



# Dartmouth in Namibia

**Dartmouth College, Environmental Studies  
Program, Hanover NH USA**

**October-November 2017**

## **Table of Contents**

<b>Assessing the Carrying Capacity of the Kuiseb River Ecosystem for Topnaar Livestock ....</b>	<b>3</b>
References .....	30
Appendices.....	32
<b>Topnaar Livestock Management in the Lower Kuiseb .....</b>	<b>35</b>
References .....	62
Appendices.....	65
<b>!Nara Herbivory: Implications for Plant Growth, Productivity, and Associated Animal Communities.....</b>	<b>79</b>
References .....	110
Appendices .....	115

# !Nara Herbivory: Implications for Plant Growth, Productivity, and Associated Animal Communities

November 10, 2017

Prepared by:

Alexander Cotnoir

Amelia Ali

Edward Darling

Jordan Swett

## Introduction

!Nara (*Acanthosicyos horridus*) is an endemic, leafless dioecious plant of the Cucurbitaceae family located in the western Namib Desert. The largest !nara population inhabits the Kuiseb Delta, which separates the gravel plains of the northwest from the large dunes of the Namib Sand Sea to the southwest. Although the Kuiseb Riverbed possesses nutrient rich soil, which supplements plant development for a variety of species within close proximity to the river, few large plants are capable of establishing themselves farther from the river aside from !nara (Moser, 2001). Previous studies found that the !nara has several features that aid in its survival in the arid environment. !Nara possess extraordinarily long taproots between 30 to 100 meters in length with one of the world's largest xylem channels, allowing them to uptake water from underground water sources in the absence of rainfall and fog events (Henschel and Moser 2004; Klopatek and Stock 1994). Alongside their root systems, recent studies suggest that !nara can utilize moisture directly from the air by intercepting fog blowing inward from the Atlantic coast, by absorbing it through their stems and thorns (Gerber et al. 2017). In addition, !nara plants possess protective thorns as opposed to leaves, thereby reducing the flat surface area exposed to the hot desert sun and increasing moisture retention (Hebeler 2000).

Along with its remarkable physiological adaptations, the !nara plant possesses an impressive ability to efficiently collect sand grains amongst its roots and thorny vegetation; thereby forming large stable mounds of sand that build up over time. Previous studies have noted that hummock formation and the growth of a protective shield of branches assists in the survival of many Namib Desert species along the Kuiseb River (Hebeler 2000). !Nara plants provide shelter, protection, a nutritional food source, and thermoregulation for an assortment of desert-adapted species. For instance, blister beetles drink nectar from the plant's flowers, and gerbils and scorpions receive shelter in the hummock's shade or the stable sand bed to construct their burrows (Rosenzweig 1973). !Nara plants form "islands" of raised sand and produce a substantial amount of vegetative material, which provides structural complexity/stability and concentrated pockets of primary productivity and nutritious detritus in the surrounding desert landscape (Henschel and Moser 2004, Latorre et al. 2011). Considering the aridity of the Namib Desert (i.e. the area around the Kuiseb receives an annual average of merely 25mm of rain), lack of shade among the dunes, and the frequent movement of the soils due to high winds, the hummock-formation, shade-provision, and concentrated nutrient resources likely play a vital role in supporting greater biodiversity in the region, which has resulted in great interest among ecologists in developing a better understanding of the plant's life strategies.

Besides providing important habitats and functioning as an important nutritional resource for wildlife, the !nara plant also arouses interest because of its longstanding cultural relationship with the local desert-dwelling people known as the Topnaar. !Nara utilization by the Topnaar community has persisted for thousands of years. Archeologists discovered stashes of dried !nara seeds stored in caves alongside human tools out on the surrounding gravel plains dated to 8,000 years old (Dentliger 1977). Among the Nama people in Namibia, such as the Topnaar community, the !nara plant retains sociocultural and economic significance through the annual !nara melon harvest. A large proportion of rural community members continue to rely upon wild !nara

harvesting and processing for income generation, nutritional supplementation and other uses (Henschel et al. 2004). Since a single !nara plant produces between 50-500 melons, which are utilized for their pulp and seeds, Topnaar !nara harvesters obtain more than a quarter of their annual income from !nara sales, in addition to obtaining a large supplement to their dietary needs (Henschel et al. 2004).

Given the perceived sociocultural, socioeconomic, and ecological importance of !nara, the current paucity in scientific understanding of the biological and ecological interactions influencing their survival and productivity is of great concern. In the Kuiseb system, one of the largest perceived threats to !nara is herbivory by Topnaar livestock, which roam and forage freely along the Kuiseb River, often consuming !nara to obtain water. Historians believe that the Topnaar began concentrated herding of large livestock as early as the 1800s in the regions surrounding the Kuiseb, and livestock remain an important part of Topnaar livelihood to the present day (Van Damme & Den Eynden 1992, Herrick et al. 2016). Although !nara plants are browsed by wild herbivores, such as springbok, the relatively recent introduction of large livestock herds centered around the Kuiseb River creates increased herbivory pressure which may affect the growth and productivity of !nara plants in the region.

Since 2013, students from Dartmouth College have collaborated with the Gobabeb Research and Training Centre to conduct monitoring experiments on !nara hummocks along the Kuiseb River and along the dunes of the Namib Desert. Data collection with each subsequent year has provided a foundation for baseline information and informed the creation of long-term data collection methods to assess the impacts of herbivory in 2016. Using previous aggregate data and methodology, the purpose of this project is to understand how !nara responds to herbivory by livestock, as well as attaining some quantifiable measurements of biodiversity and soil temperature changes associated with !nara hummocks. Given the aforementioned socioecological importance of !nara, this provides some baseline information regarding how the plant might function a keystone species in the Namib Desert environment.

We identified two central research questions: 1) What are the effects of livestock herbivory on !nara plant growth and productivity? and 2) How may !nara hummocks function to sustain and maintain biodiversity? These two areas of interest interact because of the indirect effects of herbivory pressure, including vegetation and landscape trampling, on !nara vitality. We seek to quantify and to determine if any apparent relationships can be observed in the previous year's data collected from fenced and unfenced !nara hummocks, in relation to herbivory and !nara plant vitality. We sought to couple this analysis of previously-collected data with current data collection to examine associated hummock biodiversity, along with !nara's ability to function as an ecosystem engineer in changing soil properties (i.e. soil temperatures).

### ***Herbivory***

Herbivory is a biotic interaction that affects the distribution and reproductive success of plant species (Milchunas & Lauenroth 1993). In ecological theory, herbivory by vertebrate grazing is considered as a type of disturbance. Often, herbivory limits regrowth capability because substantial plant consumption reduces available nutrient resources for regrowth, which indirectly affects

resource allocation patterns for growth. For instance, a study of two Great Basin shrub species determined that *Artemisia tridentata* cannot maintain high vigor under heavy, experimentally simulated browsing by large mammals, which makes the plant more susceptible to other environmental pressures (Bilbrough 2003). The article cites several studies that show that flower production decreased after twig removal and prevented utilization of available nutrient resources, such as nitrogen and carbohydrate, for regrowth (Bilbrough 2003). So, allocation to flowering, or other forms of regrowth, in successive growing seasons may be affected by browsing, which ultimately affects the fitness of the plant.

Additionally, herbivory may have adverse effects on !nara productivity and vitality, particularly for its fruit production capacity. An early study on !nara herbivory discovered that !nara fruit production increased 5 to 10 times without donkey herbivory versus that of herbivore impacted !nara (Henschel et al., 2004). Disturbances like herbivory may increase plant diversity in communities by reducing competitive dominance among species and allowing rarer species to grow together (Rambo & Faeth 1999). Some herbivores may also shape their surrounding environment through vegetation utilization (i.e. breaking topsoil and tree), which increases structural habitat complexity and favors other organisms (Pringle 2008). For example, a long-term study in the Kenyan savanna demonstrated that Acacia-browsing elephants increased the spatial complexity and formed crevices in damaged trees, which were preferred by arboreal geckos (Pringle 2008). Furthermore, in response to herbivory, many plant species have developed adaptations to restrict their consumption by both vertebrates and invertebrates. Some species have evolved to deter herbivores with large structures, such as thorns and spines, which reduces the rate of consumption (Hanley et al. 2007). In some instances, by creating structural complexity via disturbance (i.e. browsing) but also placing intense stress on plants in other environments, total herbivore impacts on vegetation cannot be generalized across different ecosystems accurately. Thus, herbivory dynamics may be linked concurrently with !nara productivity and vitality.

### *Herbivory Research Objectives*

We used data collected over the past year to assess patterns in !Nara plant productivity and herbivory, aiming to complete initial data analysis and improve the current long-term monitoring methodology used by the Gobabeb staff. Our hypotheses were organized around a series of research questions as follows:

#### **!Nara Herbivory and Plant Vitality:**

- 1) *How does !Nara plant growth and reproduction differ between fenced (exclosure) vs. unfenced (control) !Nara hummocks and with increasing distance from the Kuiseb River?*
  - A. *How do exclusion of livestock herbivores and distance from the Kuiseb River impact average main !nara stem length, stem diameter, number of side branches, and plant height?*

**Hypothesis 1:** Herbivore exclusion promotes !Nara growth, and thus fenced !nara hummocks will exhibit greater mean stem length, stem diameter, number of side branches,

and plant height than unfenced !Nara hummocks.

**Hypothesis 2:** Due to the concentration of livestock associated with forage and livestock drinking stations near the Kuiseb River, non-fenced !nara hummocks will exhibit greater mean stem length, stem diameter, number of side branches, and stem height farther from the Kuiseb River than unfenced !nara hummocks nearer to the Kuiseb.

*B. How do herbivore exclusion and distance from the Kuiseb River impact the production of !nara flowers and fruits?*

**Hypothesis 3:** Due to a concentration of livestock near the Kuiseb river, and because herbivore exclusion promotes the ability of !nara to invest in reproductive growth, fenced !Nara hummocks further from the river will exhibit greater numbers of fruits and flowers than unfenced hummocks near the river.

*C. How does average proportion of live biomass differ with herbivore exclusion and distance from the Kuiseb River??*

**Hypothesis 4:** Herbivore exclusion reduces browsing and trampling pressure at !nara hummocks and thus promotes !Nara plant growth, which will result in fenced !nara hummocks and !nara hummocks farther from the Kuiseb River exhibiting greater mean proportion of live biomass than unfenced !nara hummocks and !nara hummocks closer to the Kuiseb River.

2) *Are the fences used in the !nara herbivory study effectively excluding livestock?*

**Hypothesis 5:** Significantly less dung will be seen within fenced !nara hummocks compared to unfenced hummocks.

3) *How does livestock activity differ at unfenced hummocks located at different distances from the Kuiseb River?*

**Hypothesis 6:** Hummock distance from the Kuiseb River will be negatively correlated with livestock dung density (a proxy for livestock activity).

4) *Is dung density an effective proxy for herbivore pressure and how does it relate to measures of plant growth?*

**Hypothesis 7:** Herbivore exclusion promotes !nara plant productivity, and thus livestock dung density will be negatively correlated with mean plant height and the proportion of live biomass.

## ***Biodiversity***

In the Namib Sand Sea ecosystem, !nara adaptations benefit a variety of organisms. Because of its importance in the desert food web, as well as in shaping the landscape by forming hummocks, the !nara plant has been proposed as a keystone species in some literature (Klopatek & Stock 1994). Keystone species are defined as “relatively low biomass species with a structuring role in their food webs”, which strongly influences the abundances and organization of other species and the intraspecific dynamics within an ecosystem (Libralato et al. 2006; Piraino et al., 2002). These species are crucial to maintain a diversity of ecological communities. Identifying keystone species aids the maintenance of ecosystem integrity and biological diversity in the face of exploitation and other disturbances and stress (Libralato et al. 2006; Naeem and Li, 1997; Tilman, 2000).

There are a variety of many reasons why !nara may be viewed as a keystone species in the literature. First, !nara hummocks are crucial habitat and nutritional sources for various Namib Desert species. !Nara hummocks directly provide habitats for burrowing organisms by stabilizing sands in a hummock. The spine-covered stems provide aboveground protection for other small animals including gerbils. The plant also provides a vital source of moisture, protein, and carbohydrates to a wide range of species, including *Oryx gazelle* (*Oryx*), *Canis mesomelas* (Black-Backed jackal), *Camponotus detritus* (Namib Desert dune ant), and *Meroles anchietae* (Shovel-Snouted lizard) (Henschel and Moser 2004).

Another defining characteristic of keystone species is that they are exceptional relative to other species in the community in terms of their impacts (Mills et al. 1993). If a plant is a keystone species, herbivory negatively affects its plant livelihood relative to the many species that come into contact with it. Particularly, herbivory pressure on keystone species can have a cascading effect on other taxa if they rely on the plant’s resources or services (Klopatek & Stock, 1992). While it provides a significant source of nutrition and moisture to many different organisms, and it forms microhabitats by trapping sand, !nara cannot be accurately labelled a keystone species (Klopatek & Stock 1994). This claim remains persistently unsubstantiated.

Additionally, some keystone species are disproportionately important in ecosystems due to their roles as ecosystem engineers. Ecosystem engineers are organisms that create, modify, and maintain habitats, which directly or indirectly control resource availability to other organisms (Jones et al. 1997). There exists a paucity of understanding ecosystem equilibrium variations creating habitats because of the interactions among a multitude of species, the food-web linkages across trophic levels, and the landscape modulations induced by biotic and abiotic interactions (Gilad et al. 2004). In other ecosystems, plants have been shown to create structure and habitat complexity in environments that lack spatial complexity such as the ocean (Teagle et al. 2017). Similar to !nara, kelp species create “three-dimensional habitat structure” which supports a variety of species (Teagle et al. 2017). More specifically, kelp increase the volume, heterogeneity, and complexity of habitat and provide direct food and shelter to many species (Teagle et al. 2017).

Even more so, ecosystem engineering varies resource availability which affects species distribution and abundance (Wright and Jones 2004). Different areas, especially the surrounding habitat that remains unmodified by the engineer, are influenced by the presence and absence of



ecosystem engineers that influence system productivity. Ecosystem engineers increase landscape-scale species richness by creating new habitats and allowing species that would otherwise be excluded to persist (Wright and Jones 2004). For instance, at low productivity, species richness is limited by either stress or disturbance, while at high productivity, patches tend to be dominated by one or a few competitively superior species (Grime 1979). Yet, when an ecosystem engineer increases productivity in a low-productivity system, stressful conditions are ameliorated and positively affect species richness, regardless of differences in taxonomic or trophic position of the engineers (Wright and Jones 2004). !Nara hummocks demonstrate this theory of primary productivity because they provide foundational support for interconnected species amidst the low productivity of the Namib Desert ecosystem.

Additionally, since ecosystem engineers disproportionately influence the availability of resources for other species through the creation, modification or maintenance of habitats, physical structures provide a refuge that acts as thermal buffers when ambient conditions are unfavorable (Pike et al. 2013). For instance, !nara hummocks provide accessible microhabitats, such as subterranean burrows, that provide “moderate and stable thermal environments to protect against often variable and extreme environmental conditions” (Pike et al. 2013). In this report, we analyze the diversity of organisms around !nara hummocks as well as the structure and abiotic changes created by hummock formation to assess !nara as a keystone species and ecosystem engineer.

### *Biodiversity Research Objectives*

We monitored !nara with the intent of clarifying the perception of it as a keystone species and its importance within the Namib Desert environment. !Nara plant productivity and herbivory, its hummock biodiversity, and niche construction were three categorical inquiries we sought to understand. We sought to monitor the aforementioned categories, which entailed assessing and improving the current long-term monitoring methodology used by the Gobabeb staff. Our objectives and rationale for our research questions and hypotheses are as followed:

#### **!Nara Hummock Biodiversity:**

- 1) *Does livestock herbivory, hummock distance from the Kuiseb River, and !nara hummock volume influence the abundance and richness of animal species associated with !Nara hummocks?*

**Hypothesis 8:** Due to greater !nara plant vitality associated with reduced herbivory, fenced !Nara hummocks and those closer to the river will support higher species abundance and richness

**Hypothesis 9:** Because herbivore pressure decreases with increasing distance from the Kuiseb, there will be less variance in total species abundance and Shannon-Weiner Index values between fenced and unfenced hummocks farther from the river compared to fenced and unfenced hummocks closer to the river. The Jaccard Index values will decrease with increasing distance from the Kuiseb River.

**Hypothesis 10:** Due to greater habitat heterogeneity near the Kuiseb River, !Nara hummocks close to the Kuiseb will exhibit significantly greater species richness than hummocks positioned farther away.

**Hypothesis 11:** Due to a larger capacity to provide microhabitats and food sources, !Nara hummocks with greater volume and surface area will support higher species total abundance and richness.

- 2) *Do !nara hummocks support greater total abundances and richness of animal species compared to other mound-forming desert structures (i.e. rock outcroppings, acacia hummocks, and dune grass hummocks)?*

**Hypothesis 12:** Because of increased structural complexity and their ability to form large mounds, !Nara hummocks will exhibit greater species richness and abundance on average compared to rock outcroppings, acacia hummocks, and dune grass hummocks.

- 3) *How may !nara function as an ecosystem engineer, changing its surrounding environment and affecting soil properties?*

**Hypothesis 13:** Due to shading and greater belowground organic biomass, mean soil temperatures will be significantly lower in !Nara hummocks compared to surrounding bare soils.

## **Methods**

### ***Previous Data and Research***

By the end of 2016, the Gobabeb Research and Training Centre staff installed metal wire fences at 10 female !nara plant hummocks, located at various distances from the Kuiseb River, to exclude donkeys, cattle, goats, and sheep from browsing at the hummocks. All 10 fenced !nara hummocks were paired with an unfenced hummock, which permitted herbivore access and functioned as a control for comparative analysis. In November 2016, members of the Dartmouth FSP selected these 10 hummocks to conduct an herbivory and productivity monitoring experiment.

Since March 2017, to assess potential changes on the 10 unfenced and 10 fenced !nara hummocks, the Gobabeb staff collected data on a monthly and bi-monthly basis to assess plant vitality associated with herbivory levels. For the monthly data assessment, dung collection, count, and removal occurred atop and surrounding both fenced and unfenced hummocks, as well as fruit and flower counts. In addition to the monthly data collection, bimonthly assessments for growth and herbivory occurred at 10, aluminum-tagged stems from 10 thicket bushes. For example, measurements included stem diameter at 10cm from branch tip, number of pairs of thorns, and number of side stems within 30cm from the branch tip, as well as counts for burrow sizes (i.e. small, medium and large).

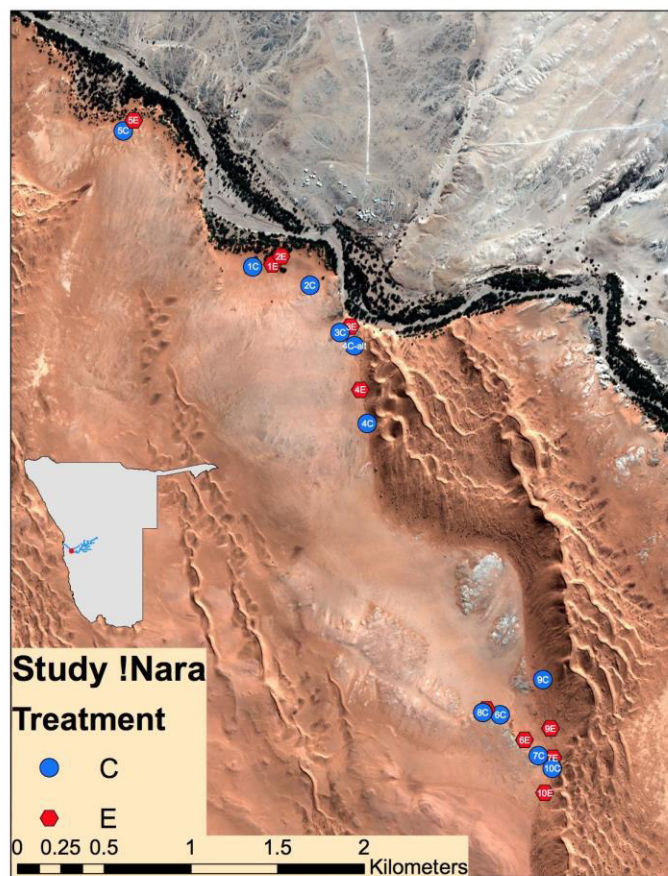
Data collection for this enclosure experiment began in March 2017. For our analysis of this past year's data, we examined plant productivity (i.e. fruit and flower counts) and plant growth (i.e. stem length and diameter) as proxies for herbivory impact. Also, we counted large herbivore dung as a proxy to examine herbivore pressure, as well as observed trends in herbivory levels corresponding to hummocks' distance from the Kuiseb River. These analyses allowed us to assess

trends in variables that could influence our hypotheses (i.e. herbivore distribution in proximity to the Kuiseb River) and to assess trends in !nara plant vitality after a year of livestock exclusion, which extends the work of Kittelberger et al. 2016.

### *Study Site Selection*

We conducted our experiment to assess plant productivity and hummock biodiversity at the ten previously selected pairs of !nara hummocks (10 fenced and 10 unfenced) selected by the 2016 Dartmouth FSP members. All hummocks were female in gender and paired with another hummock of similar size and distance from the Kuiseb River.

We randomly sampled the 10 pairs of sites to create 2 stratified groups, which each had five hummock pairs at varying distances from the Kuiseb River. We assessed the first sample, consisting of 5 hummock pairs during our first 2 days of data collection (November 1st, 2017 and November 2nd, 2017), and the second sample during our last 2 days of data collection (November 3rd, 2017 and November 4th, 2017). Thus, we collected data for all twenty !nara hummocks over the course of four days.



**Fig. 1.** – GIS map of the 20 !nara hummocks included in long-term herbivory monitoring as well as our biodiversity and temperature data collection at Gobabeb Research and Training Centre. “C” denotes a “control”, or unfenced hummock, while “E” denotes an “exclusion”, or a fenced hummock.

### ***Bi-monthly Protocol Trials***

Before conducting our data collection, we assisted a Gobabeb staff member, who currently conducts the monthly and bimonthly herbivory data collection protocols, to collect data from !nara hummocks 2E (fenced/fenced) and 2C (unfenced/unfenced) by using existing protocols for assessing !nara hummock herbivory and productivity, which Gobabeb staff has surveyed since March 2017.

After experiencing protocol methodology firsthand, we assessed the current problems with the protocols and brainstormed improvements for data collection methods. Following our field session, we considered revisions that may improve data collection efficiency, its spreadsheet coherence, and its accuracy of results.

### ***Experimental Pilot Phase***

Once we devised our initial research questions and proposed experiments for biodiversity assessment, we conducted pilot experiments to ensure that our methods would provide useful and meaningful results.

In our first trial, on the afternoon of October 29th, we deployed Sherman live animal traps, drift fences, and pitfall traps on hummocks 2E (fenced hummock) and 2C (control hummock). We conducted the following pilot experiment on each hummock as follows: we deployed fifteen Sherman traps containing a small ball of bait, composed of bread crumbs, peanut butter, and fish paste, to attract small omnivorous and carnivorous rodents. On one side of the hummock, which we chose arbitrarily, we deployed a drift fence parallel to the hummock's slope, with one pitfall at the bottom of the fence, 2 pitfalls on either side of the fence's midpoint, and one pitfall at the top of the fence. Using a small trowel, we dug a hole large enough to place the pitfall within the hummock's soil and to make it level with the soil surface, such that could catch ground-dwelling insects and other small terrestrial animals. We deployed the same arrangement of a drift fence and pitfalls on the opposite side of the hummock, yet aligned them perpendicular to the hummock's slope, to examine the possible effect of the drift fence angle on catch success. We also deployed 3 Sherman live traps at an acacia hummock positioned in between plots 2E and 2C, to see if any activity could be recorded in this alternate habitat structure. On the morning of October 30th, after collecting and assessing the pitfall and live trap data from this pilot experiment, we modified our pilot experiment to exclude live traps after receiving a low catch rate. For example, despite deploying a total of 33 traps, a single hairy-footed gerbil was captured.

On the afternoon of October 30th, we conducted a second pilot experiment to assess and to finalize our methods for data collection. We conducted the following pilot experiment on both hummocks 2E and 2C as follows: given the abundance of tracks we observed the morning following our initial pilot study, and, given that the live traps or pitfall traps did not capture much nighttime activity, we decided and used a broom to sweep standardized-sized transect to observe hummock animal

communities. The following morning, we identified these animal tracks which the transects “captured”.

On one side of hummock 2E and 2C, we swept a smooth surface parallel to the right and left of the drift fence with widths of 33 centimeters (cm) and lengths of 3 meters (m), totaling an area of 1-square meter each. We swept an additional transect of equal width and length perpendicular to the drift fence. On the opposite embankment of both 2E and 2C, we deployed 3 sweep transects in the same alignment (parallel to the right and left sides of the barrier fence and perpendicular at the hummock’s base) as 66cm long and 3m wide, for a total area of 2-square meter. With the different measurement metrics, this second deployment allowed us to assess the extent to which sweep transect width affects the number and diversity of animals whose tracks are “captured”. The drift fence and pitfall pairings remained in their previous alignments.

The following morning, we observed easily identifiable tracks within the sweep transects, as well as determined that the species number and diversity captured was not significantly different between the 1-square meter and 2-square meter transects. However, because the greater width of the 2-square meter transects made tracks more easily identifiable, we decided to sweep all future transects to 2-square meters. Additionally, after analyzing pitfall traps from our 2-day pilot data, we decided to orient all subsequent barriers parallel to the hummock slope because they yielded significantly greater capture rates compared to barrier fences placed perpendicularly to the slope.

### ***Stem Length, Stem Diameter, and Number of Side Branches***

To distinguish what, if any, effects livestock herbivory has on !nara growth rate, we calculated mean values of stem length, stem diameter, and number of side branches, utilizing data collected bimonthly from 10 !nara stems at each fenced and unfenced hummock within the long term herbivory study. Stem length had been collected from 10 branch tips, either on ten different marked !nara bushes at a hummock or on the same bush, depending on the size of the hummock. After marking ten stems 10 cm from their tips at the beginning of the study, a bimonthly measurement was recorded from the previous mark to the stem tip, and then remarked at 10 cm from the new stem tip. Stem diameter had been collected in a similar manner at the ten stem data recording locations, measured monthly using a caliper at the mark placed at 10cm two months prior. The number of side branches had been collected from these same ten stems, by counting the branch points from the top 30 cm of stem length.

### ***Mean Plant Height***

After analyzing 2017’s !nara plant vitality data and completing trial runs of the current herbivory monitoring protocols, we decided that the current methods of assessing stem growth (i.e. measuring the length of the stem tip from the previous month’s 10cm mark) did not provide a clear picture as to how plant growth rate differs between fenced and unfenced !nara hummocks. To test an alternative method of assessing the overall growth of !nara at a given hummock, we utilized a height measurement protocol developed by Dartmouth in 2016 for a student project focusing upon herbivory pressure. To calculate mean plant height, we measured heights among 6 to 10 previously-marked !nara plants (depending on the size of the hummock) from the base of the

live plant to the top of the bush, determined as the level at which a clipboard placed on top of the bush would compress the stems.

### ***Proportion of Live versus Dead Biomass***

To supplement our assessment of herbivory impacts on !nara vitality, we also utilized a DJI Phantom 4 Advanced drone, equipped with a 20 megapixel Sony Sensor, to map the proportion of live and dead !nara at both fenced and unfenced hummocks. For each hummock, dozens to hundreds of nadir and oblique geotagged photographs were analyzed using a SfM-MVS workflow in Agisoft Photoscan Pro (Carrivick et al. 2016). A georeferenced orthomosaic was then imported into ArcMap (v 10.4.1) where a Maximum Likelihood Classification was run using a user generated signature file to generate a ‘dead !nara’, ‘live !nara’, and ‘sand (or other)’ landcover map for each hummock. Finally, to calculate proportions of live and dead biomass, we divided the surface area of live and dead !nara respectively by the sum of live and dead !nara surface area coverage on the hummock (Appendix A).

### ***!Nara Live Volume, Fruit and Flower Counts***

To parameterize the fruit and flower production by hummock size, we calculated the volume of live !nara biomass utilizing the mean plant heights for each hummock, which we then multiplied by the live biomass surface area, as calculated from the UAV images utilizing ArcMap software. Also, we analyzed the total number of small fruits with flowers and open flowers from 2017’s bimonthly data collection to assess the impact of livestock herbivory on reproduction. In our analyses, we counted the cumulative number of fruits with flowers and open flowers for the year at each hummock, and then divided this number by the live !nara volume, which was calculated by the method cited above (Appendix A).

### ***Pitfall Trap and Drift Fence Set-Up***

On the afternoon of October 31st, we randomly selected our first stratified random sample and deployed drift fences and pitfalls at hummock pairs 3, 4, 6, 8, and 9. After modifying our experiments following our second pilot phase, we conducted the following procedure at each of the 10 hummocks: we deployed a drift fence on both the eastern and western embankments that was parallel to the hummock’s slope. We installed fences on the eastern and western slopes because the sun’s arc affects daytime length and exposure on the hummocks and diurnal, desert-dwelling species. Fence length was recorded using a fifty-meter tape measure. We established this measurement to act as a proxy for our catch effort, which the meters of fencing expressed. Next, we deployed 5.5cm diameter pitfalls located at the top, bottom, and both midpoints of each drift fence.

On the morning of November 2nd, we collected the drift fences and pitfalls installed at the 10 hummocks of our first stratified random sample. On the afternoon of November 2nd, we repeated this procedure for our second stratified random sample on hummock pairs 1, 2, 5, 7, and 10. On the morning of November 4th, we collected the drift fences and pitfalls that we installed at the 10 hummocks of our second stratified random sample.

### ***Track Count Transects***

On the afternoon of October 31st, we swept 2-square meter transects at the five hummock pairs of our first stratified random sample using the following procedure: on both the eastern and western embankments of the hummock, we used a broom to sweep transects 66cm wide and 3m long, for a total of 2-square meters each. We swept transects parallel to either side of the drift fence, as well as swept a transect perpendicular to the drift fence that was located at the base of the hummock. On the afternoon of November 2nd, we repeated this procedure at the five hummock pairs of our second stratified random sample.

On the afternoon of November 3rd, we swept a single transect with a 66cm width and 3m length at microhabitats within fifty-meters of each of the 10 hummocks selected for our second stratified random sample. We selected the aforementioned microhabitats for their similar mound-forming capabilities and their close proximity to the Inara hummocks. These microhabitats included rock outcroppings, Acacia hummocks, and dune grass hummocks. At each of these transects, we used a Garmin Oregon 700 GPS to tag their waypoint coordinates and recorded their location.

### ***I-buttons and Hobo Temperature Data Loggers***

On the afternoon of October 31st, we deployed twenty pairs of I-button and Hobo temperature data loggers at all twenty hummocks in our aggregate sample. We conducted the following procedure at each hummock: we attached a uniquely-numbered I-button or Hobo logger to a half-meter length stick, and we labeled the stick to match the loggers' numerical identification. Additionally, we marked the stick 5cm above the taped data logger to identify the depth of its placement it within the hummocks' soil. We placed one data logger 5-cm deep within the soil atop and on the flattest point of the hummock, so it received sunlight exposure throughout the day. The logger was placed next to a live plant, but not directly adjacent to a stem or any dead plant material. We placed another data logger at an equal depth within the soil, 20m away from the base of the hummock, which as located on the flattest, least shaded ground. On the morning of November 4th, we collected the forty data loggers that we had deployed at the twenty hummocks of our aggregate sample.

### ***Biodiversity Data Collection***

On the morning and afternoon of November 1st and the morning of November 2nd, we visited the five hummock pairs of our first stratified random sample to assess hummock biodiversity on our transect sweeps and pitfall traps. Subsequently, on the morning and afternoon of November 3rd and the morning of November 4th, we visited the five hummock pairs from our second stratified random sample. On the morning of November 4th, we visited the 10 alternative microhabitats (i.e. rock outcropping, dune grass, and Acacia hummock) located near each of the randomly selected hummock pairs within our second stratified random sample. At approximately 8:00 AM each morning, we collected "night activity" data and "daytime activity" data at approximately 4:00 PM each afternoon.

To assess pitfall traps, we used a large spoon and/or a trowel to scoop invertebrates (i.e. insects, scorpions, spiders, etc.) or lizards out of the pitfalls, carefully sifting through sand in case species burrowed inside the pitfalls. To assess sweep transects, we counted the number of species' track crossings (i.e. a distinct entry and exit) within each transect. With existing track identification knowledge provided from guidebooks and a Gobabeb researcher, Eugene Marais, we categorized observed tracks into: lizard, gerbil, caterpillar, beetle, spider/scorpion, bird, second bird, cape fox, jackal, !nara cricket, mound, sidewinding snake, skink, and unknown. While visiting all twenty !nara hummocks of our aggregate sample, we walked the length of the hummock and recorded each observed animal species. Also, after each visit to a hummock, we re-swept all transects and cleared the contents of all pitfalls.

### ***Biodiversity Indices***

*Abundance:* To calculate an overall species abundance at each hummock, we summed the total number of individuals caught in pitfall traps at the hummock to the total number of animal crossings at the six track sweeps. Note: This calculation was made from compiling individual organism counts (from pitfalls) and a proxy for animal abundance, the number of distinct crossings (defined as an animal entering and exiting) at a given track sweep.

*Richness:* To calculate overall species richness, we counted the number of different taxa found within the pitfall traps and those crossing the track sweeps at each hummock. This calculation was made from a number of different categories represented in the data, as organisms in the pitfall traps could be identified to the species level, whereas tracks could only be identified to species groups (i.e. gerbils, lizards, etc.).

*Shannon-Wiener Index:* In an attempt to combine the above parameters (species richness and abundance) we calculated a Shannon-Wiener biodiversity index value (Magurran 2004) at each hummock, for pitfall catches and track data separately, utilizing the following equation:

$$H' = - \sum_{i=1}^R p_i \ln p_i$$

To have an overall representation of biodiversity, we combined the indices calculated from the data collected via the two sampling methods (pitfalls and track sweeps) and standardized them by using the following equation to generate a combined Shannon-Wiener index:

$$\frac{H'_{\text{pitfall}_i} + H'_{\text{tracks}_i}}{H'_{\text{pitfall}_x} + H'_{\text{tracks}_x}} = H'_{\text{TOTAL FOR EACH HUMMOCK}}$$

Note:  $i = 1-20$  hummocks



*Jaccard Evenness Value:* We were also able to examine how similar the two hummocks within a pair were across the entire experiment, utilizing the following formula:

$$J = \frac{S_c}{S_a + S_b + S_c}$$

where  $S_a$ = number of species unique to sample a (fenced hummock),  $S_b$ = number of species unique to sample b (unfenced hummock), and  $S_c$ = number of species shared between the two samples (fenced and unfenced hummocks).

### ***Pollinator Collection Bowls***

To gather additional biodiversity data beyond those collected from the pitfall traps (i.e. ground-dwelling insect species) and the track-sweep transects (i.e. terrestrial hummock species), we conducted a pilot survey of Inara pollinator species. The collection bowls are also known as bee bowls.

We placed 5cm-diameter, white bee bowls atop of each fenced and control hummock at 11:30 AM in an unobstructed area and collected them after five hours. A solution of 5% propylene glycol and a drop of dish soap in water filled each bowl. Next, we placed the bowls on the eastern slope, which was away from the prevailing westward wind. Where possible, we identified each pollinator down to its species, or to its lowest taxonomic designation known from the taxonomy of the region.

### ***Data Analysis***

To analyze our hypotheses, we conducted various statistical tests using JMP Pro 13 (JMP Pro 2017). We used ANOVA to examine the effects of treatment (fenced versus unfenced ) and block (near vs. far ) on Shannon-Wiener indices, species abundance and richness, livestock dung density, mean number of branches, stem diameter, stem length, open flowers, small fruits with flowers, and mean plant height (Table 1).

We used linear regression analysis to test for relationships between livestock dung density vs. % live biomass mean plant height. We also utilized t-tests to look for statistically significant differences in soil temperatures at 5cm depth between the top of Inara hummocks and the surrounding flat ground 20 meters from the hummock base, as well as to compare Jaccard Index values between hummocks.

**Table 1.** Hummock location and treatment variables. See Appendix B for other variables used in data analysis.

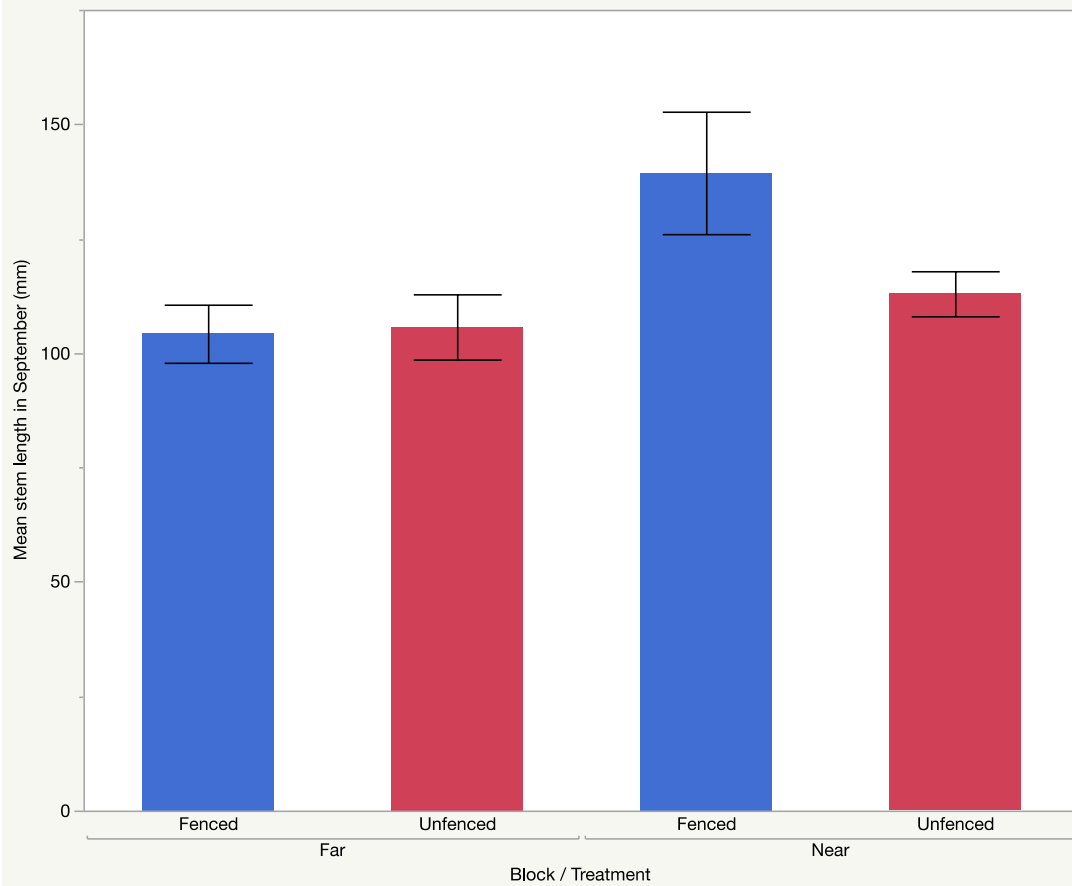
TAG	Latitude	Longitude	Treatment	Block
1E	-23.5644	15.0361	Fenced	Near
1C	-23.564515	15.034981	Unfenced	Near
2E	-23.5634	15.0366	Fenced	Near
2C	-23.5655	15.0382	Unfenced	Near
3E	-23.56766	15.04049	Fenced	Near
3C	-23.56796	15.03991	Unfenced	Near
4E	-23.57096	15.041061	Fenced	Near
4C	-23.572714	15.041466	Unfenced	Near
5E	-23.55741	15.02765	Fenced	Near
5C	-23.55685	15.02824	Unfenced	Near
6E	-23.58928	15.05035	Fenced	Far
6C	-23.587958	15.048973	Unfenced	Far
7E	-23.59021	15.05194	Fenced	Far
7C	-23.5901	15.05114	Unfenced	Far
8E	-23.587668	15.048183	Fenced	Far
8C	-23.587848	15.047976	Unfenced	Far
9E	-23.58867	15.05181	Fenced	Far
9C	-23.58611	15.05138	Unfenced	Far
10E	-23.59204	15.0515	Fenced	Far
10C	-23.59077	15.05191	Unfenced	Far
4C-alt	-23.56866	15.04072	Unfenced	Near

## **Results**

### ***Herbivory Results***

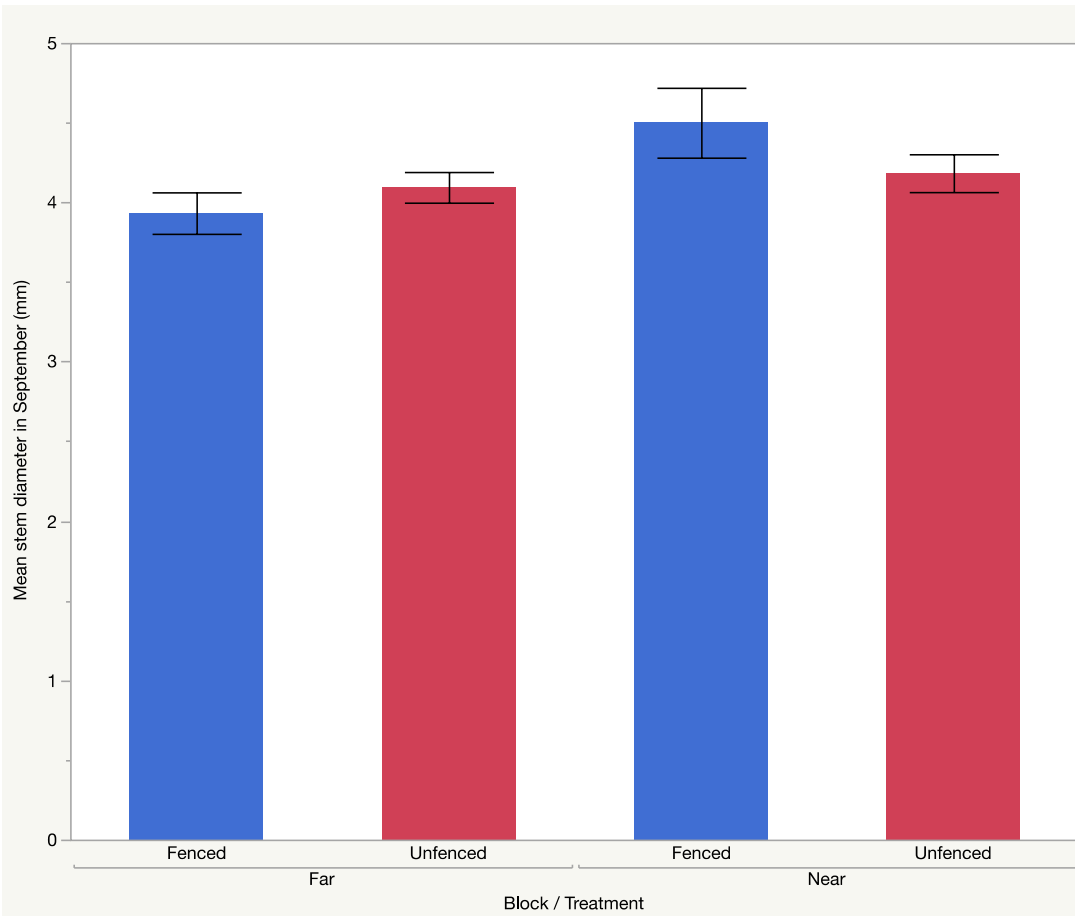
To assess the impact of herbivory pressure on plant growth in relation to treatment type and distance from the Kuiseb River, we compared the variables of !Nara mean stem length, stem diameter, number of side branches, and plant height, used as proxies for plant growth, between fenced and unfenced !Nara hummocks, and between hummocks near and from the river.

In comparing mean stem length and diameter, we excluded one data point from hummock 1C that was an obvious outlier due to data entry error. We observed a significant relationship between mean stem length and distance from the river ( $n = 20$ ,  $F = 6.1031$ ,  $df = 1$ ,  $p = 0.0251$ ) (Fig. 2), but mean stem length did not vary by treatment type ( $n = 20$ ,  $F = 2.1082$ ,  $df = 1$ ,  $p = 0.1658$ ).



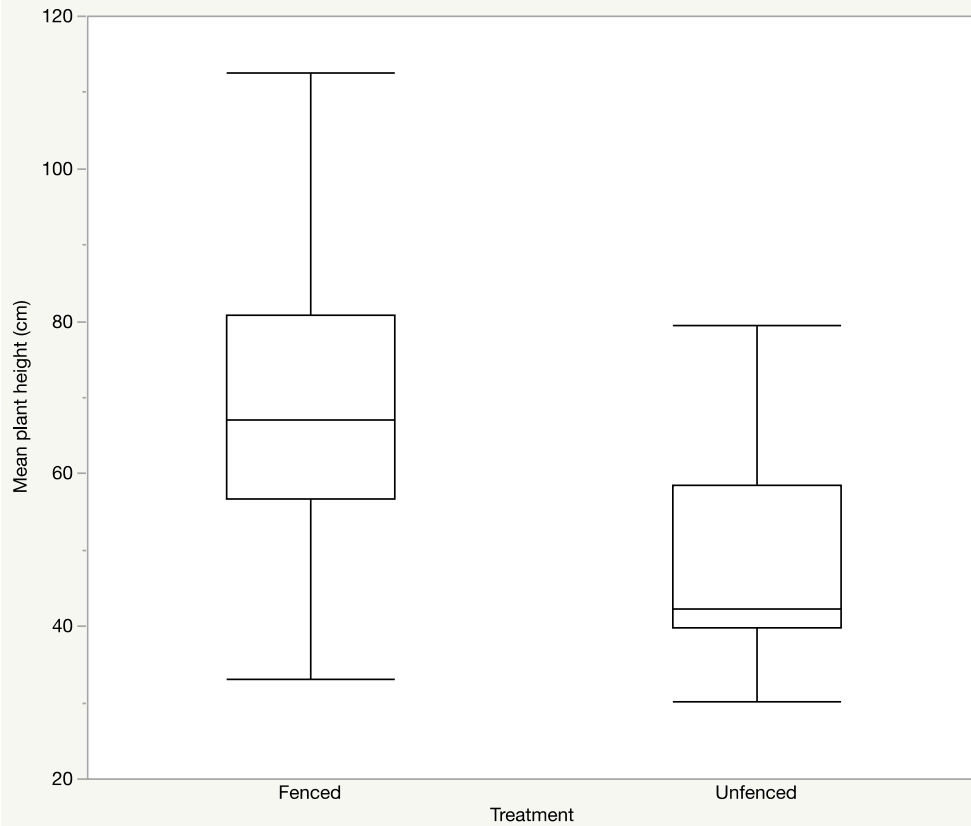
**Figure 2.** !Nara mean stem length varied between hummocks positioned near ( $\bar{x} = 126.18 \pm 6.07$  mm) and far ( $\bar{x} = 104.98 \pm 6.07$  mm) from the river. Fenced !Nara hummocks near the river exhibited the greatest mean stem length ( $\bar{x} = 139.38 \pm 13.38$  mm).

Mean stem diameter decreased with distance from the river ( $n = 21$ ,  $F = 6.08$ ,  $df = 1$ ,  $p = 0.0246$ ), but did not vary by treatment type ( $n = 21$ ,  $F = 0.0171$ ,  $df = 1$ ,  $p = 0.8976$ ) (**Fig. 3**). The mean number of side branches did not vary by treatment type ( $n = 21$ ,  $F = 0.2658$ ,  $df = 1$ ,  $p = 0.6128$ ) or with distance from the river ( $n = 21$ ,  $F = 0.2064$ ,  $df = 1$ ,  $p = 0.6553$ ).



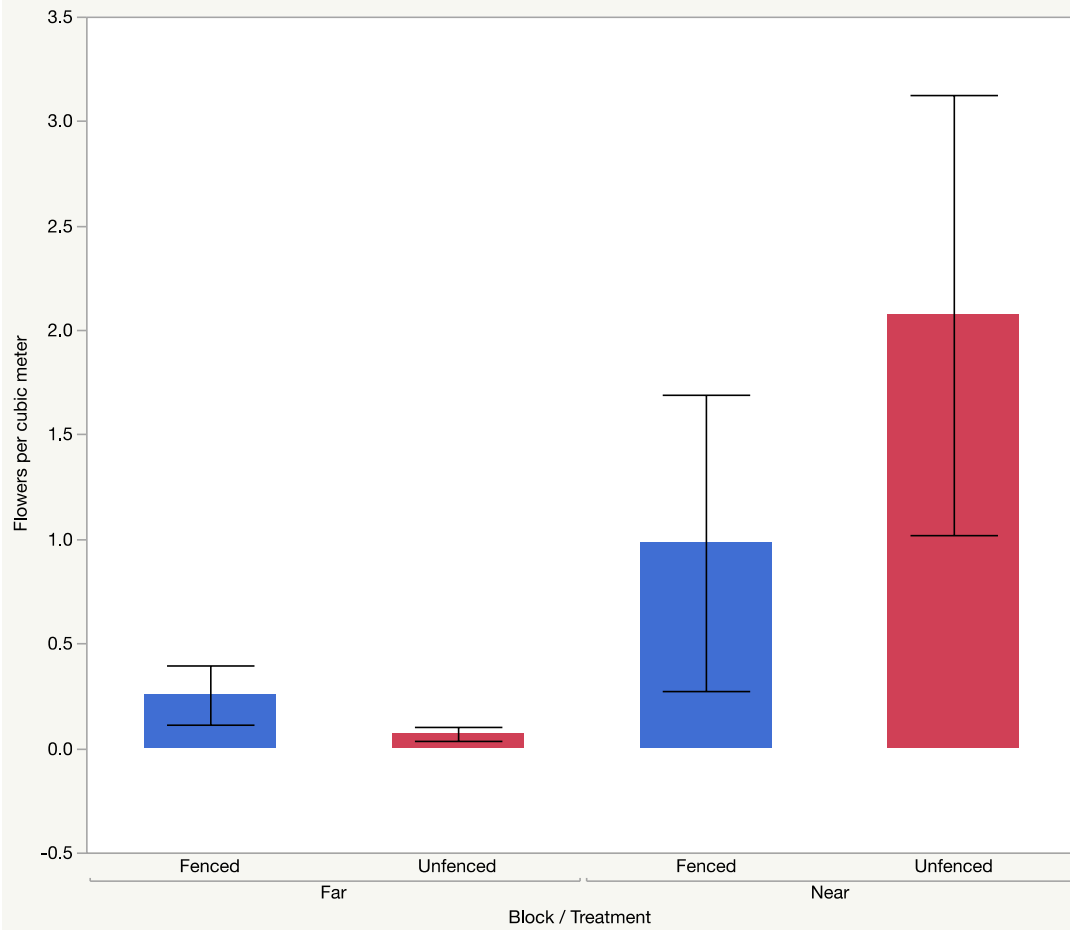
**Figure 3.** Mean !Nara stem diameter (mm) varied between hummocks positioned near ( $\bar{x} = 4.39 \pm 0.11$  mm) and far ( $\bar{x} = 4.01 \pm 0.11$  mm) from the river. Fenced !Nara hummocks near the river exhibited the greatest mean stem diameter ( $\bar{x} = 4.5 \pm 0.22$  mm).

Mean plant height is significantly greater in fenced hummocks ( $n= 21$ ,  $F= 4.5776$ ,  $df= 1$ ,  $p = 0.0472$ ) (Fig. 4), but does not vary with distance from the river ( $n= 21$ ,  $F= 0.00$ ,  $df= 1$ ,  $p = 0.99$ ).



**Figure 4.** Fenced !Nara hummocks exhibited significantly greater mean plant height ( $\bar{x} = 69.01 \pm 6.78$  cm) than unfenced ( $\bar{x} = 50.54 \pm 4.70$ cm) hummocks.

There was a significant relationship between the production of !Nara flowers and hummock distance from the river ( $n = 20$ ,  $F = 4.5718$ ,  $df = 1$ ,  $p = 0.0483^*$ ) (Fig 5), yet the production of !Nara flowers did not vary with treatment type ( $n = 20$ ,  $F = 0.5006$ ,  $df = 1$ ,  $p = 0.4894$ ). The production of small !Nara fruits with flowers did not vary with treatment type ( $n = 20$ ,  $F = 1.2915$ ,  $df = 1$ ,  $p = 0.2725$ ) or distance from the river ( $n = 20$ ,  $F = 0.0152$ ,  $df = 1$ ,  $p = 0.9034$ ).



**Figure 5.** Cumulative !Nara flower production per cubic meter varied between hummocks positioned near ( $\bar{x} = 1.53 \pm 0.45$ ) and far ( $\bar{x} = 0.16 \pm 0.45$ ) from the river. Unfenced !Nara hummocks near the river exhibited the greatest cumulative flower production ( $\bar{x} = 2.072 \pm 2.35$ ).

Proportion of live biomass did not vary with treatment ( $n = 20$ ,  $F = 1.4866$ ,  $df = 1$ ,  $p = 0.2404$ ) or distance from the river ( $n = 20$ ,  $F = 1.0758$ ,  $df = 1$ ,  $p = 0.3151$ ). Additionally, the proportion of dead biomass did not vary with treatment ( $n = 20$ ,  $F = 1.4866$ ,  $df = 1$ ,  $p = 0.2404$ ) or distance from the river ( $n = 20$ ,  $F = 1.0758$ ,  $df = 1$ ,  $p = 0.3151$ ).

In comparing the cumulative number of livestock dung, we excluded an obvious outlying observation in hummock 1C. Gobabeb staff members collected no livestock dung from fenced !Nara hummocks in the month of September 2017, which indicates and represents the effectiveness of the livestock fences in excluding herbivore activity (e.g. dung). Dung density did not vary with distance from the river ( $n = 10$ ,  $F = 0.2458$ ,  $df = 1$ ,  $p = 0.6268$ ). Additionally, there was no significance in the relationship between dung density and either mean plant height ( $n = 10$ ,  $F = 1.7357$ ,  $df = 8$ ,  $p = 0.2242$ ) or the proportion of live biomass ( $n = 9$ ,  $F = 0.0349$ ,  $df = 7$ ,  $p = 0.8570$ ).

## ***Biodiversity***

We evaluated the biodiversity in the fenced and unfenced hummocks, in relation to those near to and far from the river. We used pitfall traps to catch small animals and sweep transects to count tracks. We assessed abundance, richness, relative biodiversity (Shannon-Wiener index) and Evenness (Jaccard index). We predicted that hummocks closer to the river would have higher diversity due to the presence of riparian species. We also predicted that fenced hummocks would have higher diversity due to lower herbivore impact on animal habitat in the hummock.

There was no significant difference between track, pitfall, and combined abundance between near and far hummocks or fenced and unfenced hummocks (Table 1). There was a marginally, significant positive effect on distance to the river to the number of taxa observed in tracks but not on the number of taxa observed in the pitfalls. More taxa were observed in the hummocks near the river. There was also marginally, significant positive effect of distance to the river and treatment on the Shannon-Wiener index for tracks but the overall ANOVA was not significant. There was no significant effect of treatment or distance to the river on the Shannon-Wiener index for pitfalls and the combined Shannon-Wiener index (Table 1). We initially assumed that the fenced hummocks would have higher biodiversity in terms of richness and abundance, but the richness, Shannon-Weiner indices, and abundance results do not support that hypothesis. The Jaccard index for tracks, which measures similarities between pairs, was higher for pairs of hummocks near to the river ( $t=1.885981$ ,  $df$  8,  $p=0.048$ ). There was no difference between pairs of Jaccard index for pitfalls.

**Table 1.** Results from ANOVA tests of abundance, # of taxa (richness), and Shannon indices with treatment and distance from the Kuiseb River (near vs. far block). There was no significant difference in abundance, # of taxa, and Shannon indices in near and far hummocks or fenced and unfenced hummocks. However, there was a marginally significant difference in # of track taxa between near and far hummocks. The near hummocks had higher mean track taxa ( $7.2 \pm 0.38$ ) than the far hummocks ( $5.8 \pm 0.38$ ) There was also a marginally significant difference in the Shannon indices for tracks between near and far hummocks as well as fenced vs. unfenced hummocks. However, the fenced and near hummocks had only slightly higher mean Shannon indices for tracks ( $1.3603 \pm 0.077$ ;  $1.357 \pm 0.077$ ) than the unfenced and far hummocks ( $1.133 \pm 0.077$ ;  $1.135 \pm 0.077$ ).

Variable	N	df	F	P	Treatment P	Block P
Track abundance	20	3,19	0.5696	0.6430		
Pitfall abundance	20	3,19	1.0003	0.4181		
Combined abundance	20	3,19	1.8181	0.1845		
# of taxa (tracks)	20	3,19	2.271	0.0795*		0.0194
# of taxa (pitfalls)	20	3,19	1.4667	0.2611		
Shannon index (tracks)	20	3,19	2.7685	0.0756	0.0563*	0.0613*
Shannon index (pitfalls)	20	3,19	0.2694	0.8465		
Shannon index combined	20	3,19	2.2822	0.1182		

We found a significant relationship between the combined (pitfalls and tracks) Shannon-Wiener indices and log transformed live volume ( $N=20$ ,  $R^2=0.2163$   $p=0.0388$ ) but not between the track

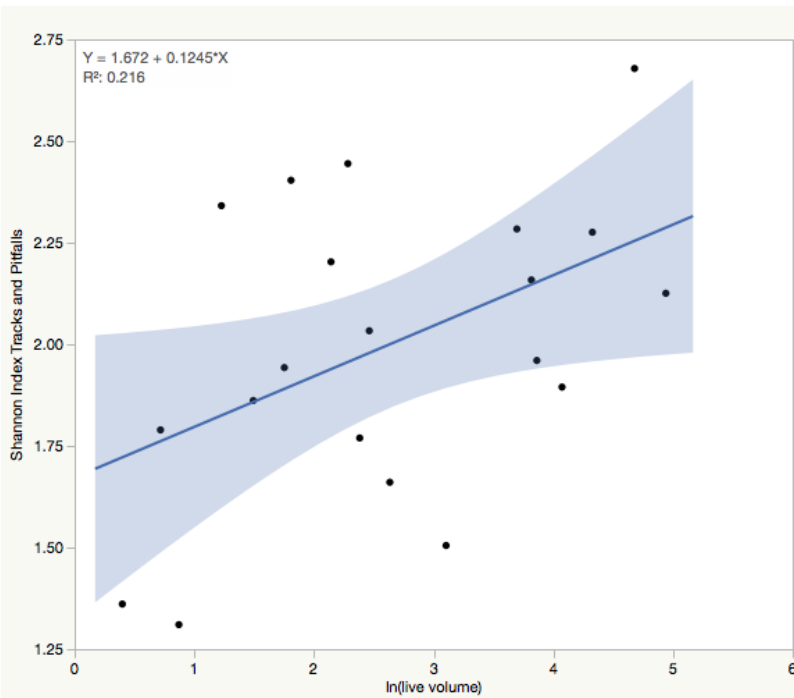


and pitfalls Shannon indices and live volume (Table 2). The combined Shannon index was positively correlated with live volume (Fig. 5). There was also a significant relationship between the tracks and combined abundance and the log transformed live volume (Table 2). For both combined and tracks abundance, there was a positive correlation with log transformed live volume (Fig. 6, Fig. 7). However, there was not a significant relationship between the number of taxa observed from the pitfalls and tracks and the log transformed live volume (Table 2). Our results showed that most measures of biodiversity (Shannon-Wiener indices and abundance) were higher in larger hummocks which supported our initial assumptions (Hypothesis 11). The only exception was the number of track and pitfall taxa observed.

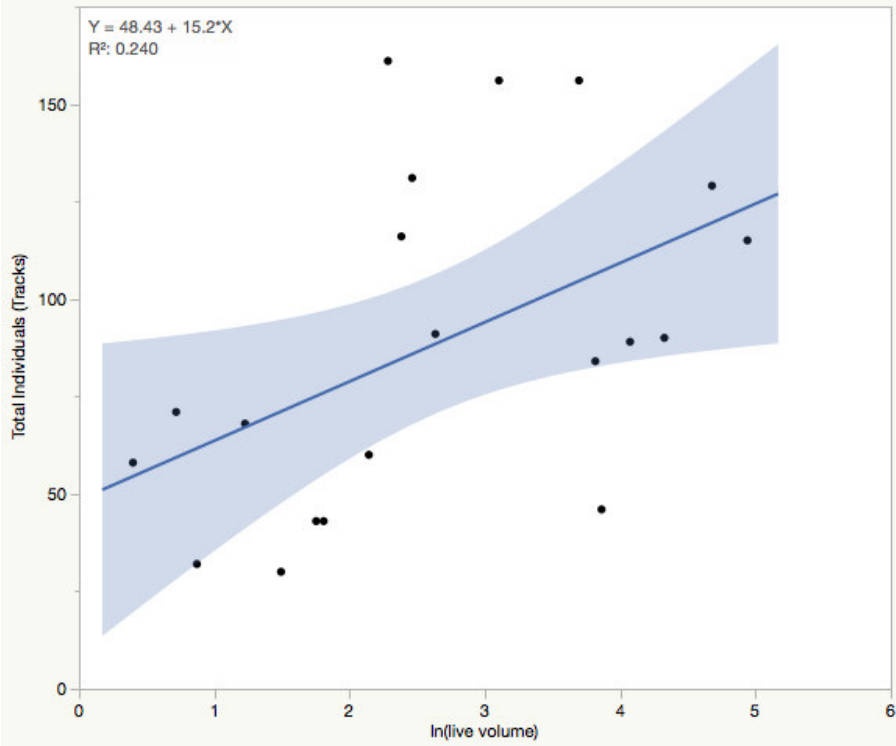
**Table 2.** Results from regressions of abundance, # of taxa (richness), and Shannon indices in relation to log transformed live volume (m<sup>3</sup>) indicate that there was a significant relation between combined Shannon indices, pitfall abundance, and combined abundance with increased log transformed volume. Larger hummocks in terms of volume had higher combined Shannon index values, track abundance, and combined abundance.

Variable	N	df	R <sup>2</sup>	P
Shannon index (combined) vs. ln (Live volume)	20	19	0.2163	0.0388*
Shannon index (tracks) vs. ln (Live volume)	20	19	0.0712	0.2553
Shannon index (pitfall) vs. ln(Live volume)	20	19	0.0868	0.2072
# of taxa (tracks) vs. ln (Live volume)	20	19	0.1604	0.0801
# of taxa (pitfalls) vs ln(Live volume)	20	19	0.2072	0.0437
Abundance (tracks) vs. ln(Live volume)	20	19	0.2399	0.0284*

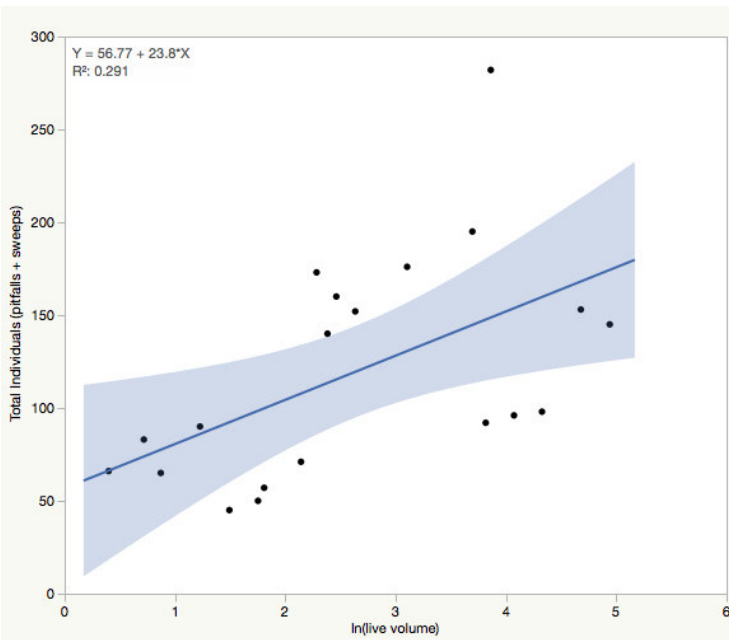
Abundance (pitfalls) vs. ln(Live volume)	20	19	0.0553	0.318
Combined abundance vs. ln(Live volume)	20	19	0.2907	0.0142*



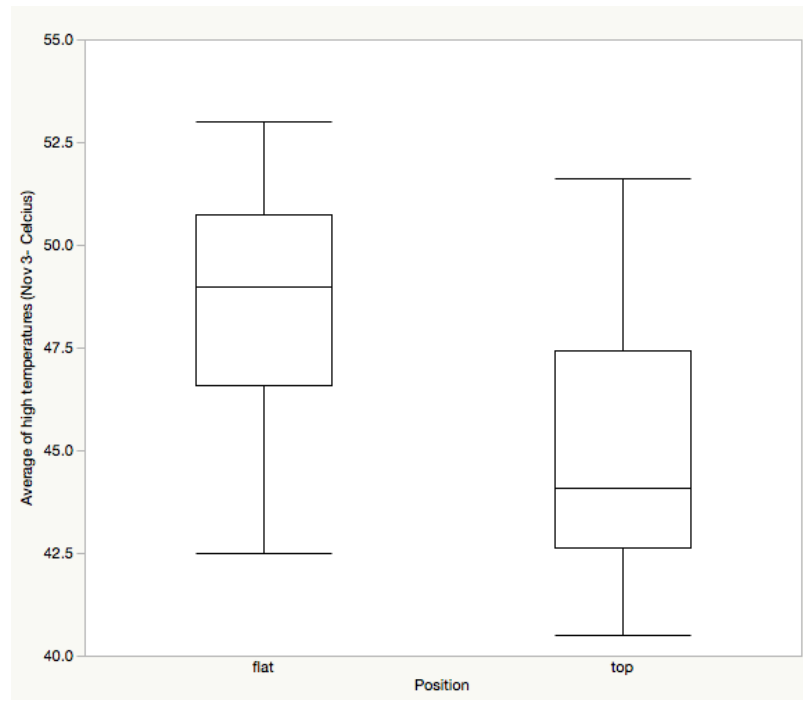
**Fig. 6.** Linear regression of log transformed live volume ( $m^3$ ) in relation to the combined Shannon-Weiner index for all !nara hummocks showed that hummocks with higher log transformed volume had higher combined Shannon indices.



**Fig. 7.** Linear regression of log transformed live volume in relation to the animal abundance observed from track sweep data for all Inara hummocks indicated that hummocks with higher log transformed volume had higher track abundance.



**Fig. 8.** Linear regression of log transformed live volume in relation to the combine abundance (pitfalls and tracks) for all !nara hummocks indicated that larger hummocks have higher combined abundance



**Fig. 9.** T-test results analyzing temperature at 5 cm depth between the top of !nara hummock and bare soil 20 m away from hummock base show that mean temperatures at 5cm depth for the hottest 30 minutes of the day are significantly lower on top of !nara hummocks compared to surrounding soils.

## Discussion

### *!Nara Plant Vitality and Herbivory Discussion*

To establish the effects of herbivory on !nara plant vitality, we first examined whether proxies of plant growth (i.e. mean stem length, stem diameter and the number of side branches) differed between fenced and unfenced hummocks. Our results indicate that for the first three proxies of plant growth assessed in the monthly and bimonthly data collection (mean stem length, stem diameter, and the number of side branches), no significant difference exists between fenced and unfenced !nara hummocks. Although these findings contradict our first hypothesis, which anticipated greater plant growth measurements in fenced hummocks, the results from our measurements taken on average plant height indicate that fenced !nara plants exhibit significantly greater heights than !nara exposed to livestock herbivore pressures. These findings indicate that the current herbivory monitoring protocol may not be providing the most accurate metric to assess herbivory impacts, or that a sufficient amount of time has not passed since fence installation for significant effects on current metrics of plant growth to be observed. On the other hand, because we did not observe significantly greater mean stem length, diameter, and number of side branches in unfenced hummocks, our data also does not suggest the existence of an alternative relationship,

whereby herbivory may stimulate plant growth, as ecologists have observed under intermediate levels of herbivory in other plant species (Bilbrough 2003).

Interestingly, although no significant difference was observed between fenced and unfenced hummocks in mean stem diameter and stem length, our ANOVA results showed that these metrics of plant growth varied significantly when considering hummock proximity (near vs. far) to the Kuiseb River. Both mean stem diameter and stem length were significantly greater at !nara hummocks near the Kuiseb River, which may be indicative of increased availability of groundwater from an elevated water table near the Kuiseb. This finding contradicts our second hypothesis, which predicted that hummocks nearer to the Kuiseb would exhibit lower mean stem diameter and stem length due to higher concentration of livestock around the river.

To establish the effect of livestock herbivory on the ability of !nara plants to invest in reproduction, we analyzed the difference in total fruit and flower production between fenced versus unfenced hummocks. We assessed the number of fruits with flowers still attached to their tips, given that this is the most ephemeral stage of fruit development, and thus the least likely to be recounted between monthly herbivory data collection. Our ANOVA analysis of fruits with flower and flower production did not support our third hypothesis, which predicted that a significantly greater number of total fruits with flowers and flowers would be observed in fenced versus unfenced hummocks. Although fruit production did not differ significantly in hummocks positioned near to versus far from the Kuiseb River, the number of flowers was observed to be significantly greater on plants closer to the Kuiseb. One possible explanation for this observation may be that !nara plants are able to produce more flowers in closer proximity to the Kuiseb due to greater access to belowground water resources. Yet, because herbivory pressure may be greater closer to the river, more of these flowers eventually become browsed prior to reaching the small fruit stage, thus reducing the difference in small fruit production near to versus far from the Kuiseb.

After observing that a large proportion of dead !nara biomass appeared to have been trampled by large herbivores, we decided to examine the impact of livestock trampling in addition to browsing on proportion of live !nara biomass. Our ANOVA results did not support the treatment component of our fourth hypothesis, which predicted that fenced hummocks would display a greater proportion of live biomass than unfenced. In addition, our examination of proportion of dead biomass revealed no significant difference between fenced and unfenced hummocks. Aside from treatment, both proportions of live and dead biomass did not differ between hummocks positioned near versus far from the Kuiseb River.

Given the wealth of data from the previous year's monthly and bimonthly data collection, we determined that the fences used in the long term herbivory study are effectively excluding livestock (Hypothesis 5), especially evident given the fact that no cattle, donkey, and/or goat dung was counted within fenced hummocks for the most recent sampling month of September. Considering the central tenets of optimal foraging theory, which includes the idea that animals will optimize nutrient intake with the least amount of energy expenditure, we had hypothesized that livestock herbivore activity (assessed utilizing cattle and donkey dung density) would be lower at hummocks positioned further out into the Namib sand sea, given the significantly lower density of plant

resource farther from the Kuiseb and the energy-intensive process of walking across sand dunes to reach these !nara hummocks (Hypothesis 6). We also predicted that signs of herbivore presence would be lower further among the dunes, given previous Topnaar livestock satellite tracking data, which indicated that cattle and donkeys only trek far into the dunes infrequently, preferring to move among the shade and concentrated forage of the Kuiseb. Results from our linear regression of September's dung density counts and hummock distance from the Kuiseb indicated that a statistically significant relationship did not exist between these two variables. A plausible reason for why no relationship was observed between hummock distance from the Kuiseb River and livestock activity may be due to the fact that the hummocks assessed in our experiment are not positioned along a wide gradient of distances from the Kuiseb. Instead, the near and far hummocks tend to occupy two clustered points, around a distance of approximately 0-500 meters and 2300-2800 meters from the Kuiseb. To distinguish a trend with a linear regression analysis, it may have been better to assess hummocks at more intermediate distances, as well as further into the Namib Sand Sea.

Considering that livestock dung density is a reliable indicator of herbivore presence/activity levels at a given hummock (based upon the lack of dung inside fenced hummocks), we also examined the relationship between cattle/ donkey dung density and mean plant height (which we concluded to provide a good metric for measuring plant vitality, based on the significant difference observed between fenced and unfenced hummocks in mean plant height), as well as proportion of live !nara biomass (which showed no variance between treatment types). Although we hypothesized (Hypothesis 7) that herbivore exclusion promotes !nara growth, we found that dung density was not significantly correlated with mean plant height. This finding does not necessarily discount our hypothesis, rather it indicates that examining the linear relation between dung density and mean plant height cannot accurately reflect significant changes in plant growth caused by herbivory pressure. The regression of dung density on proportion of biomass also showed no significance. Since we concluded that the proportion of live biomass was not a good metric for measuring plant vitality, we would no longer expect there to be a linear relationship between dung density and the proportion of live biomass.

### ***!Nara Hummock Biodiversity Discussion***

We had several main questions we addressed in our study. The first was how livestock herbivory, hummock distance from the Kuiseb River, and hummock volume affected the biodiversity (richness and abundance) of !nara hummocks. We initially assumed that hummocks with higher volume would have higher biodiversity because they contain more habitat. (Hypothesis 11). We found that larger hummocks differed significantly in terms of Shannon diversity index (combined), track abundance, and combined abundance from smaller hummocks. This is likely because hummocks provide more three-dimensional space for burrowing animals to forage and seek thermal refuge. The capacity of !nara hummocks to provide a thermal refuge for desert organisms is shown by the drastic difference in temperature between the center of the hummocks and the bare soil surrounding them ( $t=-3.209$ ,  $df= 37$ ,  $p= 0.0014$ ). The mean temperature was lower by several degrees Celsius at the top of the hummock at 5 cm depth than on bare soil 20 meters away from

the top (Fig. 9). This would support the hypothesis that !nara plays a critical role as an ecosystem engineer by changing the abiotic conditions inside of the hummock (Hypothesis 13)

In terms of livestock herbivory, we assumed that fenced !nara hummocks would have higher animal abundance and richness because the vitality of unbrowsed plants would be higher (Hypothesis 8). With higher vitality, the fenced !nara plants may provide more food resources as well as spatial complexity for the animals that utilize the hummocks. However, our results demonstrated that abundance, number of taxa, and the richness calculated with the Shannon-Weiner index were not significantly different between the different treatments and distances to the river. The Shannon-Weiner indices were likely not significantly different between near and far hummocks or fenced and unfenced hummocks because the index values are based on how many unique species are present and not on the total number of only a few species present, as with the combined abundance (total individuals). In this respect, dune ants were considerably more abundant than other species and were found in significantly higher numbers close to the river, which results in a significant difference in the combined abundance between near and far hummocks or fenced and unfenced hummocks (Appendix F). Interestingly, ant abundances were also significantly greater in enclosed hummocks, indicating that ants may choose to associate more frequently in areas that are less trampled by livestock, or that have greater biomass to forage around (which may be evident in the significantly greater mean !nara plant heights at enclosed hummocks) (Appendix F).

In terms of the proximity to the Kuiseb River, we assumed that species richness would be higher in the hummocks closer to the river because habitat heterogeneity is greater near the Kuiseb River (Hypothesis 10). In addition to higher habitat heterogeneity, we assumed that diversity would be higher in the hummocks close to the river because there would be a combination of desert-adapted species and savanna species at the margins of the river, where the river/savanna ecosystem transitions to the Namib sand sea. We found that the number of taxa (richness) and total number of individuals (abundance) were not significantly different in the hummocks near to and far from the river. However, there was a marginally significant difference between the number of track taxa with different distance from the river. Even though the overall ANOVA for the track taxa and the distance to the river was only marginally significant, the effect of distance to the river on track taxa was significant ( $p= 0.0124$ ). This result may suggest that the sample size for the track taxa data may be too small to show the effect of river proximity on diversity. The Shannon index values were likely not significantly higher close to the river because the species are less evenly distributed in the near hummocks. Perhaps there are riparian species that occur in the transition zone between the sand sea and the Kuiseb River that outcompete desert-adapted species at the near hummocks and therefore diversity is lower. There may also be no significant effect of proximity to the river or herbivore exclusion on the biodiversity of !nara hummocks because the species inhabiting them are highly specialized for the environment the plant creates. For instance, some species may depend on the lower temperatures inside of the hummock to avoid the high temperature fluctuations that naturally occur in the desert (Fig. 7) Therefore, proximity to the river or herbivore pressure would not have a large effect on the total biodiversity of the hummocks.

We also compared species richness and abundance of !nara hummocks with other hummock-forming landscape features including dune grass (*Stipagrostis sabulicola*), rock outcrops, and acacia trees (*Acacia erlioba*). We made this comparison to assess the keystone status of !nara by seeing if !nara hummocks support more diversity than the surrounding desert matrix. We initially assumed that !nara hummocks would have higher species richness and abundance than the other hummock-forming features because !nara has greater structural complexity. Our few samples indicated that more total species and more individuals of different species were found on !nara relative to other features like rock outcrops of dune grass hummocks (Appendix E). However, there is an extremely small sample size associated with these findings and the collection protocol was not always consistent between samples. Therefore, it is difficult to draw significant conclusions from this information. Future groups may be able to better evaluate the keystone status of !nara by improving upon these methods of comparison with other plants and habitats.

One final interesting finding from our biodiversity assessment was that gerbil abundances, as estimated from the total number of gerbils crossing sweep transects at each hummock, were significantly greater within fenced hummocks than unfenced hummocks (Appendix G). This finding is of particular interest, given that gerbils are cited as one of the two primary !nara seed dispersers, alongside black-backed jackals (Henschel et al. 2004). As Henschel et al. note, gerbils often bury the seeds of serve as primary short-distance seed dispersers for the !nara plant through their habits of burying caches of seeds underground, where many are forgotten and are thus well-positioned for germination. Given that significantly greater abundances of gerbils are found when livestock herbivores are excluded from hummocks, these results suggest that livestock herbivore exclusion may offer a multi-faceted benefit to !nara plant reproductive success, given that: 1) more energy could theoretically be invested in reproductive structures due to a reduction in browsing and trampling of !nara stems, and 2) dispersal and germination of !nara seeds may be significantly greater when livestock herbivores are excluded from hummocks due to the fact that gerbil abundances are significantly greater in fenced hummocks. One possible explanation for why significantly more gerbils are found within the fenced hummocks may be that gerbils are more likely to construct burrows in areas of more stable soils, as demonstrated in previous scientific literature (Brown 1989). Given that donkeys and cattle often trample heavily around the base of !nara plants within unfenced hummocks where gerbils primarily construct their burrows, gerbils may be less likely to associate with herbivore-accessible hummocks.

### **Recommendations for Future Studies**

We suggest several changes to the bi-monthly !nara monitoring protocol that would improve the accuracy and efficiency of the data collection. Firstly, we propose separating each hummock into quadrats using a pole in the center of each hummock that has several pieces of string attached. Each piece of the string would be tied off to a section of the fence to divide the hummock into 4 sections. This would help to reduce double counting of flowers, fruit, and other plant parts that are monitored in the bi-monthly protocol. This change could increase the speed of data collection while also improving the collection accuracy. We also suggest the addition of other measurements to the long-term protocol. Based on the current data in our study, we found that although the flower and fruit data did not show a significant difference with the different treatments (fenced versus



unfenced), the mean plant height for the plant was significantly different between the treatment and control. Therefore, we suggest adding the mean plant height measurement to the long-term data collection protocol.

We also suggest several changes to the biodiversity study protocol to improve the study accuracy. First, we suggest standardizing the period of time spent observing hummocks for biodiversity data (pitfall, track, and observation) to make the results more comparable. For instance, we suggest adding a section to the methods/protocol where we explain a standard way of surveying the hummock for live species observations. Second, given that pollinators are a significant component of hummock biodiversity, we suggest that further study of biodiversity include a more thorough survey pollinator species using bee bowls. To improve the bee bowl method, we suggest assessing the weather ahead of time as we encountered difficulties with a pilot study on an extremely windy day. Finally, we suggest deploying more bee bowls with attached stands so they are not blown away or filled with sand while deployed on the hummocks.

## **Conclusion**

Given the plethora of scientific literature alluding to the possibility that !nara functions as an important keystone species within the greater Namib-Kuiseb ecosystem, along with the great cultural and economic importance of the plant to local Topnaar communities, we set about in our scientific investigation to answer the following two research questions utilizing a combination of fieldwork and analysis of existing herbivory data: 1) How might livestock herbivory impact !nara plant productivity and growth? and 2) How might !nara function as an ecosystem engineer, creating a favorable environment for many desert-dwelling species and thus acting as a keystone species in the greater Namib ecosystem? From analysis of the existing herbivory study data, we determined that herbivore exclusion may promote !nara plant growth (as observed with the significantly greater mean plant heights in fenced as compared to unfenced hummocks), however enough time may not have elapsed since the beginning of the enclosure study to observe a significant difference between treatment types in other proxies for plant vitality (i.e.- mean number of fruits with flowers, open flowers, stem diameter, and stem length).

From our analysis of associated animal communities at the various hummocks, we observed that fenced hummocks do not exhibit significantly greater abundances of animals, nor greater species richness, than unfenced hummocks, indicating that livestock herbivory pressure may not be directly impacting the capacity of !nara hummocks to maintain biodiversity, or that a sufficient amount of time has not elapsed between the commencement of the experiment and our sampling for an observed effect on community structuring to be observed.

Species abundance observed from track data, combined track and pitfall species abundance, and combined Shannon-Wiener indices all appeared to be positively correlated with hummock size, indicating that herbivory may inhibit the ability of !nara plants to support biodiversity in the long term if the trampling activity of livestock inhibits the ability of !nara hummocks to enlarge. Interestingly, we found that gerbil abundances are significantly greater at fenced hummocks, indicating that herbivore exclusion may have indirect benefits on !nara reproductive success, given that these rodents are key seed dispersers of !nara. Although we only conducted a preliminary

study assessing the animal communities associated with !nara hummocks compared to other hummock-forming desert landscape features, we tentatively add that the species diversity and abundance may be greater at !nara hummocks (Appendix E). In the future, we propose an expansion of this aspect of the study, which would allow researchers to substantiate their claims that !nara functions as a keystone species.

From our temperature logging data, which indicated significantly lower mean high daytime temperatures at the top of !nara hummocks as opposed to the ground alongside them, it appears as though !nara may be functioning as ecosystem engineers, modifying their surrounding landscape in such a way that makes it more favorable to other animals. Although the exact reasons of this observed trend remain unknown, we propose that future research should extend this investigation to examine how !nara are precisely altering soil conditions.

### **Acknowledgements**

We would like to thank the incredibly committed team of Dartmouth faculty and staff, in addition to our new friends of the Gobabeb Research and Training Centre for their support and guidance in the completion of this project. Thank you to Flora Krivak-Tetley for all of her help with the logistical planning, impressive dune-driving skills, and her patience in dealing with our insatiable appetite to collect more and more field data. Thank you to Saima Shikesho, Gobabeb employee extraordinaire, for her unparalleled ability to both identify animal tracks and train a group of non-desert dwellers in the art of tracking in the Namib Desert, as well as her sage advice in constructing our final paper. We would also like to thank Liz Struder, insect connoisseur, for her ability to get all of us excited about the insect world, and for her diligent work in collecting bee bowls and supporting our final editing process. In addition, thank you to Jeff Kirby for his aerial photography skills, for all the help with analyzing our drone data, and for sharing his amazing National Geographic stories with us! We also wish to extend many thanks for Eugene Marais, known amongst the group as the master gerbil wrangler, for sharing his bountiful knowledge spanning the disciplines of desert ecology to track identification to research methods. Finally, thank you to Professor Bolger for his continued enthusiasm for ecology and belief in our project. Even when we opened our spreadsheet with over 37,000 temperature data points and questioned our ability to synthesize a final project, Professor Bolger assured us that the interesting ecological questions lay just around the corner.

## References

- Bilbrough, C. J., & Richards, J. H. (1993). Growth of sagebrush and bitterbrush following simulated winter browsing: mechanisms of tolerance. *Ecology*, *74*(2), 481-492.
- Brown, J. S. (1989) The role of resource variability in structuring desert rodent communities. *Patterns in the structure of mammalian communities*, *7*, 141-54.
- Carrivick, J., Smith, M., Quincey, D. (2016). Chapter 3. Background to Structure from Motion, in *Structure from Motion in the Geosciences*, First Edition. John Wiley & Sons, Ltd.
- Dentlinger, U. (1977). The !Nara Plant in the Topnaar Hottentot Culture of Namibia: Ethnobotanical Clues to an 8,000-year-old Tradition. *Munger Africana Library*, *38*, 12-20.
- Gerber, M., Piketh, S. J., Berner, J. M., Maggs-Kolling, G., & Marais, E. (2017). Strategies of *Acanthosicyos horridus* (! nara) to exploit alternative atmospheric moisture sources in the hyper-arid Namib Desert.
- Gilad, E., von Hardenberg, J., Provenzale, A., Shachak, M., & Meron, E. (2004). Ecosystem engineers: from pattern formation to habitat creation. *Physical Review Letters*, *93*(9), 098105.
- Hanley, M. E., Lamont, B. B., Fairbanks, M. M., & Rafferty, C. M. (2007). Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics*, *8*(4), 157-178.
- Herrick, G. S., Caspeta, D., R., & Loon, Jazz V. (2016). Perceptions of Livelihoods and Tourism Opportunities within the Topnaar Community. *Dartmouth in Namibia*.
- Hebeler, F. 2000. Structural and ecophysiological shoot features of the leafless cucurbit *Acanthosicyos horridus* , a keystone species endemic to the Namib Desert [Thesis]. Justis-Liebig Universitat Giessen. Giessen, Germany.
- Henschel, J., Dausab, R., Moser, P., & Pallett, J. (2004). !Nara: Fruit for development of the !Khuiseb Topnaar. Namibia Scientific Society, Windhoek, Namibia.
- Ito, M. (2005). Changes in the distribution of the! nara plant that affect the life of the Topnaar people in the lower Kuiseb River, Namib Desert.
- “JMP Pro Predictive Analytics Software for Scientists and Engineers.” (2017). *Jmp Statistical Discovery from SAS*, Statistical Discovery , [www.jmp.com/en\\_dk/software/predictive-analytics-software.html](http://www.jmp.com/en_dk/software/predictive-analytics-software.html).
- Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. In *Ecosystem management* (pp. 130-147). Springer New York.
- Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, *78*(7), 1946-1957.
- Klopatek, J. M., & Stock, W. D. (1994). Partitioning of nutrients in *Acanthosicyos horridus*, a keystone endemic species in the Namib Desert. *journal of Arid Environments*, *26*(3), 233-240.

- Kittleberger, K. D., Berlinghof, L. R., Catano, K., & Cheng, K. (2016). Herbivory Impacts on !Nara. *Dartmouth in Namibia*, 4-17.
- Kok, O. B., & Nel, J. A. J. (1996). The Kuiseb river as a linear oasis in the Namib desert. *African Journal of Ecology*, 34(1), 39-47.
- Latorre, C., González, A., Quade, J., Farina, J., Pinto., R., & Marquet, P. 2011. Establishment and formation of fog-dependent *Tillandsia landbeckii* dunes in the Atacama Desert: Evidence from radiocarbon and stable isotopes. *Journal of Geophysical Research*. 62: 549-566.
- Libralato, S., Christensen, V., & Pauly, D. (2006). A method for identifying keystone species in food web models. *Ecological Modelling*, 195(3), 153-171.
- Magurran, A.E. 2004. *Measuring Biological Diversity*. Blackwell
- Milchunas, D. G., & Lauenroth, W. K. (1993) Quantitative Effects of Grazing on Vegetation and Soils Over a Global Range of Environments. *Ecological Archives*, 63 (4), 327-366.
- Mills, L. S., Soulé, M. E., & Doak, D. F. (1993). The keystone-species concept in ecology and conservation. *BioScience*, 43(4), 219-224.
- Moser, P. (2001). *Root and shoot development of Acanthosicyos horridus seedlings in the Namibia desert*(Doctoral dissertation). Münster. Germany. Accessed via Gobabeb Library.
- Moser-Nørgaard, P. M., & Denich, M. (2011). Influence of livestock on the regeneration of fodder trees along ephemeral rivers of Namibia. *Journal of Arid Environments*, 75(4), 371-376.
- Naeem, S., & Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, 390(6659), 507-509.
- Pike, D. A., & Mitchell, J. C. (2013). Burrow-dwelling ecosystem engineers provide thermal refugia throughout the landscape. *Animal Conservation*, 16(6), 694-703.
- Piggot, C. D., & Grime, J. (1980). Plant strategies and vegetation processes. *The Journal of Ecology*, 68(2), 704.
- Piraino, S., Fanelli, G., & Boero, F. (2002). Variability of species' roles in marine communities: change of paradigms for conservation priorities. *Marine Biology*, 140(5), 1067-1074.
- Pringle, R. M. (2008). Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology*, 89(1), 26-33.
- Rambo, J. L., & Faeth, S. H. (1999). Effect of vertebrate grazing on plant and insect community structure. *Conservation biology*, 13(5), 1047-1054.
- Stix, G. (2003). Desert metropolis: Namibia's endless arid expanses are home to a menagerie of creatures that live nowhere else. *Scientific American*. 288: 90-92.

Teagle, H., Hawkins, S. J., Moore, P. J., & Smale, D. A. (2017). The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology*.

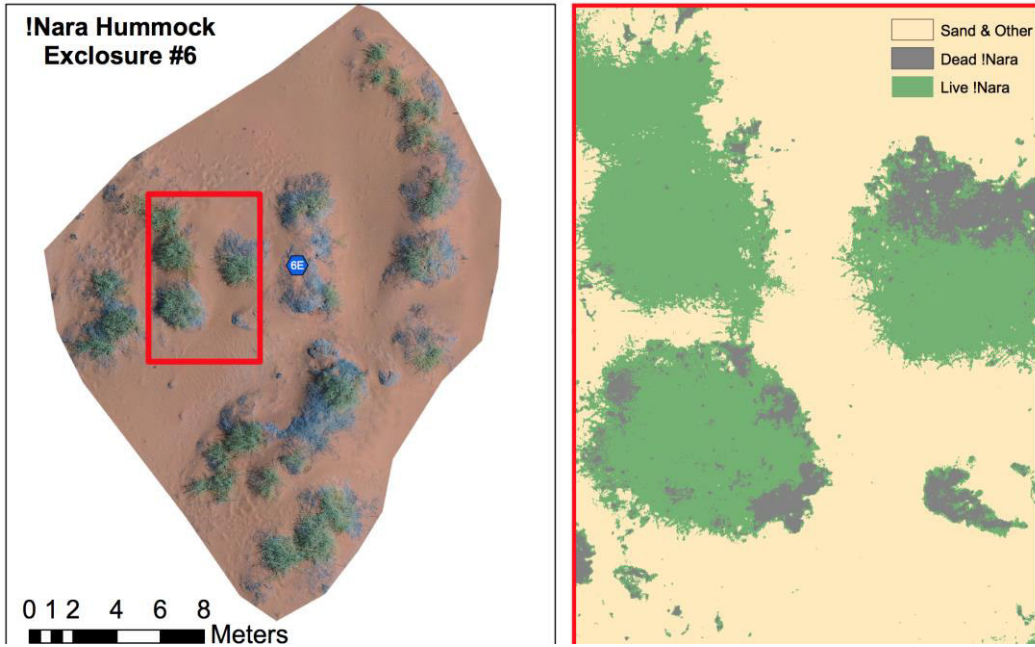
Tilman, D. (2000). Causes, consequences and ethics of biodiversity. *Nature*, 405(6783), 208-211.

Van Damme, P., & Den Eynden, V. (1992). The ethnobotany of the Topnaar. *U.N. FOA Reports*.

Wright, J. P., & Jones, C. G. (2004). Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology*, 85(8), 2071-2081.

Appendices:

**Appendix A: Classification of % Live and Dead !Nara Biomass for Hummock E6 from UAV Orthomosaic**



## Appendix B: Variables used for data analysis

TAG	Total donkey and cattle dung	Mean plant height	Mean stem length	Mean stem diameter	Mean # side branches	Small fruits with flowers	Flowers	% Live Biomass	% Dead Biomass	Live Surface Area (m <sup>2</sup> )	Live Volume (m <sup>3</sup> )
1E	0	112.5	177.4	4.63	3.8	0.08	0.5	0.435513624	0.095458243	42.3	47.58
1C	347	79.5	282.8	4.87	6.7	0.71	0.57	0.201541184	0.159751547	175.9	139.84
2E	0	68.889	144.1	3.85	2.4	0.35	0.64	0.217609726	0.030584683	156.22	107.62
2C	11	58.5	100.3	3.78	4.4	2.54	5.17	0.172717572	0.018354918	129.37	75.68
3E	0	65.2	131.1	5.182	9.9	4.28	3.77	0.300578339	0.093690661	15.05	9.81
3C	0	40.9	124.8	4.511	7.6	2.01	4.03	0.174439236	0.123761714	3.64	1.49
4E	0	75.7	95.2	4.572	9.1	0.18	0	0.459278547	0.108453303	14.31	10.83
4C	0	39.9	103.7	4.272	5.9	2.7	0.59	0.098604997	0.055297474	21.36	8.52
5E	0	33	149.1	4.268	5	0	0	0.025977891	0.08609181	10.34	3.41
5C	16	30.1	122.8	4.226	8.1	0	0	0.078767601	0.045344648	20.25	6.1
6E	0	80.4	103.7	4.085	6.9	0.31	0.09	0.233909426	0.086317982	73.03	58.72
6C	0	53.4	97.3	3.84	3.8	0.04	0.18	0.170105989	0.076441795	85.11	45.45
7E	0	60.1	97.9	4.165	4.2	0.17	0	0.2034284	0.044356131	19.52	11.73
7C	0	54.857143	98.7	4.131	9.2	11.29	0	0.155933279	0.260372695	4.36	2.39
8E	0	65.2	94.4	3.513	4.2	0.87	0.69	0.091541111	0.204044734	8.85	5.77
8C	31	75.2	101.2	4.299	5.9	0.09	0.09	0.143045042	0.156459133	29.64	22.29
9E	0	82.2	96.3	3.747	5.3	0	0	0.267038092	0.068452276	48.99	40.27
9C	0	41.9	134.1	4.299	7.6	0.86	0.07	0.217535111	0.11365897	33.25	13.93
10E	0	46.9	128.9	4.157	7.9	0.49	0.49	0.034319083	0.011573251	4.37	2.05
10C	0	39.375	97.3	3.906	4	0.22	0	0.039508072	0.104352923	11.31	4.45
4C-alt	23	42.3	113.3	4.129	7.2						

TAG	Total Individuals (Tracks)	Total Individuals (Pitfalls)	Total Individuals (Aggregate)	Track # of Taxa	Pitfall # of Taxa	Total # of taxa (aggregate)	Shannon Index Tracks	Shannon Index Pitfalls	ln(live volume)
1E	46	236	282	8	8	13	1.773843829	0.6394317	3.862412505
1C	115	30	145	7	7	12	0.984403039	1.58935049	4.940498912
2E	129	24	153	8	7	14	1.606942885	1.65330368	4.678606504
2C	90	8	98	8	5	13	1.202806985	1.559581156	4.326513925
3E	161	12	173	7	7	13	1.140336715	1.820075975	2.283402274
3C	58	8	66	7	2	9	1.301949981	0.376770161	0.39877612
4E	116	24	140	8	5	13	1.563237551	0.613481894	2.382320061
4C	60	11	71	6	4	10	1.422189942	1.263654432	2.142416341
5E	68	22	90	6	6	12	1.314082915	1.531153319	1.226712291
5C	43	14	57	7	6	12	1.26867945	1.648847072	1.808288771
6E	89	7	96	4	4	8	1.153228888	1.153741943	4.072780384
6C	84	8	92	7	5	12	1.125051869	1.494175138	3.816612821
7E	131	29	160	6	6	11	1.101015573	1.368340794	2.462149663
7C	32	33	65	4	5	9	0.672215865	0.91728616	0.871293366
8E	43	7	50	7	3	10	1.420496107	0.955699891	1.752672081
8C	156	20	176	7	2	9	1.287064973	0.562335145	3.104138147
9E	156	39	195	8	8	15	1.359216805	1.419921253	3.695606775
9C	91	61	152	5	5	9	1.44405194	0.597665869	2.634044788
10E	71	12	83	6	3	9	1.170944116	1.011404265	0.717839793
10C	30	15	45	4	6	9	0.626381237	1.617053153	1.492904096

### Appendix C: !Nara Hummock Confirmed Species List

Grouping	Species
Ants	Black ant ( <i>Oxymyrmex barbiger</i> ) Dune ant ( <i>Camponotus detritus</i> )
Beetles	Ridged dune beetle ( <i>Onymacris laeviceps</i> ) Black beetle ( <i>Onymacris unguicularis</i> ) Flat beetle ( <i>Stip stali</i> ) Shiny Black Beetle ( <i>Zophosis moralesi</i> ) Blister beetle ( <i>Mylabris zigzaga</i> ) Ladybird beetle ( <i>Coccinellidae sp.</i> )
Birds	Dune lark ( <i>Calendulauda erythrochlamys</i> )
Caterpillars	Io moth ( <i>Automeris sp.</i> )
Flies	!Nara fly ( <i>Uliidae sp.</i> ) Pollinator fly ( <i>sp. unknown, Dartmouth 2015</i> ) Blow fly ( <i>Calliphoridae sp.</i> )
Gerbils	Hairy-footed gerbil ( <i>Gerbillurus paeba</i> )
Lizards	Shovel-snouted lizard ( <i>Meroles anchietae</i> ) Namaqua desert lizard ( <i>Pedioplanis namaquensis</i> ) Wedge-snouted lizard ( <i>Meroles cuneirostris</i> ) FitzSimons' burrowing skink ( <i>Typhlacontias brevipes</i> )
Other insects	Silverfish/ fishmoths ( <i>Ctenolepisma sp.</i> ) Harvester termite ( <i>Hodotermes mossambicus</i> )



	<p>!Nara cricket (<i>Acanthoproctus diadematus</i>)</p> <p>Solifuge / Sun spider (<i>Daesiidae sp.</i>)</p> <p>Dune bee (<i>Anthrophora aune</i>)</p> <p>Black parasitoid wasp (<i>Hylaeus sp.</i>)</p>
Other mammals	<p>Cape fox (<i>Vulpes chama</i>)</p> <p>Cape hare (<i>Lepus capensis</i>)</p> <p>Steenbok (<i>Rhaphicerus silvestrus</i>)</p>
Scorpions	<p>Burrowing scorpion (<i>Opisththalmus flavescens</i>)</p>
Snakes	<p>Sidewinding adder (<i>Bitis peringueyi</i>)</p> <p>Namib sand snake (<i>Psammophis namibensis</i>)</p>
Spiders	<p>Dancing white lady spider (<i>Leucochestris arenicola</i>)</p>

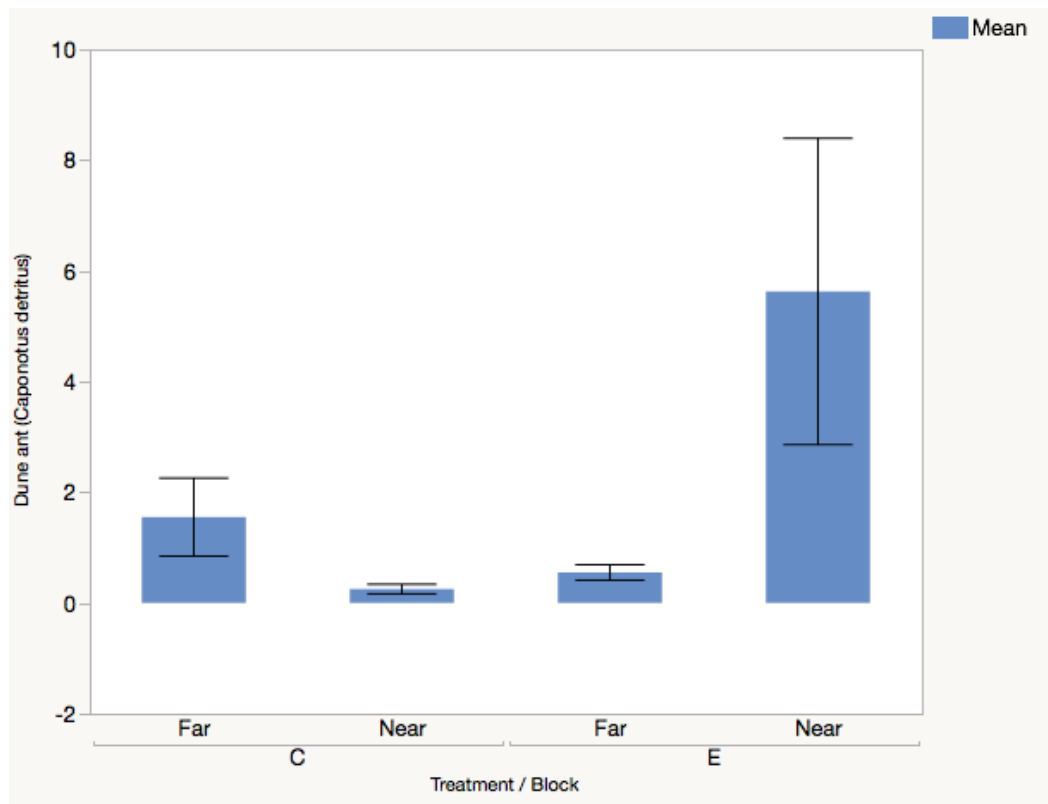
**Appendix D: Alternate Hummock Sweep Transect Positions**

<b>Waypoint #</b>	<b>Coordinates</b>	<b>!Nara hummock pairing</b>	<b>Hummock Type</b>	<b>Location relative to !Nara pairing</b>
101	S 23.56448, E 015.03638	10E	Dune Grass	northwest
102	S 23.59052, E 015.05148	10C	Rock Outcropping	northwest, across road
103	S 23.59025, E 015.05241	7E	Dune Grass	northeast, up dune
104	S 23.56461, E 015.03665	2E/2C	Acacia	between 2E and 2C, eastern side
105	S 23.56448, E 015.03638	1E	Short grass tuft	between Acacia hummock and 1E
606	S 23.59053, E 015.05091	7C	Rock outcropping	about 50m southwest
607	S 23.55659, E 015.02854	5E	Acacia	30m north
608	S 23.55715, E 015.02773	5C	Short grass tuft	20m east
609	S 23.55722, E 015.02805	5C	Rock outcropping	20m south

**Appendix E: Table for Hypothesis 12 - Sweep Transect Biodiversity For Paired  
Alternative Hummock Habitats**

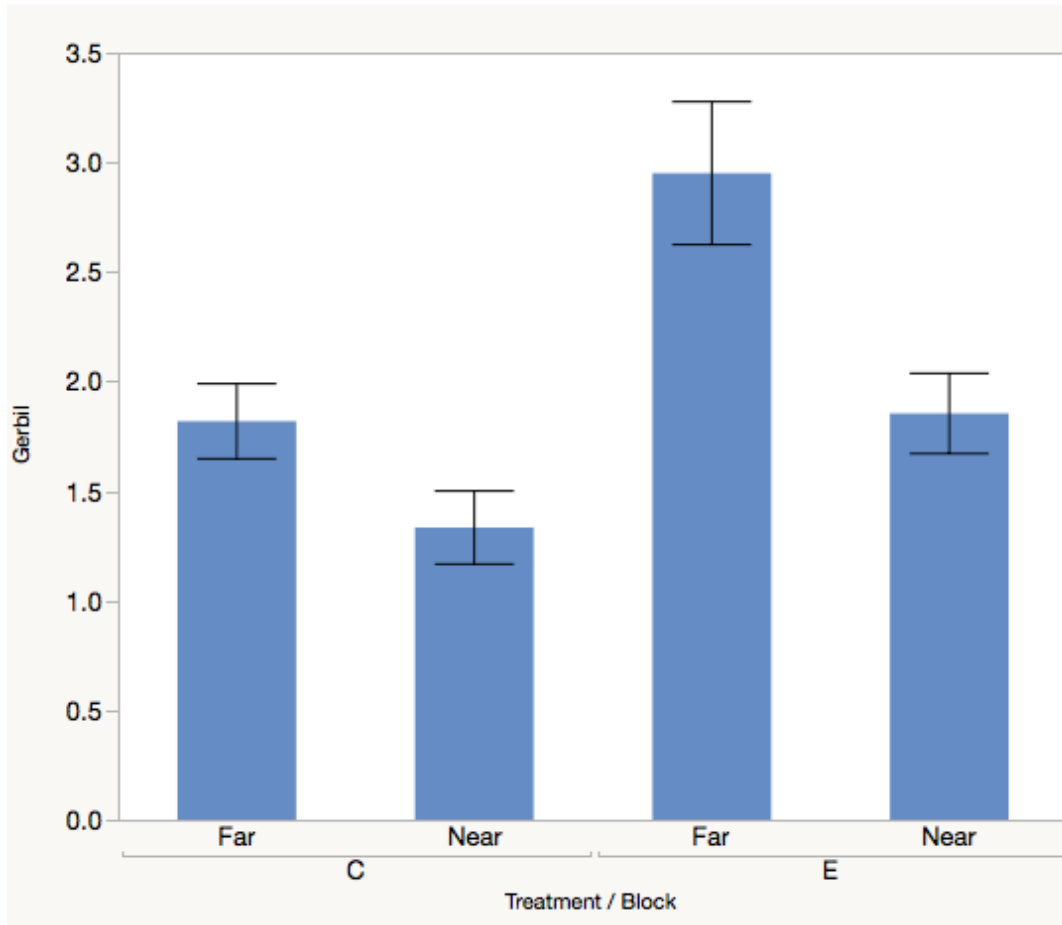
<b>ID Number</b>	<b>Hummock type</b>	<b>Track Sweep Counts- Night of Nov. 4 (2 sq. meters)</b>
101	Dune grass	2 Gerbil, 1 Spider/Scorpion
10E	!Nara	2 Beetle,
102	Rock outcropping	1 Beetle
10C	!Nara	2 Beetle
103	Dune grass	1 Gerbil, 1 !Nara Cricket, 1 Bird
7E	!Nara	3 Gerbil, 5 Beetle
104	Acacia	3 Beetle
2E	!Nara	1 Lizard, 2 Gerbil, 1 Beetle, 1 Spider/Scorpion, 2 Cape Fox
105	Dune grass	1 Lizard
1E	!Nara	3 Beetle, 1 Spider, 1 Cape fox/Jackal
605	Rock outcropping	1 Unknown
7C	!Nara	Nothing
607	Acacia	1 Gerbil
5E	!Nara	1 Gerbil, 2 Fitzsimon's Skink
608	Dune grass	Nothing
5C	!Nara	3 Lizard
609	Rock outcropping	Nothing

## Appendix F: Distribution of Ant Abundance Between Pitfall Traps at Fenced vs. Unfenced Hummocks



**App. F-** ANOVA results for total ant abundances within pitfall traps show a significant interaction between treatment (fenced vs. unfenced) and block (near vs. far to the Kuiseb River), indicating that more ants are found in fenced hummocks near to the Kuiseb than all other block and treatment combinations ( $F=3.0163$ ,  $df=3,159$ ,  $p=.0317$ ).

**Appendix G: Distribution of Gerbil Abundance, as Assessed from Track Sweeps, at Fenced vs. Unfenced Hummocks**



**App. G** - ANOVA results for total gerbil abundances (as estimated from track data) show a significant effect of treatment (fenced vs. unfenced) and block (near vs. far), indicated that: 1) more gerbils are found inside fenced hummocks than unfenced hummocks and 2) more gerbils are observed at hummocks positioned far from the Kuiseb River ( $n= 20$ ,  $F=4.9318$ ,  $df=3,142$ ,  $p=0.0028$  ).