Title

Foraging behavior of free-ranging cattle and community interactions in a tropical deciduous forest

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Publication Date

2018

UNIVERSITY OF CALIFORNIA

Los Angeles

Foraging behavior of free-ranging cattle and community interactions in a tropical deciduous forest

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Biology

by

Carlos Alberto de la Rosa

2018

ABSTRACT OF THE DISSERTATION

Foraging behavior of free-ranging cattle and community interactions in a tropical deciduous forest

by

Carlos Alberto de la Rosa
Doctor of Philosophy in Biology
University of California, Los Angeles, 2018
Professor Patricia Adair Gowaty, Co-Chair
Professor Stephen P. Hubbell, Co-Chair

North American tropical deciduous forest (TDF) is severely threatened by deforestation for livestock production and agriculture. Integrating cattle and forests, silvo-pastoral systems are an alternative to forest conversion to pasture, but the impact of cattle on TDF tree community diversity and structure in forested ranches is poorly understood. Furthermore, no research to date has quantified cattle foraging biases toward or against woody forage plant species in TDF, in order to isolate the role of cattle browsing from other variables contributing to impacts on woody vegetation. Here, I describe the foraging behavior and movements of free-ranging cattle in TDF, and differences in statistically paired TDF with and without cattle, on ranches with low stocking rates and an adjacent conservation preserve in the foothills of the Sierra Madre Occidental, Sonora, Mexico. In Chapter 1, I introduce CowPro, an animal-mounted time-lapse video, GPS and data logging system I designed and used throughout this study. CowPro units require no human intervention for periods up to seven days, allowing researchers to unobtrusively collect quantitative behavioral data on leery, forest-dwelling cattle or other large terrestrial animals. For Chapter 2, I tested hypotheses on cattle bias toward or against food resources at the plant-species level and at the plant-community level. Using CowPro, I generated a database of woody plant species and frequencies of those species occurring in cow diets. I then quantified tree community structure in TDF with arrays of 5-meter by 5-meter plant census plots on known cow foraging paths and across all available cattle habitat within ranches in the TDF, and compared species frequencies and community diversity. Cows are selective at both the individual-plant scale as well as the landscape-level, habitat scale, though the best predictor of cow preference for woody plant species overall is the prevalence of that species in foraging habitat. Additionally, repeat-visit foraging habitat is more diverse than all habitat available to cows. For Chapter 3, I tested hypotheses on the effect of cattle on TDF woody plant species abundances, species importance value indices, community diversity, and stem size class distributions in currently ranched versus cattle-free areas. To compare characteristics of forests with and without cattle, I recorded species and measured diameters of all stems greater than 1 centimeter at a height of 20 centimeters in 98 statistically matched 5-meter by 5-meter plant census plots, separated by cattle fences. In my study areas, TDF in cattle-exclusion areas is as diverse as TDF containing cattle; however, differences in stem size category distributions and species frequencies suggest cows may negatively impact some tree species, while promoting others.

The dissertation of Carlos Alberto de la Rosa is approved.

Thomas Welch Gillespie

Patricia Adair Gowaty, Committee Co-Chair

Stephen P. Hubbell, Committee Co-Chair

University of California, Los Angeles

2018

EPIGRAPH

“Un sauce de cristal, un chopo de agua,

un alto surtidor que el viento arquea,

un árbol bien plantado mas danzante,

un caminar de río que se curva,

avanza, retrocede da un rodeo

y llega siempre:”

Octavio Paz, “Piedra de sol”

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ACKNOWLEDGEMENTS

First, I am indebted to my academic advisors, Drs. Patty Gowaty and Steve Hubbell, for the significant chance they took on me as a non-traditional graduate student, and for their unshakeable faith in me. I can never thank Patty enough for our early conversations and the lessons she taught me on logic, hypothesis formation, and the philosophy of science, gifts that have enriched my thinking and my writing, and armed me with a lifelong set of problem solving tools. I thank Steve for his practical advice and his honest criticism, and for inspiring me to think and write with clarity. And I am grateful to both Patty and Steve for first introducing me to the forest and people of Álamos, the focus of my work and passion during my graduate career.

Deepest thanks also to committee members Drs. Phil Rundel and Tom Gillespie, for their enthusiasm and insight, and for encouraging me to dig deeper: into gomphotheres, African rangeland ecology, Neotropical botany, and other exciting tangents that have enriched my work.

This work would not have been possible without my partner and best friend, Katie Gostic, who read everything I wrote, provided critical feedback and advice, coached me in statistics, math, and coding, pulled me through my most challenging moments, and believed in me. I am better and more confident in my science and everyday life with you by my side. I am also grateful to my mother Tricia, and my father Carlos, for being my role models and for the lifelong gift of raising me bilingual and wild in Costa Rica, for letting me race bareback on horses with campesino kids in Murcielago, for letting me catch pargo on a shaky fishing boat of out Cuajiniquil, and for teaching me to love people and nature equally.

Estoy en deuda a mis queridxs amigxs de mis Pueblitos Mágicos, Álamos y El Sabinito Sur: a Lydia Lozano-Angulo por su apoyo y amistád invaluable; a Jeni y Daveed Mackay, por abrirme las puertas del pueblo y de la Reserva; a Suzanne y David, por compartir conmigo su pasión por las aves y los niños y niñas de Sabinito Sur; y a Lourdes “Luly” María Alcantar, por la discada, margaritas de tamarindo, y por enseñarme como hablar Sonsorense. A Leonél López-Toledo, Noé Hernández Cornejo y a Perla García, por ser mi comunidád científica, por su invaluable asistencia con permisos y trabajo de campo, y por la enseñanza valiosa que sin tortillas no se puede llenar uno. Muchísimas gracias a

Francisco “Pancho” Esquer, Raúl Álvarez, y Jesús “Chuy” Álvarez, por darme confianza y apollo, y por permitirme montar cámaritas en tus vacas. A Martín Gabriel Figueroa, por el increíble trabajo en los cuadros de referencia, por la palapa, por la lechuguilla de membrillo, por los blanquillos a 20 pesos la cartera, y mucho, mucho más. A Leocadio “Cholo” García Avendaño, sin su conocimiento de la naturaleza del mojino, de la gente y del ganado no estuviera posible este trabajo- por su amistad y su trabajo estoy profundamente agradecido. A Jonny Zayas Hermosillo, Martín García Avendaño, Felix García Caballero, Alejandro Sauceda, Alejandro “Cuate” Grajeda, Jorge “Chín” Sauceda, Juana Hermosillo, al Chapo y Juana, Andrés, Mingo, Malena, Mechelupe, Susy, y a todos los residentes de Sabinito Sur, que me ayudaron con asistencia en esta obra, me extendieron la mano, y me recibieron con posole, mojarra frita y tamales de elote, mis infinitas gracias y amor.

I am grateful for the incredible support of my UCLA and Los Angeles community. Thanks especially to my labmate Doug Booher, for his friendship and hindsight therapy; Jocelyn Yamadera and Tessa Villaseñor for their endless patience and help navigating being a grad student; Santiago Trueba for his valuable edits on Chapter 1; my undergraduate assistants Angela Chen and Chaiti Bhagawat for their hard work scoring cow videos and entering data; Evan Meyers for roping me into fun side projects; my cohort-mates Drs. Mairin Balisi and Janet Buckner for friendship and commiseration; Annabel Beichman and Jeff Potts for music and dinner invites which arrived presciently on nights when I was too tired to cook. Special thanks to Andy and Gaye Saxon for being my second family, taking me on adventures, feeding me, and much more. My eternal thanks as well to my friends and colleagues Dr. Ben Wilder, Dr. Sula Vanderplank, and Sarah Ratay, among many other reasons, for taking me through Cataviña after a rainstorm, where I first fell in love with Mexico.

This work was supported by the National Science Foundation Graduate Research Fellowship (award # DGE-1144087) and the University of California and Mexico Dissertation Fellowship (award # 20151049), and approved by the Research Safety and Animal Welfare Administration of the University of California, Los Angeles (protocol # 2018 – 030 – 01).

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de la Rosa, Carlos A. (2018). An inexpensive and open-source method to study large terrestrial animal diet and behavior using time-lapse video and GPS. Manuscript submitted for publication.

Rasheed, A. A., Hambley, K., Chan, G., de la Rosa, C. A., Larison, B., and Blumstein, D. T. (2018). Persistence of antipredator behavior in an island population of California quail. *Ethology, 124*(3), 155-160.

Vanderplank, S., Peralta-García, A., Valdez-Villavicencio, J. H., and de la Rosa, C. A. (2017). *Unique* *plants and animals of the Baja California Pacific Islands*. Botanical Research Institute of Texas (BRIT), Fort Worth, TX. 106 pages.

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CHAPTER 1

An inexpensive and open-source method to study large terrestrial animal diet and behavior using time-lapse video and GPS.

1.1 ABSTRACT

The behavior of free-ranging animals is difficult to study, especially on the large spatial and temporal scales relevant to long-lived large species. Animal-borne video and environmental data collection systems (AVEDs) directly record behavior and other data in real time as animals conduct daily activities. However, few studies to date combine systematically collected, long term AVED foraging data with environmental and movement data to test hypotheses on animal foraging. Additionally, AVEDs are often either prohibitively expensive, or require extensive fabrication and programming knowledge.

I developed an animal-mounted data collection system (CowPro) that records short, first "person" perspective videos of animal behavior on an automated time-lapse schedule. The system also captures location coordinates, elevation, speed, and other real-time metadata as study animals range through their available habitat. Moreover, CowPro is relatively inexpensive and easy to use.

I used CowPro to study the browsing habits and tree community impacts of free-ranging cattle in the western foothills of the Sierra Madre Occidental, in Sonora, Mexico. In the subset of videos featuring cow foraging on woody vegetation, most trees, shrubs, cacti, lianas, and some perennial herbs can be identified to species. As videos are georeferenced, researchers can return to the locations of specific events and collect accurate, fine-grained data on habitat characteristics that may influence animal behavior.

CowPro, combined with detailed habitat data, is a powerful tool to study semi-wild cattle foraging at multiple scales in forested areas, and could potentially apply to studies of other large terrestrial animals. Open source software and commercially available hardware make CowPro financially attainable for most researchers, land managers, students, and other user groups. I describe the system's strengths and limitations in detail, with suggestions for potential applications to different species.

1.2 INTRODUCTION

Research in animal foraging ecology requires that an investigator either directly observe and record foraging, or collect indirect proxy information on foraging. Because many animals are difficult or impossible to observe directly and continuously, many foraging studies focus instead on indirect evidence of foraging, such as records of animal movements tracked by telemetry and camera traps, among other methods (Weimerskirch, Salamolard, & Sarrazin, 1993; Bowkett, Rovero, & Marshall, 2008; Ceriani, Roth, & Evans, 2012). Inferences about foraging behavior based on indirect evidence have helped uncover fascinating new behavioral patterns and have challenged our assumptions about animal foraging. However, inferential behavioral data can be misleading, leading to Type 1 errors, or vague and incapable of ruling out alternative hypotheses. Microhistological analysis of predator fecal samples, for example, does not allow a researcher to say whether prey was killed or scavenged (Symondson, 2002). Similarly, plant or animal tissues may be overrepresented in visual analyses of feces, while soft, digestible materials may be difficult or impossible to identify by conventional visual analysis (Vavra & Holechek, 1980). Animal movements as recorded by telemetry equipment can also leave open alternative explanations of an animal's behavior: a large number of GPS coordinates in a small area could alternatively indicate that an animal was sleeping, feeding, or resting. Constraints on the type and scope of data collected during a study can limit their power to disprove or support a foraging ecology hypothesis, decrease the chances that a discovery will be relevant to other systems, and reduce the likelihood that results can be replicated by other researchers.

Ideally, an omniscient, unobtrusive observer would document a continuous record of an animal's activity, an impossible standard to reach. Nevertheless, new developments in mobile video technology come ever closer, acting as electronic stand-ins for human observers of behavior that cannot be observed directly. Animal-borne video and environmental sensors (AVEDs, Moll, Millspaugh, & Beringer, 2007) have shed light on seldom seen feeding behaviors, such as aspects of tool making and use in New Caledonian crows (Rutz, Bluff, & Weir, 2007), food selection by white tailed deer (Beringer, Milspaugh, & Sartwell, 2004), social interactions of white tailed deer (Moll et al., 2009), and the effect of cyanobacterial blooms on green turtle foraging behavior (Arthur, O'Neil, & Limpus, 2007). To understand large-scale patterns, such as the ecosystem effects of consumers, however, individual level foraging events must be interpreted in context with the community of resources.

Combining behavioral and movement data in the development of new technologies, like AVEDs, with other information on the environments where animals forage, such as remote sensing, habitat, and environmental data, can bridge the gap between individual-level behaviors and landscape-level processes (Kays, Crofoot, & Jetz, 2015; Cagnacci, Boitani, & Powell, 2010). Here, I describe an animal-mounted data collection system ("CowPro") and preliminary data from an applied study of free-ranging domestic cattle (*Bos taurus*) movement and foraging behavior in the tropical deciduous forest (TDF) of northwestern Mexico. The CowPro system yielded data on the impact of domestic cattle on the local environment, and is therefore a reliable and relatively inexpensive system that can be applied to study foraging behavior combining movement and diet observations.

1.3 METHODS

1.3.1 *CowPro, an animal mounted data collection system: summary*

A typical observation-based study protocol depending on real-time visual sightings of animals, though simple and inexpensive, can be impractical in forested systems, where dense vegetation can obstruct animal observations unless the observer is very near, yet at close distances, observer presence will almost certainly affect wary animal behavior. If sufficiently small and efficient, an automated camera and GPS system can provide a high level of detail while reducing observer effects. In addition, video files are a permanent, independently verifiable record of movement and behavior, enabling blind data entry and double-blind data analysis, as well as opportunities to exploit other aspects of the videos and GPS data at later date. With an animal-mounted, automated system, researchers can also observe multiple animals simultaneously, and sample animal behavior for multiple consecutive days, which would not have been possible using direct, human observation.

CowPro (Fig. 1-1) is an animal-mounted behavioral and spatial data collection system, designed to collect georeferenced time-lapse videos. The following configuration is optimal for free-ranging cattle or other medium to large-sized domestic or semi-domestic animals, but it could also be applicable for studies on wildlife. CowPro hardware consists of a camera unit, based on the GoPro® action camera platform (Fig. 1-1A), a GPS data logging unit, based on the I-gotU GT120, and a VHF transmitter based tracking and recovery system. I designed CowPro to address the primary limitations of an automated outdoor video system, which are battery life, digital memory, weight, and durability of the unit under field conditions. To maximize the duration of each camera deployment, I used an external 4,000 milliampere-hour (mAh) battery (Fig. 1-1C) and a 64-gigabyte micro SD card, as well as a timer that turns the camera on at a programmable interval (Fig. 1-1B). When activated, cameras access a customized script that interrupts the camera's startup protocol, executes a function, and then shuts down the camera. A customized waterproof case (Fig. 1-1D) protects the camera, battery, timer, and recovery equipment, including a VHF transmitter and sound-activated locator. The small, commercially available GPS data logger, stored separately from the camera box, records location coordinates and metadata. The system is rugged, and able to withstand high temperature, rain, concussion, and abrasion. Availability of used components that would otherwise be prohibitively expensive, such as the GoPro® cameras and Icom IC-R10 wideband receiver, kept overall cost low (Table

1-1).

Figure 1-1. Left: CowPro internals including (A) GoPro® HERO3 Black camera, (B) Cam-Do programmable scheduler, (C) Voltaic battery and SwiTronix USB battery eliminator. Right: External CowPro components including (D) customized Pelican Micro 1030 case, (E) Icom IC-R10 wideband receiver.

System unit	**Part**	**Description**	**Manufacturer link**	**Purchased at**	**Cost (2015)**
Video	Camera	GoPro® HERO3 Black	https://gopro.com	http://ebay.com	$225
Video	Timer and scheduler	Cam-Do Programmable scheduler	https://cam-do.com	https://cam-do.com	$190
Video	Battery	Voltaic 4000 mAh USB battery	http://www.voltaicsystems.com	https://www.amazon.com	$35
Video	Battery to camera link	Switronix USB GoPro battery eliminator	http://www.coreswx.com	https://www.amazon.com	$19
Video	Memory	SanDisk Extreme Plus 64GB Micro SD card	https://www.sandisk.com	https://www.amazon.com	$55
Waterproof	Case	Pelican 1030 Micro waterproof case	http://www.pelican.com	https://www.amazon.com	$16
Waterproof	Screens	GoPro® HERO3 replacement screens	https://www.amazon.com	https://www.amazon.com	$11
Waterproof	Heat shrink tubing	Uxcell 25mm diameter heat shrink tubing	https://www.amazon.com	https://www.amazon.com	$6
Data logging	GPS datalogging unit	I-GotU GT120	https://www.amazon.com	https://www.amazon.com	$60
Telemetry	VHF transmitter	Merlin 1/3n FMV transmitter	http://www.merlin-systems.com	http://www.merlin-systems.com	$95
Telemetry	Handheld wideband receiver	Icom IC-R10	http://www.icomamerica.com	https://www.amazon.com	$245
Telemetry	Yagi antenna	Merlin standard 3 element yagi antenna	http://www.merlin-systems.com	http://www.merlin-systems.com	$145
Telemetry	Signal booster	GRE Super Amplifier 20 decibel signal booster	http://magnumtelemetry.com	http://magnumtelemetry.com	$69

Table 1-1. CowPro detailed components list.

1.3.2 *Setup details*

In video mode, the highest resolution available is 4k (8 megapixel resolution) at 15 frames per second (fps). Slow motion video is available in 720p at 120 fps. All modes are compatible with ultra wide angle, providing approximately 170 degrees field of view. Although 4k at 15 fps and 1080p at 60 fps result in high quality videos under ideal conditions, camera shake from animal movements makes it difficult to clearly identify target plants. Objects in the videos were much clearer in slow motion (at 720p / 120 fps), despite the reduction in video quality compared to higher resolution settings.

For the external batteries and camera-battery links, I used 4,000 milliamp hour (15 watt-hour) 5-volt output external batteries from Voltaic, and USB battery eliminators from Switronix, which allow cameras to be powered from a 5-volt power source. The Cam-Do Programmable Scheduler (CDPS) mounts to the GoPro® 30 pin bus port, and is powered by a small amount of charge pulled from the camera battery that allows cameras to be turned on at programmed intervals. The CDPS also allows users to program an interval during which the timer schedule is active, or to program a delayed start; for example, users can specify the camera to be active only during daylight hours. As of this writing, Blink, a time-lapse and motion-sensing controller, has replaced the CDPS in Cam-Do's product line. As the CDPS and other hardware did not fit in the standard GoPro® waterproof housing, I modified a Pelican 1030 Micro waterproof case by cutting a hole in the upper right hand corner, and gluing in place a GoPro standard housing replacement lens with marine epoxy (Fig. 1-1D).

1.3.3 *GPS data logging units*

Following the example of Allan, Arnould and Martin (2013), I used I-gotU GT 120 data loggers from Mobile Action Technology. In addition to decimal degree coordinates, the single-button GPS data loggers also record date, time, elevation, speed between points, and number of satellite fixes. To maximize battery life, I programmed GPS units to record one point every 45 seconds. Recording 10- or 20-second videos results in a maximum misalignment with a given video time stamp of ± 17.5 and 12.5 seconds, respectively. To waterproof the data loggers, I encased the GT 120 data loggers in two layers of 25mm diameter heat-shrink tubing.

1.3.4 *GPS error calculation*

The maximum amount of position error (*pe,* the distance between a GPS point and the true location of a feeding event) is a function of the travelling speed of the animal (velocity, *v*, in kilometers per hour), the GPS recording interval (*r*), and the duration of the video (time video, *t*, in seconds). Subtracting *t* from *r* gives the total length of time during which a GPS point may be recorded while the camera is dormant. (*r* – *t*). As the video can match either the point before or after it, divide the difference between *r* and *t* by two. Finally, the native error *e* of the GPS chip is also a parameter to estimate the position error using the following equation (Eq. 1-1):

$$pe = (v * [r - t]/2) + e$$

Equation 1-1. Maximum position error (*pe*) between logged GPS points and true location of video-recorded behavior.

1.3.5 *Recovery and tracking system*

I used radio telemetry equipment both to locate animals carrying cameras, and as a safeguard to recover cameras lost in the course of recording. Unlike most transmitters designed for locating wildlife, the Merlin Systems 1/3n FMV transmitters in this study, designed for falconry and model rocketry, use replaceable 1/3n lithium batteries, with an individual lifespan of roughly 45 days. These were sufficiently powerful, inexpensive, and convenient for this research. I cut the 13 inch antennas to 8 inches in length in order to weatherproof them and make them more resistant, sacrificing a small amount of transmission power. To track cameras in the field, I used an Icom IC-R10 wideband receiver, Merlin Systems folding three element Yagi antenna, with a GRE Super Amplifier 20db signal booster.

1.3.6 *Time lapse automation: autoexec hack for H3B*

On startup, a H3B will boot to the most recently used camera settings and wait for the user’s input. However, the GoPro® user community (in particular, GitHub user Konrad Iturbe http://chernowii.com) discovered that a file with the name autoexec.ash containing commands written in Ambarella shell (ash), placed on the camera's SD card, can allow a user to access hidden camera functions not found in the graphical user interface. I used custom ash files adapted from scripts published on http://cam-do.com and http://chernowii.com to interrupt the camera's startup protocol and automatically take a video, photo, or turn on the camera's WiFi. The protocol I used most frequently was: 1) Camera ON (user or CDPS); 2) 10 or 20 second video; 3) 5 second delay (to allow the video file to be transferred to the camera's SD card); 4) Camera OFF. Using the CDPS, I programmed the unit to repeat the protocol every half hour from sunrise to sunset until the camera battery died or I manually shut down the camera. Autoexec scripts are available as supplementary materials of this article.

1.3.7 *Matching GPS coordinates to videos*

After downloading GPS and video data, I used the unique time and date information recorded as metadata on each video and GPS point to assign coordinates to all videos, using a customized matching program scripted in R. For a given video, the program subtracts the date and time of each GPS point from the video's date and time, appending the coordinates and metadata associated with the least difference into a CSV file (Table 1-2). R script for the matching algorithm, sample GPS track logs, and sample videos are available as supplementary materials.

Step	Data Type	Program or Language	Purpose	Description	Notes and code
1	Video	Mac Terminal (Bash shell)	Data conversion	Export file names, date and time from video files as TXT file with name <contents.txt>	`Ls –l > contents.txt`
2	Video	Sublime Text	File type conversion	Convert <contents.txt> to CSV using regular expressions	Find: `(\w+)\s*(\d{1,2})\s(\d{1,2}:\d{1,2})\s(\w+)` Replace: `\1\t\2\t\3`
3	Video	Manual	Data entry	Score video for feeding	Also score other behaviors, number of other cows in frame, species ID notes
4	GPS	igotu2gpx	File type conversion	Download GPX data from GPS	igotu2gps allows GPX file download to Mac OS. iGotU proprietary software is PC-only, and necessary to program new data collection schedules and erase GPS data.
5	GIS	Google Earth Pro (GEP)	Data visualization	Upload GPX into Google Earth Pro (GEP)	Shows spatial clustering and distribution of feeding events
6	GPS	GPS Babel	File type conversion	Convert GPX to TXT document	GPS Babel works without an internet connection.
7	GPS	Sublime Text	File type conversion	Convert TXT to CSV using regular expressions	Find: `(\d+,)(\d{1,2}\.\d*,)(-\d{1,3}\.\d*,)(\d+\.\d*,)(\d*\.\d+,)(\d*,)(\d{1,4}\S\d{1,2}\S\d{1,2},)(\d{1,2}:\d{2}:\d{2})(\.*\d*)` Replace: `\1\t\2\t\3\t\4\t\5\t\6\t\7\t\8\n`
8	GPS	R	Data conversion	Convert GPS times from GMT to MST	Script subtracts 25,200 seconds (7 hours) from all GPS times in GPS data CSV created in Step 2
9	Video + GPS	R	Combine data	Export as CSV	For loop subtracts all GPS times from each video time from video CSV (step 7), creates a vector of minima, appends times and metadata to video data frame
10	Video + GPS	R	Subset data	Export as CSV	Creates subset of data containing feeding on woody vegetation.
11	GIS	Google Earth Pro	Data visualization	Upload CSV into GEP	Create routes in GEP to efficiently access points in the field.
12	GPS	Garmin eTrex Vista C	Data entry	Upload coordinates into handheld GPS unit	Average of 20 points into a handheld GPS unit to search for during a day of field work
13	Video	iMovie	Data conversion	Compress .MP4 videos and add title screens	Convert original .MP4 video files to a smartphone-friendly format, add title screens with video name, date, and animal tag number for reference in the field.
14	Video	Manual	Data visualization	Upload MP4 files to iPhone	Upload compressed videos to an iPhone 5 to visually ground-truth eaten plant locations. I ground truthed 142 of 160 plots (~ 89%)

Table 1-2. Steps and programs to append GPS data to video data, score video, select a subset of points for plant census plots, upload to a GIS system, and generate data files.

1.4 APPLICATION EXAMPLE

1.4.1 *Foraging behavior of free-ranging cattle in tropical dry forest of Sonora, Mexico: a case study*

In the Alamos municipality, in the western foothills of the Sierra Madre Mountains in Sonora, Mexico, cows range freely on ranches containing a patchwork of primary and secondary TDF. Usually, cattle are grazers, preferring to eat grasses, forbs, and other relatively high-nutrient value vegetation. However, when ranched in predominantly forested ecosystems, cattle become facultative browsers, feeding on a wide range of woody plants, in addition to preferred vegetation types. Cattle preferences for woody plant forage species, and the effect of cattle browsing on TDF diversity and community structure, are not currently understood.

I used CowPro and plant census quadrats to collect data capable of testing a set of hypotheses on cattle foraging behavior and its potential impacts on tree community structure. I mounted CowPro camera units below the lower jaws of 20 individual cows, hanging by heavy duty cable ties from existing cow bell collars (Fig. 1-2), and data loggers at 180 degrees, nearer to the cow's nape, to improve satellite receptivity. Cows then ranged freely throughout the available habitat within a ranch division, their movements tracked by the GPS data logger (Fig. 1-3; sample track logs are available as supplementary materials) and behavior sampled by the CowPro camera (sample videos available as supplementary materials). After running for 5-7 days, I removed the cameras and data logging units and either replaced them on the same cow with fresh units, or after two consecutive running periods on the same cow, placed fresh units on new individuals in the herd.

Figure 1-2. Example of CowPro deployment and placement for foraging behavior research (red arrow). Ranchers in southeastern Sonora use bells (blue arrow) to locate cows as they range freely in ranch divisions.

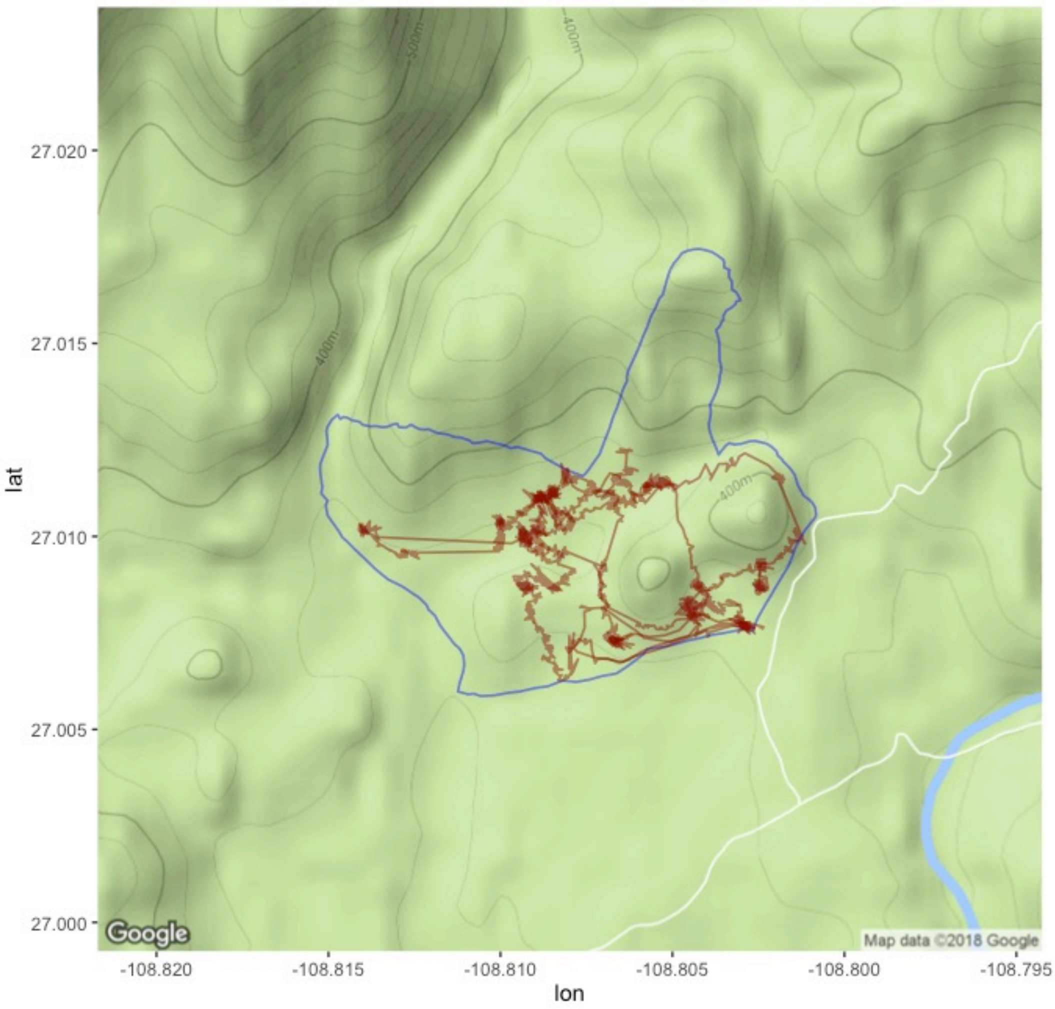

Figure 1-3. Map showing the tracklog of a study animal (red line) ranging in an 88.5 hectare division of Rancho El Brasilito (blue outline), in Álamos, Sonora, Mexico. Between the November 30 and December 4, 2015, the GPS unit logged 6,784 points. Clusters of points, indicating favored areas, are visible. Image produced using ggmap (Kahle & Wickham, 2013).

Between August and December 2015, and again between July and September 2016, I recorded 4,723 10- and 20-second videos of cow behavior for 22 unique cows. Excluding outliers, data loggers averaged 5,762 fixes over the course of 4.27 days (Table 1-3). The sampling interval I used was one 10 or 20 second video, repeated every half hour, beginning at or just before sunrise and ending at or just after sunset, over the course of 5-7 days. Using Eq. 1-1 resulted in a predicted mean position error of $pe = 9.003\ m$.

Year	N cows	GPS tracks	N videos	N vid feeding	N vid feed woody	N vid drinking	N vid traveling	N vid ruminate	N vid rest	N vid other
2015	11	23	2555	1356	367	11	111	515	521	41
2016	11	18	2168	1386	438	5	61	301	391	24
Totals	22	41	4723	2742	805	16	172	816	912	65

Table 1-3. Summary of results of the example study including number of study animals, GPS tracklogs, and videos showing feeding, drinking, traveling, ruminating, resting, and other behavior, recorded in 2015 and 2016. Other behaviors include interspecific interactions and interactions with humans.

Of the 10- and 20-second videos, 2,742 (58%) contained feeding behavior, and 805 (30% of all feeding videos) were of cows feeding on woody vegetation. I scored videos manually, and recorded one of the following behaviors per video: feeding, drinking, traveling, ruminating, resting, and other (which included interaction with other cows or people). When possible, I recorded the genus and species of the plants the cow was eating, as well as growth habit, which included tree, shrub, cactus, liana, perennial or annual herbaceous plants. If a cow ate several woody plant species, I documented the species the cow handled for the longest amount of time; if a cow ate two or more species and spent the same amount of time on each, I recorded the species of the first woody plant the animal consumed.

Results showed that cows range widely through the ranches, although they typically follow fixed routes. They prefer grasses and forbs, but browse on a broad variety of trees, shrubs, lianas, cacti and woody perennial plants. *Croton fantzianus* and *Croton flavescens* (Euphorbiaceae), a common shrub and tree, respectively, together comprise 47% of the woody plants in cow diets. It is noteworthy that *Croton fantzianus* (Euphorbiaceae), the most common woody species by far both in cow diets as well as in the ranch environment, was until this publication considered in the scientific literature to be unpalatable to cows (Felger, Johnson, & Wilson, 2001), despite its broad recognition by ranchers as an important cattle forage species. This otherwise trivial finding underscores both the lack of detailed research on domestic animal foraging in natural environments, as well as the value of local expertise.

Overall, the ratio of woody to annual plants in cow diets remained fairly stable in July, August, September, and October (Fig. 1-4). This finding is intuitive, as leafy green woody vegetation is available to cows for nearly the entire duration of the monsoonal rainy season, from late June until mid to late October. In November, the cessation of rain triggers rapid leaf loss in deciduous tree species, as well as annual plant dieback. Notably, cows in November and December eat large quantities of leaf litter, dead annual vegetation, twigs, and dried leguminous fruits (Fig. 1-4), a previously unreported phenomenon.

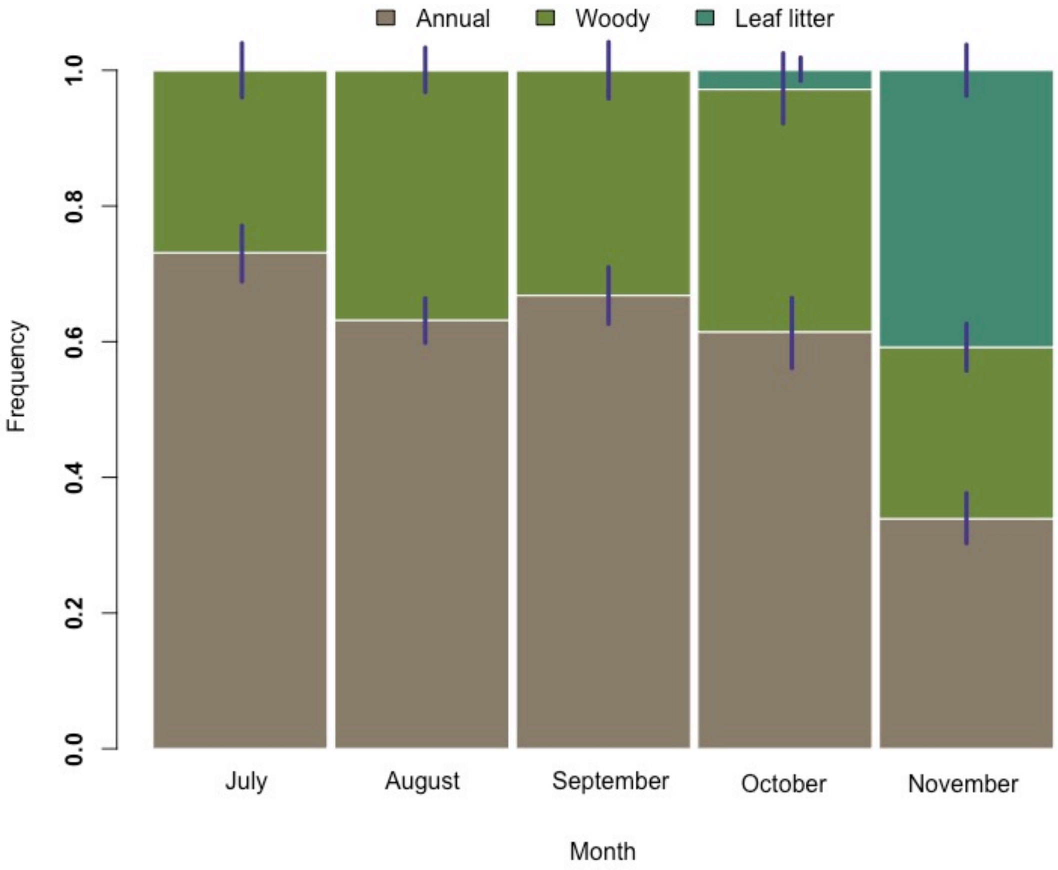

Figure 1-4. Frequency of vegetation type in cow diet by month from July through November, with bootstrapped 95% confidence intervals. The monsoonal rainy season in southeastern Sonora begins at the end of July, and lasts through October. The frequency of woody vegetation in cow diets (green) is relatively stable throughout the summer, but decreases, along with annuals (brown), as the dry season begins. By November, over 40% of cow diet consists of leaf litter (blue).

1.5 DISCUSSION

In the configuration I describe, CowPro is a robust data collection system capable of providing highly detailed, accurate information on free-ranging herbivore behavior. My use of the system in 2015 and 2016 on free-ranging cattle in Sonoran TDF resulted in a large, spatially explicit movement and foraging dataset, as well as several novel notes on cow browsing behavior in TDF. As all incidences of browsing captured by CowPro were georeferenced, I was able to return to the exact locations of browsing behavior, and record habitat data in the form of quadrat censuses, allowing for comparisons of species frequencies and community diversity in cow diets to diversity and evenness in their preferred foraging habitat.

CowPro is composed of commercially available, easily sourced components and open source software (scripts available as supplementary materials). Most components, like the GoPro® camera at the heart of the system, are meticulously engineered products stemming from industries catering to markets where competition reduces consumer costs. In 2015, a CowPro camera unit and GPS cost just $700 in parts, far less than purpose-built wildlife camera collar units. Low cost makes the prospect of fine-grained, systematic data on animal behavior attainable to students, early career researchers, conservation professionals, and other resource limited user groups.

GPS battery life and durability were the primary limiting factor determining a camera unit's active length of time and maintaining a regular data collection schedule. According to the manufacturer, the GT120 is capable of logging over 10,000 points in its memory. Modifying the unit with a higher capacity external battery, as in Allan, Arnould and Martin (2013), could allow researchers to deploy the unit for longer periods. Because of this, cattle were an ideal model system to test CowPro. However, with a professional wildlife GPS unit in addition to the portable camera, CowPro could run up to 16 days on a 20s/30min video length/time lapse interval. Improvements in camera battery capacity and size could extend length of deployment even beyond the 16-day length I achieved in field trials. At 500 grams, CowPro is less than half the weight of an average GPS collar appropriate for cows, like the 1.2 kilogram (kg) Lotek 3300, used by Augustine and Derner (2013). Large herbivores and omnivores, like elk (*Cervus canadensis,* average weight of a Rocky Mountain subspecies cow/bull: 255 and 331kg, respectively) (Quimby & Johnson, 1951) could easily carry a CowPro unit plus a commercial GPS collar. 0.5kg is also under the recommended maximum of 3% body weight for an average American black bear (*Ursus americanus*, average weight of a California sow/boar: 57 and 94kg, respectively) (Jonkel & McT. Cowan, 1971). CowPro therefore opens the possibility of exploring diet and movement behavior of a large range of wildlife and domestic animals.

1.6 SUPPLEMENTARY MATERIALS

1.6.1 Video and GPS matching program: R script

https://github.com/charliedlr/CowPro/tree/master/S1_matching_program/video_GPS_matching.R

```
######################################################################################
This script combines camera data (manually entered into datasheet.csv) and GPS data
(downloaded as GPX, converted to TXT with GPSBabel, then cleaned up with regular
expressions in Sublime Text.
## Charlie de la Rosa and Katie Gostic -- August 2015 -- Alamos, Sonora, Mexico
######################################################################################
rm(list = ls())
require('chron')

# upload video and GPS data
videos = read.csv('~/File/Source/video_datasheet.csv', stringsAsFactors = FALSE,
header = TRUE, sep = ",", quote = "\"", dec = ".", fill = TRUE) # import video master
data sheet.
```

```r
gps.tracks = read.delim('~/File/Source/gps_data.csv', header = TRUE, sep = "\t", stringsAsFactors = FALSE) # import GPS data as a tab delimited file

## TIME CONVERSION
vid.times = as.POSIXlt(paste(videos$Date, videos$Time, sep = ' '))
gps.times = as.POSIXlt(paste(gps.tracks$Date, gps.tracks$Time, sep = ' '))

# for Mountain Standard Time, i-GotU gps time stamps were offset by 7 hours (25200 seconds). Correction:
gps.times = gps.times - 25200

# initialze data frame for for loop output
# 5 columns pulled out of gps_data: latitude, longitude, elevation, speed (between points), number of satellites. time.gps and time.dif are the GPS point time data, and the difference between the minimum GPS and video date-and-time data.
lat = vector()
lon = vector()
elev = vector()
spd = vector()
sat = vector()
time.gps = vector()
time.dif = vector()

# For loop with matching algorithm
for (ii in 1:length(vid.times)){
  use.this.gps.row = which.min(abs(vid.times[ii] - gps.times)) # this gives the row number of the minimum value after subtracting all gps time values from a given video time; that is, the gps point closest in time to the video time stamp
  time.gps[ii] = strftime(gps.times[use.this.gps.row], format = "%Y-%m-%d %H:%M:%S") # strftime specifies that it's time and sets format.
  lat[ii] = gps.tracks[use.this.gps.row, 2]
  lon[ii] = gps.tracks[use.this.gps.row, 3]
  alt[ii] = gps.tracks[use.this.gps.row, 4]
  spd[ii] = gps.tracks[use.this.gps.row, 5]
  sat[ii] = gps.tracks[use.this.gps.row, 6]
  time.dif[ii] = difftime(vid.times[ii], gps.times[use.this.gps.row], units = 'sec') # difftime allows you to figure out differences between time stamps and outputs in the units you want, here seconds.
}

gps.info = data.frame(latitude = lat, longitude = lon, elevation = elev, speed.km.h = spd, sats = sat, vid.times = vid.times, nearest.time.gps = time.gps, time.dif.secs =
```

```
time.dif) # data frame of all the objects together
#sats = sat,

videos = data.frame(videos, gps.info) # attach gps info to the videos master file

## Write a new file (change name each time)
write.csv(videos, file = '~/File/Source/video_with_GPS_data.csv')

## Split out only videos with useable GPS points, where the difference between the
video and GPS time stamp is less than or equal to 45 seconds
 vid.for.map = videos[which(abs(videos$time.dif.secs) <= 45),]

###########################################################
```

1.6.2 GoPro® HERO3 Black time-lapse protocol: Ambarella Shell (ash) scripts

https://github.com/charliedlr/CowPro/tree/master/S2_ash_scripts

```
##############################################################
#  Shoot 10 second video, wait 20 seconds, turn off camera   #
#             03. Jul 2016 Charlie de la Rosa                #
##############################################################

sleep 5
t app button shutter PR
sleep 20
t app button shutter PR
sleep 5
t app button power P
sleep 2
t app button power R
```

1.6.3 Cow GPS track logs: Tab separated value files

https://github.com/charliedlr/CowPro/tree/master/S3_GPS_track_logs

1.6.4 CowPro video data: CSV file

https://github.com/charliedlr/CowPro/tree/master/S4_video_data

1.6.5 Sample CowPro videos: m4v files

https://vimeo.com/charliedlr

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CHAPTER 2

Free-ranging cattle foraging at different scales: cows that browse choose the forest, and the trees.

2.1 ABSTRACT

Domestic cattle (*Bos taurus*) seasonally browse trees in the Mexican tropical deciduous forest (TDF), raising the possibility that woody plant browsing by cows might negatively impact tree abundance and diversity in the TDF. However, few researchers have quantified cattle foraging preferences for woody plant species or tested hypotheses about the impacts of cattle browsing on TDF. Here, I describe dietary preferences and movement in relation to foraging habitat selection of free-ranging cattle in TDF.

To determine if cows are selecting or avoiding individual woody plants (trees, shrubs, cacti, lianas, and herbaceous perennials) or habitats at the landscape level, I ask: (1) how similar is the diversity of woody plants in cows' diet to the diversity of woody plants in repeatedly visited foraging habitat? And (2) are woody plant diversity and species composition different in foraging areas from diversity and species composition across all habitats available to foraging cows?

To answer these questions, I compared data generated by CowPro video and GPS to record cattle feeding behavior and movements, as well as arrays of 5m x 5m plant census plots at two scales:

on known cow foraging paths, and across all available cattle habitat within ranches in the TDF. Analyses of foraging and plant census data show that cows select and avoid certain species at the individual-plant level, although overall, the relative abundance of a given plant species in cow foraging habitat is the best predictor of the importance of that species in cow diet. Plant species relative abundances differ even more between foraging habitat compared to all habitats available for cow foraging. This indicates that cows select habitats in which to forage, as well as individual food items.

A priori, forested ranches (silvopasure), where livestock range in largely unaltered habitat, seem a much preferable alternative to intensive ranching where trees are replaced with forage crops, but management of silvopasture for conservation requires an understanding of the type and degree of cattle impacts on forest community structure. Land in this study system is currently managed as a mosaic of privately owned silvopasture and cattle-free conservation landholdings. In order to provide economic opportunities and build relationships with local ranchers, conservation land managers are actively exploring the introduction of cattle to some conservation lands, a strategy that has played out successfully in other parts of the world. To achieve conservation goals in a complex global economic and ecological landscape, silvocultural management plans must incorporate both community and scientific input. Methods and analyses of forest-dwelling cattle foraging habits, as detailed in this study, can help environmental managers make effective, data informed decisions.

2.2 INTRODUCTION

2.2.1 *Background: cattle ranching*

Over 27% of the Latin American and Caribbean landscape is dedicated to cattle ranching, a major driver of deforestation in the region (Murgueitio et al., 2011). The management of large herds of livestock, introduced to the Americas by Spanish and Portuguese colonists, evolved rapidly during the Industrial Revolution, and has since been responsible for dramatic environmental changes in the region. Specific examples are many, and include widespread deforestation for pasture development, as in the Amazonian basin (Soares-Filho et al, 2006, Walker et al., 2000), displacement of native species, such as black-tailed prairie dogs (O'Meilia et al., 1982), disease transmission, as with elk and bison in Yellowstone to (and later, from) wild bison and elk (Meagher & Meyer, 1994), and type conversion of native ecosystems, as exemplified by the reduction in native Sonoran Desert species due to non-native forage grass introductions (Franklin et al., 2006).

Pastoral systems in which small numbers of cattle forage in natural areas, however, have changed relatively little in modern times. Low-density livestock management on otherwise undisturbed or lightly managed lands is an ancient but widespread practice across the developing world (Perramond, 2010, Griscom et al., 2009, Kaufmann et al., 2013). Recently, small-scale agricultural schemes are attracting scientific interest as a means to sustain both biodiversity and local economies. For example, low-density grazing by mixed herds of domestic herbivores resulted in increased populations of breeding passerine birds in the UK (Evans et al., 2006). In Kenya, cattle diet did not overlap with that of donkeys, a hindgut fermenting equid (in the study, a stand-in for native zebras), and in low-density mixed grazing scenarios, facilitated weight gain in each other (Odadi et al., 2011). A 33% expansion in global silvopasture, where livestock graze in areas of mixed pasture and forests, could potentially result in a 31 gigaton reduction in CO2 emissions by 2050, as proposed by Paul Hawken in his proposal to reverse global warming (Hawken, 2017). In fact, the European Union has incentivized agroforestry in recent years with environmental policies (Mosquera-Losada et al., 2012). As interest in cattle silvoculture increases, so too does the need for research on cattle impacts to forest systems.

2.2.2 *Background: herbivory*

Ecologists generally classify ruminants as grazing, browsing, or intermediate / mixed feeders, based on physiological characteristics (Hofmann, 1989) or post hoc behaviors. Hofmann's predictions of foraging behavior based on anatomical differences frequently fail to find support in nature (Robbins et al., 1995; Gordon, 2003). Nonetheless, cattle are fore-stomach digesting herbivores that predominantly feed on plants whose nutritive value lies in their cell walls, like grasses, and as such researchers usually classify them as grazers (Hofmann, 1989, see Figure 2; Shipley, 1999; Clauss et al., 2008; Gordon & Prins, 2008). Many field studies document cattle preference for grasses and forbs over other vegetation types: in a mixed forest unit, Roath and Krueger (1982) found that grassy bottomlands, despite accounting for only 2% of the unit's area, contributed 81% of forage consumed by cows. Free-roaming cows in the Blue Mountains of eastern Oregon also consumed more grasses than woody shrubs, despite the fact that shrubs were more abundant (Holechek et al, 1981). And in Greek oak forests, cattle exclusively browsed herbaceous material, significantly reducing herbaceous biomass in grazed plots versus ungrazed, but having no impact on woody species (Papachristou et al., 2005).

Under certain conditions, cattle will browse facultatively, sometimes feeding on a wide range of woody plants, as I document in this study. Hereafter, the terms “woody plant(s)” or “woody vegetation” refer to trees, shrubs, lianas, cacti, and some perennial herbaceous plants. In forests where grasses and herbaceous plants are less abundant, cattle may browse more woody plants, as documented by Ralphs and Pfister (1992). High stocking rates (a measure of per unit forage production divided by animal demand over time, [Holechek, 1988]) can deplete preferred vegetation in habitats with mixed woody and annual plants, resulting in cattle diet shifts (Senft, 1989). When stocking rates are low, seasonal availability of grasses and forbs may correlate with changes in feeding strategies, as observed by Vila and Borrelli (2011) in a Patagonian forest, and de la Rosa (2018a, see Figure 4) in the tropical deciduous forest (TDF) of southeastern Sonora, Mexico.

Cattle browsing can affect tree regeneration (Vandenberghe et al., 2007), and it is possible that cattle foraging reduces species richness by causing competitive elimination of tree species preferentially browsed by cattle. On the other hand, foraging pressure may influence species composition, percent cover, stem class size differences, and other forest characteristics, without affecting species richness. A study comparing heavily grazed communal lands and lightly grazed commercial lands in succulent Karoo on opposite sides of a fence line in Namaqualand, South Africa, showed that species diversity was roughly the same in paired plots. Nevertheless, perennial cover was 20% higher in lightly grazed plots, and annual cover was 11% higher in heavily grazed plots (Todd & Hoffman, 1999). And Breceda et al. (2005) found that the growth habit of mauto (*Lysiloma divaricatum,* Fabaceae), a common leguminous tree in the TDF of northwestern Mexico, varies significantly in height and basal diameter between ungrazed and grazed areas, where they are stunted due to cattle herbivory.

Understanding the impact of cattle browsing on forests is impeded by lack of understanding of dietary preferences of free-ranging, browsing cattle. Cafeteria, smorgasbord, or free-choice experiments, where animals are allowed to select from a controlled range of food options, can provide estimates of degree of preference for certain foods (Stewart & Dunsdon, 1998; Schmidt et al., 2001), as well as show relationships between plant functional traits and herbivory (Caldwell et al., 2015), and show seasonal differences in palatability of a forage crop (Stobbs, 1997), but have limited power to predict herbivore choices in a mixed environment (Tribe, 1950, Pérez-Harguindeguy et al., 2003, Pollock et al., 2007). In forest-dwelling cattle, foraging preference on woody vegetation is complicated by the variable but typically low nutritional value of acceptable browse material, the potential for toxicity, the spatial patchiness of browse material, behavior of conspecifics, and other factors.

Palatability is the relationship between a food's taste (the texture, taste, and odor of food), and post-ingestive feedbacks that can be positive, due to nutritional benefits, or negative, due to toxic chemicals (Provenza, in Stephens et al. (eds), 2007). Palatability of woody plants to cows are potentially influenced by plant anti-herbivore defenses. Most plants have evolved under at least some feeding pressure from herbivores, resulting in a wide range of defensive traits (Howe & Westley, 1988). Plant defenses are usually grouped as either mechanical or chemical, although there area cases of overlap, as with the sticky, toxic sap of plants in the genus *Bursera* (Burseraceae) (Becerra et al., 2001). Mechanical defenses are structures that cause injury to a potential consumer, such as spines, or that prevent the plant from being eaten, such as very thick bark, or sticky sap. Chemical defenses operate in a similar, but more complex way. Plants produce a wide range of secondary metabolites, such as alkaloids, tannins, terpenes, polypeptides, amines, saponins, among many others, which are unpalatable, toxic, or inhibit digestion in herbivores. Some of these compounds are profoundly toxic and can cause death if ingested, such as mimosine, in *Leucaena glauca* (Fabaceae), when fed to rabbits (Freeland & Janzen, 1974).

Herbivory on chemically defended plants has resulted in herbivore counter strategies to detoxify or eliminate toxic plant products (Freeland & Janzen, 1974), with the result that many herbivores are capable of obtaining nutrients from plants which are toxic to other animals. Small herbivores with low food requirements, such as koalas, can afford to develop specialized diets and evolve ways to detoxify their specific host plants. However, large herbivores that have requirements for a large amount of food achieve this by having a very diverse diet, such that the toxin load per unit body weight from any one plant species is reduced. Cows, as large herbivores, presumably reduce their toxin load by diversifying their diet of plant foods. By constraining herbivore diets, plant defenses contribute to both plant and herbivore community structure (Freeland & Saladin, 1989).

In plant communities with high diversity and high species turnover from one location to the next, large herbivores face a complex foraging landscape with many potential food choices. Herbivore foraging decisions occur at multiple spatial scales (Senft et al., 1987): animals must discriminate between toxic and palatable plants within reach, at the foraging station level (Goddard 1968), and, when plants are patchily distributed, they must focus their foraging efforts on areas with preferred food species. With herbivores, selective bias can thus occur at multiple scales, towards or against food items or habitat components. Assuming that herbivore foraging can lead to differential mortality in consumed plants, the spatial scale at which herbivore preference operates would dictate the patchiness of herbivore impact on plant communities.

2.2.3 *Background: tropical deciduous forest*

North American TDF is a seasonally deciduous, monsoon-driven ecosystem that occurs along the Pacific slope of Mexico and Central America. In Mexico, TDF is widespread, occupying an estimated 15.6 million hectares (Martínez-Yrízar et al., 2000) and supporting local economies based on abundant natural resources (Yetman & Van Devender, 2002). Still, TDF is the least studied and most threatened of tropical forest types (Janzen, 1988): an estimated 60% of TDF in Mexico had been clearcut by the 1990s (Trejo & Dirzo, 2000).

TDF near Pueblo de Álamos, in the state of Sonora, Mexico, constitutes the northernmost extent of TDF in the Americas. In the foothills of the Sierra Madre Occidental Mountains, TDF grows in rocky soils between 300 and 1200 meters of elevation, and is surrounded by thorn-scrub to the west, Sonoran desert north of Guaymas, and at high elevations, pine and oak-dominated forests. TDF near Álamos receives 500-900 mm of rainfall annually, the heaviest rains beginning in late June, and ending in mid-September (Martinez-Yrízar et al., 2000). Beginning with the onset of the summer monsoon, local ranchers move cattle between fenced divisions in their ranches. Besides property limitations, ranch divisions demarcate different physiographic and hydrological features that provide different forage resources for free-ranging cattle throughout the year. Cattle may directly impact TDF species richness and abundance through browsing, trampling, or soil compaction (Álvarez-Yépiz et al., 2008, Stern et al., 2002); however, to date, no research has incorporated empirical data on cattle diet, or foraging theory models, into studies comparing areas with and without cattle.

2.3 QUESTIONS AND HYPOTHESES

The purpose of this study was to test hypotheses on patterns of cattle selective foraging and impacts on a diverse forest community, the tropical deciduous forest (TDF) of southeastern Sonora, Mexico. I used cow foraging and vegetation census data to statistically test hypotheses on cattle selective foraging on woody plants, by comparing species frequencies and diversity of woody plants in cow diet (WPC), versus repeatedly visited foraging habitat (RVFH). Then, to test hypotheses on unique characteristics of repeatedly visited foraging areas, I compared RVFH data to species frequencies and abundances in an array of plant census plots evenly distributed across all available habitat to cows (AAH).

2.3.1 *Question 1: are cows picky eaters at the individual woody plant level?*

Local ranchers know of cattle browsing on woody vegetation, and they regard certain species of tree and shrub to be desirable cattle forage during the rainy monsoon season. However, to date no research has quantified cattle preferences for woody vegetation in Mexican TDF. Thus, my first goal was to determine if cows are selecting (or avoiding) particular species of woody plants (trees, shrubs, herbaceous perennials).

Given that cows range freely within fenced, forested divisions of ranches, and that a percentage of their diet consists of woody plant vegetation, patterns of cattle selection for or against woody plant species should support one of three hypotheses:

1a. Cows show no foraging bias for or against particular woody plant species, opportunistically feeding on available plants as they encounter them in repeat-visit foraging habitat. The null hypothesis is that cows neither select nor avoid woody plant species, and thus, the diversity and frequency of plants in WPC should be proportional to the diversity and frequency of the same plants in RVFH.

1b. Cows feed primarily on palatable woody plant species, rejecting others. In this scenario, cows feed on a subset of woody plant species, passing over others available to them. Thus, WPC should be less diverse than woody plant diversity in RVFH.

1c. Cows feed evenly across available woody plant species, in order to maximize woody plant diversity in their diet. Evenness is a metric of community diversity that incorporates both number of species and number of individuals (Eq. 2-1). In this scenario, WPC should be more diverse than RVFH, and would mean that cows seek out rare plants, and/or limit their feeding on common plant species. Because tropical forests contain a diverse spectrum of plant secondary chemicals toxic to herbivores (Coley & Barone, 1996), an herbivore's best strategy may be to limit intake of any one species to minimize the herbivore's body burden of species-specific secondary chemicals (Freeland & Janzen, 1974).

$$E_H = \frac{-\sum_{i=1}^{S} p_i * \ln(p_i)}{\ln(S)}$$

Equation 2-1. Shannon's Equitability E_H, a measure of community evenness, is the negative sum of the proportion of species *i* relative to the total number of species, times the natural log of that probability, divided by the maximum diversity possible given *S* species.

2.3.2 *Question 2: Are woody plant diversity and abundance in repeat-visit foraging areas different from diversity and abundance in other accessible areas?*

Plants are often distributed heterogeneously in the environment, and landscape features can affect the nutritional payoff of an herbivore's foraging effort. Thus, some components of an herbivore's habitat will be browsed more frequently than others. Cows spend between 50 and 90% of daylight hours feeding (Kilgour, 2012; de la Rosa, 2018b). A cow's persistent exploitation of particular foraging habitats components intensify her impact on plant abundance and diversity in repeat-visit feeding areas, while reducing her impact on other, less frequently used areas across her overall habitat. Assuming cow impact can be measured in differences in species abundances and frequencies, cow selectivity for particular foraging areas could therefore be measured by comparing species frequencies and community diversity in RVFH, the component of habitat used for foraging, against AAH.

Comparing species frequencies and diversity between repeat-visit foraging areas and all available habitat should result in one of three potential patterns:

2a. There are no statistical differences between woody plant communities in repeat-visit foraging areas and across all available habitat. In the null scenario, cows browse randomly across all available habitat. Since cows use all areas with equal probability, no statistically discernable differences between the null species frequencies and diversity in AAH and the observed species frequencies and diversity in RVFH are detectable.

2b. Repeat-visit foraging habitat is less diverse than all available habitat. Here, cow presence is related to decreases in woody plant evenness in RVFH, as compared to AAH, which could be the result of increased mortality in preferred species of plants. Cow presence could also decrease diversity by trampling sensitive species, compacting or disturbing soil, or altering soil chemistry due to accumulation of urine or feces. Competitive dominance due to differential mortality of plant species in response to cattle could also result in low woody plant evenness.

2c. Repeat-visit foraging areas are more diverse than all available habitat. Greater diversity in areas repeatedly visited by foraging cows could be due to cattle preference for high-diversity habitats, or preference for landscape characteristics that are correlated with high woody plant diversity. Cows could also be avoiding habitat components characterized by low woody plant community diversity, such as monocultures. Alternatively, it could mean that cows increase diversity by transporting weedy species, or releasing competition on species otherwise suppressed.

2.4 METHODS

2.4.1 *Study area*

I conducted this study on two ranches, El Carricito and El Brasilito, in the Alamos municipality of southeastern Sonora, Mexico. Both ranches are adjacent to the Reserva Monte Mojino (ReMM), managed by Naturaleza y Cultura Internacional – Sierra Madre, a nonprofit conservation land management organization. The ReMM and surrounding ranches are situated within the 93,000,000-hectare Área de Protección de Flora y Fauna (APFF) Sierra Álamos – Río Cuchujaqui, a federally managed conservation easement with large areas of conserved primary tropical dry forest. Ranching and other extractive economic practices are regulated but permitted in the APFF.

El Carricito and El Brasilito contain a patchwork of primary forest, secondary forest in states of regeneration ranging from 15 – 40 years, riparian habitat, and managed non-native grasslands. Both ranches are fenced into divisions between 39 and 138 hectares in size, that seasonally hold 30 – 60 head of cattle. Ranchers move cattle every 1.5 – 3 months depending on availability of leafy green vegetation, as well as factors related to husbandry such as calving, milking, and vaccination.

Cows on El Carricito and El Brasilito are multipurpose herds. Most of their economic value comes from the calves, which ranchers sell annually to feedlots in northern Sonora and the United States for finishing and slaughter. Cows also provide milk, cheese, and other dairy products, for personal consumption and local sale. Herds are comprised of mixed breeds, with Charolais, Brangus, Jersey, Zebu, Criollo, and other small, hardy breeds and crosses. Cows in my study were relatively small, averaging an estimated 250-300 kg.

2.4.2 *Power analysis*

In summer of 2014, I collected TDF tree community diversity and stem category data from 49 pairs of 5-meter by 5-meter plant census plots, half of which were in actively ranched forests, and the other half in a biological preserve where cattle are excluded. In each plant census plot, I recorded the species and number of individuals for every woody plant equal to or greater than 1cm in diameter at a height of 20cm (de la Rosa, 2018c). I used TDF species richness and frequency data from the 49 CR plots as test data for a power analysis, to estimate an expected effect size when comparing diversity of woody plants in WPC with woody plants in cow RVFH.

The null hypothesis for a dietary choice study is that foraging individuals randomly choose food items as forage. Thus, in the cow/woody plant system, any given individual woody plant in a plot has an equal probability of being consumed by a foraging cow. If true, the frequency of each woody species in cow diet would be proportional to the frequency of that species in the element of habitat where they forage. However, if cows forage in a way that maximizes woody plant diversity in their diet (alternative hypothesis 1b), any particular species in a plot would have an equal probability of selection, regardless of its relative abundance in the plot.

To model the null hypothesis, I constructed a bootstrapping algorithm that randomly selects a plot from the test data plots with cattle. The computer then randomly selects a random individual plant from among all individuals in the plot, which is stored in a "null" vector. From among all unique species, the algorithm then selects an individual species name from among all unique species occurring in that plot, and stores it in an "alternative" vector. To simulate RVFH, the program compiles a vector of all individual plants occurring in the randomly selected plots.

The length of the null and alternative vectors is *m,* representing potential sample sizes of observations of random and non-random cow foraging.

To compare the number of observations I would need to make in order to statistically detect a difference between random and non-random cow foraging, I wrote an algorithm that bootstraps null and alternative vectors, and simulated RVFH, 1,000 times each for 12 values of *m* (10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 200, and 300). For each simulation, the algorithm calculated community evenness (Eq. 2-1) of the null and alternative vector, and subtracted them from the simulated RVFH, generating a null and alternative hypothesis evenness distributions of evenness differences for each value of m.

As m increases, community differences become more distinct (Fig. 2-1). I achieved power of β = 0.8 at around 180 observations, or individual plants in the null and alternative vectors. I then repeated the analysis modeling a slight increase and decrease in effect size, by sorting test plots into low and high diversity pools (less than and greater than or equal to 10 species), and limited the algorithm to select from these pools. I achieved sufficient power at about 165-185 observations (Fig. 2-2), and thus set a target goal of 165-200 video observations and corresponding foraging habitat plots.

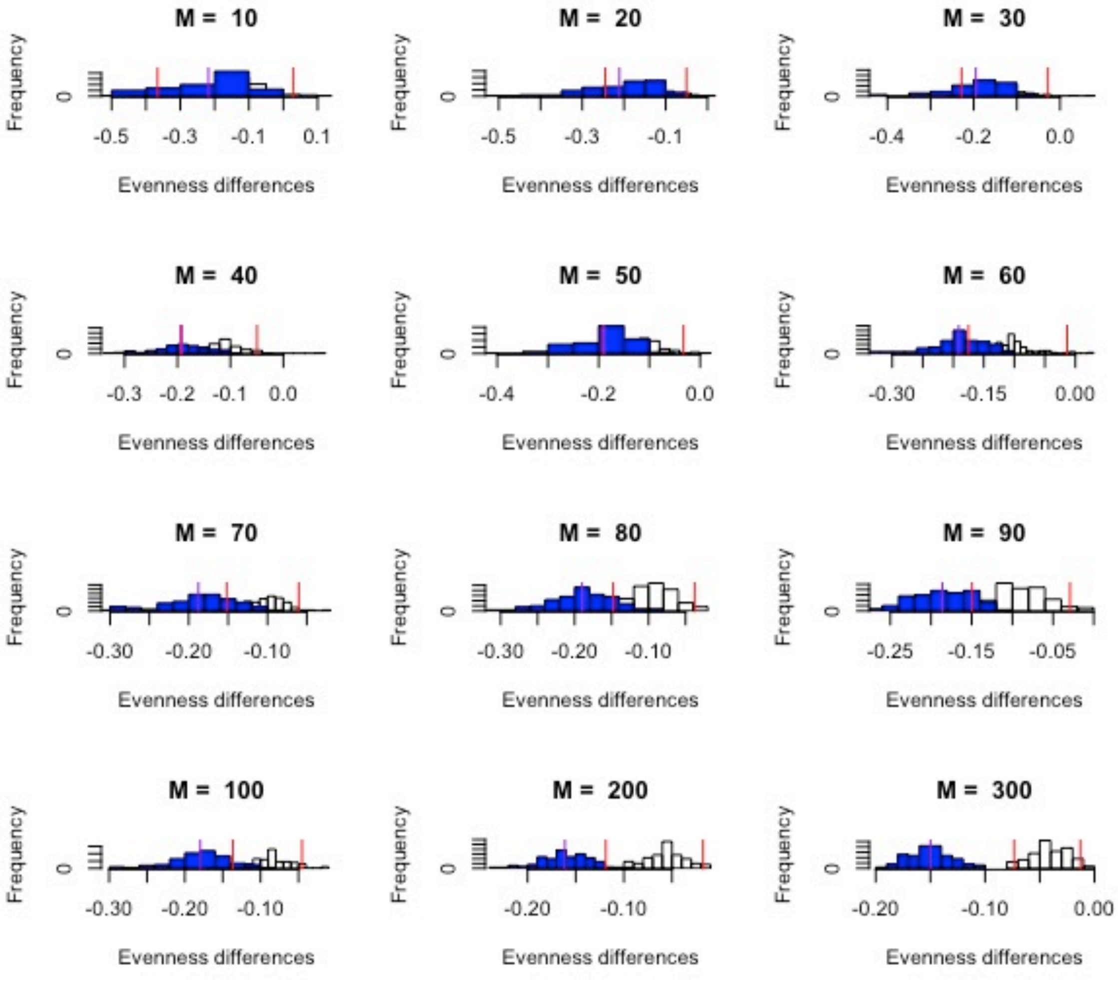

Figure 2-1. Bootstrapped null hypothesis significance tests for different sample sizes (*m)*. Evenness differences between repeat-visit foraging habitat and the alternative hypothesis, which assumes that any species in a 5m x 5m plot has an equal probability of selection, are in blue. The null distribution, which assumes an equal probability of drawing any individual plant from a 5m x 5m plot, is in white. Red lines are 95% confidence intervals. As *m* increases, the probability distributions become more distinct. Confidence intervals of the alternative and null hypotheses are distinct between *m* of 100 and 200 observations.

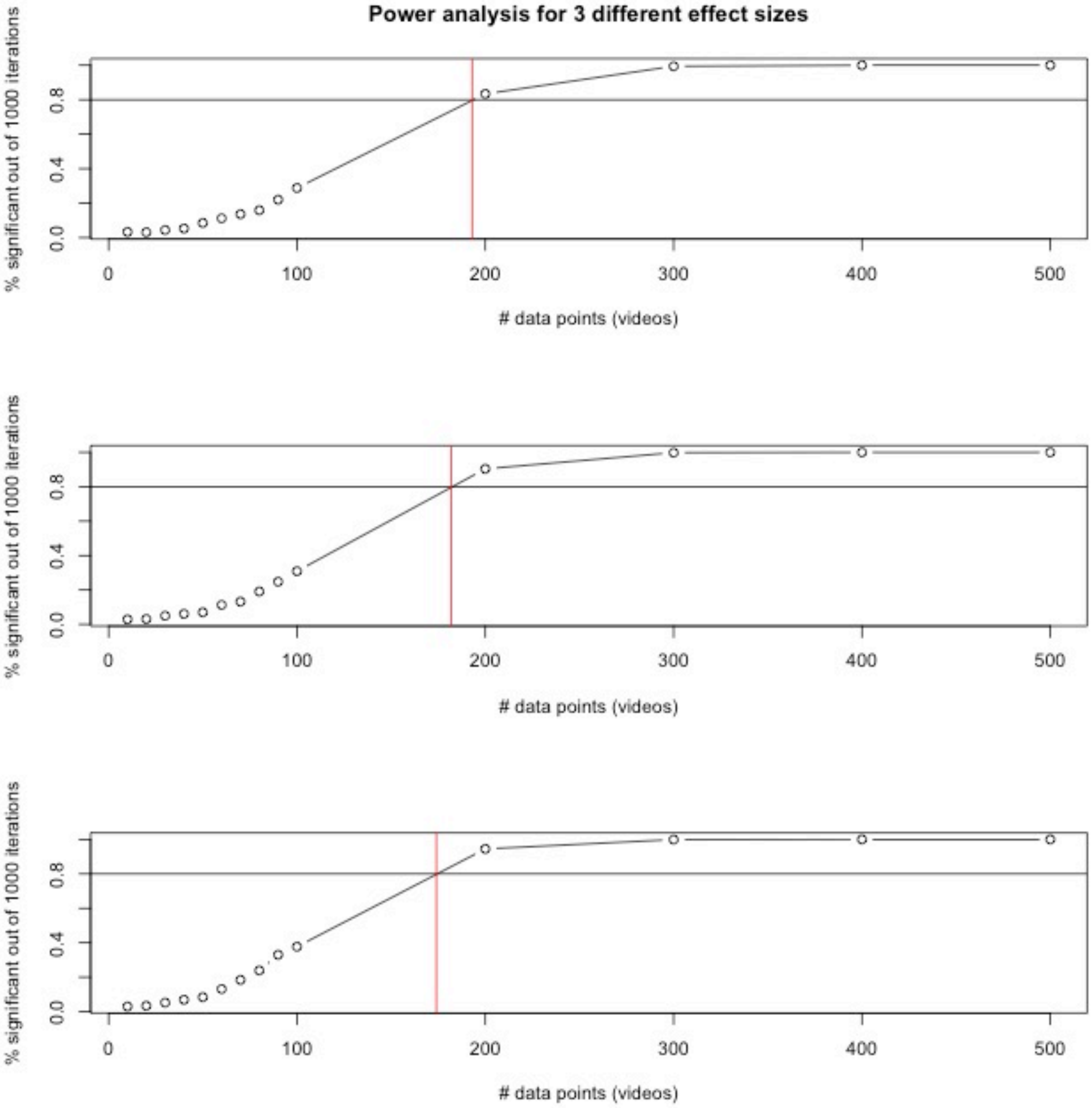

Figure 2-2. Power analysis curves for small, medium, and large effect sizes, top to bottom respectively. On the X axes, the number of data points refer to the number of observations of cow foraging on woody plants, as recorded by CowPro units, necessary to achieve power of $\beta = 0.8$.

2.4.3 *Cattle foraging data: CowPro video scoring and analysis*

CowPro is a customized, animal-mounted time lapse video and GPS system built on the GoPro® action camera platform. The system provides visual and spatial data to give a detailed window into the lives of free-ranging livestock as they interact with their environments. CowPro units consist of a scheduler, timer, external battery, VHF tracking transmitter, and customized scripts that automate functioning in GoPro® Hero 3 Black cameras, encased in waterproof cases. During the rainy seasons of 2015 and 2016, CowPro units collected 778 first-person perspective videos from 20 individual cows, each video containing a foraging event on a woody plant. I programmed a time-lapse schedule of one 20 second video, every half hour, beginning at or just before sunrise and ending at or just after sunset, repeating over 5-7 consecutive days. I determined GPS intervals and run time based on the constraints imposed by battery life, equipment wear and tear, and logistical considerations. At the end of a camera run (defined as the length of time between deploying and collecting a camera and GPS), I removed the camera and GPS from the cow with the help of the owner, and replaced them with fully charged units (de la Rosa, 2018a).

2.4.4 *Repeat-visit foraging habitat data: foraging station plant census plots*

To accurately sample RVFH, I uploaded the coordinates of videos where cows browsed on woody plants into a hand-held GPS unit, as well as compressed copies of videos into a smart phone. Using unique vegetation or landscape characteristics in the videos, I verified the locations of about 80% of the georeferenced feeding locations, meaning I was able to visually find and identify the exact plant browsed by a cow in the particular video. Of sites I was able to find, the average discrepancy between estimated GPS coordinates and the actual verified site was +/- 15m. GPS error, low quality videos, and/or input errors in the GPS unit could account for the 20% of sites that I was unable to verify.

Once I established the location of a browsing event documented by CowPro, I counted, identified, and vouchered herbarium specimens for plants greater than 1cm in diameter at a height of 20cm within a 25m^2 area surrounding the eaten plant (see Appendix II for details on quadrat construction). In total, I recorded plant census data in 165 5m x 5m plots (Fig. 2-3). In addition to hypothesis testing, returning to video documented foraging locations allowed me to confirm identifications of plant species from video.

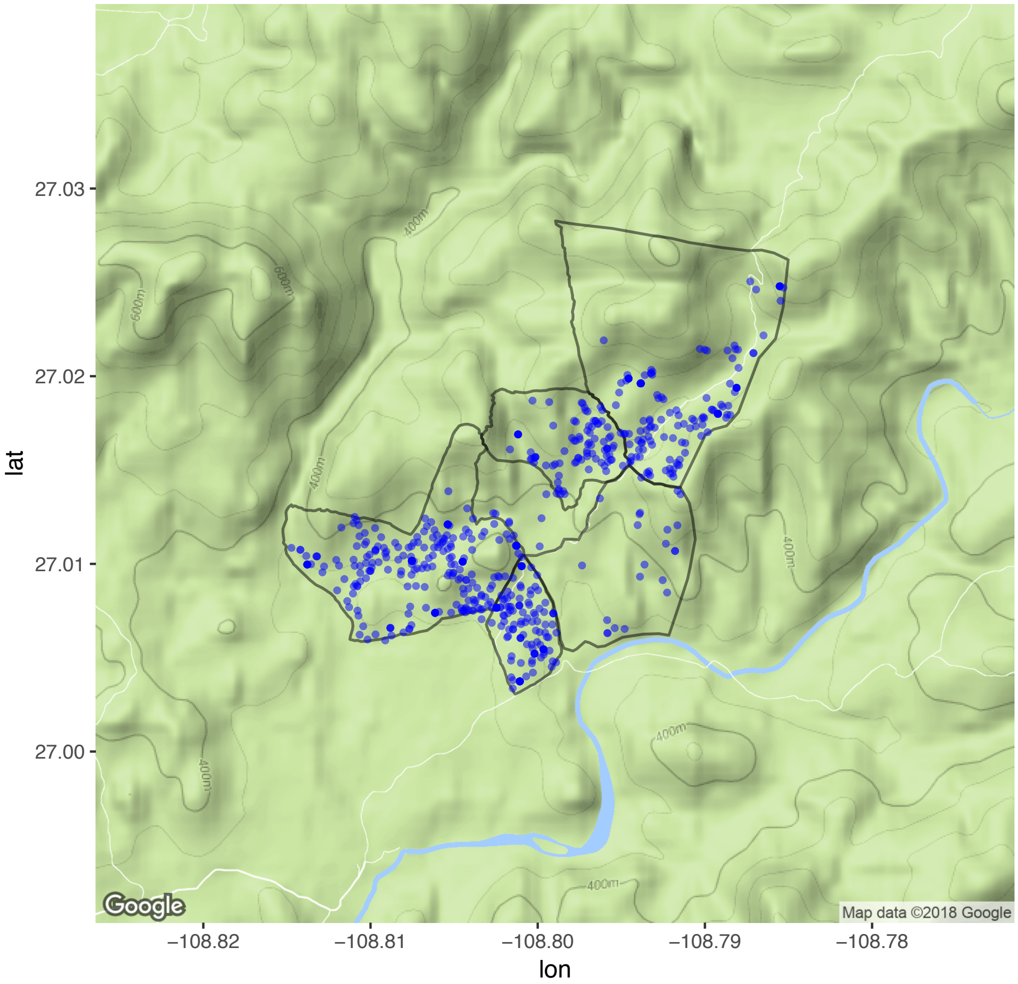

Figure 2-3. Map of RVFH plot locations. Grey lines are division fence lines in both El Carricito and El Brasilito. Each blue point corresponds both to a video where a cow fed on woody vegetation, and a 5m x

5m plant census plot occurring at the location of a particular foraging event.

2.4.5 *All available habitat data: plant census plots evenly distributed across ranches*

To sample AAH, I recorded woody plant species frequencies in plant census plots (as described above), spaced at 100-meter intervals in a grid within fenced divisions where cattle roamed freely (Fig. 2-4). Divisions in this study ranged from 22 – 118 hectares, across an elevational gradient of roughy 100 meters.

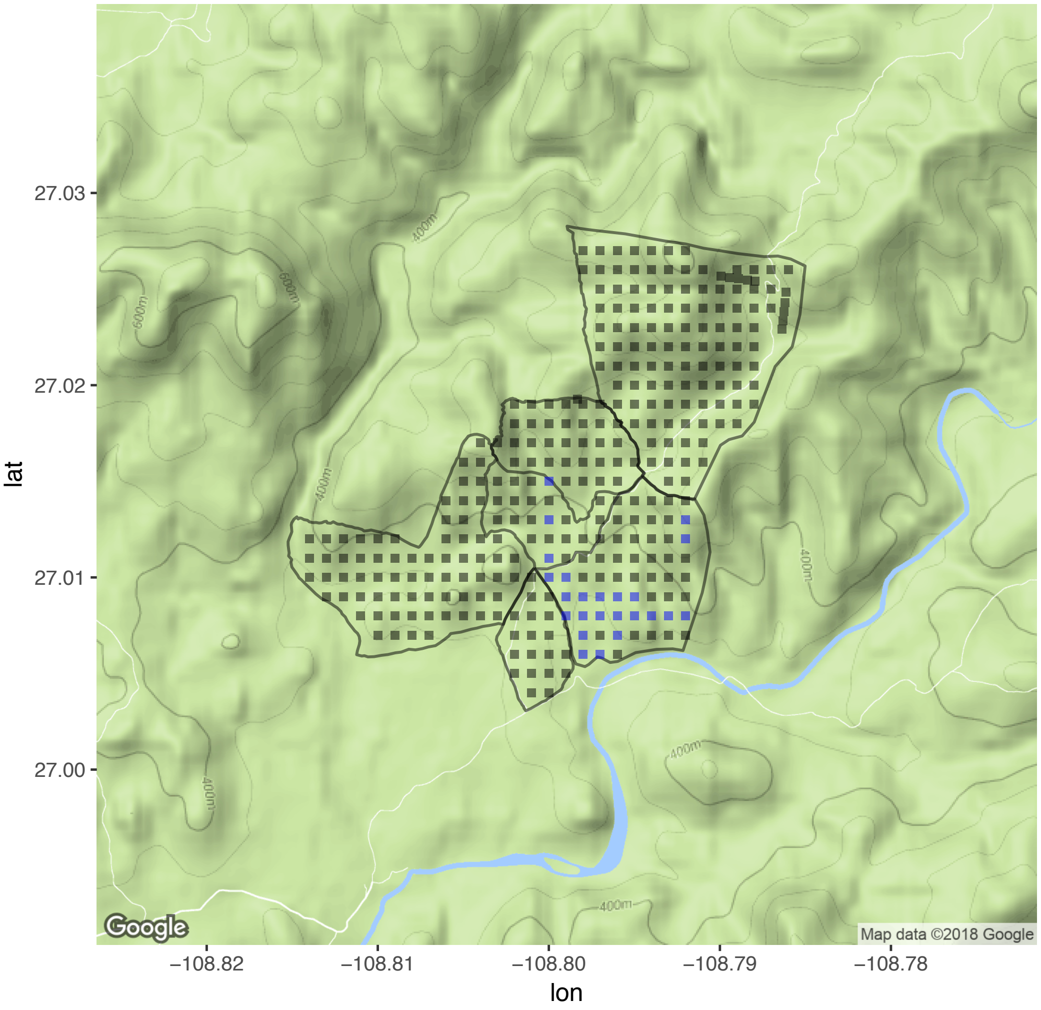

Figure 2-4. Map of AAH plant census plots, spaced at 100m intervals throughout the 5 divisions of

Rancho El Carricito and Ranch El Brasilito. Blue points indicate plot locations where there were no woody plants and were thus not included in AAH.

2.4.6 *Statistical analyses*

Question 1: foraging bias (for or against species of woody plants)

To test whether cows are biased toward or against species of woody plant in RVFH, I compared relative frequencies of 74 woody plant species occurring in RVFH or WPC plots. To generate 95% confidence intervals on each species, I bootstrapped 10,000 species frequency tables from the RVFH and WPC datasets, scaled WPC to the larger RVFH dataset, log transformed the data, and subtracted the log transformed means and 95% confidence intervals for each species. I generated confidence intervals on mean differences by finding the 250th and 9750th indexed frequency for each species in the bootstrap. Where confidence intervals overlap with zero, there is no significant difference in the frequency of the species in diet as compared to the community context from which cows selected individual plants (Fig. 2-5).

To test if the overall difference between RVFH and PFH was significant, I first calculated the observed difference between community evenness of all woody plants in cow diet and/or RVFH by subtracting evenness values for each dataset with Shannon's equitability index to measure community evenness (Eq. 2-1).

Assuming that the evenness distributions are the same, and assuming that plants in cow diet are contained within repeat-visit foraging habitat, I generated a null distribution of evenness difference values by bootstrapping 10,000 pairs of samples from the repeat-visit foraging habitat dataset, each of equal length as the original diet and RVFH dataset, and calculating an evenness value for each. Subtracting each pair of evenness values resulted in a null distribution and 95% confidence intervals at the 250th and 9750th indexed value.

Question 2: differences between woody plant communities in RVFH and all available habitat (AAH)

I repeated the analyses as above, comparing RVFH and AAH. I log transformed species frequencies for woody plants in RVFH and AAH, bootstrapping confidence intervals from each dataset (Fig. 2-7). Under the null hypothesis, if cows randomly forage across all habitats available to them, there should be no difference in community evenness between RVFH and AAH. I generated the null distribution as above, by bootstrapping samples from all available habitat of lengths equal to the observed RVFH and AAH samples, calculating evenness values for each sample data set, subtracting them, and plotting the resulting distribution.

2.5 RESULTS

2.5.1 *Question 1 results*

Cows consumed 48 woody plant species (Table 2-S1). Among the woody plant species found in WPC and/or RVFH, 12 species are eaten more frequently than expected by their frequency in the environment: *Croton flavescens* (Euphorbiaceae), *Randia echinocarpa* (Rubiaceae), *Pouzolzia occidentalis* (Urticaceae), *Lysiloma divaricatum, Acacia cochliacantha* (Fabaceae), *Haematoxylum brasiletto* (Fabaceae), *Guazuma ulmifolia* (Malvaceae), *Randia obcordata* (Rubiaceae), *Berndardia viridis* (Euphorbiaceae), *Coursetia glandulosa* (Fabaceae), *Erythroxylum mexicanum* (Erythroxylaceae), and *Bursera fagaroides.* Twenty-one species are more abundant in RVFH than they are in WPC: *Croton fantzianus* (Euphorbiaceae)*, Croton ciliato-glandulifer* (Euphorbiaceae)*, Mimosa palmeri* (Fabaceae)*, Zanthoxylum fagara* (Rutaceae)*, Brongniartia alamosana* (Fabaceae)*, Desmanthus bicornutus* (Fabaceae)*, Hybanthus mexicanus* (Violaceae)*, Gouania rosei* (Rhamnaceae)*, Sebastiania pavoniana* (Euphorbiaceae)*, Ipomoea bracteata* (Convolvulaceae)*, Senna uniflora* (Fabaceae)*, Nissolia schottii* (Fabaceae)*, Caesalpinia pulcherrima* (Fabaceae)*, Opuntia pubescens* (Cactaceae)*, Opuntia thurberi* (Cactaceae)*, Stenocereous thurberi* (Cactaceae)*, Jatropha cordata* (Euphorbiaceae)*, Fouquieria macdougalii* (Fouquieriaceae)*, Callaeum macropterum* (Malpighiaceae)*, Karwinskia humboldtiana* (Rhamnaceae)*, Pachycereus pecten-aboriginum* (Cactaceae)*,* and *Jatropha malacophylla* (Euphorbiaceae). The remaining 39 species are not statistically distinguishable (Fig. 2-5).

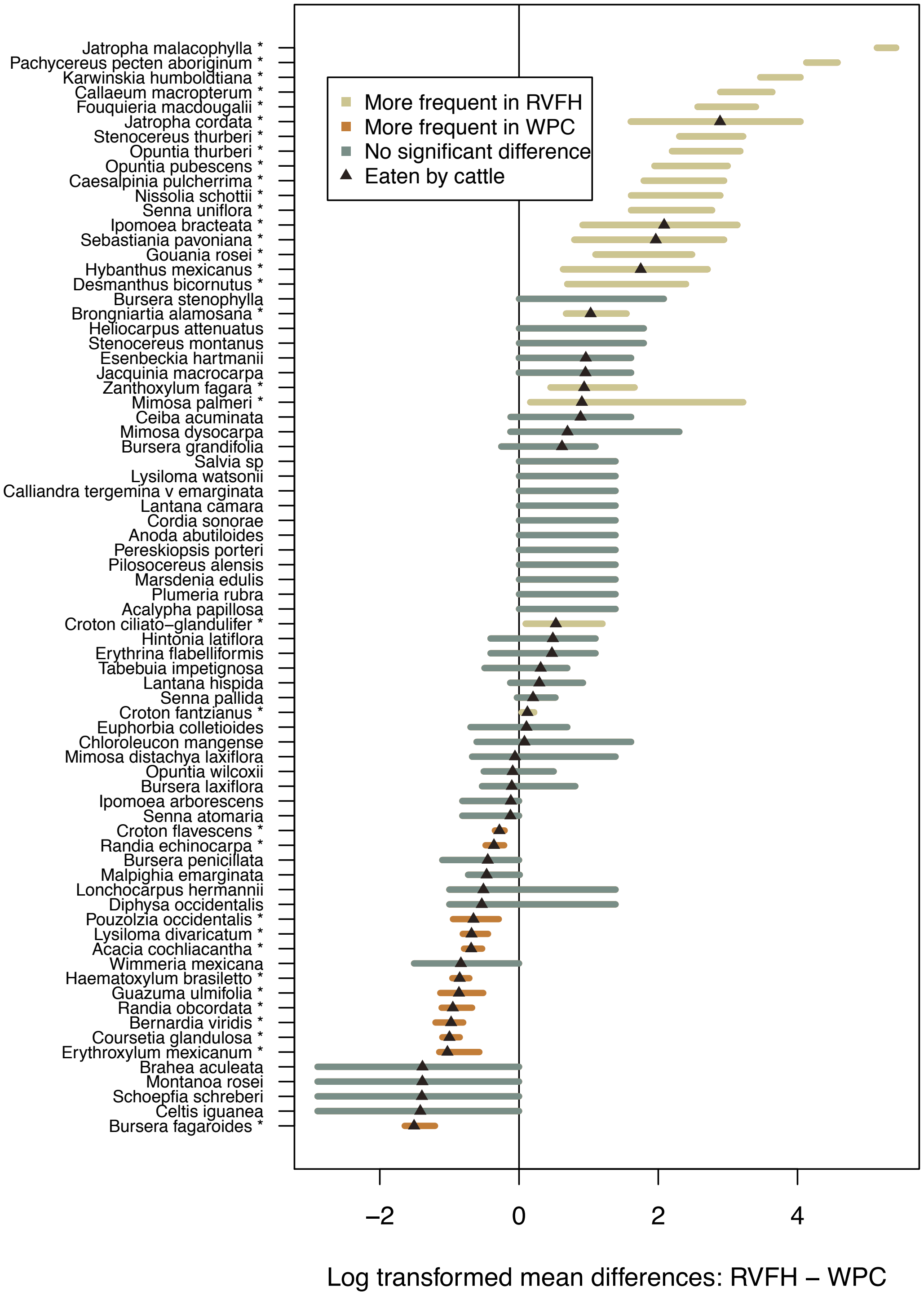

Figure 2-5. Bootstrapped confidence intervals for log transformed mean frequency differences of 74 woody plant species in cow RVFH and WPC. On the left, orange bars indicate species that are

significantly more frequent in cow WPC than would be expected based on their frequencies in RVFH. In tan are species that are common in RVFH, but infrequent in cow WPC. Short bars indicate common species, while species with wide bars were less common. Species eaten by cows are marked with a triangle. Species with a positive or negative significant difference are marked on the Y-axis with an asterisk.

The observed evenness difference, plotted on the null distribution, falls within the confidence intervals (Fig. 2-6). Thus, although some species differ in their frequencies, cow RVFH was only slightly less even than diet **(RVFH: 0.6774, diet: 0.6795, p = 0.113).**

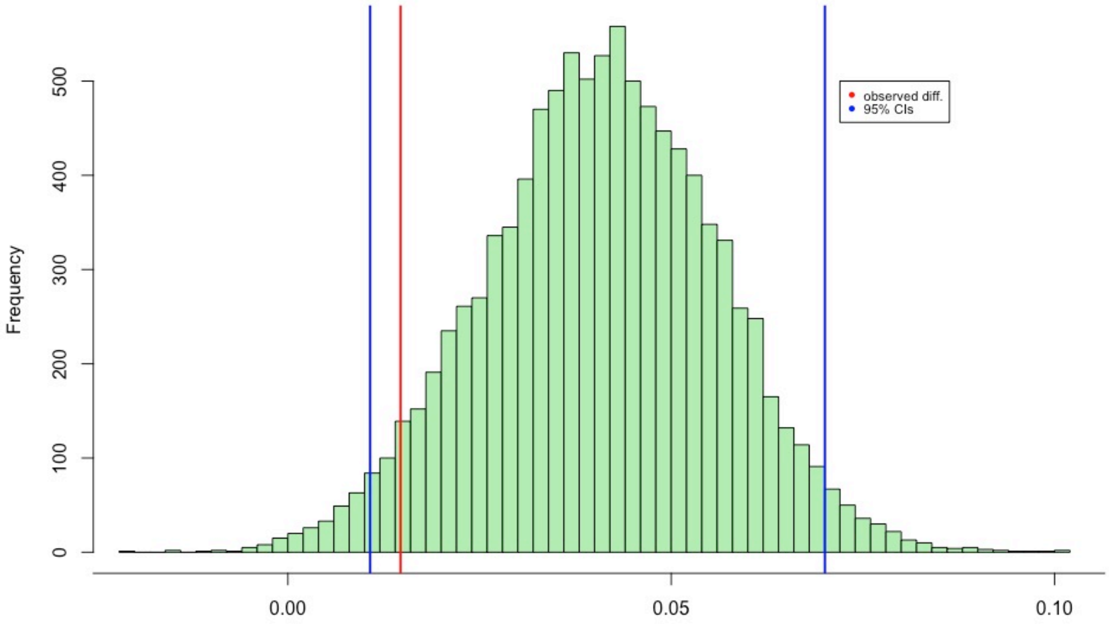

Figure 2-6. Null hypothesis significance test (NHST) of community evenness differences between WPC and RVFH. The observed difference (in red) falls within the 95% confidence intervals of the bootstrapped distribution of differences- thus, there is no significant difference in community evenness.

2.5.2 *Question 2 results*

Of 81 woody plant species occurring in either RVFH and/or AAH, more than half (45 species) are significantly more frequent in RVFH compared to the frequency of the same species in AAH: *Brongniartia alamosana, Bursera fagaroides, Jatropha cordata, Senna pallida* (Fabaceae), *Mimosa palmeri, Haematoxylum brasiletto, Lysiloma divaricatum, Croton flavescens, Randia echinocarpa, Karwinskia humboldtiana,* are among the most common. Fifteen species were more common in AAH compared to RVFH, including *Croton fantzianus, Fouquieria macdougalii, Stenocereous thurberi, Bursera laxiflora*, and *Bursera grandifolia*, among others (Fig. 2-7).

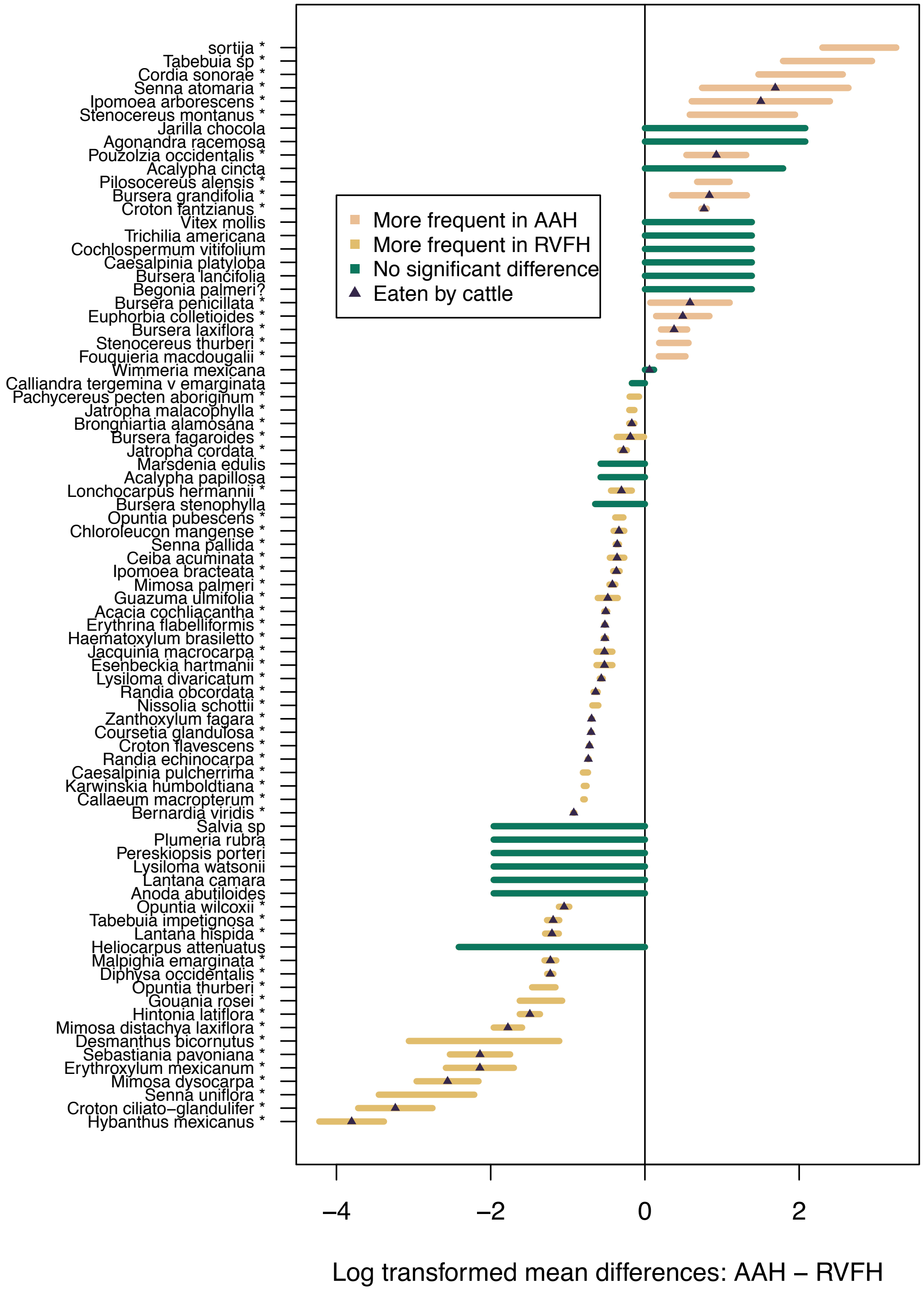

Figure 2-7. Bootstrapped confidence intervals for log transformed mean frequency differences of 81 woody plant species in cow AAH and RVFH. On the left, yellow bars indicate species that are

significantly more frequent in cow RVFH than would be expected based on their frequencies in AAH. In peach trending to the right are species that are significantly more frequent in AAH compared to RVFH. Short bars indicate common species, while species with wide bars were less common. Species eaten by cows are marked with a triangle. Species with a positive or negative significant difference are marked on the Y-axis with an asterisk.

A null hypothesis significance test confirmed that RVFH was indeed more diverse than AAH, the observed difference falling well outside of the confidence intervals of the bootstrapped null distribution **(RVFH: 0.6774, AAH: 0.4830, p < 0.0001)** (Fig. 2-8).

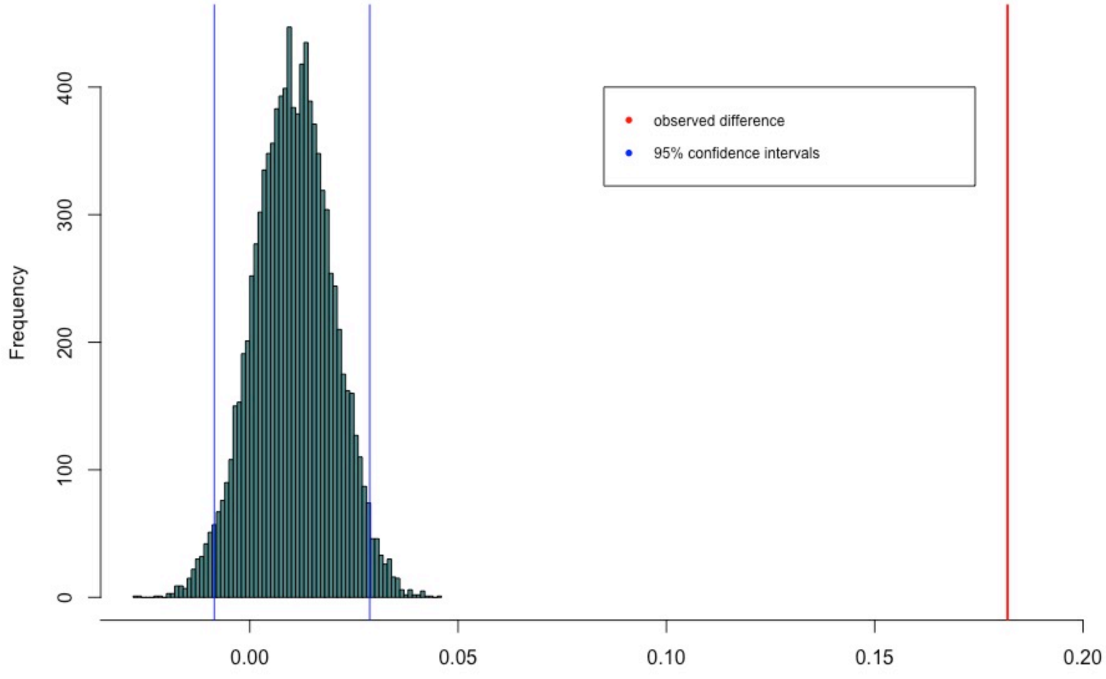

Figure 2-8. Null hypothesis test showing a distribution of 10,000 bootstrapped evenness differences comparing cow RVFH with AAH. In red, the observed difference (RVFH – AAH) falls well outside the confidence intervals, indicating that RVFH is a significantly more even community than AAH.

2.6 DISCUSSION

In this discussion, I focus on "common" species, those with at least 10 records in the null hypothesis data sets (RVFH in Question 1, AAH in Question 2), as is difficult to say whether a species that is rare in both the experimental treatment and null comparison group- in WPC compared to RVFH, or RVFH compared to AAH- is rare because of the effect of cattle, or simply because it is rare.

Comparisons of individual plant frequencies in cow RVFH versus WPC, and again in AAH versus RVFH, indicate that cows select or avoid both food species (at a fine-scale, individual plant level) as well as foraging habitat (at a large-scale, landscape level). At the individual plant level, cows are selecting or avoiding some woody plants more or less frequently than expected by the prevalence of those species in RVFH. Overall, however, WPC is as even as RVFH. Common examples of species more frequent in WPC compared to RVFH include *Croton flavescens*, *Randia echinocarpa, Acacia cochliacantha*, and *Haematoxylum brasiletto*. Foraging cows therefore selected these species at the expense of more frequently occurring food choices. Bias toward these over other, more readily available species could be a function of nutritional payoff, or lack of significant chemical or mechanical defenses, although the spines of *A. cochliacantha* and *H. brasiletto* are impressive deterrents to humans.

Common species occurring more frequently in RVFH compared to their frequencies in WPC fall into two groups: those eaten, and those never eaten by cows. *Croton fantzianus* and *Brongniartia alamosana* fall into the first group. Interestingly, they are the second and third most commonly eaten woody plant species, yet they still occur in cow WPC less frequently than predicted by their abundance in RVFH. These species are extremely common in the null datasets: in RVFH, *B. alamosana* accounts for 6% of all woody plants, and *C. fantzianus* for a full 25%; in AAH, they are 5% and an impressive 54% of all woody plants, respectively. Were they nutritionally sufficient, or tolerably non-toxic, cows would consume them more frequently.

It is also noteworthy that *Croton fantzianus*, the most common woody species by far both in RVFH and cow diets, was until this publication, considered in the scientific literature to be unpalatable to cows (Felger et al., 2001), despite its broad recognition by ranchers as an important cattle forage species. This otherwise minor finding underscores both the paucity of detailed research on domestic animal foraging in natural environments, and the value of local expertise.

Jatropha malacophylla, *Pachycereus pecten-aboriginum*, and *Karwinskia humboldtiana* are common species (6%, 2%, and 1% in RVFH; 5%, 2%, and 0.6% in AAH) yet are completely absent from cow diets. All of these species are significantly chemically or mechanically defended. Species of the genus *Jatropha* contain tannins, phorbol esters, and other toxic secondary chemicals (Devappa et al., 2010, Gámez-Meza et al., 2013), and *J. malacophylla*, when cut, bleeds a prolific, viscous red sap that is at the root of its common name, *sangrengado*, or *sangre de drago*, dragon’s blood (Yetman & Van Devender, 2002). *K. humboldtiana* is neurotoxic (Muñoz-Martínez and Chavez, 1978), and *P. pecten-aboriginum*, a columnar cactus, is protected by fiercely sharp, stout thorns.

In addition to selection of plants at the 5m by 5m scale, selection is occurring at a larger, landscape level, with cows consuming woody vegetation in more diverse habitat than that which is available to them overall. Thus, either the diversity of RVFH itself, or some related variable associated with the RVFH subset is responsible, although the mechanism underlying the discrepancy is unclear.

Why RVFH is more diverse than AAH is not clear. However, two hypothetical scenarios could explain RVFH and AAH community evenness differences: engineering, and selection/avoidance. Cattle could be engineering their foraging environment, altering community evenness in places they forage by introducing weedy species. This hypothesis is extremely unlikely, as it would require evidence of abundant species present in RVFH, but not AAH. In reality, species richness in both RVFH and AAH are very similar (77 and 80 species, respectively). Fourteen species (18%) are found in AAH but not RVFH; similarly, 14 species (18%) are in RVFH but not AAH. All are rare: half are singletons (8 in RVFH, 8 in AAH), and none account for more than 0.6% of all individuals in either community.

Cows could also engineer their ecosystems by releasing rare natives present in both RVFH and AAH, by suppressing other native competitors. Figure 7 shows a few species common in RVFH but rare in AAH, which, combined with higher frequencies of common species, could be contributing to the observed difference in diversity.

Selection/avoidance of variables associated with heterogeneous diversity of woody plants is a logical framework to understand RVFH and AAH evenness differences. Cattle could be seeking diversity as a means to dilute the toxic effect of any single plant secondary chemical, as predicted by Freeland and Janzen (1974). However, variables correlated with diversity, but unrelated in terms of the animals' decision-making processes, are equally plausible explanations for cattle ranging patterns. Slope, for example, has a well documented negative relationship on cattle land use (Mueggler, 1965; Cook, 1966; Gillen et al., 1984, Ganskopp & Vavra, 1987), although pasture layout, breed and individual differences affect whether cattle will graze on steep slopes (Ditsch et al., 2006). Elevation, aspect, distance from water and fences, and even cardinal direction (Callaway, 2008) could play a role.

Some evidence suggests that cattle avoidance of dense, low-diversity patches dominated by *Croton fantzianus* may underlie evenness differences between treatments. *Croton fantzianus* is an abundant, small-statured tree with stem diameters mostly between 2 – 10cm (de la Rosa, 2018a). The most common woody species on both ranches, it is widely distributed in the TDF and frequently eaten by cattle (Fig. 2-5). In some locations, it forms dense stands, where few other trees grow. In locations such as in the northeastern corner of Rancho El Carricito, *C. fantzianus* occurs as densely as 59 plants in a 5m x 5m area (de la Rosa, 2018a), resprouting vigorously even under moderate to heavy harvest rates.

Where dominant, *C. fantzianus* is associated with low species richness (Fig. 2-9). It is a preferred woody forage plant to cows; however, cows seem not to forage in a large area where it forms a monoculture (Fig. 2-10). Correlational evidence for the *C. fantzianus* avoidance hypothesis justifies further study.

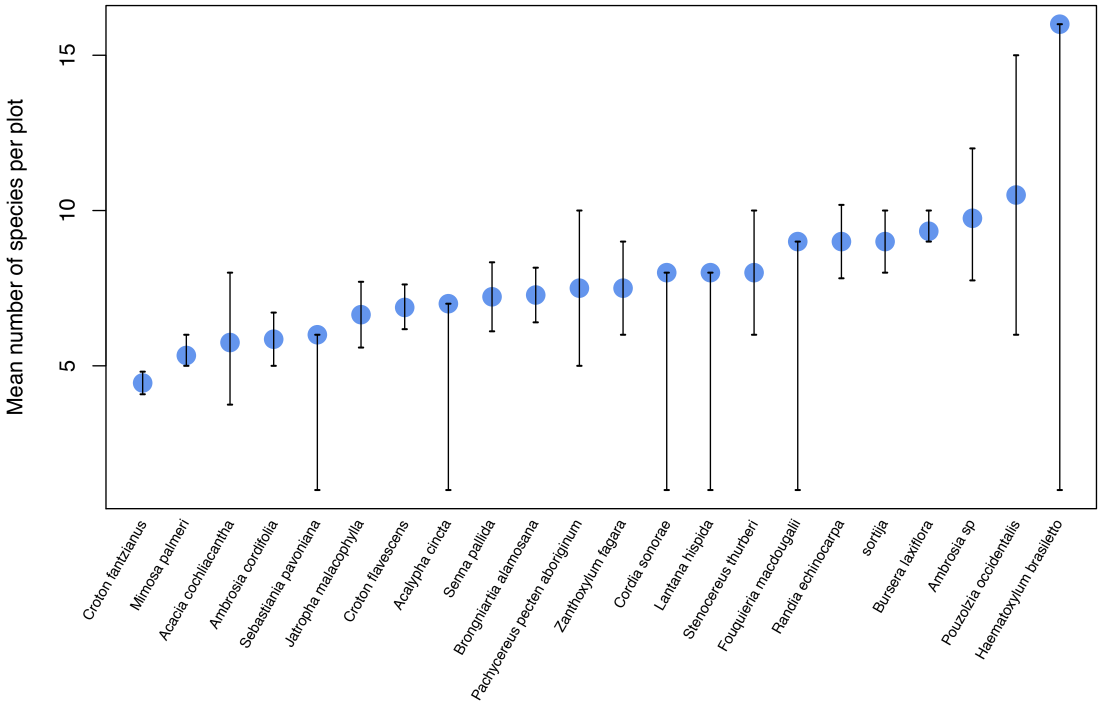

Figure 2-9. Mean species richness of plots where species listed on the x-axis are most abundant. *Croton fantzianus* and *Mimosa palmeri*, both woody small-statured trees that form dense, naturally occurring stands, are associated with the lowest mean plot diversity overall.

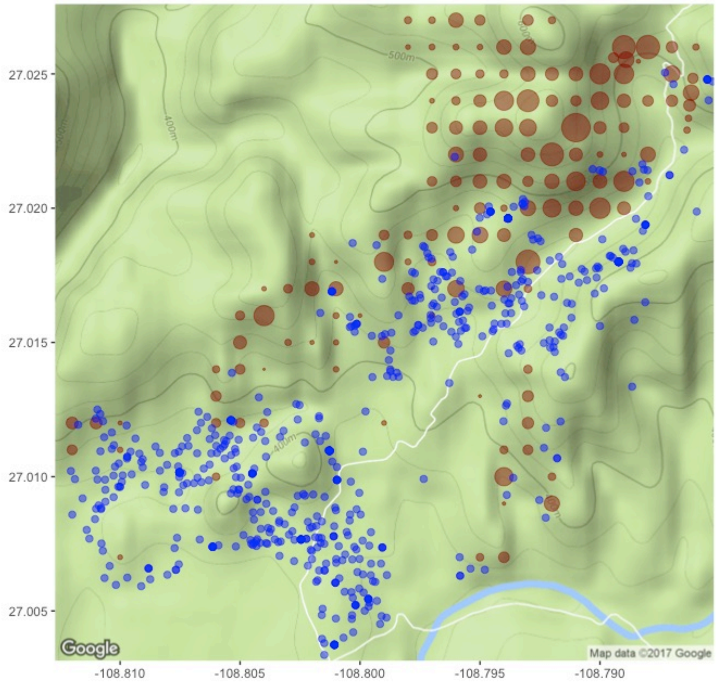

Figure 2-10. In red, AAH plant census plots dominated by *C. fantzianus* are scaled according to the number of *C. fantzianus* stems occurring in each plot. In blue are locations corresponding to videos where cows consume woody vegetation. The northeastern corner of El Carricito (top center) is noteworthy as an area largely avoided by foraging cows, despite the nearby presence of a watering hole, road, and abundant edible vegetation.

2.7 CONCLUSIONS

Cows eat some woody plant species at higher rates than expected based on their occurrence in nature, indicating they are more palatable than others, and thus worth the extra search effort. Likewise, cows consume some woody plants at rates much lower than expected under a null hypothesis scenario, where they eat randomly what is available in front of their noses.

The replicability of cow foraging behaviors is dependent on consistent stocking rates, rotational schedules, and weather, however. More cattle, or similar numbers held in fenced divisions for longer periods of time, would exhaust preferred forage plants earlier, forcing them to feed on less palatable vegetation. Similarly, palatable forage material is dependent on consistent seasonal rainfall. Assuming the stocking rates, rotational schedule, and rainfall in this study were average for the region, cow biases for and against forage plants reported here should be a good foundation for future work on woody plant species palatability and differential mortality due to browsing.

That RVFH is more diverse than AAH indicates that cattle foraging has little impact on the diversity of plants in areas repeatedly visited while feeding. Cattle foraging habitat preferences, and the resulting differences in species abundances and community evenness between RVFH and AAH, could be due to a negative response by cows to decreased diversity, and the behavioral response may to be driven by cattle avoidance of a low-diversity area dominated by *C. fantzianus*. The particular variable or variables underlying cow preference for high-diversity habitat, however, is still not clear. Future work should attempt to rule out the effects of variables correlated with diversity, for example using mixed effect models (Bolker et al., 2009) or resource selection functions (Manly et al., 2007, Clark et al., 2014).

2.8 SUPPLEMENTAL MATERIALS

1	Croton flavescens	151
2	Croton fantzianus	138
3	Randia echinocarpa	46
4	Acacia cochliacantha	39
5	Haematoxylum brasiletto	31
6	Senna pallida	23
7	Lysiloma divaricatum	22

8	Coursetia glandulosa	21
9	Brongniartia alamosana	14
10	Randia obcordata	11
11	Malpighia emarginata	10
12	Erythroxylum mexicanum	7
13	Croton ciliato-glandulifer	6
14	Lantana sp	6
15	Zanthoxylum fagara	6
16	Bursera laxiflora	5
17	Bernardia viridis	4
18	Bursera fagaroides	4
19	Guazuma ulmifolia	4
20	Opuntia wilcoxii	4
21	Pouzolzia occidentalis	4
22	Diphysa occidentalis	3
23	Lonchocarpus hermannii	3
24	Mimosa palmeri	3
25	Chloroleucon mangense	2
26	Mimosa distachya laxiflora	2
27	Mimosa dysocarpa	2
28	Brahea aculeata	1
29	Bursera grandifolia	1
30	Bursera penicillata	1
31	Ceiba acuminata	1
32	Celtis iguanea	1
33	Erythrina flabelliformis	1
34	Esenbeckia hartmanii	1
35	Euphorbia colletioides	1
36	Hintonia latiflora	1
37	Hybanthus mexicanus	1
38	Ipomoea arborescens	1
39	Ipomoea bracteata	1
40	Jacquinia macrocarpa	1
41	Jatropha cordata	1
42	Mimosa sp	1
43	Montanoa rosei	1
44	Schoepfia schreberi	1
45	Sebastiania pavoniana	1
46	Senna atomaria	1
47	Tabebuia impetignosa	1
48	Wimmeria mexicana	1

Table 2-1S. Woody plant species and frequencies of occurrence as forage in CowPro videos.

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CHAPTER 3

Effect of cattle on tropical deciduous forest plant community diversity and structure

3.1 ABSTRACT

Free-range cattle ranching is widespread in developing areas, particularly in tropical forests in the Americas, and deforestation for ranching is responsible for the loss of large tracts of tropical deciduous forest (TDF). Silvo-culture agroforestry, where livestock range in forested areas, presents an alternative to clear-cut agriculture. However, few researchers have investigated how cattle change forest tree communities in agroforestry systems, or how landscape and forage quality influence cattle-forest interactions.

In this study, I (1) tested a set of hypotheses on the effect of cattle on TDF community structure, species composition and stem size class distribution, and (2) investigated the role of cattle browsing in creating community differences. To study cattle ranching's effect on tree community structure in TDF, I constructed 49 statistically independent 5m by 5m plant census quadrat pairs. I matched quadrats with similar forest type and hydrological characteristics along fence lines separating active cattle ranches with low stocking rates (currently ranched areas, CR) and a cattle-free nature preserve (unranched, UR) in southeastern Sonora, Mexico. I then tagged, identified, and measured stem diameters for 1,609 individual plants. I compared the frequency and diversity of species and stems in CR versus UR plots, and compared results to a database of

species and frequencies of local woody plants consumed by cows, collected with CowPro, an automated animal-mounted data collection system.

Although CR and UR plots were equally diverse, community structure was significantly different, with some species occurring more frequently, or having a higher importance value index score, in CR compared to UR plots, as well as in UR compared to CR plots. Only four out of 49 plot pairs (8%) had similarity scores greater than 50%, indicating a high amount of community heterogeneity, and potential effect of cattle. Cattle also had an effect on tree stem size class distribution: CR plots had significantly fewer stems in small (10-19mm) size classes compared to UR plots.

At low stocking rates, the effect of cattle on TDF is complex but minimal. Overall, CR and UR forests are equally diverse. Species differences between CR and UR forests are likely due in part to differential mortality induced by cattle, but also partly to naturally high heterogeneity of the forest. Future work should focus on understanding the mechanisms underlying differences in ranched and unranched forests and on using scientific findings to promote sustainable, economically viable ranching recommendations.

3.2 INTRODUCTION

Tropical deciduous forest (TDF) (also, seasonally dry tropical forest (Trejo et al., 2000), tropical dry forest (Murphy et al., 1986, Gillespie et al., 2000), short tree forest (Gentry, 1942), *bosque tropical caducifolio* (Rzedowski et al., 1987), is a seasonally deciduous, monsoon-dependent tropical biome, acutely threatened by forest conversion for cattle ranching and agriculture (Janzen, 1988). Though damage to TDF trees by clear cutting is self evident, less obvious are the impacts of cattle on TDF trees in silvo-pastoral systems (Mestre et al., 2018), where livestock range in forested ranches. The aim of this study was to evaluate the effect of cattle on TDF tree diversity, structure, and stem size class distribution in an agroforestry system in southeastern Sonora, Mexico, the northernmost extent of TDF in North America.

North American TDF is widespread between northwestern Costa Rica and northwestern Mexico, occurring between 0 and 2000m elevation, typically receiving less than 2000mm of annual rainfall (Murphy and Lugo, 1995). At the time of Spanish contact, TDF covered 550,000 square kilometers of the Mesoamerican Pacific slope; today, a fraction of a percent remains (Janzen 1988). Historically overlooked by scientists and the conservation community in favor of tropical rainforest, TDF is understudied and under-protected.

In Mexico, 60% of the historical 15.6 million hectare distribution of TDF had been lost to clearcutting by the 1990s (Trejo et al., 2000), much to make way for agriculture and buffelgrass (*Pennisetum ciliare)*, an African perennial introduced for livestock forage. Livestock feature prominently in the literature as a threat to biodiversity (Noss, 1994; Fleischner 1994; Wilcove et al., 1998; Stern et al., 2002;). However, with the global human population rapidly approaching 10 billion (Cohen, 2003), livestock are an inevitable component of a complex economic and biological tapestry (Brown and McDonald, 1995; Pascual and Perrings, 2007; Odadi et al., 2011).

The Mexican state of Sonora is perhaps as famous for its high-density cattle feedlots as it is the for expansive fields of wheat nourished by the Yaqui River, where Norman Borlaug's Green Revolution was born. Sonora produced an estimated roughly 1,477,686 steers in 2001 (Sonoraganadera.com), supplying a robust domestic as well as international market. On the streets of Hermosillo, the northern state's capital city, an estimated 3,057,600 kilograms of *carne asada* (charcoal-fired beef) are consumed annually, in taco form alone (Narchi et al., 2015).

Perhaps the most ancient form of cattle management is on an open range, a style imported to northwestern Mexico in the 16th Century from the Iberian Peninsula (especially Andalusia and Extremadura), and significantly regionally adapted over the centuries (Doolittle, 1987; Butzer, 1988). Ranching quickly exploded in the rich grasslands of the north: notarized records establish that some ranchers were branding herds of more than 40,000 cows on the border of Zacatecas and Durango, and contemporary writers estimate other herds in the region at 130-150,000 animals. Cattle were established in coastal Sinaloa as early as the 1530s (Brand, 1961).

Modern cattle ranching in the Sonoran TDF is a combination of new techniques and ancient traditions. The open range is gone, replaced by a network of fences and often complex property ownership. However, in silvo-pastoral systems, cows still range freely within a natural ecosystem otherwise largely unaltered by humans, as they did hundreds of years ago. Ranchers use division fencing taking advantage of natural geographic and hydrological features, allowing them to invest minimally in supplemental feed and management. Throughout the rainy season, cattle range freely through their habitat, feeding on a variety of annual and perennial grasses, herbs, and woody species.

Detailed studies on free-ranging cattle behavior and community interactions are few, leaving unanswered a wide range of questions in foraging ecology, community ecology, and evolution. Further, because a vast amount of global intact natural land is privately owned, and much of this land is managed for cattle, studies investigating ecosystem responses to cattle have strong potential conservation benefits. Cattle can negatively affect tree species regeneration and diversity (Bakker et al, 2004; Álvarez-Yépiz et al., 2008). For example, by virtue of clearing existing vegetation cover for ranching, cattle may also release some species from competition, facilitating the establishment and growth of plants that are avoided or missed when feeding (Vandenberghe et al., 2005). Domestic cattle are not native to any natural ecosystem, but in some cases, they may mimic ancient dispersers or ecosystem engineers (Janzen & Martin, 1982; Bergman et al., 2001). Even less is known about their foraging and functional ecology, particularly outside of rangelands: as grazers, cattle strongly prefer grasses to woody species (Gordon, 2003) but under certain conditions will eat a wide range of trees, shrubs, lianas, cacti, and even leaf litter (de la Rosa, 2018b), with preferences related to the nutritional payoff of available forage (Ayantunde et al., 1999). Among woody plants, cattle generally select young vegetation (de la Rosa, 2018b), despite the fact that young trees and shoots may be better chemically defended (Rooke et al., 2004).

3.3 QUESTION, HYPOTHESES, ASSUMPTIONS, PREDICTIONS

Goals of this study were (1) to test a set of hypotheses on the effect of cattle on TDF in Álamos Municipality, Sonora, Mexico, either negatively, through browsing, trampling, soil compaction, or positively, through competitive release or facilitation; and (2), to use cow browsing data to investigate the role of cattle foraging in creating differences between TDF with cattle versus protected, cattle-free TDF.

This study assumes that (a) cattle had been in CR TDF a long enough time that cumulative cattle impact to mature woody plant species would have already occurred, and (b) that UR TDF had been cattle-free sufficiently long enough that, were there differences due to cattle in the community composition and stem class size distribution of woody plants, they would be detectable by the methods I discuss below. In other words, within the amount of time that had elapsed since the exclusion of cattle, I assume that some woody plant species would have either resprouted or recovered from the seed bank and achieved stem diameters of at least 1cm at a height of 20cm. Cattle have been present in the Álamos Municipality since 1683 and ranching has been a significant regional economic driver since the 1930s (Vásquez-León & Liverman, 2004). At the time of data collection in the summer of 2014, all UR ranches had been cattle-free for 6 to 9 years, according to Biol. Lydia Lozano, Program Director of the reserve containing cattle-free ranches in this study (personal communication, June 18, 2018).

3.3.1 *Question: are there differences in forest community structure and diversity in TDF with cattle compared to cattle-free TDF?*

Hypothesis: Currently ranched (CR) forest should have statistically detectable differences in measurements of plant stem size class distribution, community structure, species richness, and abundances of woody plants compared to the same measurements in cattle-free, unranched (UR) TDF. The hypothesis assumes: (a) woody plant assemblages in matched CR and UR plots are the same except for differences due to the presence of cattle; (b) cattle consume woody vegetation, which has been shown in de la Rosa, 2018b; (c) cattle will negatively affect plant productivity and reduce plant biomass in ranched areas; (d) when browsing woody vegetation, cows prefer small-diameter stems (seedlings as well as new growth on mature plants) to large-diameter stems.

Given these assumptions, I tested the following predictions:

1. Number of plants and stems in CR should be lower than in UR.
2. Small stem size classes should be less frequent in CR compared to UR quadrats.
3. Overall diversity in CR compared to UR quadrats will be lower.
4. Cattle browsing and trampling of woody plants will alter woody plant community structure among paired plots.
5. Some species will be less frequent in CR compared to UR plots.
6. Within species density, frequency and dominance and scores (components of the Importance Value Index, or IVI) will differ in UR compared to CR plots.
7. Species with lower mean frequencies and IVI scores in CR versus UR plots will be those browsed most frequently by cows.
8. Species with significant differences in stem size class frequencies should be those eaten by cows.

3.4 METHODS

3.4.1 *Study area*

I conducted this study within the 93,000-hectare Área de Protección de Flora y Fauna Sierra Álamos – Río Cuchujaqui (the APFF), a federally managed conservation easement situated on the Pacific slope of the Sierra Madre Occidental, in the Álamos Municipality of southeastern Sonora, Mexico. Located in the boot heel of Sonora, the APFF abuts the state border with Chihuahua and comes within 8 kilometers of Sinaloa. The APFF encompasses the Sierra Álamos, an isolated volcanic sky island, and the greater watershed of the Cuchujaqui river, an undammed tributary of the Río Fuerte and a Ramsar Wetland of International Importance. Designated a protected area in 1996, the APFF is overseen by the National Commission of Natural Protected Areas (CONANP, www.conanp.gob.mx). In 2007 it became part of the UNESCO World Network of Biosphere Reserves' Man and Biosphere Program. Within the APFF, residents are permitted to ranch livestock and grow subsistence crops, as well as mine and log forests on a limited basis. The protected area contains large areas of conserved primary and secondary TDF, small managed grasslands, and traditional *milpas* (non-irrigated croplands).

Within the APFF-SARC is the Reserva Monte Mojino (ReMM), an approximately 7000-hectare protected area consisting of 8 former forested cattle ranches, now managed by Nature and Culture International, a San Diego, CA-based nonprofit conservation organization (Fig. 3-1). The ReMM follows the Cuchujaqui watershed from roughly 108.8 to 108.655 degrees West, and 26.99 to 27.12 degrees North, and is surrounded by actively managed private cattle ranches. This study was conducted on 5 former cattle ranches in the ReMM (Guayabo, Palmarito, Sitorijaqui, San Pedro, San Francisco), and 6 neighboring ranches with seasonal free-ranging cattle (El Carrizito, El Pinto, Los Llanos de San Benito, San Pablo, Los Llanos de San Pedro, El Mango).

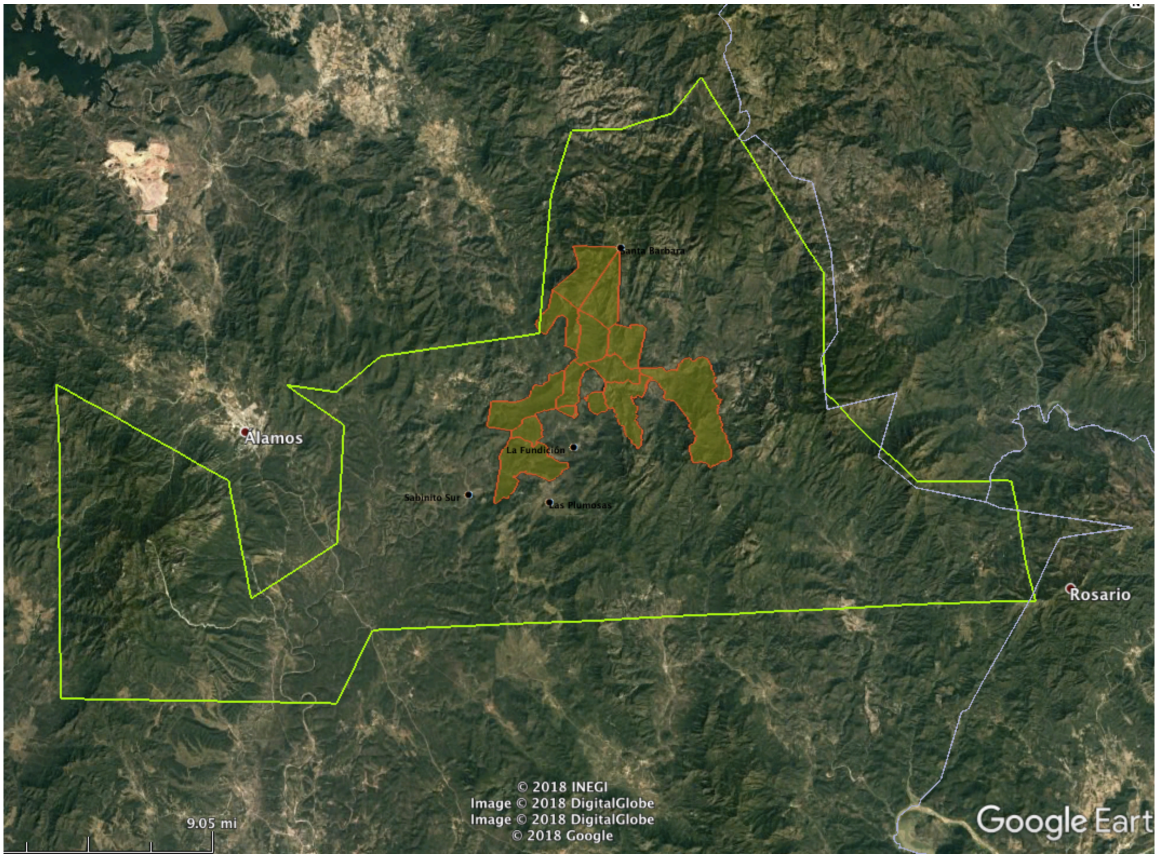


Figure 3-1. Map of the Reserva Monte Mojino (orange outline), approximately 22 km east of Pueblo Álamos, Sonora, Mexico. Boundary line of the Área de Protección de Flora y Fauna – Sierra Álamos / Río Cuchujaqui is in light green.

3.4.2 *Power analysis*

To determine the number of paired quadrats necessary for my study, I used the package PWR (Power) in R. Cohen's *d* is the difference between population means divided by the standard deviation. Since I had no *a priori* knowledge, I calculated n for the following Cohen's recommended (1977) medium effect size of d=0.5, at a significance level of alpha = 0.05.

To achieve a power of beta = 0.09 I would have needed n=44 pairs. I divided this n by the asymptotic relative efficiency (ARE) for the Wilcoxon Signed-Rank test, which estimates the ratio of observations needed for a nonparametric statistical test to reject a null hypothesis as efficiently as a similar parametric test. The ARE for the Wilcoxon signed-rank test relative to the paired t test is 3/!, or 0.955, resulting in a corrected n of 46.0686, or 46 paired quadrats.

3.4.3 *Study design*

I constructed 49 pairs of 5m by 5m plant census quadrats, placing each pair in primary TDF along a fence line that separates active cattle ranches and cattle-free properties, and assumed statistical independence of pairs by placing them 100 meters apart (Fig. 3-2). I selected paired areas with matching forest type, slope, and slope aspect, choosing fence lines that captured a range of topographic and geomorphological variation. Plot pairs ranged in elevation from 397 to 786 meters.

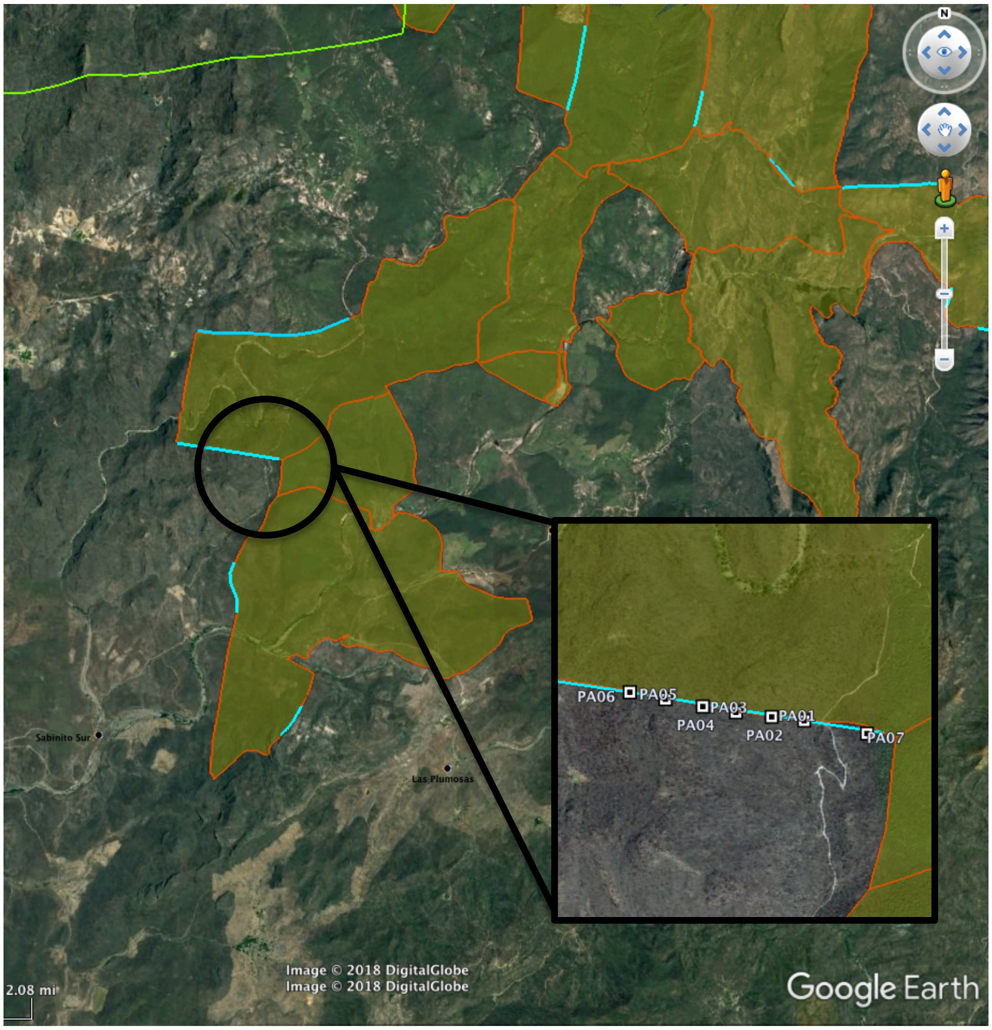


Figure 3-2. In blue, plot pair locations along fence lines delineating the Reserva Monte Mojino and neighboring cattle ranches. Points PA02 – PA07 in the inset are markers along the fence line indicating plot pair locations. Plant census plots are located roughly 10 meters north (in ReMM property El Palmarito) and south (in Rancho El Pinto, a cattle ranch). The community of Sabinito Sur is visible in the center left.

Because fence lines are frequently followed by humans as well as domestic and wild animals and often have adjacent trampled pathways, I established plot centers at a perpendicular distance of 10 meters from fences. All plots were 5x5 m squares with edges facing the four cardinal directions. To ensure that plots were 25m^2 regardless of terrain (that is, floating over the ground), I calculated north, south, east, and west-facing degree of slope from the plot midpoint using a Suunto Tandem clinometer (www.suunto.com). I then used the angle to adjust the length of each sloped vertex half to create a 90° angle between the midpoint and the floating vertex (for upslope lines), or between the corner point and the floating vertex (for downslope lines). I marked each corner with a 1m length of iron rebar and orange flagging, and returned between 2 weeks and 1 month later to census woody plants, defined here as any perennial (i.e., woody stemmed) tree, shrub, liana, or herbaceous perennial measuring at least 1cm diameter on at least one stem at a height of 20cm from the ground.

3.4.4 *Plant census protocols*

My field assistants and I used a 50m measuring tape to demarcate the edges of each square, as well as crossed vertices within the square in order to divide each into four equal parts (see Appendix II for additional details). If an edge included more than 50% of the trunk of a tree, I included it in the quadrat. I censused plants, adapting methods described by Condit (1998), recording the species, measuring the diameter with calipers (or, if greater than 15cm, the circumference, with DBH tape) of each stem greater than 1cm in diameter at a height of 20cm, and then the diameter or circumference of each stem greater than 1cm in diameter at a height of 130cm (diameter at breast height, DBH). Later, I converted all circumference measurements to diameter by dividing by pi. We marked individual plants with aluminum tree tags, each bearing the year and a unique number, by either tying tags to the base of a stem with fishing monofilament, or, when greater than ~100cm in circumference, by attaching the tag with a small stainless steel nail. We then created a map of all tree locations and relative sizes in the quadrat. If we could not identify a plant, we photographed the leaves, bark, flowers and/or fruits including the individual's tag in the periphery of the photo, to identify later. Photographic vouchers were necessary at this stage of the project, because I was unable to secure a permit to collect herbarium vouchers in 2014. However, in the fall of 2015 I retuned to each plot to re-confirm species identifications, and collect herbarium voucher specimens of individuals I was initially unable to classify. Taxonomic information is from Martin et al. (1998).

3.4.5 *Woody plant component of cattle diet (WPC)*

I collected cow foraging data with CowPro, an automated animal-mounted video and GPS data recording system (de la Rosa, 2018a).

3.4.6 *Statistical analysis*

To characterize tree community structure, I calculated and compared diversity (community evenness [Shannon's equitability] and Simpson's D), beta diversity (Bray-Curtis similarity), species frequencies, and species Importance Value Indices (relative density, relative frequency, and relative dominance). To see if cows are responsible for differences, I compared lists of eaten species to lists of species showing the greatest differences in structure and diversity.

1 & 2. Plant and stem abundances

I used bootstrapped stems in 4 stem diameter size categories: 10-19mm, 20-49mm, 51-100mm, and 101+ mm at 20 and 130cm height, in CR versus UR plots. To generate the bootstraps, I sampled a list containing all stems labeled with species name and size class 10,000 times, each time generating a table sorted by size class, for CR and UR stems at both 20cm and 130cm. 95% confidence intervals were the 250th and 9750th value of the sorted categories.

3. Overall diversity

a. Repeated measures test: community evenness differences

I compared diversity of all CR versus UR plots combined by first calculating the observed species evenness for CR and UR data, using Shannon's equitability index (evenness, Eq. 3-1):

$$E_H = \frac{-\sum_{i=1}^{S} p_i * \ln{(p_i)}}{\ln{(S)}}$$

Equation 3-1. Shannon's Equitability Index or community evenness.

Here, the numerator is Shannon's diversity index H, and the denominator is the maximum diversity possible given *S* species.

Under the null hypothesis that cows have no effect on tree community diversity, CR and UR plot pairs should be indistinguishable. I conducted a repeated measures test by first calculating the difference between CR and UR evenness scores between all plot pairs. I then simulated a distribution of likely differences by bootstrapping the vector of evenness differences.

b. Null hypothesis significance test using differences in Shannon's equitability and Simpson's index (λ)

I simulated a null hypothesis distribution by randomly switching the signs of evenness differences and Simpson's index differences (CR – UR) 10,000 times. Simpson's index gives the probability that two randomly sampled individuals belong in the same species. I calculated Simpson's index for plot pairs using the following equation (Eq. 3-2):

$$\lambda = \sum_{i=1}^{S} p_i^2$$

Equation 3-2. Simpson's Diversity Index λ.

Here, S is the total species richness of the sample, and p_i is the relative frequency of the ith species.

4. Community structure: Beta diversity in CR compared to UR plots

The Bray-Curtis similarity measure (SBC) is similar to Sørensen's index except that SBC incorporates counts (abundances) as well as presence/absence data into a quantitative difference measure. I calculated SBC using the formula (Eq. 3-3):

$$S_{BC} = 1 - \frac{\sum_{j=1}^{S} \left| n_{ij} - n_{i'j} \right|}{(n_{i.} + n_{i'.})}$$

Equation 3-3. Bray-Curtis Similarity measure.

The numerator is the sum total of the absolute value of the differences in number of individuals of a given species between paired samples, and the denominator is the total of all individuals in both samples. For each plot pair, I calculated SBC and bootstrapped confidence intervals.

5 & 6. Comparison of mean species frequency and IVI differences between sites and relationship to cow foraging preferences

I calculated CR and UR means, subtracted them, and bootstrapped confidence intervals for all 81 woody plant species occurring in CR and UR plots (Fig. 3-4). IVI is the sum of relative density, relative frequency, and relative dominance of a species (Nguyen et al., 2014). I calculated CR and UR IVI differences and bootstrapped confidence intervals for all woody plants occurring in CR and UR plots.

7 & 8. Role of cattle browsing in CR vs UR species mean frequency, IVI, and stem size class differences

To test the role of cow foraging preferences on species differences in mean frequency and IVI, I compared a list of eaten species to plots of mean frequency and IVI differences (5 and 6). To test the effect of cow browsing on woody plant stem size class distribution, I compared stem measurements in species eaten by cows (de la Rosa, 2018b) and in species not eaten by cows as a control. I binned stem measurements taken at 20cm and 130cm height into four stem size diameter classes described in 1, and then plotted CR and UR bootstrapped mean frequencies and confidence intervals for each size class. Where confidence intervals overlap, there is no statistically detectable difference in frequency of stems of a certain size.

3.5 RESULTS

3.5.1 *Summary data on community composition, species abundances and rarity*

Plant species in twenty-four families occurred in this study. A majority of tagged plants was in the family Euphorbiaceae, and the two most abundant woody Euphorb species were *Croton fantzianus* and *C. flavescens*, in both UR and CR plots (Table 3-1). Fabaceae was the most species-rich family (Fig. 3-3), although Euphorbiaceae contained more individuals overall (Fig. 3-4). Only one family (Solanaceae) occurred in UR but not CR plots; likewise, Caricaceae was the only family occurring in CR but not UR plots.

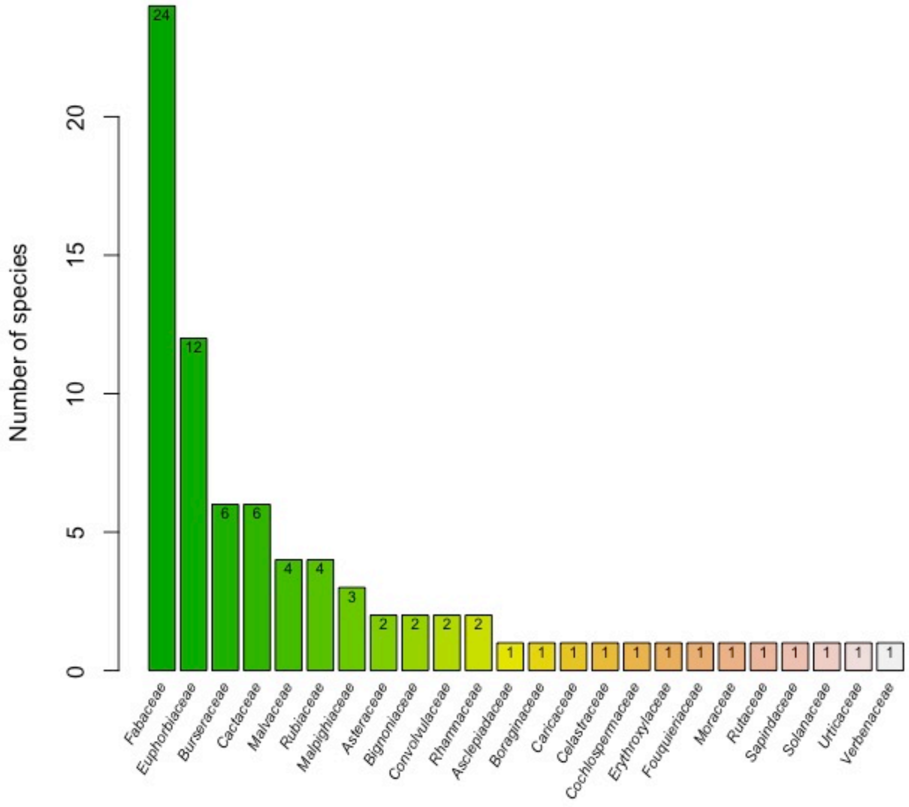


Figure 3-3. Dominant plant families in this study. Number of species per family is at the top of each bar.

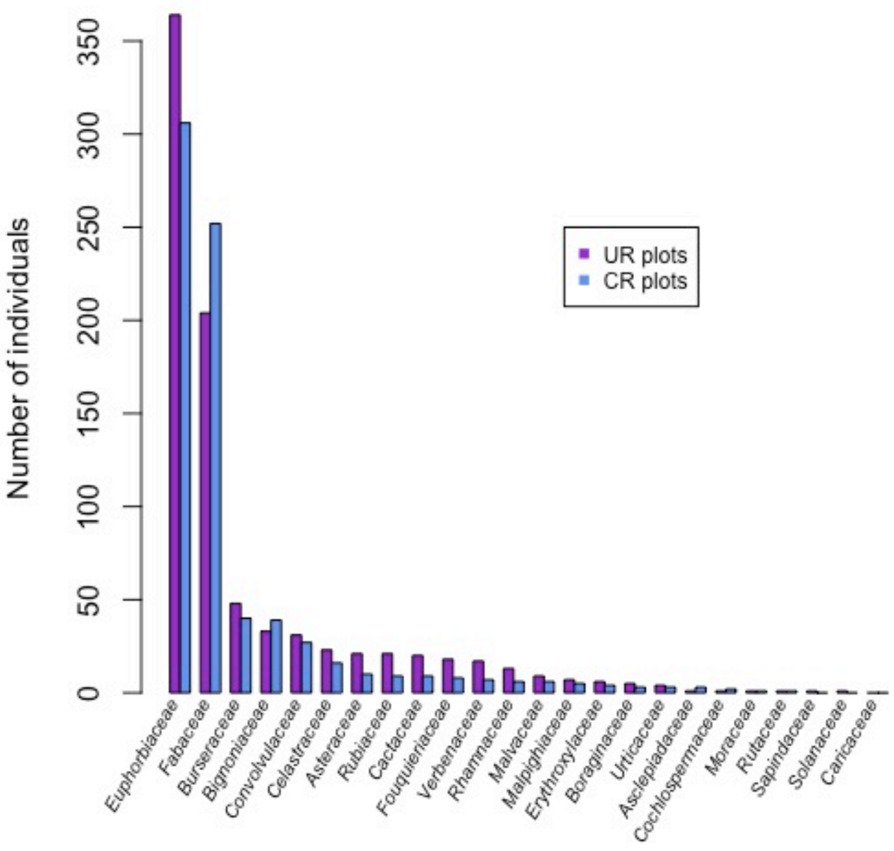


Figure 3-4. Number of tagged plants by family for CR and UR plots.

The top five most abundant species in this study were all in the families Euphorbiaceae and Fabaceae. The most abundant species in UR plots tended to also be abundant in CR plots, with some differences (Table 3-1). *Croton fantzianus* was the most abundant woody plant in both UR and CR plots, averaging 4 and 4.4 individuals per 25m^2, respectively. *Croton flavescens* was more abundant in UR plots, averaging 1.9 versus 0.9 individuals, while *Brongniartia alamosana* (Fabaceae) was slightly less abundant in UR plots, averaging 1 compared to 1.5 plants per 25m^2 in CR plots.

	Species	Family	Number	Average number per $25m^2$ plot
Unranched plots	Croton fantzianus	Euphorbiaceae	194	3.96
	Croton flavescens	Euphorbiaceae	91	1.86
	Brongniartia alamosana	Fabaceae	48	0.98
	Lysiloma divaricatum	Fabaceae	45	0.92
	Haematoxylum brasiletto	Fabaceae	40	0.82
Currently ranched plots	Croton fantzianus	Euphorbiaceae	213	4.35
	Brongniartia alamosana	Fabaceae	73	1.49
	Croton flavescens	Euphorbiaceae	44	0.90
	Haematoxylum brasiletto	Fabaceae	42	0.86
	Senna pallida	Fabaceae	41	0.84

Table 3-1. Top five most abundant species in unranched and ranched plots. The column labeled Number is the total abundance of the given species in all 49 plots in either UR or CR sites.

In UR plots, 19 species from 12 families were rare, here defined as having only one tagged individual in either data sets. Four of these species (*Eysenhardtia orthocarpa* (Fabaceae), *Nissolia schottii* (Fabaceae), *Pilosocereus alensis* (Cactaceae), and *Zanthoxylum fagara* (Rutaceae)) were also rare in CR plots. In CR plots, 11 species from 8 families were rare.

3.5.2 *Results: tests of predictions*

1. No significant difference in number of stems

We tagged and measured a total of 759 and 850 plants in CR and UR plots, respectively, with an average of 15.5 and 17.3 plants per plot. Total number of stems at 20cm and 130cm height was 983 and 1100 for CR, and 1138 and 1170 for UR plots (Table 3-2).

Stems at 20cm height	**CR**	**UR**
Total stems	983	1138
Stem diam 10-20mm	430	615
Stem diam 21-50mm	320	307
Stem diam 51-100mm	124	112
Stem diam 101+mm	105	99
Average stem diam	43.3mm	38.9mm
Max stem diam	439mm	456mm

Stems at 130cm height	**CR**	**UR**
Total stems	1100	1170
Stem diam 10-20mm	500	648
Stem diam 21-50mm	331	321
Stem diam 51-100mm	156	104
Stem diam 100+mm	111	84
Average stem diam	41.2mm	33.5mm
Max stem diam	388mm	307mm

Total number of tags	759	850
Average tags per plot	15.5	17.3

Table 3-2. Summary of Chapter 3 results.

T-tests showed no significant differences in number of tagged woody plants or total stems at either measuring height.

2. Differences in stem size distributions

In CR plots, number of stems in the 10-20mm diameter size class were significantly lower than in UR plots at both 20cm and 130cm height (Fig. 3-5). Interestingly, all larger stem size classes are slightly more represented in CR compared to UR plots. In 20-49mm stems at 20cm height, the difference is also significant.

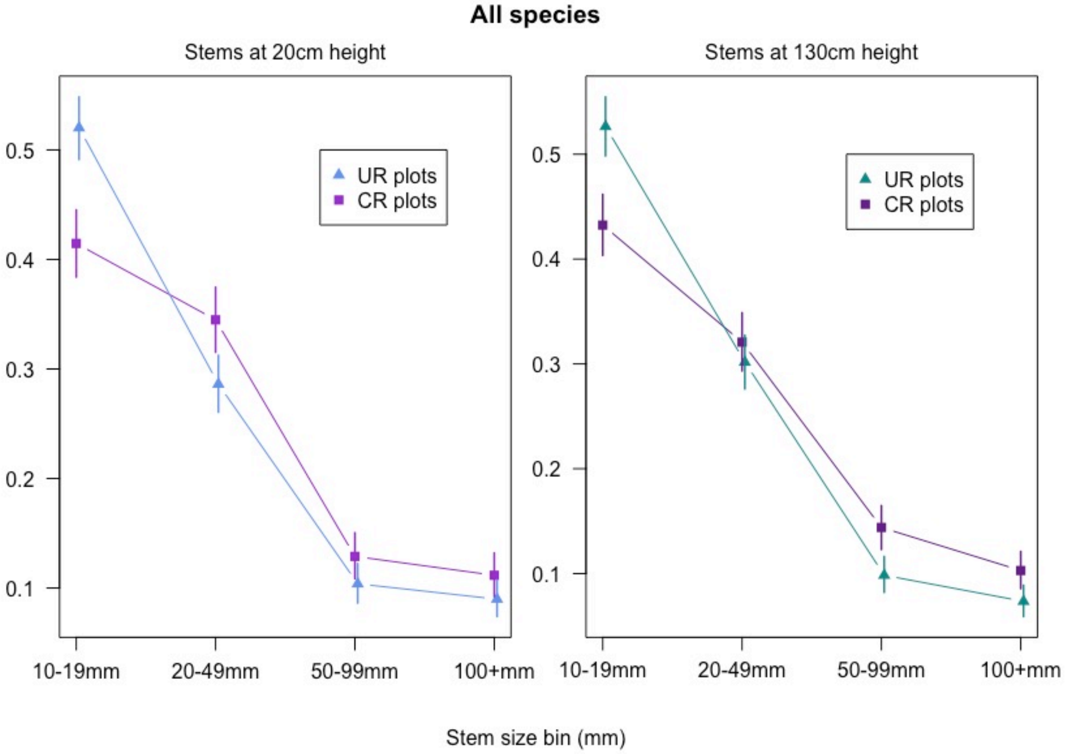


Figure 3-5. Stem diameter size class comparisons at 20cm and 130cm measuring height. At both measuring heights, CR plots had significantly fewer stems in the smallest size class than UR plots.

3. Overall diversity – no significant differences between CR and UR plots

(a) Repeated measures test of community evenness differences

The average evenness difference between CR and UR plots is the mean of the resampled distribution (0.018). The bootstrapped 95% confidence intervals overlap zero (-0.051, 0.081), thus a zero effect is consistent with the observed difference (Fig. 3-6).

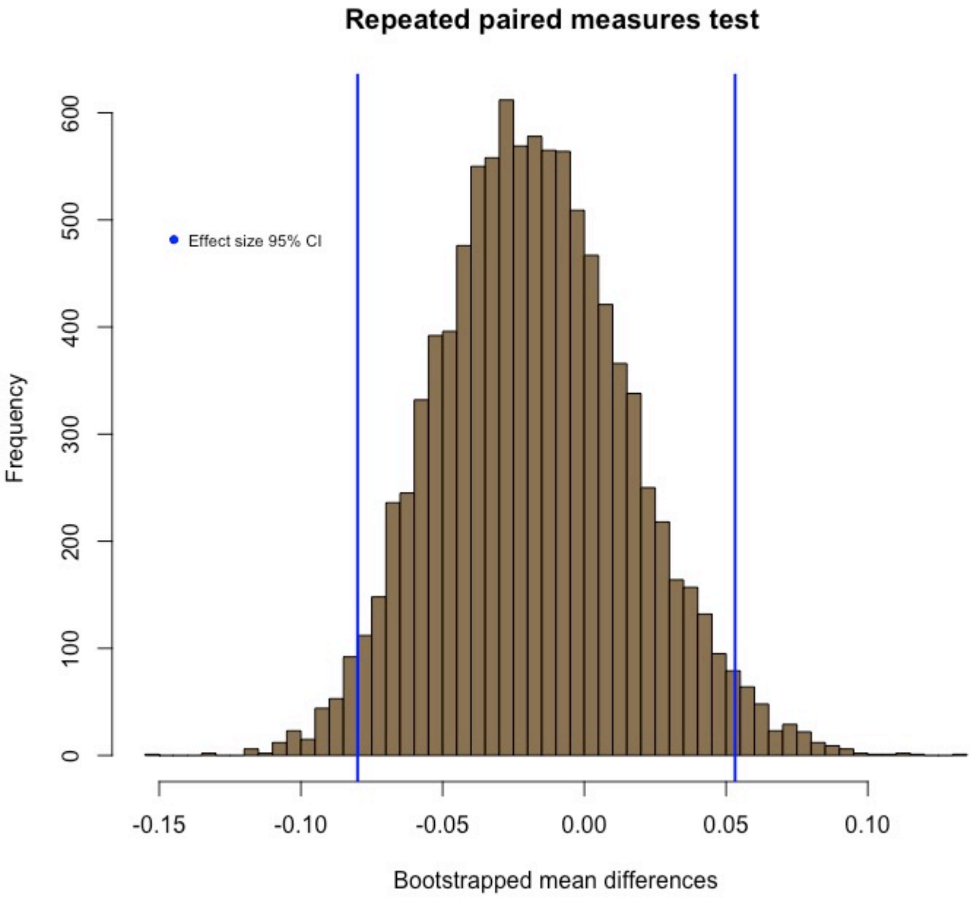
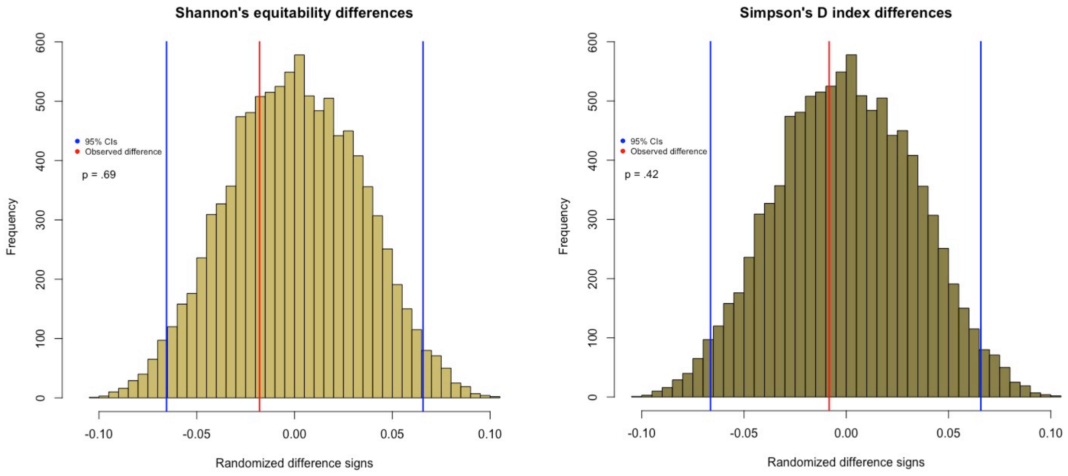


Figure 3-6. Sample test for repeated paired measures.

(b) Null hypothesis test using differences in Shannon's equitability and Simpson's index

As the actual mean evenness difference between CR and UR plots (0.018) falls within the null distribution's 95% confidence intervals (-0.065, 0.065), the test fails to reject the null hypothesis. The same null hypothesis significance test also failed to detect a difference between mean Simpson's index differences (Fig. 3-7).


Shannon's equitability differences

Simpson's D index differences

Figure 3-7. Given a null hypothesis where the evenness difference between CR and UR plots is zero, the order of the difference – that is, CR – UR or UR – CR – should not make a difference. Here, the null distribution consists of mean plot evenness scores with randomly assigned signs, simulating randomly switched order among the pairs. Null distribution of mean Simpson's D differences between CR and UR plots, with 95% confidence intervals in blue, and observed mean difference in red.

4. Community structure: strong differences in Bray-Curtis similarity measure of community composition between paired plots

Of the 49 plot pairs included in this study, 33 were less than 50% similar, and only 4 had a minimum confidence interval value that was equal to or was greater than 50% similarity (Fig. 3-8).

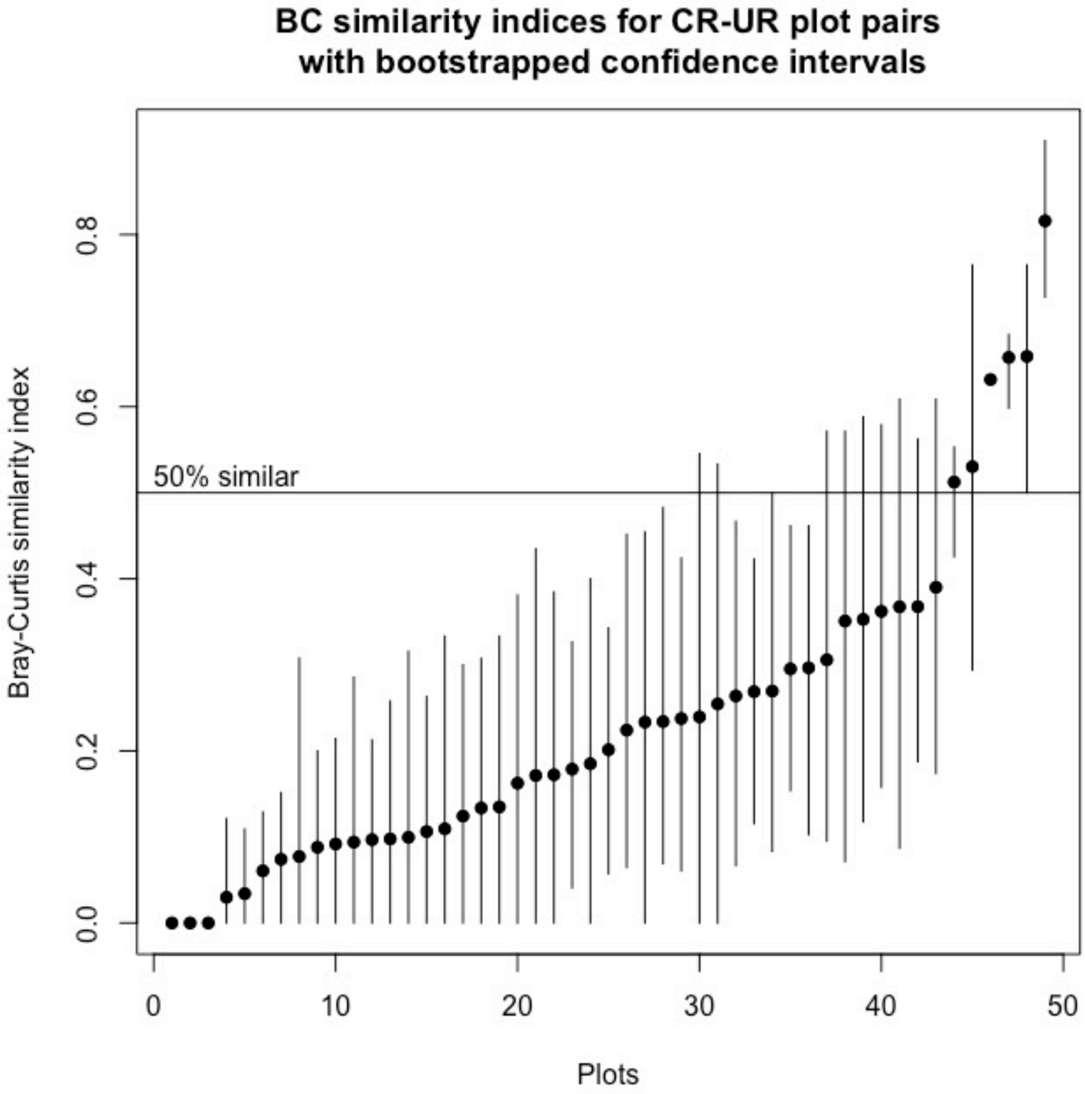


Figure 3-8. Bray-Curtis similarity measures comparing 49 CR and UR plot pairs, with bootstrapped confidence intervals. Tree community species composition is less than 50% similar in 33 plots.

5. Mean species differences: some significant differences

Of the 80 species occurring in CR and UR plots, 67 have confidence intervals overlapping zero, indicating no significant abundance differences between areas with and without cattle. However, 10 species are more abundant in UR versus CR plots (*Croton flavescens, Tabebuia chrysantha*

(Bignoniaceae), an unidentified shrub in the family Euphorbiaceae ("spotty"), *Wimmeria mexicana* (Celastraceae), *Ipomoea bracteata* (Convolvulaceae), *Lasianthaea fruticosa* var. *alamosana* (Asteraceae), *Lantana* sp. (*hispida* and *camara*) (Verbenaceae), *Euphorbia colletioides* (Euphorbiaceae), *Guazuma ulmifolia* (Malvaceae), and *Sebastiania pavoniana* (Euphorbiaceae)). Four are significantly more common in CR plots, compared to their abundances in UR plots (*Dodonaea viscosa* (Fabaceae), *Pachycereus pecten aboriginum* (Cactaceae), *Senna pallida* (Fabaceae), and *Brongniartia alamosana*) (Fig. 3-9; x axis labels in Table 3-S1).

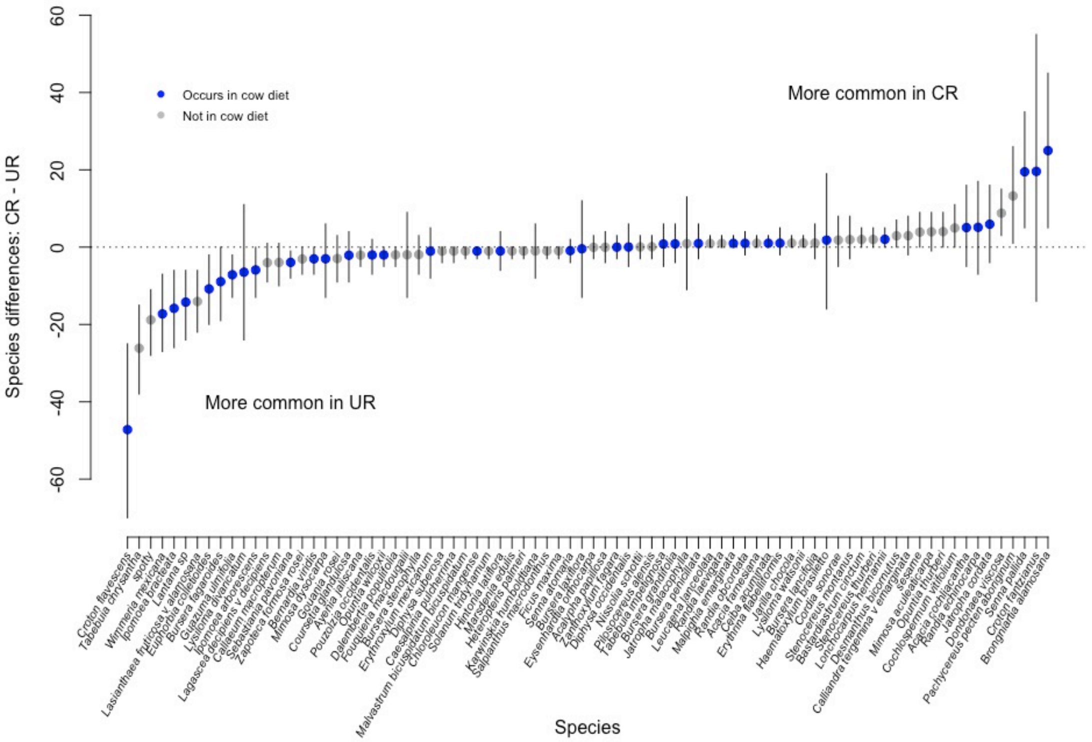


Figure 3-9. Eighty woody plant species occur in the tropical deciduous forest (TDF) currently ranched for cattle (CR), and a neighboring unranched (UR) property where cattle are excluded. Mean differences between species show that the majority (67 species) have confidence intervals overlapping zero,

indicating no significant difference in mean frequency between CR and UR. Species consumed by cows are in blue.

6. Importance Value Indices (IVI): some significant differences

Eleven species have significantly higher IVI scores in UR plots, indicating a negative effect of cattle ranching: *Jatropha malacophylla* (Euphorbiaceae)*, Croton flavescens, Tabebuia chrysantha, Ipomoea bracteata, Wimmeria mexicana, "spotty," Lasianthaea fruticosa v. alamosana, Lantana sp., Euphorbia colletioides, Guazuma ulmifolia*, and *Sebastiania pavonianna*. Seven have significantly higher IVI scores in CR, indicating a positive effect of cattle ranching: *"sesame"* (Euphorbiaceae), *Opuntia thurberi* (Cactaceae)*, Dondonaea viscosa, Senna pallida, Pachycereus pecten aboriginum, Croton fantzianus*, and *Brongniartia alamosana* (Fig. 3-10, x axis labels in Table 3-S1).

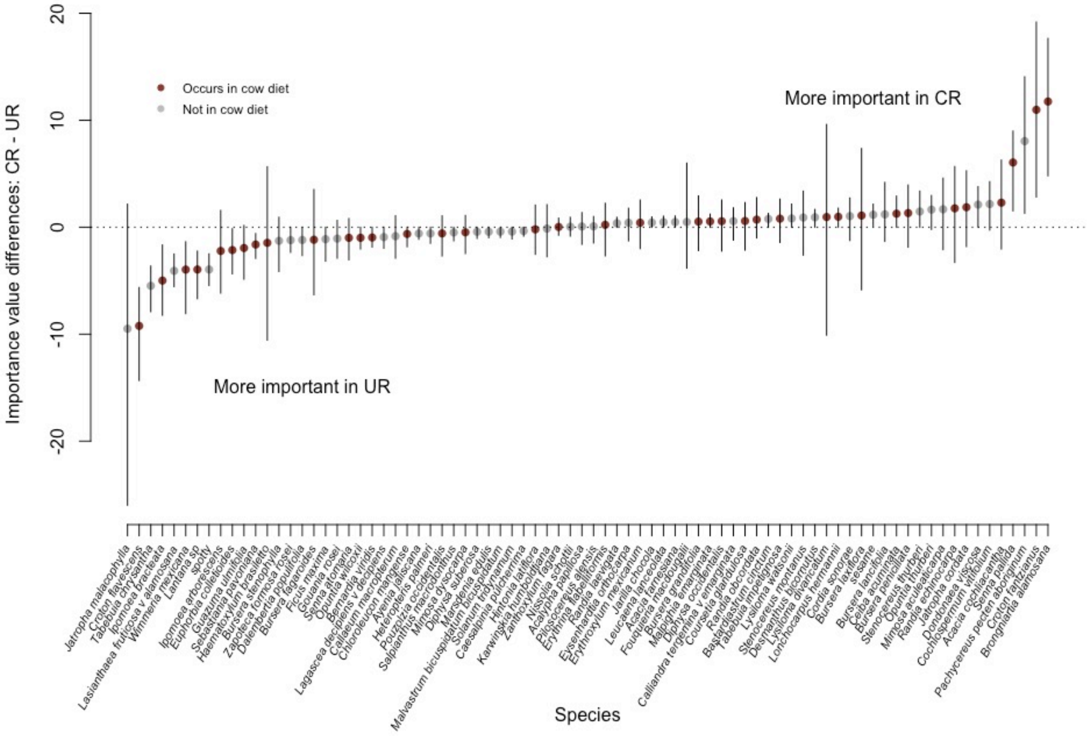


Figure 3-10. Importance Value Index (IVI) differences between species in currently ranched (CR) and unranched (UR) plots. Species consumed by cows are in brown.

7. Cattle browsing and mean frequency and IVI differences: no clear pattern

The relationship between cow consumption of woody plants and their frequencies and IVId in ranched versus exclusion areas is unclear. Cows consume thirty-seven woody species occurring in CR and UR plots, indicated by blue points in Fig. 3-4. *Croton flavescens*, for example, makes up 25% of the woody plant component of cow diets (WPC), and is significantly less common in CR compared to its frequency in UR, indicating a negative response to browsing. On the other hand, *Brongniartia alamosana* and *Senna pallida*, also consumed by cows (2 and 4% of WPC, respectively), are both significantly more common in CR versus UR. Differences between other commonly consumed species, such as *Croton fantzianus* (23% WPC), *Randia echinocarpa* (Rubiaceae) (8% WPC), *Acacia cochliacantha* (Fabaceae) (7% WPC), and *Haemotoxylum brasiletto* (Fabaceae) (5% WPC), are not statistically distinguishable from zero.

Of species with higher IVI scores in UR plots, seven occur in cow diets documented by CowPro: *Croton flavescens*, *Ipomoea bracteata*, *Wimmeria mexicana, Lantana sp., Euphorbia colletioides, Guazuma ulmifolia,* and *Sebastiania pavonianna*. However, of the six species with significantly higher IVI in CR plots, cattle consume three: *Senna pallida, Croton fantzianus*, and *Brongniartia alamosana*.

8. Cattle browsing and stem size differences: some differences

Frequencies of CR and UR stem size classes in eaten species are similar to those among all species (Figure 5): the smallest stems (10-19mm) are more frequent in UR plots, while larger size classes are equally or more frequent in CR plots. At 20cm height (Fig. 3-11, left panel), stems between 20 and 49mm in diameter in CR plots were significantly more frequent than in UR plots. There were no statistically detectable differences at 130cm height.

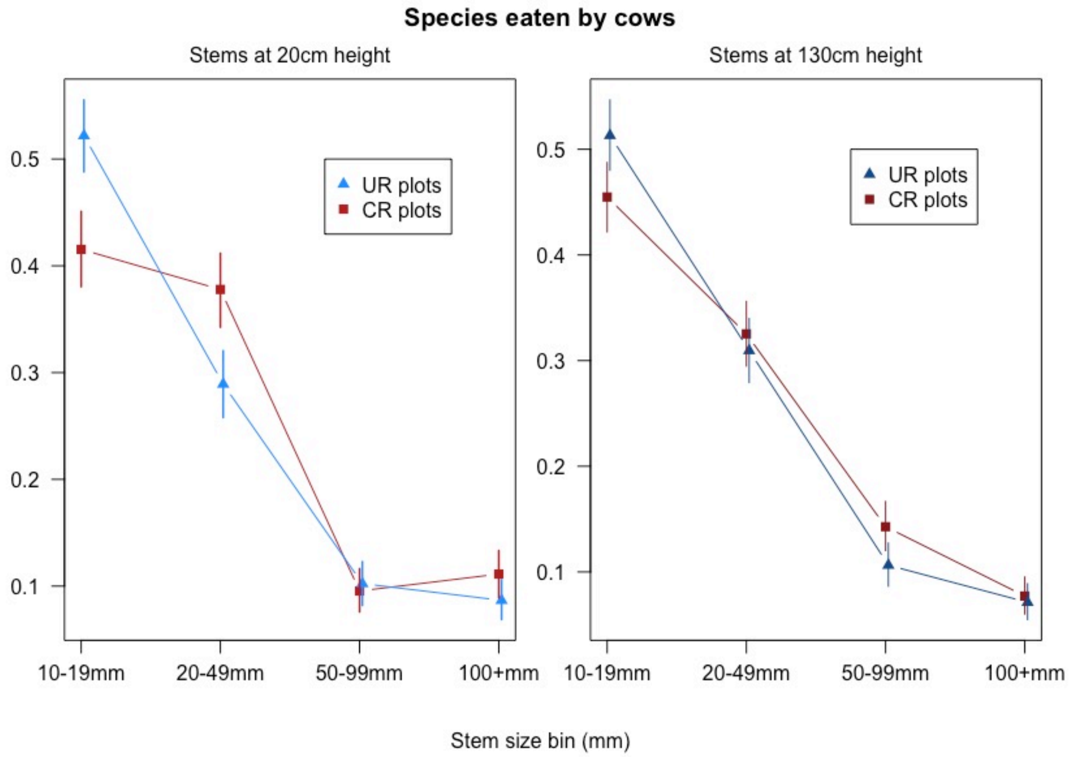


Figure 3-11. Stem size differences at 20cm (left) and 130cm height (right) for species commonly eaten by cows. At 20cm height, small stems between 10-19mm in diameter are significantly less frequent in CR compared to UR plots, thought the trend reverses for stems 20-49mm. At 130cm height, there are no statistically detectable differences.

Among species not eaten by cows in de la Rosa (2018b), UR plots had more frequent small diameter stems at 130cm, but not at 20cm height (Fig. 3-12, right and left panel respectively). Large class stems (50-99mm at 20cm height, and 101+mm at 130cm height) were significantly more frequent in CR plots.

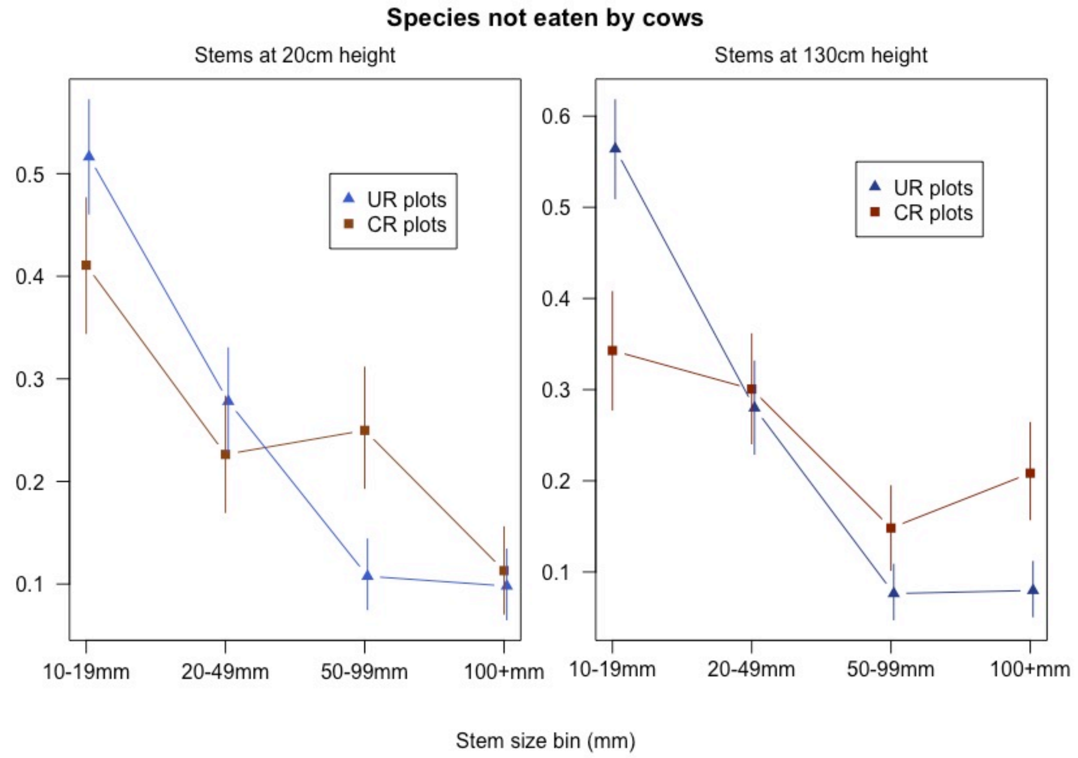


Figure 3-12. Stem size differences at 20 and 130cm height (left and right) for species not occurring in de la Rosa (2018b) cattle browsing data. At 20cm height, stems between 50-99mm in diameter were significantly more frequent in CR plots; at 130cm height, small class stems (10-19mm) were more frequent in UR plots, while large stems (100+mm) were more frequent in CR plots.

3.6 DISCUSSION

3.6.1 *Stem size class differences*

Data on stem size class differences indicate that cattle browsing influences plant stem size class distribution. Cattle are grazers, preferring grasses and annual species to woody vegetation (Vandenberghe et al., 2007), resorting to woody vegetation in areas where annuals are exhausted or absent (Holechek et al., 1982; de la Rosa, 2018b). When browsing, cattle prefer small stems of easily digestible species, like seedlings and saplings (de la Rosa, 2018b), behavior that can reduce tree regeneration, as in Australian white box woodlands (Allcock and Hik, 2004). It is intuitive, therefore, that smaller stems would be less abundant in areas with cattle: at lower heights, seedlings may be clipped below a measurable threshold or killed, while at breast height, small branches may be pruned or broken by browsing (as shown in Fig. 3-5).

Less intuitive is that, within a subset of only local species eaten by cows, the pattern is actually weaker than overall (Fig. 3-11). Stem differences are in fact more pronounced within a subset of species *not* eaten by cows at all in Chapter 2, at least in stems at breast height (Fig 12). Cattle could be having a negative effect on these species not due to browsing. Additionally, there are no within-species significant differences in the five most commonly browsed species (*Croton flavescens*, *Croton fantzianus, Randia echinocarpa, Acacia cochliacantha*, and *Haematoxylum brasiletto*) (Fig. 3-S1). Given (a) no overly strong support for a significant difference between browsed and unbrowsed species' responses in size class distribution to cattle, (b) that the pattern persists in the control group (unbrowsed species), and (c) that the pattern completely disappears at the single species level among commonly eaten plants, some other variable or variables must be behind the significant differences in Figure 5.

Two hypotheses could explain the phenomenon. First, some other action of cattle not related to browsing might be affecting tree species size class distributions. As large, mobile herbivores, cattle crush and break small shrubs and tree branches in the course of their normal daily activities. Soil compaction, through the repeated action of hooves during movement, or though dust bathing and ruminating, during which cows are usually prostrate and in contact with the ground, could stunt seedling recruitment or kill individuals by crushing.

Alternatively, it could be something missed by CowPro, the video and GPS data collection system at the heart of the database of diversity and frequency of species eaten by cows (de la Rosa, 2018a). CowPro data are limited to mature trees: seedlings, in addition to most annual plants and small perennial herbs, are too small to be accurately identified from videos. Furthermore, rare species may be underrepresented due to the CowPro sampling protocol. If certain species are predisposed to seedling mortality or pruning below a detectable level, and/or if those species are rare, CowPro data would be a poor predictor of stem size differences in areas with and without cattle.

3.6.2 *Woody plant community differences*

Species composition was significantly different in comparisons of 67% of the plot pairs. Of the 80 woody plant species occurring in this study, mean frequencies were significantly different from zero in 14 (17%) and importance value indices (IVI) were significantly different from zero in 18 (22%). None of these species were particularly rare: of the species more common and important in UR plots, all had at least 4 individuals in UR plots, and only three ("spotty," *Guazuma ulmifolia*, and *Sebastiania pavoniana*) had one or zero individuals in CR plots. Likewise, species more common or important in CR plots were not rare. Of six, only one (*Opuntia thurberi*) had fewer than 10 individuals overall. Common species, therefore, seem to be responsible for the majority of species composition dissimilarity between CR and UR plots.

Additionally, it is not possible to evaluate whether rare species are dissimilar because of the effect of cattle or because of other variables that limit their abundance.

Significant differences in species frequencies and importance values are likely partly due to the effect of cows, and partly to high local plant community heterogeneity. Beta diversity in TDF is exceptionally high. Across Mexico, Trejo and Dirzo found mean similarity between 20 sites, measured by number of shared species and Sorensen's similarity index, to be just 9% (2002). At the local scale, Álamos TDF is impressively heterogeneous. In this study, the mean number of species shared between sites within CR plots was just 1.17; likewise, mean number of shared species within-UR plots was 1.3. Though no within-treatment data exist at the 20-meter level to compare to between-treatment plot similarity indices, at 100 meters distance, any effect of cattle on community assemblage is completely obscured by the forest's natural heterogeneity. To see whether an effect of cattle is detectable at the 100m scale, I calculated Bray-Curtis similarity scores for 80 within-treatment plot pairs (within-CR and within-UR), and 80 diagonally adjacent between-treatment pairs, the centers separated by ~102m. The means of CR and UR within-treatment plot pair Bray-Curtis similarity indices are nearly identical (mean CR: 0.20 (0.07, 0.35); mean UR: 0.21 (0.09, 0.34)) (Fig. 3-13). Combined within-treatment mean Bray-Curtis similarities were also not statistically distinguishable (mean between treatment: 0.18 (0.06, 0.32); mean within treatment: 0.20 (0.08, 0.35)) (Fig. 3-14). However, this result does not mean that at

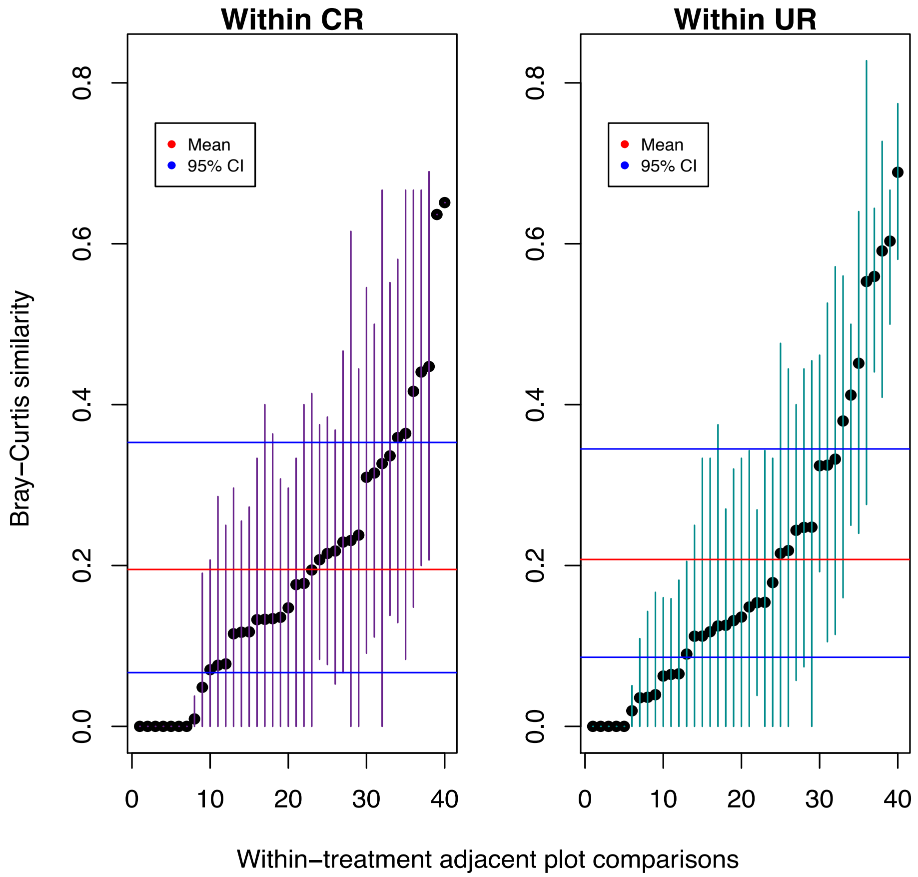


Figure 3-13. Within-treatment adjacent plot comparisons for 40 adjacent plot pairs show that species turnover within CR and UR plots is nearly identical.

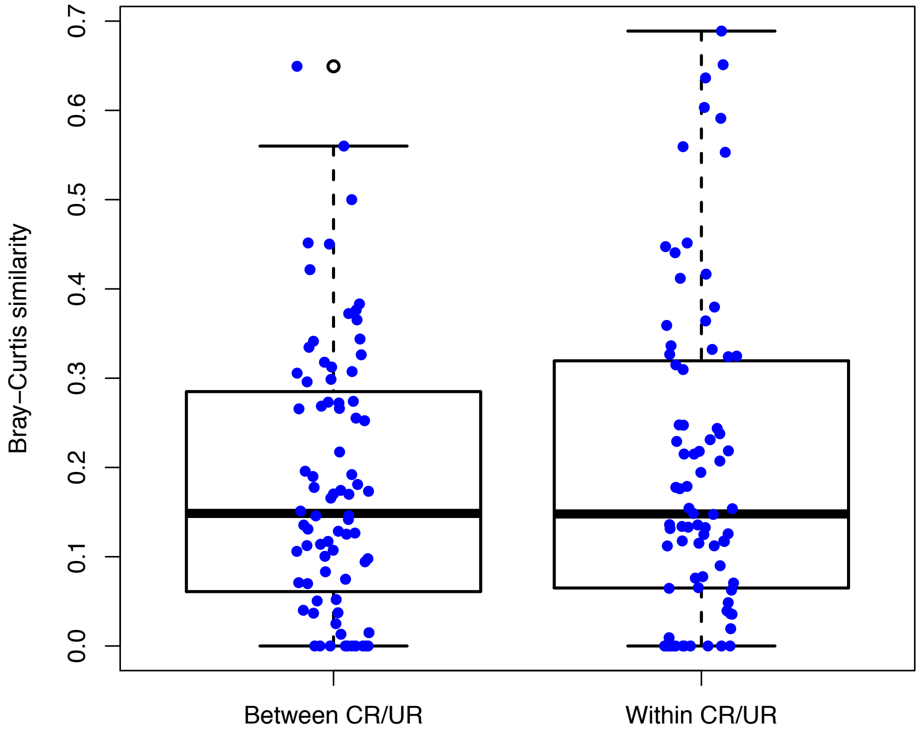


Figure 3-14. Species turnover at ~100 meters distance is not statistically distinguishable between within-treatment groups (right) and between-treatment groups.

It is possible that cow foraging impacts different tree species more severely, while others are more resistant to browsing. CowPro data I describe in de la Rosa (2018b) show that cows eat some woody plant species (such as *Croton flavescens, Acacia cochliacantha, Haematoxylum brasiletto*, and *Coursetia glandulosa*) more frequently than suggested by their abundance in the local environment. Results of this study show that there is no relationship between these species and differences in frequency or importance when comparing CR and UR plots. However, as I was only able to identify mature woody plants consumed by cows from CowPro videos, some species may be underrepresented in WPC of cow diets. *Tabebuia chysantha*, for example, is significantly more frequent in UR compared to CR plots, but does not occur in CowPro videos of cattle foraging. However, their absence in the CowPro database does not mean they are not browsed by cattle: as mature trees, their canopies spread at heights of up to 15 meters (Martin, 1998), where the majority of their leafy vegetation would be out of a cow's reach. Furthermore, *Tabebuia* species form prodigious carpets of small seedlings, which would be both tempting to browsing cattle (as I discuss in de la Rosa, 2018b), as well as impossible to document accurately using CowPro.

Also contrary to the prediction that species browsed by cattle would be less abundant, *Acacia cochliacantha* is significantly more important in CR plots compared to UR plots (Fig. 3-10). *A. cochliacantha* is a fast-growing shrubby legume, especially common in secondary TDF. Besides the apparent lack of effect of cattle browsing on *A. cochliacantha* IVI values, some evidence suggests that cattle may in fact be aiding its dispersal. In the Alamos TDF, many species of woody plant begin to shed their leaves in late September, and are largely bare from mid-October through November and December. As leafy and grassy green vegetation becomes scarce, cows begin to consume relatively large amounts of leaf litter and legume seed pods, especially *A. cochliacantha* and *Lysiloma divaricatum*, which drop their fruit at this time (see Fig. 3-4, de la Rosa, 2018a). In a common garden experiment on secondary forest colonizers, *A. cochliacantha* seedlings recruited poorly when planted on their own (Hernandez-Cornejo, unpublished data); however, in November and December of 2014 and 2015, I observed seedlings sprouting vigorously from cow feces (Fig. 3-15). Future work should investigate the potential role of cattle as a disperser of *A. cochliacantha.*

Figure 3-15. *Acacia cochliacantha* seeds in cow feces (left), *A. cochliacantha* and *Lysiloma divaricatum* seedlings sprouting from cow feces (right).

3.7 CONCLUSIONS

A key assumption of this study was that CR and UR plots, matched for similar slope, aspect, and other conditions, should in the absence of cattle be statistically indistinguishable. At the 100m level, however, the effect of cattle on TDF community structure is statistically indistinguishable from the natural heterogeneity of the TDF (Figs. 3-13 and 3-14). It is therefore possible that heterogeneity at the 20m level (the distance from center to center of matched CR and UR plot pairs) is responsible for differences in species assemblage and frequency reported in this study. Future work could quantify the role of natural heterogeneity at the 20m scale by censusing plants in quadrats at that distance within the CR and UR conditions.

The strongest effect of cattle on TDF uncovered in the course of this study was on stem size classes: cattle, presumably through browsing, significantly reduce the frequency of small stems at both sapling height (20cm) and breast height (130cm) (Fig. 3-5). Seedling mortality due to browsing could thus be responsible for community differences. However, CowPro foraging data (de la Rosa, 2018b), showing the frequency and diversity of woody plant species consumed by cows, map imperfectly onto species with the greatest differences in mean frequency (Fig. 3-9) and importance (Fig. 3-10) compared between CR and UR treatments. This is probably due to the fact that browsing on mature woody plants, the central theme of de la Rosa (2018b), accounts for only 20-30% of overall cow foraging behavior (de la Rosa, 2018a). The majority of cattle foraging effort is devoted to annual and perennial ground-covering herbaceous plants, grasses, and woody plant seedlings (“small plants”), mostly indistinguishable in CowPro videos. Additionally, among rare species, differences in abundance due to rarity are hard to untangle from differences due to cattle. A new methodological approach would be needed to resolve cow forage species at the seedling stage.

3.8 SUPPLEMENTAL MATERIALS

	Species.mean.diff	**Species.IVI.diff**
1	Croton flavescens	Acacia cochliacantha
2	Tabebuia chrysantha	Acacia farnesiana
3	spotty	Acalypha papillosa
4	Wimmeria mexicana	Ayenia jaliscana
5	Ipomoea bracteata	Bastardiastrum cinctum
6	Lantana sp	Bernardia viridis
7	Lasianthaea fruticosa v alamosana	Brongniartia alamosana
8	Euphorbia colletioides	Bursera fagaroides
9	Bursera fagaroides	Bursera grandifolia
10	Guazuma ulmifolia	Bursera lancifolia
11	Lysiloma divaricatum	Bursera laxiflora
12	Ipomoea arborescens	Bursera penicillata

13	Lagascea decipiens v decipiens	Bursera stenophylla
14	Callaeum macropterum	Caesalpinia pulcherrima
15	Sebastiania pavoniana	Callaeum macropterum
16	Zapoteca formosa rosei	Calliandra tergemina v emarginata
17	Bernardia viridis	Ceiba acuminata
18	Mimosa dysocarpa	Chloroleucon mangense
19	Gouania rosei	Cochlospermum vitifolium
20	Coursetia glandulosa	Cordia sonorae
21	Ayenia jaliscana	Coursetia glandulosa
22	Pouzolzia occidentalis	Croton fantzianus
23	Opuntia wilcoxii	Croton flavescens
24	Dalembertia populifolia	Dalembertia populifolia
25	Fouquieria macdougalii	Desmanthus bicornutus
26	Bursera stenophylla	Diphysa occidentalis
27	Erythroxylum mexicanum	Diphysa suberosa
28	Diphysa suberosa	Dondonaea viscosa
29	Caesalpinia pulcherrima	Erythrina flabelliformis
30	Malvastrum bicuspidatum bicuspidatum	Erythroxylum mexicanum
31	Chloroleucon mangense	Euphorbia colletioides
32	Solanum tridynamum	Eysenhardtia orthocarpa
33	Hintonia latiflora	Ficus maxima
34	Marsdenia edulis	Fouquieria macdougalii
35	Heteropteris palmeri	Gouania rosei
36	Karwinskia humboldtiana	Guazuma ulmifolia
37	Salpianthus macrodonthus	Haematoxylum brasiletto
38	Ficus maxima	Heteropteris palmeri
39	Senna atomaria	Hintonia latiflora
40	Bursera laxiflora	Ipomoea arborescens
41	Eysenhardtia orthocarpa	Ipomoea bracteata
42	Acalypha papillosa	Jarilla chocola
43	Zanthoxylum fagara	Jatropha cordata
44	Diphysa occidentalis	Jatropha malacophylla
45	Nissolia schottii	Karwinskia humboldtiana
46	Pilosocereus alensis	Lagascea decipiens v decipiens
47	Tabebuia impetignosa	Lantana sp
48	Bursera grandifolia	Lasianthaea fruticosa v alamosana
49	Jatropha malacophylla	Leucaena lanceolata
50	Bursera penicillata	Lonchocarpus hermannii
51	Leucaena lanceolata	Lysiloma divaricatum
52	Randia laevigata	Lysiloma watsonii
53	Malpighia emarginata	Malpighia emarginata
54	Randia obcordata	Malvastrum bicuspidatum bicuspidatum
55	Acacia farnesiana	Marsdenia edulis

56	Ceiba acuminata	Mimosa aculeaticarpa
57	Erythrina flabelliformis	Mimosa dysocarpa
58	Jarilla chocola	Nissolia schottii
59	Lysiloma watsonii	Opuntia thurberi
60	Bursera lancifolia	Opuntia wilcoxii
61	Haematoxylum brasiletto	Pachycereus pecten aboriginum
62	Cordia sonorae	Pilosocereus alensis
63	Stenocereus montanus	Pouzolzia occidentalis
64	Bastardiastrum cinctum	Randia echinocarpa
65	Stenocereus thurberi	Randia laevigata
66	Lonchocarpus hermannii	Randia obcordata
67	Desmanthus bicornutus	Salpianthus macrodonthus
68	Calliandra tergemina v emarginata	Sebastiania pavoniana
69	sesame	Senna atomaria
70	Mimosa aculeaticarpa	Senna pallida
71	Opuntia thurberi	sesame
72	Cochlospermum vitifolium	Solanum tridynamum
73	Acacia cochliacantha	spotty
74	Randia echinocarpa	Stenocereus montanus
75	Jatropha cordata	Stenocereus thurberi
76	Dondonaea viscosa	Tabebuia chrysantha
77	Pachycereus pecten aboriginum	Tabebuia impetignosa
78	Senna pallida	Wimmeria mexicana
79	Croton fantzianus	Zanthoxylum fagara
80	Brongniartia alamosana	Zapoteca formosa rosei

Table 3-S1. List of index numbers and species corresponding to indices in Figure 9 (left column) and Figure 10 (right column).

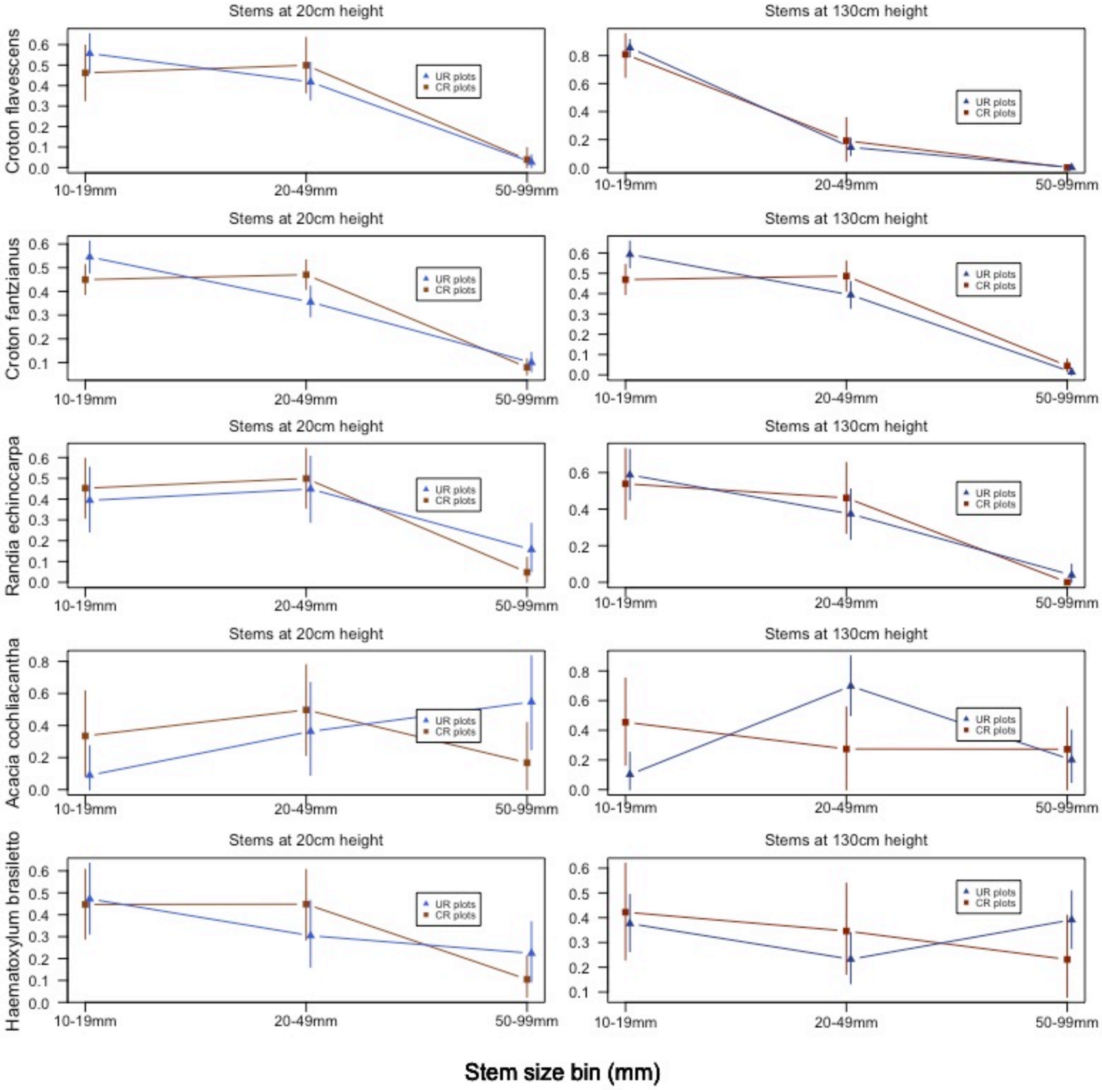


Figure 3-S1. Comparison of stem frequencies in three size categories for five woody plant species frequently eaten by cows (Croton flavescens, Croton fantzianus, Randia echinocarpa, Acacia cochliacantha, and Haematoxylum brasiletto). There are no statistically detectable differences in plant stem size frequency between CR and UR plots for these species.

3.9 APPENDIX I

Species	**Family**	**Common Name**	**Habit**	**WPC**	**RVFH**	**AAH**	**CR**	**UR**
Acacia cochliacantha	Fabaceae	Guinolo	Tree	39	110	134	16	11
Acacia farnesiana	Fabaceae	Vinorama	Tree	0	0	0	1	0
Acalypha cincta	Euphorbiaceae		Shrub	0	0	2	0	0
Acalypha papillosa	Euphorbiaceae		Shrub	0	1	1	2	2
Agave vilmorinia	Asparagaceae	Amole	Agave	0	1	2	0	0
Agonandra racemosa	Opiliaceae	Matachamaco, palo verde	Tree	0	0	3	0	0
Anoda abutiloides	Malvaceae		Perennial herb	0	1	0	0	0
Ayenia jaliscana	Sterculiaceae		Shrub	0	0	0	0	2
Bastardiastrum cinctum	Malvaceae		Perennial herb	0	0	0	2	0
Begonia palmeri	Begoniaceae		Shrub	0	0	1	0	0
Bernardia viridis	Euphorbiaceae		Shrub	4	7	5	0	3
Brahea aculeata	Arecaceae	Palmilla	Palm	1	0	0	0	0
Brongniartia alamosana	Fabaceae	Piojo	Tree	14	218	373	73	47
Bursera fagaroides	Burseraceae	Torote papelillo	Tree	4	4	6	9	18
Bursera grandifolia	Burseraceae	Palo mulato	Tree	1	7	27	3	2
Bursera lancifolia	Burseraceae	Torote copal (papelillo)	Tree	0	0	1	3	2
Bursera laxiflora	Burseraceae	Torote prieto	Tree	5	23	66	20	20
Bursera penicillata	Burseraceae	Torote de incienso	Tree	1	2	6	3	2
Bursera stenophylla	Burseraceae	Torote copal	Tree	0	3	3	2	4
Caesalpinia platyloba	Fabaceae	Palo colorado	Tree	0	0	1	0	0
Caesalpinia pulcherrima	Fabaceae	Tavachin	Shrub	0	11	10	0	1
Callaeum macropterum	Malpighiaceae	Batanene	Liana	0	26	24	2	6
Calliandra tergemina v emarginata	Fabaceae	Pata de venado, guamuchilillo	Shrub, tree	0	1	2	5	2
Ceiba acuminata	Bombacaceae	Pochote	Tree	1	9	12	1	0
Celtis iguanea	Celtidaceae	Garambullo	Tree	1	0	0	0	0
Chloroleucon mangense	Fabaceae	Palo fierro, palo pinto	Tree	2	9	13	0	1
Cochlospermum vitifolium	Cochlospermaceae	Palo barril	Tree	0	0	1	6	1
Cordia sonorae	Boraginaceae	Palo de asta	Tree	0	1	21	7	5
Coursetia glandulosa	Fabaceae	Cau samo	Shrub	21	43	43	4	6
Croton ciliato-glandulifer	Euphorbiaceae	Vara prieta peluda	Shrub	6	54	4	0	0
Croton fantzianus	Euphorbiaceae	Vara blanca	Tree	138	883	3871	213	194
Croton flavescens	Euphorbiaceae	Vara prieta	Shrub	151	646	641	44	91

Dalembertia populifolia	Euphorbiaceae	Jicama de palo	Shrub	0	0	0	0	2
Desmanthus bicornutus	Fabaceae	Dais	Shrub	0	5	0	3	0
Diphysa occidentalis	Fabaceae	Guiloche	Tree	3	8	4	4	4
Diphysa suberosa	Fabaceae	Corcho	Tree	0	0	0	0	1
Dodonaea viscosa	Sapindaceae		Shrub	0	0	0	10	1
Erythrina flabelliformis	Fabaceae	Chilicote, pionilla	Tree	1	6	7	2	1
Erythroxylum mexicanum	Erythroxylaceae	Momoa	Tree	7	13	3	5	6
Esenbeckia hartmanii	Rutaceae	Palo amarillo	Tree	1	10	11	0	0
Euphorbia colletioides	Euphorbiaceae	Candililla	Perennial herb	1	4	12	6	17
Eysenhardtia orthocarpa	Fabaceae	Palo dulce	Tree	0	0	0	1	1
Ficus maxima	Moraceae	Chalate de burro	Tree	0	0	0	0	1
Fouquieria macdougalii	Fouquieriaceae	Torote verde	Tree	0	20	56	16	18
Gouania rosei	Rhamnaceae	Guirote de violin	Liana	0	6	3	3	6
Guazuma ulmifolia	Sterculiaceae	Guasima	Tree	4	8	9	1	8
Haematoxylum brasiletto	Fabaceae	Brasil	Tree	31	74	89	42	40
Heliocarpus attenuatus	Tiliaceae	Samo	Shrub	0	2	0	0	0
Heteropteris palmeri	Malpighiaceae		Liana	0	0	0	0	1
Hintonia latiflora	Rubiaceae	Palo amargo	Tree	1	6	2	3	4
Hybanthus mexicanus	Violaceae		NA	1	23	0	0	0
Ipomoea arborescens	Convolvulaceae	Palo santo	Tree	1	3	18	3	9
Ipomoea bracteata	Convolvulaceae	Jicama	Liana	1	32	45	6	22
Jacquinia macrocarpa	Theophrastaceae	San Juanico	Tree	1	10	11	0	0
Jarilla chocola	Caricaceae	Chocola	Shrub	0	0	3	1	0
Jatropha cordata	Euphorbiaceae	Papelillo	Tree	1	72	110	16	10
Jatropha malacophylla	Euphorbiaceae	Sangrengado	Shrub	0	196	337	20	19
Karwinskia humboldtiana	Rhamnaceae	Cacachila	Shrub, tree	0	43	40	6	7
Lagascea decipiens v decipiens	Asteraceae		Shrub	0	0	0	1	5
Lantana camara	Verbenaceae	Confiturilla amarilla	Shrub	0	1	0	0	0
Lantana hispida	Verbenaceae	Confiturilla blanca	Shrub	0	42	26	0	0
Lantana sp	Verbenaceae	Confiturilla	NA	6	0	0	3	17
Lasianthaea fruticosa v alamosana	Asteraceae		Shrub	0	0	0	2	16
Leucaena lanceolata	Fabaceae	Guaje	Tree	0	0	0	1	0
Lonchocarpus hermannii	Fabaceae	Nesco	Tree	3	8	11	2	0
Lysiloma divaricatum	Fabaceae	Mauto	Tree	22	62	71	39	45
Lysiloma watsonii	Fabaceae	Tepeguaje	Tree	0	1	0	1	0

Malpighia emarginata	Malpighiaceae	Mora	Tree	10	34	20	1	0
Malvastrum bicuspidatum bicuspidatum	Malvaceae	Malva roja	Perennial herb	0	0	0	0	1
Marsdenia edulis	Asclepidaceae	Tonchi	Liana	0	1	1	0	1
Mimosa aculeaticarpa	Fabaceae	Chopo negro	Tree	0	0	0	6	2
Mimosa distachya laxiflora	Fabaceae	Gato blanco	Tree, shrub	2	8	2	0	0
Mimosa dysocarpa	Fabaceae	Gato negro	Tree, shrub	2	17	2	9	12
Mimosa palmeri	Fabaceae	Chopo	Tree	3	35	46	0	0
Montanoa rosei	Asteraceae	Batayaqui	Tree	1	0	0	0	0
Nissolia schottii	Fabaceae		Liana	0	10	10	1	1
Opuntia pubescens	Cactaceae	Civiri	Cactus	0	12	17	0	0
Opuntia thurberi	Cactaceae	Cholla	Cactus	0	15	8	5	1
Opuntia wilcoxii	Cactaceae	Nopal	Cactus	4	18	13	0	2
Pachycereus pecten aboriginum	Cactaceae	Etcho	Cactus	0	78	137	26	13
Pereskiopsis porteri	Cactaceae	Jejeri	Cactus	0	1	0	0	0
Pilosocereus alensis	Cactaceae	Pitahaya barbona	Cactus	0	1	7	1	1
Plumeria rubra	Apocynaceae	Cascalosuchil	Tree	0	1	0	0	0
Pouzolzia occidentalis	Urticaceae	Jicama de cochi	Shrub	4	10	46	2	4
Randia echinocarpa	Rubiaceae	Papache	Tree	46	181	176	21	16
Randia laevigata	Rubiaceae	Sapuche	Tree	0	0	0	1	0
Randia obcordata	Rubiaceae	Papache borracho	Tree	11	23	24	2	1
Salpianthus macrodonthus	Nyctaginaceae		Perennial herb	0	0	0	0	1
Salvia mexicana	Lamiaceae	Salvia	Shrub	0	1	0	0	0
Schoepfia schreberi	Olacaceae	Palo cachora	Tree	1	0	0	0	0
Sebastiania pavoniana	Euphorbiaceae	Brincador	Tree	1	28	7	0	4
Senna atomaria	Fabaceae	Zorrillo	Tree	1	3	22	1	2
Senna pallida	Fabaceae	Garbancillo	Shrub	23	158	224	41	22
Senna uniflora	Fabaceae	Ejotillo del monte	Perennial herb	0	9	0	0	0
Solanum tridynamum	Solanaceae	Sacamanteca	Perennial herb	0	0	0	0	1
Stenocereus montanus	Cactaceae	Pitahaya sahuira	Cactus	0	2	12	5	3
Stenocereus sp	Cactaceae	Pitahaya	Cactus	0	8	1	0	0
Stenocereus thurberi	Cactaceae	Pitahaya marismena	Cactus	0	16	45	2	0
Tabebuia chrysantha	Bignoniaceae	Amapa amarilla	Tree	0	0	0	4	30
Tabebuia impetignosa	Bignoniaceae	Amapa rosada	Tree	1	5	2	4	3
Tabebuia sp	Bignoniaceae	Amapa	Tree	0	0	11	0	0
Trichilia americana	Meliaceae	Piocha	Tree	0	0	1	0	0

Vitex mollis	Verbenaceae	Igualama	Tree	0	0	1	0	0
Wimmeria mexicana	Celastraceae	Algodoncillo	Perennial herb	1	1	3	6	23
Zanthoxylum fagara	Rutaceae	Matalased	Shrub	6	81	82	1	1
Zapoteca formosa rosei	Fabaceae	Tosapolo	Shrub	0	0	0	0	3
Resolved to morphotype								
like chiltepin			Perennial herb	0	2	0	0	0
sesame			Shrub	0	0	0	5	1
sortija			Liana	0	0	16	0	0
spotty			Shrub	0	0	0	0	19

Table A-I-1. All woody plant types (trees, shrubs, lianas, cacti, agaves, and herbaceous perennials) occurring in this study, identified when possible to species, and including common names used in the community of Sabinito Sur. Columns 5, 6, 7, 8, and 9 are the number of individuals occurring in five datasets: the woody plant component of cow diets (WPC), repeat-visit foraging habitat (RVFH), all available habitat (AAH), currently ranched TDF (CR), and unranched TDF (UR).

3.10 APPENDIX II

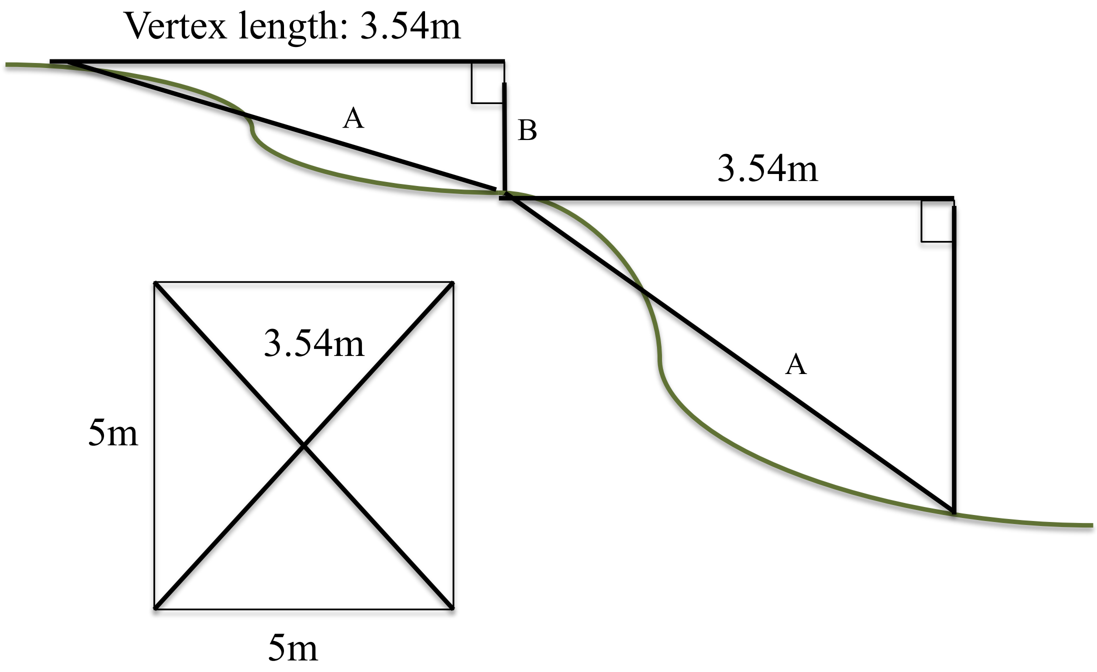


Figure A-II-1. 25m^2 plant census plot schematic. In uneven terrain, the hypotenuse (A) can be calculated by measuring the angle from a known height at the center (B) to the same height at the corner.

Plot installation checklist
Notebook
GPS
Flagging tape
Rebar
Compass/Clinometer
Tent stake (for marking the center point)
4 pound hammer
Tripod
30m tape
Extra batteries

Table A-II-1. Equipment checklist for installing 5m x 5m plant census plots. Rebar with orange flagging mark the corners.

Plot outlining checklist
10m DBH tape
30m rope
Clinometer
Machete

Plant tagging and stem measurement checklist
130cm staff with a mark at 20cm
Metric calipers (2)
Clipboard, data sheets, pencils, pens
Thread / fishing line for tying on tags
Small nails and hammer
Aluminum tags
Flagging tape
Camera

Plant collecting checklist
Plant press, newspaper, cardboard
Notebook
GPS
Leatherman multitool with saw
Pruning shears

Table A-II-2. Equipment checklists for delineating plots, tagging and measuring plants, and collecting specimens.

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