interspaces between trees. The trees selected for this study were within the Koranna-Langeberg Mountain Bushveld and the Olifantshoek Plains Thornveld (Mucina & Rutherford 2006).

Study design

I randomly selected 61 trees that contained sociable weaver nests out of over 250 nest trees mapped in the study area. I chose a nearby tree of the same species without a weaver nest as the control for each selected nest tree. These 'control' trees were chosen in the proximity of nest trees (mean 78 m: range 16 m – 192 m). The sampling resulted in 33 camelthorn trees with weaver nests paired with 33 control camelthorns without a weaver nest. Similarly, 28 shepherd trees with a sociable weaver nest and 28 paired control trees without a nest. Camelthorn and shepherd trees comprise 96% of the trees that host sociable weaver nests in the study area (Olubodun *et al*. 2023). I measured the diameter at breast height (DBH) with a tape measure and the heights of all 122 trees using a hypsometer (Nikon Forestry Pro, Nikon Vision Co., Ltd, Tokyo, Japan). Sociable weaver nests exist as a collection of individual chambers; the number of nesting chambers per colony was counted. The number of chambers is a good proxy for the colony size and the number of individual sociable weavers (Leighton & Echeverri 2014).

Field measurements

I measured the leaf area index (LAI) of all nest and control trees using the gap fraction method with a CI-110 digital canopy imager (CID Bio-Sciences, Washington, USA). I also measured the nest and canopy area of each nest tree by photographing the nest trees from a distance (10 m – 20 m), allowing a full view of the entire tree. Images were taken at a height that allowed lateral mid-canopy views of the tree by mounting a camera on a tall monopod. I included a 1-meter pole and a 297 x 210 mm white card (A4 paper) in the frame of each image to serve as a scale of measurement among the images.

To measure the area of the tree canopy in pixels, I used the magic wand selection tool of Adobe Photoshop CS5 Extended software (Adobe Systems Incorporated, Version 12.0) to select the area covered by the entire tree canopy in the image and the corresponding area in pixels given by the histogram output in the software. A similar procedure was followed to calculate the areas of the nest and the white card in pixels and scaled to the area of the card (0.062 m^2).

I counted the number of living and dead primary branches (primary branch here refers to the branch that grows directly on the main stem) per tree to assess the condition and fall of branches from both nest and control trees. I also evaluated the extent of branch fall by counting the number of fallen branches (twigs less than 5cm in diameter were not counted as fallen branches) and measured the diameter of fallen branches per tree. Further measurements were carried out only in nest trees to quantify the degree of nest-branch survival. I counted the number of dead (dry wood with no leaves) and living nest branches in the 61 selected trees. I also counted the number of terminal branches alive or dead on each nest branch. I recorded all nest branch fall at the end of the rainy season for three years (2019, 2020, and 2021). I used these data to determine the factors that contribute to the fall or survival of the nest branch. To assess tree mortality, I assessed individual nest trees in 2021 to document the death of part or all of the tree. Death of a branch or tree was defined as the loss of leaves on the branch or entire tree coupled with dried terminal and main branches.

I sampled the terminal shoots of the current year (10 – 20 cm long, usually light-coloured, tender and smaller in size) from the north, south, west, and east axes of each of the 122 selected nest and control trees. For the nest trees, the terminal branches sampled did not host the sociable weaver nest. However, I expected that the branch that hosted the nest would have a higher cost than other branches on the same nest tree that did not host the nest. Therefore, to determine the possible effect of nest cover on the biomass of the leaf and terminal shoots of the nest branches, I sampled the terminal shoots from the current year growth indicated by the seasonal intercalation on the stem or changes in the stem colour (10 – 20 cm) at the tip of the branches that hosted the nest (referred to as 'nest branch' hereafter). Therefore, there were three categories of the branch (termed ‘branch type’ below): nest branch (the branch that hosted the nest), control branch in nest tree (those not host the nest), and control branch in control tree (branches in the tree without a nest). I weighed each terminal shoot, stripped the leaves, measured the length and the diameter and weighed the leaves from the four sampling points of each tree. The diameter (D) was measured at the base of each current-year terminal shoot with digital callipers. I calculated the cross-sectional areas of the current year terminal shoots from the diameter using the formula; (CSA) CSA = $\pi D^2/4$ (Sone *et al*. 2005). The leaves of each branch type were pooled and oven dried at 70 ^{o}C to constant weight for the analysis of the nutrients and isotopes.

Analysis of leaf nutrients and isotopes

The oven-dried leaves of camelthorn and shepherd trees were crushed in a mortar and pestle and then milled to powder using a ball mill (MM200, Retsch, Germany). The powdered leaf samples were placed in XRF sample cups sealed with a 4 µm Polypropylene thin film (Chemplex Industries Inc, Florida, USA) at the bottom. They were then inserted into an Energy Dispersive benchtop X-Ray Fluorescence (EDXRF) Spectro Xepos spectrometer (Spectro, Amatek materials analysis division, Kleve, Germany). The analysis was controlled by a computer data acquisition system using a specialized software program Spectro X-Lab Pro which incorporates the TurboQuant software for automatic matrix effect correction. The instrument was calibrated using a certified standard GBW07312 (National Research Centre for Certified Reference Materials, Beijing, China), for which elemental concentrations were obtained from the NOAA Technical Memorandum NOS ORCA 68 (1992). The elements of interest to this study were P, K, Ca, and Zn, as these minerals were recorded in higher concentrations in the faecal matter of the sociable weaver (Prayag *et al*. 2020) and the soils under the selected trees (Aikins *et al*. 2023).

The analyses of C, N, $\delta^{15}N$, and $\delta^{13}C$ were performed using a mass spectrometer. The oven-dried and milled leaves of the shepherd and camelthorn trees were weighed into tin capsules (Elemental Microanalysis Ltd, Devon, UK). These were then combusted in a Flash 2000 organic elemental analyzer (Thermo Scientific, Bremen, Germany) and the gases were passed to a Delta V Plus isotope ratio mass spectrometer (IRMS) via a Conflo IV gas control unit (Thermo Scientific, Bremen, Germany). Results were calibrated using two in-house standards and one IAEA standard.

Data analysis

I performed a linear mixed model analysis in R with the nlme package (Pinheiro *et al*. 2022). Data were checked for normality (qqnorm plots) and homogeneity (using the Breusch-Pagan Test from the lmtest package; Breusch and Pagan 1979) of the variances, and I used the appropriate variance functions: model = lme (Y ~ X, random=~1|S, data=df, weights=varIdent(form=~1|X), method = “REML”) to address the issues of heteroscedasticity. I tested leaf nutrients, leaf biomass, and terminal shoot biomass as response variables. I used the 'branch type' and tree species (i.e., camelthorn and shepherd trees) as fixed factors and their interaction in the models. The interaction term determines whether the nest impacts the two species of trees differently. A measure of tree size was also included as a fixed effect to control for differences in tree size. The interaction term was removed in all models if they did not explain significant variation ($p > 0.05$). I included 'tree pair identity' (nest tree and control tree numbers) as a random effect. I used the 'Anova' function to test whether the model terms explain a significant proportion of the variation in the data. Where significant variation was found, it was followed by pairwise comparison (Tukey's post-hoc test) of the group levels conducted using the emmeans package (Lenth 2019) in R. A similar analysis was used to analyse each tree species independently for the branch type effect and each branch type independently for the species effect. I also used the same analysis to compare the canopy area, nest area, branch fall, diameter of fallen branches, leaf area index, proportion of dead to living main stem and living and dead terminal branches between tree species.

To evaluate the relationships between nest branch outcome (i.e., fall or survive) and nest tree characteristics, I ran a generalized linear model (GLM) with binomial distribution using the logit link function in R. Firstly, I assessed tree species as an explanatory variable affecting the occurrence probability of nest branch outcome as response variables. Secondly, we tested nest tree characteristics (number of nest chambers, diameter of the base of the main nest branch, diameter of the tip of the main nest branch, percentage dead terminal nest branch, and percentage cover of the nest area cover), as an explanatory variable in predicting the occurrence probability of nest branch outcome. Model plots were made using the *visreg* R package (Breheny & Burchett 2017).

Results

Characteristics of the study system

Despite selecting similarly-sized trees in an area of 200 m radius from focal nest trees, camelthorn nest trees were significantly larger (mean DBH, $\chi^2 = 14.33$, $p < 0.001$) and taller ($\chi^2 = 28.57$, $p < 0.001$) than camelthorn control trees (Table 4.1). For shepherd trees, there were no differences in DBH between nest trees and control trees, but the nest trees were taller than the control trees (Table 4.1). The nests in camelthorn trees had more nest chambers than the nests in shepherd trees ($t = 5.76$, $p < 0.001$) and more chambers per DBH (2.23 vs 1.29 per cm).

Table 4.1: Characteristics of trees with and without sociable weaver nests selected for the study. The range, mean and standard error (SE) of diameter at breast height (DBH), height, and the number of nest chambers are provided. Different letters associated with mean values in columns indicate significant differences ($P < 0.05$) between values for the specific measures as determined by the Tukey post-hoc test (DBH and height) and the Student's t-test (nest chambers).

Tree species	**DBH (cm)**		**Height (m)**		**Nest Chambers**	
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Camelthorn						
Nest tree (n = 33)	42 ± 1.9^b	14–70	5.72 ± 0.23^c	2.8–8.6	94 ± 7^b	12–189
Control tree (n = 33)	35 ± 1.3^a	22–50	4.96 ± 0.20^b	3.2–7.4		
Shepherd						
Nest tree (n = 28)	34 ± 1.2^a	23–52	4.81 ± 0.16^b	4.0–7.0	44 ± 4^a	7–93
Control tree (n = 28)	31 ± 1.6^a	21–56	4.26 ± 0.13^a	3.0–6.0		

Plant Nutrition

There was a significantly higher foliar N in the camelthorn control branch in control trees than in the shepherd control branch in control trees. Foliar N was significantly higher in the shepherd nest branch than in the control branch in control trees but not higher than in the control branch in nest trees (Figure 4.2, Table S4.1). The interaction between tree species and branch types explains the variation in foliar $\delta^{15}N$. The nest branch and control branch in nest trees of both tree species had a higher $\delta^{15}N$ than their control branch in control trees. Foliar P was higher in camelthorn than in shepherd tree species. Foliar P was significantly higher in the nest branches of both species of trees than in their respective control branches in nest trees and control branches in control trees. There was significantly higher foliar K in shepherd than in camelthorn control branches in nest trees and control branches in control trees. The foliar K of camelthorns varied between branch types, with a higher concentration in the nest branch than its control branch in nest trees and the control branch in control trees. However, foliar K in shepherd did not vary between branch types (Figure 4.3, Table S4.1). Foliar Ca was higher in shepherd than in camelthorn tree species. Foliar Ca in shepherd trees varied between branch types, with higher foliar Ca in nest branches than in control branches in nest trees but not control branches in control trees. In camelthorn trees, the foliar Ca did not vary between the branch types. Foliar Zn did not, however, vary with tree species or branch types (Figure 4.3, Table S4.1).

Foliar C:N and Zn:P ratios were higher for the camelthorn and shepherd control branch in control trees than for the nest branch but not the control branch in nest trees (Table 4.2, Table S4.1). There was no difference between the control branch in nest trees and the nest branch for these ratios (Table 4.2, Table S4.1). The foliar N:P ratio was higher in the control branch in control trees and the control branch in nest trees than in the nest branch of both tree species. There was, however, no difference in K:P and Ca:P ratios between branch types of both tree species. The foliar N:P, K:P, and Ca:P ratios were higher in shepherd trees than in camelthorn trees.

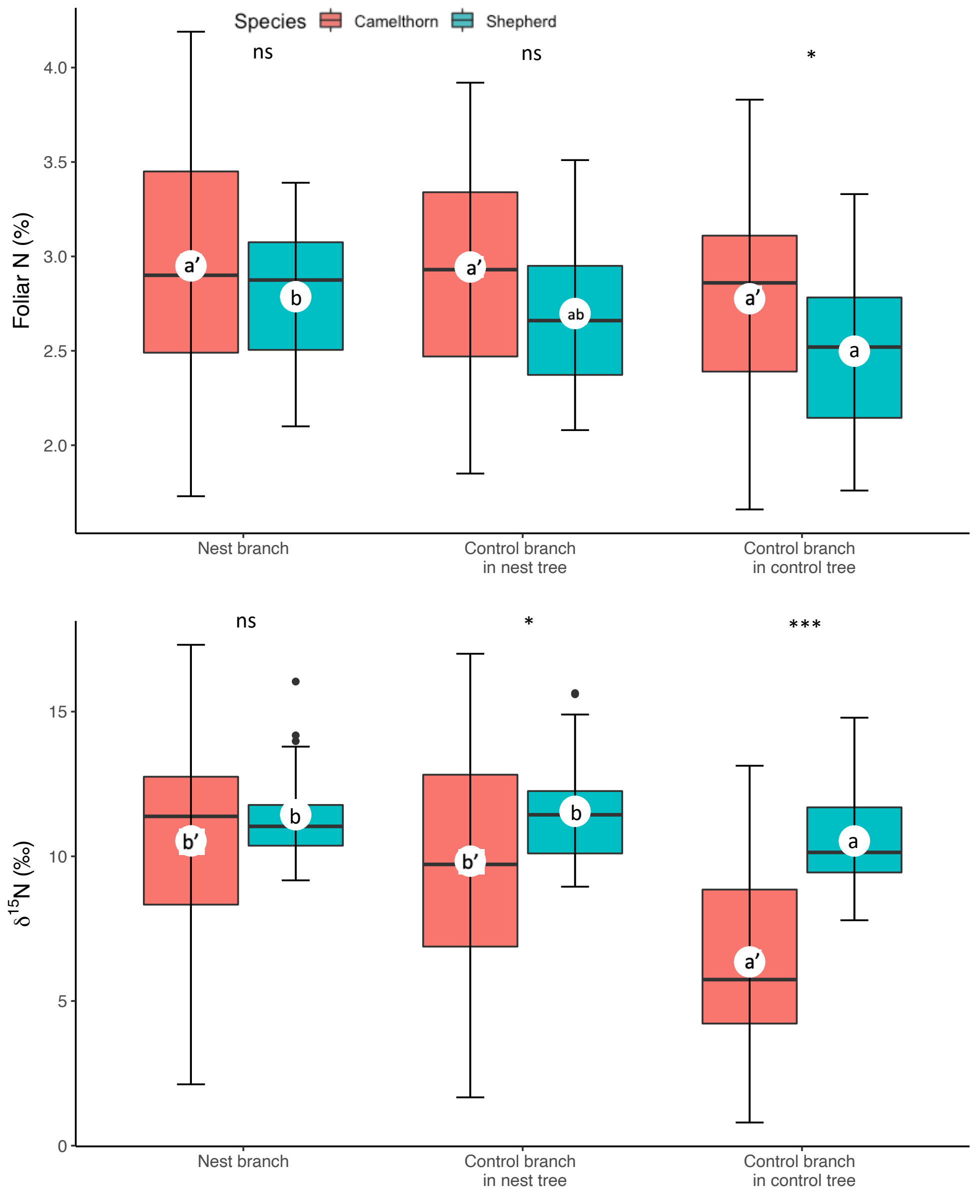

Figure 4.2: Foliar nitrogen and isotope (N and δ^{15}N) per branch type for camelthorn and shepherd trees. Circles represent the mean, and the boxes and horizontal lines represent the first and third quartiles and the medians, respectively. The whiskers represent 1.5 × the interquartile range. Outliers above/below are shown as dark points. Each species was analyzed independently for branch type effect using Tukey's post-hoc test. Letters indicate statistical differences based on Tukey's post hoc test, and error bars represent the standard error (SE). Each branch type was also analyzed independently for species effect using Tukey's post-hoc test with significant and non-significant species comparisons for each site denoted by * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ and 'ns', respectively.

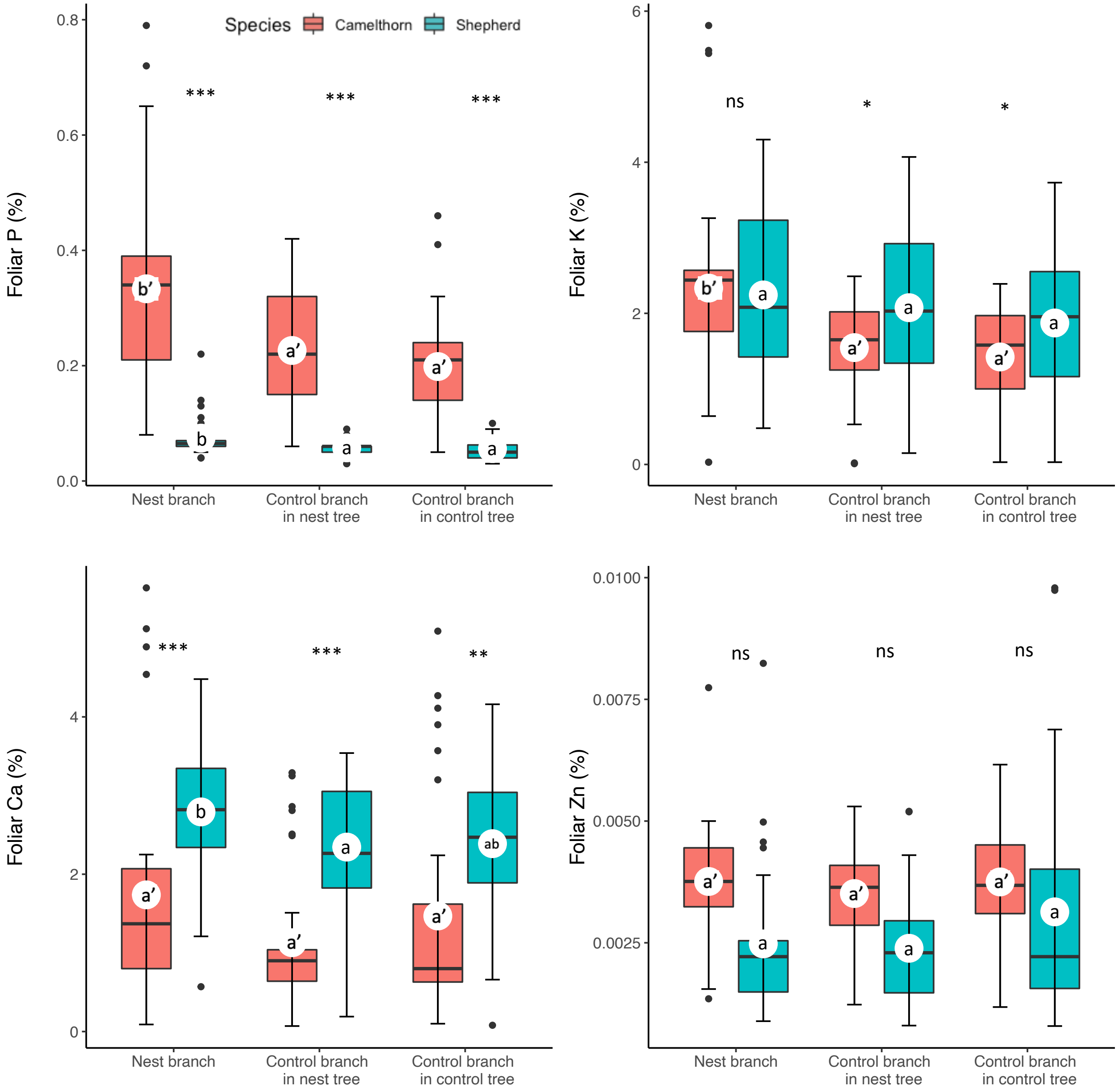

Figure 4.3: Mean foliar minerals (P, K, Ca, and Zn) per branch type for camelthorn and shepherd trees. Circles represent the mean, and the boxes and horizontal lines represent the first and third quartiles and the medians, respectively. See other figure details in figure 4.2.

Table 4.2: Foliar nutrient stoichiometry (g/g) of a mature camelthorn and shepherd tree from the nest branch, the control branch in the nest trees, and the control branch in the control trees. The mean ± SE is reported for each branch type and the nutrient stoichiometries. Means with the same letters in columns did not differ significantly after a Tukey post-hoc test.

Branch type	**Foliar nutrient stoichiometries (mean ± SE)**				
	C:N ratio	N:P ratio	K:P ratio	Ca:P ratio	Zn:P ratio
Camelthorn					
Nest branch (n= 33)	15.9 ± 0.74^{ab}	11.6 ± 1.63^{a}	6.71 ± 1.93^{a}	8.87 ± 2.93^{a}	0.014 ± 0.003^{a}
Control branch in nest tree (n= 33)	17.0 ± 0.50^{abc}	17.1 ± 1.63^{b}	8.10 ± 1.93^{a}	8.51 ± 2.93^{a}	0.018 ± 0.003^{ab}
Control branch in control tree (n= 33)	18.3 ± 0.59^{c}	17.5 ± 1.63^{b}	7.34 ± 1.93^{a}	13.70 ± 2.93^{a}	0.029 ± 0.005^{bc}
Shepherd					
Nest branch (n= 28)	15.2 ± 0.77^{a}	42.4 ± 1.72^{c}	34.27 ± 2.05^{b}	43.40 ± 3.10^{b}	0.039 ± 0.003^{c}
Control branch in nest tree (n= 28)	16.4 ± 0.53^{abc}	47.9 ± 1.72^{d}	35.66 ± 2.05^{b}	43.04 ± 3.10^{b}	0.042 ± 0.003^{cd}
Control branch in control tree (n= 28)	17.7 ± 0.62^{bc}	48.2 ± 1.72^{d}	34.90 ± 2.05^{b}	48.23 ± 3.10^{b}	0.054 ± 0.005^{d}

Leaf biomass

There was significantly lower leaf weight per branch length in the nest branch than in the control branches of both the nest and the control trees (Figure 4.4A), but the control branch in the nest trees did not differ from the control branch in the control trees. Leaf weight per branch cross-sectional area was significantly higher in shepherd control trees than in camelthorn control trees (Figure 4.4B). Branch weight per branch length was, however, significantly higher in camelthorn than in shepherd trees (Figure 4.4C). Leaf weight per branch cross-sectional area, branch weight per branch length and cross-sectional area, and leaf moisture as a percentage of dry weight did not vary between the branch types.

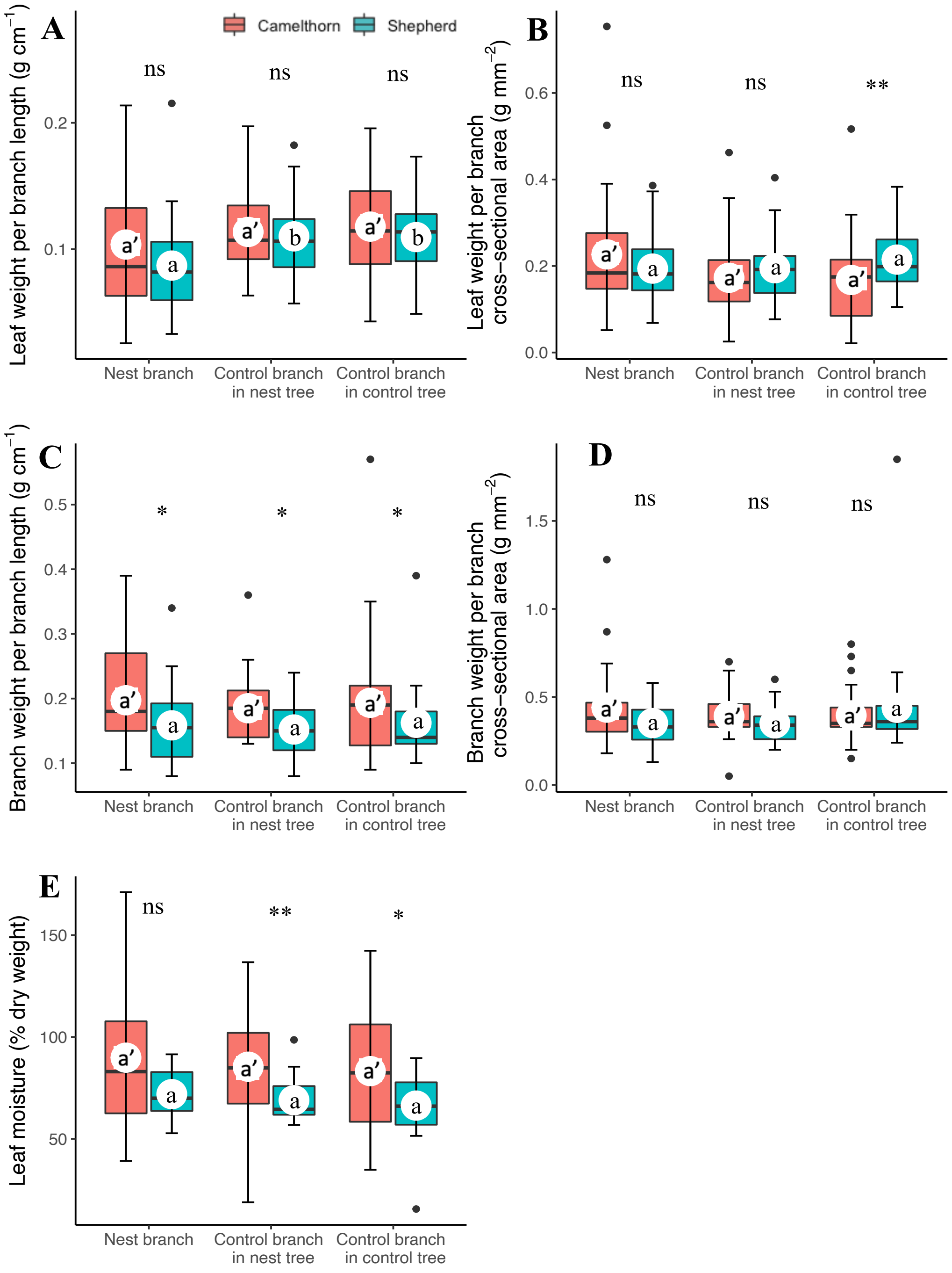

Figure 4.4: Mean leaf weight per branch length and cross-sectional area, branch weight per branch length and cross-sectional area, and leaf moisture as a percentage of dry weight. Circles represent the mean, and the boxes and horizontal lines represent the first and third quartiles and the medians, respectively. See other figure details in figure 4.2.

Nest cover

Camelthorn nest trees have significantly larger tree canopy areas (1.4-fold) and nest areas (1.6-fold) than shepherd nest trees (Table 4.3). Although camelthorn trees have significantly larger nests than shepherd trees, the percentage of total canopy area cover lost to the nest did not vary between these tree species (Table 4.3), with approximately 30% of the nest tree canopies of both tree species lost due to the sociable weaver nest.

Table 4.3: Tree canopy and nest area of the tree selected in this study. The mean, standard error (SE) and range are provided. Different letters associated with mean values in columns indicate significant differences between species ($P < 0.05$) as determined by the linear mixed model.

Tree species	**Canopy Area (m^2)**		**Nest Area (m^2)**		**% Nest Cover**	
	Mean ±SE	Range	Mean ±SE	Range	Mean ±SE	Range
Camelthorn **(n=33)**	16.4±1.06^b	6.3-32	4.9±0.37^b	1.70-8.6	31±2.3^a	10.4-64
Shepherd (**n=*28*)**	11.7±0.94^a	3.9-29	3.0±0.25^a	0.87-5.9	29±3.2^a	9.4-75
	χ^2 = 10.6 **p = 0.001**		χ^2 = 15.7 **p <0.001**		χ^2 = 0.29 p = 0.590	

Branch fall and leaf area index

The number of fallen branches varied significantly with the interaction between the tree species and tree type (Table S4.3). Shepherd nest trees had a significantly higher number of fallen branches than shepherd control trees and also camelthorn nest and control trees (Figure 4.5A). There were, however, no significant differences in the number of fallen branches in camelthorn nest and control trees. There was a significantly larger diameter of fallen branches in nest trees than in control trees of both tree species (Figure 4.5B). This variation did not vary with tree species. The leaf area index did not vary with tree species and type (Figure 4.5C). The presence of a nest in trees did not significantly affect the proportion of dead to the living main branch of camelthorn and shepherd trees (Figure 4.5D).

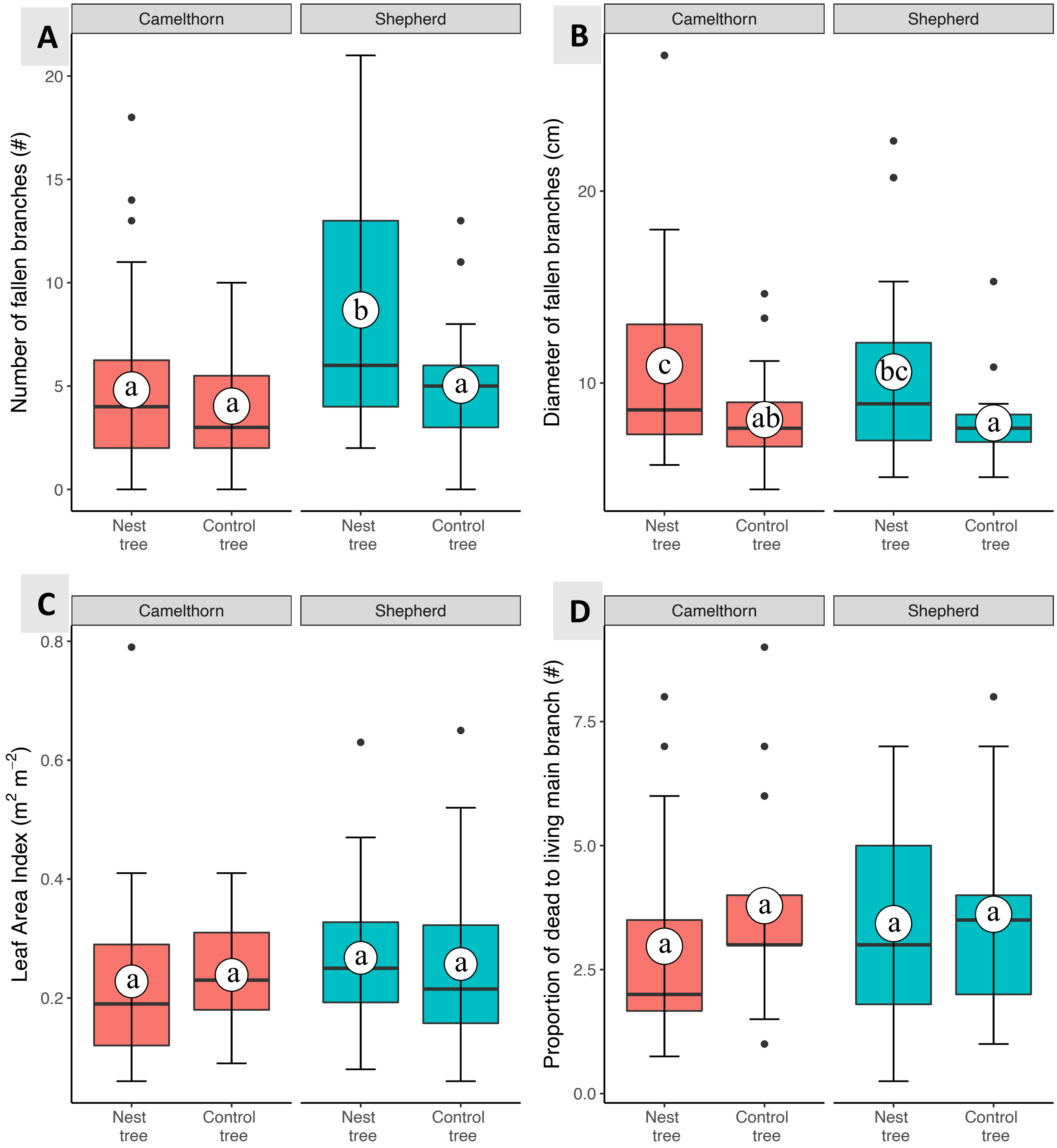

Figure 4.5: Number and diameter of fallen branches, leaf area index, and proportion of dead to living main branch under both nest trees and trees for camelthorn and shepherd trees. Circles represent the mean, and letters indicate a Tukey's pairwise comparison between species and sites. The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. Whiskers represent 1.5 × the interquartile range. Outliers above/below are shown as dark points.

Nest branch mortality

For camelthorn trees, 88% of the main nest branches were alive, with about 12% dead, while none of the shepherd tree's main nest branches was dead. There was a significantly higher number (1.59-fold) of dead terminal nest branches on camelthorn nest trees than on shepherd nest trees (Table 4.4). The percentage of dead terminal branches to living terminal branches was significantly higher in camelthorn nest trees than in shepherd nest trees (Table 4.4). The ratio of living to dead terminal branches in camelthorn nest trees was 3:1, while shepherd nest trees had a ratio of 4:1.

Table 4.4: Living and dead terminal nest branches of camelthorn and shepherd nest trees. The mean, standard error (SE), and range of living and dead terminal branches are provided. Different letters associated with mean values in columns indicate significant differences ($P < 0.05$) as determined by the linear mixed model.

Tree species	**Living terminal nest branch**		**Dead terminal nest branch**		**% of dead terminal nest branch**	
	Mean ±SE	Range	Mean ±SE	Range	Mean ±SE	Range
Camelthorn (n=33)	8.6 ± 0.82^a	0-18	6.5 ± 0.66^b	0-15	46 ± 4.1^b	17-100
Shepherd (n=28)	11.9 ± 2.24^a	2-47	4.1 ± 0.59^a	0-10	31 ± 3.6^a	9-75
	$\chi^2 = 2.258$		$\chi^2 = 7.450$		$\chi^2 = 8.073$	
	$p = 0.133$		**$p = 0.006$**		**$p = 0.004$**	

Predicting nest branch fall

The assessment of the nest branch fall shows that nest branch fall varied significantly with tree species ($\chi^2 = 5.72$, $p = 0.017$; Figure 4.6A). There was a significantly higher nest branch fall in the camelthorn nest trees (36%) than in the shepherd nest trees (11%). The probability of a nest branch fall was higher in camelthorn trees and lower in shepherd trees. I also found that the percentage of dead terminal nest branches significantly predicted the probability of the nest branch fall in camelthorn trees ($\chi^2 = 5.49$, p-value = 0.019; Figure 4.6B).

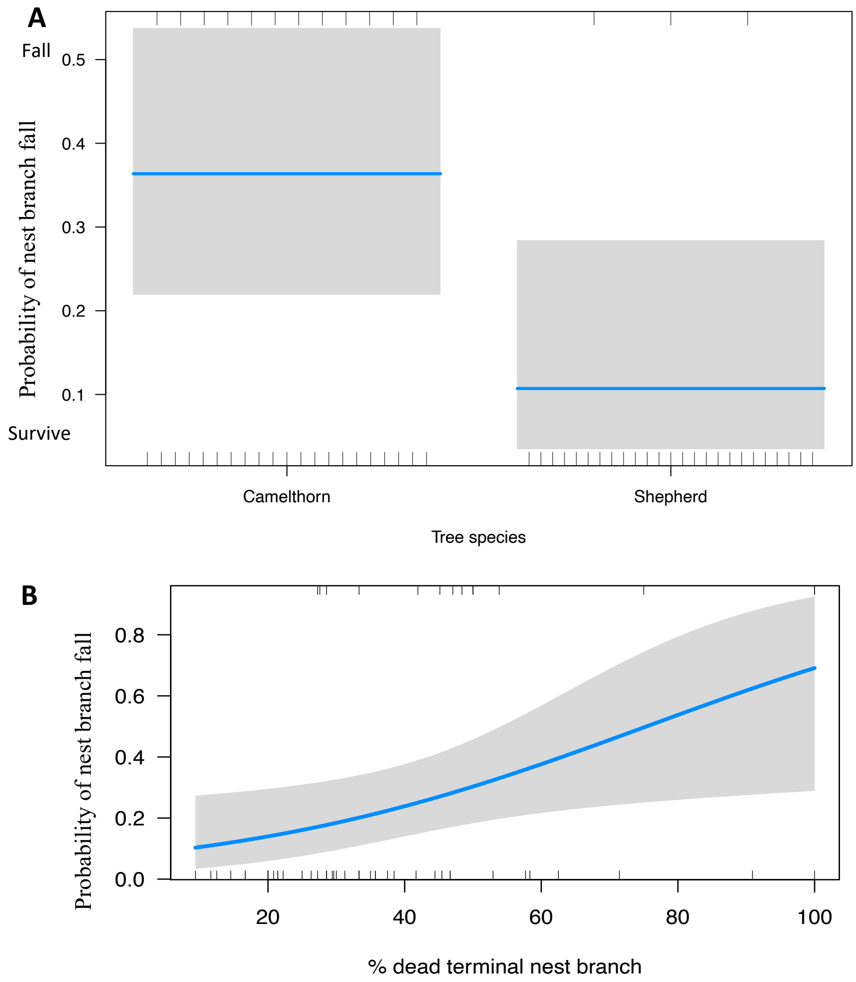

Figure 4.6: Effects of tree species (X-axis) on the occurrence probability of nest branch fall (Y-axis) in sociable weaver colony trees (Figure 4.6A). Effects of % dead terminal nest branch (X-axis) on the occurrence probability of nest branch fall (Y-axis) in sociable weaver colony trees (Figure 4.6B). Observations along the x-axis are indicated by the vertical rug lines while the dark band along the blue line indicates a 95% confidence interval. The blue line is the prediction line.

Mortality of host trees

I found that tree mortality was significantly higher in nest trees than in trees without a nest ($\chi^2 = 36.08$, $p < 0.001$; Figure 4.7). There was approximately 4-fold higher tree mortality in camelthorn nest trees than camelthorn control trees. In shepherd trees, there was 11-fold higher tree mortality in nest trees than in control trees. Tree mortality did not vary significantly between camelthorn and shepherd trees ($\chi^2 = 2.79$, $p = 0.095$; Figure 4.7; Table S4.3).

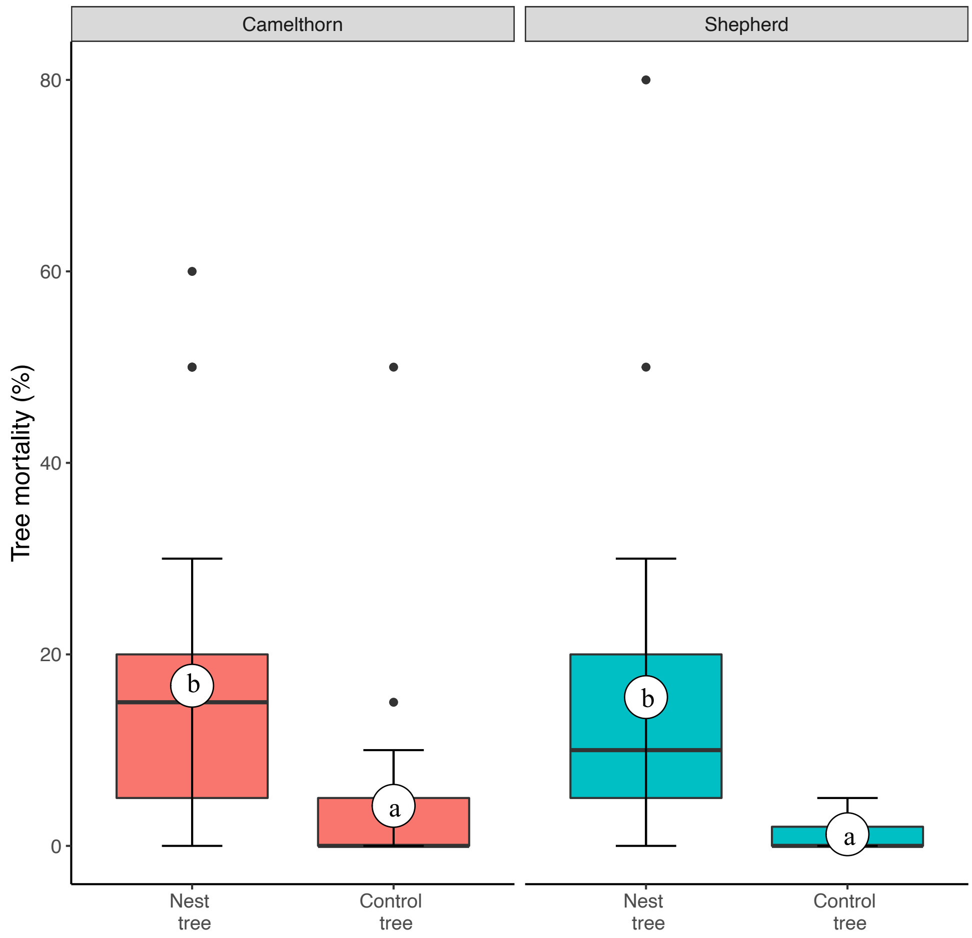

Figure 4.7: Tree mortality in nest and control trees of camelthorn and shepherd. The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. Whiskers represent 1.5 × the interquartile range. Circles represent the mean, and letters indicate a Tukey pairwise comparison between species and sites. Outliers above/below are shown as dark points.

Discussion

The benefits of the sociable weaver nest for host trees include high foliar N and Ca for shepherds, high foliar K for camelthorns, and higher P for both tree species. On the contrary, for shepherd trees, I found lower leaf weight per branch length for the nest branch than in the control branch in nest trees and the control branch in control trees. However, I did not find any difference in leaf weight per branch length of camelthorn trees. The costs identified include a reduction in the photosynthetic area of nest trees, significantly more branch fall (only in shepherd trees) and larger branch fall in nest trees and high dead terminal nest branches. I also found that tree mortality was higher for nest trees than for control trees.

The benefits of hosting a weaver nest for the trees are largely restricted to potential gains in nutrient availability. One of the main nutrients that might play a role is N since the weaver faeces are rich in N (Prayag *et al*. 2020) and N is a scarce resource in this sandy environment (Aikins *et al*. 2023). The higher foliar N in the nest branches and nest trees than the control trees in shepherd trees could be attributed to the high faecal deposition by the sociable weavers under the host trees. The high $\delta^{15}N$ in nest branches in nest trees and control branches in nest trees suggest assimilation of faunal-derived N, since the $\delta^{15}N$ in sociable weaver-enriched soils (Prayag *et al*. 2020; Aikins *et al*. 2023) had similarly high values. Additionally, the lower foliar $\delta^{15}N$ values in camelthorn tree species than in shepherd tree species may indicate N_2 fixation by the camelthorn trees.

The nutritional benefits of hosting the sociable weaver nest included higher foliar P, K, and Ca in the nest branch than in the control branch in the nest trees and in the control branch in the control trees. This could be due to roots that support the nest branch growing in the direction of the branch carrying the nest, and accessing more nutrients from the sociable weaver faecal matter deposited under the nest. Smethurst (2004) found that the rate of uptake of soil nutrients depends on the concentration in the soil solution immediately adjacent to the root. The higher foliar P, K, and Ca also suggest that the fewer terminal leaves on the nest branch in nest trees undergo more photosynthesis to support the whole branch covered by the nest and consequently have higher elemental concentrations. This is explained by the findings of Glanz-Idan *et al*. (2019), who found photosynthetic rate upregulated in partial defoliation or shading, and during this process, mineral nutrition, especially P and K, plays an important role (Jakli *et al*. 2017; Jin *et al*. 2015). Differences in foliar nutrients in branch types could also be explained by the concept of branch autonomy, which suggests that branches operate independently of neighbouring branches driven mainly by environmental factors (Sprugel *et al*. 1991), like soil nutrients. The higher foliar P in camelthorn than in shepherd trees could also be attributed to N_2 fixation, as leguminous plants are highly efficient in P acquisition due to their cluster root system (Lambers *et al*. 2006; Lambers *et al*. 2013). Ribet and Drevon (1996) reported high P efficiency in *Acacia mangium*. The high N:P ratio in camelthorn and shepherd control branch in nest tree and control branch in control tree than in nest branch could indicate an increased limitation by P relative to N. The astonishingly high N:P ratios in shepherd trees compared to those in camelthorn show a massive environmental signal due to limited P in that context.

The costs in sociable weaver-host tree interactions are diverse. I found significantly lower leaf weight per branch length in the nest branch, which I attributed to the loss of photosynthetic area caused by the nest cover; hence the terminal branches on the nest branch produce fewer leaves. Shading has been reported to decrease leaf thickness, dry matter content and mass per unit area (Yang *et al*. 2019). The difference in leaf thickness and size between camelthorn and shepherd tree leaves, as observed in the field, may explain why shepherd trees have a higher leaf weight per branch diameter in the control branch in control trees. Leaf thickness has been reported to determine leaf mass per area (Poorter *et al*. 2010; Ye *et al*. 2020).

There was also a high cost of loss of photosynthetic area in nest trees. The nest trees lost a mean of about 30% of their canopy area to the sociable weaver nest, implying fewer leaves involved in photosynthesis which could affect the productivity of these trees. Although there are larger nests on camelthorn trees, the sociable weavers only build their nests to cover the same percentage of the tree canopy, irrespective of the tree species. The area of the tree canopy covered by the nest depends on the sociable weaver population; therefore, larger colonies occupy more canopy area, resulting in more cost in terms of loss of photosynthetic area. Aizen *et al*. (2014) reported that the higher population of a partner in a mutualism than the host's carrying capacity could result in more cost to the host. Several authors have also reported the effect of colonial birds on host trees (Hobara *et al*. 2001; Hebert *et al*. 2005; Veum *et al*. 2019).

Branch fall is a significant carbon, productivity, reproductive and nutritional cost to trees, and I found more branch fall in shepherd nest trees than in control trees, and larger branch falls in nest trees than in trees without a nest in both tree species. The branch fall could be due to the nest covering the canopy area resulting in the death of terminal branches and subsequently leading to branch fall. Furthermore, the weight of the nest, especially when wet, could cause the living branches to break. In our field trial, we found that the weight of the nest could double when soaked by rainfall. Apart from branch fall, there was a high cost in terms of significantly more dead terminal branches on camelthorn nest trees than on shepherd nest trees. This could be attributed to the tree's architecture. The branching architecture of camelthorn trees attracts sociable weavers to build their nests on a selected secondary branch. However, in shepherd trees, the secondary branches are not large enough to support a nest; hence they build in several primary branches, which becomes less vulnerable to complete takeover by the nest.

Nest trees were more susceptible to mortality than trees without a nest, and this could be attributed to the large size of the sociable weaver nest, which covers most of the leaves and branches of the tree. I found a mean of 30% (up to 75%) of the tree canopy could be covered with nest materials. This reduces the photosynthetic area of the nest trees, implying less nutrient supply to support the branches. The long-term effect is the death of the terminal branches, the main branches, or the entire tree. With about 4-fold higher mortality in camelthorn nest trees than control trees and 11-fold higher mortality in shepherd nest trees than control trees, tree mortality is therefore more severe in nest than in control trees. Similar to our findings, colonial nesting birds have also been documented to damage trees through their branch breaking and leaf removal for nest construction (Hobara *et al*. 2001; Hebert *et al*. 2005), which subsequently leads to the death of host trees (Lafferty *et al*. 2016).

Conclusions

Our study shows that the occupation of camelthorn and shepherd trees by the sociable weavers leads to nutritional benefits due to the high faunal nutrient supply, which results in high foliar nutrients compared to trees without the sociable weaver nests. However, the presence of the nest exerts a severe cost on the host trees, mainly in terms of reduction in photosynthetic area, branch fall, death of terminal branches and high mortality of nest trees. I, therefore, cannot equate the nutritional benefits to the physical damage of the branch breaking, but cost-benefit evaluation requires analysis of the reproductive fitness consequences for the host trees. Investigating the reproductive benefits and costs to the host trees would give a better understanding of whether this interaction is more of a cost or benefit to the host trees.

Supplementary Materials

Table S4.1: Linear mixed model analysis with foliar nutrients and isotopes as response variables and branch types (3 levels- nest branch, control branch in nest tree, control branch in control tree) and tree species (2 levels- camelthorn and shepherd) as factors. We included pairs as a random effect. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis.

Response Variables	**Factors**	χ^2	**df**	**P-value**
N	Branch type	9.62	2	0.008
	Tree species	5.53	1	0.019
$\delta^{15}N$	Branch type* Tree species	16.95	1	< 0.001
P	Branch type	22.44	2	< 0.001
	Tree species	137	1	<0.001
K	Branch type	15.58	2	< 0.001
	Tree species	6.45	1	0.011
Ca	Branch e type	9.95	2	0.006
	Tree species	29.85	1	<0.001
Zn	Branch type	5.50	2	0.064
	Tree species	0.22	1	0.639
C:N	Branch type	10.73	2	0.005
	Tree species	1.09	1	0.296
N:P	Branch type	15.21	2	<0.001
	Tree species	255	1	<0.001
K:P	Branch type	0.63	2	0.730
	Tree species	128.82	1	<0.001
Ca:P	Branch type	4.04	2	0.133
	Tree species	94.53	1	<0.001
Zn:P	Branch type	11.28	2	0.004
	Tree species	42.39	1	<0.001

Table S4.2: Linear mixed model analysis with leaf biomass and moisture as response variables and branch types (3 levels- nest branch, control branch in nest tree, control branch in control tree) and tree species (2 levels- camelthorn and shepherd) as factors. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis. We included pairs as a random effect.

Response Variables	**Factors**	χ^2	**df**	**P-value**
Leaf weight per branch length	Branch type	14.95	2	< 0.001
	Tree species	1.12	1	0.290
Leaf weight per branch cross-sectional area	Branch type	2.29	2	0.319
	Tree species	2.194	1	0.139
Branch weight per branch length	Branch type	0.52	2	0.773
	Tree species	11.70	1	<0.001
Branch weight per branch cross-sectional area	Branch type	2.23	2	0.328
	Tree species	2.91	1	0.088
Leaf moisture (% of dry weight)	Branch type	3.72	2	0.156
	Tree species	14.07	1	<0.001

Table S4.3: Linear mixed model analysis with the number of fallen branches, the diameter of fallen branches, leaf area index and tree mortality as response variables and tree types (2 levels- Nest tree, Control tree) and tree species (2 levels- camelthorn and shepherd) as factors. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis. We included pairs as a random effect.

Response Variables	**Factors**	χ^2	**df**	**P-value**
Number of fallen branches (#)	Tree type * Tree species	5.77	1	0.016
Diameter of fallen branches (cm)	Tree type	18.36	1	< 0.001
	Tree species	0.44	1	0.509
Leaf Area Index	Tree type	0.003	1	0.958
	Tree species	1.69	1	0.194
Proportion of dead to living main branches	Tree type	1.574	1	0.210
	Tree species	0.057	1	0.811
Tree mortality (%)	Tree type	36.08	1	<0.001
	Tree species	2.79	1	0.095

Chapter 5: Reproductive consequences for savanna trees hosting large sociable weaver colonial nests

Abstract

Changes in soil conditions affect the reproduction of trees, but research investigating the consequences of ecosystem changes often does not consider the reproductive ecology of trees. Given the alteration of soil properties and complex growth costs and benefits to the trees hosting sociable weaver nests, a better understanding of how this interaction impacts the reproduction of the host trees is essential to understand the nature of this interaction and to inform conservation decisions. This study tests the hypothesis that the greater supply of nutrients to camelthorn trees that host sociable weaver nests would increase the quantity and quality of seeds relative to trees without nests, which should also positively influence seed germination and emergence. Furthermore, I test the hypothesis that the presence of sociable weaver nests that attract animal activity might also attract beetles that may damage the seeds. I evaluated pod weight, number of seeds per pod, seed weight, beetle infestation, seed nutrients, seed germination, and the emergence of camelthorn trees hosting nests and camelthorn trees without nests. There was no difference in seed pod weight, number of seeds per pod and seed weight between trees with and without a sociable weaver colony. However, there was a high probability of seed beetle infestation in nest trees than in trees without nests. The concentrations of K and Cu in seeds were higher in the trees without nest than in trees with nest, while the concentration of seed Bo was higher in the nest trees than in the trees without nest. These differences in seed nutrition did not drive significant differences in seed germination and emergence. However, there was a significantly shorter germination time in seeds infested with beetles than in seeds without beetle infestation, but beetle-infested seeds had significantly lower percentages of seed germination and emergence. Seed

quality, germination and emergence did not substantially differ between trees with and without sociable weaver nest. There is therefore no substantial difference in the costs and benefits of hosting a sociable weaver nest in terms of tree reproduction.

Introduction

In many environments, the nature of the physical environment limits plant reproduction (Lambers *et al.* 2008; Fernández-Marín *et al.* 2020). Some species can facilitate the growth of other species by improving their environment (Brooker *et al*. 2008; Gross *et al*. 2013; Schöb *et al*. 2013), and these facilitative interactions can ameliorate environmental conditions, which play a significant role in the growth and presence of plant communities in these extreme habitats (Callaway 1995; Callaway & Walker 1997; Brooker & Callaghan 1998; Cavieres & Badano 2009). Some studies have shown that facilitation occurs more and stronger in arid than in moist environment (Callaway & Walker 1997; Sthultz *et al*. 2007; Tylianakis *et al*. 2008).

In facilitative interactions between species where both benefit, costs may still be involved. Biotic interactions like seed dispersal (Cantor *et al*. 2013), pollination (Dupont *et al*. 2014; Tur *et al*. 2014; Valverde *et al*. 2015), and ant-plant interactions (Dáttilo *et al*. 2014) involve mutualistic partners and hence both parties benefit. However, in interactions which involve partly antagonistic partners, the outcome of the mutualistic interaction could be altered (McCall & Irwin 2006; Thompson & Fernandez 2006). For example, yucca moths decrease the viable seed production of yuccas by 0.6 to 19.5% through oviposition and feeding, leading to a loss of up to 30% of the benefits yuccas derive from interaction (Addicott 1986). Therefore, facilitative interactions involve costs and benefits.

Interactions between plants and birds, including pollination, seed dispersal, and the associated reproductive benefits, have received much attention (Richardson *et al.* 2000; Bascompte & Jordano 2014). About 50% to 90% of plants in the tropical forest produce seeds that are required to pass through the guts of animals, especially birds, before they can germinate (Howe & Smallwood 1982); therefore, many plant-bird interactions function to disperse seeds (Marjakangas *et al*. 2019). This mutuality between plants and birds is crucial to sustaining ecological functions within the plant community (Whelan *et al*. 2008; Schleuning *et al*. 2015). However, interactions between plants and birds are not always mutually beneficial. For example, Natusch *et al*. (2017) found that although colonially breeding metallic starlings increase soil fertility below host trees, trees hosting these birds die in the long-term from possible nutrient toxicity. Similarly, nesting and roosting cormorant colonies defoliate host trees and kill mature trees from faecal 'whitewash' and the highly acidic nature of their faecal matter (Moore *et al*. 1995; Shieldcastle & Martin 1997). What is unclear from these studies is whether host trees benefit in the short-term from the nutrient influx provided by the birds. Indeed, breeding or roosting birds using trees as substrates for their colonies is common in many systems, yet the consequences to the host trees are seldom investigated. While some structural damage to the host trees could be expected, any positive reproductive consequences from increased nutrient input, especially in nutrient-poor (oligotrophic) arid systems, remain unstudied. Understanding these interactions at the individual plant level is crucial to clarify such interactions' reproductive costs and benefits.

I studied reproductive investment in terms of costs and benefits for camelthorn trees *Vachellia erioloba* that host a sociable weaver *Philetairus socius* nest colony. My study system occurs in the Kalahari, an oligotrophic desert savanna where the input of faunal nutrients may positively impact the host trees. Indeed, previous studies have shown that trees hosting sociable weaver colonies use the nutrients deposited by birds, increasing the growth of host trees (Prayag *et al*. 2022, Chapter 3). However, the large size of the nest colonies reduces the host tree's photosynthetic area, and their high mass causes branch fall (Chapter 4). Camelthorn trees are threatened and are a protected species due to their important role in the ecosystem (Seymour and Milton 2003). They are considered key ecosystem engineers in the Kalahari (Dean *et al*. 1999). Similarly, the sociable weaver colonies are considered ecosystem engineers (Lowney & Thomson 2021, 2022). These nests serve as a resource and refuge for several organisms, including insects (Lowney & Thomson 2022). Beetles have been reported to infest camelthorn seeds (Seymour and Milton 2003), and the presence of the nest may provide suitable conditions for these beetles. The growth benefits and costs of this interaction with the host trees of sociable weavers have been documented (Chapter 4). However, our understanding of the reproductive fitness of host trees of the sociable weaver is limited, and research on this aspect would contribute to the conservation of host trees.

Most research on ecosystem changes often does not consider the reproductive ecology of trees, yet long-term changes in reproduction relate to trees' response to changing soil conditions (Richardson *et al*. 2005; Pérez-Ramos *et al*. 2010). High nitrogen fertilisation has been reported to increase tree growth, seed production, and seed size (Callahan *et al*. 2008; Smaill *et al*. 2011). Seed minerals have also been documented to significantly influence seed germination and emergence (Mandizvo & Odindo 2019). Naegle *et al*. (2005) found that the growth of seedlings in the first week is sustained by the amount of N stored in the seed. Furthermore, seed-stored phosphorus (P) is the only source for seed germination and emergence (Mandizvo & Odindo 2019). Molybdenum (Mo) is required for plant development and growth (Brodrick & Giller 1991; Brodrick *et al*. 1995), while Bo increases the production and retention of flowers and subsequently increases the development of seed and fruit as well as germination (Bell *et al*. 1989; Archana *et al*. 2021). Therefore, tree with access to nutrients should invest these into their seeds to enhance their reproductive output.

The lack of information on changes in host tree reproduction undermines our ability to predict the responses of host trees to the sociable weaver colonisation of trees. Given the complex growth costs and benefits to camelthorns as hosts of sociable weaver nests already established (Chapter 4), a better understanding of how this interaction impacts the reproduction of the host trees is crucial. This study represents a first attempt to empirically quantify the reproductive costs and benefits of the interaction between the sociable weaver and camelthorn host trees. I hypothesised that the higher nutrient supply to camelthorn trees hosting sociable weaver nests would increase the quantity and quality of pods and seeds. I predicted that camelthorn trees with a nest would have larger pods, higher seed weight, higher seed nutrients, higher germination and emergence percentage, and fast germination and emergence time than trees with no nest. I further hypothesised that the sociable weaver nest in camelthorn trees would attract beetles to damage the pods and seeds, decreasing the quality of the seeds produced. I predicted that camelthorn trees with sociable weaver nests would have greater seed damage; therefore, infested seeds would have poor germination and emergence.

Materials and Methods

Study Area

This study was carried out at Tswalu Kalahari, a reserve in the Northern Cape Province of South Africa (27.225° S, 22.478 ° E). The climate in this area is hot and arid, with an annual mean temperature of 20.3ºC, an annual mean maximum of 29.5º C and a minimum of 11.1º C (Cromhout 2006). Tswalu Kalahari experiences summer rainfall (generally December-March), which is highly variable, with a mean of 325 per annum (range 175 mm to 595 mm; van Rooyen & van Rooyen 2017). Tswalu Kalahari lies in the Desert biome of South Africa. The trees selected for this study were within the Koranna-Langeberg Mountain Bushveld and the Olifantshoek Plains Thornveld. The vegetation cover is mostly grasses and herbs, visible mainly after summer rainfall. The area has sparsely distributed trees, primarily camelthorn and shepherd trees. Shrubs such as *Senegalia mellifera* (blackthorn) and *Rhigozum trichotomum* (three thorn) grow in interspaces between trees. Camelthorns begin to flower in September and mature pods are visible on trees in February of the following year.

Study design

I used the same camelthorn trees selected in Chapter 3 (Aikins *et al*. 2023) for this study. This resulted in 33 camelthorn trees that contained sociable weaver nests (hereafter nest trees) out of about 190 camelthorn nest trees that have been mapped in the study area. I used the same control trees in chapter 3 (Aikins *et al*. 2023), which were chosen from camelthorn trees with similar height and DBH as each selected nest tree. Control trees were chosen in the proximity of nest trees (mean 78 m: range 16 m – 192 m). Matching selected trees by size and location aimed at limiting differences in the life stage and local conditions. My sampling resulted in 33 camelthorn trees with weaver nests paired with 33 control camelthorns without a weaver nest.

Pod and seed sampling

All 66 trees were visited in September/October 2021 to determine if they contained seed pods. If pods were present, I collected freshly dropped (mature) pods from the base to assess the variation in the pod and seed mass, seed numbers, and beetle infestation. When available, a maximum of 10 pods per tree were collected (range 1 – 10 pods per tree). I weighed each pod, counted the number of seeds per pod, weighed all the seeds in each pod together, and divided by the number of seeds per pod to obtain the average weight per seed. To obtain the average seed size per pod, I measured the size of 4 randomly selected seeds per pod. I examined each seed for beetle infestation, and the number of infested seeds per pod was recorded. Approximately 20 beetle-free seeds were randomly sampled, milled into powder, and analysed for nutrients. The remaining seeds from each tree were used for seed germination and emergence trials.

Analysis of seed nutrients

To assess the nutrient content of seeds from the nest and control trees, I obtained matured pods from 16 nest and 12 control trees between July and August 2022. The seeds were analysed for N, P, K, Ca, and Zn, as they were recorded in the faecal matter of the sociable weaver and the soils under trees (Prayag *et al*. 2020; Aikins *et al*. 2023). Other essential and trace minerals, including Mg, Na, Bo, Fe, Mn, Al, and Cu, were also analysed. All nutrient analyses were duplicated using the official methods of the Association of Official Agricultural Chemists (AOAC) (AOAC International 1997) and the methods of the Southern African Agricultural Laboratory Association (ALASA) (ALASA 1998). The samples were re-analysed when the duplicate results differed by 5% or more (CV >3.5%). Dry milled seeds were analysed for these minerals using an inductively coupled plasma analyser (Thermo Jarrel Ash Iris/AP HR Duo: Boston, Massachusetts). To analyse seed total N, the standard Kjeldahl method was used (ALASA 1998). Approximately 0.2 g were digested with 5 ml concentrated sulfuric acid and HgO catalyst in a Kjeldahl flask. The mixture was then distilled with 10 ml of 40% w/v sodium hydroxide and titrated to pH 4.7 with 0.01 N HCl with an auto-titrator (Rapidstill I, Labconco, Kansas City, MO, USA).

Seed germination trials

I conducted a germination and emergence test on seeds from sampled trees. From the 33 nest and 33 control camelthorn trees selected initial for the research, I obtained camelthorn pods from 16 nest and 12 control trees during July and August 2022. The seeds were extracted from the pods and the seeds infested with beetles were separated from each group. I scarified part of the seed coat of the nest and control beetle-free seeds with sandpaper to expose the cotyledon for easy water absorption. To determine the effect of beetle infestation on germination, beetle-infested seeds (only bruchid beetle-infested seeds) and seeds with no beetle infestation were germinated, but none of these two sets of seeds was scarified. In all, there were six seed sources/treatments; nest seed scarified (n = 16), control seed scarified (n = 12), nest seed beetle infested (n = 14), control seed beetle infested (n = 12), nest seed unscarified (n = 12), control seed unscarified (n = 12). The seeds were soaked in water for 24 hours. Subsequently, each set of seeds was transferred to a petri dish with cotton wool as substrate. The seeds were kept in the growth chamber for germination and emergence at 20 °C. The seeds were watered daily throughout the trial. When the cotton substrates became contaminated with fungi, the seeds were immediately removed and transferred into a new petri dish with a new substrate. Seeds producing a 2 mm radicle were scored as germinating (following Mavi 2010), and scoring was completed every 24 h. Seeds with radicle and shoot elongation (sprouting) were considered to have emerged (Fyfield & Gregory 1989; Mavi 2010). The distinction between germination and emergence is necessary because seeds might germinate but fail to emerge (Fenner 1987) due to several reasons, including low stored seed nutrients. The number of seeds that germinated or emerged was counted until approximately 15 days, during which there were no further seed germination and emergence. The seed germination time (days), emergence time (days), germination percentage (%), and emergence percentage (%) were determined.

Data analysis

I performed a linear mixed model analysis in R with the nlme package (R Core Team 2022). Data were checked for normality (qqnorm plots) and homogeneity of variances (using the Breusch-Pagan Test from the lmtest package; Breusch & Pagan 1979), and I used the appropriate variance functions: model = lme (Y ~ X, random=~1|S, data=df, weights=varIdent(form=~1|X), method = "REML") to address the issues of heteroscedasticity. I tested pod weight, number of seeds per pod, seed weight, seed size, number of beetle-infested seeds, and seed nutrients as response variables. I used tree type (i.e., nest tree and control tree) as an explanatory variable. I included the identity of the 'tree pair' as a random effect, although I was unable to match all tree pairs due to the lack of pods in some of the trees selected for this study. I used the 'Anova' function to test whether the model terms explain a significant proportion of the variation in the data. Where a significant variation was found, it was followed by a pairwise comparison (Tukey's post-hoc test) of group levels conducted using the emmeans package in R (Lenth 2019). For the number of beetle-infested seeds, I tested the probability of seed infestation using the glmmTMB with a binomial distribution (Brooks *et al.* 2017). The numbers of infested and non-infested seeds were bound together using the cbind () function as a response variable for the binomial model.

The final percentage of germination and the percentage of emergence were calculated. The time taken for 50% germination (T50) is considered a good measure of germination time (Ranal & García De Santana 2006). T50 estimated using the formula of Coolbear *et al.* (1984) as modified by Farooq *et al.* (2005). $T_{50} = t_i + [(N / 2 - n_i)(t_i - t_j)] / n_i - n_j$. Where N = final number of germination, n_i, n_j = cumulative number of seeds germinated by adjacent counts at times t_i and t_j, respectively, when $n_i < N / 2 < n_j$. A similar calculation was repeated for the time taken for 50% emergence. Seed germination and emergence percentages and germination and emergence times were tested as response variables. Seed sources/treatments (nest seed scarified, control seed scarified, nest seed beetle infested, control seed beetle infested, nest seed unscarified, and control seed unscarified) were used as fixed factors. The tree pair identity (nest tree and control tree) was included as a random effect. I used the 'Anova' function to test whether the model terms explain a significant proportion of the variation in the data. Where significant variation was found, it was followed by a pairwise comparison (Tukey's post-hoc test) of the group levels conducted using the emmeans package in R (Lenth 2019).

Results

Pod and seed characteristics

Pods were obtained in 20 of the 33 nest trees and 13 of the 33 control trees. A total of 194 pods were collected from all trees: 125 from the nest and 69 from the control trees. The probability of finding a pod in a tree tended to be higher in nest tree compared to control trees (Figure 5.1), although this was not strictly significant ($\chi^2 = 3.44$, $p = 0.064$). A mean (± SE) of 5.95 ± 0.63 and 4.31 ± 0.82 pods were obtained from nest and control trees, respectively, and a range of 1-10 pods for both trees. The mean number of pods collected per tree did not differ between nest and control trees ($\chi^2 = 3.61$, $p = 0.058$). There were no significant differences in pod weight, number of seeds per pod, or seed weight between nest trees and trees without nests (Table 5.1; Table S5.1).

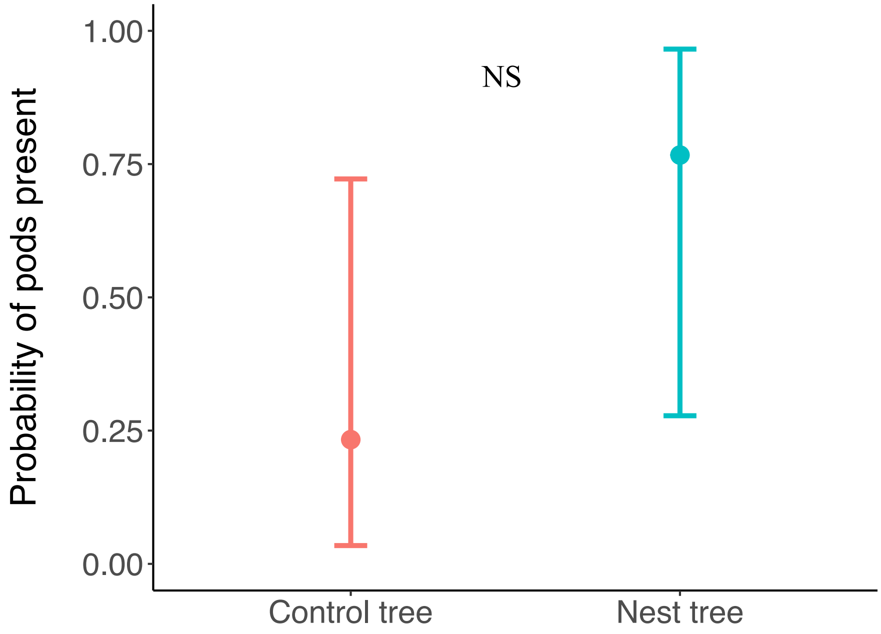

Figure 5.1: The probability of finding a pod in the nest and control trees (model produced values ± 95% CI; NS denotes $p > 0.05$).

Table 5.1: Characteristics of pods and seeds from nest trees and trees. The mean and standard error (SE) of pod weight, the number of seeds per pod, and seed weight are provided. Statistical differences were tested using a linear mixed model.

Pod and seed characteristics	**Mean ± SE**		**χ^2**	**P-value**
	Nest tree (n=125)	Control tree (n = 69)		
Pod weight (g)	9.58 ± 0.71	9.98 ± 0.81	0.407	0.524
Seeds per pod (#)	11.7 ± 0.81	12.4 ± 0.94	0.731	0.393
Seed weight (g)	0.16 ± 0.013	0.17 ± 0.015	0.665	0.415

Beetle infestation

There was a significantly higher probability of seed infestation in the nest than in control trees ($\chi^2 = 35.67$, $p < 0.001$: Figure 5.2). With the mean of 12 seeds per pod, there was a mean of 6.15

infested seeds per pod in nest trees compared to 4.43 in trees without nests. Two species of beetles were identified to invade camelthorn pods and seeds: Bruchid beetle *Bruchus rufimanus* (Figures 5.3A, 5.3B and 5.3D) and yellow mealworm beetle *Tenebrio molitor* (Figure 5.3C). Bruchid beetles create holes in the pods (Figure 5.3A) to access the seeds and make holes to eat the content (Figures 5.3B and 5.3D). The yellow mealworm beetles chew the seed coat and the content (Figure 5.3C).

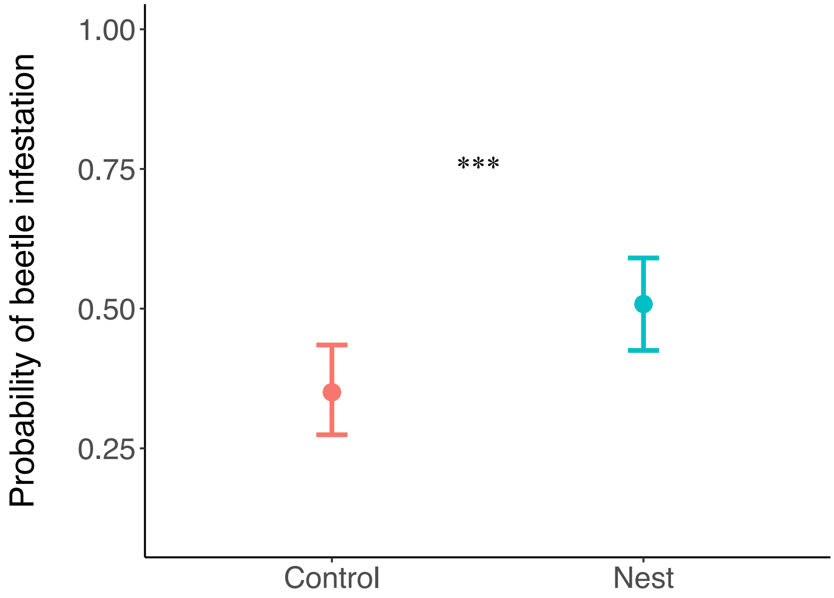

Figure 5.2: The probability of beetle infestation of pods in nest and control trees (model produced values ± 95% CI; *** denotes p <0.001).

Figure 5.3: Bruchid beetles create holes in camelthorn pods to access seeds (A). Infestation of camelthorn seeds by the *Bruchus rufimanus* bruchid beetles (B and D). Damage to the camelthorn pod and seeds by the *Tenebrio molitor* yellow mealworm beetle (C).

Seed nutrients

There were significantly higher concentrations of K (1.1-fold) and Cu (1.2-fold) in the seeds of control trees than in nest trees (Table 5.2; Table S5.2). However, the concentration of Bo was 1.2-fold higher in seeds from the nest than in control trees. The seed concentrations of N, P, Ca, Zn Mn, Mg, Na, Al, and Fe did not vary between the nest and control trees (Table 2; Table S5.2).

Table 5.2: Elemental composition of camelthorn seeds collected from camelthorn nest and control trees. Mean ± SE is given for each faecal nutrient. Statistical differences were tested using a linear mixed model. Means with the different letters in the rows indicate a significant difference ($P < 0.05$).

Seed nutrient	**Mean ± SE**		χ^2	**P-value**
	Nest tree seed	Control tree seed		
N (%)	6.58 ± 0.180	6.39 ± 0.200	0.950	0.330
P (%)	0.45 ± 0.014	0.47 ± 0.015	1.192	0.275
K (%)	1.30 ± 0.032^a	1.41 ± 0.037^b	5.727	**0.017**
Ca (%)	0.37 ± 0.029	0.36 ± 0.033	0.027	0.870
Mg (%)	0.34 ± 0.011	0.34 ± 0.013	0.196	0.658
Zn (mg/kg)	37.10± 1.56	39.3 ± 1.76	1.308	0.253
Mn (mg/kg)	39.2 ± 5.32	31.6 ± 5.97	1.480	0.224
Na (mg/kg)	41.9 ± 8.53	47.1 ± 8.85	1.056	0.304
Cu (mg/kg)	5.71 ± 0.334^a	6.84 ± 0.385^b	4.930	**0.026**
Bo (mg/kg)	31.3 ± 1.78^b	25.9 ± 2.05^a	3.885	**0.049**
Al (mg/kg)	6.72 ± 0.550	6.00 ± 0.623	1.069	0.301
Fe (mg/kg)	81.5 ± 2.45	94.1 ± 9.18	2.002	0.157

Seed germination and emergence

There were no significant differences in the seed germination and emergence percentage between seeds from nest and control trees for scarified, unscarified and beetle-infested seeds (Figures 5.4A and 5.4C; Table S5.3). However, there was a significantly higher percentage of seed germination and emergence in scarified seeds than in unscarified and beetle-infested seeds. Seed germination and emergence percentages did not differ between beetle-infested and unscarified seeds (Figures 5.4A and 5.4C). Germination and emergence time did not differ between nest and control tree seeds for scarified, unscarified, and beetle-infested seeds (Figures 5.4B and 5.4D; Table S5.3).

There were significantly shorter germination and emergence times in scarified and beetle-infested seeds than in unscarified seeds. However, the germination and emergence time did not differ between the scarified seeds and the beetle-infested seeds. The percentage of germinated seeds that did not emerge was significantly higher in beetle-infested nest seeds than in beetle-infested control seeds ($\chi^2 = 13.97$, $p = 0.016$: Figure S5.1). However, there was no significant difference in the nest and control seeds of scarified and unscarified seeds (Figure S5.1).

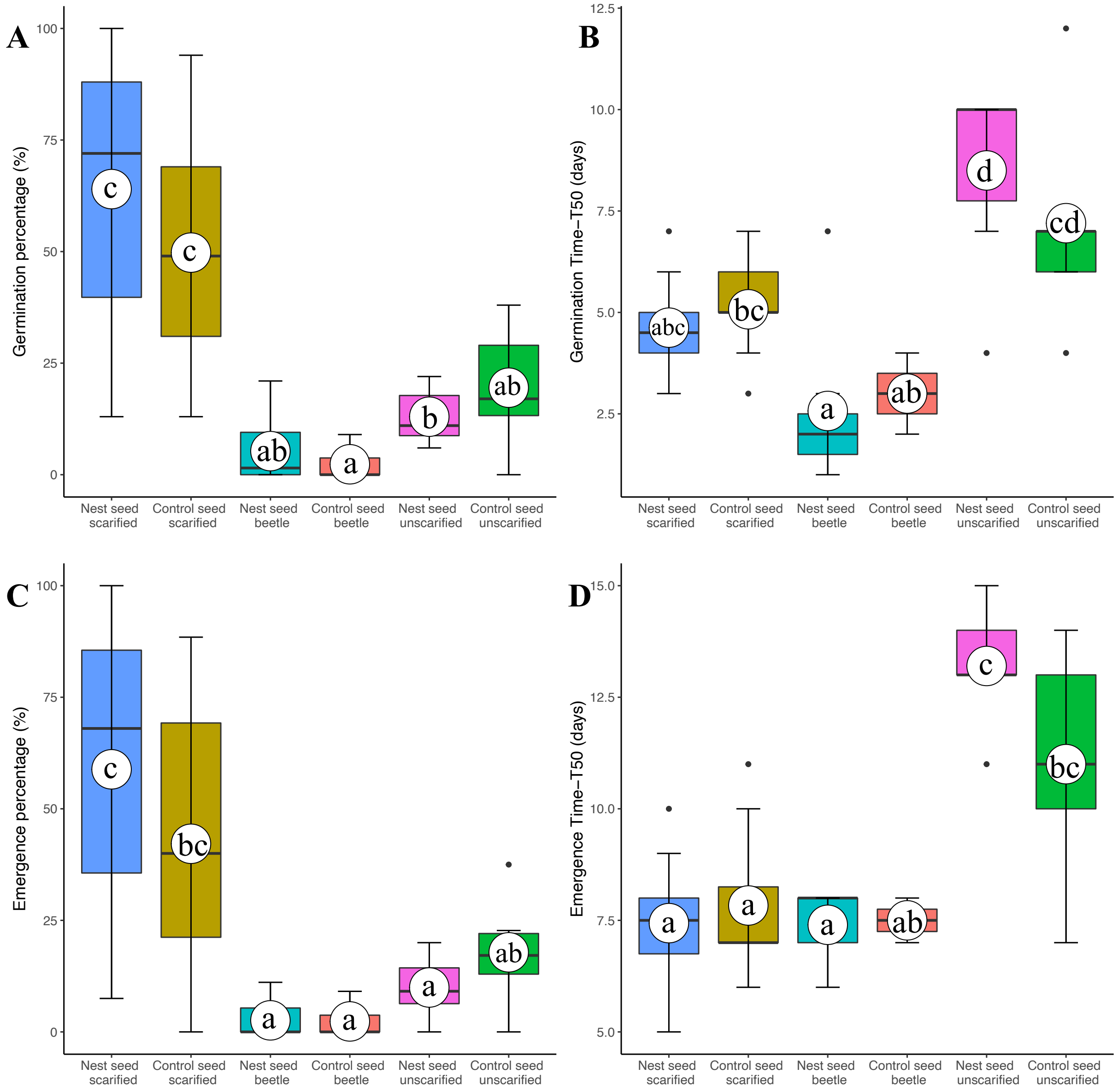

Figure 5.4: Germination percentage of various camelthorn seed sources and treatments (A). Germination time (the time to reach 50% germination-T50) of various camelthorn seed sources and treatments (B). Emergence percentage of various camelthorn seed sources and treatments (C). Emergence time (the time to reach 50% emergence-T50) of various camelthorn seed sources and treatments (D). The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. The whiskers represent 1.5 × the interquartile range, and the outliers above/below are shown as dark points. Circles represent means, with letters indicating pairwise comparison between seed sources/treatments.

Discussion

Overall, there were few differences in reproductive characteristics between the camelthorn trees hosting sociable weaver nests and those without. Pod and seed characteristics did not differ between nest and control trees, although there was a tendency for trees hosting weaver nests to contain pods during my single main sampling event. Despite having access to more soil nutrients, my study found that almost all the major seed nutrients did not differ between nest and control trees. Seed germination and emergence did not vary between the nest and the control trees. There was, however, a higher beetle infestation in seeds from nest trees than in control trees.

I expected pods from nest trees to have a higher pod numbers, pod weight, more seeds per pod, and a higher seed weight than seeds from control trees. There was, however, no difference in these pod and seed characteristics between the nest and control trees. This could mean that camelthorn trees invest resources in the production of quality seeds to ensure adequate stored nutrients to initiate germination, regardless of the soil nutrients in which the parent plants grow. Obeso (2012) found that seed mass variation is controlled by paternal genetic effect, brood size, and sibling rivalry within a tree. This implies that seed characteristics are more of a genetic makeup than the soil nutrient effect. This lack of differences in seed characteristics between nest and control trees might also explain why there were no significant differences in seed germination and emergence percentages and time.

The mineral nutrients of seeds are expected to drive the germination and emergence of seeds (Mandizvo & Odindo 2019). Despite the higher seed K and Cu in the seeds of the control tree compared to the nest trees and the higher Bo in the seeds of the nest tree compared to the control trees, there were no differences in the germination and emergence percentages and time. This could mean that the differences in these nutrients in the seeds of the nest and control trees were not significant to drive the differences in germination and emergence. Bo has been documented to increase flower production and retention and, subsequently, increase seed and fruit development and germination (Archana *et al*. 2021). But this did not drive the differences in germination and emergence between the nest and the control trees. Therefore, the levels of Bo might be sufficient in both nest and control tree seeds to initiate germination.

The high beetle infestation of seeds is a significant reproductive cost found in the interaction between the sociable weaver and its camelthorn tree host. There was a higher beetle infestation of the seeds in the trees hosting nests than in the control trees. The high beetle infestation subsequently decreased seed germination and emergence percentages in beetle-infested seeds only. I found that bruchid beetles eat the cotyledon of seeds and, in most cases, eat the embryo; in this case, the seeds do not germinate. The embryo grows when the beetle eats only part of the cotyledon. Miller (1994) reported that the extent of bruchid beetle damage would determine the germination of seeds. Hence seeds with more damage would have lower germination percentages. I found that seeds infested with beetles germinated faster than seeds without beetle infestation. I also found no differences in germination and emergence time between beetle-infested seeds and mechanically scarified seeds. This means that the beetles' holes help the seeds absorb water to initiate quick germination. Coe and Coe (1987) reported that undetectable bruchid beetle holes in camelthorn seeds could have contributed to the high germination rate in undigested seeds than seeds that passed through the guts of elephants and cattle. According to Lamprey *et al*. (1974), seeds with undamaged embryos from bruchid beetle infestation would still be viable and germinate faster due to high water uptake from holes created by the beetles. This might explain why there was a shorter germination time in beetle-infested seeds than in seeds without beetle infestation and unscarified mechanically. The high percentage of germinated seeds that did not emerge in the beetle-infested nest seeds than in the beetle-infested control seeds could mean that the extent of beetle damage in individual seeds from nest trees was high, hence less emergence.

Conclusions

The study findings show that the occupation of camelthorn trees by sociable weavers did not influence pods and seed characteristics, although higher soil nutrients have been reported under nest trees than in control trees (Aikins *et al.* 2023). However, the presence of the nest results in high beetle infestation of seeds, leading to poor seed germination and the emergence of beetle-infested seeds. All nutrients found to be higher in the faecal matter of the sociable weaver and the nest soil (Prayag *et al*. 2020; Aikins *et al*. 2023) did not vary between the nest and the control tree seeds. In addition, seed germination and emergence did not differ between nest and control trees, but mechanical scarification of seeds resulted in higher percentages of germination and emergence. Except for a high infestation of beetles, the presence of a nest in the camelthorn tree does not affect the reproduction success of the host trees differently from trees without a nest. Therefore, it can be deduced that camelthorn trees invest in producing quality seeds irrespective of soil nutrient status, and the presence of the nest mass does not influence the reproductive success of the host trees.

Supplementary Materials

Table S5.1: Linear mixed model analysis with pod weight, seeds per pod, and seed weight as response variables and tree types (2 levels- nest tree, control tree) as a factor. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis. We included pair as a random effect.

Response Variables	**Factor**	χ^2	**df**	**P-value**
Pod weight (g)	Tree types	0.407	1	0.524
Seeds per pod (#)	Tree types	0.731	1	0.393
Seed weight (g)	Tree types	0.665		0.415

Table S5.2: Linear mixed model analysis with seed nutrients as response variables and tree types (2 levels- nest tree, control tree) as factors. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis. We included pair as a random effect.

Response Variables	**Factor**	χ^2	**df**	**P-value**
N (%)	Tree types	0.950	1	0.330
P (%)	Tree types	1.192	1	0.275
K (%)	Tree types	5.727	1	0.017
Ca (%)	Tree types	0.027	1	0.870
Mg (%)	Tree types	0.196	1	0.658
Zn (mg/kg)	Tree types	1.308	1	0.253
Mn (mg/kg)	Tree types	1.48	1	0.224
Na (mg/kg)	Tree types	1.056	1	0.304
Cu (mg/kg)	Tree types	4.930	1	0.026
Bo (mg/kg)	Tree types	3.885	1	0.049
Al (mg/kg)	Tree types	1.069	1	0.301
Fe (mg/kg)	Tree types	2.002	1	0.157

Table S5.3: Linear mixed model analysis with percentage germination, percentage emergence, germination time, and emergence time as response variables and seed sources/treatments (6 levels- nest seed scarified, control seed scarified, nest seed beetle infested, control seed beetle infested, nest seed unscarified, and control seed unscarified) and seed thickness as factors. Wald Chi-square values (χ^2), degrees of freedom (df), and p-values are provided for each analysis. We included pair as a random effect.

Response Variables	**Factors**	**χ^2**	**df**	**P-value**
Germination (%)	Seed sources/treatments	116.98	5	<0.001
	Seed thickness	5.45	1	0.020
Emergence (%)	Seed sources/treatments	96.50	5	< 0.001
	Seed thickness	0.963	1	0.327
Germination time (days)	Seed sources/treatments	52.69	5	<0.001
	Seed thickness	0.45	1	0.501
Emergence time (days)	Seed sources/treatments	87.79	5	<0.001
	Seed thickness	0.011	1	0.915

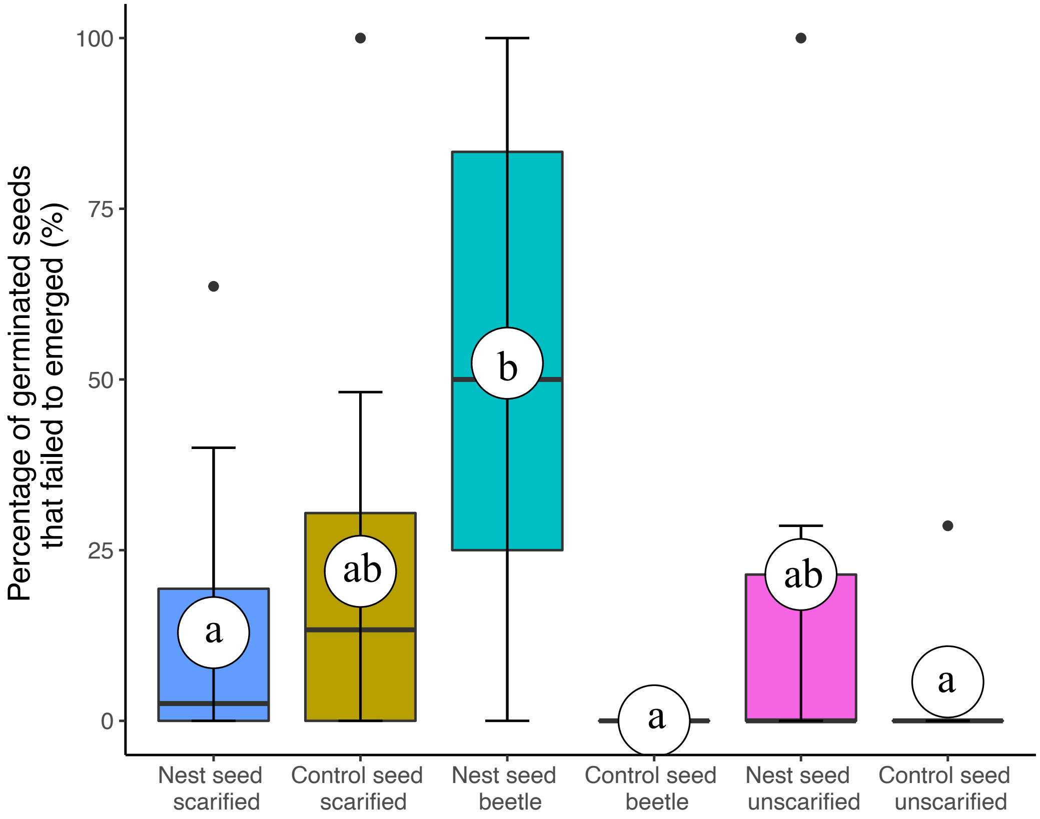

Figure S5.1: Percentage of germinated seeds that failed to emerge across various camelthorn seed sources and treatments. See figure 4 for other figure details.

Chapter 6: General Discussion and Synthesis

This chapter concludes the study by discussing the key research findings related to the overarching research hypothesis and the contribution to knowledge thereof. The chapter also discusses the limitations of the study and proposes areas for future research. This study tested the hypothesis that the interactions between animals and plants in the savanna ecosystem enhance the islands of fertility created by trees, which influence the growth and survival of vegetation in the environment. Specifically, the thesis aimed to test the benefits that host trees derive from this interaction, such as improved soil fertility, improved host tree growth, foliar nutrient concentrations and stoichiometries, and reproductive benefits. It also tested the costs to the host trees such as loss of photosynthetic area, branch fall, terminal branch death, tree mortality, insect infestation of host tree seeds, and its effects on host tree reproduction.

Trees and grasses grow together in savannas and compete for limited resources (Scholes & Archer 1997). The co-existence of grasses and trees in the savanna ecosystem is made possible through biological processes like competition acting together with resource partitioning and facilitation (den Boer 1986; Walter 1991; Fargione & Tilman 2005; Callaway 2007). My study established that trees in the Kalahari Desert facilitate their environment for plants by creating islands of fertility, which I found to have high soil N, P, K, Ca, and Zn than grassland soils (Aikins *et al.* 2023). Trees may facilitate grass growth through hydraulic lift or shade provision (Ludwig *et al.* 2004). Facilitation may also occur by creating islands of fertility under the tree through processes such as litter fall (Treydte *et al.* 2008; Ludwig *et al.* 2008). These islands of fertility created by trees are characterised by higher soil and plant N and lower water loss from soil and plants (Bernhard-Reversat 1982; Belsky *et al.*1993; Moyo *et al.* 2010). Similarly, Schlesinger *et al.*

(1996) found higher soil N, P, and K under *Larrea tridentata* shrubs than in the grassland between the shrubs in the Chihuahuan Desert. Trees also redistribute nutrients and water by accessing them from deeper layers and moving them to the upper layer for use by shallow-rooted subcanopy plants (Jackson *et al*. 2002; Caylor *et al*. 2005; D'Odorico *et al*. 2010). Through this ecological process, savanna trees influence inter-plant interactions (Dawson 1993).

It is suggested that nitrogen fixation by trees or subcanopy species under these trees are the main contributor to increased soil fertility of tree islands of fertility (Vitousek & Walker 1989; Sitters *et al.* 2015). I found higher soil C and N under leguminous camelthorn trees than under non-leguminous shepherd trees (Aikins *et al*. 2023). This could be attributed to nitrogen fixation by camelthorn trees and also to the high decomposition of leaf litter under these large trees. Fernández *et al*. (2020) reported that leguminous trees and shrubs improve soil fertility through N_2 fixation and biomass accumulation. Cramer *et al*. (2007) established that leguminous trees and shrubs in the savanna fix nitrogen, especially when in competition with grasses. Acacia trees in the savanna therefore contribute to nitrogen availability in these N-limited soils (Ludwig *et al*. 2001; Aikins *et al*. 2023). The high availability of nutrients under trees in the savanna improves the quality of forage and subcanopy plants, hence attracting herbivores (Treydte *et al*. 2007, 2008; Ludwig *et al*. 2008). The attraction of the herbivores results in increased faunal faecal deposits, further increasing soil nutrients and enhancing the fertility island effect (Belsky *et al*. 1989; Belsky 1994; Dijkstra *et al*. 2006). Tree, grass, and herbivore interactions could have a positive, neutral, or negative effect on trees.

In Chapter 2, I established that soils under trees in the savanna have high soil nutrients, which are probably formed through the interaction of the trees with large mammals (Aikins *et al*. 2023). In Chapter 3, I also found that mammalian faeces collected from under the canopy of trees have high levels of N, C, P, K and Ca, which could potentially increase soil fertility under these trees. Animals attracted to savanna trees deposit faecal materials, which contribute to the fertile vegetation island effect (Dean *et al*. 1999; Cao *et al*. 2018; Mashizi & Sharafatmandrad 2020). Large herbivores in African savannas regulate the establishment of vegetation through their feeding. Grazing by herbivores influences the abundance of plants they feed on and alters the competition between trees and grasses (Thompson Hobbs 1996; Scholes & Archer 1997; Riginos & Young 2007; van der Waal *et al*. 2011). The influence of herbivores on the savanna ecosystem also depends on the species of herbivores, the vegetation type, and the environmental factors (Sebata 2017). Herbivores therefore influence soils in the savanna ecosystem by creating nutrient hotspots through their urine and faecal deposits under trees (McNaughton 1988; Thompson Hobbs 1996; van der Waal *et al*. 2011; Aikins *et al*. 2023).

It can be expected that the nutrient stoichiometry of plants growing on islands of fertility that differ in their origins will vary based on the soil nutrient stoichiometry in these islands of fertility as influenced by the sources of faunal nutrients (e.g., mammalian or avian sources). In this study, evidence supports the general hypothesis that interactions between animals and plants in the savanna ecosystem influence the growth of vegetation in the environment (Chapter 3). I established that the islands of fertility created by the sociable weaver and the host trees influenced the nutrient stoichiometries and significantly increased the growth and foliar nutrient concentrations of camelthorn seedlings than soils from tree islands of fertility and the grasslands (Chapter 3). This shows that the faunal faecal input on islands of fertility increases vegetation growth in the environment better than on islands of fertility created by trees alone. Faunal input at tree islands of fertility results in localised changes in the physical and chemical properties of the soil and alters plant growth (Schlesinger *et al*. 1996; Dean *et al*. 1999; Prayag *et al*. 2020; Aikins *et al*. 2023). Since the stoichiometric composition of the animal's food, its body size, and body nutrients influence the nutrient stoichiometry (e.g., N:P ratios) in their faecal matter (Sitters *et al*. 2017; Sitters & Venterinka 2021; le Roux *et al*. 2020), mammals and birds will not have the same nutrient contributions at islands of fertility. Furthermore, the amounts of faeces/urine deposited, together with nutrient stoichiometry, determine how plants grow in response to the faunal input (le Roux *et al*. 2020).

Coloniality is a common occurrence in many animal species, and birds especially form conspicuous colonies, with about 13% of bird species breeding in colonies (Lack 1968). Colonies are known to influence habitat characteristics the structure and composition of the vegetation and the chemical and physical properties of the soil (García *et al.* 2002; Ellis 2005). In Chapter 2, I established that the high faecal deposit by the colonial sociable weaver under the nests creates a bare patch with no vegetation growth in this patch. The results show that this bare patch is due to physiological drought formed by the high deposition of faecal matter and the poor water infiltration created by the faecal mat in these patches (Aikins *et al*. 2023). These changes could be beneficial due to the input of faunal nutrients or detrimental to the host trees and other plants in the environment due to physiological drought. Faunal nutrient input has the potential to affect the host plant positively. The benefits of the large amounts of nutrients supplied by colonial breeding birds have been documented to increase leaf N, P and Zn concentrations (Erskine *et al.* 1998; Anderson & Polis 1999; García *et al.* 2002). The interactions between colonial birds and their host vegetation can also lead to costs. Excessive nutrient faunal nutrient deposition can perpetuate soil damage, squash woody vegetation, and dramatically alter soil chemistry changes (Weseloh & Ewins 1994; Hebert *et al.* 2005).

The cost of hosting colonial birds also includes physical vegetation damage through branch breaking, death of host plants and deposit of excreta on leaves (Mulder & Keall 2001; Ellis 2005; Havik *et al.* 2014; Otero *et al.* 2015). This study provided novel findings and a greater understanding of the benefits and costs of arid zone savanna trees that host large colonial birds (Chapter 4). I established that the interactions between the sociable weavers and the host trees result in high foliar nutrients in the host trees than in trees without the nest (Chapter 4). The interactions, however, also pose costs to host trees, including branch breaking, loss of canopy area, death of terminal branches, death of part or the whole tree, higher seed damage by beetles, and its consequences on the reproduction of host trees (Chapters 4 and 5). The benefits and costs of hosting colonial birds in the desert ecosystem are relatively less explored. Previous studies investigating the influence of colonial birds on host trees have focused on forest species and seabirds, this study provided the first attempt to fully understand the impacts of these interactions on savanna trees in arid climatic conditions. These findings provide value information for land owners on the need to maintain colonies of sociable weavers on their properties, as this interaction facilitates the conditions of the arid environment to support the growth of other plants.

The costs and benefits of a specific biotic interaction could change depending on the stage of life of the species, the environment, or the climate (Newman 2021). The cost may outweigh the benefits, or the benefits may outweigh the cost during certain times in the lifespan of the individuals involved in the interaction (Newman 2021). In this study, I established that the interaction between the sociable weaver and its host trees could not strictly be classified as mutualism or parasitism but depends on the stage of the interaction and the population of the sociable weavers as reflected in the size of the nest they build (Figure 6.1). At the early stages of the interaction, host trees benefit from the high input of faunal nutrients by sociable weavers, but as the nest becomes more extensive, the trees lose most of their canopy to the nest, leading to the death of branches, the whole tree, and the branch fall (Figure 6.1). The net effect of the costs and benefits of a biotic interaction on the general fitness of the host is the theoretical basis for assigning mutualism, parasitism, or commensalism tags (Ewald 1987; Johnson *et al*. 1997). Biotic interactions could start as mutualistic but could change to parasitic with the length of the relationship, host age, or environmental conditions, making costs greater than benefits (Ewald 1987; Johnson *et al*. 1997; Newman 2021). Mutualism and parasitism are therefore described as extremes of a dynamic continuum of species interactions, as described by Ewald (1987) and Johnson et al. (1997) as a 'mutualism-parasitism continuum'.

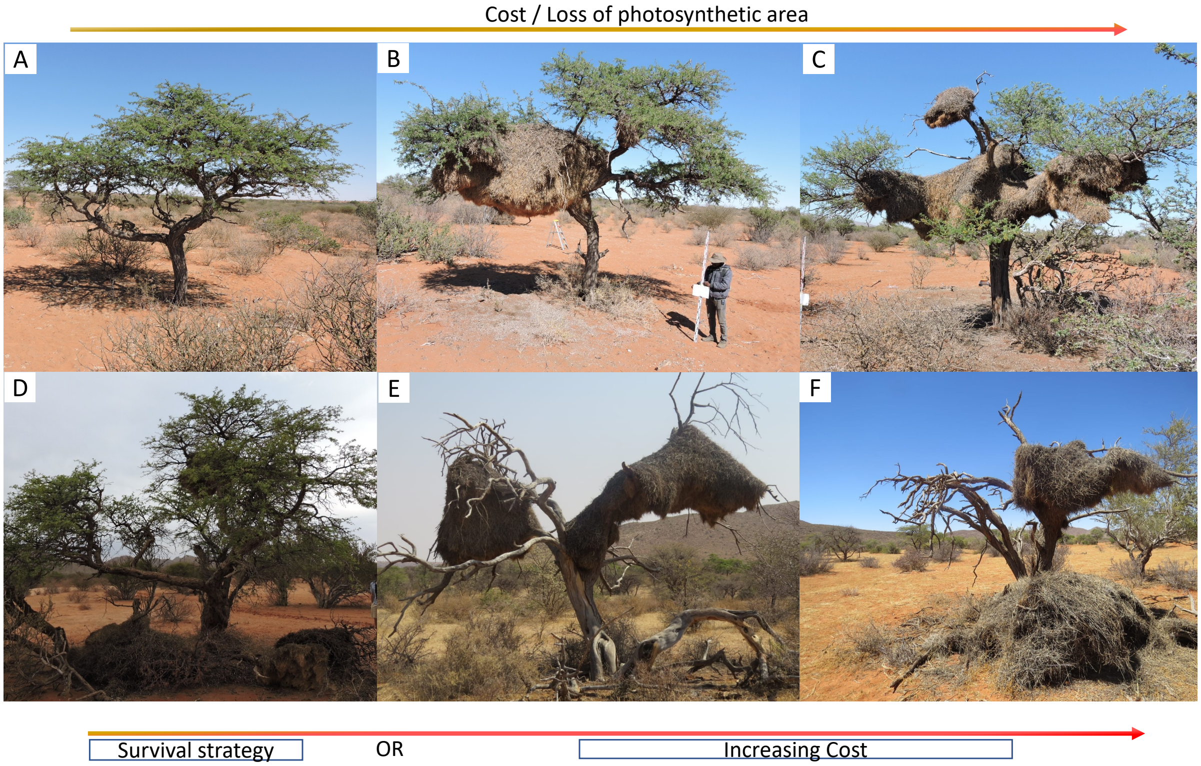

Figure 6.1: A tree without a sociable weaver nest has a full canopy cover of leaves and creates islands of fertility through litter fall, nitrogen fixation, and the attraction of large herbivores (Figure 6.1A; Chapter 2). Once the sociable weavers build their massive nest in the tree, the faecal matter

of the sociable weaver increases soil nutrients leading to larger tree growth, but also, the tree has greater chances to lose some of its leaves to the nest cover (Figure 6.1B, C; Chapters 2, 3 and 4). The sociable weavers continue to build and increase the nest size to cover a mean of 30% of the tree canopy but, at times, up to 75% of the tree canopy (Figure 6.1C; Chapter 4). Trees with a large nest have less of the leaves involved in active photosynthesis, which may not be able to support the entire tree's food requirement. At this point, the supply of nutrients to a part of the tree that does not produce food for the other parts to survive may be reduced. This could lead to the death of terminal branches in some nest branches (Figure 6.1C; Chapter 4). Branch fall may be a survival strategy of host trees to avoid total tree mortality (Figure 6.1D). Trees unable to break branches could end in the death of most branches or the whole tree (Figure 6.1E; Chapter 4). When the tree dies, the nest masses can fall after soaking up a lot of rainwater (Figure 6.1F).

Conclusions

In this thesis, I have presented the first attempt to quantify the costs and benefits to trees that host the colonial nest of the sociable weavers. Specifically, I showed that savanna trees create an island of fertility, but the presence of colonial sociable weaver nests on these trees further increases the soil fertility created by the trees. I also found that a larger colony size means high faunal nutrient input, and leguminous camelthorn increases soil fertility more than non-leguminous shepherd trees. However, the islands of fertility created by trees differ from those made by colonial birds and host trees. These islands of fertility support growth, foliar nutrient concentration, and stoichiometries differently. My findings also show evidence of growth, nutritional and reproductive costs, and the benefits of hosting the colonial nest of the sociable weaver. This study also represents the first attempt to empirically quantify the reproductive costs and benefits of the interaction between the sociable weaver and its camelthorn host trees.

This study contributes to the growing literature on islands of fertility and colonial birds' influence on soil nutrient improvement. The study established that colonial birds in the arid zone savanna also create an island of fertility with trees, which significantly increases soil fertility in this ecosystem. The study also contributes to the literature on ecological engineering, showing how the association between the sociable weavers and savanna trees ameliorate conditions in N-limited desert soils which drives the growth of plants in this soil condition. These contributions have important implications for conservation and management, as the protection of sociable weaver colonies and their host trees would facilitate the conditions of the arid environment to support the growth of other plants. This study highlights the role of interactions between fauna and flora in contributing to savanna ecosystem heterogeneity and species richness, and consequently to ecosystem resilience.

This study was carried out in one location of the range of sociable weavers and host trees. According to the stress gradient hypothesis, facilitative interactions increase in a drier environment (Bertness & Callaway, 1994). Exploring how this interaction change at different parts of the range (across aridity gradient) of this interaction where environmental conditions differ would help to make a generalisation of these findings. Future research to assess the costs and benefits to the subcanopy plants under host trees would provide a holistic understanding of the effect of the interaction on the savanna plant community.

References

Abril, A., Villagra, P., & Noe, L. (2009). Spatio-temporal heterogeneity of soil fertility in the Central Monte desert (Argentina). *Journal of Arid Environment,* 73, 901-906. https://doi.org/10.1016/j.jaridenv.2009.04.019

Addicott, J. F. (1986). Variation in the costs and benefits of mutualism: the interaction between yuccas and yucca moths. Oecologia, 70, 486-494. https://doi.org/10.1007/BF00379893

Aganga, A. A., Adogla-Bessa, T., Omphile, U.J., & Tshireletso, K. (2000). Significance of browses in the nutrition of Tswana goats. *Archivos de Zootecnia,* 49, 469-480.

Ågren, G. I., Wetterstedt, J. A., & Billberger, M. F. (2012). Nutrient limitation on terrestrial plant growth-modeling the interaction between nitrogen and phosphorus. *New Phytologist*, 194, 953-960. https://doi.org/10.1111/j.1469-8137.2012.04116.x

Aguilera, L. E., Gutiérrez, J. R., & Meserve, P. L. (1999). Variation in soil microorganisms and nutrients underneath and outside the canopy of *Adesmia bedwellii* (Papilionaceae) shrubs in arid coastal Chile following drought and above-average rainfall. *Journal of Arid Environments* 42, 61-70. https://doi.org/10.1006 /jare.1999.0503

Aikins, T. K., Cramer, M. D., & Thomson, R. L. (2023). Positive feedbacks between savanna tree size and the nutritional characteristics of "Islands of fertility" are amplified by sociable weaver colonies. *Journal of Arid Environments*, 209 (104903). https://doi.org/10.1016/j.jaridenv.2022.104903

Aikins, T. K., Thomson, R. L., & Cramer, M. D. (2023a unpublished). All savanna islands of fertility are not equal: colonial birds influence soil nutrient stoichiometries with consequences for tree seedling growth.

Aikins, T. K., Cramer, M. D. & Thomson, R. L. (2023b unpublished). Growth benefits and costs to trees hosting colonial birds that build large avian nests.

Aizen, M. A., Morales, C. L., Vázquez, D. P., Garibaldi, L. A., Sáez, A., & Harder, L. D (2014). When mutualism goes bad: density-dependent impacts of introduced bees on plant reproduction. *New Phytologist*, 204 (2), 322-328. https://doi.org/10.1111/nph.12924

ALASA (1998). Handbook of Feeds and Plants Analysis. Palic, D. (Ed).

Alias, D., & Milton, S. (2003). *A collation and overview of research information on Boscia albitrunca (Shepherd's tree) and identification of relevant research gaps to inform protection of the species.* Department of Water Affairs and Forestry. https://www.dffe.gov.za/sites/default/files/reports/bosciaalbitrunca_researchinformation.pdf

Anderson, W. B., & Polis, G. A. (1999). Nutrient fluxes from water to land: Seabirds affect plant nutrient status on Gulf of California islands. *Oecologia,* 118(3), 324-332. https://doi.org/10.1007/s004420050733

AOAC International. (1997). Official Methods of Analysis (16th ed.). AOAC International, Gaithersburg, MD.

Archana, A., Verma, P., & Pandey, N. (2021). Impact of Inadequate Concentration of Boron in Seed Storage Proteins Content in Oilseed Crops. In (Ed.), Grain and Seed Proteins Functionality. IntechOpen. https://doi.org/10.5772/intechopen.95873

Austin, A., Yahdjian, L., Stark, J., Belnap, J., Porporato, A., Norton, U., Ravetta, D., & Schaeffer, S., (2004). Water pulses and biogeochemical cycles in arid and semi-arid ecosystems. *Oecologia,* 141, 221-235.

Barker, J. L., & Bronstein, J. L. (2016). Temporal Structure in Cooperative Interactions: What Does the Timing of Exploitation Tell Us about Its Cost? *PLoS Biology,* 14(2), e1002371. https://doi.org/10.1371/journal.pbio.1002371

Barnes, M. E. (2001a). Seed predation, germination and seedling establishment of *Acacia erioloba* in Northern Botswana. *Journal of Arid Environments,* 49, 541-554. https://doi.org/10.1006/jare.2001.0805

Barnes R. D. (2001b) The African Acacias - A thorny subject. *The Southern African Forestry Journal,* 190(1), 9–18. https://doi.org/10.1080/20702620.2001.10434110Bascompte, J., & Jordano, P. (2007). Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 38, 567-593.

Baumann, P., Lee. J., Frossard, E., Schönholzer, L. P., Diby, L., Hgaza,V. K., Kiba, D. I., Sila, A., Sheperd, K., & Six, J. (2021). Estimation of soil properties with mid-infrared soil spectroscopy across yam production landscapes in West Africa. *Soil*, 7(2), 717–731, https://doi.org/10.5194/soil-7-717-2021

Becker, J. N., Gütlein, A., Sierra Cornejo, N., Kiese, R., Hertel, D., & Kuzyakov, Y. (2017). Legume and non-legume trees increase soil carbon sequestration in Savanna. *Ecosystems*, *20(5)*, 989-999.

Bell, R.W., McLay, L., Plaskett, D., Dell, B., & Loneragan, J. F. (1989). Germination and vigour of black gram (Vigna mungo (L.) Hepper) seed from plants grown with and without boron. *Australian journal of Agricultural Research*, 40, 273-279.

Belsky, A. J. (1994). Influences of trees on savanna productivity: Tests of shade, nutrients and tree-grass competition. *Ecology,* 75(4), 922–932.

Belsky, A. J., Amundson, R. G., Duxbury, J. M., Riha, S. J., Ali, A. R., & Mwonga S. M.. (1989). The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology,* 26(3), 1005–1024.

Belsky, A. J., S. M. Mwonga, R. G. Amundson, J. M. Duxbury, and A. R. Ali. (1993). Comparative effects of isolated trees on their under-canopy environments in high and low rainfall savannas. *Journal of Applied Ecology,* 30(1), 143–155.

Bernhard-Reversat, F. (1982). Biogeochemical cycle of nitrogen in a semi-arid savanna. *Oikos*, 38(3), 321–332.

Bogie, N. A., Bayala, R., Diedhiou, I., Conklin, M. H., Fogel, M. L., Dick, R. P., & Ghezzehei, T. A. (2018). Hydraulic Redistribution by Native Sahelian Shrubs: Bioirrigation to Resist In-Season Drought. *Frontiers in Environmental Science*, 6, 98. https://doi.org/10.3389/fenvs.2018.00098

Bond, W. J. (2008). What limits trees in C4 grasslands and savannas? *Annual Review of Ecology Evolution and Systematics,* 39, 641-659. https://doi.org/10.1146/annurev.ecolsys.39.110707.173411

Boström, B., Comstedt, D., & Ekblad, A. (2007). Isotope fractionation and 13C enrichment in soil profiles during the decomposition of soil organic matter. *Oecologia,* 153, 89-98. https://doi.org/10.1007/s00442-007-0700-8

Breheny, P., & Burchett, W. (2017). Visualization of regression models using Visreg. *The R Journal*, 9, 56-71.

Breuning-Madsen, H., Ehlers-Koch, C., Gregersen, J., & Løjtnant, C. L. (2010). Influence of perennial colonies of piscivorous birds on soil nutrient contents in a temperate humid climate. *Geografisk Tidsskrift-Danish Journal of Geography*, 110(1), 25-35. https://doi.org/10.1080/00167223.2010.10669494

Breusch, T. S., & Pagan, A. R. (1979). A Simple Test for Heteroscedasticity and Random Coefficient Variation. *Econometrica*, 47 (5), 1287-1294. https://doi.org/10.2307/1911963

Briers, J. H. (1988). *'n Ondersoek na aspekte van die vestiging van inheemse bome en struike op versteurde gebiede* [Masters' Thesis, Potchefstroom University for Christian Higher Education]. Potchefstroom.

Brodrick, S. J., & Giller, K. E. (1991). Root nodules: efficient scavengers of molybdenum for N_2-fixation. *Journal of Experimental Botany,* 42(5), 679–686. https://doi.org/10.1093/jxb/42.5.679

Brodrick, S. J., Amijee, F., Kipe-Nolt, J. A., & Giller, K. E. (1995). Seed analysis as a means of identifying micronutrient deficiencies of Phaseolus vulgaris L. in the tropics. *Tropical Agriculture (Trinidad),* 72(4), 277-284.

Bronstein, J. L. (1994a). Our current understanding of mutualism. *The Quarterly Review of Biology,* 69(1), 31-51. https://doi.org/10.1086/418432

Bronstein, J. L. (1994b). Conditional outcomes in mutualistic interactions. *Trends in Ecology & Evolution*, 9(6), 214– 217. https://doi.org/10.1016/0169-5347(94)90246-1

Bronstein, J. L. (2001a). The Costs of Mutualism. *American Zoologist*, 41(4), 825-839, https://doi.org/10.1093/icb/41.4.825

Bronstein, J. L. (2001b). The exploitation of mutualisms. *Ecology Letters*, 4(3), 4277-287.

Bronstein, J. L. (2009). The evolution of facilitation and mutualism. *Journal of Ecology*, *97*(6), 1160-1170. https://doi.org/10.1111/j.1365-2745.2009.01566.x

Brooker, R. W., & Callaghan, T. V. (1998). The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos,* 81, 196-207.

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., Liancourt. P., Tielbörger, K., Travis, J. M. J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C. L., Saccone, P., …

Michalet, R. (2008). Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology,* 96, 18-34. https://doi.org/10.1111/j.1365-2745.2007.01295.x

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378-400. https://doi.org/10.32614/RJ-2017-066.

Brown, D., Ng'ambi, J. W., & Norris, D. (2016). Voluntary intake and palatability indices of Pedi goats fed different levels of Acacia karroo leaf meal by cafeteria method. *Indian Journal of Animal Research*, 50, 41-47.

Brust, G. E. (2019). *Management Strategies for Organic Vegetable Fertility*. In Safety and Practice for Organic Food. Biswas, D., Micallef, S.A. (Eds). Academic Press, pp 193-212, https://doi.org/10.1016/B978-0-12-812060-6.00009-X

Callahan, H. S., Del Fierro, K., Patterson, A. E., & Zafar, H. (2008). Impacts of elevated nitrogen inputs on oak reproductive and seed ecology. *Global Change Biology*, 14(2), 285–293. https://doi.org/10.1111/j.1365-2486.2007.01483.x

Callaway, R. M. (1995). Positive interactions among plants. *The Botanical Review*, 61(4), 306-349. https://doi.org/10.1007/bf02912621

Callaway, R. M. (2007). *Positive interactions and interdependence in plant communities*. Springer Science & Business Media.

Callaway, R. M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas C., Kikodze, D., Cook B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417(6891), 844-848. https://doi.org/10.1038/nature00812

Callaway, R. M., & Walker, L. R. (1997). Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology,* 78(7), 1958-1965. https://doi.org/10.1890/0012-9658(1997)078[1958:cafasa]2.0.co;2

Camara, A. S. (2021). Do woody plants create 'fertile islands' in dryland New Zealand? *New Zealand Journal of Ecology,* 45(1), 1-7. https://doi.org/10.20417/nzjecol.45.20

Cantor, M., M. M. Pires, G. O. Longo, P. R. Guimarães, & Setz, E. Z. F. (2013). Individual variation in resource use by opossums leading to nested fruit consumption. *Oikos,* 122(7), 1085-1093. https://doi.org/10.1111/j.1600-0706.2012.00070.x

Cao, J., Xu, X., Deo, R. C., Holden, N. M., Adamowski, J. F., Gong, Y., Feng, Q., Yang, S., Li, M., Zhou, J., Zhang, J., & Liu, M. (2018). Multi-household grazing management pattern maintains better soil fertility. *Agronomy for Sustainable Development* 38, 1-7. https://doi.org/10.1007/s13593-017-0482-2

Cavieres, L. A., & Badano, E. I. (2009). Do facilitative interactions increase species richness at the entire community level? *Journal of Ecology,* 97(6), 1181–1191. https://doi.org/10.1111/j.1365-2745.2009.01579.x

Caylor, K. K., Shugart, H. H., & Rodriguez-Iturbe I. (2005). Tree canopy effects on simulated water stress in southern African Savannas. *Ecosystems,* 8(1), 17–32.

Choler, P., Michalet, R., & Callaway, R. M. (2001). Facilitation and competition on gradients in alpine plant communities. *Ecology*, 82 (12), 3295-3308. https://doi.org/10.1890/0012-9658(2001)082[3295:facogi]2.0.co;2

Coates-Palgrave, K. (1983). *Trees of Southern Africa*. Cape Town : C. Struik, South Africa. 959 pp.

Coe, M. & Coe, C. (1987). Large herbivores, Acacia trees and bruchid beetles. *South African Journal of Science,* 83, 624-635.

Coolbear, P., Francis, A., & Grierson, D. (1984). The effect of low temperature pre-sowing treatment on the germination performance and membrane integrity of artificially aged tomato seeds. *Journal of Experimental Botany,* 35(11), 1609–1617. https://doi.org/10.1093/jxb/35.11.1609

Craine, J. M., Brookshire, E. N. J., Cramer, M. D., Hasselquist, N. J., Koba, K., Marin-Spiotta, E., Wang, L. (2015). Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils. *Plant Soil,* 396, 1-26. https://doi.org/10.1007/s11104-015-2542-1

Cramer, M. D., Chimphango, S. B. M., van Cauter, A., Waldram, M. S., & Bond, W. J. (2007). Grass competition induces N^2 fixation in some species of African Acacias. *Journal of Ecology*, 95(5), 1123–1133. https://doi.org/10.1111/j.1365-2745.2007.01285.x

Cramer, M. D., van Cauter, A., & Bond, W. J. (2010). Growth of N_2-fixing African savanna Acacia species is constrained by below-ground competition with grass. *Journal of Ecology*, 98(1), 156–167. https://doi.org/10.1111/j.1365-2745.2009.01594.x

Cromhout, M. (2006). *The ecology of the African buffalo in the eastern Kalahari region, South Africa.* [Master's Thesis], University of Pretoria, Pretoria.

D'Odorico, P., Laio, F., Porporato, A., Ridolfi, L., Rinaldo, A., & Rodriguez-Iturbe, I. (2010). Ecohydrology of terrestrial ecosystems. *BioScience,* 60(11), 898–907.

Dáttilo, W., Fagundes, R., Gurka, C. A. Q., Silva, M. S. A., Vieira, M. C. L., Izzo, T. J., Díaz-Castelazo, C., Del-Claro, K., & Rico-Gray, V. (2014). Individual-based ant-plant networks: diurnal-nocturnal structure and species-area relationship. *PLoS ONE,* 9(6), e99838.

Dawson, T. E. (1993). Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia,* 95, 565–574.

Dayton, P. K. (1975). Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs,* 45, 137–159.

Dean, W. R. J., Milton, S.J., & Jeltsch, F. (1999). Large trees, fertile islands and birds in arid savanna. *Journal of Arid Environments,* 41(1), 61-78. https://doi.org/10.1006/jare.1998.0455

den Boer, P. J. (1986). The present status of the competitive exclusion principle. *Trends in Ecology and Evolution,* 1(1), 25-8. https://doi.org/10.1016/0169-5347(86)90064-9

Díaz, M., Tietje, W.D., & Barrett, R. H. (2013). Effects of management on biological diversity and endangered species. In P. Campos, L. Huntsinger, J. L. Oviedo, P. F. Starrs, M. Díaz, R.B. Standiford & G. Montero (Eds), *Mediterranean Oak Wood- land Working Landscapes* (pp. 213–243). Springer.

Dijkstra, F.A., Wrage, K., Hobbie, S.E. & Reich, P.B. (2006). Tree patches show greater N losses but maintain higher soil N availability than grassland patches in a frequently burned oak savanna. *Ecosystems*, 9(3), 441–452.

Ditlhogo, M. K., Setshogo, M. P, & Mosweunyane, G. (2020). Comparative nutritive value of an invasive exotic plant species, Prosopis glandulosa Torr. var. glandulosa, and five indigenous plant species commonly browsed by small stock in the BORAVAST area, south-western

Botswana. *Botswana Journal of Agriculture and Applied Sciences,* 14(1), 7-16. https://doi.org/10.37106/bojaas.2020.25

Domingues, T. F., Ishida, F. Y., Feldpausch, T. R., Grace, J., Meir, P., Saiz, G., Sene, O., Schrodt, F., Sonké, B., Taedoumg, H., Veenendaal, E. M, Lewis, S., & Lloyd, J. (2015). Biome-specific effects of nitrogen and phosphorus on the photosynthetic characteristics of trees at a forest-savanna boundary in Cameroon. *Oecologia*, 178(3), 659-672. https://doi.org/10.1007/s00442-015-3250-5

Dupont, Y. L., Trøjelsgaard, K., Hagen, M., Henriksen, M. V., Olesen, J. M., Pedersen, N. M. E., & Kissling, W. D. (2014). Spatial structure of an individual-based plant-pollinator network. *Oikos,* 123(11), 1301-1310. https://doi.org/10.1111/oik.01426

Dusi, J. L. (1977). Impact of egrets on an upland colony area. *Proceedings of the Colonial Waterbird Group* 1:128-130.

Ellis, J. C. (2005). Marine birds on land: A review of plant biomass, species richness, and community composition in seabird colonies. *Plant Ecology,* 181(2), 227-241. https://doi.org/10.1007/s11258-005-7147-y

Ellis, J. C., Fariña, J. M., & Witman, J. D. (2006). Nutrient transfer from sea to land: the case of gulls and cormorants in the Gulf of Maine. *Journal of Animal Ecology*, 75(2), 565–574 https://doi.org/10.1111/j.1365-2656.2006.01077.x

Elser, J. J., Dobberfuhl, D. R., MacKay, N. A., Schampel, J. H. (1996). Organism size, life history, and N:P stoichiometry. *Bioscience,* 46(9), 674-684. https://doi.org/10.2307/1312897

Elser, J. J., Fagan, W. F., Kerkhoff, A. J., Swenson, N. G., & Enquist, B. J. (2010). Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. *New Phytologist,* 186, 593-608.

Erskine, P. D., Bergstrom, D. M., Schmidt, S., Stewart, G. R., Tweedie, C. E., & Shaw, J. D. (1998). Subantarctic Macquarie Island: A model ecosystem for studying animal-derived nitrogen sources using N-15 natural abundance. *Oecologia*, 117(1–2), 187– 193. https://doi.org/10.1007/s004420050647

Ewald, P. W. (1987). Transmission modes and evolution of the parasitism- mutualism continuum. Annals of the New York Academy of Sciences, 503(1), 295-306.

Fargione, J., & Tilman, D. (2005). Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass. *Oecologia,* 143, 598–606.

Fargione, J., & Tilman, D. G. (2002). Competition and coexistence in terrestrial plants. In U. Sommer and B. Worm, editors. *Competition and coexistence*. Springer Verlag, Berlin, Heidelberg. pp 165–206

Farooq, M, Basra, S. M. A., Hafeez, K., Ahmad, N. (2005). Thermal hardening: a new seed vigour enhancement tool in rice. *Journal of Integrative Plant Biology,* 47(2), 187-193. https://doi.org/10.1111/j.1744-7909.2005.00031.x

Fedriani, J. M., García, L. V., Sánchez, M. E., Calderón, J., & Ramo, C. (2017). Long-term impact of protected colonial birds on a jeopardized cork oak population: conservation bias leads to restoration failure. *Journal of Applied Ecology*, 54(2), 450–458. https://doi.org/10.1111/1365-2664.12672

Fenner, M. (1987). Seedlings. *New Phytologist*, 106, 35-47. https://doi.org/10.1111/j.1469-8137.1987.tb04681.x

Fernández-Marín, B., Gulías, J., Figueroa, C. M., Iñiguez, C., Clemente-Moreno, M. J., Nunes-Nesi, A., Fernie, A. R., Cavieres, L. A., Bravo, L. A., García-Plazaola, J. I., & Gago, J. (2020). How do vascular plants perform photosynthesis in extreme environments? An integrative ecophysiological and biochemical story. *The Plant Journal*, 101(4), 979-1000. https://doi.org/10.1111/tpj.14694

Fernández, M., Alaejos, J., Andivia, E., Madejón, P., Díaz, M. J., & Tapias, R. (2020). Short rotation coppice of leguminous tree Leucaena spp. improves soil fertility while producing high biomass yields in Mediterranean environment. *Industrial Crops and Products*, 157, 112911. https://doi.org/10.1016/j.indcrop.2020.112911

Franklin, K. A., Sommers, P. N., Aslan, C. E., López, B. R., Bronstein, J. L., Bustamante, E., Búrquez, A., Medellín, R. A., & Marazzi, B. (2016). Plant biotic interactions in the Sonoran Desert: current knowledge and future research perspectives. *International Journal of Plant Sciences*. 177(3), 217-234. https://doi.org/10.1086/684261

Fujita, M. S., & Kameda, K. O. (2016). Nutrient Dynamics and Nutrient Cycling by Birds In: Çagan H. Sekercioglu, Daniel G. Wenny, Christopher J. Whelan (Eds). *Why Birds Matter: Avian Ecological Function and Ecosystem Services.* University of Chicago Press. https://doi.org/10.7208/chicago/9780226382777.003.0009

Fyfield, T. P., & Gregory, P. J., (1989). Effects of temperature and water potential on germination, radicle elongation and emergence of mungbean. *Journal of Experimental Botany*, 40(6), 667-674. https://doi.org/10.1093/jxb/40.6.667

García, D. (2016). Birds in ecological networks: insights from bird-plant mutualistic interactions. *Ardeola*, 63(1), 151-180. https://doi.org/10.13157/arla.63.1.2016.rp7

García, L. V., Marañón, T., Ojeda, F., Clemente, L., & Redondo, R. (2002). Seagull influence on soil properties, chenopod shrub distribution, and leaf nutrient status in semi-arid Mediterranean islands. *Oikos*, 98(1), 75–86. https://doi.org/10.1034/j.1600-0706.2002.980108.x

Gerlach, R. W., Dobb, D. E., Raab, G. A., & Nocerino, J. M. (2002). Gy sampling theory in environmental studies. 1. Assessing soil splitting protocols. *Journal of Chemometrics*, 16(7), 321–328. https://doi.org/10.1002/cem.705

Gherardi, L. A., Sala, O. E., & Yahdjian, L. (2013). Preference for different inorganic nitrogen forms among plant functional types and species of the Patagonian steppe. *Oecologia*, 173(3), 1075–1081. https://doi.org/10.1007/s00442-013-2687-7

Gillson, L. (2015). Evidence of a tipping point in a southern African savanna? *Ecological Complexity*, 21, 78-86. https://doi.org/10.1016/j.ecocom.2014.12.005

Gilmore, A. R., Gertner, G. Z., & Rolfe, G. L. (1984). Roosting birds kill pine trees but no toxic effect to soil under roost. *Communications in Soil Science and Plant Analysis*, 15(5), 599-605. https://doi.org/10.1080/00103628409367500

Glanz-Idan, N., Tarkowski, P., Turečková, V., & Wolf, S. (2019). Root–shoot communication in tomato plants: cytokinin as a signal molecule modulating leaf photosynthetic activity. *Journal of Experimental Botany*, 71(1), 247–257. https://doi.org/10.1093/jxb/erz399.

Greenlee, J. T., & Callaway, R. M. (1996). Abiotic Stress and the Relative Importance of Interference and Facilitation in Montane Bunchgrass Communities in Western Montana. *The American Naturalist,* 148(2), 386-396. https://doi.org/10.1086/285931

Gross, N., Börger, L., Duncan, R. P., & Hulme, P. E. (2013). Functional differences between alien and native species: do biotic interactions determine the functional structure of highly invaded grasslands? *Functional Ecology,* 27(5), 1262–1272. https://doi.org/10.1111/1365-2435.12120

Güsewell, S. (2004). N : P ratios in terrestrial plants: variation and functional significance. *New Phytologist*, 164(2), 243–266. https://doi.org/10.1111/j.1469-8137.2004.01192.x

Güsewell, S., & Koerselman, W. (2002). Variation in nitrogen and phosphorus concentrations of wetland plants. *Perspectives in Plant Ecology, Evolution and Systematics*. 5(1), 37–61. https://doi.org/10.1078/1433-8319-0000022

Hale, K. R. S & Valdovinos, F. S. (2021). Ecological theory of mutualism: Robust patterns of stability and thresholds in two-species population models. *Ecology and Evolution*. 11(24), 17651-17671. doi: 10.1002/ece3.8453

Han, W. X, Tang, L. Y, Chen, Y. H., & Fang, J. Y (2013). Relationship between the relative limitation and resorption efficiency of nitrogen vs phosphorus in woody plants. *PLoS ONE,* 8(12), e83366. https://doi.org/10.1371/journal.pone.0083366

Han, W., Fang, J., Guo, D., & Zhang, Y. (2005). Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytologist*, 168(2), 377-385. https://doi.org/10.1111/j.1469-8137.2005.01530.x

Harder, L. D., & Barrett, S. C. H. (1992). The Energy Cost of Bee Pollination for Pontederia cordata (Pontederiaceae). *Functional Ecology*, 6(2), 226-233. https://doi.org/10.2307/2389759

Hartshorn, A. S., Coetsee, C., & Chadwick, O. A. (2009). Pyromineralization of soil phosphorus in a South African savanna. *Chemical Geology*, 267(1–2), 24–31. https://doi.org/10.1016/j.chemgeo.2009.03.021

Hattersley, P.W. (1982). δ^{13} values of C_4 types in grasses. *Functional Plant Biology*, 9(2), 139–154. https://doi.org/10.1071/pp9820139

Havik, G., Catenazzi, A., Holmgren, M. (2014). Seabird nutrient subsidies benefit non-nitrogen fixing trees and alter species composition in South American coastal dry forests. *PLoS ONE,* 9(1), e86381. https://doi.org/10.1371/journal.pone.0086381

Hayes, P., Turner, B. L., Lambers, H., Laliberté, E. (2013). Foliar nutrient concentrations and resorption efficiency in plants of contrasting nutrient-acquisition strategies along a 2-million-year dune chronosequence. *Journal of Ecology,* 102(2), 396-410. https://doi.org/10.1111/1365-2745.12196

Haynes, R. J., & Goh, K. M. (1978). Ammonium and nitrate nutrition of plants. *Biological Reviews*, 53(4), 465–510. https://doi.org/10.1111/j.1469-185x.1978.tb00862.x

Hebert, C. E., Duffe, J., Weseloh, D. V. C., Senese, E. M. T., & Haffner, G. D. (2005). Unique island habitats may be threatened by Double-crested Cormorants. *Journal of Wildlife Management* 69(1), 68-76. https://doi.org/10.2193/0022-541x(2005)069<0068:uihmbt>2.0.co;2

Hobara, S., Koba, K., Osono, T., Tokuchi, N., Ishida, A., Kameda, K. (2005). Nitrogen and phosphorus enrichment and balance in forests colonised by cormorants: Implications of the influence of soil adsorption. *Plant and Soil*, 268(1), 89-101. http://dx.doi.org/10.1007/s11104-004-0231-6

Hobara, S., Osono, T., Koba, K., Tokuchi, N., Fujiwara, S., Kameda, K. (2001). Forest floor quality and N transformations in a temperate forest affected by avian-derived N deposition. *Water, Air, and Soil Pollution,* 130, 679-684.

Högberg, P. (1997). ^{15}N natural abundance in soil-plant systems. *New Phytologist* 137(2), 179-203. https://doi.org/10.1046/j.1469-8137.1997.00808.x

Holland, J. N. (2002). Benefits and costs of mutualism: demographic consequences in a pollinating seed–consumer interaction. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1498), 1405-1412. https://doi.org/10.1098/rspb.2002.2027

Holland, J. N., Deangelis, D. L., Schultz, S. T. (2004). Evolutionary stability of mutualism: interspecific population regulation as an evolutionarily stable strategy. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1550), 1807-1814. https://doi.org/10.1098/rspb.2004.2789

Hoogsteen, M. J. J., Lantinga, E. A., Bakker, E. J., Groot, J. C. J., & Tittonell, P. A. (2015). Estimating soil organic carbon through loss on ignition: effects of ignition conditions and structural water loss. *European Journal of Soil Science*, 66(2), 320-328. https://doi.org/10.1111/ejss.12224

Howe, H. F., & Smallwood, J. (1982). Ecology of Seed Dispersal. *Annual Review of Ecology and Systematics*, 13(1), 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

Huntley, B. J., & Walker, B. H. (2012). Ecology of tropical savannas. Springer Science+Business Media BV.

Irick, D. L., Gu, B., Li, Y. C., Inglett, P. W., Frederick, P. C., Ross, M. S., Wright, A. L., & Ewe, S. M. L. (2015). Wading bird guano enrichment of soil nutrients in tree islands of the Florida Everglades. *Science of The Total Environment*, 532, 40-47. https://doi.org/10.1016/j.scitotenv.2015.05.097

Iwasaki, S., Ikazaki, K., Bougma, A., & Nagumo, F. (2022). Appropriate Use of Local Phosphate Rock Increases Phosphorus Use Efficiency and Grain Yield of Sorghum and Cowpea in the Sudan Savanna. *Frontiers in Soil Science*, 1. https://doi.org/10.3389/fsoil.2021.709507

Jackson, R. B., Banner, J. L., Jobbágy, E. G., Pockman, W. T., & Wall D. H. (2002). Ecosystem carbon loss with woody plant invasion of grasslands. *Nature,* 418(6898), 623–626.

Jakli, B., Tavakol, E., Trankner, M., Senbayram, M., & Dittert, K. (2017). Quantitative limitations to photosynthesis in K deficient sunflower and their implications on water-use efficiency. *Journal of Plant Physiology*, 209, 20–30. https://doi.org/10.1016/j.jplph.2016.11.010

Jin J., Tang, C., & Sale, P. (2015). The impact of elevated carbon dioxide on the phosphorous nutrition of plants: a review. *Annals of Botany,* 116(6), 987-999. https://doi.org/10.1093/aob/mcv088

Johnson, N. C., Graham, J., H., & Smith, F. (1997). Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *New Phytologist*, 135(4), 575-585.

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as ecosystem engineers. *Ecology*, 78(7), 1946-1957. https://doi.org/10.1890/0012-9658(1997)078[1946:paneoo]2.0.co;2

Jones, D. B. (1931). Factors for converting percentages of nitrogen in foods and feeds into percentages of protein (Slightly revised in 1941). US Department of Agriculture Circular 183. https://archive. org/details/factorsforconver183jone

Kahiya, C., Mukaratirwa, S., & Thamsborg, S. M. (2003). Effects of Acacia nilotica and Acacia karoo diets on Haemonchus contortus infection in goats. *Veterinary Parasitology*, 115(3), 265–274. https://doi.org/10.1016/s0304-4017(03)00213-9

Kang, J. G., & van Iersel, M. W. (2004). Nutrient solution concentration affect shoot: root ratio, leaf area index, and growth of subirrigated salvia (Salvia splendens). *HortScience,* 39(1), 49-54. https://doi.org/10.21273/hortsci.39.1.49

Kaur, M. & Kumar, M. (2020). Nesting preferences of birds in relation to exotic trees in Ludhiana, Punjab. *Journal of Animal Research*, 10(1), 105-109. https://doi.org/10.30954/2277-940x.01.2020.14

Keeler, K. H. (1985). Cost: benefit models of mutualism. Pages 100–127 in D. H. Boucher (Ed), *The biology of mutualism*. Oxford University Press, New York.

Klein, A.M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2006). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 303–313. https://doi.org/10.1098/rspb.2006.3721

Koh, S., Tanentzap, A. J., Mouland, G., Dobbie, T., Carr, L., Keitel, J., Hogsden, K., Harvey, G., Hudson, J., & Thorndyke, R. (2012). Double-crested Cormorants alter forest structure and increase damage indices of indi- vidual trees on island habitats in Lake Erie. *Waterbirds*, 35 (Special Publication 1), 13-22. https://doi.org/10.1675/063.035.sp103

Kolb, G., Ekholm, J., & Hambäck, P. (2010). Effects of seabird nesting colonies on algae and aquatic invertebrates in coastal waters. *Marine Ecology Progress Series*, 417, 287–300. https://doi.org/10.3354/meps08791

Kołodziejek, J. (2019). Growth and competitive interaction between seedlings of an invasive *Rumex confertus* and of co-occurring two native Rumex species in relation to nutrient availability. *Scientific Reports,* 9(1), 3298, 1-12. https://doi.org/10.1038/s41598-019-39947-z

Lack, D. (1968). *Ecological adaptations for breeding in birds*. London: Methuen.

Lafferty, D. J. R., Hanson-Dorr, K. C., Prisock, A. M., & Dorr, B. S. (2016). Biotic and abiotic impacts of Double-crested cormorant breeding colonies on forested islands in the southeastern United States. *Forest Ecology and Management*, 369, 10-19. https://doi.org/10.1016/j.foreco.2016.03.026.

Laity, J. J. (2009). *Deserts and desert environments* (Vol. 3). John Wiley & Sons.

Lambers, H., Chapin, F.S. III, & Pons, T. L. (2008). *Plant physiological ecology*. Springer.

Lambers, H., Clements J. C., & Nelson, M. N. (2013). How a phosphorus-acquisition strategy based on carboxylate exudation powers the success and agronomic potential of lupines

(Lupinus, Fabaceae). *American Journal of Botany*, 100(2), 263-288. https://www.jstor.org/stable/23433125

Lambers, H., Shane, M. W., Cramer M. D., Pearse, S. J., & Veneklaas, E. J. (2006). Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Annals of Botany,* 98(4), 693-713. https://doi.org/10.1093/aob/mcl114.

Lamprey, H. F., Halvey, G. & Makacha, S. (1974). Interactions between Acacia, bruchid seed beetles and large herbivores. *East African Wildlife Journal*, 12(1), 81-85. https://doi.org/10.1111/j.1365-2028.1974.tb00109.x

Lang, J. M. & Benbow, M. E. (2013). Species interactions and competition. *Nature Education Knowledge*, 4(4), 8.

le Roux, E., van Veenhuisen, L. S., Kerley, G. I. H., & Cromsigt, J. P. G. M. (2020). Animal body size distribution influences the ratios of nutrients supplied to plants. *Proceedings of the National Academy of Sciences,* 117(36), 22256–22263. https://doi.org/10.1073/pnas.2003269117

Leighton, G. M., & Echeverri, S. (2014). Non-linear influence of nest size on thermal buffering of sociable weaver nests and the maintenance of cooperative nest construction. *Avian Biology Research*, 7(4), 255–260. https://doi.org/10.3184/175815514x14151918723245

Leistner, O. A. (1961). On the dispersal of *Acacia giraffae* by game. *Koedoe*, 4(1), 101-104.

Lemmon, C. R., Bugbee, G. & Stephens, G. R. (1994). Tree damage by nesting Double-crested Cormorants in Connecticut. *Connecticut Warbler,* 14, 27-30.

Lenth, R. V. (2019). emmeans: Estimated Marginal Means, aka Least-Squares Means. https://cran.r-project.org/package=emmeans

Lindenmayer, D. B., Laurance, W. F., Franklin, J. F., Likens, G. E., Banks, S. C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A. D., & Stein, J. A. R. (2013). New Policies for Old Trees: Averting a Global Crisis in a Keystone Ecological Structure. *Conservation Letters*, 7(1), 61–69. https://doi.org/10.1111/conl.12013

Lowney, A. M. (2020). *Sociable weaver nests as a resource to local animal communities.* [PhD Thesis], University of Cape Town. http://hdl.handle.net/11427/36892

Lowney, A. M., & Thomson, R. L. (2021). Ecological engineering across a temporal gradient: sociable weaver colonies create year-round animal biodiversity hotspots. *Journal of Animal Ecology*, 90(10), 2362-2376. https://doi.org/10.1111/1365-2656.13544

Lowney, A. M., & Thomson, R. L. (2022). Ecological engineering across a spatial gradient: sociable weaver colonies facilitate animal associations with increasing environmental harshness. *Journal of Animal Ecology*, 91(7), 1385–1399. https://doi.org/10.1111/1365-2656.13688

Lowney, A. M., Bolopo, D., Krochuk, B. A., & Thomson, R. L. (2020). The large communal nests of sociable weavers provide year-round insulated refuge for weavers and pygmy falcons. *Frontiers in Ecology and Evolution*, 8, 357. https://doi.org/10.3389/fevo.2020.570006

Ludwig, F., Dawson, T. E., Prins, H. H. T., Berendse, F., & Kroon, H. (2004). Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. *Ecology Letters*, 7(8), 623–631. https://doi.org/10.1111/j.1461-0248.2004.00615.x

Ludwig, F., De Kroon, H., & Prins, H. H. T. (2008). Impacts of savanna trees on forage quality for a large African herbivore. *Oecologia*, 155(3), 487–496. https://doi.org/10.1007/s00442-007-0878-9

Ludwig, F., De Kroon, H., Prins, H. H. T., Berendse, F., Kroon, D., & Herbert, H. T. (2001). Effects of nutrients and shade on tree-grass interactions in an East African savanna. *Journal of Vegetation Science,* 12(4), 579–588.

Luna, L., Vignozzi, N., Miralles, I., & Sole-Benet, A. (2018). Organic amendments and mulches modify soil porosity and infiltration in semi-arid mine soils. *Land Degradation and Development*, 29(4), 1019-1030. https://doi.org/10.1002/ldr.2830

Maclean, G. L. (1973a). The sociable weaver, Part 1: Description, distribution, dispersion and populations. *Ostrich,* 44(3-4), 176-190. https://doi.org/10.1080/00306525.1973.9639158

Maclean, G. L. (1973b). The sociable weaver, Part 2: Nest architecture and social organization. *Ostrich,* 44(3-4), 191-218. https://doi.org/10.1080/00306525.1973.9639159

Maclean, G. L. (1973c). The Sociable Weaver, Part 5: Food, feeding and general behaviour. *Ostrich,* 44(3-4), 254-261. https://doi.org/10.1080/00306525.1973.9639162

Mandizvo, T., & Odindo, A. O. (2019). Seed mineral reserves and vigour of Bambara groundnut (Vigna subterranea L.) landraces differing in seed coat colour. *Heliyon*, 5(5), e01635. https://doi.org/10.1016/j.heliyon.2019.e01635

Mapiye, C., Chimonyo, M., Dzama, K., Strydom, P. E., Marufu, M. C., & Muchenje, V. (2009). Nutritional status, growth performance and carcass characteristics of Nguni steers supplemented with Acacia karroo leaf meal. *Livestock Science,* 126(1-3), 206-214. https://doi.org/10.1016/j.livsci.2009.07.001

Marjakangas, E., Abrego, N., Grøtan, V., Lima, R. A. F., Bello, C., Bovendorp, R. S., Culot, L., Hasui, É., Lima, F., Muylaert, R. L., Niebuhr, B. B., Oliveira, A. A., Pereira, L. A., Prado, P. I., Stevens, R. D., Vancine, M. H., Ribeiro, M. C., Galetti, M., & Ovaskainen, O. (2019). Fragmented tropical forests lose mutualistic plant-animal interactions. *Diversity and Distributions*, 26(2), 154-168. https://doi.org/10.1111/ddi.13010

Marschner, H. (2012) *Marschner's Mineral Nutrition of Higher Plants*. Vol. 89, Academic Press, London, 651. https://www.elsevier.com/books/marschners-mineral-nutrition-of-higher-plants/marschner/978-0-12-384905-2

Marume, U., Chimonyo, M., Dzama, K. (2012). Influence of dietary supplementation with Acacia karroo on experimental haemonchosis in indigenous Xhosa lop-eared goats of South Africa. *Livestock Science*, 144, 132-139.

Mashizi, A. K., & Sharafatmandrad, M. (2020). Assessing the effects of shrubs on ecosystem functions in arid sand dune ecosystems. *Arid Land Research and Management*, 34(2), 171-187. https://doi.org/10.1080/15324982.2019.1634655

Materechera, E. K., and Materechera, S. A. (2001). Breaking dormancy to improve germination in seeds of Acacia erioloba. South African Journal of Plant and Soil, 18, 142-146.

Mavi, K., (2010). The relationship between seed coat color and seed quality in watermelon Crimson sweet. *Horticultural Science*, 37(2), 62-69. https://doi.org/10.17221/53/2009-hortsci

McCall, A. C., & Irwin, R. E. (2006). Florivory: the intersection of pollination and herbivory. *Ecology Letters*, 9(12), 1351-1365. https://doi.org/10.1111/j.1461-0248.2006.00975.x

McCarthy, E. L. (1934). Mariotte's bottle. *Science*, 80(2065), 100-100. https://doi.org/10.1126/science.80.2065.100

McLean, E. O. (1982). Soil pH and lime requirement. In Page, A.L. (ed). *Methods of soil analysis*. Part 2, 199. American Society of Agronomy, Wisconsin.

McNaughton, S. J. (1988). Mineral nutrition and spatial concentrations of African ungulates. *Nature,* 334(6180), 343–345. https://doi.org/10.1038/334343a0

Miller, M. F. (1994). Large African herbivores, bruchid beetles and their interactions with Acacia seeds. *Oecologia*, 97(2), 265–270. https://doi.org/10.1007/bf00323159

Milton, S. J., & Dean, W. R. J. (1995). How useful is the keystone species concept, and can it be applied to *Acacia erioloba* in the Kalahari Desert. *Zeitschrift für Ökologie und Naturschutz,* 4, 147-156.

Mira, S., Schnadelbach, A., Correa, E.C., Pérez-García, F. & González-Benito, M.E. (2017). Variability of physical dormancy in relation to seed mechanical properties of three legume species. *Seed Sci. Technol.* 45, 540-556 https://doi.org/10.15258/sst.2017.45.3.11

Mnisi, C. M., & Mlambo, V. (2016). Influence of harvesting site on chemical composition and potential protein value of *Acacia erioloba*, *A. nilotica* and *Ziziphus mucronata* leaves for ruminants. *Journal of Animal Physiology and Animal Nutrition,* 101(5), 994-1003. https://doi.org/10.1111/jpn.12535

Mo, Q., Zou, B., Li, Y., Chen, Y., Zhang, W., Mao, R., Ding, Y., Wang, J., Lu, X., Li, X., Tang, J., Li, Z., & Wang, F. (2015). Response of plant nutrient stoichiometry to fertilization varied with plant tissues in a tropical forest. *Scientific Report 5*, 14605. https://doi.org/10.1038/srep14605.

Mokoboki, H.K., Ndlovu, L.R., Ngambi, J.W., Malatje, M.W., Nikolovav, R.V. (2005). Nutritive value of Acacia tree foliages growing in the Limpopo Province of South Africa. *South African Journal of Animal Science*, 35(4), 221–228. https://doi.org/10.4314/sajas.v35i4.3963

Moore, A., Van Niekerk, J. P., Knight, I. W., & Wessels, H. (1985). The effect of tebuthiuron on the vegetation of the thorn bushveld of the Northern Cape – a preliminary report. *Journal of the Grassland Society of South Africa,* 2(4), 7-10. https://doi.org/10.1080/02566702.1985.9648012

Morris, W. F., Vázquez, D. P., Chacoff, N. P. (2010). Benefit and cost curves for typical pollination mutualisms. *Ecology,* 91(5), 1276-1285. 1276-1285. https://doi.org/10.1890/08-2278.1

Moyo, C. S., Frost, P. G. H., & Campbell, B. M. (2010). Modification of soil nutrients and micro-climate by tree crowns in a semi-arid rangeland of south-western Zimbabwe. *African Journal of Range and Forage Science,* 15(1-2), 16–22.

Mucina, L., & Rutherford, M.C., eds. (2006). The Vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. Pretoria: South African National Biodiversity Institute.

Mulder, C. P. H., Jones, H. P., Kameda, K., Palmborg, C., Schmidt, S., Ellis, J. C., Orrock, J. L., Wait, D. A., Wardle, D. A., Young, H., Croll, D., & Vidal, E., (2011). Impact of seabirds on plant and soil properties. In Mulder, C.P.H., Anderson, W., Towns, D.R., Bellingham, P., eds. *Seabird Island: Ecology, invasion and restoration*. New York, USA: Oxford University Press.

Mulder, C. P., & Keall, S. N. (2001). Burrowing seabirds and reptiles: impacts on seeds, seedlings and soils in an island forest in New Zealand. *Oecologia*, 127(3), 350–360. https://doi.org/10.1007/s004420000600

Naegle, E. R., Burton, J. W., Carter, T. E., & Rufty, T. W. (2005). Influence of seed nitrogen content on seedling growth and recovery from nitrogen stress. *Plant and Soil,* 271(1–2), 329-340. https://doi.org/10.1007/s11104-004-3242-4

Natusch, D. J. D., Lyons, J. A., Brown, G. P., & Shine, R. (2017). Biotic interactions mediate the influence of bird colonies on vegetation and soil chemistry at aggregation sites. *Ecology*, 98(2), 382–392. https://doi.org/10.1002/ecy.1642

Neff, J. C., Reynolds, R., Sanford, R. L., Fernandez, D., & Lamothe, P. (2006). Controls of bedrock geochemistry on soil and plant nutrients in Southeastern Utah. *Ecosystems*, 9(6), 879-893. https://doi.org/10.1007/s10021-005-0092-8

Nel, J. A., Craine, J. M., & Cramer, M. D. (2018). Correspondence between δ^{13}C and δ^{15}N in soils suggests coordinated fractionation processes for soil C and N. *Plant Soil,* 423, 257–271. https://doi.org/10.1007/s11104-017-3500-x

Newman, J. A., Gillis, S., & Hager, H. A. (2022). Costs, Benefits, Parasites and Mutualists: The Use and Abuse of the Mutualism–Parasitism Continuum Concept for Epichloë Fungi. *Philosophy, Theory, and Practice in Biology*, 14(9), 1-41. https://doi.org/10.3998/ptpbio.2103

Obeso, J. R. (2012). Mineral nutrient stoichiometric variability in Hedera helix (Araliaceae) seeds. *Annals of Botany*, 109(4), 801–806. https://doi.org/10.1093/aob/mcr306

Offenberg, J. (2001). Balancing between mutualism and exploitation: the symbiotic interaction between Lasius ants and aphids. *Behavioral Ecology and Sociobiology*, 49(4), 304–310. https://doi.org/10.1007/s002650000303

Olde Venterink, H. (2011). Does phosphorus limitation promote species-rich plant community? *Plant Soil*, 345(1-2), 1-9. https://doi.org/10.1007/s11104-011-0796-9

Olofsson, J. (2004). Positive and negative plant–plant interactions in two contrasting arctic–alpine plant communities. *Arctic Antarctic and Alpine Research*, 36(34), 464-467. https://doi.org/10.1657/1523-0430(2004)036[0464:panpii]2.0.co;2

Olubodun, O.P., Lowney, A.M., Bolopo, D., Thomson R. L. (2023). Breeding biology of the African Pygmy Falcon: long-term variation and seasonal decline in breeding performance of an arid zone raptor. Journal of Ornithology, 164, 689–704. https://doi.org/10.1007/s10336-023-02065-9

Otero, X. L., De La Peña-Lastra, S., Pérez-Alberti, A., Ferreira, T. O., Huerta-Diaz, M. A. (2018). Seabird colonies as important global drivers in the nitrogen and phosphorus cycles. *Nature Communications,* 9(1), 1-8. https://doi.org/10.1038/s41467-017-02446-8

Otero, X. L., Tejada O., Martin-Pastor M., De La Pena S., Ferreira T. O., & Perez-Alberti, A. (2015). Phosphorus in seagull colonies and the effect on the habitats. The case of yellow-legged gulls (Larus michahellis) in the Atlantic Islands National Park (Galicia- NW Spain). *Science of the Total Environment,* 532,383–397.

Parsons, A. J., Abrahams, A. D., & Simanton, J. R. (1992). Microtopography and soil-surface materials on semi-arid piedmont hillslopes, southern Arizona. *Journal of Arid Environments*, 22(2), 107–115. https://doi.org/10.1016/s0140-1963(18)30585-8

Pataki, D. E., Billings, S. A., Naumburg, E., Goedhart, C. M. (2008). Water sources and nitrogen relations of grasses and shrubs in phreatophytic communities of the Great Basin desert. *Journal of Arid Environment* 72(9), 1581–1593. https://doi.org/10.1016/j.jaridenv.2008.03.011

Paterson, W. (Lieut.) (1789). A Narrative of four Journeys into the Country of the Hottentotts and Caffria. In the Years One Thousand Seven Hundred and Seventy-Seven, Eight, and Nine. London: J Johnson. https://archive.org/details/narrativeoffourj1789pate/page/n1/mode/2up

Pellew, R. A., & Southgate, B. J. (1984). The parasitism of Acacia tortilis seeds in the Serengeti. *African Journal of Ecology*, 22(1), 73-75. https://doi.org/10.1111/j.1365-2028.1984.tb00679.x

Pellmyr, O., & Leebens-Mack, J. (2000). Reversal of mutualism as a mechanism for adaptive radiation in yucca moths. *The American Naturalist*, 156(S4), S62–S76. https://doi.org/10.1086/303416

Peñuelas, J., & Sardans, J. (2009). Elementary factors. *Nature*, 460(7257), 803–804. https://doi.org/10.1038/460803a

Pérez-Ramos, I. M., Ourcival, J. M., Limousin, J. M. & Rambal, S. (2010). Mastseeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. *Ecology*, 91(10), 3057-3068. https://doi.org/10.1890/09-2313.1

Pinheiro, J., Bates, D., R Core Team (2022). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-161, https://CRAN.R-project.org/package=nlme.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New phytologist*, 182(3), 565-588. https://doi.org/10.1111/j.1469-8137.2009.02830.x

Prayag, K. D., du Toit, C. J., Cramer, M. D., Thomson, R. L. (2020). Faunal input at host plants: Can camel thorn trees use nutrients imported by resident sociable weavers? *Ecology and Evolution*, 10(*20*), 11643-11656. https://doi.org/10.1002/ece3.6798

Qiu, T., Andrus, R., Aravena, M-C, Ascoli, D., Bergeron, Y., Berretti, R., Berveiller, D., Michal Bogdziewicz, M., Boivin, T., Bonal, R., Bragg, D. C., Caignard, T., Calama, R., Camarero, J. J., Chang-Yang, C-H., Cleavitt, N. L., Courbaud, B., Courbet, F., Curt, T., Das, A. J., … Clark, J. S. (2022). Limits to reproduction and seed size-number trade-offs that shape forest dominance and future recovery. *Nature Communications*, 13, 2381. https://doi.org/10.1038/s41467-022-30037-9

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Ranal, M. A., & Garcia De Santana, D. (2006). How and why to measure the germination process? *Revista Brasileira de Botânica*, 29(1), 1-11. https://doi.org/10.1590/s0100-84042006000100002

Ravhuhali, K. E., Mlambo, V., Beyene, T. S., & Palamuleni, L. G. (2020). Effects of soil type on density of trees and nutritive value of tree leaves in selected communal areas of South Africa. *South African Journal of Animal Science*, 50(1), 88–98. https://doi.org/10.4314/sajas.v50i1.10

Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *PNAS*, 101(30), 11001-11006. https://doi.org/10.1073/pnas.0403588101

Ribet, J., & Drevon, J. -J. (1996). The phosphorus requirement of N2-fixing and urea-fed Acacia mangium. *New Phytologist*, 132(3), 383-390. https://doi.org/10.1111/j.1469-8137.1996.tb01858.x

Richardson, D. M., Allsopp, N., D'Antonio, C. M., Milton, S. J., Rejmánek, M. (2000). Plant invasions-the role of mutualisms. *Biological Reviews*, 75(1), 65-93. https://doi.org/10.1111/j.1469-185x.1999.tb00041.x

Richardson, S. J., Allen, R. B., Whitehead, D., Carswell, F. E., Ruscoe, W. A., & Platt, K. H. (2005). Climate and net carbon availability determine temporal patterns of seed production by Nothofagus. *Ecology*, 86(4), 972–981. https://doi.org/10.1890/04-0863

Rico-Gray, V., & Oliveira, P. S. (2007). *The Ecology and Evolution of Ant-Plant Interactions.* Chicago, IL: Chicago University

Riginos, C., & Young, T. P. (2007). Positive and negative effects of grass, cattle, and wild herbivores on Acacia saplings in an East African savanna. *Oecologia*, 153(4), 985-995

Roques, K. G., O'Connor, T.G., & Watkinson, A. R. (2001). Dynamics of shrub encroachment in an African savanna: Relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, 38(2), 268-280

Rotundo, J. L., & Aguiar, M. R. (2005). Litter effects on plant regeneration in arid lands: a complex balance between seed retention, seed longevity and soil–seed contact. *Journal of Ecology* 93(4), 829–838. https://doi.org/10.1111/j.1365-2745.2005.01022.x

Roughgarden, J. (1975). Evolution of marine symbiosis -- a simple cost-benefit model. *Ecology* 56(5), 1202–1208. https://doi.org/10.2307/1936160

Ryan, P. G., & Watkins, B. P. (1989). The influence of physical factors and ornithogenic products on plant and arthropod abundance at an inland nunatak group in Antarctica. *Polar Biology*, 10(2), 151-160. https://doi.org/10.1007/bf00239162

Safriel, U., Adeel, Z., Niemeijer, D., Puigdefabregas, J., White, R., Lal, R., … Mcnab, D. (2005). Dryland Systems, Millenium Ecosystem Assessment. New York, NY: Island Press.

Sandhu, S. K. (1993). *Ecological studies on the association of birds with trees with special reference to nest-site selection* [PhD Thesis]. Punjab Agricultural University, Ludhiana, India.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K. K., Coughenour, M. B., Diouf, A., Ekaya, W., Feral, C. J., … Zambatis, N. (2005). Determinants of woody cover in African savannas. *Nature*, 438(7069), 846–849. https://doi.org/10.1038/nature04070

Sardans, J., & Peñuelas, J. (2015). Potassium: a neglected nutrient in global change. *Global Ecology and Biogeography*, 24(3), 261–275. https://doi.org/10.1111/geb.12259

Schlesinger, W. H., & Pilmanis, A. M. (1998). Plant-soil interactions in deserts. *Plant-Induced Soil Changes: Processes and Feedbacks*, 169–187. https://doi.org/10.1007/978-94-017-2691-7_9

Schlesinger, W. H., Abrahams, A. D., Parsons, A. J., & Wainwright, J. (1999). Nutrient losses in runoff from grassland and shrubland habitats in Southern New Mexico: I. rainfall simulation experiments. *Biogeochemistry*, 45(1), 21–34. https://doi.org/10.1007/bf00992871

Schlesinger, W. H., Raikes, J. A., Hartley, A. E., & Cross, A. F. (1996). On the spatial pattern of soil nutrients in desert ecosystems. *Ecology,* 77(2), 364-374. https://doi.org/10.2307/2265615

Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Huenneke, L. F., Jarrell, W. M., Virginia, R. A., & Whitford, W. G. (1990). Biological feedbacks in global desertification. *Science* 247(4946), 1043-1048. https://doi.org/10.1126/science.247.4946.1043

Schleuning, M. , Fründ, J. & García, D. (2015). Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant-animal interactions. *Ecography*, 38(4), 380–392. https://doi.org/10.1111/ecog.00983

Schöb, C., Armas, C., Pugnaire, F. I. (2013). Direct and indirect inter- actions co-determine species composition in nurse plant systems. *Oikos,* 122(9), 1371-1379. https://doi.org/10.1111/j.1600-0706.2013. 00390.x

Scholes, R. J., & Archer, S. R. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, 28(1), 517-544. https://doi.org/10.1146/annurev.ecolsys.28.1.517

Schoonhoven, L. M., van Loon J. J. A., & Dicke, M. (2005). *Insect–Plant Biology.* Oxford University Press. https://doi.org/10.1007/978-1-4899-3200-6

Sebata, A. (2017). Ecology of Woody Plants in African Savanna Ecosystems. *Plant Ecology - Traditional Approaches to Recent Trends*. https://doi.org/10.5772/intechopen.69865

Seymour, C., & Milton, S. (2003). A collation and overview of research information on *Acacia erioloba* (Camelthorn) and identification of relevant research gaps to inform protection of the species. Department of Water Affairs and Forestry. Contract No. 2003/089.

Shapiro, S. S., Wilk, M. B., & Chen, H. J. (1968). A comparative study of various tests of normality. *Journal of the American Statistical Association*, 63(324), 1343-1372. https://doi.org/10.1080/01621459.1968.10480932

Shieldcastle, M. C. & Martin, L. (1997). Colonial waterbird nesting on west sister island national wildlife refuge and the arrival of double-crested cormorants. *Symposium on Double-Crested Cormorants: Population Status and Management Issues in the Midwest.* 12. https://digitalcommons.unl.edu/nwrccormorants/12

Sitters, J., & Venterinka, H. O. (2021). Body size–fecal nutrient patterns of mammalian herbivores. *PNAS,* 118(6), e2020137118. https://doi.org/10.1073/pnas.2020137118

Sitters, J., Bakker, E. S., Veldhuis, M. P., Veen, G. F., Venterink, O. H., Vanni, M. J. (2017). The Stoichiometry of Nutrient Release by Terrestrial Herbivores and Its Ecosystem Consequences. *Frontiers in Earth Science,* 5(32), 1-8. https://doi.org/10.3389/feart.2017.00032

Sitters, J., Edwards, P.J., Suter, W., & Olde Venterink, H. (2015). Acacia tree density strongly affects N and P fluxes in savanna. *Biogeochemistry,* 123(1/2), 285–97.

Smaill, S. J., Clinton, P. W., Allen, R. B., & Davis, M. R. (2011). Climate cues and resources interact to determine seed production by a masting species. *Journal of Ecology*, 99(3), 870–877. https://doi.org/10.1111/j.1365-2745.2011.01803.x

Smethurst, P. (2004). Tree Physiology | Nutritional Physiology of Trees. Editor(s): Jeffery Burley. *Encyclopedia of Forest Sciences*. https://doi.org/10.1016/B0-12-145160-7/00103-4

Smith, R. I. L. (1984). Terrestrial plant biology of the sub-Antarctic and Antarctic. In Laws, R. M. (ed.), *Antarctic Ecology, vol. 1*(pp. 61-162). Academic Press.

Sone, K., Noguchi, K., & Terashima, I. (2005). Dependency of branch diameter growth in young Acer trees on light availability and shoot elongation. *Tree physiology*, 25(1), 39-48. https://doi.org/10.1093/treephys/25.1.39

Spottiswoode, C. N. (2005). Sociable weaver, *Philetairus socius*. In: Hockey, P. A. R., Dean, W. R. J. and Ryan, P. G. (eds), *Roberts – birds of Southern Africa*. Trustees of the John Voelcker Bird Fund, Cape Town, pp. 1007-1010.

Sprugel, D. G., Hinckley, T. M., & Schaap, W. (1991). The theory and practice of branch autonomy. *Annual Review of Ecology and Systematics*, 22(1), 309-334. https://doi.org/10.1146/annurev.es.22.110191.001521

Stachowicz, J. J. (2001). Mutualism, Facilitation, and the Structure of Ecological Communities: Positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend, *BioScience*, 51(3), 235–246. https://doi.org/10.1641/0006-3568(2001)051[0235:MFATSO]2.0.CO;2

Sterner, R. W., & Elser, J. J. (2002). *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press, UK

Sthultz, C. M., Gehring, C. A., & Whitham, T. G. (2007). Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. *New Phytologist*, 173(1), 135-145.

Sugihara, S., Shibata, M., Mvondo-Ze, A. D., Araki, S., Kosaki, T., Funakawa, S. (2017). Soil phosphorus of stable fraction differentially associate with carbon in the tropical forest and savanna of eastern Cameroon. *Soil Science and Plant Nutrition*, 63(6), 616-627. https://doi.org/10.1080/00380768.2017.1403841

Tao, Y., Zhou, X. B., Zhang, Y. M., Yin, B. F., Li, Y. G., & Zang, Y. X. (2021). Foliar C:N:P stoichiometric traits of herbaceous synusia and the spatial patterns and drivers in a temperate desert in Central Asia. *Global Ecology and Conservation*, 28 (e01620). https://doi.org/10.1016/j.gecco.2021.e01620

Thompson Hobbs, N. (1996). Modification of ecosystems by ungulates. *The Journal of Wildlife Management,* 60(4), 695–713.

Thompson, J. N., & Fernandez, C. C. (2006). Temporal dynamics of antagonism and mutualism in a geographically variable plant-insect interaction. *Ecology,* 87(1), 103-112. https://doi.org/10.1890/05-0123

Throop, H. L. & Belnap, J. (2019). Connectivity dynamics in dryland litter cycles: moving decomposition beyond spatial stasis. *BioScience,* 69, 602-614.

Tölgyesi, C., Török, P., Hábenczyus, A. A., Bátori, Z., Valkó, O., Deák, B., Tóthmérész, B., Erdős, L., Kelemen, A. (2020). Underground deserts below fertility islands? Woody species desiccate lower soil layers in sandy drylands. *Ecography*, 43(6), 848-859. https://doi.org/10.1111/ecog.04906

Tongway, D. J., Ludwig, J. A. (1994). Small-scale resource heterogeneity in semi-arid landscapes. *Pacific Conservation Biology,* 1(3), 201-208. https://doi.org/10.1071/pc940201

Traveset, A., & Richardson, D. M. (2014). Mutualistic interactions and biological invasions. *The Annual Review of Ecology, Evolution, and Systematics,* 45(1), 89-113. https://doi.org/10.1146/annurev-ecolsys-120213-091857

Treydte, A. C., Heitkönig I. M. A., Prins H. H. T., and Ludwig F. (2007). Trees improve grass quality for herbivores in African savannas. *Perspectives in Plant Ecology, Evolution and Systematics,* 8(4), 197–205.

Treydte, A. C., Looringh van Beeck, F. A., Ludwig, F., & Heitkönig, I. M. A. (2008). Improved quality of beneath-canopy grass in South African savannas: local and seasonal variation. *Journal of Vegetation Science,* 19(5), 663–670. https://doi.org/10.3170/2008-8-18435

Tur, C., Olesen, J. M., & Traveset, A. (2014). Increasing modularity when downscaling networks from species to individuals. *Oikos*, 124(5), 581–592. https://doi.org/10.1111/oik.01668

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11(12), 1351-1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Valverde, J., Gómez, J. M., & Perfectti, F. (2015). The temporal dimension in individual-based plant pollination networks. *Oikos*, 125(4), 468-479. https://doi.org/10.1111/oik.02661

Van Bael, S.A., Brawn, J. D., & Robinson, S. K. (2003). Birds defend trees from herbivores in a Neotropical forest canopy. *Proceedings of the National Academy of Sciences*, 100 (14), 8304-8307; https://doi.org/10.1073/pnas.1431621100

van der Waal, C., Kool A., Meijer S. S., Kohi E., Heitkönig I. M. A., de Boer W. F., van Langevelde F., Grant R. C., Peel M. J. S., Slotow R., de Knegt H. J., Prins H. H. T., & de Kroon H. (2011). Large herbivores may alter vegetation structure of semi-arid savannas through soil nutrient mediation. *Oecologia,* 165(4), 1095–1107.

Van der Walt, P., & le Riche, E. (1999). *The Kalahari and its plants*. Van der Walt & le Riche, Pretoria.

van Rooyen, N. & van Rooyen, G. (2017). Ecological Evaluation of Tswalu Kalahari Reserve-November, 2017.

Venables WN, Ripley BD (2002) Spatial statistics. In: Ripley BD (ed) Modern applied statistics with S. Springer, New York, pp 419–434https://doi.org/10.1007/978-0-387-21706-2

Verboom, G. A., Stock, W. D., & Cramer, M. D. (2017). Specialization to Extremely Low-Nutrient Soils Limits the Nutritional Adaptability of Plant Lineages. *The American Naturalist*, 189(6), 684-699. http://orcid.org/0000-0003-2475-2963

Veum, L. M., Dorr, B. S., Hanson-Dorr, K. C., Moore, R. J., & Rush, S. A. (2019). Double-crested cormorant colony effects on soil chemistry, vegetation structure and avian diversity. *Forest Ecology and Management*, 453(117588). https://doi.org/10.1016/j.foreco.2019.117588

Vitousek, P.M., & Walker, L.R. (1989). Biological invasion by Myrica faya in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecological monographs*, 59(3), 247–65.

Vona, V., Centeri, C., Biró, Z., Vona, M., Kalocsai, R., Jakab, G., Kauser, J., Kulmány, I. M., Kovács, A. J., & Milics, G. (2022). Comparing Different Phosphorus Extraction Methods: Effects of Influencing Parameters. *Sustainability*, 14(4), 2158. https://doi.org/10.3390/su14042158

Wagner, T. C., Richter, J., Joubert, D. F., & Fischer, C. (2018). A dominance shift in arid savanna: An herbaceous legume outcompetes local C4 grasses. *Ecology and Evolution*, 8(13), 6779-6787. https://doi.org/10.1002/ece3.4188

Walter, G. H. (1991). What is resource partitioning? *Journal of Theoretical Biology,* 150(2),137–143.

Weseloh, D. V., & Ewins, P. J. (1994). Characteristics of a rapidly increasing colony of double-crested cormorants (*Phalacrocorax auratus*) in Lake Ontario: population size, reproduction parameters and band recoveries. *Journal of Great Lakes Res*earch, 20(2), 433-456.

Whelan, C. J., Wenny, D. G., & Marquis, R. J. (2008). Ecosystem services provided by birds. *Annals of the New York Academy of Sciences*, 1134, 25–60. https://doi.org/10.1196/annals.1439.003

Wood, S. N. (2017). Generalized Additive Models: An Introduction with R (2nd ed.). Chapman and Hall/CRC. https://doi.org/10.1201/9781315370279

Wookey, P.A., Robinson, C.H., Parsons, A.N., Welker, J.M., Press, M.C., Callaghan, T.V., & Lee, J.A. (1995). Environmental constraints on the growth, photosynthesis and reproductive development of Dryas octopetala at a high arctic polar semi-desert, Svalbard. *Oecologia*, 102, 478–489. https://doi.org/10.1007/bf00341360

Yahdjian, L., Gherardi, L., & Sala, O. E. (2011). Nitrogen limitation in arid-subhumid ecosystems: A metaanalysis of fertilisation study. *Journal of Arid Environments,* 75(8), 675–680.

Yan, Y. C., Yan, R. R., Chen, J. Q., Xin, X. P., Eldridge, D. J., Shao, C. L., Wang, X., Lv, S. J., Jin, D. Y., Chen, J. Q., Guo, Z. J., Chen, B. R., & Xu. L. J. (2018). Grazing modulates soil temperature and moisture in a Eurasian steppe. *Agricultural and Forest Meteorology,* 262, 157-165. https://doi.org/10.1016/j.agrformet.2018.07.011

Yan, Y., Xu, D., Xu, X., Wang, D., Wang, X., Cai, Y., Chen, J., Xin, X., & Eldridge, D. J. (2019). Shrub patches capture tumble plants: potential evidence for a self-reinforcing pattern in a semiarid shrub encroached grassland. *Plant and Soil*, 442(1–2), 311–321. https://doi.org/10.1007/s11104-019-04189-5

Yang, M., Liu, M., Lu, J., & Yang, H. (2019). Effects of shading on the growth and leaf photosynthetic characteristics of three forages in an apple orchard on the Loess Plateau of eastern Gansu, China. *PeerJ,* 7(e7594). https://doi.org/10.7717/peerj.7594

Ye, M., Zhang, Z., Huang, G., Xiong, Z., Peng, S., & Li Y. (2020). High leaf mass per area *Oryza* genotypes invest more leaf mass to cell wall and show a low mesophyll conductance, *AoB PLANTS*, 12(4), 1-12. https://doi.org/10.1093/aobpla/plaa028

Zhang, P. J., Yang, J., Zhao, L.Q., Bao, S., & Song, B. Y. (2011). Effect of *Caragana tibetica nebkhas* on sand entrapment and fertile islands in steppe–desert ecotones on the Inner Mongolia plateau, China. *Plant Soil,* 347, 79–90. https://doi.org/10.1007/s11104-011-0813-z

Zhao, H., Wei, D., Yan, Y., Wu, J., & Wang, X. (2020). Alpine Hummocks Drive Plant Diversity and Soil Fertile Islands on the Tibetan Plateau. *Wetlands,* 40, 1217–1227 https://doi.org/10.1007/s13157-020-01275-8

Zhao, Y., Wu, J., He, C., & Ding, G. (2017). Linking wind erosion to ecosystem services in drylands: A landscape ecological approach. *Landscape Ecology,* 32, 2399–2417. https://doi.org/10.1007/s10980-017-0585-9

Ziółek, M., & Melke, J. (2014). The impact of seabirds on the content of various forms of phosphorus in organic soils of the Bellsund coast, western Spitsbergen. *Polar Research,* 33, 19986. https://doi.org/10.3402/polar.v33.19986

Żółkoś, K., & Meissner, W. (2008). The effect of Grey Heron (Ardea cinerea L.) colony on the surrounding vegetation and the biometrical features of three undergrowth species. *Polish Journal of Ecology,* 56, 65-74. https://doi.org/10.1007/s11284-015-1288-9

Zwolicki, A., Zmudczyńska-Skarbek, K. M., Iliszko, L., & Stempniewicz, L. (2013). Guano deposition and nutrient enrichment in the vicinity of planktivorous and piscivorous seabird colonies in Spitsbergen. *Polar Biology,* 36, 363-372. https://doi.org/10.1007/s00300-012-1265-5