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Foreword

The papers that follow were authored by the students in the 2024 Dartmouth College, Department of Environmental Studies Foreign Study Program in Namibia. Dartmouth College is a liberal arts university in Hanover, New Hampshire, USA. The students were tasked with engaging productively in the socio-ecological system in and around Gobabeb Namib Research Institute. They worked closely with research station staff and interns as well as field mentors from a range of disciplines to develop and complete novel group research projects in this system. This work builds on over a decade of collaboration with Gobabeb and other community partners. These four papers are some of the products of the engagement in 2024.

The students were: Solange Acosta Rodríguez, Phoebe Altman, Anna Block, FT Chiu, Mia Compton-Engle, Reah Donohue, Marina Frayre, Jacob Garland, Lauren Heller, Mikhaila Hurley, Paulie Horvath, Corey Huebner, Evan Kaye, Lindsey Lu, Jadin Scott, and Tobin Yates.

There were many people who made this work possible – too many to mention individually. But we would particularly like to thank Gillian Maggs-Kolling, Eugene Marais, Bernice Coetzee, Leena Kapulwa, and the rest of the Gobabeb staff and interns. Our extraordinary field teaching team - Saima Shikesho, Rebecca Finger, Jonathan Davies, Elizabeth Wolkovich, Michael Butler Brown, Doug Bolger, and course TA Miranda Zammarelli - acted as intellectual catalysts and provided technical expertise and undying encouragement. Finally, thank you to Jeff Muntifering, Karen Bieluch, and Kim Wind for everything you do to make this program a success.

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Hosting the Hungry Heights: Variation of Woody Vegetation Along Namibia's Kuiseb River and Its Implications for Giraffe Translocation

November 16, 2024

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Abstract

The successful translocation of wildlife is a critical conservation tool in reversing biodiversity loss and ensuring stable species populations. In a giraffe translocation assessment, diet, or woody vegetation availability, plays a crucial role. The Kuiseb River, an ephemeral river along the Namib coast of Namibia, houses a diverse mix of woody vegetation species. However, their composition differs with distance from the coast due to varying fog, rainwater and groundwater inputs. Therefore, to determine the suitability of the Kuiseb River for a giraffe translocation, we compared woody vegetation compositions at different distances from the coast with other ephemeral rivers—including the Hoanib, Hoarusib, and Khumib Rivers—where there is existing giraffe presence. For our samples, we selected four sites along the Kuiseb River distanced 28 kilometers from each other. In each site, we designated six transects and collected woody vegetation data to derive plant density, biomass density, and diversity. To account for both ecological and translocation-applicable considerations, we separated our data into two spatial scales: riparian woodland (the actual length of riparian vegetation) and riparian zone (a set distance from the river channel within which giraffes forage). We concluded that, on average, plant density along the Kuiseb River was higher in sites further inland. Log biomass followed a similar pattern, though anomalous results rendered this trend less consistent. However, alpha and beta diversity testing produced contrasting results, with greater diversity closer to the coast. Nonetheless, diversity is not necessarily indicative of giraffe diet availability, so plant density and biomass density remain more useful metrics. These findings ultimately suggest that woody vegetation composition varies along the Kuiseb River's coastal gradient and is more favorable for giraffes further inland, making this area more suitable for a giraffe translocation.

Introduction

Global wildlife populations have dramatically declined in the past 50 years, with monitored wildlife populations decreasing by an average of 73% (*World Wildlife Fund*, 2024). These declines are primarily driven by human influences, including pollution, habitat reduction, human-wildlife conflict, poaching, and climate change (Habibullah, 2022). Concerned about biodiversity loss and its implications, governments, NGOs, and private actors have turned to various strategies to reverse the declining trends, such as conducting population assessments, engaging local communities, establishing protected areas, and employing active interventions like species translocations (Gašparová, 2024; Muller et al., 2018).

Translocation involves the moving of species individuals to a new location with sufficiently similar resources, in such a way that allows the population to thrive over the long term without harming other wildlife or nearby communities (Muller et al., 2020). It can be used to maintain the genetic diversity of existing populations, increase the numbers of struggling populations, and reintroduce new populations into areas that the species once inhabited (Gaywood et al., 2023). Such practices have succeeded for the white rhinoceros and the sea otter, whose wild populations are now making a significant comeback (Tsavo Trust, 2024; Learn, 2021). However, many translocation practices fall short of intended outcomes, with many attempts failing within the first four years of release (Bubac et al., 2019). Thus, to truly succeed, translocations must assess several factors in both the original and the post-translocation sites, including but not limited to the genetic background of the population (Bertola, 2022), its previous behavioral patterns (M. Brown, personal communication, November 8, 2024), any biological or anthropological factors that would threaten the population (Patel, 2021), human resources available to conduct the translocation (Patel, 2021), and the availability of food and water resources (Gaywood et al., 2023). Availability of food and water becomes particularly important in arid habitats, as both resources tend to be scarce due to the lack of rainfall (Qu, 2024).

One arid habitat species for which translocation has shown great promise is the giraffe (*Giraffa camelopardalis*; M. Brown, personal communication, November 8, 2024). According to the last global assessment published in 2018, giraffes are not only classified as a vulnerable species, but have had decreasing populations for nearly thirty years, or as long as those populations have been measured (Muller et al., 2018). Such trends come primarily from human-wildlife conflict, poaching, competition between livestock and wild animals (Di Marco et al., 2014), and climate change (Beever et al., 2011). However, certain countries have managed to combat declining population trends. Namibia, a country with a giraffe population of around 12,000 individuals (Giraffe Conservation Fund, 2016), has found success in maintaining healthy populations due in part to its effective translocations (M. Brown, personal communication, November 8, 2024; Giraffe Conservation Fund, 2016). That being said, though standardized translocation practices exist for many other important species (Muller et al., 2020; IUCN/SSC, 2013), standardized rules and guidelines for the translocation of giraffes are still under development (M. Brown, personal communication, November 8, 2024).

Even in the absence of standardized guidelines, giraffe translocation assessments tend to focus on the same characteristics as translocations for other species when deeming a suitable location: genetics, biological and anthropological threats, human resources available to conduct the translocation, and food availability (Muller et al., 2020). Giraffes are obligate browsers, feeding on leaves and twigs from woody vegetation, which comprise around 95% of their diet (Fennessy, 2004). Giraffes favor these woody vegetation species due to their high moisture content, and finding moist, woody vegetation drives the majority of giraffe habitat use and foraging behavior (M. Brown, personal communication, November 8, 2024). Around 60-70% of giraffe diet in the Hoarusib and Hoanib rivers of Namibia is comprised of *Acacia erioloba* (Camel Thorn), *Salvadora persica* (Mustard Tree), and *Faidherbia albida* (Apple-Ring Acacia) due to their high water and nutrient content (Fennessy, 2004). However, giraffes also subsist on other woody species such as *Acanthosicyos horridus* (!Nara), *Euclea pseudebenus* (Black Ebony), *Tamarix usneoides* (Wild Tamarix), and *Nicotiana glauca* (Wild Tobacco) to meet their nutritional needs (Fennessy, 2004). Therefore, vegetation diversity and where woody vegetation is distributed in both space and time help to determine whether a translocated giraffe population could survive.

One location currently being considered for giraffe translocation is the Kuiseb River (M. Brown, personal communication, November 8, 2024), a 560 km ephemeral river system located in the Central Namib Desert of Namibia (Morgan, 2019). Ephemeral river systems like the Kuiseb have a uniquely linear spatiotemporal configuration of vegetation and are vitally important to Namibia, as around 20% of the country's land area and people reside within their catchments (Jacobson, 1995). While most of the Namib Desert experiences a harsh and variable climate, ephemeral rivers provide a diversity of natural resources and spectacular landscapes. Aquifer storage from river flooding provides essential water for farmers and towns, as well as sustains forests that support livestock and wildlife (Jacobson, 1995).

The flood pulses of the Kuiseb River in particular also serve as a barrier between two uniquely distinct ecosystems of the Central Namib Desert: the gravel plains to the north and the Namib Sand Sea to the south (Morgan, 2019). The river is a hydrologically losing system, meaning that the riverbed and shallow soil of the riparian zone remain dry nearly year-round (Morgan et al., 2024). The river experiences sporadic, seasonal flooding between December and April, allowing the aquifer in the lower reaches of the Kuiseb (within ~150 km of the coast) to recharge (Morgan, 2019). Rainfall in the lower Kuiseb ranges from 15 to 50 mm per annum, which is far too little to contribute to river flow (Morgan 2020); however, heavier rainfall (~350 mm per annum) occurs in the Khomas Hochland and escarpment zone in the higher Kuiseb ranges. Thus, a gradient emerges, with the river receiving more rainfall overall as one moves farther from the coast. The opposite gradient is present for fog, with much higher concentrations around the river sections closer to the coast (Gottlieb et al., 2019). Groundwater, though dependent on rainfall for recharge, does not seem to follow easily identifiable gradients (NamWater groundwater level data). Given that giraffe-favored vegetation predominantly rely on groundwater and deep soil moisture (Morgan et al., 2020) and such groundwater is impacted by rainfall, one might expect to see a gradient of vegetation as well.

Understanding this vegetation gradient will help to determine if the Kuiseb is a suitable location for a giraffe translocation and where the initial release point should occur along the river. Currently, multiple reasons point to the Kuiseb being an effective translocation area. Despite the low rainfall and sporadic flooding, the Kuiseb supports numerous non-desert species and provides necessary resources for local wildlife. Certain anecdotal accounts suggest that giraffes have been observed only ~10 km away from the river (E. Marais, personal communication, November 1, 2024). And giraffes in other ephemeral river systems, such as the Hoarusib and Huanib, have flourished (M. Brown, personal communication, November 8, 2024), as the riparian woodlands provide critical food sources for desert-dwelling giraffes throughout the entire year (Fennessy, 2004).

However, with the Kuiseb River system's wide gradients in rainfall and fog as one moves farther from the coast, as well as its inconsistent groundwater recharge patterns, concerns arise about whether woody vegetation would be consistently available for giraffes along the Kuiseb. Given these concerns, we set out to test if the distance from the coast affects the composition of woody vegetation along the Kuiseb, as well as compare the Kuiseb's vegetation composition to other ephemeral rivers with successful giraffe translocations. Given the gradients present for rainwater, groundwater recharge, and the reliance of Kuiseb vegetation on groundwater availability, we expected our variables of plant density, biomass density, and diversity to increase further from the coast. Thus, the vegetation composition would become more suitable for a giraffe translocation further from the coast as well.

Methods

Site Selection

To get a representative sample along the Kuiseb River, we selected four discrete sites along the river. Those sites, listed from nearest to farthest from the coast, are Rooibank, Swartbank, Gobabeb, and Homeb. Each site was 28 km apart (Figure 1). At each site, we selected six transects, and the positioning of each transect depended on whether or not the site's main river channel could be identified. At sites where a main river channel could be identified, we created three pairs of transects on either side of the riverbed extending perpendicular to the river's flow (as seen in Homeb [A] and Gobabeb [B]; Figure 2). At sites without a clearly defined riverbed, we sampled three pairs of transects (6 total) with at least 10 m of distance between the end of the first transect and the beginning of the second transect (as seen in Swartbank [C] and Rooibank [D]; Figure 2).

Figure 1: Map of the Kuiseb River marked with our four sites: Rooibank, Swartbank, Gobabeb, and Homeb.

Regardless of whether or not a main river channel could be identified, each pair of transects was 200 m apart from an adjacent pair (Figure 2). Each transect was measured perpendicular to the river's flow as best we could distinguish. The transects were rectangular, spanning 10 m wide and either 300 m long maximum or until we hit the end of the river's vegetation. Consequently, some transects were shorter than others, which presented a unique challenge to our analyses: do we standardize the length of transects, and potentially include stretches of desert which lower our overall densities? Or do we keep the original transect lengths, which may not, in our density statistics, reflect the fact that the vegetation available to giraffes is collected in a small area? To remedy this issue, we designated two types of areas: the "riparian woodland" includes only the vegetation along the Kuiseb, keeping the original transect lengths even if they were less than 300 m, and the "riparian zone" includes the empty area that did not have vegetation, extending the transects to a uniform length of 300 m. We chose 300 m because telemetry data suggests that giraffes typically forage within 300 m of the main river channel in other ephemeral river systems (M. Brown, personal communication, November 8, 2024).

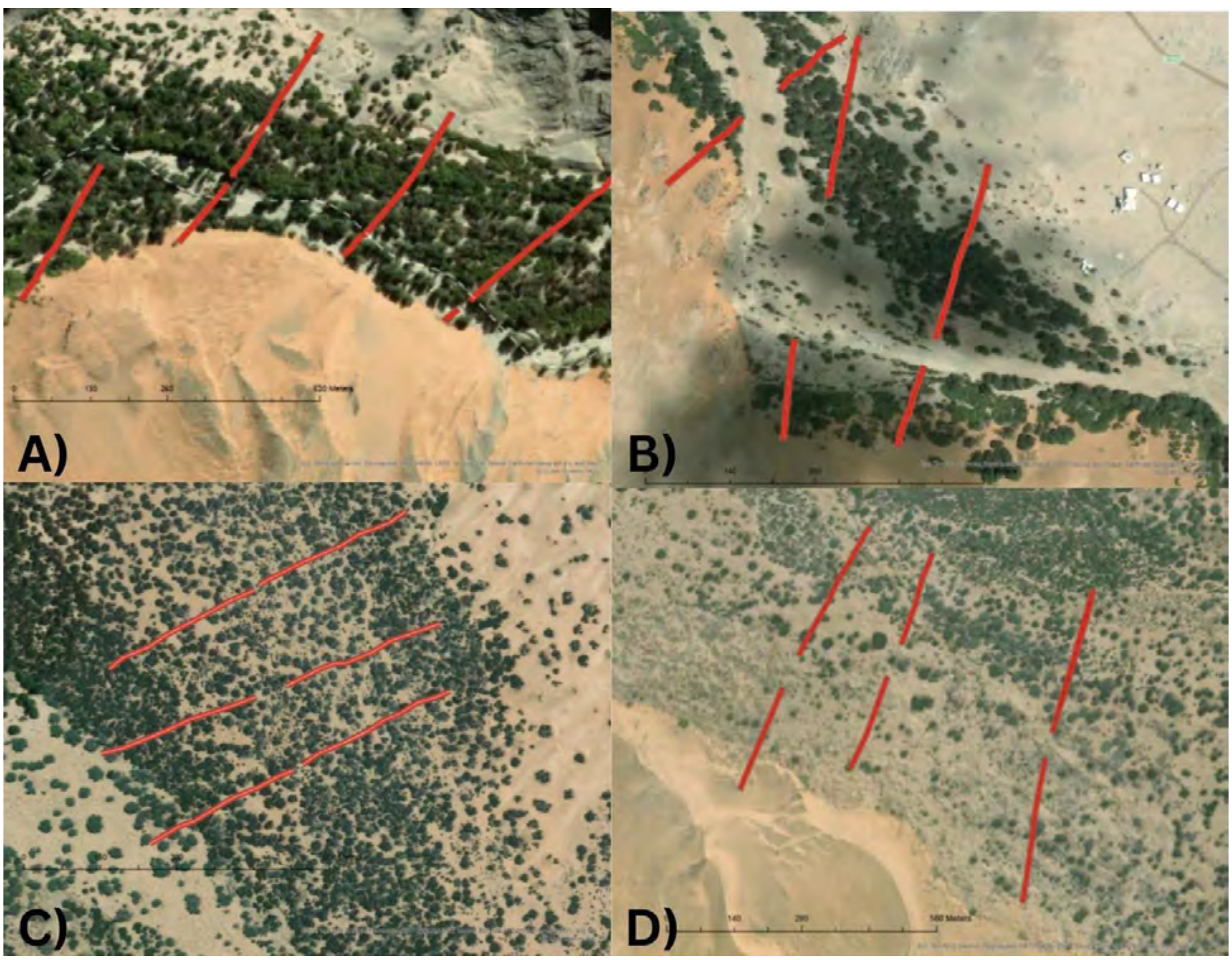

Figure 2: Transects taken at the Homeb (A), Gobabeb (B), Swartbank (C), and Rooibank (D) sites (ordered by proximity to the coast from far to near). We took 7 transects at the Homeb (A) site because the transects on the dune side were short with sparse data. The other three sites each had 6 transects. Each transect was 10 m wide and ran until we reached the end of vegetation or until a maximum of 300 m.

Vegetation Survey

Within each transect, we surveyed all living woody vegetation above breast height which could potentially be browsed by giraffes (M. Brown, personal communication, 2024). We recorded the species and circumference at breast height (CBH) of each vegetation individual. Then, we divided each of our CBH measurements by pi to calculate the diameter at breast height (DBH). To measure the individual's height, we took the observer's angle and distance from the crown by means of a range finder. Then, with the observer's height, angle, and distance from the crown, we used the Pythagorean theorem to calculate that individual's height (Equation 1):

$$HHHHHHHHhtt_{vvvvvvvvvvvvvvvvvvvvv} = ssHHssss * DDHHssttDDssDDHH_{vvoooovvoovvvvoo} + HHHHHHHHhtt_{vvoooovvoovvvvoo} \quad \textbf{Eq. 1}$$

Then, with that individual's DBH and height, we used either a general allometric equation for species in the African extratropical region (Equation 2; Chave et al., 2014) or a species-specific allometric equation for *A. erioloba* (Equation 3; Tietema, 1993) and *F. albida* (Equation 4; Beedy et al., 2015) to calculate that individual's biomass:

$$AAAAAA_{vvoovv} = 0.0673 * (\rho\rho DD^2HH)^{0.976} \text{ where } \rho\rho = 0.648HHmm^{-3} \quad \textbf{Eq. 2}$$

$$AA = 0.1376 * AAAA^{1.2562} \quad \textbf{Eq. 3}$$

$$LLssLLAAAAAA = -2.68 + 2.5 * LLss(DDAAHH) \quad \textbf{Eq. 4}$$

For shrub-like species, such as *S. persica*, *A. horridus,* and *Pechuel-loeschea leubnitziae* (Stinkbush), we recorded the width, length, and height to get a volume measurement to calculate biomass. For *S. persica*, we gathered a 0.5 m cubic sample that we deemed an accurate representation of the average *S. persica* density. We separated the sample into three categories – leaves, green stems, and wood – and set the samples on a drying rack at 60 °C for 48 hours. The dry mass was used to calculate *S. persica's* biomass.

For *A. horridus* and *P. leubnitzia*, we used a generalized shrub mass equation to determine biomass (Equation 5; Guy, 1981):

$$MMDDssss = (DDDDsscccccc\ vvccvvvvmmHH)^{0.9138} * 1{,}2102 \quad \textbf{Eq. 5}$$

When collecting vegetation measurements, we also encountered several instances where case-specific solutions were necessary. For vegetation that split into multiple stems below breast height, we included a measurement for each stem larger than 10 mm in circumference, indicating that they belonged to the same tree (Tree Index, Giraffe Data). If the individual stems had similar heights, only one height was measured. However, if the stems greatly differed in height, each height was recorded. Further, if all of the protrusions below breast height were less than 10 mm in circumference, we selected the largest stem for measurement. For vegetation that could not be safely accessed – either due to dense, non-traversable patches of *S. perscia* or dense clusters of thorns – an estimation of CBH was made based on comparable stem measurements of CBH. For any vegetation whose height could not be obtained by the range finder, an estimation of height was made based on comparison to the height of the observer. Lastly, any dead vegetation or vegetation whose crown was below breast height was not included in our survey.

Analyses

To analyze our data, we used R Statistical Software (R Core Team, 2023) and JMP Statistical Software (JMP Pro, 2018). We used a logarithmic transformation on our biomass data set, which allowed us to minimize the impact of outlier values and thus standardize our data set across a normal distribution.

We ran analysis of variance (ANOVA) tests to determine differences in abundance, plant density, and log biomass density across sites. We performed ANOVAs for our response variables in terms of the riparian woodland area and the riparian zone area. When ANOVA testing revealed significant differences, we ran post-hoc Tukey tests to determine the differences between pairings of sites. Additionally, we ran models testing for the interaction between site and species and whether the interaction affected plant and log biomass densities. Finally, we ran diversity testing – Shannon index, species richness, and Bray-Curtis dissimilarity on a non-metric multidimensional scale (NMDS) – to determine species richness, evenness, and distinctiveness. Shannon diversity was calculated for each site using the R ‘diversity’ function, which computes the negative sum of the products of each species’ proportion in the sampled population at each site (p_i) and the natural logarithm (ln) of that proportion (Equation 6). Species richness was calculated by counting the number of different species at each site, while Bray-Curtis dissimilarity was calculated by first creating a species abundance matrix organized by site, then removing the site column to compute pairwise dissimilarities, which were subsequently used to derive NMDS metrics for visualization. Bray-Curtis dissimilarity between two sites is calculated as one minus the ratio of twice the shared species abundance (C_{ij}) to the total abundance across both sites ($S_i + S_j$) (Equation 7).

$$HH = -\sum^{oo}_{„} \; cc_{vv} vvsscc_{vv} \quad \textbf{Eq. 6}$$
$$AACC_{vvii} = 1 - (2 * CC_{vvii})/(SS_{vv} + SS_{ii}) \quad \textbf{Eq. 7}$$

To directly compare the plant densities between the Kuiseb River and the Hoanib River of Fennessy’s study (2004), we averaged those densities across species across our four Kuiseb sites. We did so for both the riparian woodland and the riparian zone (see *Comparison to Analogous Ephemeral River Systems and Implications for Giraffe Translocation* section for further details).

Results

Across the four Kuiseb sites, we encountered 11 different species. *Tamarix usneoides* had the highest abundance at 322 individuals, while *M. schinzii* and *N. glandulosa* had the lowest with only one individual recorded for each (Table 1). Homeb had the greatest number of individuals overall, followed by Swartbank, Gobabeb, and Rooibank (Figure 4). *Tamarix usneoides*, *F. albida*, and *E. pseudebenus* abundances increased across sites with distance from the coast (Figure 3). Homeb had the highest biomass by individual, followed by Gobabeb, Swartbank, and Rooibank (Table 1). *Acacia erioloba* had the highest total biomass, and *S. plumosa* had the lowest total biomass (Table 1). Swartbank had the highest total biomass overall, followed by Homeb, Gobabeb, and Rooibank (Table 1). Notably, a majority of species – specifically *A. horridus, M. schnizii, N. glandulosa, P. leubnitzia, S. plumosa*, and *N. glauca* – were not found within every site (Table 1). Certain species, such as *T. usneoides* and *S. persica*, differed between the abundance of individuals and the total biomass of those individuals. *Tamarix usneoides* had high abundance but low total biomass, while *S. persica* had low abundance but high total biomass (Table 1).

Table 1: Abundance and Biomass across Sites by Species. Abundance and biomass are presented by site, ordered by proximity to the coast from near to far. Species marked "N/A" were not present in that site. Means are prior to log transformation.

Abundance (Individuals / Site)					
Species	**Rooibank**	**Swartbank**	**Gobabeb**	**Homeb**	**Total**
A. erioloba	33	146	66	23	268
A. horridus	30	N/A	2	N/A	32
E. pseudebenus	4	10	14	25	53
F. albida	11	15	57	136	219
M. schinzii	N/A	1	N/A	N/A	1
N. glauca	3	1	10	N/A	14
N. glandulosa	1	N/A	N/A	N/A	1
P. leubnitzia	35	83	1	N/A	119
S. persica	N/A	N/A	7	28	35
S. plumosa	N/A	9	N/A	N/A	9
T. usneoides	N/A	24	112	186	322
Total	117	289	269	398	1073
Average Biomass (Kg / Site)					
Species	**Rooibank**	**Swartbank**	**Gobabeb**	**Homeb**	**Total Average**

A. erioloba	447.41 ± 1035.83	1669.95 ± 16383.23	367.16 ± 793.70	752.34 ± 888.54	1085.71 ± 11882.90
A. horridus	7.09 ± 14.77	N/A	0.45 ± 0.18	N/A	6.68 ± 14.38
E. pseudebenus	28.22 ± 24.58	86.51 ± 99.33	7.46 ± 7.14	30.24 ± 59.01	31.59 ± 58.12
F. albida	886.35 ± 1203.19	93.93 ± 289.73	274.97 ± 895.94	521.14 ± 1075.74	413.73 ± 989.94
M. schinzii	N/A	919.28	N/A	N/A	919.28
N. glauca	15.01 ± 16.68	0.38	0.2 ± 0.23	N/A	4.17 ± 10.27
N. glandulosa	2637.32	N/A	N/A	N/A	2637.32
P. leubnitzia	15.84 ± 15.49	9.32 ± 9.24	0.64	N/A	11.16 ± 11.76
S. persica	N/A	N/A	1248.39 ± 1113.68	1082.92 ± 1992.78	1115.10
S. plumosa	N/A	6.06 ± 2.56	N/A	N/A	6.06 ± 2.56
T. usneoides	N/A	7.49 ± 11.08	13.92 ± 22.70	14.81 ± 22.97	13.85 ± 22.24

Sum Biomass (Kg / Site)					
Species	**Rooibank**	**Swartbank**	**Gobabeb**	**Homeb**	**Total**
A. erioloba	37582.36	433952.78	45160.98	21817.90	538514.01
A. horridus	212.77	0.00	0.91	N/A	213.68
E. pseudebenus	536.19	1211.18	201.33	1179.18	3127.88
F. albida	15954.22	2348.28	34645.69	82340.86	135289.05
M. schinzii	N/A	919.28	N/A	N/A	919.28
N. glauca	60.06	0.38	2.05	N/A	62.49
N. glandulosa	2637.32	N/A	N/A	N/A	2637.32
P. leubnitzia	554.47	773.33	0.64	N/A	1328.44
S. persica	N/A	N/A	8738.72	31404.80	40143.52
S. plumosa	N/A	54.50	N/A	N/A	54.50
T. usneoides	N/A	247.07	3132.17	3020.52	6399.77
Total	57537.39	439506.80	91882.49	139763.26	728689.95

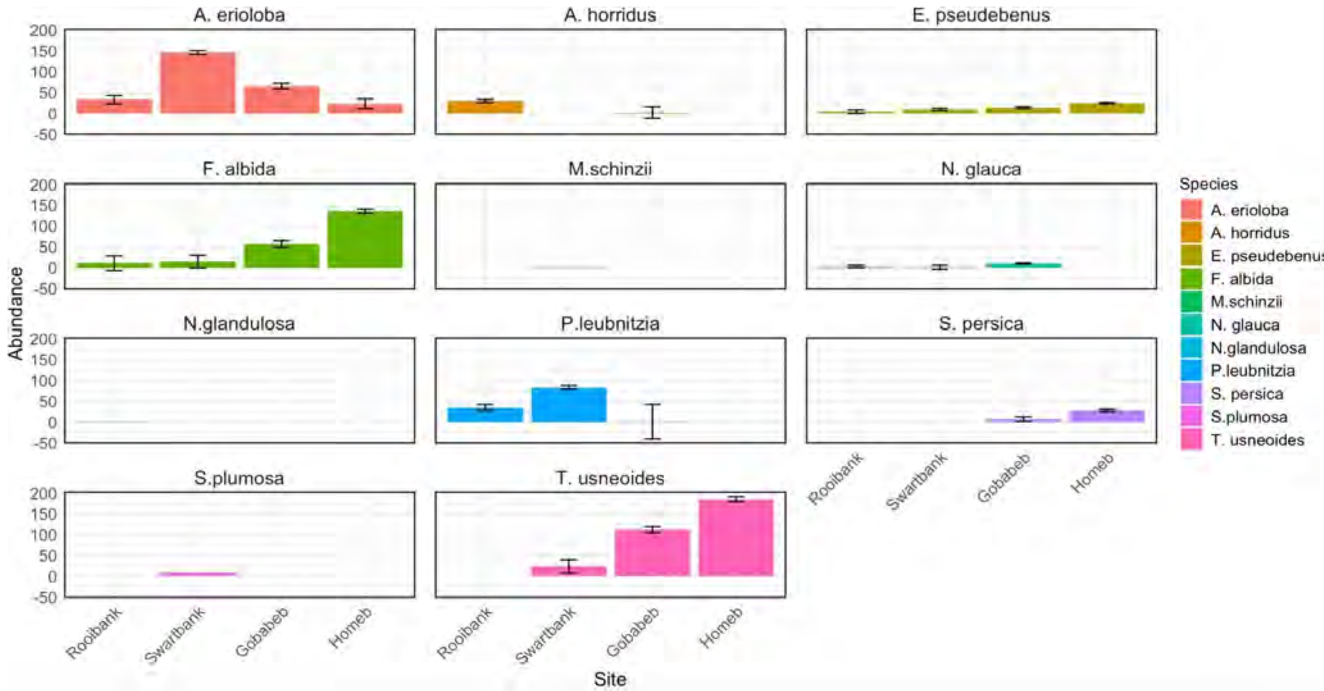

Figure 3: Abundance by species across sites (ordered by proximity to the coast from near to far). *Tamarix usneoides*, *F. albida*, and *E. pseudebenus* abundances increased across sites with distance from the coast.

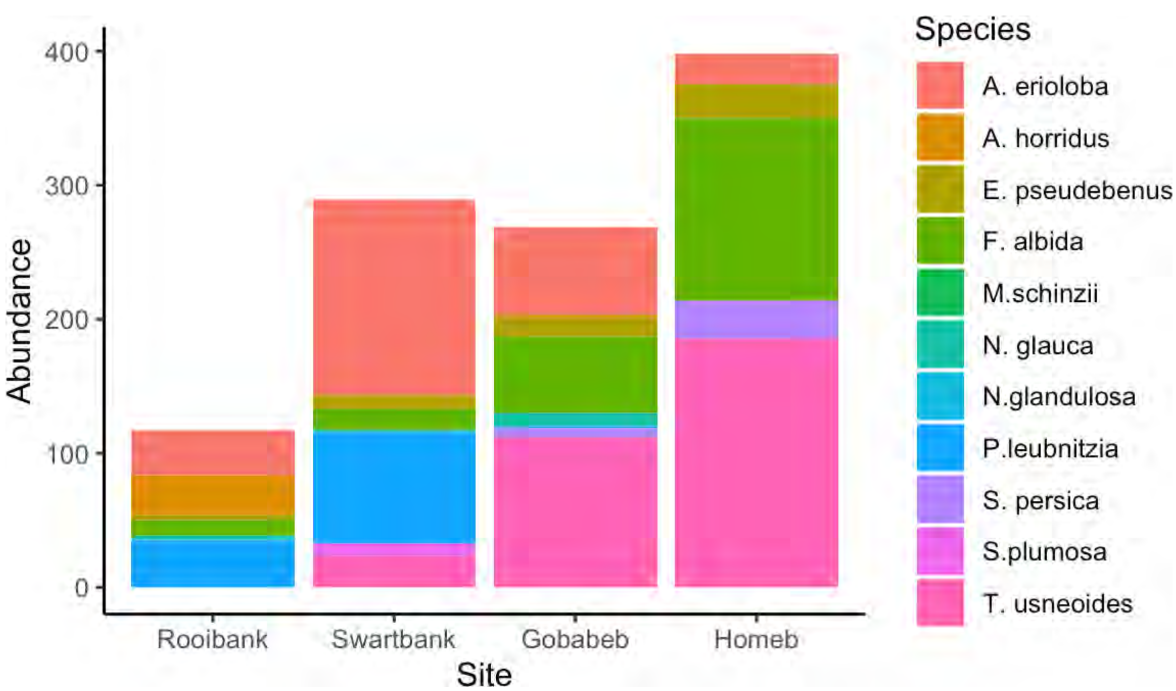

Figure 4: Stacked distribution of abundance and species across sites (ordered by proximity to the coast from near to far). *Tamarix usneoides*, *A. erioloba*, and *F. albida* had the highest abundances across sites.

Kuiseb Riparian Woodland

Riparian woodland plant density (plants ha^{-1}) differed between sites ($F_{3,21} = 9.29$, $P = 0.00041$). Homeb had the highest plant density overall, while Rooibank had the lowest plant density overall (Figure 5). Homeb had a higher plant density than both Rooibank (post-hoc Tukey test: 259.15 ± 51.39; P = 0.00030) and Swartbank (post-hoc Tukey test: 172.43 ± 51.39; P = 0.015), and Gobabeb had a higher plant density than Rooibank (post-hoc Tukey test: 168.51 ± 53.33; P = 0.023). However, we did not find a difference between other pairings of sites (Appendix 2). In essence, as distance from the coast increases, plant density also increases.

When we included the interaction between site and species in our model, patterns in plant density across sites varied among species ($F_{14,77} = 2.12$, $P = 0.020$). Certain species such as *T. usneoides* and *F. albida* had higher plant densities at sites further from the coast (Figure 6). These species drove the overall trend of plant density increasing further from the coast (Figure 5). However, other species such as *A. erioloba* did not follow this trend, with higher plant densities at the middle sites (Figure 6).

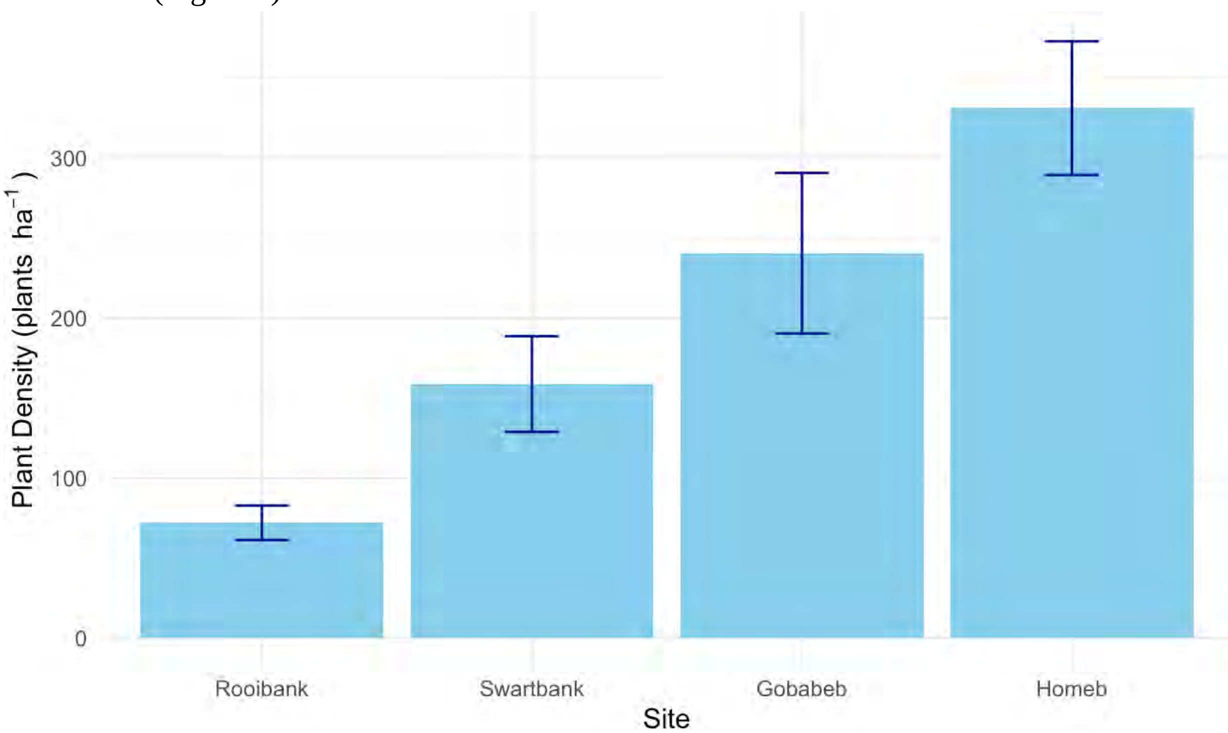

Figure 5: Plant density across sites (ordered by proximity to the coast from near to far) in riparian woodland samples. Mean plant density was 331.08 (SD = 110.52) at Homeb, 240.40 (SD = 122.94) at Gobabeb, 158.65 (SD = 73.29) at Swartbank, and 71.93 (SD = 26.40) at Rooibank. Means are presented with standard error bars.

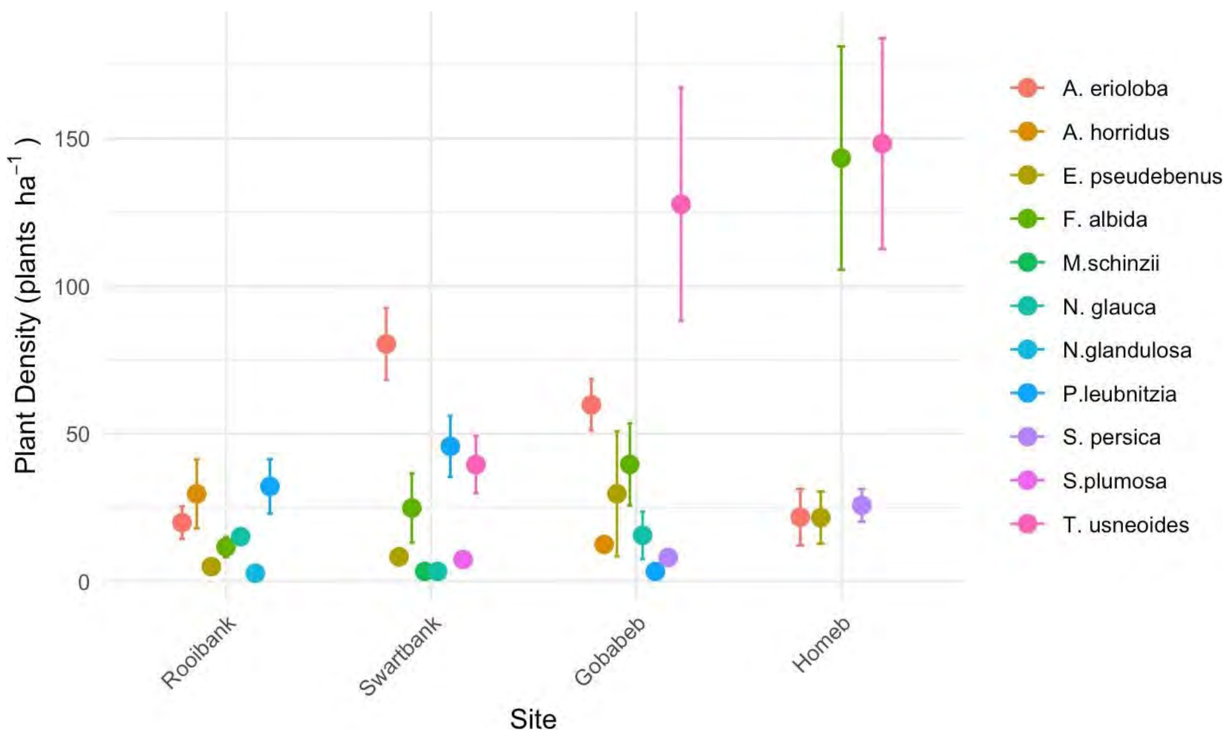

Figure 6: Plant density by species across sites (ordered by proximity to the coast from near to far) in riparian woodland samples. Means are presented with standard error bars.

Riparian woodland biomass density (kg ha^{-1}) varied significantly between sites ($F_{3,21} = 5.27$, $P = 0.0072$). Gobabeb had a higher biomass density than Rooibank (post-hoc Tukey test: 840.37 ± 215.32; $P = 0.0042$). However, we did not find a difference between other pairings of sites (Appendix 2). Gobabeb had the highest biomass density overall, while Rooibank had the lowest biomass density overall (Figure 7).

When we included the interaction between site and species in our model, patterns in biomass density across sites varied among species ($F_{14,77} = 2.56$, $P = 0.0046$). Certain species such as *A. erioloba*, *F. albida*, and *T. usneoides* drove the overall trend of the highest biomass density at Gobabeb and the lowest biomass density at Rooibank (Figure 6). However, *A. erioloba* actually had the highest biomass density at Swartbank, and *F. albida* actually had the highest biomass density at Homeb (Figure 8). Nevertheless, *A. erioloba*, *F. albida*, and *T. usneoides* all had high biomass densities at Gobabeb (Figure 8).

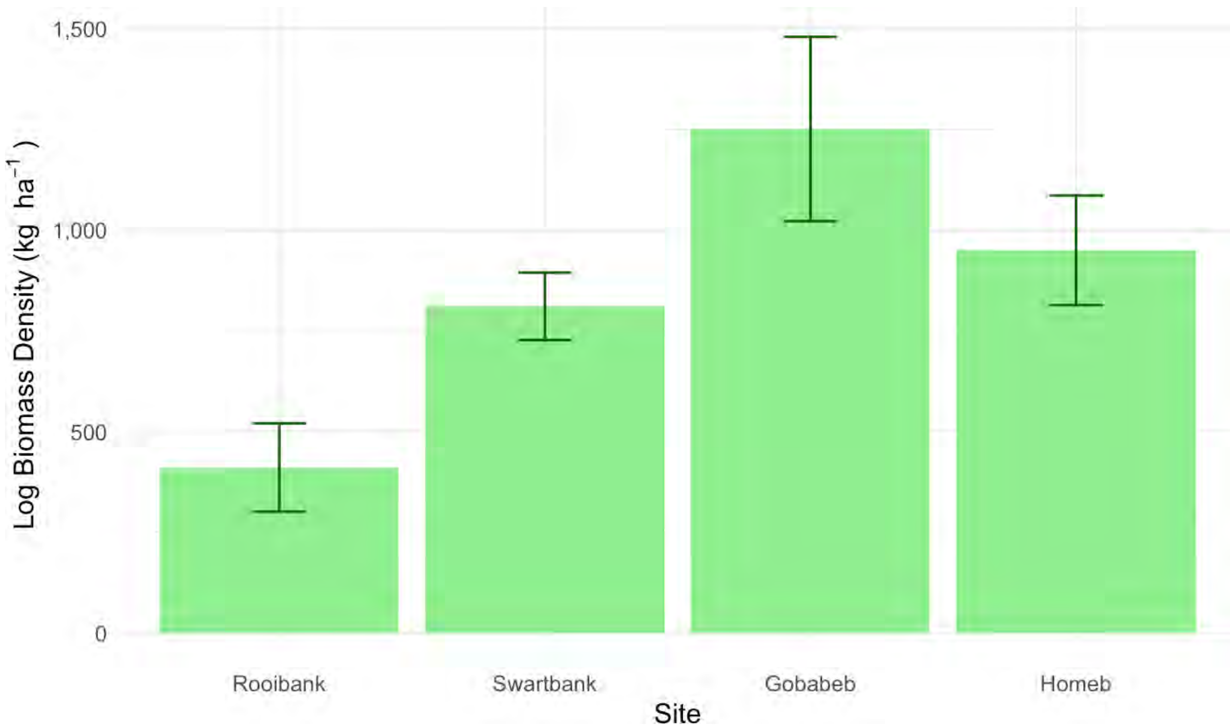

Figure 7: Biomass density (in log units) across sites (ordered by proximity to the coast from near to far) in riparian woodland samples. Mean log biomass density was 950.04 (SD = 360.25) at Homeb, 1251.08 (SD = 560.70) at Gobabeb, 810.87 (SD = 204.97) at Swartbank, and 410.71 (SD = 268.41) at Rooibank. Mean biomass density (back-transformed from log units) was 22,268.83 (SD = 30,406.47) at Homeb, 15,427.80 (SD = 21,120.80) at Gobabeb, 555,40.87 (SD = 189,385.64) at Swartbank, and 8,986.18 (SD = 19,746.31) at Rooibank. Means are presented with standard error bars.

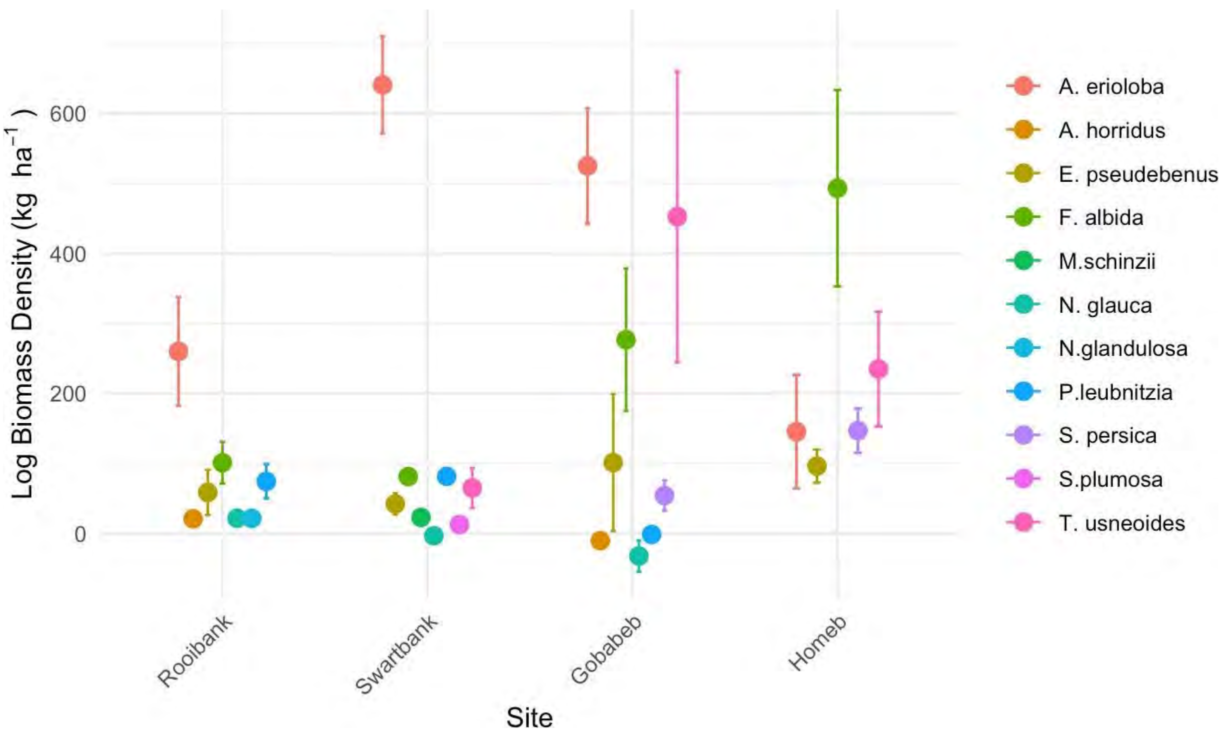

Figure 8: Biomass density (in log units) by species across sites (ordered by proximity to the coast from near to far) in riparian woodland samples. Means are presented with standard error bars.

Kuiseb Riparian Zone

Riparian zone plant density differed only marginally between sites ($F_{3,21} = 2.42$, $P = 0.094$). However, visually comparing Rooibank to Homeb, there was a clear increase in plant density (Figure 9).

When we included the interaction between site and species in our model, patterns in plant density across sites varied only marginally among species ($F_{14,77} = 1.33$, $P = 0.21$). *Tamarix usneoides*, *F. albida*, *E. pseudebenus*, and *S. persica* plant densities all increased across sites with distance from the coast (Figure 10). These species drove the overall trend of plant density generally increasing further from the coast (Figure 9). However, site ($F_{3,77} = 4.36$, $P = 0.0069$) and species ($F_{10,77} = 3.79$, $P = 0.00035$) individually were significant, suggesting that site influences plant density and species influences plant density. For example, species such as *A. erioloba* did not follow the overall trend of plant density generally increasing further from the coast, with *A. erioloba* having a higher plant density at Swartbank (Figure 10). *Acacia erioloba* drove overall plant density higher at Swartbank than Gobabeb, diverging from the trend of plant density increasing further from the coast that was found generally between sites in the riparian zone (Figure 9) and uniformly between sites in the riparian woodland (Figure 5).

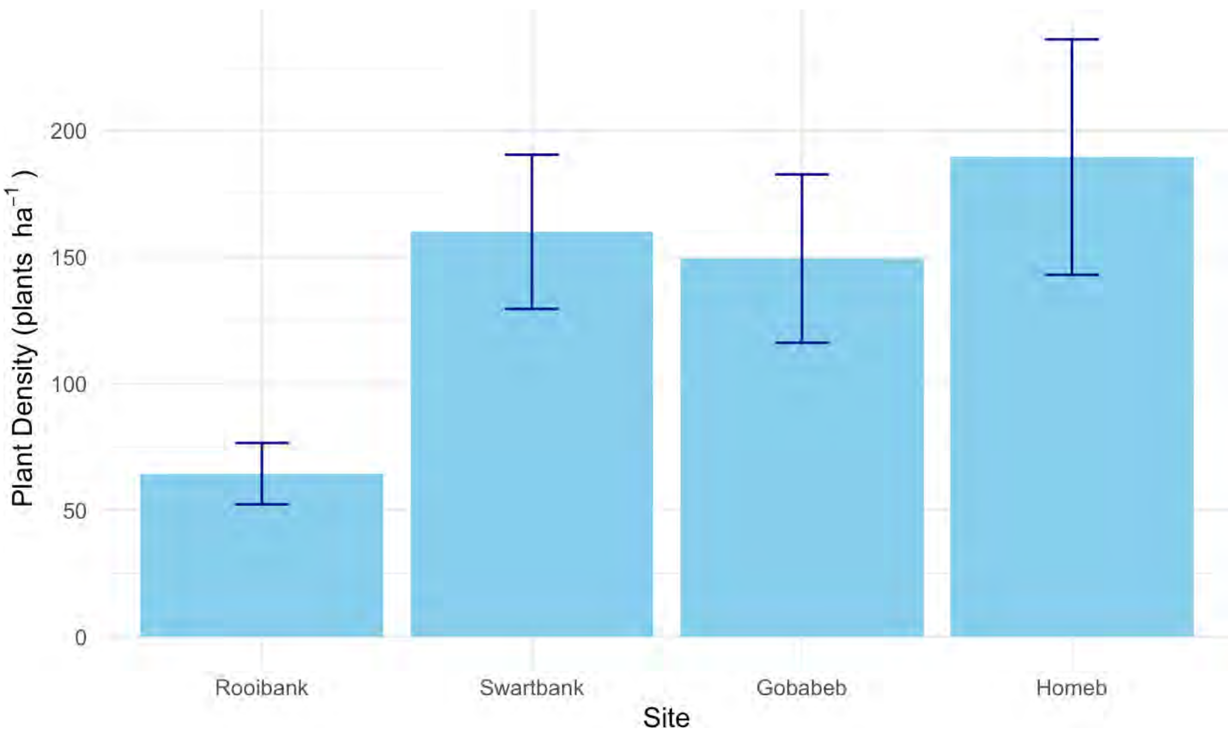

Figure 9: Plant density across sites (ordered by proximity to the coast from near to far) in riparian zone samples. Mean plant density was 189.52 (SD = 123.11) at Homeb, 149.44 (SD = 81.52) at Gobabeb, 160.00 (SD = 74.65) at Swartbank, and 64.44 (SD = 29.71) at Rooibank. Means are presented with error bars.

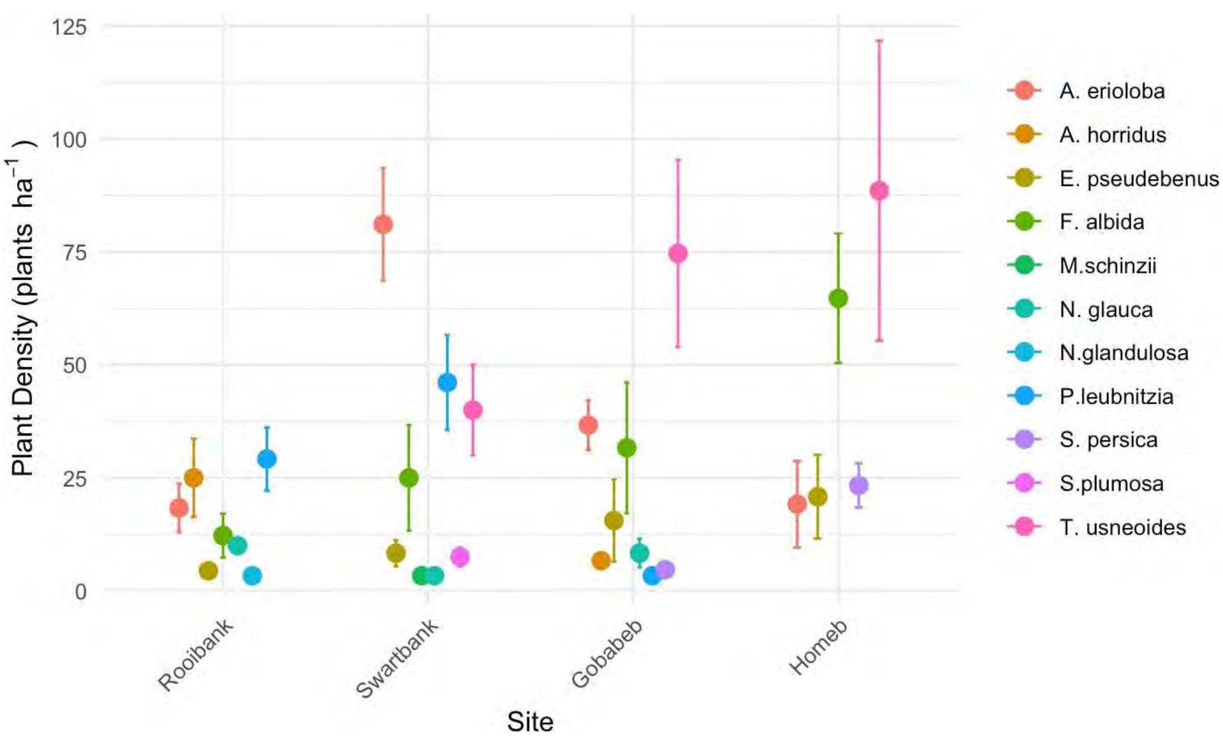

Figure 10: Plant density by species across sites (ordered by proximity to the coast from near to far) in riparian zone samples. Means are presented with error bars.

Riparian zone biomass density did not vary significantly between sites ($F_{3,21} = 2.12$, $P = 0.13$). Swartbank had the highest biomass density overall, while Rooibank had the lowest biomass density overall (Figure 11).

When we included the interaction between site and species in our model, patterns in biomass density across sites varied among species ($F_{14,77} = 3.14$, $P = 0.00066$). *Acacia erioloba* had a much higher biomass density at Swartbank (Figure 12), which drove the overall trend of highest biomass density at Swartbank (Figure 11).

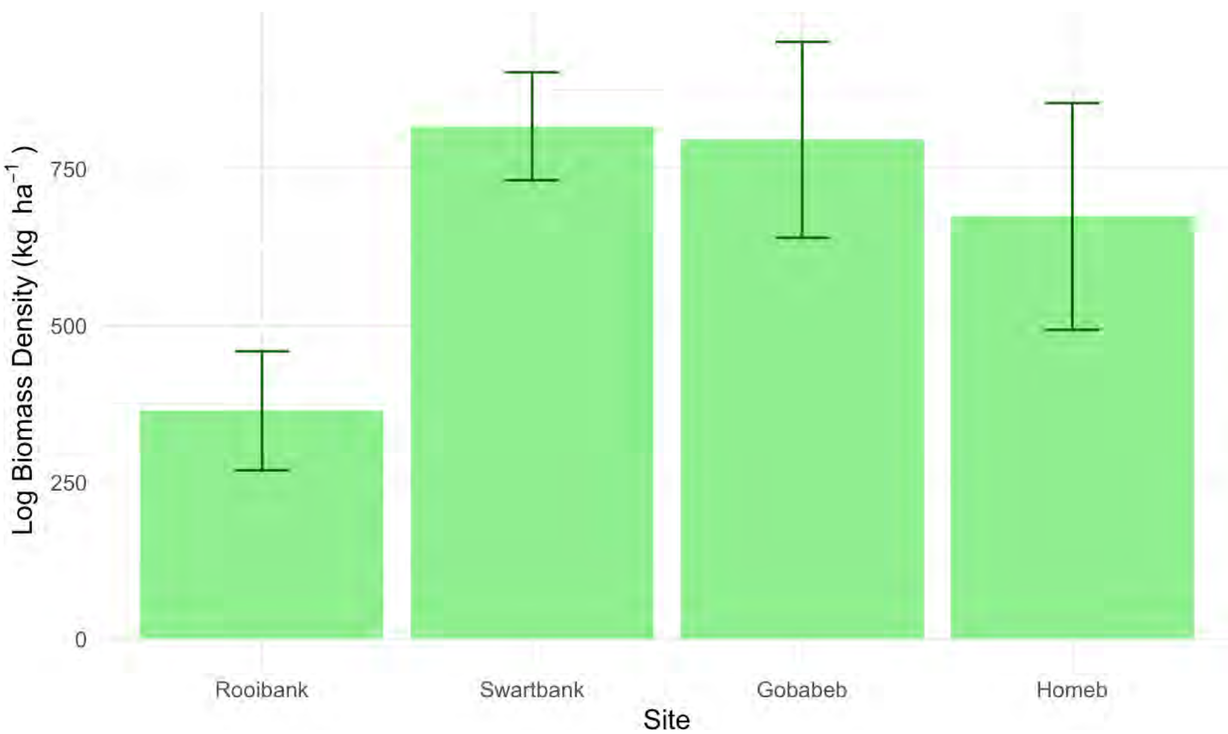

Figure 11: Biomass density (in log units) across sites (ordered by proximity to the coast from near to far) in riparian zone samples. Mean log biomass density was 673.60 (SD = 478.41) at Homeb, 795.85 (SD = 382.57) at Gobabeb, 817.47 (SD = 210.78) at Swartbank, and 363.61 (SD = 232.36) at Rooibank. Mean biomass density (back-transformed from log units) was 17,918.38 (SD = 24,609.91) at Homeb, 9,879.84 (SD = 14,343.43) at Gobabeb, 56,347.03 (SD = 193,110.46) at Swartbank, and 8,717.78 (SD = 20,028.72) at Rooibank. Means are presented with error bars.

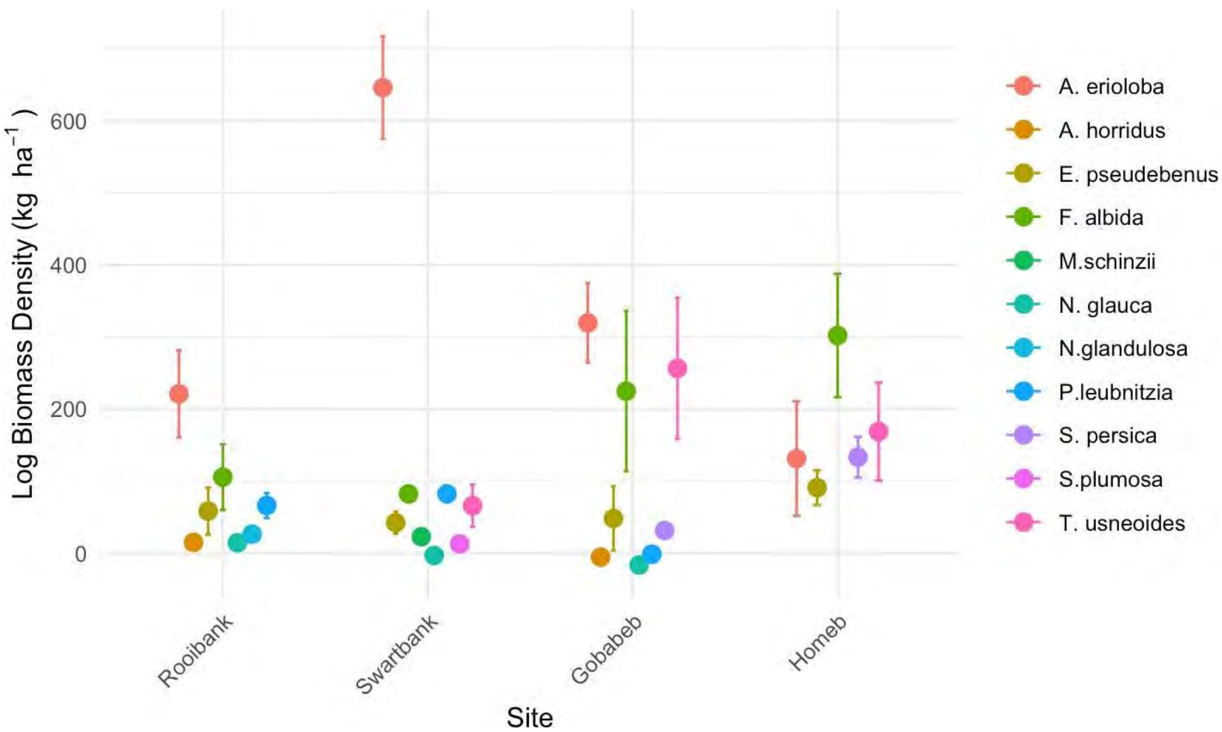

Figure 12: Biomass density (in log units) by plant species across sites (ordered by proximity to the coast from near to far) in riparian zone samples. Means are presented with error bars.

Diversity Indices

Overall for each site, the Shannon index (Figure 13) reveals highest alpha diversity – specifically more species richness and evenness – at Rooibank (1.52), followed by Gobabeb (1.37), Homeb (1.29), and Swartbank (1.21). Species richness (Figure 14) was highest at the middle sites, Swartbank and Gobabeb (8), followed by Rooibank (7) and Homeb (5). Bray-Curtis dissimilarity testing for beta diversity reveals more distinct species compositions between Rooibank, Swartbank, and Homeb, but more homogenous species compositions between Gobabeb and Homeb (Figure 15) . Distance from the coast does not seem to relate to a trend in woody vegetation species richness, evenness, and distinctiveness.

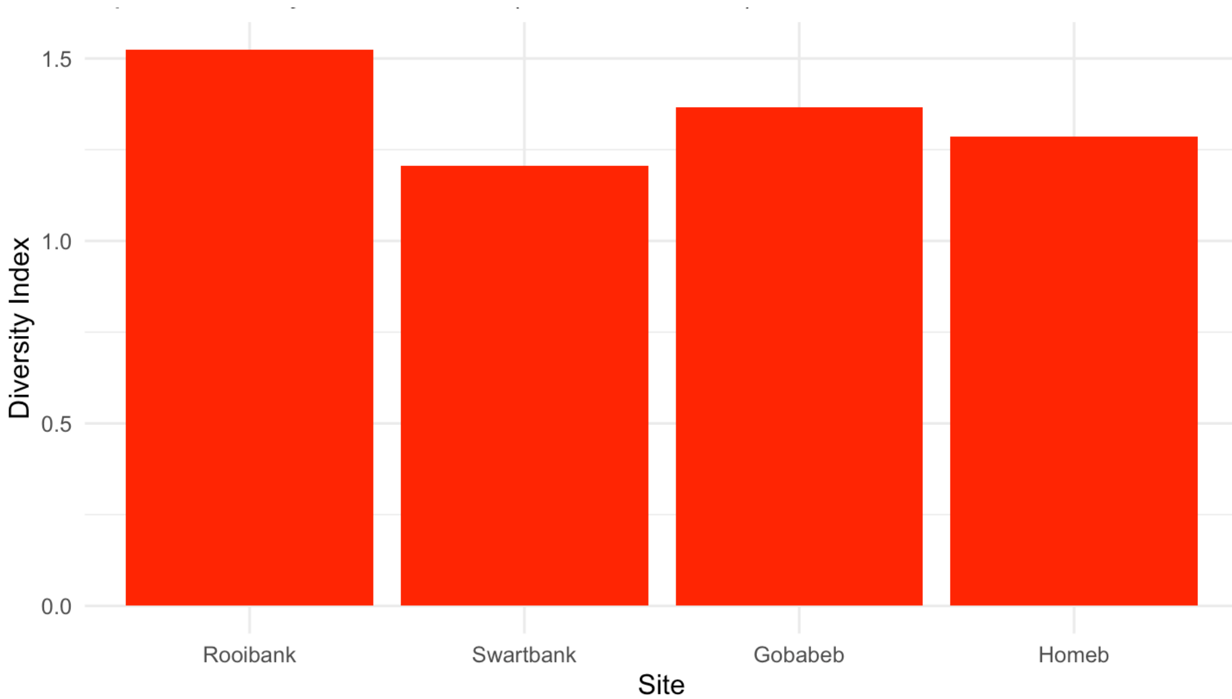

Figure 13: Alpha diversity by Shannon index across sites (ordered by proximity to the coast from near to far). Higher Shannon index values indicate greater diversity, meaning that there are more species present and/or that species are more evenly distributed (species richness and evenness).

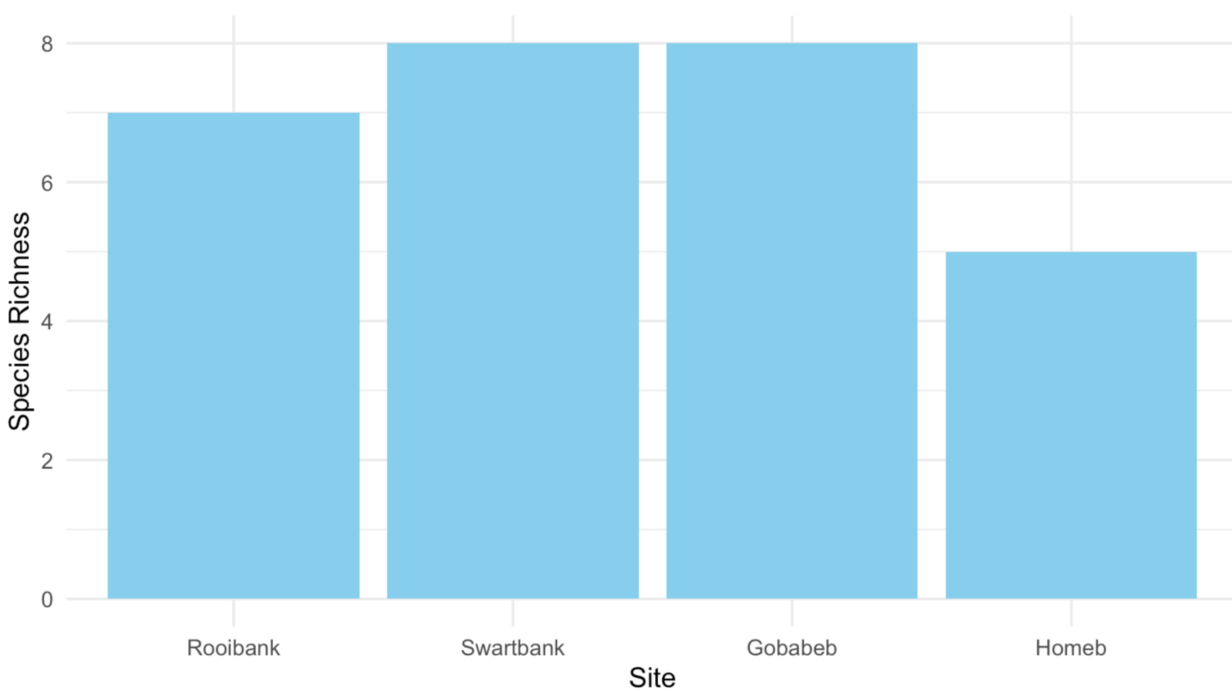

Figure 14: Alpha diversity by species richness across sites (ordered by proximity to the coast from near to far). Higher species richness means that there are more species present, indicating greater diversity.

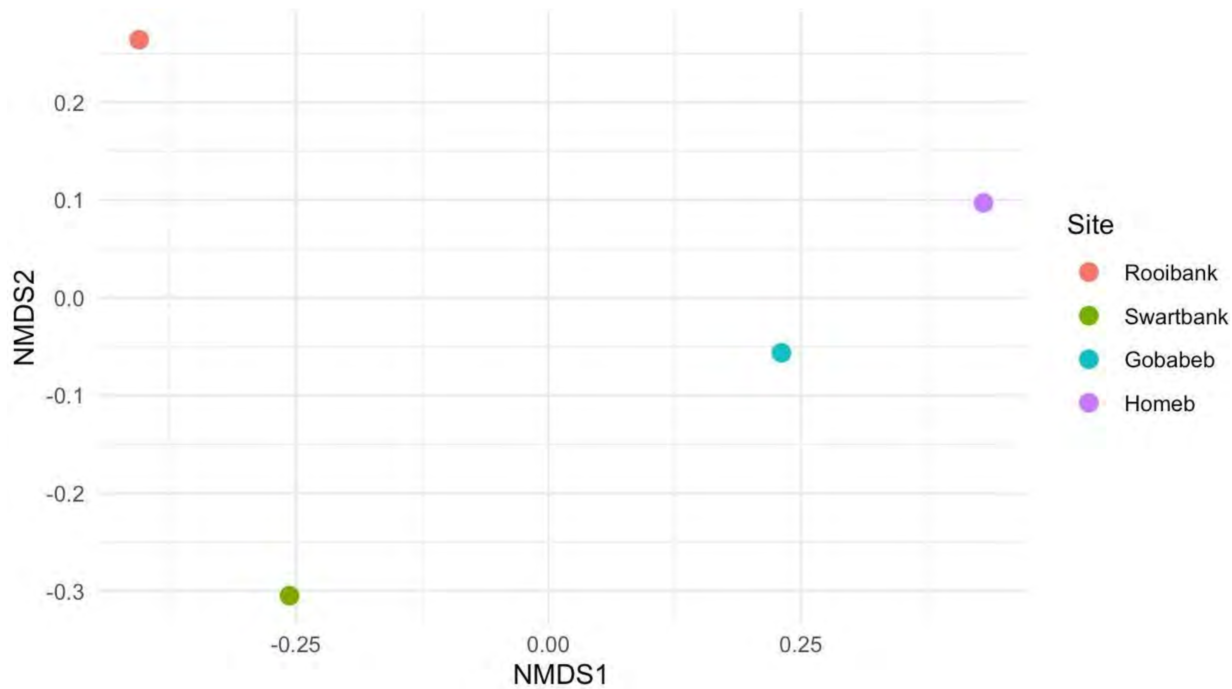

Figure 15: Beta diversity by Bray-Curtis dissimilarity on a non-metric multidimensional scale (NMDS). Greater distance between points on the NMDS plot represents sites with more distinct species compositions and indicates greater diversity.

Comparison to An Analogous Ephemeral River System

To further assess the suitability of the Kuiseb for giraffe translocation, we compared our data with existing vegetation data along the Hoanib River, an analogous ephemeral river system with existing giraffe presence. After averaging plant density across species along the Kuiseb, we found that plant density was significantly different between the Kuiseb River and the Hoanib River ($F_{2,21} = 4.29$, $P = 0.027$) (Figure 16). Specifically, the Kuiseb riparian woodland had a higher plant density across species than the Hoanib (post-hoc Tukey test: 32.63 ± 11.49; $P = 0.026$). *Taramix usneoides* had a much higher plant density in the Kuiseb riparian woodland (Figure 17), which drove the overall trend of higher plant density in the Kuiseb riparian woodland than the Hoanib (Figure 16). However, no significant difference between the Kuiseb riparian zone and the Hoanib was found (Appendix 2).

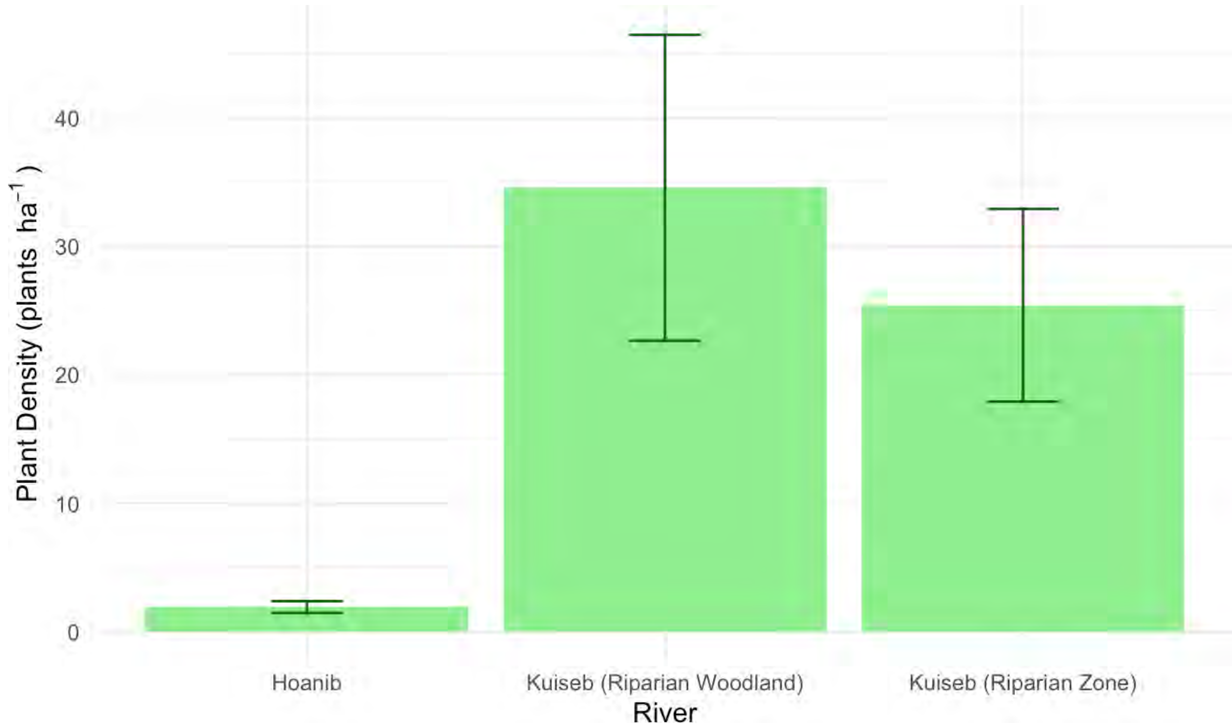

Figure 16: Plant density between the Hoanib and Kuiseb River's riparian woodland and riparian zone samples. Mean plant density was 1.92 (SD = 1.29) at Hoanib and 34.55 (SD = 33.66) at Kuiseb for the riparian woodland and 25.41 (SD = 21.21) for the riparian zone. Means are presented with error bars.

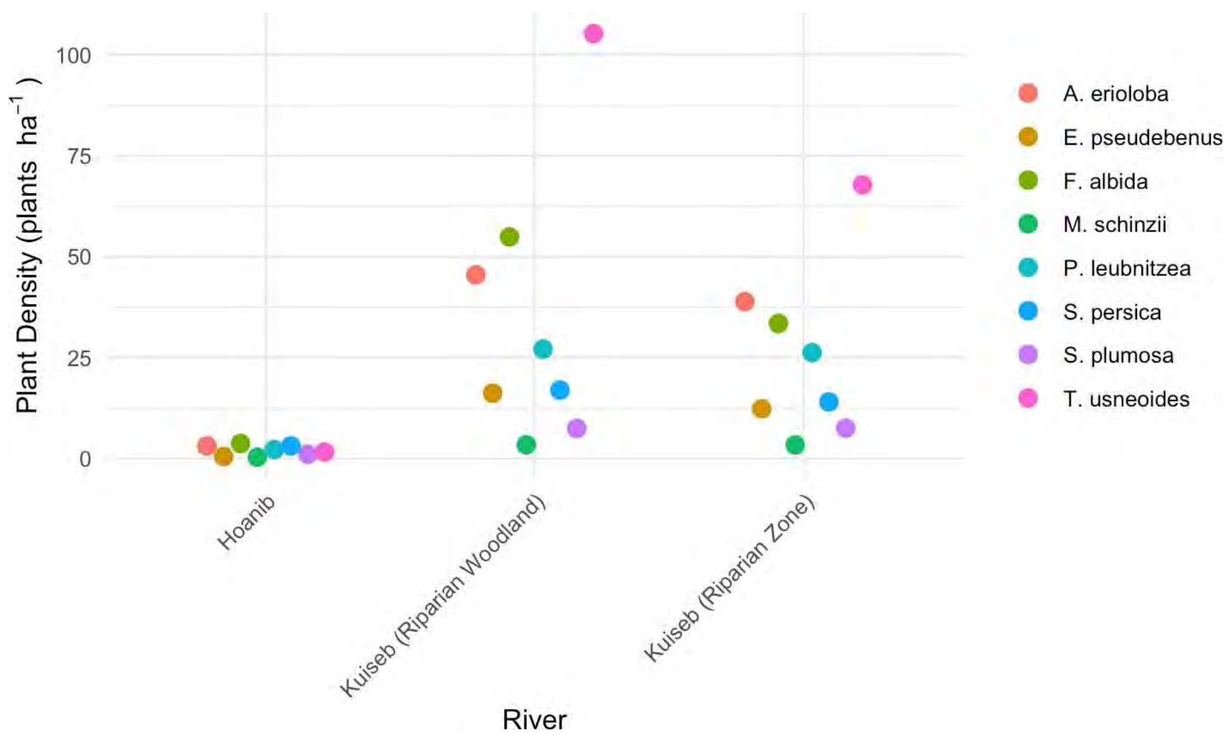

Figure 17: Plant density by species between the Hoanib and Kuiseb River's riparian woodland and riparian zone samples. Means are not presented with error bars as the vegetation data along the Hoanib River only includes means.

Discussion

We found that the gradient of vegetation density moving away from the coast was not as strong as initially predicted. In our riparian woodland assessment, the plant density was greater at our two sites furthest from the coast than the ones closest to it, and the biomass density was greatest at our second farthest site from the coast, Gobabeb, than it was at the sites closest to the coast. In our riparian zone assessment, plant density was lowest in the site closest to the coast. While these findings align with our prediction of an increasing vegetation gradient moving away from the coast, our biomass densities and diversity indices followed different trends.

Swartbank's high biomass density was heavily influenced by its *A. erioloba* biomass, which was far greater than at other sites (Figure 7 and Figure 11). *Acacia erioloba* biomass may be greater due to higher groundwater levels (as *A. erioloba* has deeper roots, they can better compete for groundwater than other species) and more old-growth trees at the site (Seymour and Milton, 2003), although there is insufficient literature on or data collected at the Swartbank site to support such theories. However, a lot of the *A. erioloba* biomass was dead wood and thus not necessarily representative of giraffe food availability.

In terms of alpha diversity, barring Swartbank, the Shannon index generally decreased with distance from the coast, suggesting richer and/or more evenly distributed vegetation composition near the coast (Figure 13). Similarly, species richness was higher in sites closer to the coast (Rooibank, Swartbank, and Gobabeb) than furthest from the coast (Homeb; Figure 14). While Swartbank had the highest species richness, it also had the lowest Shannon index. This contradictory result may be due to Swartbank's large number of *A. erioloba*, which could have outcompeted other species (Hilmers et al., 2018). Swartbank's low Shannon index suggests that *A erioloba* is common while other species are rarer. In terms of beta diversity, Bray-Curtis dissimilarity testing shows that species compositions are more distinct near the coast (Figure 15), though the assessment of additional sites would be necessary to solidify this trend. While lower diversity further inland contradicts our gradient prediction, it does not necessarily imply reduced diet availability for giraffes. As this lower diversity coincides with a general increase in vegetation density, there may be greater food availability – specifically of giraffe-favored woody vegetation species – further inland.

When comparing the Kuiseb to the Hoanib River, where there is giraffe presence, we found that the Kuiseb River's riparian woodland and riparian zone both have higher plant density than the Hoanib River (Figure 16). In particular, the Kuiseb River's riparian woodland varies significantly from the Hoanib River due to the high plant density of its *T. usneoides* (Figure 17). *Tamarix usneoides* is not one of the more significant giraffe food sources; however, the Kuiseb also has higher plant densities of *A. erioloba, F. albida,* and *S. persica* (Figure 17).

Though plant density cannot be considered a direct proxy for giraffe food availability, the fact that the Kuiseb has higher plant density of giraffe-favored woody vegetation species does provide one piece of evidence to suggest that giraffes may survive there.

Another piece of evidence to support giraffe survival in the Kuiseb is a qualitative comparison to two other rivers that currently host giraffes: the Khumib River and the Hoarusib River (M. Brown, personal communication, November 8, 2024). In the Hoarusib River, around 75% of giraffe diet is covered by just four species: *A. erioloba, F, albida, S. persica,* and *B. welwitschii* (Fennessy, 2004). Similar trends exist in the Khumib River (Fennessy, 2004), with other species serving only a minor role in the composition of giraffe diet. Though we did not find *B. welwitschii* within the Kuiseb sites, *A. erioloba, F, albida,* and *S. persica* had the three highest biomass counts across those sites, collectively making up well over 75% of the vegetation biomass present. Without major *A. erioloba* and *F. albida* presence, it is unlikely that giraffes could survive year-round in these ephemeral river systems (Fennessy, 2004), so it is reassuring to see their large abundance in our study area.

However, a giraffe translocation assessment requires consideration of not only giraffe diet availability but also the ecological and social implications of their introduction. When considering these implications, five major concerns emerge: first, introducing a large herbivore such as a giraffe could impact vegetation composition (Danell et al., 2006), especially along the Kuiseb. However, species such as *A. erioloba* and *F. albida* are well adapted to high browsing pressure (Fennessy, 2004). Additionally, giraffe browsing may induce a physiological response in some woody vegetation species that stimulates higher quantity and quality of foliage production (Fennessy, 2004). This positive feedback loop suggests that giraffe browsing could actually benefit woody vegetation growth, thereby enhancing the riparian woodland ecosystem.

Second, giraffes could potentially outcompete other herbivores for woody vegetation. Along the Kuiseb, the primary herbivores are livestock (cows and goats) from the Indigenous Topnaar communities (Morgan et al., 2020). In fact, *A. erioloba* and *F. albida* – both significant giraffe food sources – have been proposed as conservation priorities in Southern Africa due to their importance in feeding the livestock of the Topnaar (Mizuno & Yamagata 2005). Introducing giraffes could result in the over-browsing of these woody vegetation species and reduce available resources for the Topnaar. However, while both livestock and giraffes eat the seed pods of *A. erioloba* and *F. albida*, giraffes tend to feed on canopy leaves and twigs, allowing them to browse at different height levels than livestock (Fennessey, 2004).

Third, giraffes could potentially forage *A. horrida* (Fennessy, 2004), which is the most important food source and of great cultural significance for the Topnaar (Mizuno, 2005). Although, as Fennessy (2004) explains, giraffes were observed to feed on *A. horrida* melons only in the Khumib River, likely as a result of the Khumib's increased aridity and reduced forage availability. While we do not have directly comparable vegetation density data between the

Kuiseb and the Khumib, our findings suggest a high level of forage availability within the Kuiseb. However, with the Kuiseb being dry the majority of the year, we suspect similar levels of aridity that may drive giraffes to consume these moisture-rich melons. Thus, to ensure that giraffe foraging of *A. horrida* will be minimal, a social impact assessment is needed. It is vital to include the Topnaar in these conversations, to inform them of potential impacts and to understand and mitigate their concerns. This collaboration will ensure that Topnaar perspectives directly contribute to any final decision regarding a giraffe translocation.

The fourth concern that arises from giraffe translocation is the escalation of human-wildlife conflict, primarily poaching (Kahler & Gore, 2015). While discussing a similar giraffe translocation project at Iona National Park in Angola, Hamuteyna (2022) explains that in the past, poaching drove Iona's giraffe populations to extinction (Huntly & Russo, 2019). At present, Hamuteyna does not know the community's attitudes towards giraffe reintroduction, so poaching could still be a potential threat despite its otherwise suitable conditions (Hamutenya, 2022). Thus, poaching should be an anticipated risk for a giraffe translocation to the Kuiseb.

Finally, while all of these considerations are essential in the decision to translocate giraffes, it is important to acknowledge that these systems and factors constantly change. For example, with projected climate change, annual rainfall is predicted to decrease in Namibia, which would reduce the frequency and magnitude of flooding in Namibia's ephemeral river systems (Brunette, 2024). Furthermore, evapotranspiration is predicted to increase as well, which will cause groundwater decline to accelerate (Dirkx et al., 2008). These compounding factors could increase tree mortality in all of Namibia's ephemeral river systems. Morgan et al. (2020) found that there was an overall increase in fractional vegetation cover over the last 35 years along the Kuiseb River, further highlighting how Kuiseb vegetation can shift in response to climate change. Whether it be changes to vegetation composition, flooding, rainfall, groundwater levels, or all of the above, these changes will directly affect the communities along the Kuiseb River, how they interact with nearby wildlife, and thus the success of any giraffe translocation.

Conclusion and Recommendations for Future Research

Though it seems that the Kuiseb River's vegetation gradient was not as strong as we initially predicted, the story of giraffe translocation does not end there. The similarities found between the woody vegetation composition along the Kuiseb and Hoanib Rivers suggest that the Kuiseb may have appropriate food availability for a giraffe translocation. That being said, to fully determine whether the Kuiseb River is a suitable habitat for a giraffe translocation, further ecological and social considerations are needed.

Further research and extensions of this study should focus on six key areas: first, sampling more contiguous sites along the river would allow for a more continuous vegetation gradient to be established. Second, surveying wider and longer transects would allow for more representative sampling. Third, utilizing more species-specific equations to calculate biomass would allow for more accurate biomass density assessments. Fourth, further woody vegetation studies should analyze not just water availability, but also temperature, light, nutrient availability, and herbivory, all of which could influence vegetation distribution as well. Fifth, vegetation chemical content (e.g. levels of moisture and crude protein) and seasonal phenology are also worth investigating, as they may drive giraffe foraging behavior more directly than density (Fennessy, 2004). Finally, future research should assess broader ecological and social impacts of potential giraffe translocation to the Kuiseb, with particular emphasis on the perspectives of the Topnaar.

All of these considerations, when combined, would not only lead to more effective surveying of the Kuiseb River's vegetation but contribute vital data to the future translocation of giraffes. As climate change and human encroachment upon giraffe habitat continues, such translocations will become increasingly important to ensure the longevity of the species. On a global scale, continuing to refine translocation strategies will be essential for the world's conservation efforts to prevent the rapid loss of biodiversity.

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Appendices

Appendix I

Appendix 1: Giraffe-Favored Woody Vegetation Species and their Water Sources (*Namibia Biodiversity Database*)

Giraffe-Favored Woody Vegetation Species	**Characteristics**	**Water Sources**
A. erioloba	perennial, deciduous, leguminous (white pods), endemic, spiny, high moisture content, deep roots	Groundwater
F. albida	perennial, deciduous, leguminous (red pods), endemic, highly adaptable, spiny, high moisture content	Groundwater
S. persica	perennial, evergreen, dense leafy bush, widespread, highly adaptable, high moisture content	Groundwater
T. usneoides	perennial, evergreen, endemic	Groundwater
E. pseudebenus	perennial, evergreen, near-endemic	Groundwater
N. glauca	perennial, evergreen, yellow flowers, widespread	Groundwater
A. horridus	perennial, dense branched bush, yellow flowers, melons, near-endemic, deep taproot	Groundwater

Appendix II

Appendix 2: Included Differences with Post-Hoc Tukey Test Results Associated with Figures

Figure	Difference	Post-Hoc Tukey Test
5	Gobabeb and Homeb	90.64 ± 0.51.39; P = 0.32
5	Rooibank and Swartbank	86.72 ± 53.33; P = 0.39
5	Swartbank and Gobabeb	81.79 ± 53.33; P = 0.44
7	Rooibank and Homeb	539.33 ± 207.49; P = 0.073
7	Swartbank and Gobabeb	440.21 ± 215.32; P = 0.20
7	Rooibank and Swartbank	400.16 ± 215.32; P = 0.28
7	Gobabeb and Homeb	301.04 ± 207.49; P = 0.48
7	Swartbank and Homeb	139.18 ± 207.49; P = 0.91
16	Kuiseb (Riparian Zone) and Hoanib	23.49 ± 11.49; P = 0.13
16	Kuiseb (Riparian Woodland) and Kuiseb (Riparian Zone)	9.14 ± 11.49; P = 0.71

Resource Pod-tential: Assessing Forage Availability for Herbivores Along the Kuiseb River

November 15, 2024

Prepared By:

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Abstract

Resource limitations and competition are central drivers of ecological dynamics in arid ecosystems. This study examines how tree size, density, and herbivore interactions shape pod availability in *Vachellia erioloba* and *Faidherbia albida* trees along the Kuiseb River in Namibia. Using field measurements of tree parameters, pod phenology monitoring, and experimental analysis, we found no significant relationships between tree size or density and pod production. This may be due to high variability of pod density on the ground and pod deposition among individual trees, which could suggest that other environmental factors play a greater role in reproductive success. Seasonal deposition patterns of pods varied by species, resulting in staggered production and deposition across a year of phenological camera observations. Pod removal rates were higher among dense tree clusters compared to isolated pod-producing trees, highlighting the impact of forest structure on herbivore browsing. These findings underscore the need to incorporate environmental variables such as water availability and climatic variability to better understand forage resource distribution in riparian ecosystems.

Introduction

Arid regions, which cover more than 40% of the Earth's land surface, are crucial terrestrial ecosystems that support 50% of the world's livestock and wild ungulate populations (Gaur & Squires, 2018; Huang et al., 2015; Singh & Chudasama, 2021). These ecosystems exhibit significant seasonal and annual variations in environmental conditions, driven by extreme temperatures and infrequent, unpredictable pulses of precipitation (resource pulses) (Noy-Meir, 1973 & Chesson et al., 2004). These variabilities lead to limited water resources and alter ecosystem processes such as plant productivity and species interactions, ultimately posing significant challenges for native organisms. In recent decades, prolonged drought conditions have become increasingly prevalent in various arid regions, severely restricting plant growth and productivity (Schachtschneider, 2010). These limitations in plant productivity have cascading impacts, affecting ecosystem services such as foraging availability of herbivore populations. Thus, in arid landscapes, the ability of key plant species to maintain sufficient forage resources is crucial to biodiversity and overall ecosystem stability.

The Namib Desert in Namibia, one of the most extreme hyper arid environments on the planet, annual rainfall averages as low as 25 mm. Ephemeral rivers such as the Kuiseb River play a crucial role as ‘linear oases,’ providing intermittent yet essential water sources to support life (Jacobson et al., 1995). Rising in the Khomas Hochland near Windhoek, and extending through the Namib Desert, the Kuiseb shapes a unique ecosystem along its path, before exiting into the

Atlantic ocean (Jacobson et al., 1995). The Kuiseb typically flows only a few weeks each year, sustaining a riparian forest and a variety of plant and animal species, including *Vachellia erioloba* (Camelthorn) and *Faidherbia albida* (Ana tree). These keystone tree species have adapted to utilize groundwater reserves to survive in the harsh desert conditions. However, during sporadic floods, the flow rarely reaches the coast, leading to transmission loss, decreased water availability (Wekesa et al., 2020), and less dense woody vegetation (Morgan et al., 2020) downstream.

Resource availability, particularly in the form of water, is fundamental to sustaining the Kuiseb ecosystem. Prior research links water scarcity to reduced pod production, as limited water can result in seed abortion and decreased pod growth rates, constraining reproductive output (Bianchi et al., 2020). In hyperarid environments, competition for such resources is a primary factor influencing plant growth, reproductive success, and, consequently, forage availability for dependent herbivores (Minor & Kobe, 2019). Theories on resource competition indicate that close tree proximity intensifies competition, often resulting in diminished resource access and reduced reproductive success per tree (Ngaruka, 2011). In high-density tree stands, individual trees may experience increased competition for water, nutrients, and sunlight. Larger trees tend to support greater pod production due to their enhanced ability to access and utilize resources (Ouedraogo et al., 2020; Joubert et al., 2013), so competition between trees that reduces tree size may impact reproductive capacity. In fact, previous research indicates that tree density may negatively impact leaf area index and pod yield per tree (Jaaffar & Gardner, 1988). This suggests that while a dense forest may collectively produce a high volume of pods, individual trees may yield fewer pods than those in less crowded areas. For *V. erioloba* and *F. albida*, this could mean that trees that secure more resources through advantageous positioning or competitive traits are generally more successful in pod production.

Herbivore survival is closely tied to the forage availability of nutrient-rich vegetation from species core to the food web, such as *V. erioloba* and *F. albida*. Both *V. erioloba* and *F. albida* produce seed pods rich in proteins and carbohydrates, serving as primary food sources for grazing herbivores, including cattle, goats, and wild ungulates like oryx. Studies conducted along the Kuiseb River suggest that dense stands of *F. albida* experience higher browsing impacts from cattle, goats, and sheep than isolated trees. This indicates that pod removal rates may be greater in more dense clusters (Moser-Nørgaard & Denich, 2011). These pods provide essential nutrients that sustain these animals through the dry season when alternative resources are scarce (Jacobson et al., 1995; Hoffman et al., 1989). Additionally, these species hold significant social and economic value for the local Topnaar community, supplying fodder for livestock farming, fuel for the economy, and raw materials for traditional uses, including firewood and building materials.

Vachellia erioloba and *F. albida* exhibit unique adaptations that allow them to endure hyperarid conditions. *Vachellia erioloba* grows farther from the riverbank, and has an extensive taproot system reaching depths of up to 60 meters, enabling it to access deep groundwater reserves in the arid soil (Vandenbelt, 1991). *Faidherbia albida* grows closer to the riverbank, and has taproots reaching approximately 40 meters. Another adaptation that *F. albida* has is an "inverted" phenology, leafing out during the dry season and shedding leaves in the wet season. This strategy conserves moisture and allows the tree to survive even in extreme conditions (Schachtschneider, 2010). The staggered timing of pod production between *V. erioloba* and *F. albida* plays an essential role in maintaining forage availability year-round. *Vachellia erioloba* produces pods primarily during the winter months, while *F. albida* provides pods later in the summer, extending from September to February (Wood 1992; Van der Merwe et. al., 2019; Seymour & Milton, 2003). This seasonal spread of resources provides herbivores with food year-round, shaping their distribution and density within the ecosystem and ensuring sustained foraging opportunities across seasons.

We define several terms related to the ecosystem's forage dynamics. Pod availability refers to the presence of pods on the ground, shaped by factors like tree density, seasonal timing, and pod "residence time," or the period pods remain accessible on the ground before removal by herbivores or natural processes. Pod deposition is the rate at which pods fall from the canopy and onto the ground, where most herbivores access *V. erioloba* and *F. albida* pods (Hanya & Aiba, 2010. Pod removal describes the rate at which herbivores or other factors clear the pods (Smith & McWilliams, 2013). Both pod deposition and pod removal rate are key components that impact pod residence time and forage availability over time. According to theories of resource allocation, larger trees with greater canopy cover and trunk diameter are expected to produce more pods, as their increased capacity to capture resources allows for greater investment in reproductive efforts. Past research has specifically shown a positive relationship between tree circumference and *F. albida* pod production (Cervenka et al., 2017). These metrics—tree size, density, and pod availability—are crucial to understanding the resource distribution in the Kuiseb's ecosystem, especially when viewed from the competing perspectives of trees, which allocate resources to reproduction, and herbivores, which consume these resources for survival.

For this study, we aim to understand factors affecting forage resource supply for large herbivores along the Lower Kuiseb River in the Namib Desert. This research aims to understand resource dynamics in arid land ecosystems where the scarcity of water and nutrients exerts considerable pressure on tree productivity. Specifically, we examine tree size, density shapes, pods availability, pods deposition rate and pods removal rate for *V. erioloba and F. albida*. We hypothesize that competition, tree size and density, and water availability determine pod availability for herbivores in the Kuiseb River. We predict that larger trees likely have higher pod density on the ground due to increased pod production and greater energy allocation to reproduction. Furthermore, large trees and those in less densely populated areas may also exhibit higher deposition rates as a result of increased pod production. As tree density increases, we predict that pod availability per tree may decrease due to resource competition among closely spaced individuals. Lastly, higher tree density may attract more herbivores, increasing browsing pressure and pod removal rates. Through this approach, our study contributes to a broader understanding of resource dynamics in hyper-arid landscapes, informing conservation and land management practices crucial to sustainable resource use.

Methodology (Materials and Methods)

Study Area

Our study was conducted along a 68-kilometer stretch of the Lower Kuiseb River. Data was collected from four key sites: Upstream, Homeb, Natab, and Swartbank (Figure 1). These sites were identified based on prior research (Saima Shikesho, personal communication) and selected due to the availability of camera trap data, enabling us to analyze pod deposition and removal rates at the individual tree level. Each site represents a unique segment of the river ecosystem, providing a comprehensive view of pod dynamics influenced by environmental gradients along the river's course.

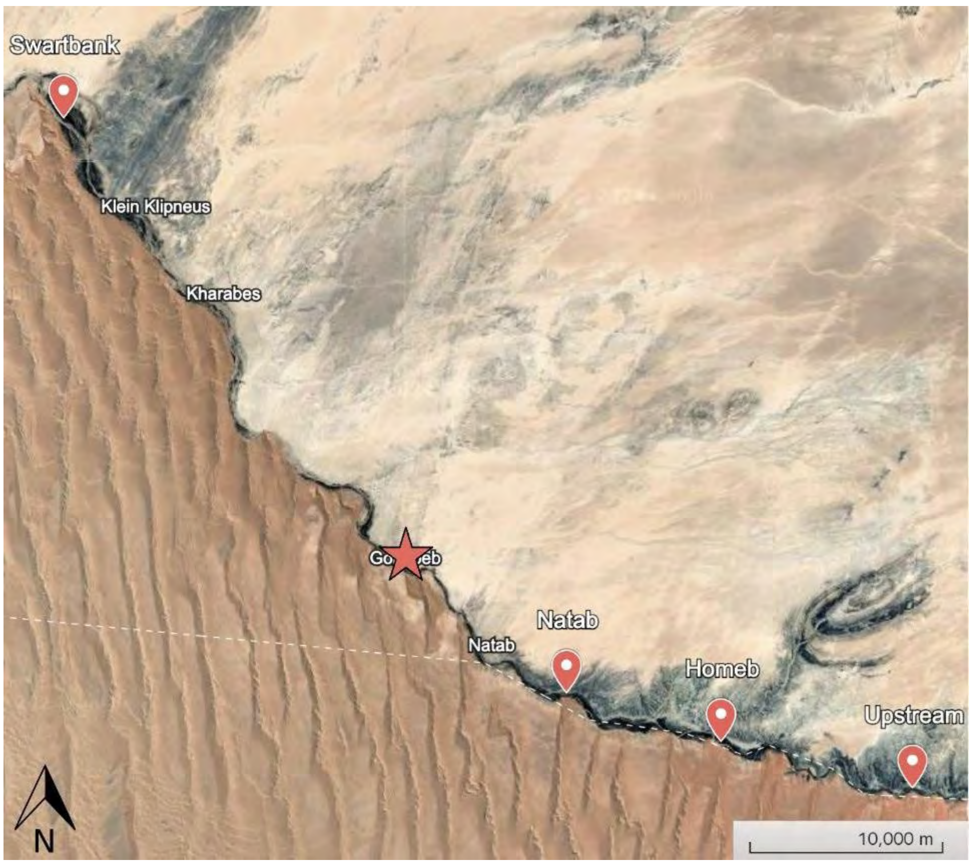

Figure 1: Geographic map of the total study area in the Lower Kuiseb River, with key sites marked with pins from left to right: Swartbank, Natab, Homeb, and Upstream. Created using GPS coordinates taken during data collection and Google Earth. A star is placed at Gobabeb Research Center, where our removal experiment was based.

Field Measurements

Though we lack direct measurements of pod production, the maturation of pods in the canopy, canopy cover, and tree size serve as our primary indicators of potential pod productivity for *V. erioloba* and *F. albida*. To investigate these factors, we focused on selected trees equipped with Saima's cameras at each site, referred to as our focal trees. Most sites contained two focal trees per species; however, due to camera theft, certain locations had data gaps. For each focal tree, we recorded species, diameter at breast height (DBH), tree height, canopy foliage cover, and GPS location over one week in November 2024. Instead of using DBH directly in our analysis, we converted this measurement to calculate area at breast height due to multiple stems at breast height from the same tree. Plants with main stems smaller than 2 cm DBH were excluded from the study to reduce potential outliers, allowing our analysis to focus on trees that significantly impact resource availability (Ngaruka, 2011).

Additionally, we examined each focal tree's two nearest neighbors (NN1 and NN2) to assess potential competition. Tree competition has traditionally been inferred from the relationship between focal tree size and surrounding forest density, offering insight into stand dynamics (Woodall et al., 2009). By applying the nearest neighbor method (Shackleton, 2002), which is widely used to analyze competition based on the spatial proximity of trees, we aimed to understand the influence of neighboring trees on pod production. Neighboring trees' competitive capacity is shaped by their spatial influence, providing a framework for exploring species distribution and pod production within the riparian landscape (Minor & Kobe, 2019). NN1 and NN2 were identified by measuring the distance from the bottom of the focal tree's trunk to the trunks of the nearby living trees. For NN1 and NN2, we measured distance from the focal tree, DBH, height, and canopy cover.

The DBH was measured using a tree diameter tape, providing the trunk's diameter at breast height (1.3 m). Area at breast height was done by calculating the area of each stem from its DBH and adding together for all the stems of the same tree.

Tree height was estimated using the WorkingTrees app, a beta tool leveraging iPhone LiDAR technology to measure tree size accurately (provided by Joseph Tumber-Dávila). WorkingTrees functions similarly to the default iPhone Measure app by operating on a three-dimensional plane, allowing height measurements between the tree base and the highest point with improved precision (Figure 2).

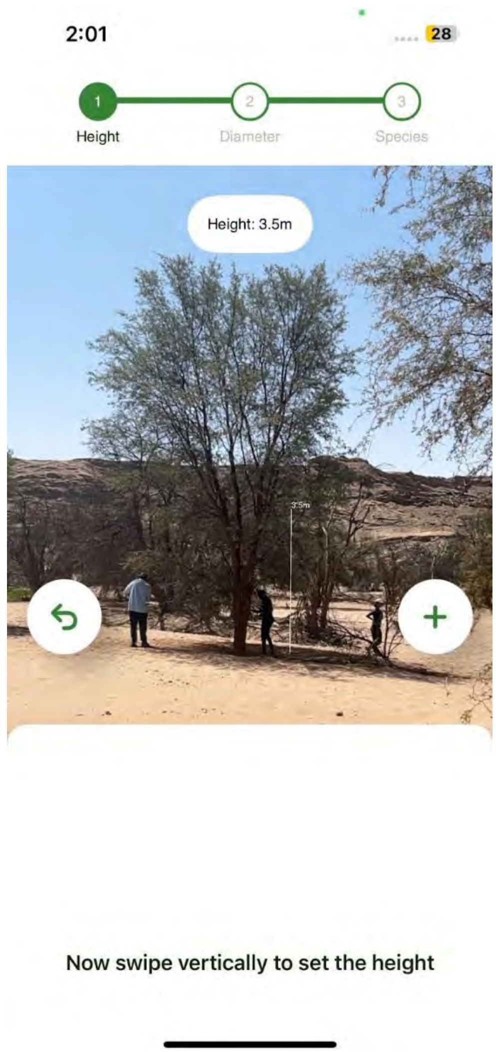

Figure 2: Example of tree height measurement using WorkingTrees app.

Canopy foliage cover was measured by capturing an upward-facing photograph directly under the camera trap using an iPhone. These photos were processed with the coveR R package, which provides an automated, fast, and reproducible method for analyzing Digital Cover Photography images to estimate canopy cover and leaf area index (Figure 3). The package performs single-image analysis or batch-processing and has been validated as a reliable tool for routine canopy monitoring, making it accessible for field studies (Chianucci et al., 2022).

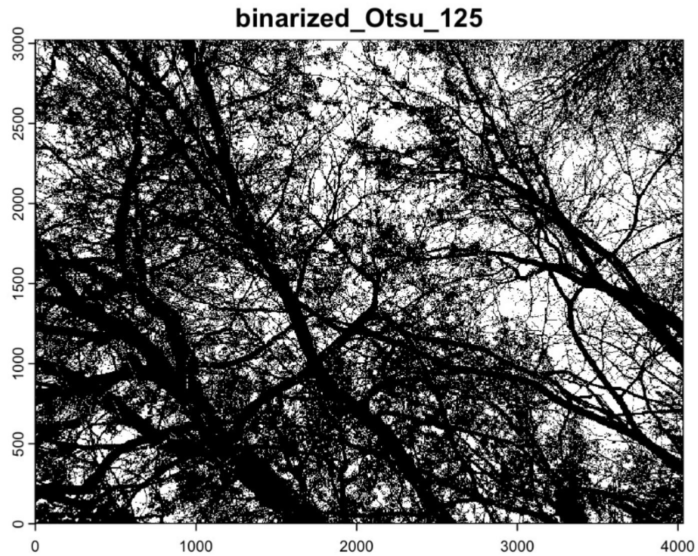

Figure 3: Example of a binarized image used to calculate foliage cover and leaf area index created by the coveR R package.

To broaden our dataset, we conducted transects to assess a larger sample of *V. erioloba* and *F. albida* trees at each site, allowing for comparative analysis of tree growth and density across locations. We opted for transect sampling of randomly selected individual trees, a method supported by prior Namibian studies on tree density and competition (Ngaruka, 2011). We established two transects at each site, one for each species, running parallel to the river channel. Transects were established in zones where our target species were more dominant: for *F. albida*, we ran the transect closer to the river channel, while for *V. erioloba*, we ran a transect closer to the edge of the riparian zone. Each transect spanned 140 meters, and at 20-meter intervals, we recorded data for the nearest tree of the target species, as well as its NN1 and NN2. Nearest neighbors were not required to be the same species as the focal tree, enabling a diverse representation of tree interactions. Using this method, we gathered data on 24 individual trees per transect, providing a robust sample to understand inter- and intraspecific competition across riparian zones.

Camera Analysis

Our image analysis relied on time-lapse camera data collected from 2022 to 2024 across our four sites along the Lower Kuiseb River, where current researcher Saima set up cameras to monitor pod-producing trees. For our analysis, we focused on images from August 2023 to July 2024, to capture key periods of pod deposition and removal across seasons. A total of fifteen cameras—two per species at each site—captured daily images, with each site representing varied habitats, including areas near Topnaar settlements where grazing by cattle and goats may affect pod dynamics. To ensure high-quality and consistent images, we prioritized images captured in the morning from each day's data. Morning light not only provided stable illumination and minimized shadows, enhancing the visibility and clarity of pods in each frame, but it also coincided with peak herbivore feeding activity, which is critical for capturing pod removal events. Our analysis focused on an average of the first 14 days of each month available (see Appendix I for the available months for each camera), prioritizing months with higher pod activity as indicated by phenological cues. This 14-day rolling observation window offered a balanced approach, capturing detailed short- term fluctuations while managing data volume. It allowed us to detect weekly trends and minimized the influence of isolated anomalies, making it a practical timeframe for observing pod dynamics.

Using ImageJ software, we tagged individual pods in the initial image of each monthly series to establish a baseline reference for tracking over time (Figure 4). Stacking images in sequence enabled each tagged point to persist throughout the series unless a pod was removed, which was then documented accordingly. This tagging process streamlined tracking, as tagged pods remained visible across frames, allowing for consistent monitoring of pod deposition and removal. For each day within this observation window, we recorded three main variables: pods added, pods removed, and the total pod count. From the removal rate each day, we also calculated the proportion of pods removed from the total pod count from the previous day to control for the variation between pod availability among days and trees. Then, from the daily count of total pods, deposition rate, and removal rate, monthly means in pods per day were calculated for each tree. Monthly means were used to calculate yearly means for each focal tree.

Figure 4: Example of camera analysis using ImageJ software, tagging individual pods in monitoring of pod deposition and removal.

Pod Removal Experiment

To examine the impact of tree density on the rate of herbivore pod removal, we conducted a controlled experiment at the Gobabeb Research Center along the Kuiseb River. Prior research on the Kuiseb has found a positive relationship between herbivore browsing and *F. albida* density, indicating that higher tree density may attract more browsing activity (Moser-Nørgaard & Denich, 2011). We selected 12 *F. albida* trees, as *V. erioloba* trees in the area were not currently producing pods, and divided them into two treatment groups: isolated and crowded. In the isolated treatment, each site contained a single pod-producing tree (or two trees sharing a single canopy) and was positioned at least 50 meters from any other pod-producing tree. The crowded treatment, in contrast, consisted of high-density sites with a minimum of three *F. albida* trees. For each treatment, we established a 5x5 meter quadrat directly beneath the tree canopy where pods would naturally accumulate, clearing all vegetation prior to experimental set-up. We randomly distributed 50 mature pods within each quadrat, sourced either from the riverbed or by shaking nearby *F. albida* branches where mature pods were stuck. To maintain consistency, all quadrats were set up within the riverbank, minimizing potential variability in herbivore feeding patterns and selection. Also, only trees that currently had no more pods on their leaves were selected, which ensured that no deposition occurred to alter pod counts. Motion-sensor cameras were installed to monitor herbivore activity in one quadrant per treatment. We observed the quadrats daily at the same time over a one-week period, beginning on November 3, 2024. This setup allowed us to document differences in pod removal rates based on tree density, providing insights into how herbivore interactions with pods might vary between isolated and crowded tree environments.

Statistical Analysis

Relationships between tree parameters, such as area at breast height, height, canopy cover, average pod deposition, pod removal, and total pod count, were assessed using linear regressions. A square root transformation adjusted variables with a skewed distribution to achieve normality before performing statistical analyses. Tree parameter comparisons across sites were analyzed with ANOVA to determine whether there was a difference between means, followed by a Tukey HSD test to assess the differences in means between each site. We used the same statistical methods to assess the difference in pod deposition, pod removal, and total pod count means across months. To statistically compare the exponential decay rates between crowded and isolated treatments, we fit separate non-linear models to each group and compared their decay parameters using an ANOVA test. All analyses were completed in R and visualized with the ggplot2 R package.

Results

Site Differences

Across all four sites in the Lower Kuiseb, *F. albida* and *V. erioloba* trees vary in parameters such as distance to NN1 and NN2, area at breast height, species composition of NN1 and NN2, and tree height. Distance to NN1 across transects ranges from 0 m to 14.6 m. Distance to NN2 ranges from 0.86 m to 24.1 m. In addition, area at breast height ranged from 2.01 cm^2 to 14,377.1454 cm^2, and tree height ranged from 1.63 m to 23.44 m.

We found that for both *F. albida* ($F_{3, 37} = 0.37$, $P = 0.78$) and *V. erioloba* ($F_{3, 34} = 2.56$, $P = 0.07$) focal trees, the distance to NN1 did not vary across sites. However, we found that for *F. albida*, the mean distance to NN2 varies across sites ($F_{3, 37} = 3.44$, $P = 0.026$; Figure 5). The difference in NN2 distances is driven by Swartbank, the most downstream site, exhibiting the greatest average distance (8.22 ± 1.14 m) to NN2 compared to the Upstream site, with the shortest average distance (3.35 m; Tukey HSD test: -4.87 ± 4.25, P = 0.019; see Appendix II for all Tukey test values).

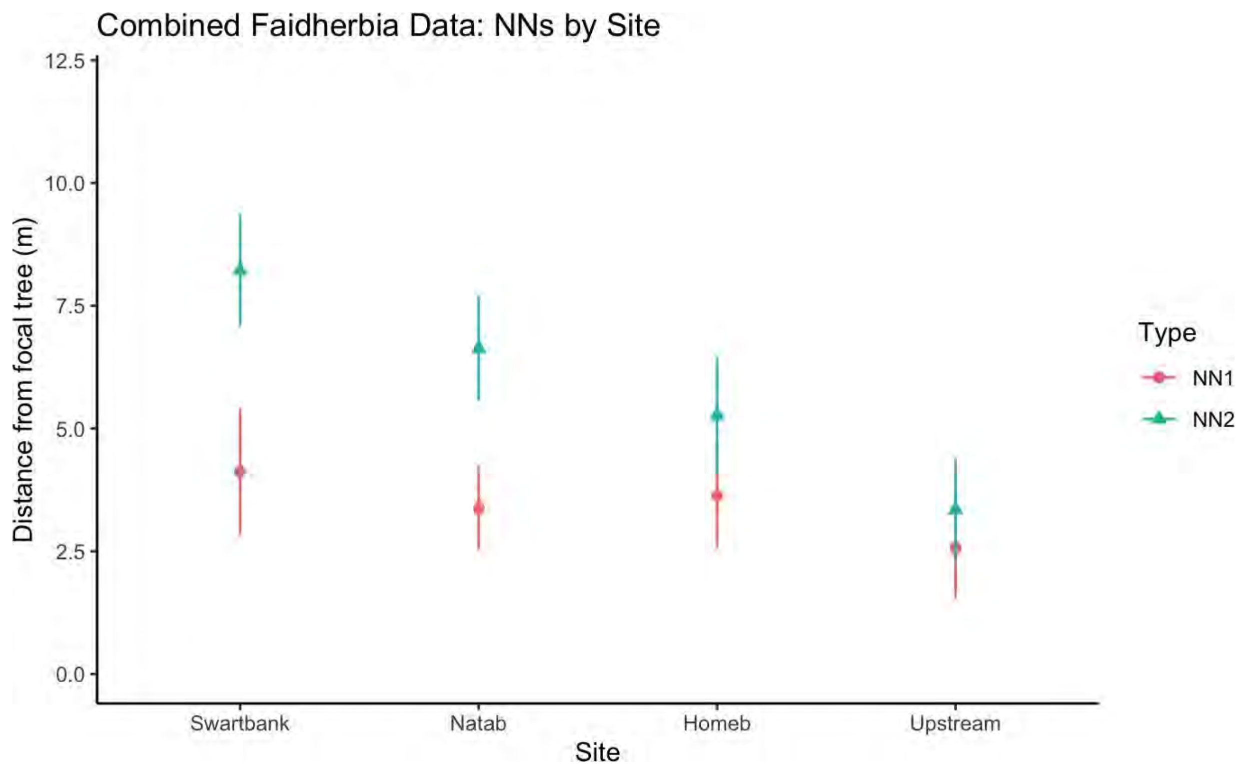

Figure 5: Mean distance from focal tree of *F. albida* to NN1 and NN2 in meters, ranging across sites from downstream to upstream in the Lower Kuiseb River. Means are presented with standard error bars.

For *V. erioloba* trees, the distance from the focal tree to NN2 was significantly different across sites ($F_{3, 34} = 3.06$, $P = 0.04$) (Figure 6). The distance to NN2 was shorter at Homeb compared to Natab (Tukey HSD test: 5.18 ± 5.19, P = 0.05) and Swartbank (Tukey HSD test: 4.78 ± 5.19, P = 0.08), but there was no difference between the other sites: Upstream, Natab, and Swartbank sites (all $p>0.05$).

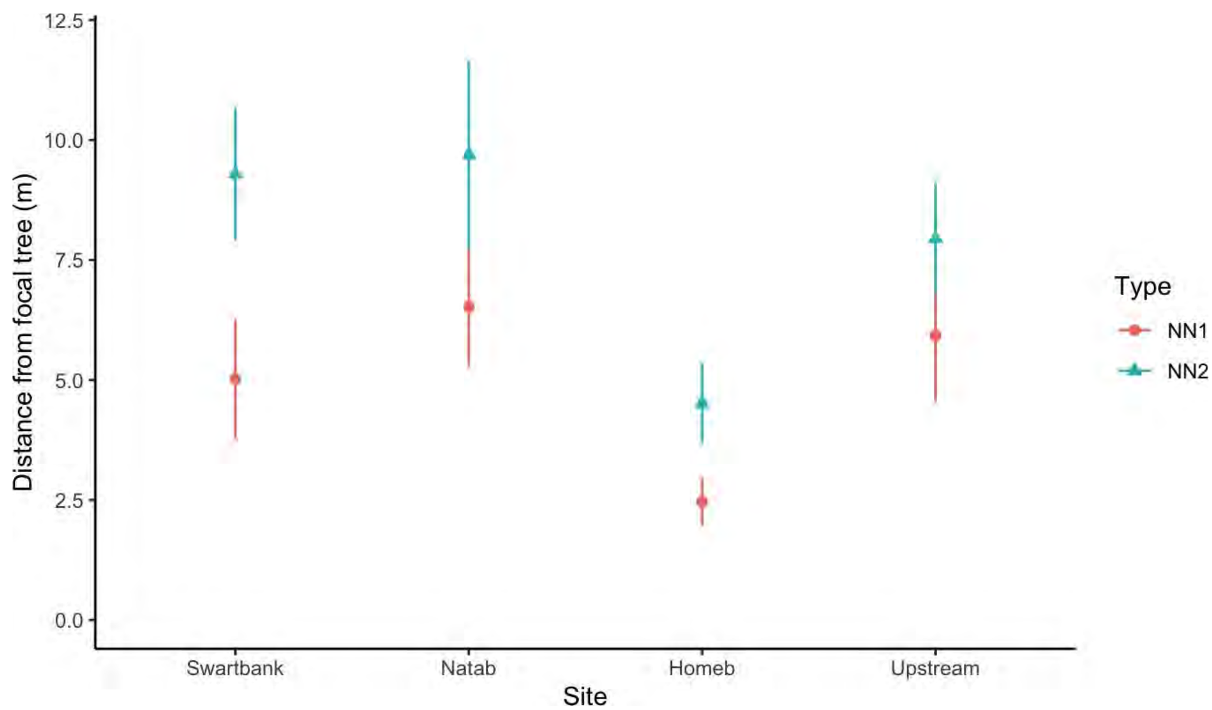

Figure 6: Mean distance from focal tree of *V. erioloba* to NN1 and NN2 in meters, ranging across sites from downstream to upstream in the Lower Kuiseb River. Means are presented with standard error bars.

Faidherbia albida and *V. erioloba* had different compositions of neighboring tree species. Most of the neighboring tree species for *F. albida* were pod-producing species, with conspecific making up 76.2%, followed by *V. erioloba* (14.3%) and then non-pod producing species (*Euclea pseudebenus, Salvadora persica)* comprising less than 10% (Figure 7). Similarly, most neighboring species for *V. erioloba* are pod-producing species, with conspecifics making up 65.8%, followed by *F. albida* (21.1%) and lastly, *E. pseudebenus* (13%, Figure 7).

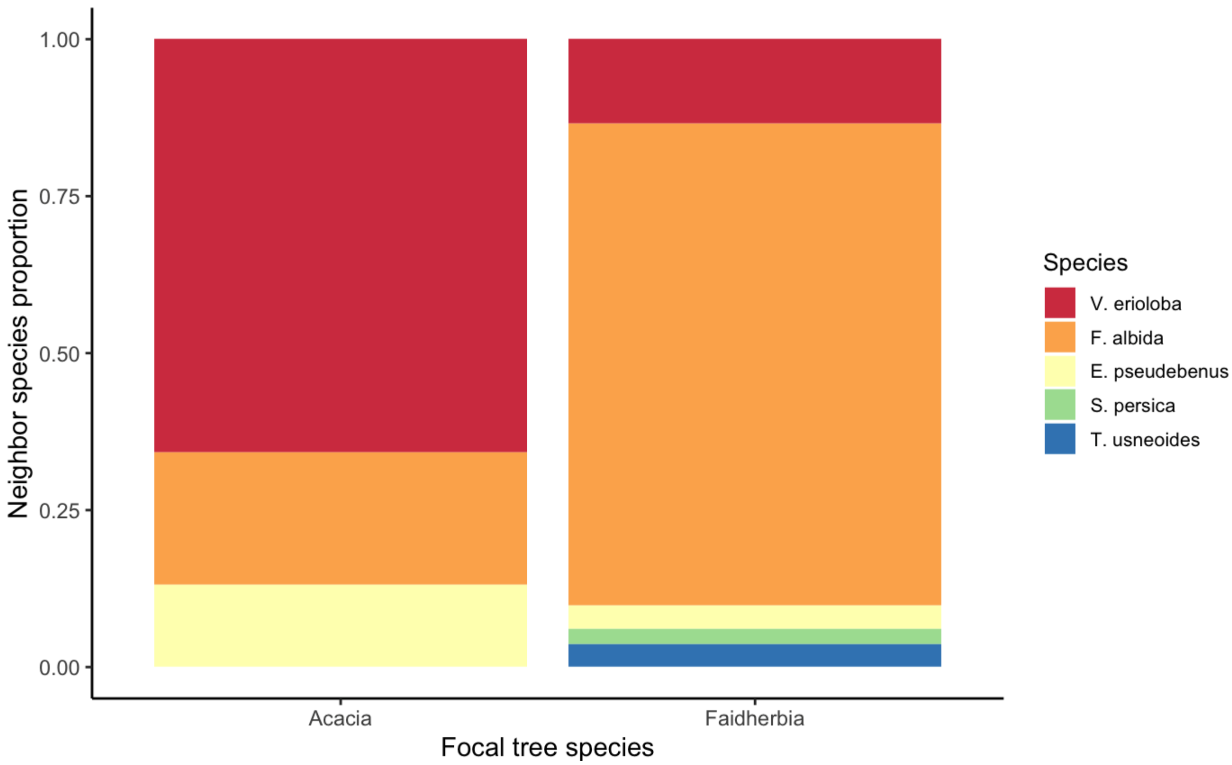

Figure 7: Proportion of Species Richness of neighboring tree species sorted by focal tree species.

Relationship Between Nearest Neighbors and Focal Trees

We found no relationship between the distance of NN1 from the focal tree and the focal tree's area at breast height (slope = 0.46 ± 1.00, P = 0.65, R^2 = 0.003), height (slope = -0.25 ± 0.17, P = 0.15, R^2 = 0.03), or canopy cover (slope = -0.002 ± 0.004, P = 0.59, R^2 = 0.004). There was a slight positive relationship between NN1 area at breast height and the focal tree's area at breast height (slope = 0.27 ± 0.15, P = 0.07, R^2 = 0.04). Overall, there is a positive correlation between NN1 height and the focal tree's height (slope = 0.31 ± 0.12, P = 0.01, R^2 = 0.08). In general, there was no trend between canopy cover, area at breast height, and height across sites (p>0.05?).

Pod Fall Phenology

From the phenology cameras, we observed that *V. erioloba* pods began to mature in October, with full maturation achieved by mid-November. The greatest deposition of mature *V. erioloba* pods occurred from mid-November through the end of December. While the trees ceased pod production in January, mature pods remained stuck on the trees, gradually falling and persisting on the ground through mid-May.

For *F. albida*, flowering started in August, with pods appearing on the trees towards the end of December and peaking from December through February. Although *F. albida* stopped actively producing pods by March, a significant number of pods remained attached to the branches. These pods, though not freshly deposited, were still accessible to herbivores as they lingered on the trees and were deposited throughout the year.

Forage Availability

Through analyzing time-lapse cameras of pods on the ground, we found high variability between both individual trees and across months for total pod count, pod deposition, and pod removal. Specifically, the daily total number of pods on the ground within the camera frame ranged from zero to 531 pods for *F. albida* and from zero to 617 pods for *V. erioloba*. In terms of daily pod deposition, the rate at which pods dropped to the ground each day, ranged from zero to over 173 for *F. albida* and from zero to 67 for *V. erioloba* for each day. Similarly, daily pod removal, the rate at which pods were removed from the ground each day, ranged from zero to 176 for *F. albida* and from zero to 40 for *V. erioloba*. Notably, pod deposition, removal, and total pod count data were skewed toward zero, with 21.4% of mean month deposition rates, 21.4% of mean month removal rates, and 12.6% of mean month total pod counts being zero.

This high daily variability was reflected in the monthly averages for total pod count and deposition. In general, there was more variability in the number of pods on the ground for *V. erioloba* compared to *F. albida*. For example, the mean monthly pod count ranged from zero to 597.7 pods for *V. erioloba*, compared to a range of 39.3 to 182.0 pods for *F. albida* (Table 1). For monthly pod deposition, the mean deposition rate of individual trees ranged from 0 to 11.5 pods per day for *V. erioloba* and from 0.39 to 7.7 pods per day for *F. albida* (Table 1). Mean monthly pod removal had similar variability to pod deposition across both species, with pod removal rate higher in months with higher pod deposition and lower in months with lower pod deposition for both *V. erioloba* (Figure 8) and *F. albida* (Figure 9). However, variability of pod removal rates did not necessarily mean variability in the proportion of pods removed from the previous day's total pod count. Though the proportion of *F. albida* pods removed varied across months ($F_{11, 486} = 2.58$, $P = 0.003$), the proportion of pods removed from *V. erioloba* was not significantly different across months ($F_{10, 480} = 1.64$, $P = 0.09$).

Table 1: Pod Availability Across Months. For September, October, and November, *V. erioloba* had one camera operating.

	V. erioloba			***F. albida***		
Month	**Mean Deposition Rate ± st. dev. (pods/day)**	**Mean Removal Rate ± st. dev. (pods/day)**	**Mean Total Count ± st. dev.**	**Mean Deposition Rate ± st. dev. (pods/day)**	**Mean Removal Rate ± st. dev. (pods/day)**	**Mean Total Count ± st. dev.**
August	1.27 ± 4.39	1.13 ± 2.13	36.80 ± 4.39	6.02 ± 21.86	7.70 ± 29.17	120.48 ± 21.86
September	16.00	14.00	597.71	8.60 ± 10.91	6.47 ± 2.58	193.13 ± 10.91
October	3.54	2.15	509.21	10.33 ± 13.86	5.77 ± 0.75	202.07 ± 13.86
November	11.54	15.23	525.79	4.79 ± 2.22	4.05 ± 1.36	204.19 ± 2.22
December	8.65 ± 4.10	5.54 ± 4.25	261.86 ± 4.10	3.09 ± 2.14	3.08 ± 2.55	115.07 ± 2.14
January	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	3.78 ± 5.43	3.09 ± 3.41	39.31 ± 5.43
February	1.10 ± 2.54	1.24 ± 2.95	102.53 ± 2.54	1.37 ± 2.03	2.69 ± 5.73	151.65 ± 2.03
March	2.11 ± 3.45	2.66 ± 3.36	64.71 ± 3.45	0.38 ± 1.20	1.48 ± 1.61	181.99 ± 1.20
April	1.56 ± 1.46	1.45 ± 1.48	74.17 ± 1.46	0.49 ± 1.25	0.87 ± 1.75	130.76 ± 1.25
May	1.97 ± 2.38	1.82 ± 1.23	73.93 ± 2.38	0.68 ± 1.80	0.39 ± 1.20	120.31 ± 1.80
June	1.98 ± 2.32	1.84 ± 0.78	77.78 ± 2.32	3.78 ± 16.56	0.58 ± 1.76	177.53 ± 16.56
July	0.26 ± 0.94	0.78 ± 0.86	29.08 ± 0.94	1.33 ± 2.47	2.08 ± 10.84	136.55 ± 2.47

Pod Deposition

Throughout the year, there was notable variability in deposition patterns. For *V. erioloba*, mean daily deposition rate peaked in September (16 pods per day), while *F. albida* experienced a mean daily pod deposition peak in October (10.3 pods per day). However, deposition rates do not directly reflect the overall pod count on the ground throughout the year, due to the persistence of pods from previous months on the ground. Although deposition rates tapered off after December for *V. erioloba* (Figure 8) and after January for *F. albida* (Figure 9), residual pods on the ground and unfallen pods on trees continued to provide forage resources across these periods (Figure 10, 11).

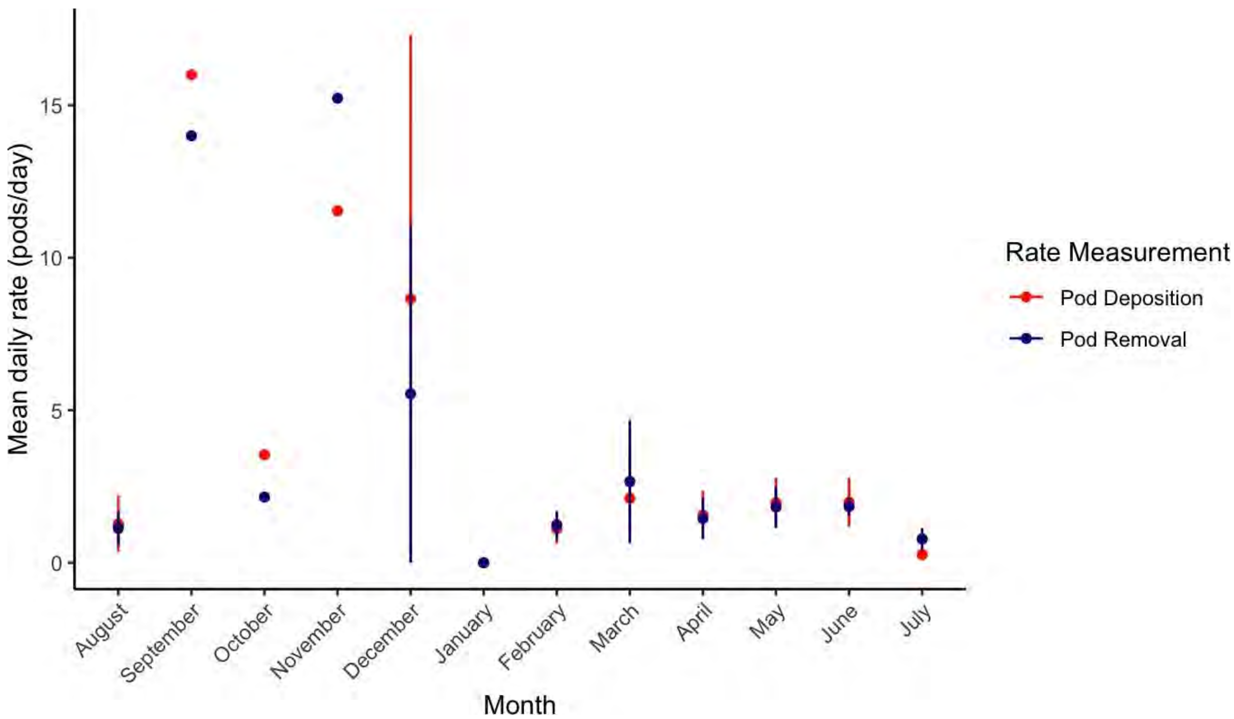

Figure 8: Mean monthly pods deposition rate (red) and removal rate (blue) of *V. erioloba* plotted from August 2023 to July 2024. Means are presented with standard error bars. For September, October, and November, only one camera was operating.

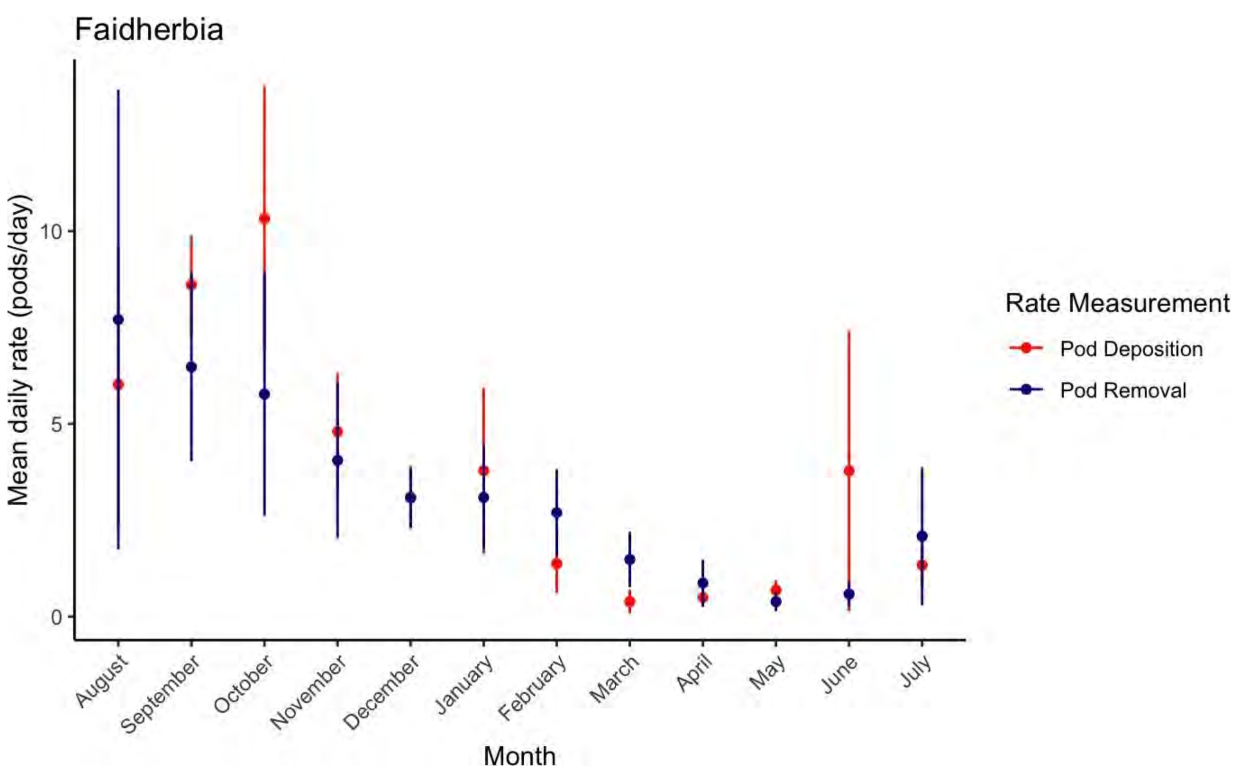

Figure 9: Mean monthly pods deposition rate (red) and removal rate (blue) of *F. albida* plotted from August 2023 to July 2024. Means are presented with standard error bars.

Pod Availability on the Ground

The mean total pod count on the ground for *F. albida* remained substantial for the months of February (151.7), March (151.7), April (182.0), and May (130.7; Table 1), even though deposition rates significantly declined for those months (Figure 9). This indicates that pods deposited in previous months persisted on the ground (Table 1). Similarly, *V. erioloba* experienced low deposition rates in January through July (Figure 8), yet the mean total pod count for these months was still notable (Figure 10), showing that resources were still accessible from prior high- deposition periods (Table 1). In February, while deposition rates slowed, the mean total count for both *V. erioloba* and *F. albida* was still relatively high (Table 1).

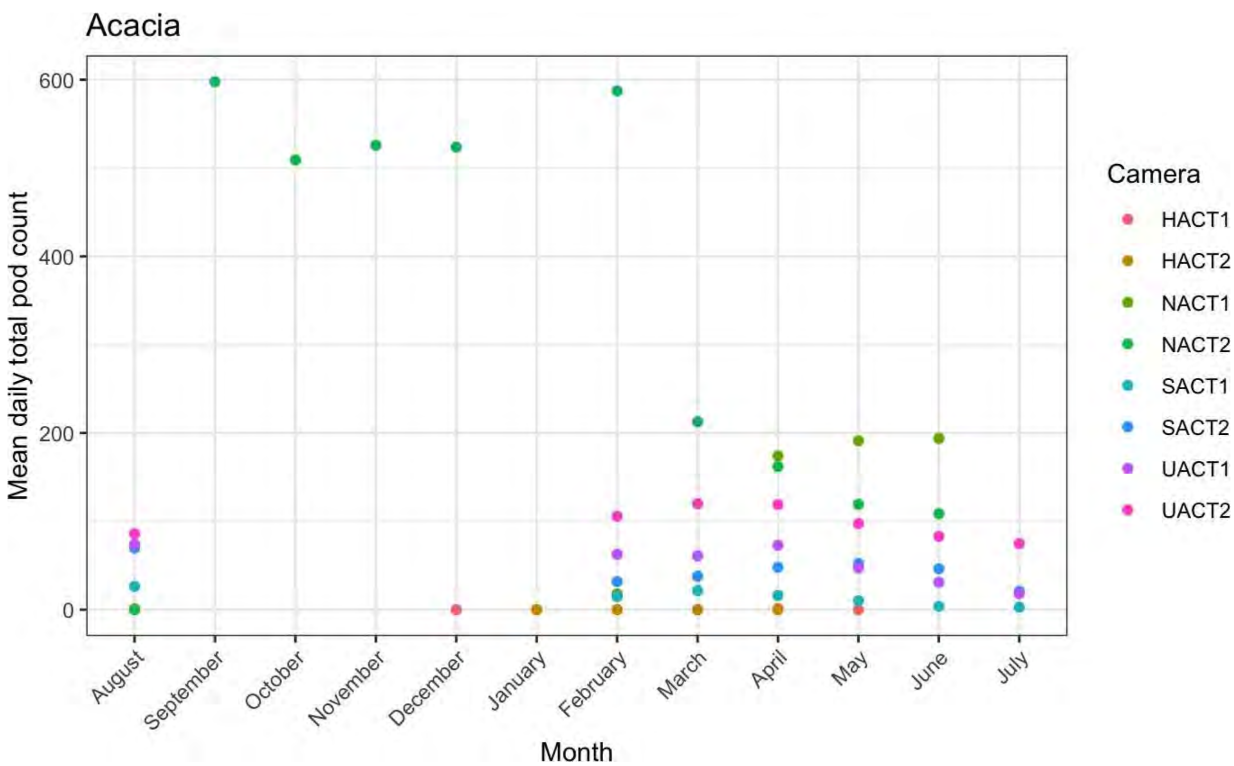

Figure 10: Mean monthly total pod count per day for *V. erioloba* trees from August 2023 to July 2024 for each tree. Sample size varies from n=1 to n=7 for each month based on camera data availability.

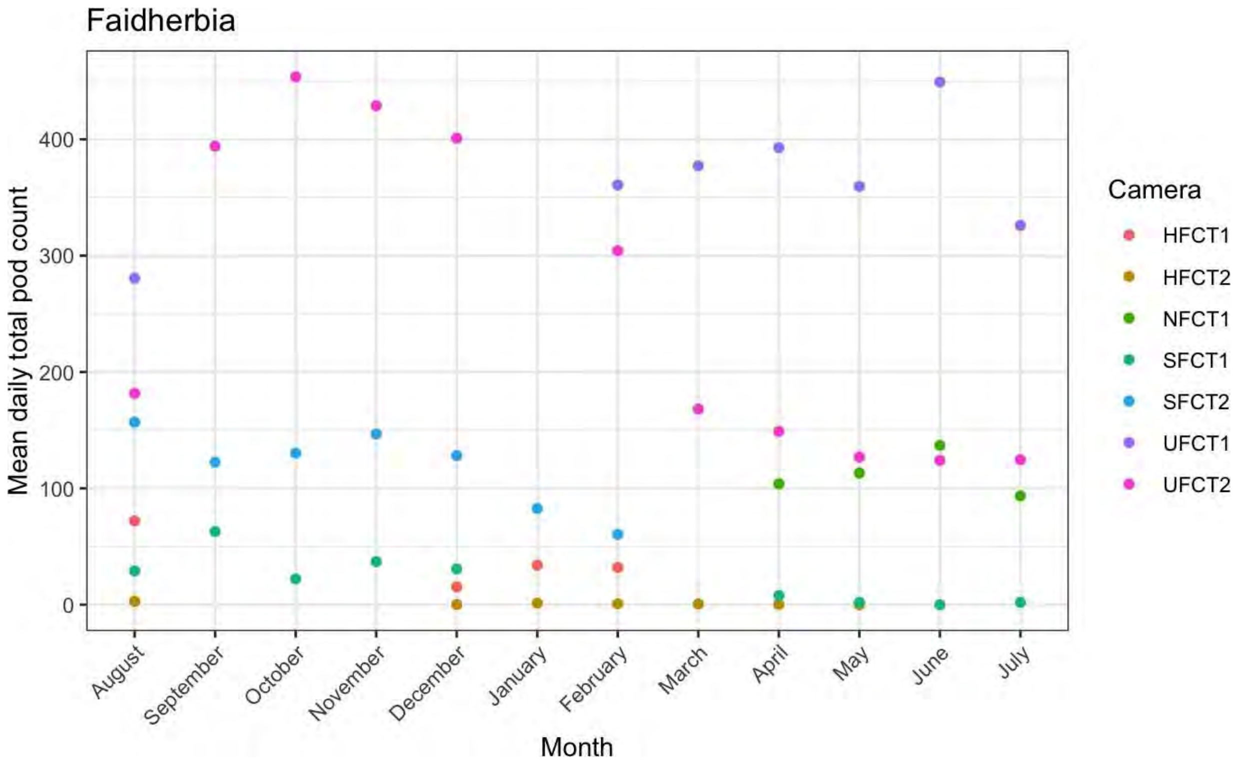

Figure 11: Mean monthly total pod count per day for *F. albida* trees from August 2023 to July 2024 for each tree. Sample size varies from n=1 to n=7 for each month based on camera data availability.

Herbivore Pod Consumption Rate Experiment

Through our pod removal experiment, where we set up 50 pods around each of six crowded and six isolated *F. albida* trees, we observed faster removal rates of pods by herbivores in crowded *F. albida* trees than isolated trees over time (Figure 12). After one day, 90% of the provisioned pods (n=50) were consumed by herbivores (confirmed with motion sensor imagery) around crowded trees, while in isolated trees, only 30% of the provisioned pods were consumed. We found a significant difference between sites, with crowded trees containing fewer remaining pods compared to isolated trees ($t = -3.72$, $df = 6.45$, $P = 0.009$). Across six days of observation, the crowded sites' trend had reached close to zero while isolated sites leveled out around 15, leading to a statistically significant difference between the crowded and isolated treatment groups' decay functions ($F_{1, 41} = 43.05$; $P < 0.0001$).

Motion sensor cameras at crowded and isolated sites captured images of goats and springbok consuming pods. Goats were most abundant and were seen at both clustered and isolated sites. One springbok was seen only at the isolated site (Appendix III).

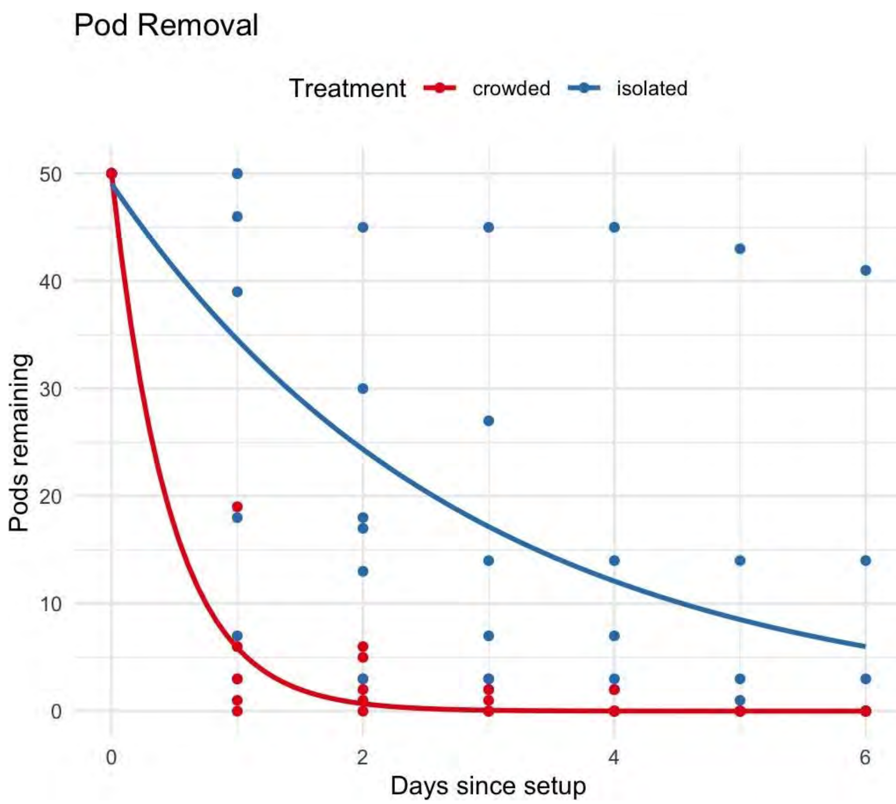

Figure 12: Exponential decay function of pod removal over six days at crowded *F. albida* sites ($y = 49.97 * e^{-2.14x}$) and isolated *F. albida* sites ($y = 49.04 * e^{-0.35x}$) at Gobabeb Research Center.

Relationships Between Forage Availability and Tree Parameters

In general, tree size and tree density did not impact total pod count and pod deposition rate at time- lapse camera sites. Canopy cover was not an indicator for pod deposition rate for *V. erioloba* (slope = 0.01 ± 1.41, P = 0.75, R^2 = 0.02; Figure 13) or *F. albida* (slope = -0.004 ± 1.41, P = 0.75, R^2 = 0.02; Figure 13). In addition, there was no significant relationship between area at breast height and total pod count (slope = 1.18 ± 0.98, P = 0.25, R^2 = 0.11; Figure 14) and pod deposition rate (slope = 3.28 ± 7.60, P = 0.67, R^2 = 0.02). For tree density, there was no significant relationship observed between the distance to NN1 and total number of pods (slope = -0.008 ± 0.21, P = 0.97, R^2 = 0.05; Figure 15) and pod deposition rate (slope = -0.08 ± 1.50, P = 0.96, R^2 = 0.02; Appendix IV) of the focal tree.

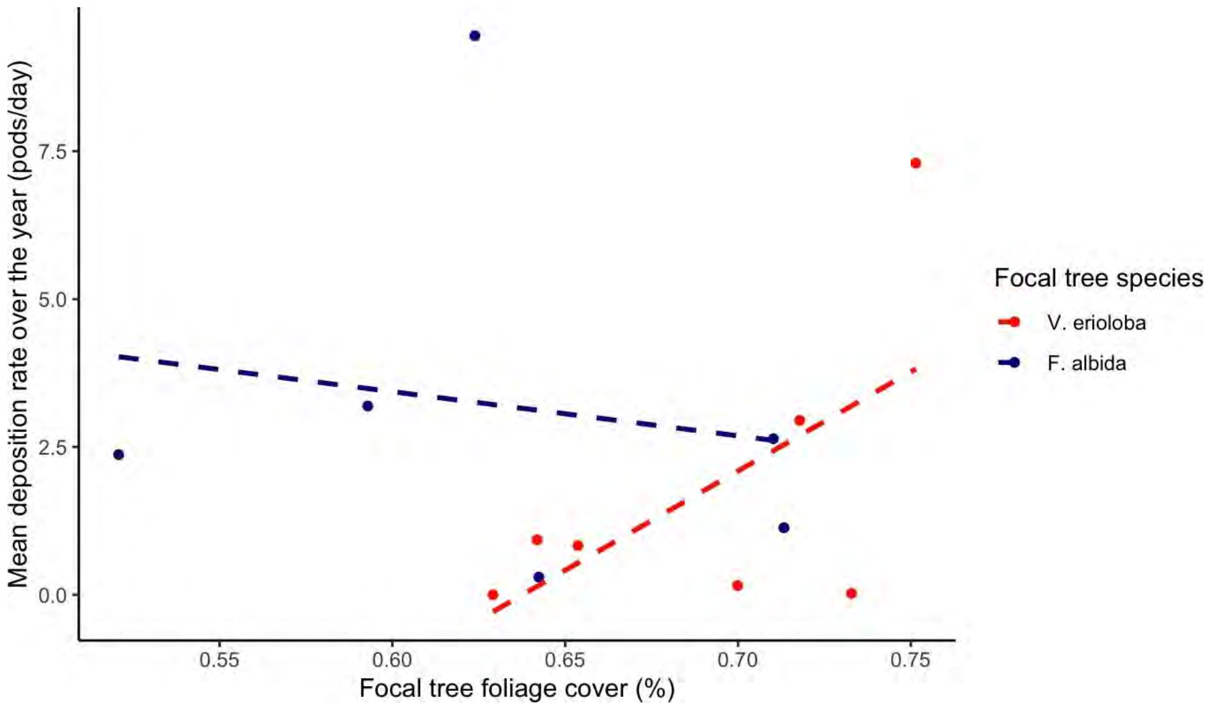

Figure 13: Mean daily pod deposition rate for *V. erioloba* and *F. albida* trees from August 2023 to July 2024 and percent foliage cover of each focal tree.

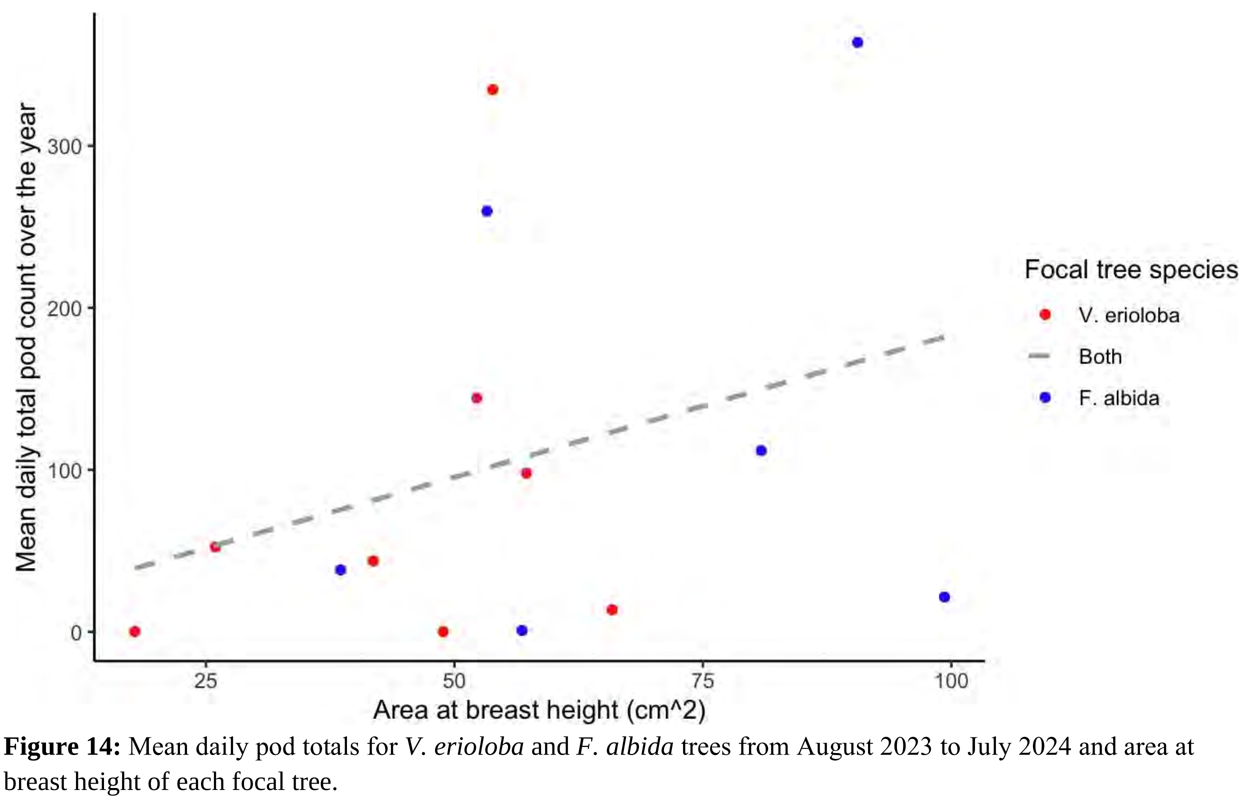

Figure 14: Mean daily pod totals for *V. erioloba* and *F. albida* trees from August 2023 to July 2024 and area at breast height of each focal tree.

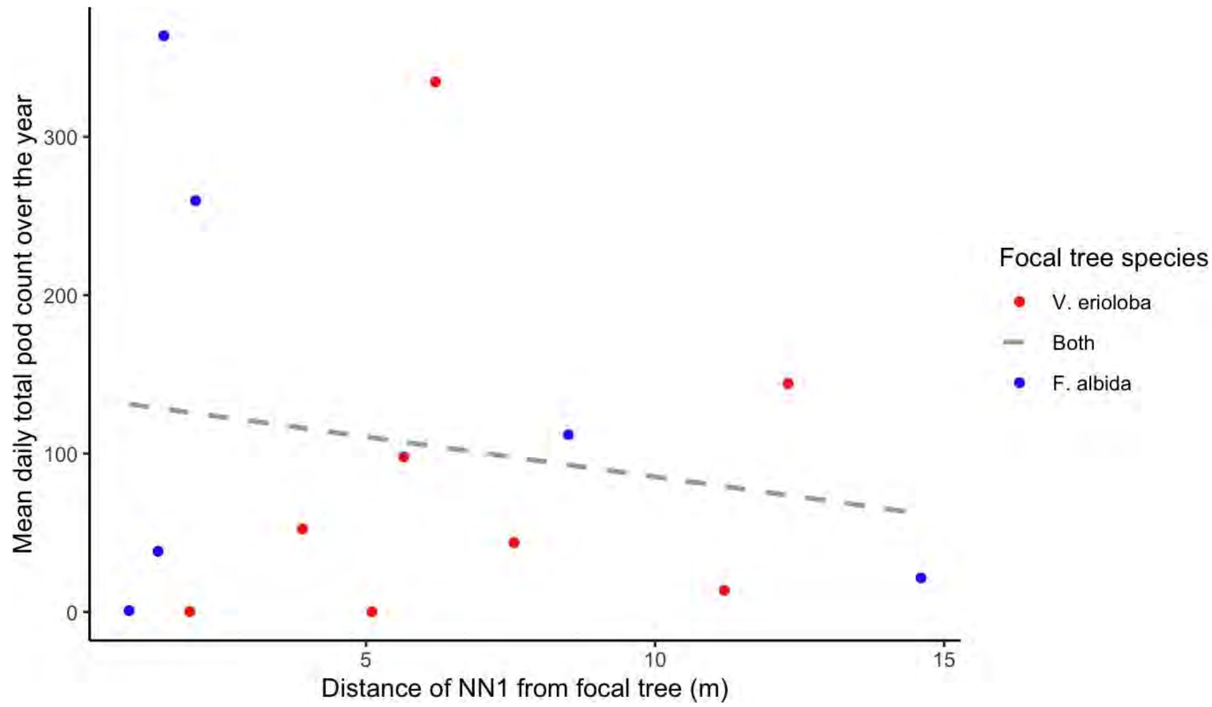

Figure 15: Mean daily pod totals for *V. erioloba* and *F. albida* trees from August 2023 to July 2024 and NN1 distances from each focal tree.

Discussion

Our study hypothesized that tree density would influence both tree size and pod availability, with denser areas leading to increased competition as well as reduced individual tree growth and pod production. Across the four sites, nearest neighbor (NN) parameters and distances generally had limited measurable effects on focal tree size, canopy cover, or pod availability. This suggests that tree proximity and tree size alone do not directly influence resource availability or reproductive output.

Site Differences

We saw differences between NN2 distances across sites but not for NN1 distances. Visually, we observed differences among sites in tree density. Trees were denser at upstream sites, where we found it harder to navigate undergrowth. However, this gradient was not present in our statistical analysis, which found no difference in NN1 distances across sites. Our observations in density may not be properly represented by NN1 data given clustered growth patterns, which could have manufactured NN distance uniformity despite changing distances between separate clusters. This separation between clusters might be better represented with distances to NN2: as specifically for *F. albida*, NN2 distances decreased upstream, indicating denser tree populations in these areas. This pattern corroborates past research indicating greater woody vegetation density upstream

(Morgan et al., 2020) and aligns with our hypothesis that upstream sites, benefiting from stable groundwater recharge and greater water availability, create more favorable conditions for vegetation growth and potentially higher pod production. Since this clear decreasing density trend is only reflected in *F. albida* and not *V. erioloba,* which saw differences in NN2 distances across sites but not in correlation to the flow gradient, may also reflect *F. albida's* greater sensitivity to water availability. *Faidherbia albida* trees grow closer to the riverbed compared to *V. erioloba* (Wood, 1992), as *V. erioloba* can thrive further from the Kuiseb River due to its ability to survive on minimal water. On the other hand, *F. albida*—though also drought-resistant—requires a more consistent groundwater source (Wood, 1992).

Despite finding differences in nearest neighbor distances, the distance of the focal tree's first nearest neighbor (NN1) and second nearest neighbor (NN2) did not impact the focal tree's size or canopy cover. In addition, the focal tree's nearest neighbors' tree size and canopy cover had no impact on the focal tree's parameter. Thus, we found no relationship between tree size and tree density in the Lower Kuiseb riverine system and no evidence to support our hypothesis that competition, in the form of a focal tree's nearest neighbors, impacts tree growth.

We observed many large trees growing in close proximity to each other, which may explain the lack of any relationship between tree density and size. There are multiple potential explanations for this growth pattern. First, the prevalence of NN1 and NN2 trees conspecific to the focal tree suggests a potential lack of interspecies competition, but existing intraspecies competition (Ngaruka 2011). Past studies of *V. erioloba* trees in Namibia found clustered monotypic growth to be common in arid ecosystems, suggesting that individual growth may be maximized in the absence of other tree species (Ngaruka 2011). Second, tree clustering could induce the creation of favorable microenvironments. These spaces contain higher contents of soil macronutrients, as both *V. erioloba* and *F. albida* are nitrogen-fixers, increased leaf litter, and concentrated herbivore droppings (Ngaruka 2011). Greater canopy density also limits soil evaporation through shading, lengthening root access to rainfall, groundwater, and condensation (Ngaruka 2011). Third, our observations of trees–particularly *F. albida*–found complexities in trunk stem growth. Some trees grew in horizontal directions immediately after emerging from the ground, others grew upwards originally before curving out horizontally at their midsection, while the remainder grew straight upwards. The structural variation existed within distinct, same-species clusters, indicating potential for resource partitioning as their growth patterns trended towards open spaces and access to light. Rather than competing and consequently thinning out upon maturity, clustered individuals manage to coexist by optimizing spatial niches through diverse growth. Ultimately, our observations suggest competition plays less of a controlling factor in tree size and density than other factors, such as water availability. This conclusion has implications for pod availability, as prior research has directly linked water availability to pod production (Bianchi et al., 2020).

Forage Availability

There was no relationship between tree size and canopy cover on pod availability. Even examining the direct connection between the distance of NNs on pod availability illustrated no relationship. Therefore, not only is there no impact of NNs on focal tree size, it is also not an indicator of pod availability for herbivores providing insufficient support for our hypothesis that larger trees and lower densities would correlate with greater pod availability. This lack of correlation could be due to high variability in pod production, which might obscure discernible patterns. This outcome aligns with findings in other competitive woody savanna ecosystems, where factors beyond tree size or density—such as microclimate variations or localized water availability—may play a more influential role in reproductive success (Ngaruka, 2011). For instance, both species showed high daily and monthly variability in total pod count, pod deposition, and removal from time lapse camera data, which may indicate that other factors are at play.

One potential explanation for the pod variability might be due to "masting," where a synchronized, large-scale pod production occurs periodically. Although masting is not well-documented in *Acacia* species, the high variability we observed in pod deposition at the Natab site hints at similar behavior. For instance, last year, one *V. erioloba* tree (NACT2) had over 500 pods on the ground during the months of September through February, while a nearby tree, only 18 meters away, had fewer than half that amount of pods on the ground. In fact, the timing of this high pod deposition and pod availability contradicts past literature that suggests that *V. erioloba* pods typically drop from May to September (Seymour & Milton, 2003). Moreover, when we visited the site in November 2024, the ground beneath both trees was clear of pods. This discrepancy suggests that pod production and deposition might fluctuate between years, potentially in response to environmental factors like drought. Similarly, a prior study on seed production in trees found a highly skewed distribution of annual seed production, with large variation ranging from 0 to more than 100 seeds for samples of the same species (Davi et al., 2016). Similar to past conclusions on interindividual variability in seed production, our variation points to a potential episodic strategy or sensitivity to diverse environmental triggers, encouraging further research to understand these fluctuations.

Pod Deposition

Our phenology data provide a timeline for pod maturation and deposition for both *V. erioloba* and *F. albida*, highlighting seasonal patterns that stagger pod availability across species. *Vachellia erioloba* pods begin maturing in October, with peak deposition from mid-November to December. In contrast, *F. albida* begins flowering in August, with pods available from September to February. These seasonal differences ensure resources are available to herbivores at various times of the year. Furthermore, total pod count on the ground remained more consistent than deposition rate, providing sustained forage resources even during periods of low deposition. For instance, in February, pod deposition begins to taper off for both *F. albida* and *V. erioloba*, while total pod count on the ground remains relatively high. This month may serve as a critical transitional period, with lingering pods from previous deposition peaks remaining on the ground, demonstrating that low deposition rates do not necessarily imply a lack of available resources. Remaining pods, both on the ground and attached to trees, ensure continuous availability even during months with minimal or no new deposition, providing sustained forage resources for herbivores throughout the year. For example, *F. albida* pods, with their thick, curled structure, often get stuck on branches, remaining available for an extended period, but variable environmental factors like wind can cause these pods to fall in clusters, creating sudden bursts of resources on the ground. The shapes and structures of the pods further influence these deposition patterns and availability. *V. erioloba* pods fall whole without dehiscing, providing concentrated bursts of resources when they hit the ground. These structural differences in pod morphology affect each species' unique deposition pattern, ultimately shaping how pods are available for herbivores and seed dispersers over time.

The observed variability in pod deposition highlights the complex localized environmental factors, such as water access, soil quality, or sunlight, that influence pod availability. This variability complicates the predictability of forage availability in heterogeneous landscapes, where even slight differences in environmental factors can lead to significant changes in resource distribution.

Pod Removal

Pod removal appears to be closely linked to tree density, with our experiment revealing significant differences between crowded and isolated sites of *F. albida*. Pods were consumed at a greater rate within crowded sites, supporting our experimental hypothesis. We theorize that several variables may have an effect on this relationship, such as shading and attraction of herbivores to pools of foraging resources.

Our camera data showed that herbivores consumed pods during two distinct times of the day: the early morning around 7 AM, and the late afternoon between 3 and 4 PM. Herbivores like springbok and goats may be more active early in the morning due to temperature differences, as the mean temperature at Gobabeb Research Center at 7 AM in the month of November is 12.9℃, as compared to 29.5℃ at 4 PM (Schulze, 1969). Shading also appears to play a critical role in determining feeding times, with crowded sites cameras strictly capturing herbivory when the quadrat was fully shaded.

One notable outlier in our study was an isolated tree with insufficient canopy cover to provide shade at any point during the day. This tree received the least amount of feeding of all 12 sites, with only 9 pods consumed over 6 days. Additionally, large packs of animals were the primary consumers of pods at crowded sites, while single individuals feeding were strictly observed at isolated sites. Larger canopy shade areas can accommodate a larger number of grazers, and individuals may be less likely to stray from the pack if there is more shade and more resources (Mizuno & Yamagata, 2005; Randle et al., 2018).

Human activity may also influence pod removal rates. Gobabeb Research Center is located near several Topnaar settlements along the Kuiseb River, where cattle and goat herders interact with the landscape. One of our cameras captured a dog herding goats, suggesting that herders may direct livestock to areas with greater pod density. Evidence of this influence was observed in a crowded quadrat, where a previously tracked herbivore path crossed the site, resulting in the removal of 49 pods within the first 24 hours. Additionally, large piles of pods beneath some trees indicate that the Topnaar community may redistribute pods, potentially increasing removal rates in these areas (Appendix V).

Implications and Future Research

Forage resources form the foundation of the food chain, making it essential to study how seasonal variations in pod availability affect ecosystem dynamics. Understanding these effects is crucial for predicting and managing future ecological changes. Determining that competition may not be the primary factor tree growth, density, or pod availability in the Kuiseb River ecosystem is crucial for herbivores and local communities who rely on pods for food and fodder. We found high variation in pod availability among trees unrelated to tree size or tree density, which indicates that other environmental factors are at play. Especially in an arid environment, where ecosystems are subject to high climate variability, identifying which factors are key determinants for pod availability will provide important insights for how to ensure sufficient future foraging resources.

Further research to increase our understanding of forage availability could include refining our understanding of water availability, another contributing factor. Although our study assessed this through site differences, adding data on tree distance from the riverbed would provide insight into the Kuiseb River's specific influence on tree growth and distribution across differing proximities. Additionally, long-term data collection of rainfall and the local groundwater table would contextualize individual sample observations within broader environmental conditions, such as ongoing drought.

Distance from the riverbed may also have implications for future studies on pod removal rates, as it can help us better understand feeding habits of grazers that do not just eat from resources in the river, and may graze across differing distances from the riverbed. Also, sites were selected for this study because they currently had no more pods on their leaves, which ensured that no deposition occurred. However, this may have created an unnatural feeding environment, gifting pods to animals that may have consumed all pods in one feeding. In the future, our pod removal experiment could be broadened with these more specific variables.

To better contextualize pod deposition data, future monitoring could benefit from canopy-facing cameras on the same trees with time-lapse cameras to track the exact timing and amount of pod availability on trees. This would allow us to correlate ground deposition more accurately with canopy observations, distinguishing new pods from those left from previous depositions. Directly linking canopy observations with ground depositions will also inform whether no pods seen on the ground are an indication of no pod production on the tree or due to other factors, such as quick removal by herbivores. In addition, long-term monitoring of pod production and deposition of individual trees may help us understand variability year-to-year. This approach would provide a clearer picture of the dynamics of pod availability over time and offer insights into potential masting behavior in these species.

This study's findings emphasize the complex interplay of ecological factors in shaping tree growth, pod availability, and resource competition. While tree size showed limited correlation with pod production, the proximity of *F. albida* trees emerged as a significant factor, aligning with ecological theories on resource competition in hyperarid environments. In areas with limited water, such as the Kuiseb River, competition for scarce resources intensifies, affecting both tree growth and reproductive success. However, our results suggest that other factors, such as groundwater availability, play a critical role in shaping tree productivity and herbivore resource use. This underscores the need to consider a range of ecological factors, beyond just competition, in understanding resource dynamics in arid regions.

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Appendices

Appendix I: Table of months with available data from time-lapse cameras

Camera ID	Aug. 2023 (Y/N)	Sep. 2023 (Y/N)	Oct. 2023 (Y/N)	Nov. 2023 (Y/N)	Dec. 2023 (Y/N)	Jan. 2024 (Y/N)	Feb. 2024 (Y/N)	Mar. 2024 (Y/N)	Apr. 2024 (Y/N)	May. 2024 (Y/N)	Jun. 2024 (Y/N)	Jul. 2024 (Y/N)	Total Months
NACT1	N	N	N	N	N	N	Y	N	Y	Y	Y	Y	5
NACT2	Y	Y	Y	Y	Y	N	Y	Y	Y	Y	Y	Y	11
NFCT1	N	N	Y	Y	Y	N	N	N	Y	Y	Y	Y	7
NFCT2	N	N	N	N	N	N	N	N	N	N	N	N	0
HACT1	Y	N	N	N	Y	Y	Y	Y	Y	Y	N	N	7
HACT2	Y	N	N	N	N	Y	Y	Y	Y	N	N	N	5
HFCT1	Y	N	N	N	Y	Y	Y	N	N	N	N	N	4
HFCT2	Y	N	N	N	Y	Y	Y	Y	Y	Y	N	N	7
SACT1	Y	N	N	N	N	N	Y	Y	Y	Y	Y	Y	7
SACT2	Y	N	N	N	N	N	Y	Y	Y	Y	y	Y	7
SFCT1	Y	Y	Y	Y	Y	N	N	N	Y	Y	Y	Y	9
SFCT2	Y	Y	Y	Y	Y	Y	Y	N	N	N	N	N	7
UACT1	Y	N	N	N	N	N	Y	Y	Y	Y	Y	Y	7
UACT2	Y	N	N	N	N	N	Y	Y	Y	Y	Y	Y	7
UFCT1	Y	N	N	N	N	N	Y	Y	Y	Y	Y	Y	7
UFCT2	Y	Y	Y	Y	Y	N	Y	Y	Y	Y	Y	Y	11

Figure I:

Appendix II: Tukey Test Pairwise Comparison Values for *F.albida* NN2.

Sites	Difference Between Mean	Standard Error of Difference	P-value
N-H	1.37	4.15	0.81
S-H	2.96	4.25	0.26
U-H	-1.92	4.25	0.62
S-N	1.59	4.15	0.73
U-N	-3.28	4.15	0.16
U-S	-4.87	4.25	0.02*

Figure II: Tukey test results display the difference between pairwise comparisons of mean NN2 distances of *Faidherbia albida* across sites (Swartbank, Natab, Homeb, Upstream), with shorter distances upstream. Significance values are marked with a *.

Appendix III: Herbivore Activity captured by motion sensor cameras

Figure III: Herbivores grazing on pods at experimental sites captured by motion sensor cameras**.** A) Multiple goats walking by the camera and consuming the pods at a crowded site. B) A springbok eating pods at an isolated site.

Appendix IV: Distance of NN1 on Deposition and Removal Rate of Pods

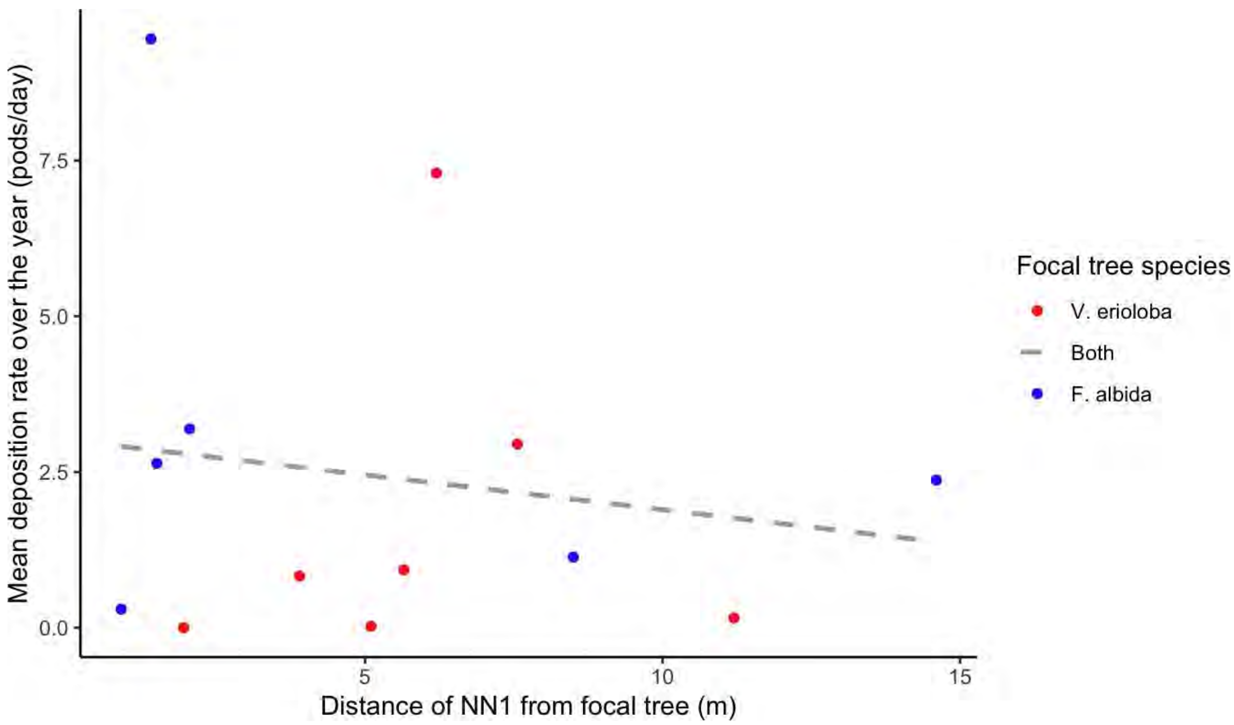

Figure IV: Mean daily pod removal rate for *V. erioloba* and *F. albida* trees from August 2023 to July 2024 and NN1 distances from each focal tree.

Appendix V: Human Influence on Pod Removal

Figure V: A large pile of pods underneath a focal camera tree at Upstream site.

As the Fly Flies: The Effects of Habitat Connectivity on Invertebrate Biodiversity

November 15, 2024

Prepared By:

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Abstract

Biodiversity loss through fragmentation is accelerating globally at unprecedented rates, threatening invertebrates that provide essential ecosystem services such as pollination, pest control, and nutrient cycling. We studied how biodiversity may (1) differ between !nara hummocks that are connected to or isolated from the Kuiseb River, and (2) how this biodiversity changes as distance from each !nara habitat increases. Guided by the principles of island biogeography theory, (1) species diversity would be greater at patches connected to the Kuiseb River corridor, and (2) invertebrate diversity will decrease at a faster rate in connected habitats than isolated habitats as distance from the !nara increases, which also aligns with the resource concentration hypothesis. To test our hypotheses, we placed Malaise and pitfalls traps at four !nara hummocks, two connected to the Kuiseb corridor and two isolated in the Namib Desert Sand Sea. Every 24 hours for six consecutive days, we moved the traps 20 m further away from the hummocks into the Sand Sea matrix, and classified all invertebrates captured in that period. Shannon-Wiener diversity index values were the same for isolated and connected landscapes and decreased at the same rate as distance from the !nara patch increased. These data imply that connectivity is not the main driver in the distance that invertebrates travel from a habitat source. These observed invertebrate distribution patterns elicit important implications for habitat fragmentation, biodiversity management, and metapopulation theory in the Namib Desert landscape.

Introduction

Biodiversity loss, driven by habitat destruction, climate change, pollution, invasive species, and unsustainable use of resources, is occurring at an alarming rate, higher now than at any point in human history (Medellin, 2024). Biodiversity, encompassing variation from within species to across landscapes, is crucial for the long-term resilience of ecosystem functions and the services that they uphold (Oliver et al., 2015). While plant and animal populations across the globe are suffering from this immense decline in diversity, invertebrates are amongst the most affected (Wagner et al., 2021). Some scholars have described this global insect apocalypse as the "Ecological Armageddon," resulting in the demise of human civilization (Cardoso & Leather, 2019). Invertebrates comprise the most diverse group of multicellular organisms on Earth, and provide multiple ecosystem services (Chowdhury, 2017). These services include, but are not limited to, pollination, biocontrol of pests, decomposition and biodegradation, and transference of energy through food chains, providing some of the most important functions in habitat communities (Chowdhury, 2017). Due to their crucial role in ecosystem services, invertebrates serve as valuable indicators of ecosystem health and stability, attributable to their high sensitivity to environmental changes (Blanckenhorn, 2018; Chowdhury et al., 2023). Much attention has been given to the contribution of pollution, including pesticides and insecticides, to invertebrate declines, but habitat loss remains the primary driver of biodiversity loss. As the world continues to develop, fragmentation of natural ecosystems will continue to be one of the biggest threats to invertebrate populations.

Habitat fragmentation threatens biodiversity by altering the connectivity between crucial habitats. Fragmentation has been shown to negatively influence invertebrate abundance and diversity due to both a decrease in habitat size and an increase in distance between habitats (Didham et al., 1996). Isolated ecosystems are less productive, as the ability for invertebrates to pollinate, decompose, predate, etc. in more fragmented landscapes is limited (Didham et al., 1996). Isolated areas may experience decreased fruit production and dung decomposition, two effects intrinsically linked to invertebrate ecosystem services (Didham et al., 1996). Smaller and disconnected environments lead to limited organism fitness due to increased inbreeding. This reduces genetic diversity and can have long-term consequences for the resilience of invertebrate populations that must adapt to shifting environments (Schlaepfer et al., 2018). Beyond those effects, fragmentation also directly and indirectly alters relationships between trophic levels and higher-order interactions between invertebrates and other organisms (Didham et al., 1996). For example, fragmented environments alter pollinator behavior and flight patterns, resulting in reduced flower pollination (Didham et al., 1996). Habitat fragmentation can also lead to the truncation of food chains via the loss of natural predators which increases the probability of uncontrolled invertebrate growth (Hunter, 2002). Overall, measures of invertebrate species richness in a community offer the strongest indicator of the amplified consequences of fragmentation at higher trophic levels (Nouhuys, 2005). The most effective approach to combat the effects of fragmentation is by maintaining habitat connectivity.

Large and well-connected habitats tend to support greater biodiversity. Island biogeography theory suggests that larger habitats facilitate larger population sizes and lower extinction rates due to an increase in resource access, which allows for more species to accumulate (MacArthur & Wilson, 2001). As distance between islands increases, species richness and diversity typically decreases. Island biogeography theory predicts that immigration rates should decrease inversely with increasing distance of a fragment from a population source (Collinge, 2000). This concept suggests that the connection between habitat patches is the most important driver of biodiversity (Thiele et al., 2017). High connectivity among habitats can enhance colonization rates and increase local species richness, thus contributing to the overall health of ecosystem patches (Taylor et al., 1993). Corridors of suitable habitat reduce patch isolation, thereby decreasing species loss and enhancing colonization rates (Collinge, 2000). At the species level, corridors are essential for the movement of invertebrates – for example, Coleoptera travel almost exclusively on corridors (Collinge, 2000) and some Hymenoptera will not travel between islands due to "altered microclimatic conditions" (Didham et al., 1996).

Metapopulation theory, applied to the dynamics of species in habitat fragments, suggests that corridors between fragments should increase regional persistence of native species by reducing isolation effects and increasing colonization probability (Collinge, 2000). As populations become more connected, corridors allow for higher levels of invertebrate movement between patches, resulting in a system that is effectively a single extinction-resistant population (Harrison, 1991). Finally, metapopulation theory provides the most common theoretical construct for considering the impacts of invertebrate movement driven by habitat connectivity: dispersal allows for the reestablishment of populations at risk of extinction by allowing a greater flow of invertebrates (Bohonak & Jenkins, 2003).

The extent to which habitats are connected depends on the movement patterns of invertebrates and the distances at which they are able to travel from one habitat source to another. Different groups of invertebrates respond differently to landscape structure due to their resource specialization and dispersal ability (Diekotter et al., 2008). Invertebrates disperse as a means to reduce inbreeding, access habitat and resources, avoid competition, and to allow for adaptation to changing environments (Kral-O'Brien & Harmon, 2021; Bohonak & Jenkins, 2003). The resource concentration hypothesis states that larger host plant patches should have larger insect densities because the probability of an insect finding a large patch is higher and the probability of an insect leaving the large patch is lower (Fahrig & Jonsen, 1998). Additionally, many invertebrates utilize the movement patterns described by the Lévy flight foraging hypothesis, which maximizes foraging efficiency and is used most often in resource-poor environments such as a desert (Gautestad & Mysterud, 2013). These patterns are classified as many short movements stochastically interspersed by long moves (Gautestad & Mysterud, 2013). However, in more arid environments, long distance dispersals become even more rare compared to short distances, suggesting that habitats must be closer to each other to maintain effective connectivity (Suhling et al., 2016).

While existing literature addresses much about habitat connectivity and its effects on invertebrate biodiversity and dispersal patterns, little is known about how these relationships may change in arid environments and what the implications of habitat fragmentation may be on invertebrate populations in such extreme conditions. We conducted our research at the Gobabeb Namib Research Institute in Namibia. Gobabeb sits at the heart of the hyperarid Namib Desert, between the Sand Sea to the south and Gravel Plains to the north, and along the riparian woodlands of the ephemeral Kuiseb River. !Nara, *Acanthosicyos horridus*, is an endemic melon plant in the Namib Desert. It has adapted to the sandy desert environment, and grows on the banks of dry river beds, on slip faces of dunes, and in the interdune valleys. The plant provides essential shelter and food to various Namib fauna, particularly invertebrates (Berry, 1991). The presence of !nara plants along both the Kuiseb River riparian corridor and in the vast Sand Sea desert provides examples of similar habitat patches at varying levels of connectivity to a larger ecosystem. Empirical evidence suggests that species richness is enhanced by connectivity particularly in dry ecosystem conditions (Collinge, 2000), providing valuable context for arid areas facing worsening drought conditions due to climate change.

In this study, we sought to quantify the relationship between !nara patch connectivity and invertebrate biodiversity by studying invertebrate populations in both connected and isolated !nara patch habitats. Island biogeography and connectivity theories would support that !nara patches connected to the Kuiseb River, compared to the !nara patches lacking proximity to a larger source of vegetation or habitat, are expected to have greater invertebrate biodiversity. We suspected this increase would occur because the !nara patches closer to the Kuiseb River will be part of a greater Kuiseb island which provides for more access to habitat, resources, and advanced trophic level interactions. In contrast, the isolated !nara patches are smaller islands with limited connectivity, separate from any larger source pool of invertebrate or vegetative diversity, and will thus support lower invertebrate biodiversity (Wilson, 1992).

The second goal of this study was to quantify the distribution patterns of invertebrate taxa from !nara patches connected to and isolated from the Kuiseb River into the Sand Sea to better understand implications of habitat connectivity and fragmentation. Island biogeography theory predicts that individuals found in larger populations are less likely to disperse in resource-abundant areas than in areas lacking resources (Summerville & Crist, 2004). We also draw from the resource concentration hypothesis that states that invertebrates will be more abundant in connected patches of host plants and will thus stay longer in those patches with a lower probability of dispersal (Fahrig & Jonsen, 1997). Thus, invertebrates in isolated patches will travel further from habitats and demonstrate a less significant decline in diversity, as greater habitat fragmentation increases the need to disperse (Kral-O'Brien & Harmon, 2021, Marcantonio et al., 2023).

Methods

Site Selection

We selected four locations along !nara population edges at two distinct distances from the Kuiseb River (Table 1; Figure 1). We defined an isolated site to be >1 km from the Kuiseb River corridor. Connected sites are directly attached to the Kuiseb River. Sites Angela and Betty are located 0 m from the Kuiseb River habitat. Sites Claudine and Delores are isolated from the river, located 2.96 km and 3.03 km from Angela and Betty, respectively (Figure 1). We selected !nara patches located a significant distance from other vegetation patches to increase the likelihood that trapped invertebrates likely originated from the specific !nara plant (Figure 2; see Vegetation Survey).

Table 1. Site Descriptions. Site name, connection versus isolation level, GPS location, and distance to the Kuiseb River.

Site	Connected/ Isolated	GPS Coordinates	!Nara Patch Distance to Kuiseb River Corridor (km)
Angela	Connected	-23.563916 S 15.034247 E	0
Betty	Connected	-23.564722 S 15.035833 E	0
Claudine	Isolated	-23.587837 S 15.047880 E	2.96
Delores	Isolated	-23.588056 S 15.048889 E	3.03

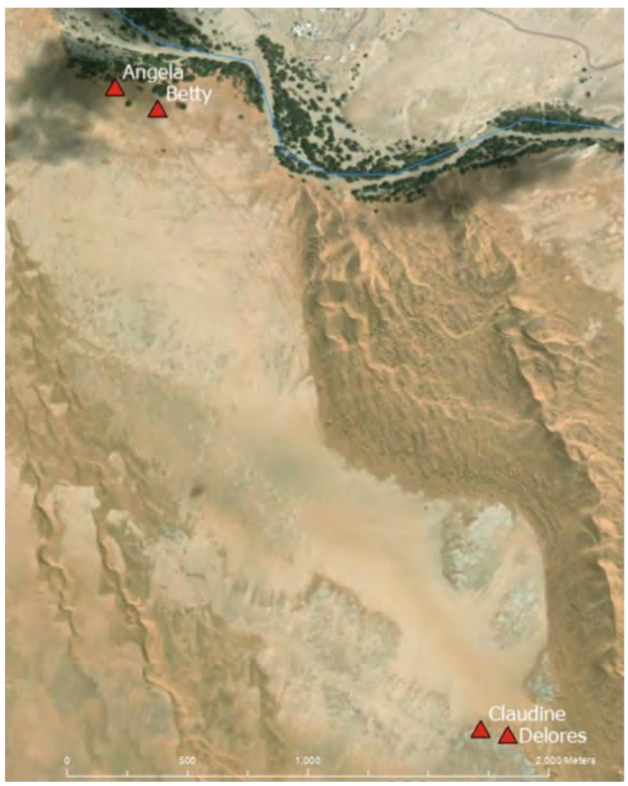

Figure 1. Site Map. Map depicting the location of each of the four trap sites selected for invertebrate observation.

Figure 2. Zoomed in Site Selection. The left image (Angela and Betty) map out the connected habitats to the Kuiseb River whereas the right image (Claudine and Delores) depict the isolated habitats. Light green patches under each site depict !nara habitats. The dark green vegetation surrounding Angela and Betty are part of the Kuiseb River habitat. The lighter gray colors surrounding Claudine and Delores are rocks.

Background Data

Vegetation Survey

To compare the level of habitat connectivity at each of the sites, we conducted a vegetation survey in the surrounding areas of the trap. A dedicated walker with an equal stride (L.G.H) used a compass to measure and walk 50 left-foot steps (~75 m total) in perpendicular directions to the left and to the right of the line at each 20 meter interval starting at our initial trap location (Figure 3). We surveyed 100 m in the direction of trap placement, and 100 m in the opposite direction. For each step, the walker classified the vegetation either under their feet or above their head. The descriptive categories for the terrain were sand, rock, dune grass, !nara, shrub (<1.5 m tall), tree (>1.5 m tall), and dead woody vegetation. We considered vegetation to be trees, shrubs, !nara, dune grass, and dead woody vegetation. We calculated percent vegetation cover at each site by summing the amount of vegetation and dividing it by the total number of cover observations. We plotted this data on a vegetation map of each testing site and used it to quantify the level of vegetation through diversity indices, as well as calculate the biotic versus abiotic makeup of each site.

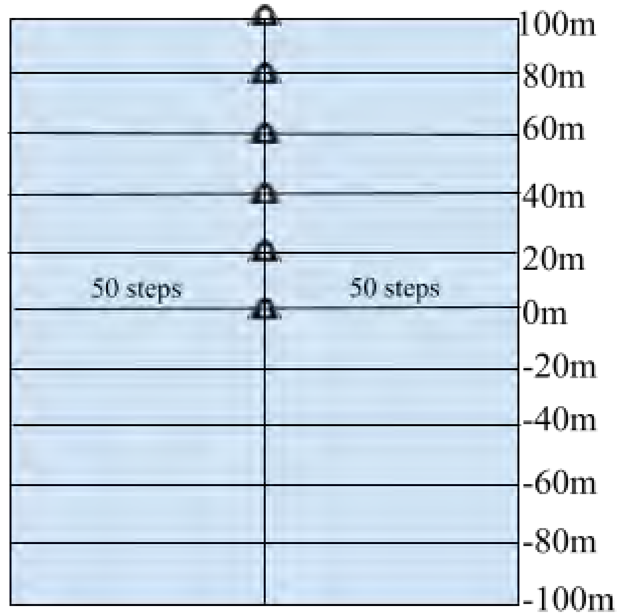

Figure 3. Vegetation Survey Map. Map displaying the layout of traps and the method of vegetation surveying. The tents depict where each of the trapping sites were located every 20 m going out into the Sand Sea (0 to 100 m). We surveyed the area behind the traps (-20 m to -100 m) to account for surrounding vegetation from the Kuiseb River.

Weather Data

We obtained hourly weather data from the Aussinanis station near Gobabeb. We accounted for air temperature (°C), wind speed (m/s), and wind direction (deg.). We calculated mean values for each 24-hour invertebrate sampling period.

Invertebrate Trapping

We used a combination of Malaise and pitfall traps to collect both flying and non-flying invertebrates (Appendix I). At each site, ten pitfall traps surrounded one Malaise trap (Figure 4). The pitfall traps were haphazardly placed to achieve greater randomization of species captured at each site. Since flying insects are heavily affected by wind patterns (Pasek, 1988), we consistently angled each trap toward ~75 ºSE to prevent a significant impact of wind direction on flying invertebrate trapping.

To measure invertebrate dispersal from the !nara patches, we placed the traps at a starting point (indicating 0 m) on the edge of a !nara patch, and moved the traps 20 m further down a linear path from the origin every 24 hours. We chose a 24-hour data collection period to include the bimodal spikes in the daily activity cycle of insects (Holm & Edney, 1973). Across the 6 collection periods of our study from November 2, 2024 to November 8, 2024, the traps reached a maximum distance of 100 meters away from the !nara plant.

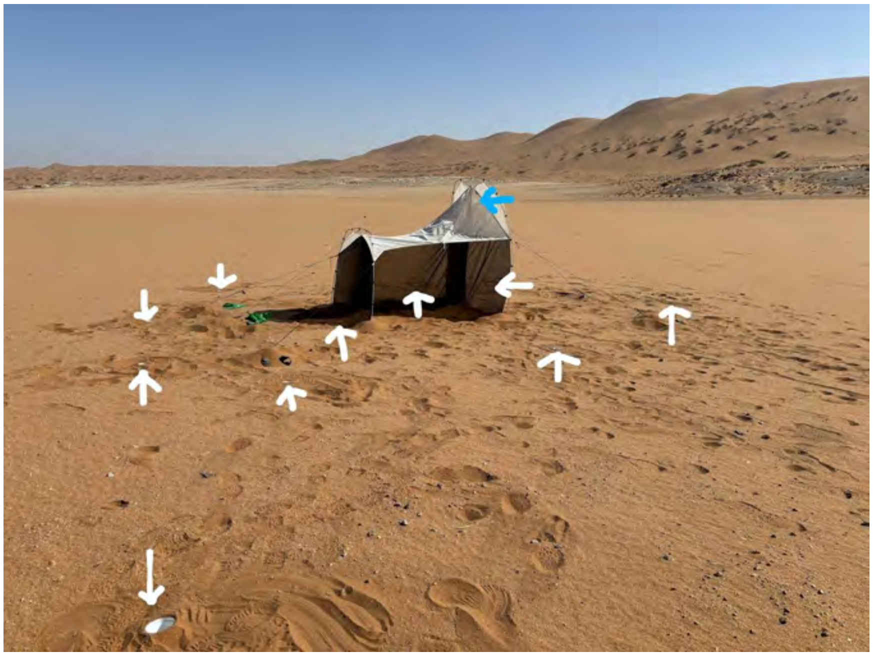

Figure 4. Trap Design. Example Malaise trap (blue arrow) surrounded by 10 pitfall traps (white arrows). One set of these 11 traps was set up at each of the four sites (Angela, Betty, Claudine, Delores) for a 24-hour period. After each 24-hour period, the traps were moved 20 m further from the origin.

Insect Identification

Every 24 hours, we visited each site and collected the insects in each of the 44 traps (1 Malaise, 10 pitfalls at each of the 4 sites) before moving them 20 meters out. We then identified each individual insect by Order (Diptera, Hymenoptera, Hemiptera, Lepidoptera, Coleoptera, Trichoptera, Arachnid, Orthoptera, Blattodea) and then to a Family or Genus depending on the available information for the individual invertebrate (Appendix II). For invertebrates we were unable to identify through our own research and reverse-image searching on Google, we utilized the help of Eugene Marais, Gobabeb Research Manager and entomologist.

Formulas

We quantified vegetation diversity using ANOVA tests. If ANOVA results were significant, we ran a post hoc Tukey test.

We quantified alpha diversity using the Shannon-Wiener Diversity Index:

Shannon-Wiener: $H' = \sum_{i=1}^{s} p_i \, ln p_i$ Eq. 1

where H' is the species diversity index, s is the number of Orders, and p_i is the proportion of individuals of each Order belonging to the ith Order of the total number of individuals (Nolan & Callahan, 2006).

We quantified beta diversity using the Bray-Curtis Diversity Index:

$$\textbf{Bray-Curtis: } BC_{ij} = 1 - \frac{2C_{ij}}{S_i + S_j} \qquad \text{Eq. 2}$$

where i and j are the two sites, S_i is the total number of specimens counted on site i, S_j is the total number of specimens counted on site j, and C_{ij} is the sum of only the lesser counts for each species found in both sites (Gauch, 1973).

We chose both of these models to account for invertebrate abundance as a factor of biodiversity (see Appendix III for alternative methods of calculating diversity).

Data Analysis

All analyses and figure preparations were done in RStudio (4.3.2). We used a combination of ANOVA tests for differences between sites, linear regressions for differences between site and distance, and Akaike Information Criterion (AIC) for determining best-fit models. We classified a significant difference in AIC as a delta > 3, and tested the following models:

I. lm(diversity ~ distance)
II. lm(diversity ~ distance + isolation)
III. lm(diversity ~ distance * isolation)
IV. lm(diversity ~ poly(distance, 2))
V. lm(diversity ~ poly(distance, 2) + isolation)
VI. lm(diversity ~ poly(distance, 2) * isolation)

We evaluated both invertebrate species diversity and distribution through regression models, with the intercept depicting the initial biodiversity differences in isolated versus connected habitats and the slope depicting the direction and strength of the relationship between species diversity and distance from !nara. When separating invertebrates by Order to run further diversity tests, we included only Orders that had at least 40 individuals to ensure patterns were significant.

Results

Background Data

Vegetation Cover

The connected sites had a mean surrounding vegetation cover of 35.1% ± 10.7% (42.6% and 27.5% for Angela and Betty, respectively), whereas the isolated patches only had a mean surrounding vegetation cover of 6% ± 2.7% (4.1% and 7.9% for Claudine and Delores, respectively; Figure 5). We found a significant difference between mean vegetation surrounding isolated versus connected !nara patches ($F_{df1, df2} = 254.9$, $P < 0.0001$). All pairs of sites lacked significantly different vegetation covers (F-statistic = 13.41, $P < 0.0001$ for all pairs, df = 21), except for Claudine and Delores – the two isolated sites – whose difference in vegetation was marginally significant (F-statistic = 13.41, P = 0.08, df = 21). While the two connected sites have differing levels of vegetation cover from each other, we found that both have significantly more vegetation compared to the isolated sites.

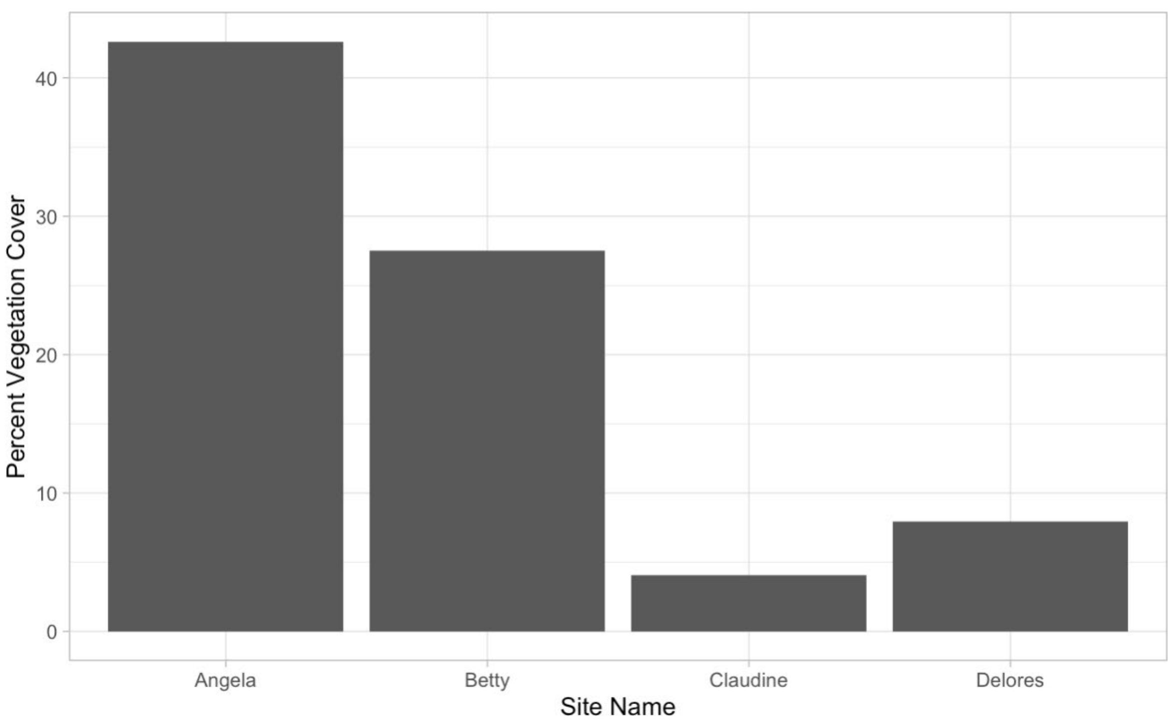

Figure 5. Vegetation Cover. Bar graph depicting % surrounding vegetation at each of the four sites. Vegetation included dune grass, shrubs, !nara, trees, and dead woody vegetation. Non-vegetation consisted of rock and sand. Angela and Betty (connected) have a higher percentage of vegetation than Claudine and Delores (isolated).

We also calculated the Shannon-Wiener diversity index to quantify the diversity of cover surrounding each of the sites. It is important to note that these indices do not measure the diversity of vegetation, but rather the diversity of ground cover type, including sand and rocks. A higher value index corresponds to higher diversity in cover type and its abundance. Angela and Betty had the highest cover diversity, with Shannon-Wiener values of 1.2 and 0.9 respectively. Claudine had the lowest value of 0.6 and Delores was second lowest with 0.7. The isolated sites had the lowest values due to the high abundance of few cover types (primarily sand and rock). In contrast, Angela and Betty had higher values of cover diversity – including the presence of trees, shrubs, and a higher abundance of grasses – due to their proximity to the riparian corridor (Figure 5).

In Figure 6, the high density of green surrounding Angela and Betty depicts the vegetation from the Kuiseb River corridor. The high density of sand surrounding the sites portrays the Sand Sea matrix that all sites border (Figure 6). Therefore, while trap sites at all four locations were placed in the same Sand Sea matrix, Angela and Betty had more surrounding vegetation.

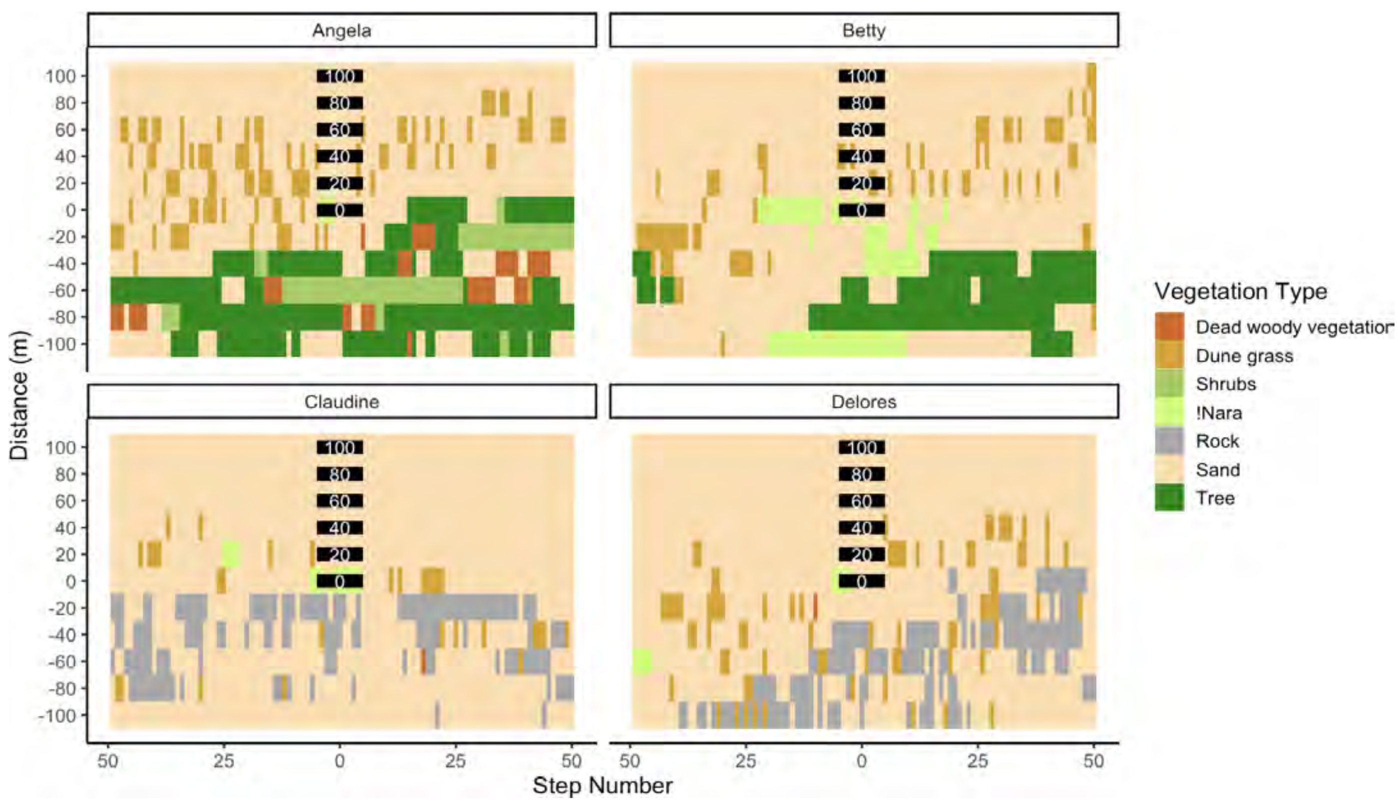

Figure 6. Vegetation map. Maps for each site depicting the vegetation surrounding the !nara patches. Each black rectangle indicates the intervals at which traps were set up. The legend on the right describes the color associated with each cover type.

Weather Data

We ran linear regressions to test if weather variables had a significant effect on the total number of invertebrates caught. We found that neither the wind speed (F-statistic = 0.64, P = 0.46, df = 5), wind direction (F-statistic = 0.22, P = 0.66, df = 5), nor air temperature (F-statistic = 0.54, P = 0.49, df = 5) had a significant effect on the total abundance of invertebrates caught.

Invertebrate Data Overview

Over the sequence of six collection periods, we collected a total of 1153 invertebrates in 9 distinct Orders and 59 unique species across all pitfall and Malaise traps (Table 1, Appendix II). We collected the greatest number of invertebrates in traps closest to the !nara patch (0 m), with 287 total individuals, and the fewest at 40 m, with 85 total individuals. By site, we trapped the largest number of invertebrates at Delores with a total of 312 individuals, and the smallest at Claudine with 262 individuals.

Table 1. Total invertebrates collected by trap and distance. Sum of total invertebrates caught in all Malaise and pitfall traps grouped by trap distance and site. M indicates Malaise trap and P indicates pitfall trap.

	0m		20m		40m		60m		80m		100m		
	M	P	M	P	M	P	M	P	M	P	M	P	**Total**
Angela	12	51	8	7	4	19	5	93	14	19	7	36	**275**
Betty	23	30	18	10	6	8	3	71	23	66	14	32	**304**
Claudine	28	42	13	16	12	17	2	19	8	20	53	32	**262**
Delores	43	58	16	25	6	13	0	47	5	14	45	40	**312**
Total	**106**	**181**	**55**	**58**	**28**	**57**	**10**	**230**	**50**	**119**	**119**	**140**	**1,153**

Diptera was overwhelmingly the most frequent Order caught, with a total of 854 individuals (Figure 7). Lepidoptera was the second most frequent Order with 98 total invertebrates (Figure 7). The least common Orders were Orthoptera, Hemiptera, and Blattodea with 1, 6, and 7 individuals captured, respectively (Figure 7).

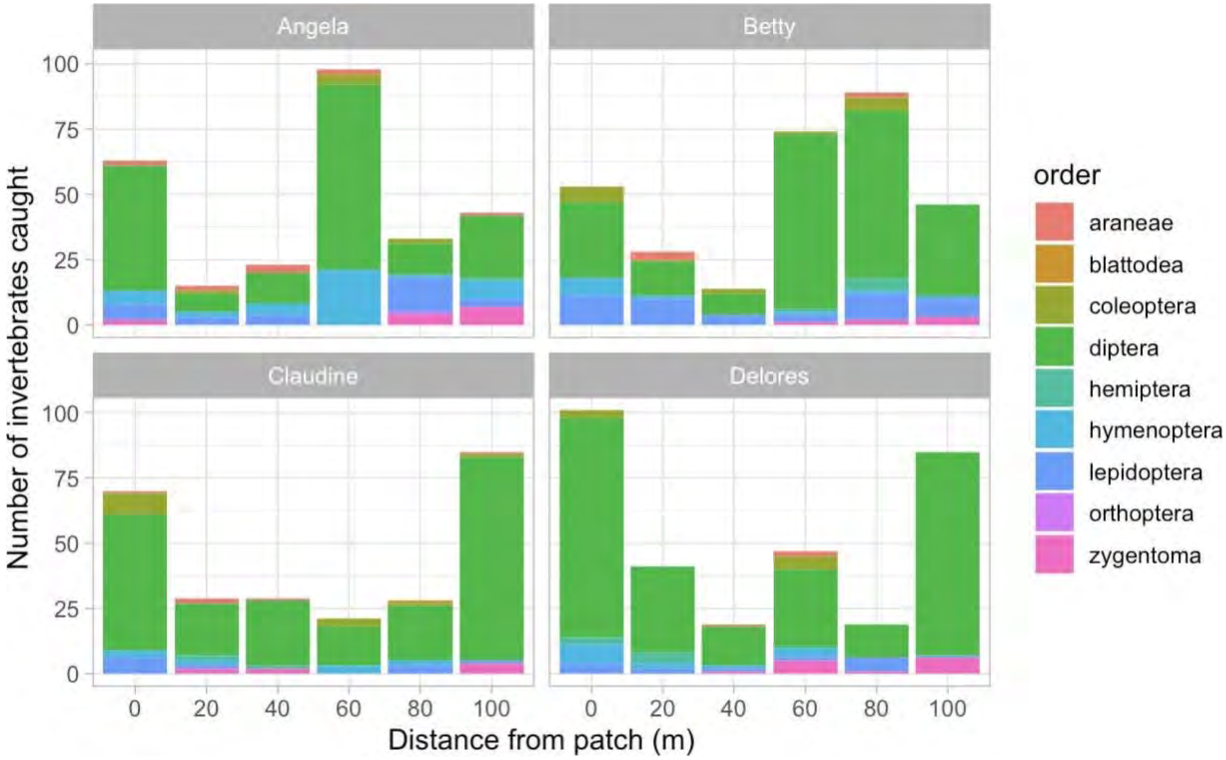

Figure 7. Order Count by Site and Distance. Bar graph depicting the number of invertebrates collected at each distance of every site. The colors describe the specific Order that each individual invertebrate belongs to.

Shannon-Wiener Index for Invertebrate Alpha Diversity

To compare Order-level (Appendix II) invertebrate biodiversity levels (Shannon-Wiener Index) and distribution based on habitat connectivity, we utilized a linear regression model (Figure 8). We accounted only for the species found at 0 m and 20 m from the origin to increase the likelihood of modeling species associated with the !nara patch as traps moved further into the Sand Sea (Figure 8).

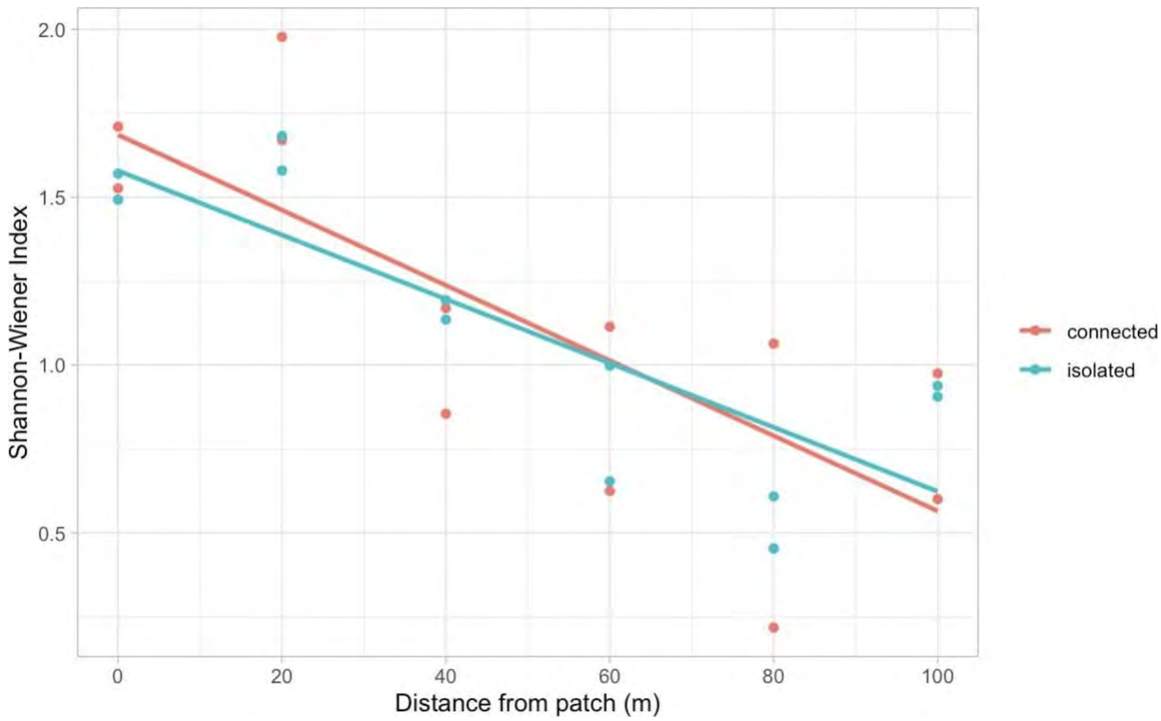

Figure 8. Shannon-Wiener Index (0-20 m species) on Distance from !nara patch. Linear regressions distinguished by connected versus isolated habitats analyzing the relationship between invertebrate biodiversity (Shannon-Wiener Index) and distance from the !nara patch (meters). This graph only accounts for the species identified at 0 m and 20 m and thus does not include new species caught at 40 m and beyond.

Using AIC calculations, we determined that a linear model that does not account for isolation as a factor or interaction was best fit to describe the relationship between Shannon-Wiener Index and the distance from the !nara patch (delta AIC = 0.87). The regression model suggests a significant negative linear relationship between distance from !nara patch and Shannon-Wiener alpha diversity ($P < 0.0001$, adjusted $R^2 = 0.60$, F-statistic = 35.82, df = 22).

The y-intercept describes the level of invertebrate diversity at 0 m from the !nara patch (Figure 8); These values provide a baseline for invertebrate diversity based on habitat connectivity. While connected !nara habitats have higher initial levels of invertebrate diversity compared to isolated !nara habitats (Figure 8), the model that includes isolation level is weaker than the model that excludes this factor (delta AIC = 1.95).

The slopes describe the inverse relationship between distance from !nara patch and invertebrate diversity. While distance from !nara patch and invertebrate diversity have a strong, negative linear relationship, we found no difference in the rate of decline between the connected versus isolated patches.

When accounting for all species collected, regardless of when they were first recorded, the linear regression model changes slightly (Figure 9). Using AIC calculations, we concluded that a model capturing distance and isolation level was preferable, though the difference in AIC when accounting for isolation versus not lacks statistical significance (delta AIC = 1.60). The y-intercepts of the two lines, indicating invertebrate biodiversity levels at 0 meters from the !nara patch, is marginally significant (t-value = -1.84, P= 0.08).

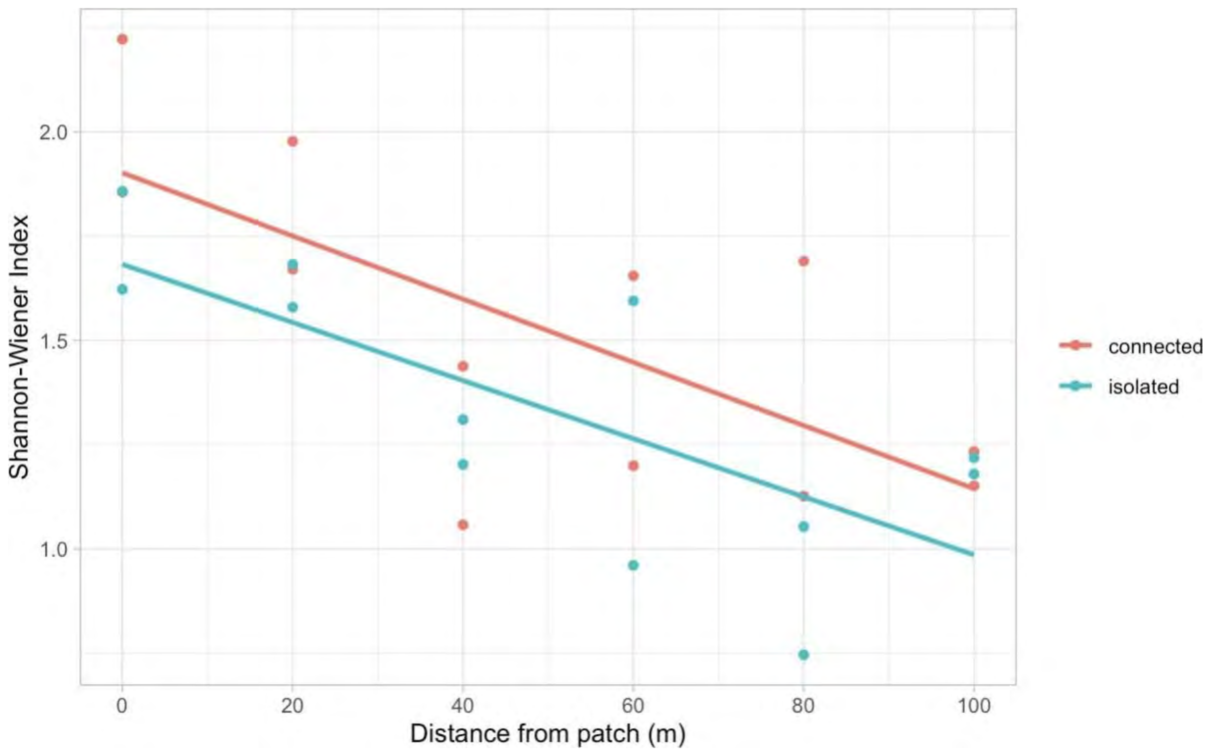

Figure 9. Shannon-Wiener Index on Distance from !nara patch. Linear regressions distinguished by connected versus isolated habitats analyzing the relationship between invertebrate biodiversity (Shannon-Wiener Index) and distance from the !nara patch (meters). This graph accounts for all species collected.

With increasing distance from the !nara patch, we found no difference between the connected and isolated patches in the direction or magnitude of the decline in species diversity. The negative relationship between Shannon-Wiener diversity and distance remains strong for this linear regression model ($P < 0.0001$, adjusted $R^2 = 0.52$, F-statistic = 13.41, df = 21).

We also examined the relationship between alpha diversity and distance from !nara patch by each Order (Figure 10). The only Order in which the AIC best-fit model included both distance and isolation factors was Lepidoptera (delta AIC = 7.13). Thus, the y-intercepts are statistically different (t-value = -3.135 P = 0.00603) indicating that the Lepidopteras were significantly more diverse at 0 m from the !nara patch in connected habitats compared to isolated habitats. The negative relationship between Lepidoptera alpha diversity and distance from !nara patch is strong

(P = 0.0004, adjusted $R^2 = 0.7$, F-statistic = 13.13, df = 17). However, the slopes between connected and isolated habitats are not statistically different (delta AIC = 0.49).

The best-fit linear models for Diptera, Hymenoptera, and Araneae accounted for only distance as a factor (respective delta AICs = 1.44, 1.47, and 1.53). Thus, we found no significant difference in the intercepts for alpha diversity at 0 m from the !nara patches based on isolation (Diptera t-value = 15.06, Hymenoptera t-value = 7.18, Araneae t-value = 3.27). The negative linear relationship between diversity and distance (slope) was significant for Diptera (P = 0.03, F-statistic = 5.51, df = 22) and Hymenoptera (P = 0.002, F-statistic = 13.37, df = 18), even though the level of connectivity had no significance on this relationship. The linear model for Araneae had no significant relationship between diversity and distance (P = 0.4, F-statistic = 0.75, df = 11), indicating that distance had no effect on alpha diversity.

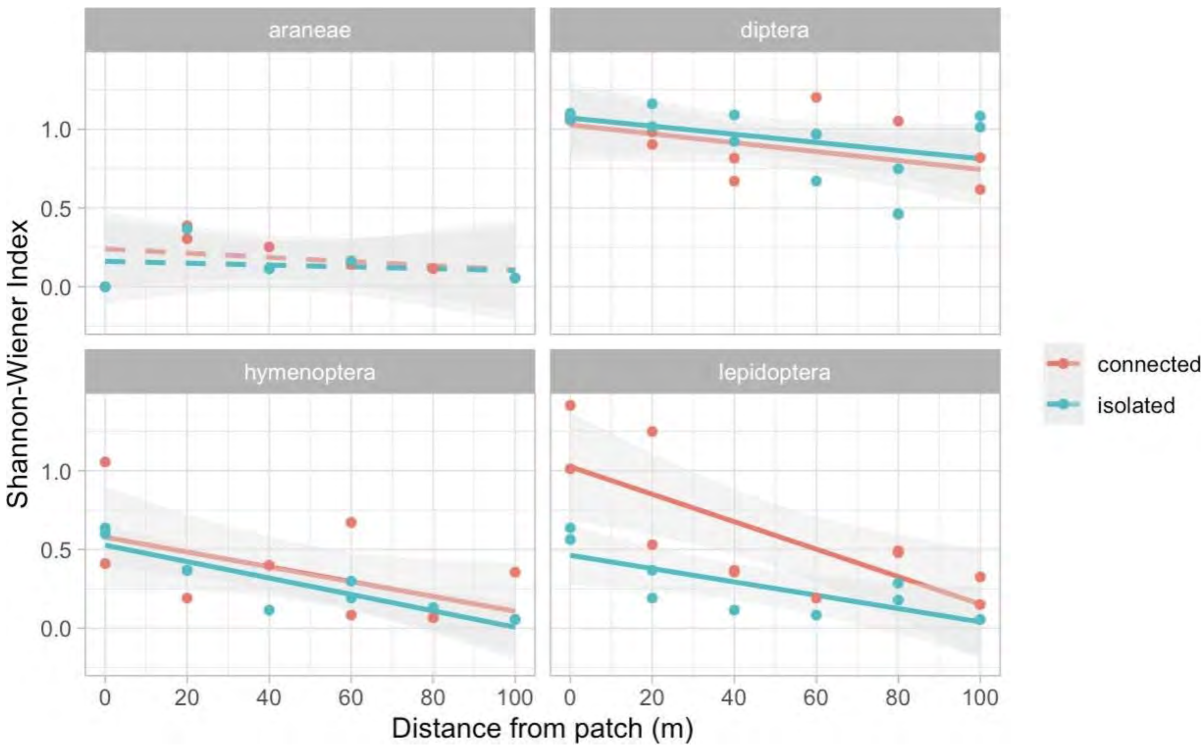

Figure 10: Shannon-Wiener Index as distance increases, by Order. Linear regressions distinguished by connected versus isolated habitats for each common order (Araneae, Diptera, Hymenoptera, Lepidoptera), analyzing the relationship between invertebrate biodiversity (Shannon-Wiener Index) and distance from the !nara patch. Dotted lines indicate no significance.

Beta Diversity: Bray-Curtis Model

To quantify species turnover as distance from the patch increases, we used the Bray-Curtis Index to calculate the difference in beta diversity between the connected and isolated patches (Figure 11). The AIC metric determined that the best fit model for this Bray-Curtis graph takes both distance and isolation level into consideration (delta AIC = 2.2). However, isolation level was only marginally significant when considered ($P = 0.06$ for isolation factor, t-value = -1.96). The AIC also concluded that the best-fit regression for these data is nonlinear. Shown by the dissimilar y-intercepts, the isolated patches had a lower initial Bray-Curtis value than the connected patches ($P < 0.0001$, adjusted $R^2 = 0.68$, F-statistic = 17.13, df = 20; Figure 11). This smaller value suggests that isolated !nara patch invertebrates are initially less similar to those of the Sand Sea than in connected patches.

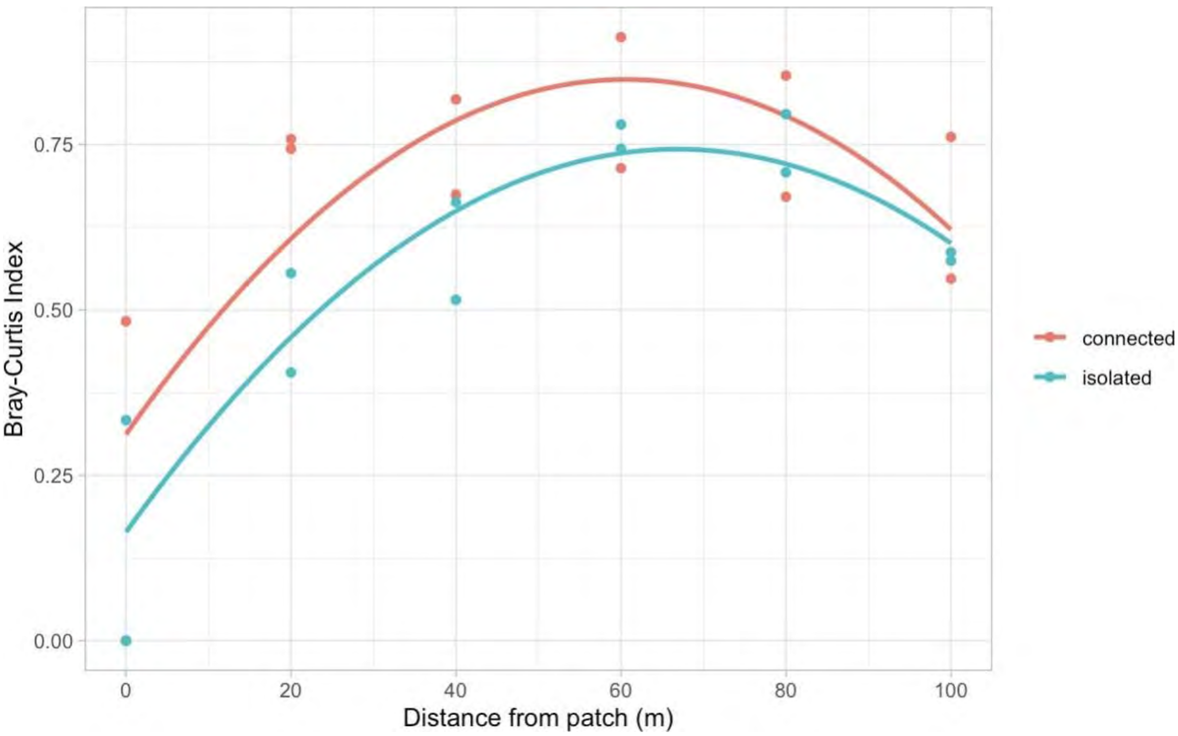

Figure 11. Bray-Curtis Index as distance from !nara patch increases. Nonlinear model reflecting Bray-Curtis Index between connected versus isolated habitats as distance increases from the !nara patch.

As distance from the patch increases, the species turnover climbs before eventually slowing down/plateauing. The curve takes a somewhat parabolic shape, suggesting that the species turnover rate decreases towards the initial patch makeup following a peak at 80 m; however, this decrease is likely due to the nonlinear graphing function rather than reflecting an accurate depiction of biodiversity changes. Thus, the upward slope of the curve is more indicative of species turnover as distance from the patch increases. Finally, it is important to note that a Bray-Curtis graph that subsets for invertebrates found in either the Malaise traps or the pitfall traps yields a similar curve (Figure 7), suggesting that trap type does not significantly affect species turnover rate.

Discussion

Overall, our study found no difference in invertebrate diversity between connected and isolated !nara patches. Further, we found that although there is a strong, negative relationship between distance from the !nara patch and invertebrate diversity, this relationship did not differ in direction nor magnitude between the connected and isolated habitats. We identified several factors that may influence these patterns and highlight key implications of our findings for the Namib Desert ecosystem and invertebrate diversity theories.

Our finding that invertebrate diversity is similar between connected versus isolated !nara patches counters connectivity theory, which claims that connection between habitat patches is the most important determinant of species diversity (Thiele et al., 2017). Rather, our study suggests that a factor independent of connectivity is the main driver of invertebrate abundance and distribution across patch types. A study on an ephemeral river in the Australian desert yielded similar results, observing that invertebrate diversity did not increase with greater proximity to the river corridor; rather, rainfall and other changes in abiotic factors drove biodiversity levels (Free et al., 2013). Thus, connectivity between habitats may not necessarily serve as the primary factor influencing diversity, since abiotic elements such as rain, nutrient availability, soil composition, and other environmental factors likely play a significant role.

One such factor could be the microclimates established by the !nara plant that provide resources to invertebrates. !Nara have long taproots that reach deep underground water supplies and thorns that minimize evaporation and transpiration (Berry, 1991). These physiological structures allow fog accumulation under the plant, creating a relatively moist microclimate that many invertebrates depend on (Berry, 1991, Free et al., 2013). Further, the !nara provide essential shade for invertebrates, with uncovered surface temperatures reaching over 66°C while shaded ground stays around 38°C, allowing invertebrates to tolerate extreme heat (Holm & Edney, 1973). In the absence of shelter and moisture deeper into the arid Sand Sea, the !nara patches support a higher diversity of invertebrates. This rare, productive habitat sustained by the isolated !nara plants may also explain the similarity in diversity between the connected and isolated environments. Increased biodiversity on these patches is particularly present in times of drought, like the one Namibia has faced for years, as individuals flock to more rich/fertile habitats (Free et al., 2013). Small but productive patches, like the isolated !nara hummocks, may serve as a refuge for invertebrates and thus foster more concentrated biodiversity.

Our findings revealed a strong, negative relationship between invertebrate diversity and distance from !nara patches, confirming that !nara patches are more biologically diverse than the Sand Sea matrix. Beta diversity initially increases with distance from !nara patches before eventually becoming less steep (Figure 11). These findings suggest high levels of species turnover as traps moved deeper into the Sand Sea before reaching a maximum turnover rate and plateauing, indicating that population makeup in the Sand Sea is different from that of the !nara. This beta diversity curve is driven by the negative correlation between alpha diversity and distance from !nara patches.

The inverse relationship between !nara patch distance and invertebrate diversity suggests that vastly empty matrices in between habitat patches are unable to support diverse invertebrate populations. This trend has been demonstrated in other habitat types, such as forests, where matrix landscapes have a strong effect on the movement of certain invertebrates, often limiting access to their needs at different life stages (Jules & Shahani, 2003). Certain invertebrates, particularly beetles, need "stepping stones" to travel further, and habitats that have bare ground in the matrix increase the costs associated with attempting to disperse towards new habitats (Yang et al., 2022). Pulling from these trends, our observations further imply that either increasing the size of a matrix or adding a matrix in the Sand Sea will have a gradient effect of decreasing diversity as distance increases.

While we found a strong negative relationship between distance and invertebrate diversity, this relationship did not differ between connected and isolated !nara patches. This counters the idea that species in more isolated areas disperse further for resources and therefore have a shallower loss in biodiversity (Marcantonio et al., 2023). Given that we only included species found at 0 and 20 meters from hummocks, our findings suggest that in species associated with the !nara, diversity decreases evenly over distance, regardless of habitat type. These comparable declines could imply that invertebrates do not change their behavior and distribution even if close to larger biodiversity hotspots. Another possible explanation could be that, the further out into the matrix we sampled, the less surrounding vegetation we found, regardless of !nara patch isolation level (Figure 6). Since complexity of ground cover mosaics has been correlated with the number of fly species present, it is reasonable to believe that diversity would fall at similar rates at all sampling sites (Haslett, 2001).

These findings suggest that connectivity does not influence invertebrate distribution. Rather, the driver of invertebrate distribution may be their food-driven behavior. Firstly, a number of fixed rate mechanisms could drive invertebrates to disperse. For example, invertebrates may disperse once a fixed amount of food is obtained or when food capture rate is low (Hassell & Southwood, 1978). If the invertebrates we caught are relying mostly on the !nara for food, not on other resources from the riparian, then food-related movements likely occur at similar rates across varying levels of connectivity. Alternatively, if time-limit related mechanisms are the primary drivers of movement, then invertebrates would leave a !nara patch with the same frequencies, regardless of surrounding resources (Hassell & Southwood, 1978).

Other studies have supported both proximate and ultimate motivations for invertebrate movement; proximate motives are based on genetics and physiology while ultimate motives are based on adaptation, natural selection, and evolution (Asplen, 2018). Ultimate motivations suggest that invertebrates have evolved to know where their resources are – !nara patches – and they have optimized their behavior to remain there. Several of the invertebrate species found in the Namib Desert are already specially adapted to the patchy environment, thus making connectivity less of a factor for movement. From a proximate standpoint, species at varying levels of habitat connectivity would disperse at the same rate, as these behaviors are genetic and not influenced by the environment (Asplen, 2018). Both motivations may be present in the Namib Desert, and can account for the patterns we found between connected and isolated patches.

Our results further suggest that invertebrate Order may impact diversity at differing levels of connectivity. Lepidoptera possessed more initial diversity in connected sites than isolated sites, perhaps because moths require large, dense environments to maintain population stability (Botham et al., 2015). Interestingly, no other Order indicated difference in habitat preference, or differences in loss of diversity with distance from a patch. Our reliance on morphological identification, rather than more exact measures such as DNA barcoding, may influence this result. For example, Order Coleoptera is notorious for cryptic species (Singhal et al., 2018), and without differentiating morphologically identical species, we may find less diversity than actually exists in the Namib.

Our findings hold crucial management implications for the long-term diversity of invertebrates in the Namib Desert. We found that the effect of distance from !nara patches on invertebrate diversity were the same regardless of connectivity, which implies that even isolated patches of habitat are still essential for protecting diversity and providing ecosystem services, and should still be conserved (Proesmans et al., 2019). Thus, fragmenting habitats can disproportionately affect species in desert landscapes like the Namib. Studies have found that the more specialist a species, the less resilient they are to landscape fragmentation and disturbance (Devictor et al., 2008). Since the invertebrates in the Namib are specialized to survive in extreme arid conditions by relying on !nara (Yan et al., 2022), they are incredibly vulnerable to habitat fragmentation, regardless of whether the fragmentation occurs near the larger Kuiseb River corridor or in the middle of the Sand Sea matrix.

Our data has further implications for metapopulation theory. A future study could use relative abundances to try to quantify the maximum distance that invertebrates will travel from the !nara patches. This would provide an understanding of where a specific patch is no longer a metapopulation of a greater habitat but rather an island. If the patches are too far apart to even connect and interact with each other, perhaps through fragmentation, metapopulations are no longer functional. Since metapopulations are essential to the health and longevity of invertebrates, quantifying their dispersal abilities would provide important implications for habitat fragmentation.

Ultimately, this study provides important information for several aspects of the Namib Desert invertebrate communities and habitat connectivity in general. The Namib Desert is one of the oldest in the world, and is a biodiversity hotspot with many important endemic species. However, the increase of mining projects and other extractive activities for economic gain threatens the crucial biodiversity that keeps this ecosystem healthy and resilient (Wassenaar et al., 2013). Small, patchy desert habitats are generally viewed as areas that harbor little life or diversity; however, our study found that these isolated habitats still have an equal diversity of life and thus deserve broader protection. Given that deserts already have low overall diversity (our calculation of the Namib Desert yielded a Shannon-Wiener Index of 1.5, when typical values range from 1.5-3.5), further threats to diversity (e.g. fragmentation) could significantly disrupt communities. As climate change worsens and habitat fragmentation becomes evermore present, understanding the behaviors and habitat utilizations of crucial organisms, particularly invertebrates, is vital for the health of our ecosystems.

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Appendices

Appendix I

Figure A1. Malaise Trap. Example Malaise trap site.

A Malaise trap (Figure A1) is a tent-like trap made of fine mesh material used primarily for the collection of flying insects. Insects collide with a middle mesh, fly upward into a funnel at the peak of the trap, and fall into a bottle of ethanol to both peacefully kill and preserve the specimen. During our fieldwork trial period, we found that the Malaise traps easily fell over from the strength of the wind. To solve this issue, we tied sandbags to each support string and buried them in the sand to ensure extra stability. We also buried the lower portion of the Malaise trap frame to make sure the foundation was sturdy and stable.

Figure A2. Pitfall Trap. Example Pitfall trap site.

A pitfall trap (Figure A2) is a plastic cup buried in the desert sand, positioned flush with the ground surface to capture crawling insects. We poured a water and dish soap solution into each cup to break the water's surface tension to ensure trapped insects could not escape. Due to the wind in the Sand Sea, some of the pitfall traps would fill with sand by the time we collected them the next day. To solve this issue, we carefully sifted through the sand to ensure we collected all samples present in the trap.

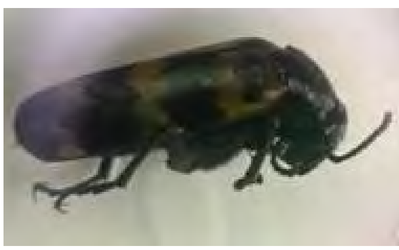
Appendix II

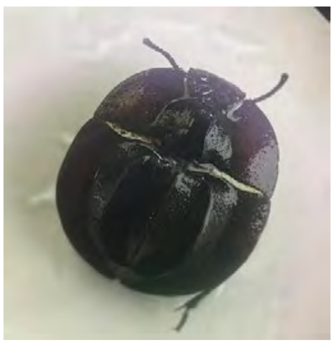
Table A2. Table of invertebrates caught. This table shows each unique species we captured, classified to the most specific nomenclature we could accurately find. F refers to the Family, O refers to the Order, and G refers to the Genus. When available, the species name was added.

PHOTO	CLASSIFICATION
	F: Tineidae **O: Lepidoptera**
	F: Tineidae **O: Lepidoptera**
	F: Tineidae **O: Lepidoptera**

	F: Tineidae **O: Lepidoptera**
	F: Therevidae (Stiletto fly) **O: Diptera**
	F: Eremiaphilidae **O: Mantodea** G: Tarachodes
	F: Asilidae **O: Diptera**
	F: Muscidae **O: Diptera** G: Musca

	F: Muscidae **O: Diptera** G: Musca
	F: Scarabaeidae **O: Coleoptera** G: Aphodius
	F: Coccinellidae **O: Coleoptera**
	F: Musca **O: Diptera** G: Atherigona (stem borer fly)
	F: Tineidae **O: Lepidoptera**

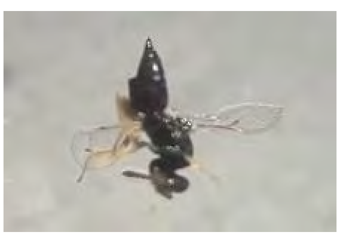
	F: Araniella **O: Araneae**
	F: Curculionoidea (Weevil) **O: Coleoptera**
	F: Meloidae **O: Coleoptera** G: Hycleus
	F: Formicidae **O: Hymenoptera** G: Camponotus S: *Camponotus detritus*
	F: Musca **O: Diptera** G: Atherigona

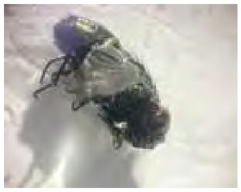
	F: Coccinellidae **O: Coleoptera**
	F: Chrysomelidae **O: Coleoptera**
	F: Tenebrionidae **O: Coleoptera** G: Stips S: *Stips stali*
	F: Geometridae **O: Lepidoptera**
	F: Chrysomelidae **O: Coleoptera**
	F: Noctuidae **O: Lepidoptera**

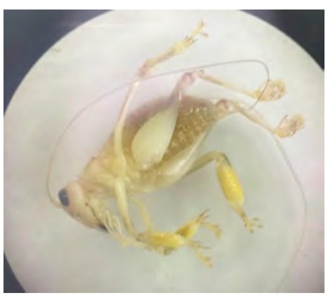
	F: Tenebrionidae **O: Coleoptera** G: Adesmia S: *Adesmia cribripes*
	F: Salticidae **O: Araneae**
	**O: Coleoptera** G: Toktokkus
	F: Sphecidae **O: Hymenoptera**
	F: Formicidae **O: Hymenoptera** G: Crematogaster
	**O: Zygentoma** G: Ctenolepisma

	F: Formicidae **O: Hymenoptera** S: *Ocymyrmex robustior*
	F: Colletidae **O: Hymenoptera**
	F: Sphecidae **O: Hymenoptera**
	**O: Diptera** G: Sarcophaga

	F: Noctuidae **O: Lepidoptera**
	**O: Coleoptera** G: Agrilus
	F: Sparassidae **O: Araneae**
	F: Noctuidae **O: Lepidoptera**
	**O: Zygentoma** G: Ctenolepisma S: *Namiblepisma wygodzinskyi*

<table>
<tr><td></td><td>O: Zygentoma
G: Ctenolepisma</td></tr>
<tr><td></td><td>F: Chloropidae
O: Diptera</td></tr>
<tr><td></td><td>O: Hymenoptera</td></tr>
<tr><td></td><td>F: Drosophilidae
O: Diptera</td></tr>
<tr><td></td><td>F: Pyralidae
O: Lepidoptera</td></tr>
</table>

	**O: Diptera** G: Lucilia
	F: Mythicomyiidae **O: Diptera**
	**O: Hymenoptera** G: Anoplius
	F: Daesiidae O: **Araneae**
	**O: Hymenoptera** G: Pheidole
	F: Formicidae **O: Hymenoptera**

	**O: Coleoptera** G: Hycleus (larval stage)
	F: Noctuidae **O: Lepidoptera**
	F: Fulgoroidea **O: Hemiptera**
	F: Ichneumonidae **O: Hymenoptera**
	**O: Orthoptera** S: *Comicus compestrus*

	F: Cleridae **O: Coleoptera**

	**O: Diptera** G: Bactrocera
	F: Miridae **O: Hemiptera**
	F: Miridae **O: Hemiptera**
	**O: Blattodea** G: Blatta
	F: Ichneumonidae **O: Hymenoptera**
	F: Pyralidae **O: Lepidoptera**

Appendix III

Simpson and Sorensen Indices as secondary measures of diversity

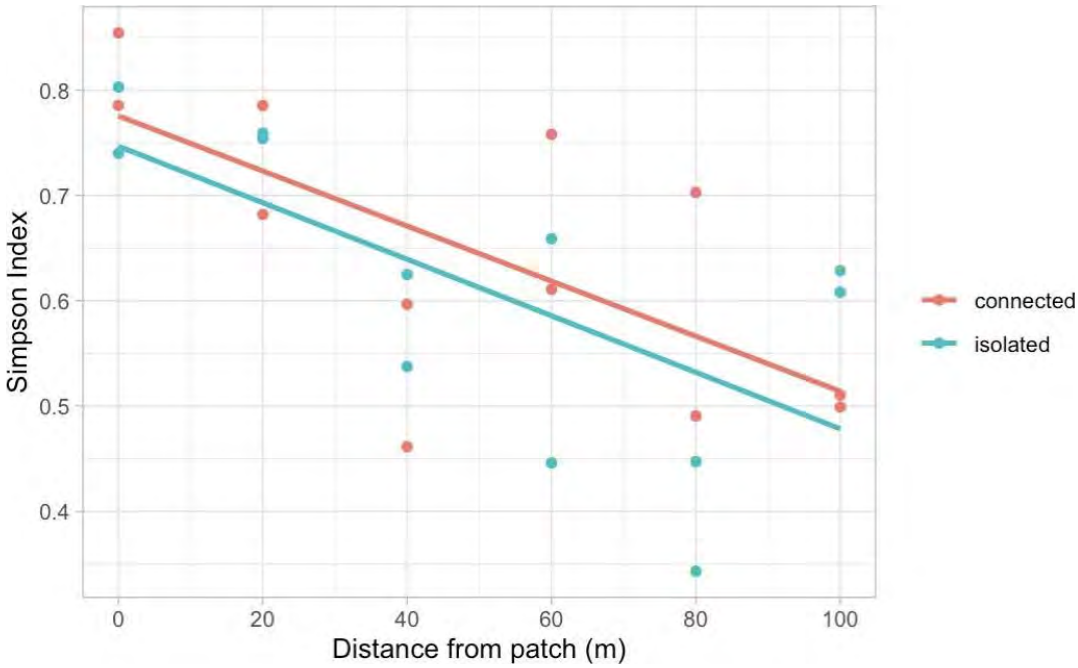


Figure A3. Simpson Index on Distance from !nara patch. Linear regressions distinguished by connected versus isolated habitats analyzing the relationship between invertebrate diversity (Simpson Index) and distance from the !nara patch (meters).

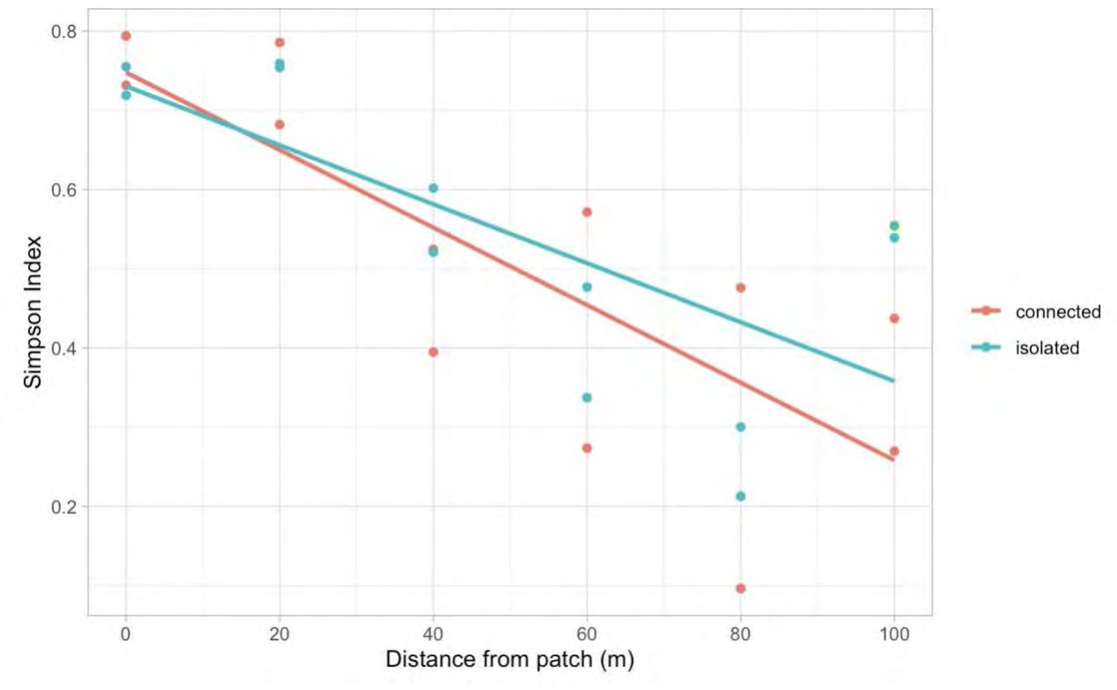


Figure A4. Simpson Index (0-20 m species) on Distance from !nara patch. Linear regressions distinguished by connected versus isolated habitats analyzing the relationship between invertebrate diversity (Simpson Index) and distance from the !nara patch (meters). This graph only accounts for the species identified at 0 m and 20 m and thus does not include new species caught at 40 m and beyond.

The Simpson Index favors species abundance, while the Shannon-Wiener Index favors species richness. We include these Simpson figures to illustrate that trends in loss of biodiversity as distance from a patch increased are similar across distinct indices. When accounting for all species present (F-statistic = 17.91, $P = 0.0003$, df = 22), or for species present at just 0 m and 20 m (F-statistic = 27.28, $P < 0.0001$, df = 22), distance from patch decreased the Simpson Index, without isolation level as a factor (delta AIC = 1.37; delta AIC = 1.41).

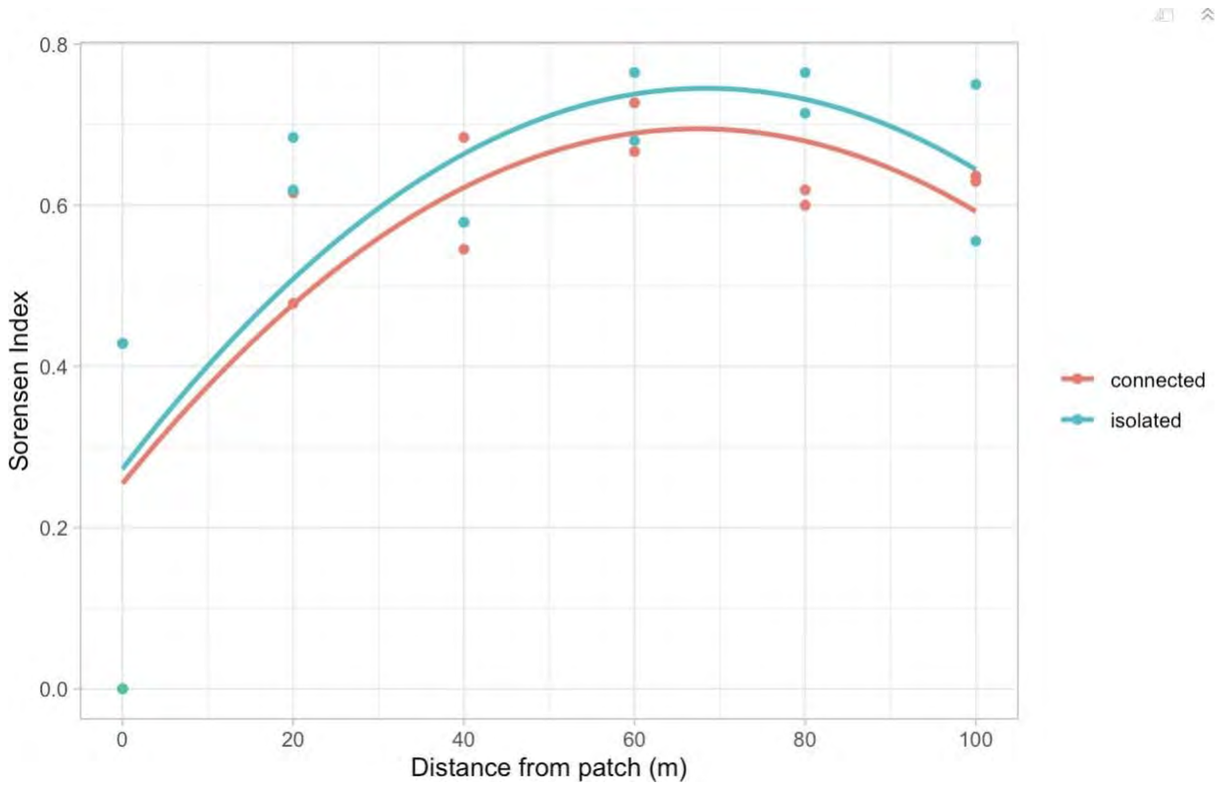


Figure A5. Sorensen Index as distance from !nara patch increases: Nonlinear model reflecting changes in Sorensen species turnover index between connected versus isolated habitats as distance (meters) from the !nara patches increased. This graph only accounts for the species identified at 0 m and 20 m and thus does not include new species caught at 40 m and beyond.

Unlike the Bray-Curtis Index, the Sorenson model does not weigh species abundance as a factor in species turnover and thus elicits different results. The AIC metric determined that the best fit model takes distance into consideration, while isolation level does not play a significant role. AIC calculations also concluded that these data follow a nonlinear regression that suggests that invertebrate species turnover levels increased with growing distance from the !nara patch ($P < 0.0001$, adjusted $R^2 = 0.60$, F-statistic =18.53 , df = 21). Much like the Bray-Curtis model, this curve follows a parabolic path, though it likely faces the same data and mathematical limitations aforementioned in Figure 11.

Appendix IV

Visualizing Bray-Curtis Dissimilarity

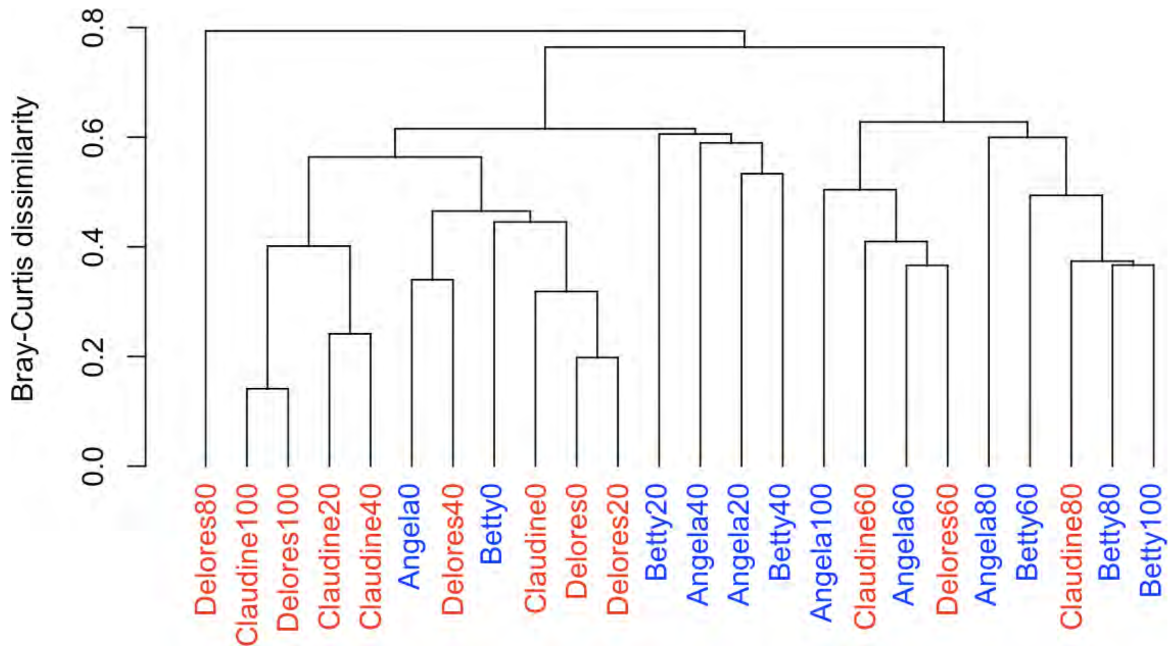


Figure A6. Cluster Dendrogram of Bray-Curtis Dissimilarity: Differences in Bray-Curtis beta diversity index represented by a cluster dendrogram. Sites are represented by their unique name and distance from the edge of the !nara patch. The red labels indicate isolated sites and the blue labels indicate connected sites.

While we found little significant difference between initial invertebrate diversity in connected and isolated habitats, small observational trends are notable. Figure A6 demonstrates that sites with similar distances from patch edge and similar isolation level have the closest Bray-Curtis dissimilarities. For example, Claudine and Delores 100 m locations are closely related, as well as Angela and Betty 20 m and 40 m locations.

Busted Biocrust: Examining the Effects Of Off-Road Tracks on Soil and Rock Surface Communities in the Namib Desert

November 15, 2024

Prepared By:

Phoebe Altman, Jadin Scott, Solange Acosta Rodríguez, Evan Kaye

Abstract

Anthropogenic disturbances are an increasing threat to ecosystems around the globe, with arid ecosystems being particularly vulnerable due to their high degree of fragility. As mining and tourism activities continue to increase in the hyper-arid Namib Desert, delicate elements within this ecosystem are threatened by off-road driving. A lack of research has become apparent in evaluating the specific impact of these vehicle tracks on the biodiversity of soil and rock-surface communities (SRSCs), which is necessary for informing effective management of the national parks that span most of the Namib region. This study aims to contribute to the growing understanding of road disturbances in the Namib desert by assessing if the evidence of ecosystem disturbance on soil erodibility and soil surface communities radiates beyond off-road vehicle tracks. We found that lichen biodiversity and percentage of biological soil cover were lowest within the track, but these factors did not vary between the track and varying distances away from the track, suggesting that for low-intensity use off-road tracks, the ecological impacts do not radiate. Future research should be undertaken to evaluate the connection between soil erodibility and biological soil cover in these ecosystems, and further classification efforts on soil and rock surface communities are necessary for improved understanding of these lichen communities.

Introduction

Disturbance ecology studies the causes and effects of disturbances and how they impact interactions between biological communities and human societies (Newman, 2019; Newman et al., 2024). A *disturbance* can be defined as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource, substrate availability, or the physical environment” (White & Pickett, 1985, p. 7). Disturbances can be differentiated based on their spatiotemporal extent and severity, as well as whether they are autochthonous or anthropogenic in origin (Newman et al., 2024; Dornelas, 2020). While the intermediate disturbance hypothesis suggests that moderate “natural” disturbances promote higher levels of biodiversity (Connell, 1978; Huston, 1979; Turner et al., 2003), severe disturbances can trigger extreme shifts that restructure an ecosystem entirely.

One way to describe the transformation of an ecosystem after a disturbance is through an *alternative stable states* model, wherein an ecosystem transitions from one “stable” and relatively “resilient” form to another (Holling, 1973). However, these restructurings have the potential to take many forms, which are not reliably predictable and not necessarily stable (Graham et al., 2021). The impacts of anthropogenic disturbances specifically are of increasing concern in more fragile environments due to their potential to trigger a transition to an alternative state with lower ecosystem functioning (Möllman et al., 2009).

Ecosystem fragility is generally quantified by the degree of change in species abundance and composition following disturbance (Nilsson & Grelsson, 1995). Hyper-arid environments such as the Namib Desert have extremely limited resource availability (Pointing & Belnap, 2012; Hoover et al., 2020); these environments receive less than 100 mm of rain per year, making them largely unable to support plant life (Schieferstein & Loris, 1992). This contributes to lower species diversity overall and fewer ecosystem niches, which are both major contributors to the ability of an ecosystem to recover from a disturbance (Naeem et al., 1995; Levine & HilleRisLambers, 2009).

Hyper-arid ecosystems are dominated by *poikilohydric* life forms. These consist mostly of cyanobacteria, chlorophytes, heterotrophic bacteria, and lichens that form a thin "biological veneer" over the top few centimeters of soil and rock (Pointing & Belnap, 2012, p. 551). These communities, referred to hereafter as *soil and rock-surface communities* (SRSCs), have been found to occupy the primary producer niche in dryland ecosystems and provide important ecosystem services. While historically understudied, hyper-arid and other dryland ecosystems cover nearly ⅓ of the continental Earth's surface, and have been shown to play a vital role in global nutrient and hydrological cycles (Pointing & Belnap, 2012; Porada et al., 2013).

SRSCs in the Namib Desert are dominated by lichen growth at the soil surface, which survive off of fog events and periods of high humidity (Lalley and Viles, 2006). These lichens serve as nitrogen and carbon fixers, habitat for micro-fauna, and food sources for certain herbivorous species (Lange et al., 1994; Lalley & Viles, 2005; Lalley et al., 2006; Pointing & Belnap, 2012). The majority of these lichen are endemic and support a milieu of other endemic species, thus making them essential to Namibia's overall biodiversity (Lalley et al., 2006). They also play a critical role in stabilizing soil crusts from aeolian erosion (Webb & Wilhire, 1983; Belnap & Gillette, 1998). This is of particular importance in southern Namibia, as these areas experience consistent Berg winds that have been shown to transport dust from the interior to the western coastal cities, negatively impacting air quality in these locations (Pfiz et al., 2010; Weber et al., 2022).

Namib-Naukluft National Park, located within the southern Namib Desert, contains at least two large lichen fields near its northern border situated directly inland from Swakopmund and Walvis Bay (Ministry of Environment, Tourism and Forestry, 2021). As tourism, mining speculation, and filming activities have recently increased the amount of off-road driving in lichen fields across Namib-Naukluft and Dorob national parks, concerns have emerged about the ability of these fields to maintain their ecosystem functions (McCulloch, 2008; Margonelli, 2013; Conway-Smith, 2016). Recent road ecology literature suggests roads may harm lichens in multiple ways. Lichens are highly sensitive to disturbance, particularly disturbances such as driving that impact the soil surface, as most lichens in these environments occur in the top 3mm of soil (Garcia-Pichel & Belnap, 1996). Lichens have also been shown to be sensitive to environmental pollutants (Calvelo et al., 2009), particularly silica dust (Pystina et al., 2019) and nitrogen pollution (Britton & Fisher, 2010), both of which vehicles may contribute to through dust trails and nitrogenous exhaust gasses. A recent study on a highway in Brazil found a positive relationship between distance from the road and lichen diversity, suggesting that these pollutants created by vehicle traffic had a radiating negative impact on lichen diversity (Ishikawa & Vasconcelos, 2021).

Existing research on lichen recovery from disturbance also suggests that impacts may not only be spatially radiating, but temporally radiating as well. While there is a lack of scientific consensus on the exact lengths of time required for lichen to fully recover from a disturbance, lichens are generally understood to be slow to recover (Belnap & Warren, 2002; Evans & Belnap, 1998; Lalley & Viles, 2008; Kidron et al., 2020). There is evidence to further suggest that even when lichen population numbers recover from a disturbance, species composition and levels of photosynthetic activity fundamentally differ from comparable undisturbed populations (Evans & Belnap, 1998; Lalley & Viles, 2006). This suggests that vehicle track disturbances may have long-lasting impacts on lichen in hyper-arid ecosystems such as the Namib Desert.

Although there has been some work to classify lichens found in the Namib Desert (Wirth, 2010), as well as some research investigating the impacts of off-road driving on the productivity of these lichens (Lalley & Viles, 2006), there is a lack of research on the specific impacts that off-road driving might have on the area surrounding vehicle tracks. This is a particularly important question to ask when determining off-roading policies for entities such as national parks. We aim to assess if the negative impacts of off-road driving disturbances radiate beyond the confines of track edges, and if there is an observable connection between lichen communities and soil erodibility in the lichen fields of the southern Namib desert.

Disturbance ecology theory, particularly road ecology, suggests that the most extreme disturbances created by roads will be proximal to the road edge (Spellerberg & Morrison, 1998). Since vehicles create aeolian pollutants that have the capacity to impact SRSCs (Calvelo et al., 2009; Pystina et al., 2019), and given previous research on the radiating impact of high traffic roads (Ishikawa & Vasconcelos, 2021), measurable impacts of off-road driving might be expected to decrease with increasing distance from the tire track. We expect to find such measurable radiating impacts on lichen biodiversity, percentage of lichen cover, and soil stability. Additionally, previous evidence suggests that SRSCs promote soil stability, and since lichens represent a significant part of ground cover in the southern Namib, we expect to observe a positive relationship between percent cover of lichen and soil stability.

Methods

We conducted our study in the lichen fields of Namib-Naukluft National Park, specifically studying double tracks created by four-wheeled vehicles driving off-road. We studied areas within the track, as well as areas 1 meter and 5 meters away from the tracks to represent areas “near” and “far” from the disturbance, respectively. We collected data on soil stability, lichen biodiversity, and biological soil cover density. We also collected lichen samples to estimate the amount of carbon captured by species in this region of the Namib Desert.

Site Selection

Sites were selected based on several criteria. Due to the region’s high abundance of lichens (Wirth et al., 2007) and proximity to Gobabeb Research Centre, we chose locations within the gypsum soil lichen fields of the Namib Desert gravel plains, roughly east of Walvis Bay. Within this region, we selected locations with varying degrees of natural lichen cover. We used the *Mad Max: Fury Road* Environmental Impact Assessment, maps of lichen cover from the Namib-Naukluft Management Plan, and our own visual observations to find suitable locations. All sites selected were within the boundaries of Namib-Naukluft National Park, within several hundred meters of a graded roadway (Figure 1). All sites selected experienced either 75-100 or 100-125 days of fog per year (Appendix IV Figure IVB). Two sites were located within areas under exploratory mining licenses (Appendix IV Figure IVA).

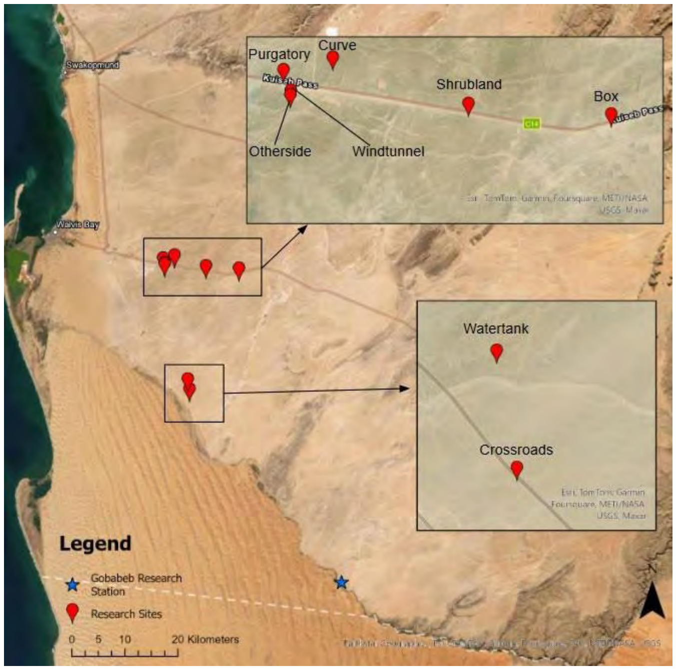


Figure 1: Map of Sampling Sites. Names for each site are either above the location marker or connected by a line. See Appendix I for specific coordinates.

Each site was also investigated on foot prior to data collection. Within each site, we chose lengths of track within a relatively flat area to reduce the likelihood of gravity-based erosional gradients. We selected tracks that had been visibly used more than once, with a clear inter-tire area in which lichen growth was present. We avoided tracks in which tread marks were still visible, ensuring that each track had a more consistent degree of recovery since disturbance. Only double (four-wheeled vehicle) tracks were selected. Finally, we selected 24-meter-long sections of track that were not intersected by other sets of tracks and did not have other tracks within ten meters of the boundaries of our study area. Some sites did not perfectly meet every one of these criteria (see Individual Site Descriptions and Appendix III for images). Track density, defined as the concentration of individual tracks within a visible radius, was noted for each site.

Individual Site Descriptions

Crossroads

This site had a relatively flat topography. The site was located several hundred meters from an unnamed unpaved road running roughly parallel to Route D1983. Track density was moderate. Lichen cover was more sparse and patchy than some other sites though lichen could be found in all areas. No single lichen species dominated.

Watertank

This site was located approximately two kilometers northwest of Crossroads. The site had similar lichen cover and topography to Crossroads, though track density was slightly higher. This site was about one-kilometer northeast of the unpaved road parallel to D1983.

Shrubland

The topography was relatively flat but included some small hills. Lichen cover was moderately thick and tinged the ground slightly green due to the high presence of *Acarospora gypsi deserti*. The site included sparse but regular shrub cover. The site was north of and adjacent to the C14 road which was used to access it.

Box

The topography was flat. Lichen cover was medium-high density and dominated by *Acarospora gypsi deserti*. The site was roughly adjacent to and north of the C14 road, which was used to access the area. Track density was very high, and there were heavy equipment tracks present.

Curve

The topography was mostly flat with some small dispersed hills. A cluster of shrubs was present nearby, but not within our sample area. Track density was very high, with few undisturbed sections. We struggled to identify a straight length of track that was not crossed by another, so we settled on a track with a slight curve. There was dense lichen cover dominated by *Acarospora gypsi deserti*. Natural patchiness in lichen cover increased at the far end of our sampling area, and overlapped with the far transect (t5). We accessed this site from an existing high-use off- road track running north off of C14.

Purgatory

The topography was composed of undulating hills with some flat sections. High-voltage electrical towers were positioned several hundred meters away. Track density was very high, with few undisturbed sections. There were also prevalent water-eroded gullies with minimal lichen presence. Lichen cover was relatively thick and dominated by *Acarospora gypsi deserti,* creating a yellow-green tinge on the landscape. There were occasional shrubs. The site was several hundred meters north of the C14 road, which we used for access.

Windtunnel

This site was within a kilometer of Purgatory. It was located south of the C14 highway and had a much lower track density than all other sites, as well as evident *Acarospora gypsi deserti* dominance. Our sampling location was adjacent to a small hill and as a result, was on a very slight incline. Wind speed was high and consistent when we sampled at this site.

Otherside

This site was several hundred meters from Windtunnel, in a more flat location. The site had comparable track density to Purgatory. The wind speed was lower than at Windtunnel. There was thick lichen cover dominated by *Acarospora gypsi deserti*. This site was accessed on foot from Windtunnel.

Data Collection

At each site, we laid three 24-meter transects: one along the outside edge of the track (t0), another one meter from the outside edge of the track (t1), and another five meters from the outside edge of the track (t5; Figure 2.). The edge of the track represented the area of direct disturbance, the one-meter mark represented the area “close” to the track, and the five-meter mark represented areas “far” from the track. Along each transect, we measured soil stability, the presence of algal crusts and lichen, and lichen species diversity.

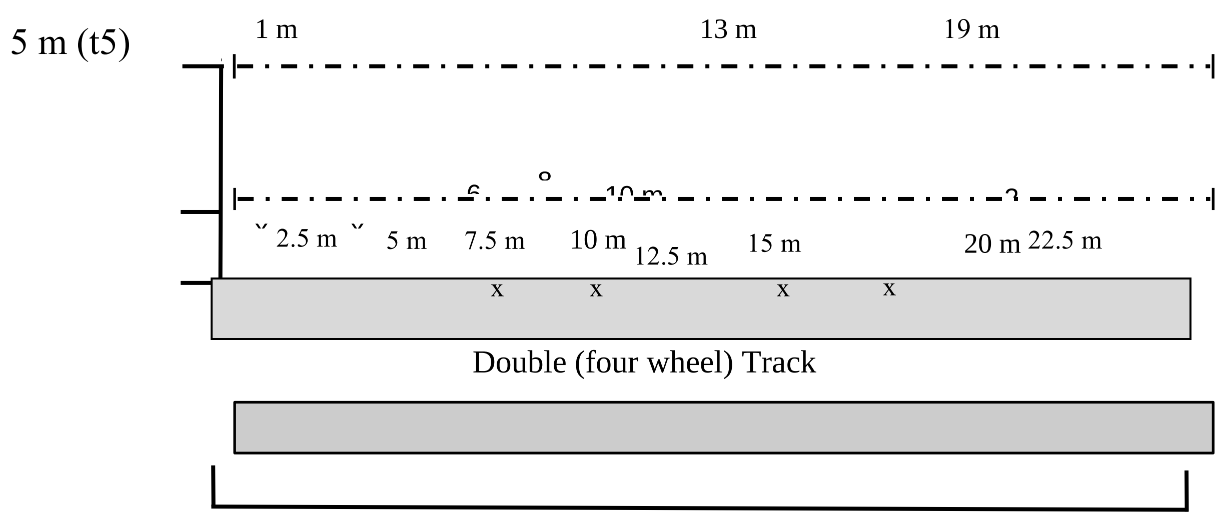


Figure 2. Transect layout schematic. Transects are marked with dotted lines. While each variable was sampled at every transect, for readability only one variable is shown per transect. Locations for sampling are included as xs. Biodiversity sampling intervals are shown for the transect at 5 m (t5), percent lichen cover intervals are shown for the transect at 1 meter (t1), and soil stability intervals are shown for the transect at 0 meters (t0).

Soil stability was measured with a soil slake test kit, using soil water erodibility as a proxy for soil aeolian erodibility. Soil crust samples were collected from the top 1 cm of the soil profile, at 2.5 m intervals along the inner edge of each transect (Figure 2). Before samples were collected, pebbles and lichen not directly attached to the soil surface were lightly brushed off so that there was a clear area of soil to sample from. Each soil sample was placed in a separate water-filled cell for five minutes. Time was tracked with a stopwatch. When time was up, it was dunked out of and into the water five times. Based on the soil’s structural response to these disturbances, each sample was assigned an ordinal score from 1 to 6, with 1 the least stable and 6 the most stable. We completed this nine times per transect for a total of 27 soil stability measurements per site.

We estimated the percent cover of lichen using a wire soil crust frame divided into 20 five cm by five cm squares in a five x four configuration. The test was repeated every two meters along the transect’s inner edge beginning at zero m (Figure 2). Each testing location along the transect was misted with water for 20 seconds prior to testing to make the lichen more visually distinct and to better identify algal crusts. Once the frame was laid on top of the soil, we used a point-sampling method to identify the material hit at the bottom right corner of each of the squares. We created five categories to describe soil surface community composition based on classifications presented in Rosentreter et al. (2007) under the guidance of U.S Geological Survey ecologist Dr. Rebecca Finger-Higgens (Table 1).

Table 1: Soil Surface Community Category Definition and Description.

Soil Surface Community Category	Description
Soil lichen (SL)	Any lichen with a soil or rock substrate that was embedded in the soil enough that it did not move when probed.
Rock lichen (RL)	Any lichen that had a non-embedded rock as its primary substrate, in which the majority of the lichen was visibly attached to the rock.
Vagrant lichen (VL)	Any lichen that was unattached to the soil surface, or was attached to a non-embedded rock with the majority of the lichen not confined to the rock.
Algal soil crust (ASC)	Any non-lichen evidently biotic soil crust, which we determined by probing the soil surface with a pin flag and assessing soil texture at that point.
N/A	Any abiotic material, which included sand or rocks without lichen cover.

We recorded the number of cells per frame for each category and proportions to calculate the percentage cover of each category per frame, and ultimately for each transect.

To estimate species diversity, a 50 cm x 50 cm quadrat was laid along each transect's inner edge at six meter intervals, beginning at one meter (Figure 2). At this location, an observer collected a sample of every visually distinct lichen species within the frame. At each additional location along the transect, the observer collected only species not found in the preceding locations, creating a collection of total species for each transect. In the lab at Gobabeb Research Centre, we examined our samples under the microscope and visually identified each species using *Lichens of the Namib Desert* by Volknar Wirth (2010) as a guide. Samples that we could not confidently identify were given provisional names based on their visual characteristics.

To estimate lichen carbon content, we collected samples of several lichen species: *Xanthoparmelia walteri*, *Acarospora gypsi deserti*, and a mix of all vagrant species found at one site. We fired two samples of each lichen type. Each sample was dried in a drying oven for 24 hours at 60º C. Once dried, the samples were ground with a mortar and pestle into a powder, placed into separate aluminum tins, and heated for three hours at 450º C to burn off carbon. Combined lichen and tin mass was weighed before and after heating. Six empty tins were placed in the oven along with the samples and weighed before and after heating so average tin mass loss after firing could be incorporated into the lichen mass loss calculations. Final lichen weight was recorded in terms of average loss on ignition (LOI), indicating the percentage of the original material that was composed of carbon.

Data Analysis

Raw data was recorded in the field in physical notebooks and then entered into Google Sheets. Maps were made in ArcGISPro and Adobe Photoshop. JMP Pro 17 was used to conduct statistical analysis and produce visualizations. Some figures were also made in R. Because our data points were collected at different intervals along transects, we calculated the means of each variable per transect and used individual transects as our unit of analysis for each site. For analyzing the relationships between transect and percent cover of lichen, species diversity, and soil stability, we ran mixed effects models with site as a random effect to account for a lack of independence in transect measurements at each site and the variability of lichen concentrations at each site. For significant results, we then ran post hoc Tukey tests to identify directional differences between transects for each response variable. For the relationships between percent cover of lichen and soil stability, as well as species diversity and soil stability, we ran linear regression analyses.

Results

Lichen Findings

Across all of our sites, we identified 20 unique species of lichen belonging to eight distinct genera (Figure 3). The majority of these species are considered endemic to the Namib. The most abundant species overall was *Lecidella crystallina* (11.9% of total abundance), while *Caloplaca testudinea* and *Pertusaria pseudomelamospora* were the least abundant species (each 1% of total abundance). We also observed six species that we were unable to identify, which we labeled as ‘unknowns 1-6.’ Species richness across all sites ranged from 10 to 17 different species (Figure 4). We saw similar distributions of genera of lichen across all sites.

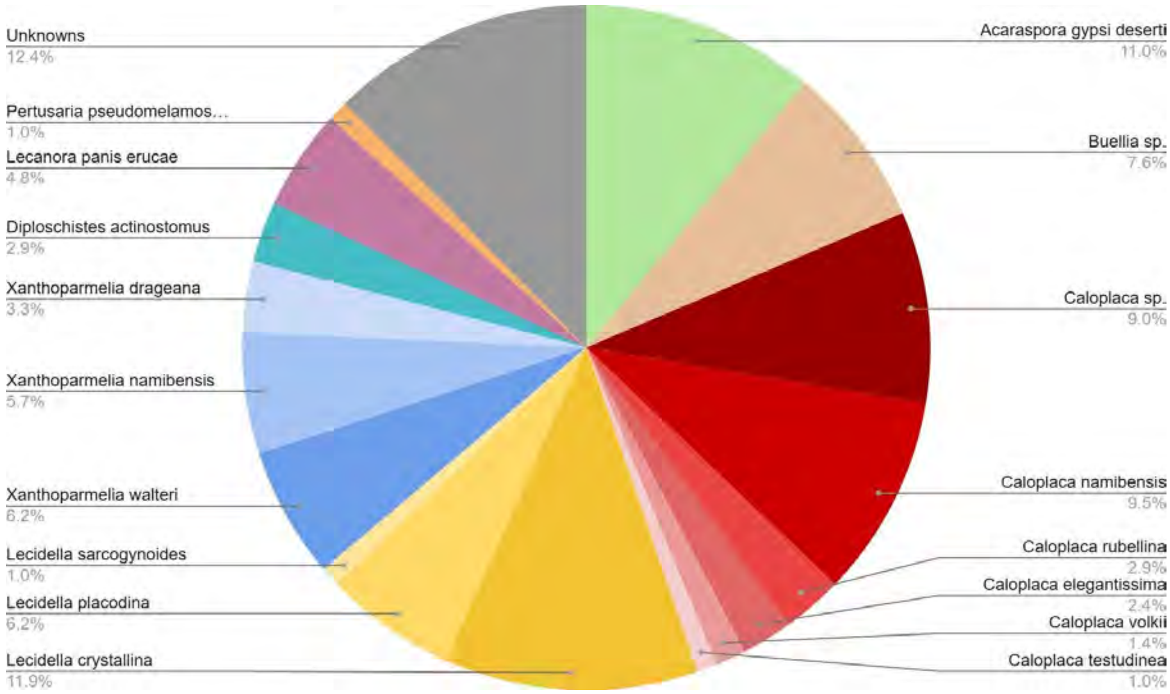


Figure 3: Species abundance across all sites. Species are grouped by color based on their genera. *Xanthoparmelia* spp. are blue, *Caloplaca* spp. are red, and *Lecidella* spp. are yellow. All other genera are excluded from this classification because there was only one species for the remaining genera.

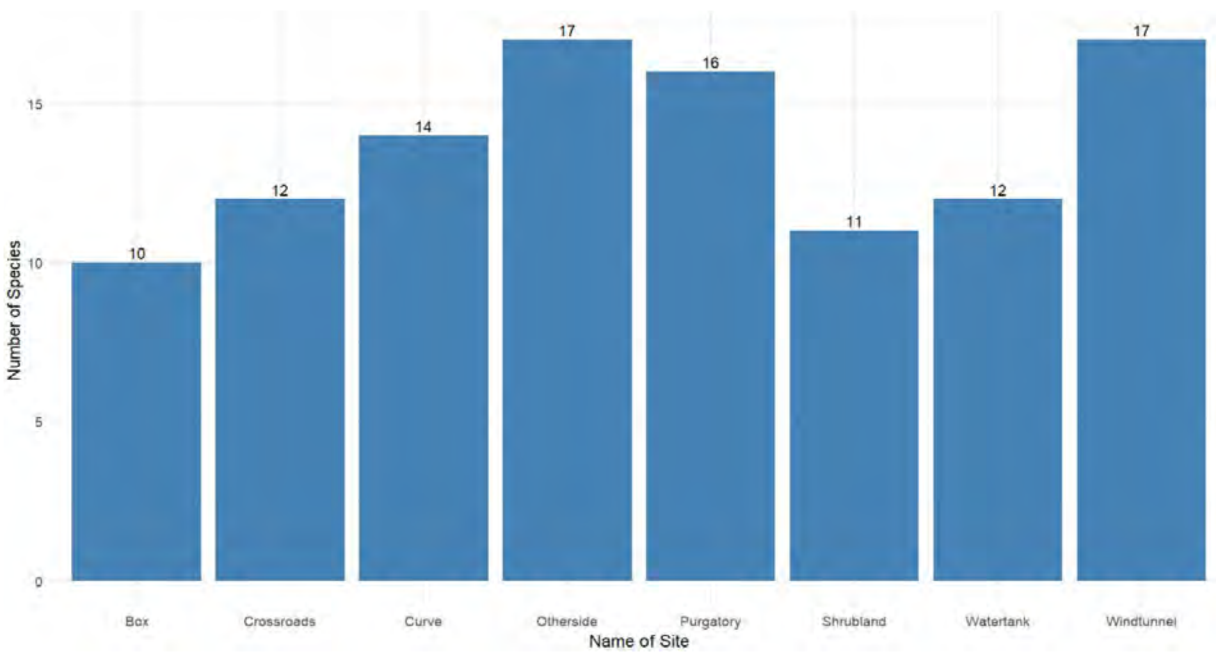


Figure 4: Overall Species Richness across all sites. Number of species counted at each site ranges from 10 to 17 species of lichen.

Our LOI tests found that *Xanthoparmelia walteri* lichens had the highest percentage of carbon per unit of mass. On average, these lichen samples had a 73% average LOI, while *Acarospora gypsi-deserti* had an average LOI of 23%, and the mixed vagrant lichen species had an average LOI of 24.56%.

Sample	Average percent composition of C
Xanthoparmelia Walteri	72.86 % ± 0.03
Acarospora gypsi deserti	21.67 % ± 0.004
Mixed vagrant lichen species	24.56 % ± 0.00007

Table 2: Percent Composition of Carbon of Fired Samples (n=2 per species)

Soil & Rock-Communities Surface Cover

We ran our analysis first on the total SRSC ground cover, in which we included all lichen types and ASCs, but not N/A. We found a difference between transects in percent SRSC cover ($F_{2,14} = 26.73$; $P < 0.0001$). There were decreases in soil and rock-surface community cover from t1 to t0 (post hoc Tukey test: -20.68% ± 3.56; P = 0.0001) and between t5 and t0 (post hoc Tukey test: -24.06% ± 3.56; P < 0.0001), but not between t1 and t5 (post hoc Tukey test: -3.39% ± 3.56; P = 0.62).

This trend persisted when we ran the same analysis on lichens alone, which included all lichen types, but not ASC or N/A. Overall, we found that percent lichen cover varied between transects (Table 3, Figure 5; $F_{2,14} = 26.23$; $P < 0.0001$), with greater lichen cover at t5 than t0 (post hoc Tukey test: -21.35% ± 3.20; P = 0.0001), and at t1 than t0 (post hoc Tukey test: -18.54% ± 3.20; P = 0.0001), but no difference in lichen cover between t5 and t1 (post hoc Tukey test: -2.81% ± 3.20; P = 0.66).

Table 3: Mean Percentage of Lichen Cover Across All Sites by Transect

Transect	Percentage lichen cover (mean ± SD)
t0	17.97 ± 11.44
t1	36.51 ± 12.22
t5	39.32 ± 16.33

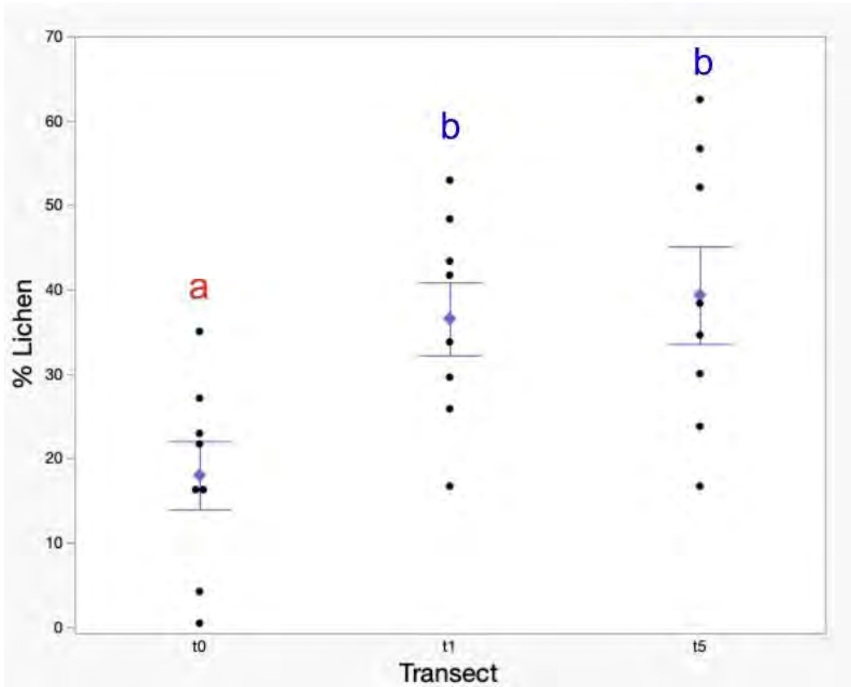


Figure 5. Percent cover lichen by transect. Mean percent cover of lichen at each transect across eight sites. Points represent the mean percent cover for each site, diamonds represent the mean across all sites with standard error bars. Letters indicate statistical differences from the post hoc Tukey test.

We then narrowed our analysis by lichen category and found this trend repeated with RL and VL (Figure 6; $F_{2,14} = 6.97$, $P = 0.0079$; $F_{2,14} = 7.49$, $P = 0.0061$). VL and RL had a decrease in lichen cover from t5 to t0 (post hoc Tukey tests: -11.82% ± 3.38, P = 0.0093; -6.41% ± 1.94, P = 0.018) and from t1 to t0 (post hoc Tukey tests: -10.78% ± 3.38, P = 0.017; -6.09% ± 1.94, P = 0.018), but had negligible differences between the outer transects (post hoc Tukey tests: -1.04% ± 3.38, P = 0.95; -0.31% ± 1.94, P = 0.99). We did not find a relationship between SL cover and distance from the track ($F_{2,14} = 2.81$, $P = 0.094$).

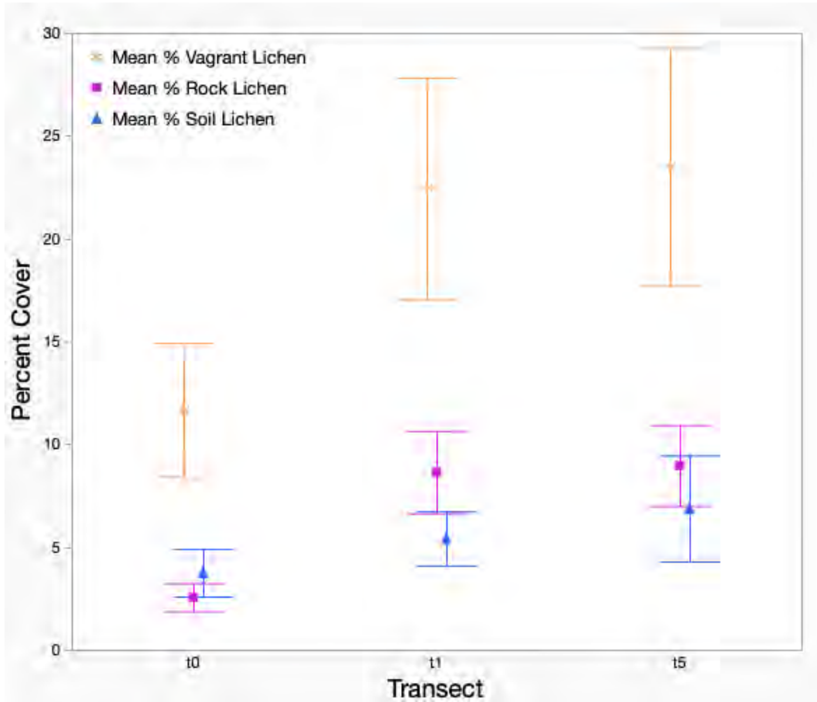


Figure 6. Average percent cover lichen by transect and lichen type. Means are presented with standard error bars.

Lichen Species Diversity

When comparing lichen species diversity by transect, we found that there were differences between transects (Table 4, Figure 7; $F_{2,14,}$ = 7.57, P = 0.0059). We found lower diversity in the track (t0) compared to the outer transects. The track (t0) had less species diversity than t5 (post hoc Tukey test: -3.50% ± 0.96, P = 0.007) and t1 (post hoc Tukey test: -2.88% ± 0.96, P = 0.025), but there was no difference between t1 and t5 (post hoc Tukey test: -0.63% ± 0.96, P = 0.79). We additionally ran a linear regression model to test for a relationship between species diversity and soil stability, and between species diversity and percent lichen cover, and found no relationship for either (slope = 0.035, $F_{1,22}$ = 0.20, P =0.66, r^2 = 0.0092; slope = 0.018; $F_{1, 22}$ = 0.37, P = 0.55, r^2 = 0.016).

Table 4: Mean Species Count Across All Sites by Transect

Transect	Mean species count ± SD
t0	6.25 ± 1.75
t1	9.13 ± 1.64
t5	9.75 ± 1.91

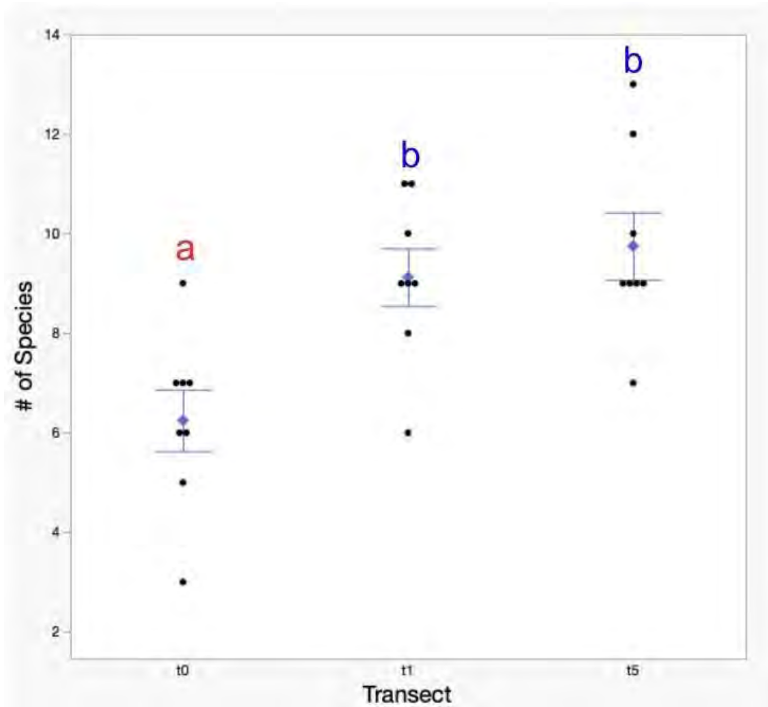


Figure 7. Species diversity by transect. Number of species identified at each transect across eight sites. Points represent the total number of species for each site, diamonds represent the mean number of species across all sites with standard error bars. Letters indicate statistical differences from the Tukey post hoc test.

Soil Stability

Though our samples from within the track had a lower range of soil stability than the transects outside of the tracks, there was no relationship between soil stability and distance from the track (Figure 8; $F_{2,14}$= 2.48, P = 0.12). We also found no relationship between soil stability and percent cover of lichen (slope = 0.10, $F_{1,22}$ = 0.94, P = 0.34, r^2 = 0.041).

Table 5: Mean Soil Stability Across All Sites by Transect

Transect	Mean soil stability ± SD
t0	2.79 ± 1.002
t1	3.42 ± 0.64
t5	3.46 ± 0.75

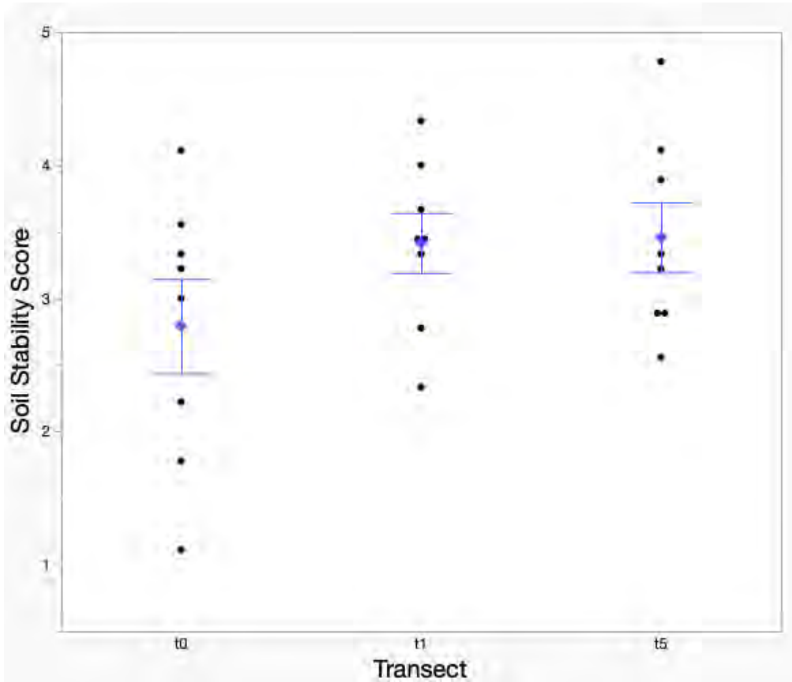


Figure 8. Soil stability by transect. Mean soil stability score (with a stability score of 1 being the least stable and a score of 6 being the most stable) at each transect across eight sites. Points represent the mean soil stability score for each site, diamonds represent the mean across all sites, and the bars represent one standard error from the mean.

Discussion

Our results found that off-road driving has negative impacts on SRCSs, but the impacts are localized to the tracks themselves and do not radiate outward. Both lichen biodiversity and percent biological soil cover were lowest in the tracks, but not did not differ between the 'near' and 'far' transects. We found no relationship between distance from tracks and soil stability, and we did not identify a relationship between soil stability and lichen cover. These findings add to the existing body of knowledge on road ecology, and suggest that road type and degree of usage matter when considering the impact of disturbance on SRCSs.

Our lichen biodiversity sampling found a high number of species that are endemic to the Namib. Lalley et al. (2006) found an association between some of these species and endemic arthropod species, reflecting this area's importance as a hub for Namibia's overall biodiversity. While endemic species of lichen were found both within and outside of the tracks, demonstrating these species' potential resilience in the face of vehicular disturbance, overall species richness was significantly lower (Figure 7). When we couple this result with previous research that has found lichen to be significantly less photosynthetically active within tire tracks compared to outside of tracks, it is clear that minimizing vehicular disturbance is important to dryland biodiversity and ecosystem functioning (Lalley & Viles, 2006; Hinchcliffe et al., 2017).

Given that we selected tracks that had visibly recovered since initial disturbance, and enough time had passed that tire tread marks were no longer visible, the fact that lichen cover and biodiversity were limited in the tracks is an important finding. It appears that even tracks not currently in use have lingering impacts on lichens. This is particularly important considering the degree to which off-road tracks of varying ages currently cover the park. Satellite imagery of Namib-Naukluft National Park has shown that the number of these tracks has increased significantly in recent decades (Google Earth, 2000; Google Earth, 2020).

Site selection was challenging because it was difficult to find sections of track to sample that were not disturbed by other sets of tracks running through or near them, as can be seen in our images of site areas, demonstrating the high degree of overall disturbance in these lichen fields (Appendix II). It was not possible to determine exact use history of our sites or track age due to imprecise records and the limited resolution of remote sensing data. We also did not have the resources to test for aeolian erodibility, which is the primary means of soil erosion in the Namib Desert, so we instead used a slake test for water erodibility as a proxy. This proved to be problematic, as we had to remove the lichen cover in order to take slake samples, which meant we could not logically conclude the degree to which these lichens would have protected the soil from wind erosion.

Our limitations evidence the need for further study of lichen fields in the Namib desert. Improved, expanded classification of Namib lichens would be useful in identifying not only species but also their ecosystem functions, which is important for understanding the role of these lichens in the greater Namib ecosystem. Further study should also be done to assess the connection between these lichens and the aeolian erodibility of the soils they cover. Other studies have found that lichen cover in arid environments does help protect soil from wind erosion, so it is likely that our study design was inadequate for assessing the soil's stability in this system, and different methods should be used (Gholamhosseinian et al., 2021; Ariyasena et al., 2024).

While our data did not show significant radiating effects of off-road double tracks, we noticed visually radiating impacts to lichen cover from graded dirt roads and higher-use roads. Pre-existing research on higher intensity use dirt roads has found a gradient of impact, thus further research should be conducted to determine the consequences of varying intensities of road use in this region. A controlled long-term recovery study in an otherwise undisturbed area would provide further clarity on lichen response over time and would minimize potential interference from other historical disturbances. More systematic investigations of lichen and biocrust carbon content in the Namib desert would also improve understanding of their role in the carbon cycle.

Our research highlights the necessity of limiting the number of new tracks, as it suggests that using one track multiple times will not have dramatic radiating impacts, whereas each new track would create significant disturbance to lichens and ultimately create a greater disturbed surface area. Based on our data and the existing body of literature, we would highly recommend that the Namib-Naukluft park management implement and better enforce policies to limit off-road driving to specific, pre-existing tracks to reduce impact on the lichen fields. While the Namibian Ministry of Environment, Forestry and Tourism has banned off-road driving in national parks outside of specific zones demarcated for guided tours, enforcement is virtually nonexistent (Ministry of Environment, Forestry, and Tourism, 2021). We also urge that non-tourism activities such as film production be encouraged to move their operations elsewhere in the country, or otherwise be meticulously managed to minimize the creation of new tracks as much as possible. Given the degree to which off-road driving has increased in recent years in Namib-Naukluft National Park, it is important to understand how these roads impact the life that keeps these fragile ecosystems functioning. As human activities continue to encroach on more previously undisturbed land, disturbance ecology is becoming an increasingly relevant field of study. This study provides an example of how understanding the intricacies of a particular ecosystem is crucial to informing land management plans that aim to counter the negative impacts of anthropogenic disturbance in more effective and ecosystem-specific ways.

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Appendices

Appendix I: Name and Location of Study Sites

Table IA: Name and Location of Study Sites

Name	Northing	Easting
Crossroads	-23.226219	14.752867
Shrubland	-23.016001	14.783536
Box	-23.020249	14.844352
Water Tank	-23.209282	14.749761
Curve	-22.997685	14.725722
Purgatory	-23.002551	14.704720
Wind Tunnel	-23.010663	14.707839
Otherside	-23.012471	14.707600

Appendix II: Photos of General Disturbance


Figures IIA *(left)* and IIB (*right*): images of extensive vehicular disturbance seen during data collection.

Appendix III: Photos of Sampling Sites

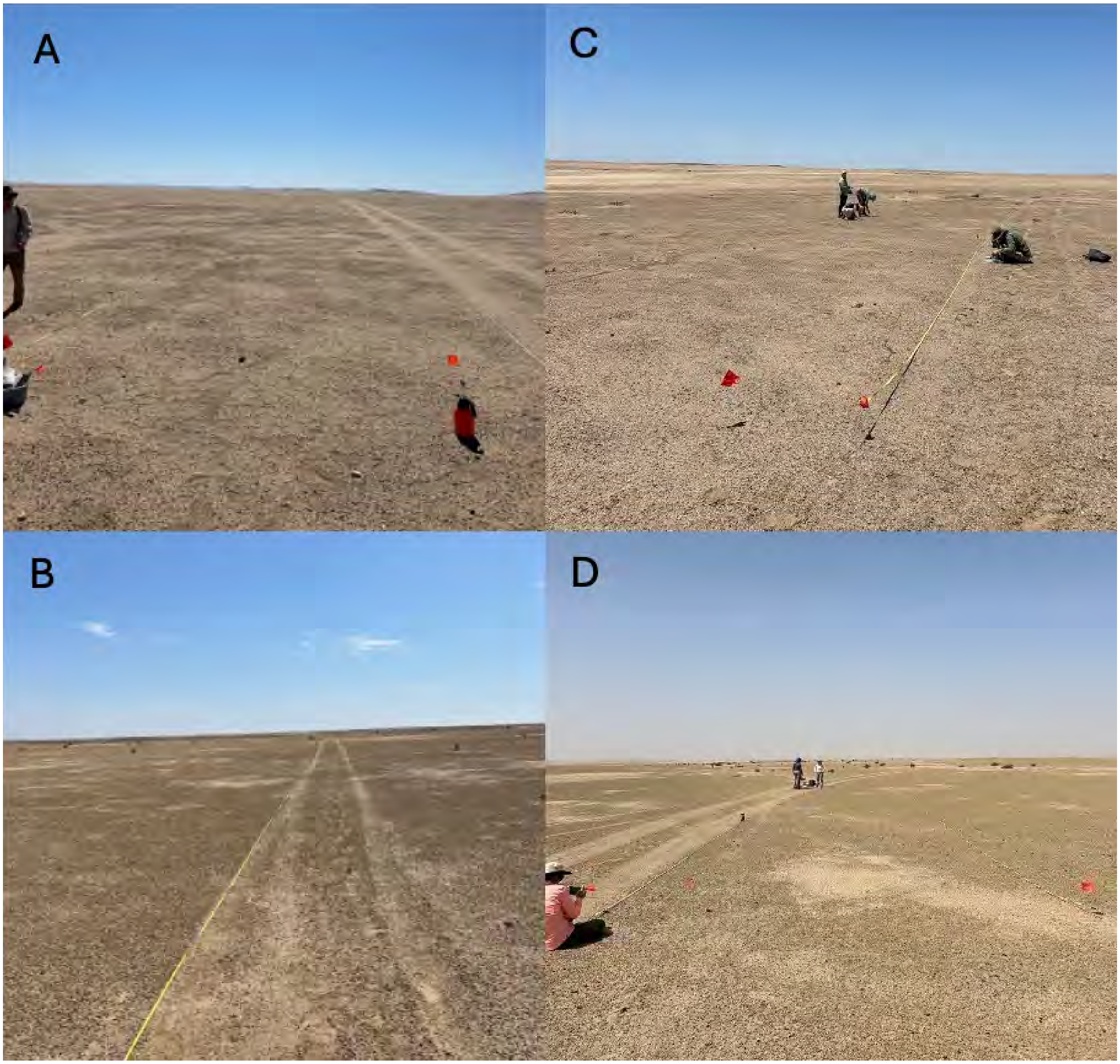

Figure III (A) Crossroads, (B) Shrubland, (C) Box, and (D) Curve.

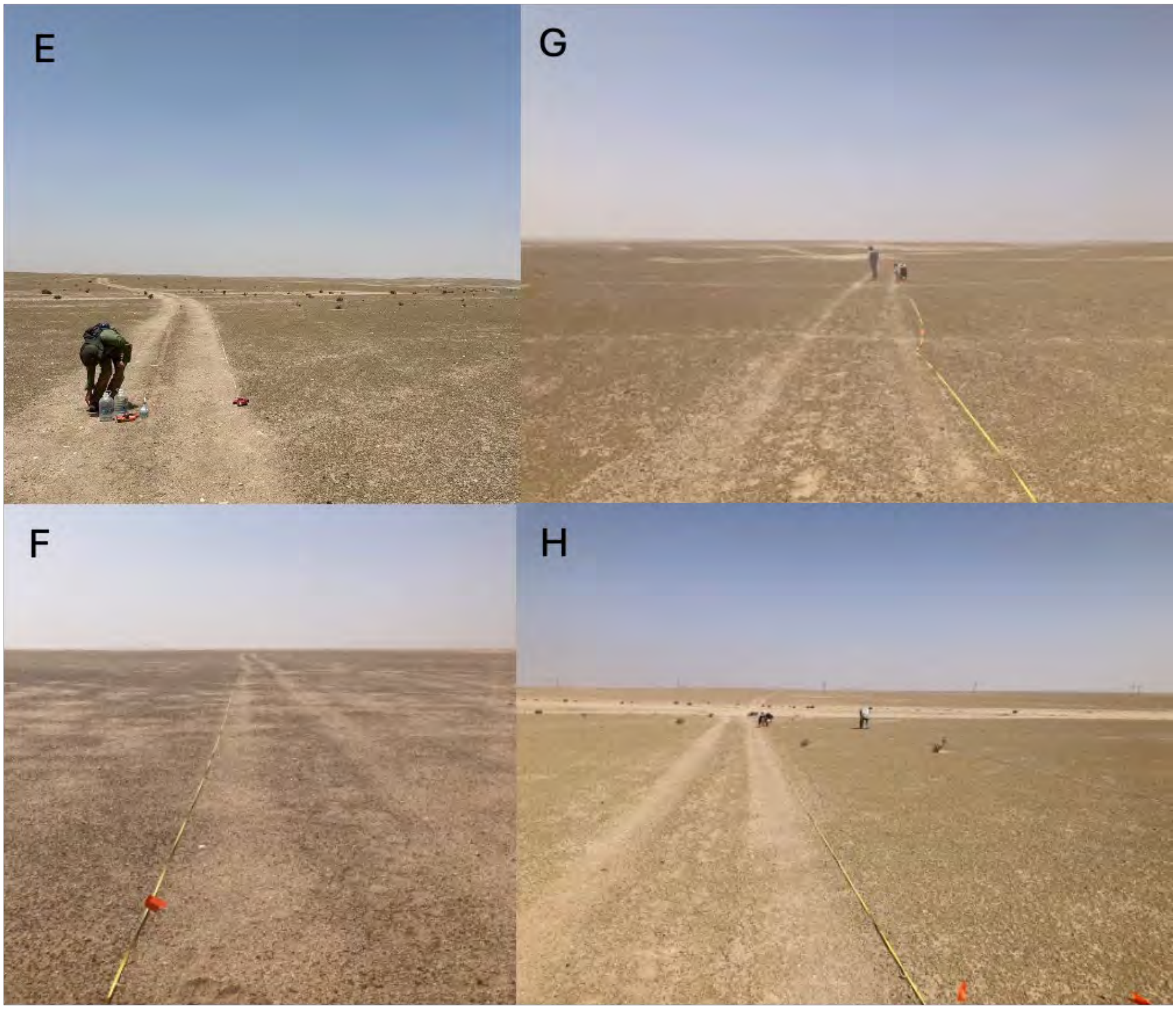

Figure III (E) Purgatory, (F) Watertank, (G) Windtunnel, and (H) Otherside.

Appendix IV: Supplementary Maps

Figure IVA: Map of research sites and mining lands

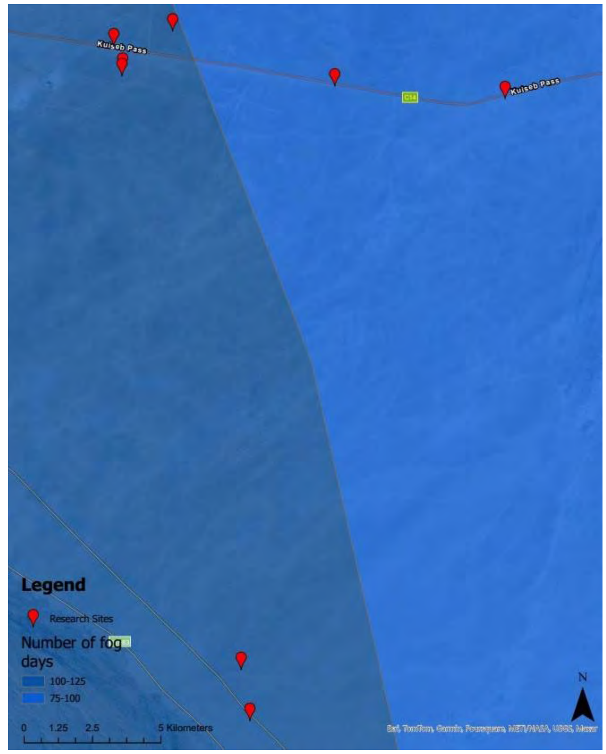

Figure IVB: Map of research sites and number of fog days