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GRADUATE SCHOOL

Dry season cattle grazing in the seasonally dry tropical forests of Costa Rica: importance in cattle ranching livelihoods and impacts on forest botanical composition and diversity

By
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Dedication

To my family: Blandine Favre, Hubert Godinot, Coline and Benjamin Godinot

To Claudia Arndt

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Biography

The author was born in Lyon, France, in April 1990. He graduated in 2011 from the ESCD 3A Business and International Development School, with a specialty on NGO management and Latin America. Throughout his studies, he discovered a fascination for forests during a six-month internship in the Peruvian Amazon, in the small town of Tamshiyacu where he helped local craftspersons to establish a distribution channel to sell their forest seed-based handicraft. He realized how important the forest was in people's everyday life, and decided to orient his career towards forest conservation. After working for a year at the forest conservation UK charity The Forest Trust, he went for a three-year trip through Latin America, working as a dive and kitesurf instructor. He then worked at the Fairtrade chocolate company Alter Eco in San Francisco, USA, for a year and a half, as a staff accountant. However, the need to spend time in forests doing fieldwork and understanding the role of forests and the services it provides in sustaining local livelihoods drove him to apply to CATIE's Master's Degree in Tropical Forests and Biodiversity Management and Conservation. The thesis subject presented in this volume is in the straight line of his research interests, as forests in Guanacaste provide a critical service to local farmers, and should be studied and understood. He now looks forward to develop and coordinate science-based conservation programs with local and international conservation organizations.

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Abbreviations

ACG: Area de Conservación Guanacaste

ANOSIM: Analysis of Similarities

ANOVA: Analysis of Variance

Bs-T: Bosque Seco Tropical

CADF: Central American Dry Forests

EbA: Ecosystem-based Adaptation

EEFH: Estación Experimental Forestal Horizontes

ENSO: El Niño-Southern Oscillation

FAO: United Nations Food and Agriculture Organization

FCGG: Federación de Cámaras de Ganaderos de Guanacaste

HDI: Human Development Index

MAG: Ministerio de Agricultura y Ganadería

MINAE: Ministerio de Ambiente y Energía

SDTF: Seasonally dry tropical forest

SINAC: Sistema Nacional de Áreas de Conservación

NMDS: Non-Metric Multidimensional Scaling

WWF: World Wildlife Fund

Resumen

El bosque seco tropical (Bs-T) centroamericano es uno de los ecosistemas más amenazados en el mundo, con poca superficie bajo estatuto de conservación formal. Aunque no quedan bosques secos maduros en Costa Rica, el bosque seco vuelve a crecer desde el colapso de los precios de la carne en los 1980, pero está sometido a dos disturbios principales. El primero es los frecuentes incendios forestales de origen antropogénico. El segundo proviene de una práctica pecuaria poco documentada que consiste en dejar que el ganado vacuno entre al bosque durante el período seco para ramonear la vegetación leñosa y para que disfruten de la sombra y así aliviar el estrés calórico típico de la temporada seca. La frecuencia de esa práctica y su impacto sobre los medios de vida ganaderos son muy poco conocidos, y el impacto del ganado sobre este ecosistema ha sido poco estudiado en la literatura científica. Los bosques en fincas representan la mayoría de la cobertura arbórea de los Bs-T costarricenses, y es de especial importancia estudiarlos para determinar si los bosques sometidos a fuego y ramoneo en bosque son diferentes a los bosques de áreas protegidas, más estudiados y menos afectados por esos disturbios. Este estudio se enfocó en caracterizar esta práctica y su impacto en bosques no protegidos.

Se realizaron 43 entrevistas semiestructuradas con ganaderos del cantón de Liberia, Guanacaste, Costa Rica, para determinar la importancia del ramoneo en bosques en los medios de vida ganaderos. Siguió un muestreo ecológico en cuatro bosques no protegidos en fincas, que se compararon con el bosque protegido de la Estación Experimental Forestal Horizontes (EEFH). El ramoneo en bosque se identificó como la suplementación más usada en temporada seca, y se considera crítico en el manejo de fincas, en un contexto de baja rentabilidad de la ganadería y de cambio climático. Esta práctica presentaba ventajas para el bienestar animal, pero complicaba la eficiencia del manejo de la finca. Esta disyuntiva podría ser el factor que impacte más la decisión del ganadero de llevar ganado al bosque, ya que pruebas tratando de relacionar ramoneo en bosques con tipos de fincas o perfiles de suplementación no fueron concluyentes.

El muestreo en bosques no encontró diferencias entre estratos de dosel en bosques protegidos o no protegidos. Un análisis de conglomerados encontró tipologías de vegetación distribuidas en todo el paisaje, que dependían parcialmente de incendios. El mismo análisis en estratos del sotobosque y de vegetación del suelo encontró una diferencia más marcada entre conglomerados con parcelas en bosques quemados o ramoneados. Una prueba de correlación encontró una asociación fuerte entre las composiciones botánicas de los estratos verticales del bosque de las parcelas, pero las asociaciones entre conglomerados de los diferentes estratos mostraron una alta variabilidad. Sin embargo, se encontraron tendencias que sugieren que el fuego o el ramoneo podrían no ser los factores de mayor influencia sobre la composición de bosque de este paisaje, aunque el fuego pueda tener más impactos que el ramoneo. Ya que el ramoneo en bosque es importante para los medios de vida locales, las instituciones agrícolas no deberían satanizar esta práctica sino más bien trabajar con ganaderos para desarrollar el uso de buenas prácticas ganaderas o apoyar esta práctica en un marco sostenible y controlado. Se requiere una investigación más detallada para confirmar las conclusiones preliminares de este estudio.

Palabras claves: Adaptación basada en ecosistemas, Bosque seco Tropical, Ganadería, Áreas protegidas

Abstract

Central American seasonally dry tropical forests (SDTFs) are one of the most endangered ecosystems in the world, with little surface area under formal conservation status. Although there are no old-growth dry forests left in Costa Rica, secondary forests are growing back since the collapse of meat prices in the 1980s, but are subject to two major disturbances. The first is the frequent forest fires of anthropogenic origin. The second comes from a poorly documented ranching practice consisting of letting cattle enter the forest during the dry period to browse on the woody vegetation and benefit from the shade, and thus relieve the heat stress of the dry season. The frequency of this practice and its impact on ranching livelihoods are very little known and the impact of livestock on this ecosystem has been studied scarcely in the scientific literature. Forests on farms represent the majority of the tree cover of the Costa Rican SDTFs, and it is important to study them to determine if forests subject to fire and browsing are different from forests in protected areas, which are more extensively studied and less affected by those disturbances. This study focused on characterizing this practice and its impact on unprotected forests.

For this, 43 semi-structured interviews were conducted with farmers in the county of Liberia, Guanacaste, Costa Rica, to determine the importance of browsing in forests in ranching livelihoods. It was followed by an ecological sampling campaign in four unprotected forests on farms, which were compared with the protected forest of the Horizontes Forest Experimental Station (EEFH). Browsing in forest was identified as the most used supplementation during dry season, and it is considered critical in the management of farms, in a context of low profitability of ranching and climate change. This practice presented advantages for animal welfare, but complicated the efficiency of farm management. Such dilemma could be the factor that most impacts the farmer´s decision to take cattle to the forest, since statistical tests trying to relate browsing in forests with types of farms or supplementation profiles were inconclusive.

Sampling in forests found no differences between canopy strata in protected or unprotected forests. A cluster analysis found vegetation typologies distributed throughout the landscape, which depended partially on fires. The same analysis in undergrowth and soil vegetation strata found a stronger difference between conglomerates with plots in burned or browsed forests. A correlation test found a strong association between botanical compositions of the vertical strata in forests of the plots, but associations between clusters of different strata showed high variability. However, trends were found suggesting that fire or browsing may not be the most influential factors on forest composition and diversity of this landscape, although fire may have more impact than browsing. Since browsing in the forest is important for local livelihoods, agricultural institutions should not demonize this practice but rather work with farmers to develop good livestock practices or support this practice in a sustainable and controlled framework. More detailed research is required to confirm the preliminary findings of this study.

Key words: Ecosystem-based adaptation, Seasonally dry tropical forests, Cattle ranching, Protected areas.

Introduction

1 Background and justification

Climate change is impacting the livelihoods of many people across the globe. The most optimistic scenario that nations of the world agreed upon as a goal for humanity is to limit global warming to 2°C by the end of this century (IPCC 2014). What is left to do is to find ways to adapt ourselves to the rising temperatures and changing rainfall patterns. In Central America, the expectations sway towards an increase in droughts and a decrease of precipitation (Imbach et al. 2018).

Central American populations have always lived with droughts, which are a yearly recurrent climatic event in a great part of the isthmus, and forests in these areas also show adaptations to this disturbance, and can withstand several months without rainfall (Murphy and Lugo 1995). As drier areas are more favorable to humans, due to the ease of access and good quality of soils for agriculture, those areas tend to have higher population densities than more humid areas (Maass 1995).

Due to this, the dry forests of Central America have been extensively cleared, in particular for cattle ranching (Arroyo-Mora et al. 2005), which is deeply embedded within Central American culture and provides the most vulnerable populations with a buffer against economic crisis, such as a bad crop harvest (Robinson et al. 2011, Rodrı́guez et al. 2016). Cattle is thus crucial for maintaining rural livelihoods in face of increase droughts to come, but extreme droughts sometimes kill cattle, due to the heat and lack of pastures, leaving the most vulnerable populations without food or income (FAO 2017). A traditional mean to face drought for cattle ranchers in dry regions of Central America is to use forests in their farms to provide their herd with shade and feed by browsing on trees and shrubs (Betancourt et al. 2003, Morillo Espinoza 2012). Dry forests are hence an element of food and financial security for cattle ranchers.

Today, SDTFs are regaining cover through secondary succession after being severely deforested (Redo et al. 2012, Arroyo-Mora et al. 2005, Aide et al. 2012). However, they remain threatened by fire and fragmentation (Miles et al. 2006), which are collateral damages of agriculture, as fires mainly start on clear pastures before spreading to forest patches (Chazdon et al. 2011). For a while, the forest browsing practice was considered the solution to the problem cattle ranching had created: It was said, without extensive studies, that cattle would help fight fire by reducing fuels in the forest, and cattle was allowed to browse in some national parks of Costa Rica (Stern et al. 2002). However, this practice was strongly criticized, and Stern and other authors (2002) demonstrated that forest browsing was affecting taxonomical diversity in endangered forests. The practice was subsequently abandoned in protected areas.

Central American seasonally dry forests are critically underrepresented within the protected areas network, with only between 4.5% to 5.7% of them under formal protection status, depending on studies (Miles et al. 2006, de Albuquerque et al. 2015). Most of SDTFs are thus privately owned, and their conservation depends on private initiatives (DeClerck et al. 2010). In the Guanacaste province of Costa Rica, which hosts all SDTFs of the country, farms are principally dedicated to cattle ranching, and forests within those farms (not including plantations and natural regeneration areas with vegetation less than 5 m in height) represent 19% of the whole province land use. Forests are regularly subject to fires, but no study has explored the extent of using cattle browsing in SDTFs during dry seasons as a supplementation practice.

To better understand the impact of human activity on the ecological integrity and connectivity of a landscape, such as the one encountered in the Guanacaste province, two main questions remain unanswered:

1) How frequent is the use of forests for cattle browsing? Answering this question encompasses more than a simple number of farms using this practice. It requires a deep understanding of cattle ranching in dry regions as well as how and why browsing in forests can be vital for farmers. Doing so will allow to fathom the advantages and inconveniences of this practice, and to identify available alternatives for farmers to eventually replace this practice, if deemed nefarious for forests, without depriving them of their livelihoods.
2) If forests in private farms are mostly browsed and subject to fire, how do they differ from forests in protected areas? Most research on SDTFs has been performed in protected areas, which are significantly more sheltered from disturbances, despite having been subject to occasional fires and browse for a time. It is thus important to assess and understand the differences between protected and unprotected forests that could be caused by those disturbances, to better understand the impacts of human activity on the Costa Rican SDTF landscape, heavily dominated by an agricultural matrix.

2 Objectives

- General objectives

Characterize the impact of the dry season cattle browsing in forests on cattle ranching livelihoods and ecological integrity of SDTFs in Costa Rica.

- Specific objectives:

Evaluate the importance of dry season forest browse by cattle in management of cattle ranches in the Liberia County, Guanacaste, Costa Rica (Chapter I).

Identify differences in the botanical composition and species diversity between burnt and browsed secondary forests in cattle ranches and non-browsed, protected, secondary forests (Chapter II).

Research questions:

- How prominent is the use of forest browsing as supplementation in cattle ranches of the study area?
- Which farm managements and supplementation types are associated with forest browsing?
- What drivers push ranchers to use forest browsing?
- What are the differences in botanical composition and diversity between protected and unprotected forests?
- Which forest strata are the most affected by browse and fire?
- How does vegetation of each stratum of a dry forest correlate with the other forest strata?

3 Conceptual framework

3.1 Central American Seasonally dry tropical forests

3.1.1 Overview

The Central American seasonally dry forests are distributed through all of the Central American isthmus, with some continuity from Northwest Costa Rica and the Guanacaste province, up to some strips of forest reaching up to northern Mexico, and with the addition of Panama's "arco seco" (Murphy and Lugo 1995). In Central America, due to the particular climatic conditions of the American isthmus, the seasonally dry region is situated on the Pacific coast, while the Caribbean side receives constant humidity and can maintain wet forests year-long (Bullock et al. 1995).

A seasonally dry tropical forest (SDTF) is primarily defined by its ability to withstand a yearly dry season as a natural part of its ecological cycle. A dry season is considered as a period showing marked decline in rainfall, regardless of the yearly precipitation, for a duration of more than two months with less than 100mm of precipitation per month (Murphy y Lugo 1986, Gentry 1995). Central American SDTFs are experiencing a dry season of between 5 and 8 months long, according to the ecoregion's description by Olson et al. (2001)**.** There is much debate regarding what can be considered a SDTF: For Janzen and Hallwachs (2016), despite the seasonal opening of the dry forest canopy, SDTFs are still distinguished from other seasonally dry or semi-arid ecosystems such as chaparrals by the existence of a canopy layer that will close during the rainy season. For other authors, such as Miles et al. (2006), shrublands and savannahs are included in the dry forest cover satellite estimates, possibly overestimating the actual extent of the dry forests in their stricter sense of a multi-layered forest. SDTFs have been reported to have a great variation in structure and composition, due to "differences in soil and flooding periodicity" (Murphy and Lugo 1995).

3.1.2 Botanical composition

A distinctive feature of SDTFs is the dominance of deciduous species, that will shed their leaves at some point during the dry season. This trait distinguishes SDTFs from tropical rainforests, which tend to be evergreen (Borchert 1998). In terms of botanical composition, dry forests are considered less complex and diverse than rainforests, possibly because the seasonally harsh conditions restrict the number of niches that can be colonized by plant species (Gentry 1995). However, there is high endemism within some of those forests, as well as a great diversity of dry forest floristic types, which should make their regional conservation globally important (DRYFLOR 2016). SDTFs from Honduras to Panama were grouped by DRYFLOR (2016) with northern South American dry forests of Colombia and Venezuela based on their taxonomical composition, rather than with Mexican dry forests, which have been long recognized for their unique configuration (Gentry 1995). Gillespie et al. (2000) censused 75 species across 33 families in Santa Rosa National Park forest, close to where our study took place.

According to many composition studies (Gentry 1995, Gei et al. 2018, Gillespie et al. 2000 and many others), the Fabaceae family represents a very high proportion of the species of the dry forests, in particular during the early stages of secondary succession, with a decreasing presence as the forest reaches maturity.

3.1.3 Characteristics and ecological processes of SDTFs

Secondary succession in SDTFs is a unique ecological pattern. Rainforest secondary succession favors fast-growing, shade-intolerant short-lived species in the first place to later give place to shade-tolerant, slow-growing and long-lived species (Finegan 1984). To the contrary, dry forests will first witness the growth of conservative species, with a slow growth rate and a better resistance to harsh abiotic conditions (Buzzard et al. 2016). Those species will create a basic nutrient cycle, increase water availability and generally reduce the climatic harshness of the habitat, allowing growth of faster metabolism species more demanding in resources, according to the "productivity filtering" hypothesis (Buzzard et al. 2016). The ability of the Fabaceae family to fix nitrogen in a nutrient-scarce environment can explain why this family dominates secondary succession in SDTFs. It is important to mention the facilitation provided by bushes or adult trees to young saplings during their first dry seasons. Dry forests have diverse compositions, but tend to have an important bushy understory (Gillespie et al. 2000), even in mature forests, due to a more open canopy (Castellanos Castro 2013). In forests with resource and water scarcity, a seed falling in a bush or close to an adult individual will benefit from the protection of the surrounding vegetation against harsh conditions, instead of being disadvantaged by competition (Derroire et al. 2016, Zamora et al. 2004). The establishment and survival of seeds depend thus a lot on the presence of vegetation in their direct surroundings. The litter from deciduous trees can preserve soil moisture and favor the germination of seeds. However, this facilitation provided by already established trees tend to reverse itself when the rainy season comes, giving place to competition for light and nutrients. This mechanism is theorized by the "stress gradient hypothesis" (Derroire et al. 2016).

The patchiness of water and nutrients availability in tropical dry forests (Hulshof et al. 2013), as well as the seasonality of their availability, is the source of a great diversity of drought-surviving strategies observed in SDTF (Hulshof et al. 2002). These strategies can be classified into two main types of functional response: Drought resistance and drought avoidance (Poorter et al. 2014, Lohbeck et al. 2015).

Drought avoidance strategy is principally characterized by deciduousness, which is the strategy of a majority of species in SDTF, who shed their leaves at different stages of the dry season to avoid excessive water loss from their leaves' stomata (Borchert 1998). According to Borchert (1988), deciduous trees comprise both low and high wood density species, that tend to have their own sub-strategies: low stem density trees have a greater capacity to store and carry water but are then more susceptible to damages due to lack of water. To conserve water, dry forests' low wood density deciduous trees shed their leaves early in the dry season and tend to be have a thick bark which insulates the trunk and prevents transpiration (Poorter et al. 2014). The savings in water are invested in heavy flowering, as the dry season is the main reproductive season in dry forests (Borchert 1998). For Borchert, denser wooded trees tend to have a greater structural integrity (stronger cell walls, allowing cells to rely less on turgor pressure), slower metabolism and less need of water, and tend to have a thinner bark and shed their leaves later in the season. Dense wood species are more common in SDTFs than in rainforests, and represent a typical trade-off between resource acquisitive (oriented towards obtaining resources) and conservative (oriented towards saving resources) strategies, as the investment realized in greater wood density is not allocated to vertical growth, hydraulic efficiency and photosynthesis (Pérez-Harguindeguy et al. 2013).

Drought resisters maintain their leaves throughout the summer and rely more heavily on extensive roots and deep taproots, allowing them to get access to the water in the lower parts of the soil, reaching sometimes groundwater tables (Poorter and Markesteijn 2007, Eamus and Prior 2001). They also have leaves with tougher tissues that have a stronger cell wall and better wilting resistnace (Slot and Poorter 2007). Drought-resistant evergreen species tend to arrive later in the secondary succession process, due to the increased water availability and facilitation provided by pioneer deciduous species previously mentioned (Lohbeck et al. 2015).

The strategies employed by trees to survive the dry season also provide collateral benefits against herbivore browse. For example, tougher leaves are less palatable to insect or mammal herbivores, and those leaves, costly to the tree, usually have a high concentration of secondary metabolites making them toxic or difficult to digest (Pérez-Harguindeguy et al. 2013). Those same drought resistance traits can also provide resistance to fire.

3.1.4 Fire in SDTFs

Contrarily to other ecosystems that have evolved with fire as a natural recurring disturbance, fires in Central America are not considered as part of the ecological processes of its SDTF, even though the anthropogenic fires from pre-Columbian populations might have shaped their composition through the Holocene (Otterstrom et al. 2006) to favor species with the most fire-resistant traits. For example, Central American dry forest tree species are in majority basal resprouters, which make dry forest trees resilient to fire, in addition to herbivory. Another alternative to surviving fire is heavy recruitment, thanks to the production of a large number of seeds easily dispersed (Otterstrom et al. 2006). Wind-dispersed species seem most likely to be the most adapted to this environment, and indeed they dominate succession in tropical dry forests (Janzen 1988, Derroire et al. 2016). In SDTF, wind-dispersed seeds are not resistant to fire and do not depend on it for scarification, although fire provides an easier access to soil and nutrients for those light and nutrient poor seeds by clearing the floor vegetation (Lloret et al. 2009).

As fire spreads in the understory, it is important for trees to protect their stem and their cambium from fire damage and prevent fire to spread up to their canopy. Dry forest trees employ various strategies to prevent this through their bark and wood, according to Poorter et al. (2014):

- Trees with thick bark and soft wood. The thick bark of soft wood deciduous trees helps them retain water during the dry season. It also helps them resist fire thanks to a thicker bark and a higher bark moisture content (Brando et al. 2012).

- Trees with hard wood and thin, hard bark. These denser wooded trees are more resistant to fire, as they have the ability to better compartmentalize damages (Brando et al. 2012) and ignite less easily. Moreover, part of their drought resistance strategy is the ability to use little water, and thus have no water to conserve. However, it is important to note that trees with denser wood and leaves with high dry matter content, once ignited, will burn for a longer time (Grootemaat et al. 2015).

3.1.5 Conservation status and the WWF Eco-region.

Janzen (1988) was among the first to point out the extensive deforestation and degradation of tropical dry forests, and urged the scientific community to focus its attention and conservation efforts towards them. However, recent studies show forest recovery in the American seasonally dry tropics, as degraded pastures and other land uses have been abandoned (Aide et al. 2012, Arroyo-Mora et al. 2005, Redo et al. 2012). Aide et al. (2012) point out that the tendency for Pacific SDTFs was one of natural reforestation, particularly in land not suited for agriculture. However, SDTFs in Central America and worldwide were still under great pressure from climate change, conversion to agriculture, forest fragmentation, fire and expansion of human population, with only 3.3% of all dry forests worldwide being spared from the mentioned threat (Miles et al. 2006). Less emblematic than tropical rainforests in the fight for preserving biodiversity, SDTF have attracted less attention to themselves for research and conservation efforts (Hulshof et al. 2002). Nevertheless, SDTFs are unique ecosystems of capital importance for the ecological well-being of the regions in which they are present.

Fragmentation of SDTFs is a major obstacle to the proper functioning of this regional ecosystem, altering pollination and reproduction, as highlighted by Quesada et al. (2011). As a matter of fact, the WWF ecoregion defined by Olson et al. (2001) and used by the FAO is described as “Patches scattered through Mexico, Guatemala, Honduras, El Salvador, Nicaragua, and Costa Rica”, under an “endangered/critical” category. The land cover recovery of dry forests is helping to maintain functional connectivity through the landscape, but the lack of representation of SDTF within the Central American protected area system leaves some important voids in conservation that can be filled only by private or local initiatives (Harvey et al. 2008, DeClerck et al. 2010) In this context, secondary forest conservation and restoration must be encouraged throughout the region by promoting its ecological importance and finding sustainable uses for it that participate to the local livelihoods, principally by improving farm management, according to Chazdon et al. (2011).

These authors suggest that dry forest landscape connectivity can only be improved by increasing tree coverage within the landscape, and restoring riparian or secondary forests in farms to help safeguard the dry forests’ ecological processes. Indeed, Miles et al. (2006) highlight that only 5.7% of SDTFs in Central America are under formal protection. In the study area of

Guanacaste, Costa Rica, most of the SDTF coverage is located in private farms, which are mostly cattle ranches, for more than 200,000 ha of forests (INEC 2014). Cattle ranching, which has been a pivotal part of Central American culture since European colonization (Janzen and Hallwachs 2016), has been the main reason for forest conversion in Guanacaste. The conservation and connectivity of this SDTF landscape relies then principally on farmers management of forests. It is thus necessary to understand the socio-economic situation of farmers, their livelihoods and agricultural practices to determine the effect that the regionally omnipresent agricultural matrix has on the fragmented and mostly secondary forests that subsist in the landscape.

3.2 Livelihoods and cattle ranching in the Central American Dry corridor

The Central American dry corridor as defined by the FAO is an ecological area which delimitation is based on the distribution of the seasonally dry areas of Central America, but also a socio-economic focus unit. Its focus is mainly centered on the food security of populations of Central America living in areas that are affected by a seasonal drought (FAO and ACF 2012), and hence on the countries that are the most affected by droughts, in terms of geographical extent of the dry regions in these countries and the vulnerability of their population to drought damages. The FAO focused its efforts on four countries in the delimitation of the dry corridor: Guatemala, El Salvador, Honduras and Nicaragua. Costa Rica and Panama were given a lower priority.

If Miles et al. (2006) do not consider agriculture as one of the main threats to Central American SDTFs, it is maybe because dry forests have a longer history of colonization and that there is not much forest left to cut down. It is at least the analysis that Redo et al. (2012) make of the situation: Redo finds a general correlation in Central American countries between Human Development Index (HDI, a composite index of life expectancy, education and income per capita) and forest transition, and shows that more developed countries have tended to reforestation in recent years, while lower-HDI countries keep deforesting. This can be explained by better government control, a shift to more intensive agricultural practices and less agricultural population, among others, in higher HDI countries. However, these authors mention a tendency of dry forests to recover while Caribbean moist forests are heavily deforested, which is explained by the possibility that a maximum agricultural development has been attained in dry forest regions and progressively scales back as the country slowly gets less dependent on the primary sector and that agriculture colonizes harder-to-reach regions.

Arroyo-Mora et al. (2005) seem to confirm that theory in the local example of the Chorotega region, in Costa Rica. The region, and in particular the Nicoya peninsula, was a case of extreme deforestation as cattle ranchers colonized and cut down almost the entire forest cover of the peninsula, driven by high beef prices and government incentives to agricultural development. Since the eighties, however, with the collapse of beef prices and the shift in environmental policy of Costa Rica, the beef sector has shrunk back and forest has regrown (Arroyo-Mora et al. 2005, Janzen and Hallwachs 2016, Jiménez M. et al. 2015). The majority of forest recovery, however, has happened in areas that were least suitable to cattle ranching, which shows not a total abandonment, but a stabilization of the cattle farming sector.

Cattle ranching is omnipresent in the Central American dry corridor and is part of the livelihoods of many rural families throughout the sub-continent (FAO and ACF 2012). In average, the cattle sub-sector represents close to 20% of the agricultural GDP of Central American countries, reaching up to 38% for Nicaragua (FAO 2014). Even though a big part of the national herd in each country is owned by big ranches that have more streamlined and efficient practices, most cattle farms in the Central American dry corridor are small operations, mostly owned by subsistence farmers, often the same that grow staple grains (FAO 2014, FAO and ACF 2012, Rodríguez et al. 2016). For these farmers, cattle plays a central role in their financial and food security, as it does not only provides an extra income, but also a way to store wealth for emergency situations, as an alternative safety net against the risks of bad harvest and low market prices inherent to agriculture, as well as an extra food source and social status (Robinson et al. 2011, FAO 2014, FAO and ACF 2012, Rodríguez et al. 2016).

Cattle has a high capacity to regulate its body temperature and to resist drought, in particular zebu cattle (Beatty et al. 2006, Cardoso et al. 2015). Its resistance helps families that have been struck by drought to be resilient to a severe drought destroying their crops. However, most pastures in the Central American corridor are degraded, and do not have improved forages that are resistant to drought (Betancourt et al. 2007). During the dry season, the pastures tend to dry and do not provide the necessary nutritional levels for cattle anymore, which often leaves the small cattle rancher facing the dilemma of letting his cattle die or sell it for a low price for slaughter, which largely diminishes the household's ability to cope with further crisis (FAO 2014, 2017, Diaz et al. 2016).

In this mostly agricultural matrix of small subsistence producers, fire is a preferred way for clearing land. It is used to boost the regrowth of pastures at the end of the dry season, prepare the land for crops and remove any secondary regeneration of woody vegetation (Janzen 1988, Chazdon et al. 2011). In the absence of proper fire control practices, those fires easily spread to larger extents than intended due to the dry nature of the abiotic environment, giving rise to forest fires that will destroy whole patches of dry forest and contribute further to the fragmentation of this habitat. Forest control practices are improving in Costa Rica since 2000, according to Arroyo-Mora et al. (2005), but clandestine or accidental fires continue to be set today.

3.3 Browsing by cattle and vulnerability to fire in Central American SDTFs

3.3.1 Dry season browsing:

The dry season can be an extremely difficult time to bear for cattle, which suffers heat stress and malnutrition, often leading to death. With longer and more intense droughts being forecasted in the future (IPCC 2014), adaptation measures are necessary for rural populations of the Central American dry corridor. A practice in seasonally dry regions from Mexico to Venezuela is for farmers to use small patches of secondary forests as a source of forage and shade for cattle, sometimes all year long, but with the most intense use taking place during the dry season when pastures are no longer available. Cows will eat leaf litter, fruits and green leaves still standing in the deciduous dry forests (Morillo Espinoza 2012) and maintain their weight as well as normal metabolic processes otherwise affected by heat stress and malnutrition (Aggarwal and Upadhyay 2013).

Dry forests hence serve as an instrument for food security and adaptation to climate change for farmers, but literature on this subject is extremely scarce, barely mentioned in some articles and manuals (Pezo y Ibrahim 1998 for example). A few studies were found on the subject, mostly in Venezuela, Mexico and in the Argentinian Chaco dry forests (Pizzani et al. 2005, Morillo Espinoza 2012, Simón et al. 1998, Ascencio-Rojas et al. 2013). Most research on browsing in Central America has been done on the nutritional value of fodder banks, remnant trees in pastures and other silvo-pastoral systems that are being promoted as a sustainable compromise between productivity and biodiversity conservation (Pérez Almario et al. 2013, Navas 2010). However, fodder banks are costly to implement and are not within the financial and technical reach of farmers in the poorest areas (FAO 2014), who prefer to rely on traditional methods.

3.3.2 Cattle grazing as a fire management tool

In the last decades, cattle grazing has been believed to be an efficient fire reduction tool and has been used as such in Costa Rica particularly until the early 2000, since a study from Vaughan et al. (1995, cited by Quesada y Stoner 2004) showed the capacity of "controlled grazing" in tropical dry forests to reduce the fire potential by suppressing both the introduced jaragua grass *Hyparrhenia rufa* and floor leaf litter, thereby reducing the risk of wildfires. Indeed, the jaragua grass, introduced in the 1920's in Costa Rica during the expansion of cattle ranching (Quesada and Stoner 2004, Janzen and Hallwachs 2016), will grow up to one or two meters high when pasture is abandoned and burn with flames, up to 4 meters when dry, easily spreading to the contiguous forest and causing stand-replacing fires (Janzen 1988). Consequently, cattle were introduced in Palo Verde National Park, Lomas Barbudal Biological Reserve and Guanacaste National Park, and farmers were allowed to bring their herd to browse in Guanacaste National Park for a small fee (Quesada and Stoner 2004). A study by Stern et al. (2002) challenged this management plan by verifying in the field the effect of cattle grazing in Palo Verde, and concluded that cattle dramatically affected the structure and composition of a dry forest, and that "The long-term ecological cost of preventing fires with the use of cattle will be much greater than the short-term economic cost of investing in alternative fire management programs".

However, the actual effect of cattle presence on SDTF flammability was not established by this study, and even though cattle have now been removed from Guanacaste National Park, the general belief is that cattle do contribute to prevent forest fires (personal communication with Area de Conservación Guanacaste park rangers). The effect of cattle in forests has been studied in other ecosystems, such as in pine forests of the US Interior West by Belsky and Blumenthal (1997). The authors found that the presence of cattle in those forests diminished their resilience to fires and changed the fire regime from low-intensity frequent fires to stand-replacing fires, by reducing competition from grasses and creating denser tree stands, and compacting the soil. A similar ecological study is much needed in Central America's dry forests.

4 Main results

4.1 Chapter I

A set of 43 semi-structured interviews was conducted with cattle ranchers of the Liberia county, Guanacaste, Costa Rica, focusing on farm management, forest composition, age and structure, use of supplementation, use of forest browsing, and incidence of fire on farm. The interviews were conducted in farms that had forest and cattle.

Cattle ranching in Liberia county is mostly composed of beef cattle breeding (breeding calves and selling them at weaning) and backgrounding farms (raising cattle up to a certain weight before selling them to fattening farms), as 72% of farms interviewed followed one of these modalities, often in combination. However, some fattening farms (fattening adult cattle up to slaughter weight) and dairy farms (oriented towards a constant milk production) were present in the landscape, although often in combination with another modality.

Cattle ranching in Liberia county was deemed by farmers as an activity suffering from low profitability due to the increasing cost of feed and lower meat prices, and vulnerable to many pressure factors. Fire, in particular, had affected most of the interviewed farms in recent years, and had destroyed pastures and sometimes forests at a critical time of the dry season. It is still common in this region that farmers burn their pastures themselves to trigger a stronger sprouting during the first rains, but the practice is becoming less popular with the progressive replacement of traditional fire-dependent *Hyparrhenia rufa* pasture by improved pastures, which have a lower tolerance to fire. However, 27% of responses to the question "Where does fire come from?" mentioned pasture or sugar cane burns from neighboring farms. Nevertheless, fire in farms often originates from causes exogenous to farm management such as hunters, fishermen or criminal hand.

Cattle theft was another frequent disturbance experienced by farmers. Twenty-six percent of farmers had gotten cattle stolen in recent years, and often had to adapt the management of their herd (e.g minimize the entrance of cattle to the forest where visibility and control over livestock is limited, or stable cattle every night) to avoid further theft.

Cattle ranching in the plains of Liberia county originates from a *latifundio* tradition, where a small number of families owned vast areas of land. However, those farms are in a fragmentation process, due to the splitting of farms between successors, the sale of land to cope with financial difficulties, development of other activities, and sometimes land squatters. Farms close to Liberia city were being engulfed by the urban development and were rare.

Farm size and land use was very variable, as small farms were often found next to bigger farms, that had sold small areas of land to them when needing liquidity. However, we identified two different patterns of farm structure and cattle dry season supplementation, based on geographic location. Farms in the plains of Liberia county were bigger, with a higher proportion of forests on farmland, while farms located on the slopes of the volcanic cordillera were smaller, with a low proportion of forest and a higher proportion of land dedicated to crops, and a higher proportion of land ownership among interviewees. Those farms tended to be more focused on subsistence agriculture, and relied more on fodder banks and silage as a dry season supplementation strategy. This was possibly due to historical and cultural reasons, but could also be attributed to different soil conditions, or to an increased presence of technical support entities that focused on smaller farms.

The use of forests in farms for browse was very common, with 70% of farms using it as a supplementation strategy during the dry season. Up to 65% of farms had their cattle in forests in the driest month of May, while two farms removed cows from the forest during those months to supplement them, as a forest was not deemed to be sufficient in providing feed to the animal and to avoid loss of energy from cattle due to long walks through the forest.

Forest browse was not associated to one particular type of supplementation or pasture type. Improved pastures were said to dry later in the season, but this did not impact significantly the presence of cattle in forests. Browsing in forest by itself was not a miracle solution either, as only 14% of farms that used cattle browsing relied only on it for dry season supplementation. No distinct supplementation profiles were found, showing that the complexity of supplementation strategies in this dry region goes further than a simple extensive/intensive management classification.

When asked for benefits and drawbacks of using forests for cattle browsing, farmers mostly mentioned benefits related to animal welfare, such as the provision of shade or feed, as a primary factor impacting their decision. Important drawbacks of this decision to put cattle in forests or not were related to farm management, as cattle could be lost or stolen while in the forest. Farmers were divided as for the ecological impacts of cattle in forest. Some farmers believed that cattle were beneficial to the forests by improving tree species regeneration through seed dispersal and elimination of herbaceous competition. Others blamed cattle for stream erosion, undesirable changes in forest composition and destruction of tree species regeneration. The use of cattle in "cleaning" forest understory and thus decreasing the intensity of fires was a widely mentioned benefit.

Farmer's knowledge of cattle behavior and feeding preferences in the forest was very variable and often contradictory, perhaps due to differences in herd behavior due to management of the animals, type of cows or type of supplementation, or to a general lack of observation of cattle's behavior in forests, as many farmers admitted to rarely step into their forests. The knowledge of plants eaten or avoided by cattle was usually limited to species found at the edge of forest or in pastures.

4.2 Chapter II

An ecological sampling was performed between four secondary unprotected forests in farms under different levels of cattle browsing and fire frequency, and in one secondary forest in a protected area. The forests were compared in terms of taxonomical composition and ecological diversity in three vertical strata of the forest.

Most common tree families for canopy individuals in the landscape were Fabaceae, Malvaceae and Rubiaceae. The understory tree family composition was similar, except that Saliaceae was the third most frequent family. Lianas were mostly represented by Bignoniaceae, followed by Malphigiaceae and Sapindaceae, at canopy and understory levels. Floor vegetation was dominated by Poaceae, in particular *Lasciasis sorghoidea*, followed by Bignoniaceae, Malphigiaceae and Acanthaceae.

A Non-Metric Multidimensional Scaling (NMDS) performed for each stratum of the forest returned no clear distinction between forests, in particular because the protected forest covered the whole range of composition found in the landscape. A cluster analysis was performed for each stratum of the forest to characterize the vegetation of plots. Each analysis returned a classification into three clusters, with their own indicator species. Clusters were all validated with an analysis of similarities (ANOSIM) which returned significant corrected p-values ($p=0.0003$).

Percentage of floor vegetation browsed and number of adult stems with damages from fire were used to characterize each plot in terms of fire and browse intensity. Plots with *Spondias mombin* and *Casearia syltestris* as canopy indicator species were burnt the most, while understory vegetation characterized by liana species *Tetracera volubilis* and *Xylophragma seemanianum*, or by *Cupania guatemalensis* and *Casearia sylvestris* were abundant in burnt areas. Fire was not a significant factor for determining the botanical composition of floor vegetation, but cattle browsing was associated to plot composition. Most browsed plots were either dominated by *Lasciasis sorghoidea* or by the association of *Ruellia inundata* and *Melanthera nivea*. Plots characterized by *Cupania guatemalensis* and *Smilax spinosa* were the least browsed, and were found mostly in the protected, non-browsed forest.

No differences between forests were found for canopy species in terms of number of individuals, species density, diversity, dominance and evenness. However, the proportion of liana species in the number of species per plot and number of individuals per plot was significantly higher in protected forests than in browsed forests. Species rarefaction curves showed higher diversity in protected forests than in browsed forests for a same number of individuals sampled, but the difference was not statistically significant. When grouping all farms vs. EEFH, diversity shown by rarefaction curves was higher in unprotected forests for the same number of individuals, although still not statistically different.

At canopy level, clusters were only separated by density of individuals per plot, with the cluster characterized by *Chomelia spinosa* and *Heteropterys laurifolia* being both the densest and the least burnt. The shrubs and saplings understory clusters showed differences in species density, diversity (Shannon index), dominance (Simpson index) and evenness. The cluster characterized by *Tetracera volubilis* and *Xylophragma seemanianum* was the most diverse, with a more even composition. The cluster composed mostly of *Cupania guatemalensis* and *Casearia sylvestris* was also ranking highest in terms of evenness. Both clusters were the most burnt. The classification of floor vegetation in three clusters returned differences only in terms of evenness and dominance, as well as browsing intensity, whereas the cluster characterized by *Lasciasis sorghoidea* had higher dominance and lower evenness indexes.

The NMDS analysis coordinates were used to compute distance matrices between plots, for each stratum of the forest. Those matrices were compared via Mantel correlation test to probe for a correlation in taxonomical composition between forest strata. Comparisons between all layers returned a significant correlation. Canopy stratum was related at 22% with the shrubs and saplings understory layer ($p=0.001$). The shrubs/saplings stratum was in turn correlated at 31% ($p=0.001$) with the floor vegetation. The highest correlation was between canopy and floor strata, with a 0.38 coefficient ($p<0.0001$).

To describe the relation between each forest layer taxonomically, we used contingency tables to determine the correspondence patterns between clusters of each stratum. Most comparisons returned Chi-squared values and attributed p-values showing a non-random attribution of clusters between strata, with the exception of the canopy/floor vegetation comparison ($p=0.0779$), contradicting the results from Mantel correlation test. This could be due to the simplification created by clustering. Trends of association were identified between strata, although no definite pattern could be established.

5 Conclusions and recommendations

Cattle browsing in forests is a frequent supplementation practice used by farmers in Liberia, Guanacaste county. It is seldom used as a standalone supplementation, but it is combined with other types of supplementations, depending on farmer's available resources, agricultural know-how and management objectives. This practice is considered a great benefit for animal well-being during dry season, but has some important management drawbacks that can prevent farmers from putting their herd into forests. We hypothesize that, given the lack of relationship found between herd management, purpose, supplementation and the forest browsing practice, the decision to browse cattle in the forest or not lies in their conception of cattle ranching, swaying either towards maintaining animal well-being or keeping a tight control over farm management and its associated costs. However, as this study was exploratory, it might have lacked some details on the supplementation provided to animals. We recommend a follow-up study relating forest browsing to a detailed supplementation profiling of farms, and with a larger sample size to allow for a sound statistical analysis.

Given the tendency of the global cattle industry to constantly increase productivity, an intensification of ranching practices might be observed in years to come, which could progressively eliminate the possibility of using of a low-cost, but hardly controllable practice like forest browse. However, the increasing costs of supplementation for farmers and of climate hardship in this region could push more ranchers to adopt such practice as means to reduce feed costs and avoid dramatic herd die-offs in extreme heat conditions.

Most of forests in cattle ranches were thus subject to cattle browsing and fire, and hence these browsed and burnt forests represent the majority of tree cover in the area. The ecological impact of cattle in forests was a dividing subject for farmers, who mentioned both positive and negative impacts. A point of agreement was the cattle's ability to "clean" forest understory during the dry season, diminishing the risk and intensity of wildfires, dry forest's main disturbance. If, as cattle ranchers declared, cattle browsing reduced the impact of fire on forests, this practice would result beneficial for SDTF's ecological integrity. Obviously, better fire control practices, the withdrawal of pasture burning as a management tool, and fire preparedness are preferred solutions to fight wildfires in the region. There has been significant progress towards this goal in Guanacaste, but there is no such thing as zero risk, and browsing in forests could be a complement to those safety measures, particularly for fires originating from forests, such as the ones lit by hunters and fishermen.

No major difference in canopy species composition or diversity was found between protected and browsed and burnt unprotected forests, highlighting the lack of major effect of cattle browsing on the botanical composition and abundance of adult trees in forests. Abiotic factors seem to be the major determinants of the botanical composition of these forests. Fire was a significant disturbance at canopy and understory level, as some composition types were related to the most burnt forest patches.

At floor level, browsing was associated with changes in composition of regeneration and herbaceous vegetation. Most browsed plots were dominated by Poaceae species highly favored by cattle and deer, herbaceous vegetation or species with cattle-dispersed seeds. It is hard to draw conclusions, as cattle could have favored those areas because of their composition, or these plants could rather have been the only ones to survive in those highly browsed plots due to a better resilience to browsing. This might be a mutualistic plant-animal strategy, as cattle ranching has been present in forests since the introduction of cattle in the XVI century.

Even though a correlation was found between canopy and floor vegetation, no clear composition pattern emerged when comparing botanical clusters between forest strata. There was a high variation of cluster association, suggesting that canopy composition was not the only driver of understory and floor vegetation composition, and that the intensity of fire or browse disturbances could have influenced the composition of forests as well. To test this hypothesis, a tightly controlled experimental design is needed, possibly enclosing parts of a browsed forest for several dry seasons to assess if a composition change would take place.

This study has demonstrated that in the Guanacaste province, forests are part of farm management and should be included in all studies related to cattle ranching and rural livelihoods. Cattle browsing does not seem to deteriorate forest condition, and this practice remains critical for local livelihoods. Forests in private farms provide connectivity between protected areas in this landscape, and if their use by cattle incentivizes their conservation and restauration, this practice should be encouraged by the conservation community. Government and technical support institutions should work with farmers to regulate this practice in controlled frameworks, helping them to maintain cattle browsing intensity within the limits of sustainability. Farmers who wish to abandon browsing in forests must be provided with low-costs alternatives and with the technical and financial assistance to transition to more controlled options for cattle well-being in the dry season, such as increased tree coverage in pastures, fodder banks, silage or locally-made concentrate.

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Chapter I: Secondary tropical dry forests are important to cattle ranchers in Northwestern Costa Rica.

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Abstract

In dry regions of Central America, the presence of trees and forests in cattle ranches benefits cattle, as it provides shade and feed to cattle herds during the dry seasons, when pastures are dry. Cattle browsing in forests as supplementation has been little studied, and we do not know how frequent this practice is, how it fits in a farm's management plan and what impacts it has on the ecological integrity of the forest. We conducted a set of 43 semi-structured exploratory interviews in farms of the Liberia county, Guanacaste, Costa Rica, to contribute to filling those knowledge gaps and to assess rural knowledge concerning this practice. Farmers in Liberia suffered from the loss of profitability of the cattle industry and were affected by droughts, fire and cattle theft. Cattle browsing in forest was used by 69% of farms, mostly between the months from March to May. No type of farm or supplementation practice was associated with forest browsing, as the practice spanned all types of farm structure and management. We could not isolate supplementation profiles, due to the great diversity of farm managements in the region. We did find a difference in farm structure and supplementation types between ranches in the plains and ranches in the slopes of the volcanic cordillera, which was possibly due to historical, edaphic or institutional reasons.

The benefits from forest browsing most cited by farmers were related to animal welfare, and most cited drawbacks were related to the complications that this practice brought to farm management. We hypothesize that the decision to put cattle in forest or not is not entirely related to supplementation strategies, but rather to the farmer choosing between animal well-being and simplification of farm management. Farmers' knowledge of cattle behavior and feeding preferences in forest was usually limited to observed behavior at the edge of forest, and very variable between farms. We recommend a more detailed follow-up on this exploratory study with an in-depth focus on supplementation types, animal behavior in the forest, browse selectivity and impact of the animal, as well as a study comparing browsed forests with protected forests in order to determine the ecological impact of cattle on forest structure, composition, diversity and functioning. This study will help decide if cattle browsing in forests can be a good example of ecosystem-based adaptation, or if alternative supplementation types must be fostered by agricultural institutions to reduce browsing in forests. In any case, this research showed that forest browsing must always be taken into account when studying ranching in dry regions.

Key words: Cattle ranching, Seasonally dry tropical forests, Cattle browsing, Ecosystem-based adaptation, Mesoamerican dry corridor.

Resumen

En las regiones más secas de Centroamérica, los bosques en fincas benefician a ganaderos, ya que proveen sombra y alimento al ganado en temporada seca, cuando las pasturas se secan. El ramoneo en bosques ha sido muy poco estudiado, y no se sabe qué tan frecuente es esa práctica, cómo cabe en el plan de manejo de las fincas, y cuáles impactos tiene sobre la integridad ecológica de esos bosques. Se realizaron 43 entrevistas semiestructuradas en fincas del cantón de Liberia, provincia de Guanacaste, Costa Rica, para llenar esos vacíos de conocimiento y evaluar el conocimiento campesino acerca de esta práctica. Los ganaderos de Liberia se veían afectados por la pérdida de rentabilidad de la actividad ganadera y eran afectados por las sequías, incendios y el robo de ganado. El ramoneo en bosques se usaba en 70% de las fincas estudiadas, mayormente entre marzo y mayo. No se pudo asociar esta práctica con un tipo particular de finca o suplementación en temporada seca, ya que se usaba en todos tipos de fincas. No se encontraron perfiles de suplementación, debido a la gran diversidad de manejos en la región. Se encontraron diferencias en la estructura y suplementación de fincas de bajura y fincas de las pendientes de la cordillera volcánica, que pudieron haber sido causadas por razones históricas, edáficas o institucionales.

Los beneficios del ramoneo en bosque más mencionados estuvieron relacionados con el bienestar animal, mientras los inconvenientes más mencionados se relacionaban con las dificultades ocasionadas en el manejo del hato. Esto sugiere que la decisión del ganadero de colocar su ganado en bosques no depende de tipos de suplementación provistos, más bien de una elección del ganadero entre el bienestar de sus animales y un manejo eficiente de su finca. El conocimiento de los finqueros sobre el comportamiento y las preferencias alimenticias del ganado en bosques era a menudo limitado a lo observado a las orillas del bosque y en pasturas, y variaba mucho entre finquero. Recomendamos un trabajo de seguimiento a este estudio exploratorio, que cubra más fincas y se enfoque con más detalles en los tipos de suplementación provistos, comportamiento animal en bosques, selectividad del ganado e impacto de los animales, así como un estudio de impacto ecológico comparando bosques secundarios protegidos con bosques ramoneados, en términos de estructura, composición y diversidad. Este estudio ayudará a decidir si esta práctica es un buen ejemplo de adaptación basada en ecosistemas, o si las instituciones agrícolas deben apoyar la implementación de otros tipos de suplementación para reducir el ramoneo en bosques. En todo caso, este trabajo destaca que el ramoneo en bosques es una práctica común que siempre tiene que ser considerada al momento de estudiar la ganadería en regiones secas de Centroamérica.

Palabras claves: Ganadería, Bosque seco tropical, Ramoneo, Adaptación basada en ecosistemas, Corredor seco mesoamericano.

1 Introduction

Since the colonization of Latin America, and with it the arrival of the first cattle herds on the continent in the XVI century (Bishko 1952), human development has progressively made of the neotropical seasonally dry forests one of the most endangered ecosystems today (Miles *et al.* 2006)**.** However, the biophysical environment of those dry regions provided the context for a situation where forests are beneficial to ranchers: as the dry season progresses, temperature rises and rainfall is close to zero for up to eight months (Sánchez-Azofeifa *et al.* 2013), pastures dry out and leave ranchers with no forest within their farm, with the options of either selling part or all of their herd at low prices, increasing spending on supplementation, transporting their herd to a non-seasonal area, or letting their cattle go through the dry season without help and risk losing part of the herd to drought. On the other hand, farmers that do have a forest on farm have the additional option to use forests as a refuge for cattle during the dry season, where the tree cover and cooler temperatures relieve cattle from heat stress and where the last green leaves and fruits from deciduous trees and shrubs can improve animals' diet (Betancourt *et al.* 2003, Vásquez *et al.* 2014, Ascencio-Rojas *et al.* 2013). Cattle can then spend most the dry months of the year within forests.

In the Americas, only a small number of studies were found about cattle behavior in the forest and its impact on it. Browsing in general has been studied worldwide in the context of silvopastoral systems (Pérez Almario *et al.* 2013, Barrientos-Ramírez *et al.* 2015), and as a source of supplementation in the arid lands of Africa for subsistence farmers (Aganga and Tshwenyane 2003, Franzel *et al.* 2014, Le Houerou 1980). However, most of those papers pay little attention to the role of forests as a source of browsing for cattle. A significant part of the research on the subject comes from the United States (Roath and Krueger 1982, Belsky and Blumenthal 1997), which despite being known as the capital of industrial farming, maintains a significant part of its beef cattle herd in rangelands, only transferring cattle to feedlots for finishing (Drouillard 2018). Other sporadic research on cattle in forests has been found in Venezuela, the Argentinian Chaco, Brazil and Mexico (Morillo Espinoza 2012, Simón *et al.* 1998, Vieira *et al.* 2006, Ascencio-Rojas *et al.* 2013).

In Central America, research on cattle ranching practices has also left out forests from analysis; most of the work performed on the characterization of farm management in dry areas of the subcontinent ignores the use of forests, and the few mentions of this practice are scattered through documents that give a broad treatment to farm management in Central America (Pezo and Ibrahim 1998, Cabrera 2007). This lack of interest for forests could simply mean that this practice is very marginal nowadays. It is true that this practice dates back to the colonial times, and does not seem to fit within today's farm management intensification strategies, which demand a tighter control of cattle rather than extensive practices. However, it is possible that cattle browsing in forests is at the crossroad between two disciplines and their different priorities regarding livestock management and landscape conservation and restoration, which makes this topic far from being a priority study interest for agronomists and conservationists alike. However, in a world where climate change is now a reality, and where Central American seasonally dry regions are projected to experience longer and more intense droughts and a shorter rainy season (Fung *et al.* 2017), it is of prime importance to characterize the local practices that farmers use to cope with climatic hardship.

A multidisciplinary approach to this subject is thus necessary. In recent years, policy makers and scientists alike agreed that one of the most efficient and least costly way to adapt to climate change is the use of local traditional practices to design new resilience solutions for the years to come. In response to this statement, the concept of Ecosystem-based Adaptation (EbA) was created, aiming to focus on local ecological conditions and livelihoods to increase local climate change preparedness (Andrade Pérez *et al.* 2010). In the framework of this concept, this paper is one of the first to explore the practice of dry season browsing in seasonally dry forests by bovine cattle and its importance for local livelihoods. As no research was available, we decided to turn to farmers in those regions to probe the extent of the traditional knowledge on the topic.

We chose to base our study in the Guanacaste province of Costa Rica, which is the beef cattle capital of Costa Rica (INEC 2014). This seasonally dry region had been heavily deforested until the 1980s, due to strong incentives for land clearing and beef cattle rearing, but has since then experienced a strong recovery of forest cover (Arroyo-Mora *et al.* 2005), and many commercial livestock farms now have extensive patches of dry secondary forests within their boundaries (INEC 2014, Arroyo-Mora *et al.* 2005). In this study, we interviewed farmers in the Liberia county of Guanacaste province, aiming to (i) determine the frequency and intensity of the dry season forest browsing practice, (ii) gather traditional knowledge about cattle browsing preference and behavior while in seasonally dry forests and (iii) understand the feeding and management factors that influence farmers´ decisions to put their cattle in the forest or not during the dry season.

2 Materials and Methods

2.1 Study area

The study took place in Liberia county, province of Guanacaste, in Northwestern Costa Rica, ranging from 10° 57' 54'' N to 10° 25' 6'' N, and 85° 17' 31'' W to 85° 49' 34'' W. The county is 1,444 km^2 and hosts 62,987 inhabitants according to the latest 2011 national census (INEC 2012), with 82% of county's population living in Liberia City. Seventy-nine percent of Liberia county population is dedicated to the tertiary sector, while only 8.4% works in the primary sector, that is, less than half of the province´s average of 17.8% (INEC 2012). Of the 650 farms of the county, 295 were dedicated to cattle ranching, with an average of approximately 89 animals per farm, compared to the national average of 35 animals per farm (INEC 2014). Ranching in Liberia and Guanacaste province in general is traditionally built on a "latifundio" model, with vast extents of land belonging to one owner or family, and focused on beef cattle rather than dairy (INEC 2014, Cabrera 2007).

The county is mostly composed of flat to mildly hilly lowlands, with more marked slopes on the foothills of the Guanacaste Volcanic Cordillera to the East. Liberia County has a strongly seasonal climate, with a dry season (< 100 mm of precipitation per month) from December through May (IMN 2013). Most of the county's lowlands have a very warm tropical dry sub-humid climate with a period of light to moderate excess of precipitation. Average rainfall is 1,600mm per year, September being the rainiest month (346 mm) and January the driest (1.3 mm). Temperatures range from 19.2°C to 37.7°C in April and from 18.9°C to 33.4°C in November, with a mean annual temperature of 27.2°C, a relative humidity ranging from 60.5% to 86.1% in March and October respectively (IMN 2013). Soils are mostly Inceptisols over a shallow layer of brittle volcanic rock in the plains, among which are interspersed many patches of clayey deep soils with low water absorption capacity, locally named "sonzocuites" (Bergoeing 2017).

Forests of Liberia county are seasonally dry tropical forests (SDTF) as defined by Sánchez-Azofeifa *et al.* (2005), with a high proportion of dry season-deciduous species and Fabaceae (Kalacska *et al.* 2004, Murphy and Lugo 1995), as it is the case for most tropical dry forests (Gei *et al.* 2018). However, forests with dominance of *Quercus oleoides* can be found in the flatlands surrounding Liberia and the slopes of Guanacaste Volcanic Cordillera (Klemens *et al.* 2011). Classified by the Holdridge life zone system as tropical dry forest, the vegetation on the slopes of the Guanacaste Cordillera transitions rapidly to premontane wet forest and lower montane rainforest at the county's maximum altitude of 1,900 m (IMN 2013). Most of the county is within the Central American Dry Forest ecoregion defined by Olson *et al.* (2001) as an ecosystem-based unit for conservation planning.

A wave of deforestation took place in Guanacaste province during the second half of the 20th century with the fast development of extensive cattle ranching, boosted by national development incentives and international meat prices (Stan and Sanchez-Azofeifa 2019). The Costa Rican golden age of beef cattle ended in the late 1970s, with a drop in meat prices and the end of those incentives, triggering the regeneration of forest on the least productive cleared areas. As a consequence, most dry forests today in Guanacaste province and Liberia county are relatively young secondary forests (Stan and Sanchez-Azofeifa 2019).

The only remaining old-growth dry forest of Costa Rica is located within Santa Rosa National Park, which marks the northern border of the county, as well as the contiguous Guanacaste National Park. Biological corridors are not present in the lowlands of the county, but the 7,317 ha Horizontes Experimental Forest Station (EEFH) studies sustainable conservation options in productive landscapes under a special status. The EEFH rents regenerating pastures within the station to cattle owners to maintain fuels low (Milena Gutierrez, Pers. Comm). Wildfires are very common in the area, most of them of anthropogenic origin (Janzen 1988). Many farms burn every year, either by accident or due to the persisting practice of pasture burning. The dry season of the year where the study was conducted was predicted to be particularly severe due to a strong El Nino South Oscillation (ENSO) phenomenon, and farmers interviewed were prepared to face serious drought and wildfires during this period.

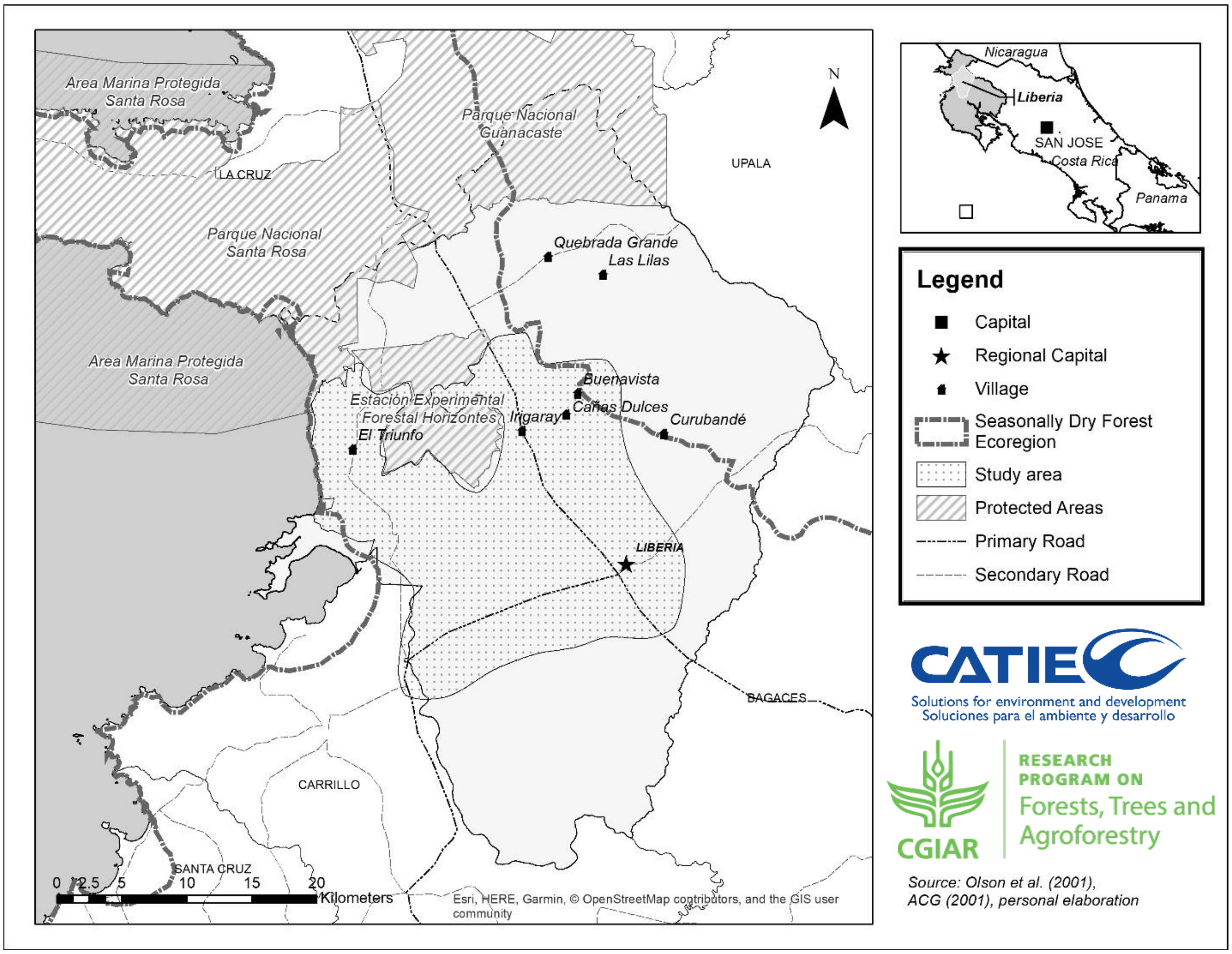


Figure 1 - Map of Liberia county. Study area is shown as the approximate area covered by farms where interviews were made.

2.2 Data Collection and Analysis

In the months of November and December 2018, 43 semi-structured interviews were conducted in cattle farms of Liberia county. The interview involved 13 open-ended questions with follow-up topics, some enquiring about farmer perceptions or opinions, and other requiring a concise answer or a list of items (Appendix 1). Interviewees were selected on the basis of their farm management knowledge, and could be either farm owners or administrators. As cattle in forest was the object of this study, selected farms had a patch of forest and livestock density indicating an active herd management. For example, one farm of 250 ha which had a herd of 5 animals was not selected for interview. Whether or not forests were used for cattle browsing was not a selection criterion. Farms had to be within the limits of the Olson *et al.* (2001) WWF Central American Dry Forest (CADF) ecoregion. For the sake of this study, the definition of cattle browsing in forests was taken in a broad sense. The selected definition of forest was "an area with dense tree cover and an understory layer, where the main forage for cattle are trees, shrubs and wild herbaceous plants". Hence, tree plantations and forests where cattle browsed on understory vegetation were included, but forests and plantations where the understory had been cleared to plant improved pastures were not. The definition provided by the Costa Rican legislation was close to our definition but also included open formations of one canopy layer (REDD/CCAD-SINAC 2015), which did not fit our study objectives.

A first part of the questionnaire aimed to learn about farm management practices, focusing on dry season cattle husbandry strategies. The second part was about cattle management and behavior in forests, to elicit farmer's knowledge on cattle behavior in the forests. A last open-ended question asked for farmer's opinions on the practice, its advantages and drawbacks. The third part was enquiring about forest age, structure and composition, as well as wildlife and particularly other herbivore presence or dangerous animals in the forest. The last part of the questionnaire was oriented towards fire and fire-based management practices. Interviews were recorded and backup notes taken to ensure a minimum loss of information.

The original interview structure was reviewed and perfected by a panel of specialists in sociology, agroforestry and livestock management. However, the first days of interviewing triggered a necessary adaptation to the interview structure and content, as new themes were repeatedly mentioned by interviewees as of critical importance. The reviewed interview is available in Appendix 1. Despite reviewing the interview, the semi-structured setup of the interview left many questions open-ended, and several items that were not meant to be specifically enquired about were mentioned spontaneously by farmers. Some other times, farmers did not know the answer to a question or the question did not apply. Those exceptions lead to some incomplete data on certain subjects, but those were deemed of enough importance to be discussed in the results section. In those cases, proportions will be presented as percentage of farmers that expressed themselves on the matter, with the total number of farmers having expressed themselves, e.g: *"24% (n=25)"*, when the number of interviews "n" was different from the total of 43 interviews.

Farmers were not randomly selected in terms of spatial distribution or farm size, as no exhaustive georeferenced map of cattle farms was available. Interviews were performed following a combination of chain of recommendation or “snowball sampling”, a list of addresses and contacts provided by the Guanacaste Cattle Ranchers Chamber Federation (Federación de Cámaras de Ganaderos de Guanacaste, FCGG), and personal contacts from employees of the Costa Rica’s System of National Conservation Areas (Sistema Nacional de Áreas de Conservación, SINAC) as well as the Ministry of Agriculture and Cattle Ranching (Ministerio de Agricultura y Ganadería, MAG).

As an extensive list of possible interviewees was gradually compiled, the selection of farmers to meet was made in order to include a wide range of different farm sizes, occupations and locations, to embrace the highest possible combination of situations and managements. The investigation headquarters were based in the EEFH for logistical and geographical ease, and all interviews took place within a 20 km radius from the station. Interviews were centered around three main population centers: El Triunfo, Liberia and Cañas Dulces, but interviews were conducted on other farms in different locations. The highest altitude registered for an interviewed farm was 338 m, in Buena Vista de Cañas Dulces, still within the CADF ecoregion.

Statistical analyses on supplementation variable and farm structure used in this paper were performed using the statistical software Infostat (Di Rienzo et al. 2018), using a simple T-test or an analysis of variance (ANOVA) when needed, with a Fisher’s LSD test for comparing means, with a statistical significance fixed at $p<0.10$.

3 Results and Discussion

3.1 General considerations

Demographics of the 43 interviewees were quite homogenous. Only two interviewees were female. The pool of interviewees was ageing, although a significant proportion of owners or administrators’ children were actively involved in farm management and decision making, hinting at some generational renewal in the sector, even though this tendency was not dominant. Sixty-three percent of the interviewees were farm owners, the other 37% being administrators. Two of the interviewees had a primary occupation that was unrelated to cattle ranching, despite owning cattle and actively managing their farm. Farm size ranged between 7 ha and 1200 ha, and herd size ranged between 9 and 500 heads of cattle.

Farmers’ opinion on the state of the cattle industry in Costa Rica were in general quite gloom and cattle ranching was described as an industry generating little profits due to low meat prices and increasing costs, particularly for feed and supplements. While the lowlands of Liberia county used to belong to immense ranches, farms have undergone a progressive fragmentation process due to the reduction of cattle herds, splitting of the land between successors, cost of land maintenance, and the lack of liquidity in times of financial hardship. For example, Hacienda Ahogados, the biggest farm in the county, who spanned more than 34,000 ha at the beginning of the 20th century (Cabrera 2007), is now reduced to a couple of thousand hectares, after selling most of its land to other farmers and to the state (the entire 7,317 ha of land of the EEFH were donated by Hacienda Ahogados). In addition, seven farms from the interviewee pool had been divided between children of the farm owner, some functioning as one management units, some not. Only one farm had experienced an increase in size in the previous decades.

3.2 Farmland and cattle herd management

The following production types were encountered throughout this study, often combined, and are briefly defined below:

Beef cattle farms were split between breeding, backgrounding and fattening farms. Breeding farms are dedicated to cattle breeding, selling calves at weaning. Backgrounding farms raise cattle up to a certain weight or age, then selling the animal to fattening/finishing farms. Breeding and backgrounding farms were the most common, representing 72% of interviewed farms, often combined. Those farms adapted their management to the hardships of the dry season, 35% of them working with seasonal breeding to avoid having lactating cows during the driest month of the year, where the scarcity of resources combined with the additional physiological strain of lactating could put their lives in jeopardy. Only four farms were part of an insemination program. As seasonal breeding requires a more intricate management plan and higher personnel costs, only 9% of farms <150 ha had implemented it, compared to 55% of farms >150 ha. In those farms, cows were mounted so the calves would be born after the first rains of May. Weaning was done between 5 and 8 months, and most calves and heifers were thus sold before the dry season, completing the annual cycle. For farms that did not implement seasonal breeding, cows with calves were usually not allowed to enter the forest and were supplemented separately from the rest of the herd, to ensure a proper nutrition and avoid the smaller calves to be prey to coyotes, big cats and thieves. The animals entering forests in those farms were thus pregnant cows, bulls and weaned calves and heifers.

Beef fattening/finishing farms buy adult cattle and fatten it up to slaughter weight. Some fattening farms were present (14% of farms), but were not a preferred type of cattle production, as the weight loss during the dry season usually would nullify all the weight gained during the rainy season. As a consequence, cattle fattening usually is done as a side activity complementing other beef production modality, as fattening allows for some flexibility: cattle can be bought from auction when pastures are green and sold for a profit at the beginning of the dry season. It results that half of farms dedicated to fattening drastically reduced their herd as soon as the rains stopped, only leaving a small number of cattle for pasture maintenance. Farms that kept fattening cattle during the dry season usually stabled and heavily supplemented it when pastures were dry. Only one of those farms purposefully brought cattle under a high tree cover.

Dairy farms focused on milk production, usually raising the heifers for replacement of older cows. Dairy farms were scarce (12% of all farms) and only two of them sold milk to the national market via the main Costa Rican cooperative Dos Pinos. Both of those farms had implemented a strong supplementation program to maintain milk production during dry season, and did not allow cows into forest due to the demanding logistics of milking twice a day. Supplementation was also capital in dairy farms due to the necessity of maintaining cows in lactation, forcing the farmers to let cows give birth at the peak of the dry season.

Dual-purpose farms were dedicated both to milk and meat production. Those farms had dairy cattle cross-bred with beef breeds to provide a good value for the carcass when cows are slaughtered, but with a lower milk production.

For all beef operations, preferred breeds were the *Bos indicus* Brahman, often mixed with Nellor (*Bos indicus*). Dairy cows were not of a dominant breed, but rather of *Bos indicus* dairy breeds (Gyr/Guzerat), *Chumeca* (Jersey x Holstein) or mixes of *Bos taurus* x *indicus*.

No two farms were the same in terms of management, structure and supplementation strategies. However, we could identify different dynamics depending on the area. Farms on the slopes of the volcanic cordillera and particularly around the village of Cañas Dulces were smaller than farms in the plains of Liberia county. There was a noticeable difference in farm structure, purpose and management between upland farms and farms in the plains (Table 1). Upland farms were smaller than in the plains, had a larger proportion of pastures and less forests on farm. Almost all farms in Cañas Dulces managed a small area of crops for self-consumption or local markets, while crop areas in the plains were dedicated to commercial production of sugar cane, rice or corn.

This difference could be explained by some historical and cultural background. As a farmer from the village explained, Cañas Dulces was founded by rural families looking for a piece of land to settle and live from subsistence agriculture. Historical literature confirms this claim. As explained by Cabrera (2007)**,** the set of land laws "*Leyes de Cabezas de Familia"* promulgated at the beginning of the 20th century, that allowed citizens to occupy and claim public land, gave rise to the idea that any uncultivated land was claimable. In addition, the poorly defined limits of big farms allowed for some confusion in determining which area belonged to whom. As a result, many families settled on the least used areas of big farms, on the mountain slopes, giving birth to violent land conflicts between farms and squatters over the years (Cabrera 2007).

Cañas Dulces farmers hence come from a subsistence agriculture background and live directly on and depend from them. This is a harshly different context from El Triunfo in the plains, where farms are bigger and belong to old ranching families. Most villagers of El Triunfo are farm workers and administrators, while people of Cañas Dulces own their land. Seventy-five percent of interviewees in Cañas Dulces were owners, living on or close to their farms, while only 48% of interviewees in El Triunfo were owners, few of them living on site. There are small farms around El Triunfo, however, those originate mostly from the more recent fragmentation of big farms, and few owners of those farms were living from cattle ranching. The social tissue in Cañas Dulces was also denser, and the local producers' association had managed to implement a community irrigation system for cattle and crops. In addition, while the herd in most beef farms in the plains was composed of almost exclusively Brahman or Nellore, only five farms on the slopes of the volcanoes were of purebred Brahman. Other herds were composed of a mix of zebu cattle and dual-purpose cows.

Table 1 - Comparison between upland farms on the slopes of the Rincón de la Vieja volcano (Altitude), Liberia farms (Plains-city) and farms in the plains of Liberia county in terms of farms size, proportion of pasture area on farm (Ppasture), proportion of forest (Pforest) and herd size. Statistical comparisons are performed with p<0.1 as level of significance.

Location	n	Farm size (SE)	Ppastures (SE)	Pforest (SE)	Herd size (SE)
Upland	13	116.19 (90.01)b	0.78 (0.07)a	0.11 (0.06)b	121 (46.05)a
Plains-City	5	126.2 (145.14)ab	0.50 (0.10)b	0.30 (0.10)a	78 (74.26)a
Plains-Countryside	24	387.5 (66.25)a	0.60 (0.05)b	0.28 (0.04)a	156.42 (33.89)a
P-value		*0.0392*	*0.0375*	*0.0673*	*0.5873*

Values in the same column with shared letters are not statistically different (p>0.1)

Small farms in any location experienced the same space challenges, mostly for farmers whose primary source of income was ranching: In a small portion of land, one must be able to stock a herd big enough to support a family's financial needs, forcing farmers to maximize the number of animals per hectare, and hence the amount of pasture space. As a consequence, small farms had either a significantly smaller proportion of forests, or managed forests in order to increase the forage output by either replacing the understory layer with pastures or selecting the understory vegetation to only leave plants edible by cattle in 12% of farms.

Forest plantations were more typical of smaller farms (<150 ha), of which 30% maintained a few hectares of *Gmelina arborea*, *Tectona grandis*, *Gliricidia sepium* or *Pachira quinata* for fences and other farm needs for wood. One interviewed farm had an active commercial plantation with its own sawing mill. Only 10% of bigger farms had forest plantations.

3.3 Threats and challenges faced by ranchers

Cattle theft has become a real issue, affecting all cattle farms but mostly the ones close to cities and settlements. Four of five farms interviewed in the surroundings of Liberia had to stable cattle every night to avoid cattle theft. Theft affects nevertheless most of the farms of the county, as even the most remote farms interviewed have been affected, and in total 26% of farmers mentioned spontaneously that they had been victims of cattle theft. As described by farmers, cattle thieves usually kill, skin and butcher cows on the spot, taking only the most valuable cuts with them, killing up to four cows in one night, as one of the interviewees mentiones. Cow thieves are believed to be either petty criminals or "frustrated hunters that need to bring some meat home". Wildlife (e.g. jaguars) attacks on cattle are usually not perceived as a real threat in comparison to criminal damage, and as one farmer described: "I never have any trouble with animals, apart from the two-legged one". The Guanacaste Cattle Ranching Federation (FCGG) has acknowledged the issue and gives classes and workshops on how to adapt farm management to avoid cattle theft.

Land encroachment has become a problem for farmers in the region, with the regular arrival of land squatters or "precaristas" on farmland. One of the interviewed farmers maintained a cattle herd on his land only to maintain pastures clear and prevent encroachment from squatters. Allegedly, those squatters form a great part of the hunters and opportunistic cattle thieves that plague private farms of Liberia county.

Wildfires are the most important threat to farmers, as well as the most recurrent one. Every dry season, fire takes its toll on farm's operations. Sixty-nine percent (30) of the farms included in the study had been burnt partially or totally during the previous five years. The reasons mostly originating fires affecting farmers are in Table 2, and have different impacts on forests in farms, as well as on cattle management.

Table 2 - Most common reasons at the origin of uncontrolled fires in the study area, according to farmers, as a proportion of farms where the reasons were mentioned (n=43). As more than one answer could be provided, the total is superior to 100%.

Origin of fire	Proportion of farms (%)
Pasture/sugar cane burning	30
Hunting	23
Criminal activity	19
Recreation	14
Fishermen	12
Natural/Accidental	9
Cigarettes/Glass bottles	7

Pasture and sugar cane burns are a common practice in Liberia, and poorly controlled agricultural burns are one of the main reasons for wildfires. If burning of sugar cane is still a standard practice for hand-harvested plantations, pasture burning seems to be decreasing within the area, as improved pastures replace the traditional Jaragua (*Hyparrhenia rufa*), criticized for its high flammability (Janzen 1988, Johnson and Wedin 1997). Only five interviewees admitted to using fire as a pasture management strategy. However, when asked for the reasons for wildfires in the dry season, 30% of respondents mentioned the neighboring farms' burning practices. Hunters were second to be mentioned in 23% of farms, as dry season hunting practices are very reliant on fire. Most of those fires start in the forest, lit by hunters wanting to clear the forest understory for better visibility and to trigger green re-sprouts from plants that would attract deer and other herbivores. Criminal activity and recreation (33% of farms when grouped) are symptoms of a "fire culture" mentioned without prompting by three interviewees, where fire can be used either by arsonists for the pleasure of burning, or as the simplest way to exert vengeance in this region, when a single well-placed match can set a whole farm on fire. The motives that have been listed by farmers for vast wildfires driven by revenge can be as petty as the fire lighting strategy can be intricate. Fires caused by fishermen are typically accidental, when a poorly extinguished fireplace lit by riverside fishermen in a forest springs back to life with a strong breeze. These fires are nevertheless common enough to be cited as one of the main reasons for forest fires in Liberia county by 12% of farms, and affect forests more than pastures, as riversides are required by law to be forested. Roadside littering was cited as a reason for fires starting from the roads, as a cigarette or allegedly a glass bottle lit by the sun can start a fire. However, this reason, a faceless scenario, has been deemed by three interviewed farmers and government employees as "an easy excuse for burning one's own farm".

Fire on private farms is a private matter. No government help is usually available to farmers. Employees of the EEFH are trained to prevent forest fires, but their range of action is limited to the territory of the experimental station and the contiguous farms. Liberia firemen are only mandated to protect infrastructure and houses, and extinguishing forest fires is not part of their official duty, according to farmers. Every farmer interviewed, but one, maintained small firebreaks between pastures and at farm limits, mostly to save the costly wooden posts of fences in case of fire, and small fire containment equipment (water tanks and pesticide sprayers recycled into water sprayers) was available on all farms interviewed.

3.4 Dry season feeding strategies and cattle in forests

3.4.1 Pasture management

Pastures are the main source of feed for cattle during the dry season, and it is important to first examine the relationship of cattle dry season browsing with pasture type. During the wet season, cattle feed mostly consists of pastures. Not all pastures were equal in terms of drought resistance once the dry season started. Jaragua grass (*Hyparrhenia rufa*), has been the preferred pasture in the region since its introduction in the 1920s, when it replaced native grasses in the Guanacaste landscape (Janzen and Hallwachs 2016). This tall savannah grass has a low nutritive value and a low palatability when dried, and requires heavy grazing and management to maintain an acceptable condition for grazing (FAO 2016). Jaragua dries early in the dry season, and without appropriate management becomes both an unpalatable pasture and a highly flammable fuel, which tempts farmers to use fire to foster re-sprouts. Although still heavily present in the landscape, Jaragua is disappearing, being dominant in only 11 farms (Table 3). It is progressively being replaced by improved pastures, and mostly by *Brachiaria* species, in particular *B. brizantha* (dominant in 21 farms), as well as a more nutritive and drought resistant, *Andropogon gayanus* (FAO 2016). *B. brizantha* was often mixed in pastures with other *Brachiaria* species.

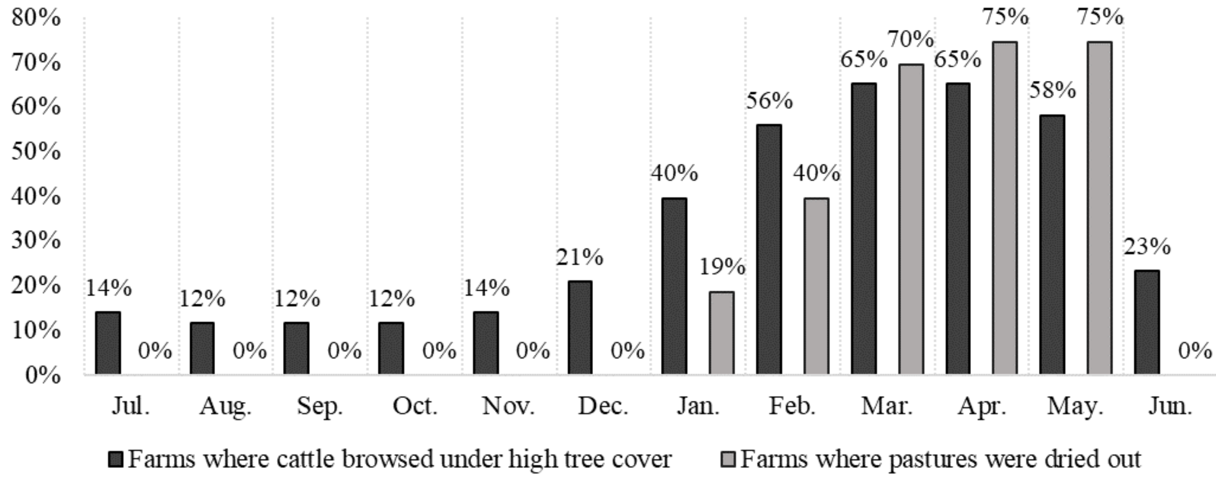
Many other pasture types were found within farms. Some were farmer's tryouts of promising pastures varieties and combinations, including *Panicum maximum cv. Masai* or legumes-pasture associations (various pastures and *Desmodium* sp. or *Stylosanthes* sp., for example) that were found mostly in farms around Liberia. Some others were used as horse pasture in small areas (*Digitaria eriantha cv. Transvala*, *Dichanthium aristatum)*, and some other bound to be made into hay bales (e.g. *Brachiaria* sp., *Digitaria eriantha cv. Transvala)*.

Table 3 - Presence and dominance of pastures in interviewed farms. All results add to above 100%, as several pastures could be present in one farm, and that dominant pastures were often mixed in paddocks or several pastures represented a high cover of pasture area according to farmers.

Common name	**Latin name**	**Present (%)**	**Dominant (%)**
Andropogon	Andropogon gayanus kunth	33	12
Angleton	Dichanthium aristatum	16	7
Brachiaria brizantha	Brachiaria brizantha	72	49
Brachiaria decumbens	Brachiaria decumbens	23	16
Brachiaria dictyoneura	Brachiaria dictyoneura	5	2
Brachiaria humidicola	Brachiaria humidicola	2	2
Brachipara	Brachiaria hybrid, b.arrecta x b.mutica	2	0
Caiman	Brachiaria hybrid cv. CIAT BR 02/1752	2	2
Desmodium	Desmodium spp.	2	0
Estrella africana	Cynodon spp.	5	0
Guinea	Panicum maximum	2	2
Guinea Massai	Panicum maximum cv. Masai	2	0
Guinea Mombasa	Panicum maximum cv. Mombasa	19	12
Jaragua	Hyparrhenia rufa	40	26
Kudzu tropical	Pueraria phaseoloides	2	0
Mulato	Brachiaria hybrid 36061 cv. Mulato	7	5
Stylosanthes	Stylosanthes spp.	2	0
Swazi	Digitaría swazilandensis	5	0
Transvala	Digitaria eriantha cv. Transvala	12	0

Improved pastures tend to dry later in the dry season, according to farmers and available literature (FAO 2016)**,** and their higher nutritive value and palatability was said to reduce the necessity for other supplementation, including browsing in forests. However, even though improved pastures are more drought resistant, the proportion of farms with improved pastures which also allowed cattle to enter forests was similar to the figures for all farms. The month of cattle entry in the forest followed the seasonal pattern of pastures drying, independently of their resistance to drought, as shown in Figure 2a and b**.**

(a)



(b)

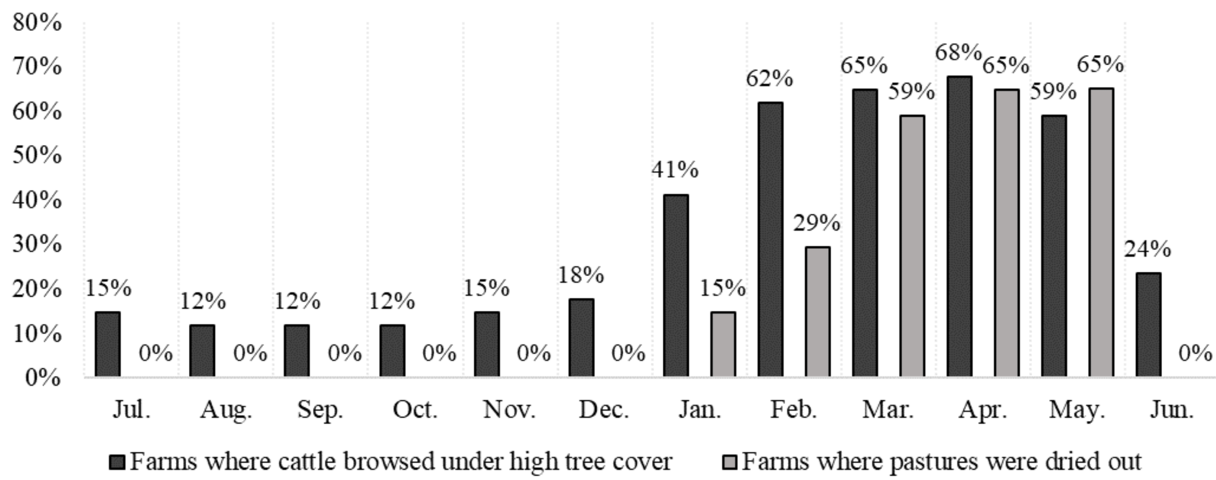


Figure 2a and b. Chronological relationship between number of farms allowing cattle to enter forests and proportion of farms with dried-out pastures, for all farms (a) and farms with improved pastures (b).

Improved pastures hence decreased the urgency that drove farmers to put their herd into forests during the dry season. Improving pastures was sometimes a management strategy to avoid having to put cattle within forests for survival. One farmer declared that “The idea for [our] farm is to have pastures that are good enough so we do not have to bring our herd into the forest”. This idea was shared by other farmers, who saw that practice only as an emergency resource, which was however still necessary almost every dry season. Twenty-five percent of farmers declared that their pastures did not fully dry during the dry season. However, the decrease in pastures palatability and digestibility as dry season progressed impacted sufficiently cow nutritional input to justify entering the forest. The months from March to May were the most critical, regardless of the type of pasture. In the last months of the dry season, two farmers stated that cows had to be removed from the forest to be supplemented, as the forest did not provide enough feed to maintain cattle in a healthy state and walking long distances in the search of feed depleted the energy of the cows. In total, 70% of farms did bring cattle into the forest as a feed supplementation strategy, but in the critical months of March to May, only 65% percent of farms had their cattle in forests for the reasons mentioned previously. In contrast, others preferred to wait until a month or two after the first rains before restarting a fully pasture-based diet and let cows return from the forest, to allow for pastures to regrow and build up a sufficient proportion of dry matter content.

Eight farms had implemented a rotational grazing system where small paddocks were grazed under high stocking rates for one or two days, with a total rotation time of approximately 30 days. Seven of them used improved pastures. Both dairy farms selling to the Dos Pinos cooperative had implemented this system. All other farms had either a longer rotation time (between two to three months for a complete rotation) with bigger pasture lots, or had a low number of animals in a small number of lots. However, five farmers mentioned their desire to implement a more intensive (shorter) rotation system to increase their use of pasture area and increase stocking rates, to "manage [a beef cattle] farm like a dairy, because today we need to produce more with less". For all systems, pasture rotation often came to a stop as the dry season settled in: to face the loss of productivity of drying pastures, 21 farms opened all paddock gates at the beginning of the dry season, to allow cattle to find food wherever it was available, without following any management plan. This practice was independent of farm size. Farms with a shorter rotation period tended to maintain the same rotation during the dry season, with a few exceptions.

Forests in farms were often included in pastures, with several paddocks including a small portion of forest. When a forest was part of the paddocks, cattle were free to enter the small portions of forests year-round, but according to farmers, cattle only tended to enter those during the dry months of the year, preferring open pastures during the rainy months and being deterred from entering forests due to the dense understory vegetation sprouting with the first rains. When only part of the forest was included within pastures, cows often were not allowed to enter further into the forest. In two farms where forest was part of the paddocks, farmers stated that cows would not enter the forest willingly during the dry season because the paddocks had a high density of fruit trees that provided both feed and shade, in addition to other kinds of supplementations.

When a forest was fenced away from the paddocks, there were diverse reasons for this separation. Some farmers had fenced their forests so cattle would not enter in order to protect the integrity of the forest or springs and streams, but the most common reason for fencing was to stop cows from entering the forest and getting lost or stolen, or disrupting the rotation plan during the rainy months. However, during the dry season, farms that used forest browsing either opened the paddocks gates to the forest at the same time as they stopped regular rotation and opened paddock gates or put cattle entirely in forest patches, enclosing them in forests as extensive separate paddocks.

3.4.2 Supplementation types

A big part of farm work in the last months of the rainy season consisted in harvesting and stocking up on various kinds of supplements to prepare an adequate supplementation for cattle during the dry season. The main supplementation types provided in the dry season were the following:

- Salt and minerals were used by all farmers year-round, and were left aside from further analysis, as the interview did not enquire about the type of minerals used.
- Hay bales were used by 26 (60%) farmers and were the most common type of supplementation aside from the use of forests for browsing. Smaller farms tended to buy or exchange the bales, while bigger farms usually had a reserved area of pastures for haymaking, in specialized paddocks on farm or in a separate area. The most common source of hay were rice stubbles and specialized pastures such as *Digitaria eriantha cv. Transvala* or *Digitaria swazilandensis*. Hay bales being the most basic type of supplementation in farms, the fact that a farmer supplemented his herd with hay or not could be an indicator of different objectives: reducing costs to the minimum by not supplementing animals, or maintaining animals healthy through the dry season. Indeed, farmers that provided hay to their herd also fed their animals more supplements (1.84 supplements, S.E.=0.23, n=26) than farmers than did not provide hay (1.12 supplements, S.E.=0.27, n=17), t-test, p=0.0488. However, this figure must be interpreted with caution, as in some cases hay was not provided to cattle due to the presence of better supplementations such as fodder banks and silage or a high number of planted fruit trees in paddocks.
- Sugar syrup or molasses were used by 23 farmers as a source of energy, widely known for its use as cattle drought-feeding. Molasses were often used in combination with hay, to encourage cattle to eat the dry forage, although there was no pattern of association between those two supplements.
- Silage was used in 7 farms, mostly in the mountain area.
- Fodder banks had been implemented in 14 farms, nine of them in the surroundings of Cañas Dulces. There was some overlap of farms using fodder banks and silage, as all or part of banks were usually used for silage in 43% of farms with fodder banks. Other farms provided the feed directly, whole or chopped, to their herd.
- Fruits and branches from trees were fed to cattle in a similar modality to fodder banks, in eight farms. Branches from trees in pastures or from the forest were pruned and fed to cattle. Fruits were either directly eaten by cows from fruit trees planted in pastures where cattle were brought purposefully (e.g. Mangoes, fruits from the *Acrocomia aculeata* palm tree). Four farms bought citrus pulp from a nearby orange plantation that sold the byproducts for a low price. Two farmers mentioned that previously melon pulp had been used for cattle supplementation in the region, but this practice had been abandoned due to the price of the pulp. In one case, cows refused to eat other feed sources once the melon season had passed, having acquired a taste for the pulp, which resulted in heavy weight losses in the herd.

- Poultry manure was mostly used in farms in the plains, and is considered by farmers a good source of protein, although not recommended by the MAG due to its potential health risks (Oscar Alvarez, Pers. Comm.). Six farms complemented their herd with poultry manure.
- Concentrate was used by seven farms. Three farms were dairy farms, and fed concentrate to all their cattle to maintain milk production during the dry season. Other farms only provided concentrate to young cattle after weaning, or to the weakest cows. The low rate of concentrate use was due to the high prices of this supplement on the market, forcing farmers to adopt other strategies. One farmer had successfully developed his own concentrate recipe.

Farms could not be grouped into distinct supplementation types because supplementation practices were extremely variable and heavily depended on each farm's structure, purpose, and owner's knowledge on good agricultural practices. Statistical tests between supplementation practices and forest browsing were not significant. Moreover, as several types of production were sometimes present in one farm, different supplements were given to cattle depending on their age, beef or dairy purpose and physical condition. However, we were able to find a difference in supplementation practices between mountain and plains farms (Figure 3). Farms in the plains relied more on hay and molasses, while fodder banks and silage were much more common in upland farms; no poultry manure was used as supplement in mountain farms. This might be due to the difference in soil types (Bergoeing 2017), where upland soils have a greater aptitude for agriculture, the existence of a subsistence farming, irrigation and extent of technical support by the Ministry of Agriculture. In the Cañas Dulces area, MAG provides more assistance to smaller farms and subsistence farmers to help them to implement fodder banks and silage (Oscar Alvarez, MAG director for Liberia County, Pers. Comm.).

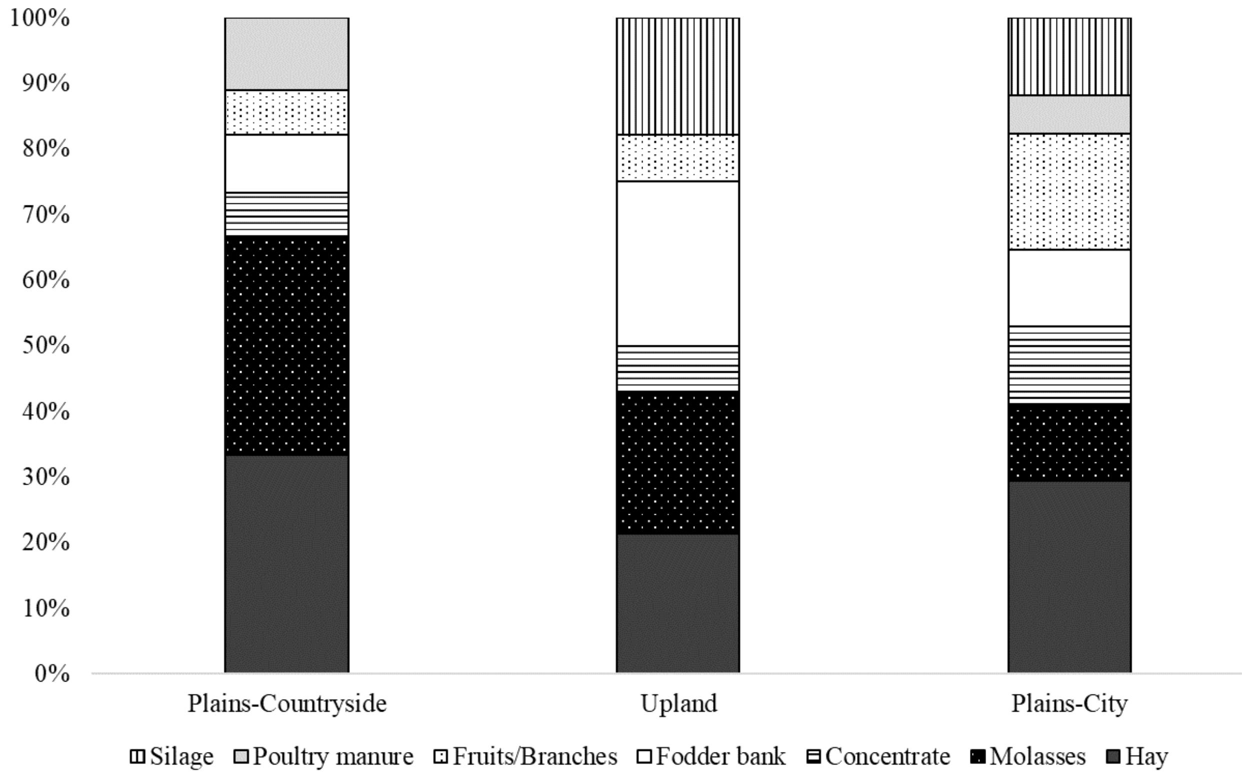


Figure 3 - Proportion of each supplementation provided to cattle in farms for the three categories mentioned in Table 1.

The amount of supplement provided to cattle might have an impact on the need for cattle to benefit from another supplement, including the use of forests. For example, the feeding behavior of cattle in forests can be influenced by nutrient deficiencies due to an improper supplementation, causing cows to eat wood, soil, plastic and otherwise unpalatable plants. One farmer mentioned that it is common in the area that cattle with nutrient deficiency would eat pieces of plastic or chew on posts. This behavior disorder is known as Pica or allotriophagia (Elshahawy and Aly 2016). These considerations highlight the need for a more thorough analysis of the amount of supplementation provided to cattle by age and production system in order to understand the need for using the forest as a supplementation strategy.

3.4.3 Factors that affect the decision to put cattle in forests

Farmers were asked about the benefits and drawbacks of using forest browsing by cattle as a dry season supplementation strategy, as an open-ended question with multiple answers possible. Reasons given by farmers were classified into three categories: Management, animal welfare and ecological impact (Figure 4).

Forest browsing benefits were cited 77 times, while drawbacks were cited only 48 times, with a more diverse number of reasons. As expected, the value of forest as a source of food and shade were the most cited and most important benefits. The improvement in animal well-being overpowered the threats found in forests, such as wounds, parasites or animal attacks. One farmer said: “We have a contract with the jaguar, we give it one cow a year, this is better that having cows dying under the sun”. However, in some cases farmers mentioned that the energy lost by cattle while walking to or within the forest cancelled the positive effects of forest browse; Most farmers preferred to maintain cows close to water and feed during dry season and did not put cattle in forest patches that did not have a water source nearby.

Ecological impact of browsing was usually not considered as a factor of great importance, with a few exceptions of interest. Three farms had forests under a Payment for Ecosystem Services (PES) program, and were therefore forbidden from using the forest, including for cattle browsing. Forest browsing is often cited as an efficient way to reduce fuels in forest, making fire more manageable and ensuring that fires affect only the forest floor and does not affect the canopy of the forest. This belief, which we will call the fire control model, is widespread in Guanacaste, and was a central piece of the Área de Conservación Guanacaste fire control and restoration strategy until the early 2000s, but mostly focused towards *Hyparrhenia rufa* overgrowth control in pastures; it is still part of the EEFH management plan. It is unclear if the fire control model promoted by farmers has sparked the ACG policies, or if the promotion of forest browsing via the ACG influence has made it part of the ranching culture of Costa Rica’s dry areas. Fire being such a prominent threat in Liberia county, farmers considered the cattle’s work “cleaning the forest” as an important secondary benefit of this practice, protecting forests against wildfire as well as maintaining firebreaks and creating new ones as they make their path in the forest.

The fire control model has been criticized by some for the damages caused to tree regeneration (Stern *et al.* 2002). Farmers were divided on this matter. Ten farmers agreed that regeneration was impaired by the cattle browsing, while seven sustained that as cattle selected wild grasses, other herbaceous plants and strangling vines over saplings, tree regeneration was improved by the lack of competition, sometimes with the negative effect of understory layers overcrowded with tree regeneration, which is an argument made by some in scientific literature (Belsky and Blumenthal 1997). This disparity of opinions shows the complexity of a little studied subject and might be depending on many factors such as the variation of browsing pressure related to animal stocking, only allowing us to estimate cattle impact on forests based on the known behavior of wild herbivores. Even though some farmers did not put their cattle in the forest in order to protect its ecological integrity, most farmers did not consider it to be critical, focusing their efforts on the protection of streams from cattle destroying streambeds.

The factors of strongest impact on farmer’s decision to keep their cattle away from the forest were related to herd and farm management. Even though the negative effect of cattle on regeneration was the most listed drawback, the risk of cattle theft and the difficulty of managing a cattle herd in a forest were strong deterrents for farmers, and were usually the main reasons cited for not allowing cattle in forests during the dry season.

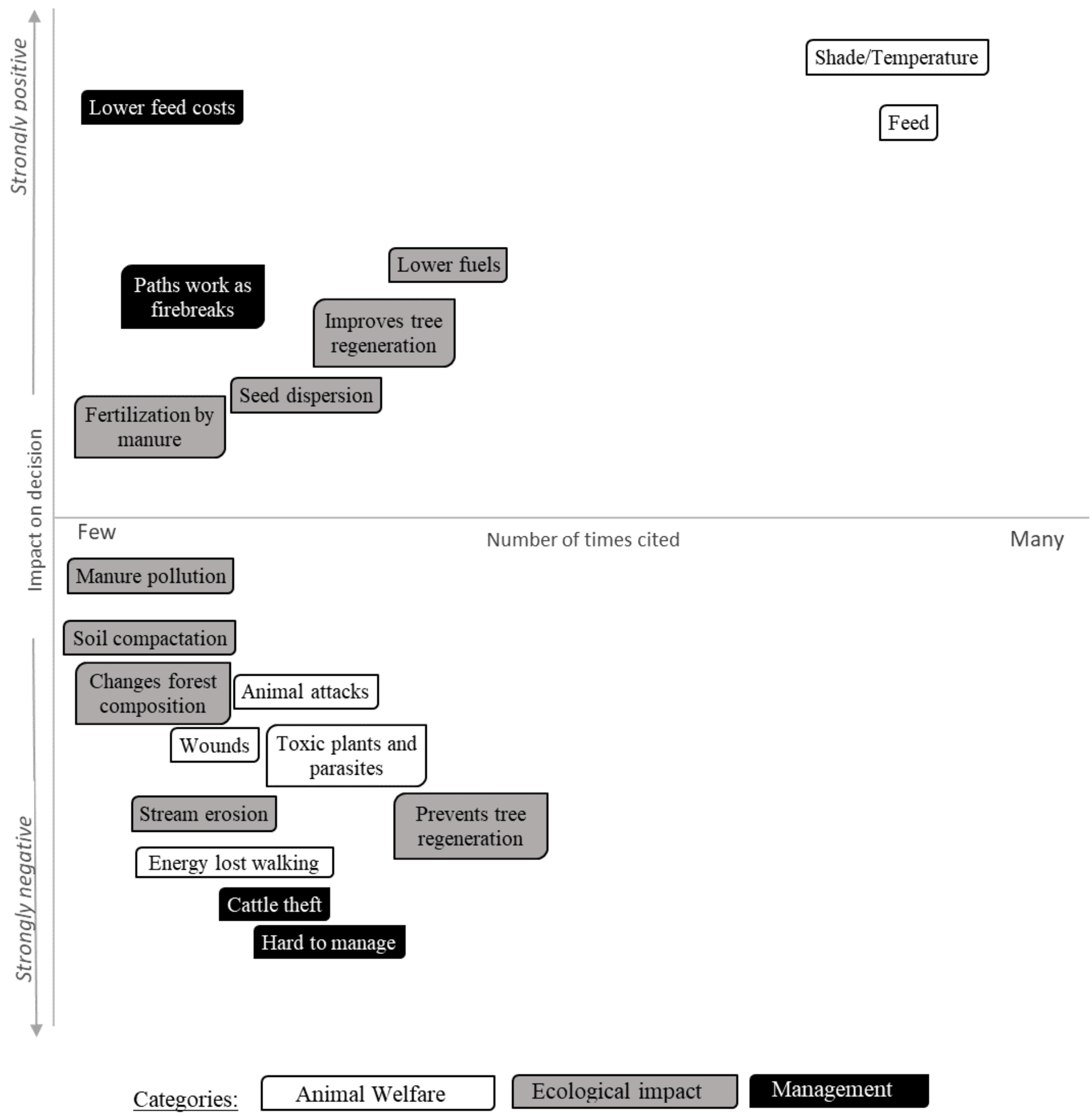


Figure 4 - Benefits and drawbacks of dry season forest browsing according to farmers (n=43), and the relative impact of each reason on farmers decision to implement or not this practice. Impact on decision was graded arbitrarily based on farmer's perception of each reason as a primary factor in their decision making. A benefit or drawback that was cited by farmer as crucial would receive the highest score on a scale of 1 to 10, while one that did not matter at all for the farmer would receive a low score. The average of answers provided the final position of the benefit or drawback on the Y axis.

3.5 *Cattle behavior in forests*

When asked about how cattle behaved while in the forest, farmers provided most of the time a wide variety of answers, often contradictory and without a clear majority prevailing. We were unable to address most of these contradictions based solely on the farm management data collected through the semi-structured interviews, meaning that either (i) cattle behavior was highly variable depending on ecological and structural factors proper to each forest that were outside of the scope of this study; or (ii) farmer knowledge on cattle behavior in forest was quite rudimentary and based on a small number of personal observations. A mix of both scenarios seems the most likely. Only two farms had a cowboy who stayed constantly with the herd and followed them in the forest, the rest of the farmers only getting into the forest to round, check and count cattle daily or fortnightly; some farmers admitted (out of the structure of the interview) that they rarely set foot in the forest, if ever. Cattle was usually trained to respond to whistling and walk out of the forest when called; in most farms, feeder for hay and water are placed close to the forest to avoid the need for farmers to step into the forest. This training aims to maintain cattle tame and close to people, as cows tend to become wild when in the forest without human contact for too long, adopting a deer-like fleeting behavior and becoming extremely hard to catch. Feral cows are common in big expanses of forests where they can escape and sometimes live several years in the forest before getting caught or killed.

3.5.1 *Distribution of cattle in forest*

Most farmers that allowed cows to enter the forest or had actively included forest browsing as a supplementation practice (n=30) indicated that cows tended to use the complete extent of forest patches (80%, n=25), while the rest indicated that cows only used the edges or parts of the forest, staying closer to rivers, drinking or feeding infrastructure. All farmers that expressed themselves (n=22) on cow distribution in the forest mentioned that cattle entering patches of forest in the dry season progressively dug paths through the forest by eating understory vegetation and compacting soil, creating “streets” between preferred spots, namely forest edge, rivers and streams, common resting places under high tree cover with low understory vegetation, and forest sections with predominance of fruit trees. Despite wet season regeneration, cattle were said to have a lasting memory of preferred spots in forests and go back to the same spots year after year, reopening the same path as the year before. Cattle was said to use man-made firebreaks that delimited forest sections as a way to avoid walking through rough vegetation, maintaining those firebreaks by compacting the soil and limiting vegetation regrowth.

3.5.2 *Herd behavior in forest*

Farmers had mixed responses regarding the size of cattle groups within forest. The most common response was that once in the forest, the cattle herd would split into several groups (61%, n=23), stay as one herd (22%, n=23) or would behave as solitary individuals roaming the forest separately (17%, n=23). Farmers’ experience was not dependent on the size of the herd, or the size of the forest, but was rather consistent with the behavior observed in cattle in forest rangelands and with the theory of herbivore herd behavior in forest (Roath and Krueger 1982, Mitchell and Rodgers 1985). Farmers mentioned that several factors could impact herd behavior in forest; a few farmers indicated that the whole herd of cows would follow either the bull, when the latter was not separated from them by the farmer, or the "alpha" cow. One interviewee who managed both beef and dairy cattle mentioned that beef cattle was more solitary than dairy cattle, that consistently stayed in a tight group, despite cows of each type being of the same sex and age. However, in most farms, cows were said to regroup to ruminate and rest at a specific place in the forest common to all groups of cows. Cows did not always spend a whole day within a forest patch, preferring to enter when temperatures were the highest, between noon and before sunset, as observed by Navas (2010) and Morillo Espinoza (2012).

3.5.3 Plants preferred and avoided by cattle, cattle selectivity and impact on the forest

We asked farmers to list cattle's favorite plants browsed in the forest and they identified 94 plant species that were either preferred, avoided, or harmful to cattle when eaten. The complete list of all plants identified is provided in Appendix III. Despite the high number of plants identified, plants most cited by farmers were the trees that are traditionally associated with cattle ranching in dry regions of Costa Rica (Table 4). Most farms in Costa Rican Northwest include trees of guácimo (*Guazuma ulmifolia*), guanacaste (*Enterolobium cyclocarpum*) and cenízaro (*Samanea saman*) in their pastures, as it is of common knowledge that those trees provide nutritious fruits during the dry season, as well as the "madero negro" tree (*Gliciridia sepium*), a Fabaceae known worldwide for its value as forage and used widely as live fences in Costa Rica due to its capacity of re-sprouting from branches once planted as a post (Gutteridge and Shelton 1994). The "bejuco engordador" ("fattening vine", *Calopogonium mucunoides*) and batatilla (*Ipomoea* sp.) were the most cited non-woody plants, also growing in pastures and known widely as forage sources. Another poorly known key species for cattle nutrition is the oak (*Quercus oleoides*); only one of the farms that had a patch of oak forest moved cattle in it, where part of the herd was sustained solely on acorns during the whole dry season.

Almost all of the cited plants could be found in open pastures as well as in forest; trees, shrubs and weeds were plants regularly observed in pastures or at forest edges. Within the top 20 plants cited (see Table 4) were also "domesticated" trees, such as *Mangifera indica* or *Gmelina arborea*, that were admittedly important for cattle nutrition in dry season. One farmer supplemented fattening cattle solely with leaves and fruits of *Gmelina arborea* re-sprouts from a partially harvested plantation. Overall, plants that did not thrive outside of forest were little listed by ranchers. 45 plants were only cited once as eaten by or harmful to cattle. This points to the conclusion that there does not seem to be an extensive shared knowledge on edible forest plants by cattle, but rather a set of personal curiosity, observations and experience, that vary a lot between farmers.

Table 4 - Twenty most mentioned species by farmers as eaten by cattle. Number of time mentioned are reported for parts of plants considered by farmers as eaten by cattle (E), avoided (A) or harmful to the animal (H). More details on harmful plants can be found in Table 5.

Common name	Scientific name	Life form	Part	E	A	H	Grows in
Guácimo	*Guazuma ulmifolia*	Tree	Fruit	33			Pastures/Forests
Guanacaste	*Enterolobium cyclocarpum*	Tree	Fruit	23		5	Forests/Pastures
Cenízaro	*Samanea saman*	Tree	Fruit	20		10	Forests/Pastures
Guácimo	*Guazuma ulmifolia*	Tree	Leaf	20	1		Pastures/Forests
Madero negro	*Gliricidia sepium*	Tree	Leaf	19	1		Pastures/Forests
Bejuco engordador	*Calopogonium mucunoides*	Liana	Leaf	16			Pastures/Forests edges
Josmeca/Ajillo	*Mansoa hymenaea*	Liana	Leaf	13		13	Forests
Escoba morada	*Melochia villosa*	Grass	Leaf	10		10	Pastures
Batatilla	*Ipomoea trifida*	Liana	Leaf	7			Pastures
Mango	*Mangifera indica*	Tree	Fruit	7		1	Domesticated
Coyol	*Acrocomia aculeata*	Palm	Fruit	6			Pastures/Scrubland/Forests
Encino	*Quercus oleoides*	Tree	Fruit	6			Pastures/Forests
Jobo	*Spondia mombin*	Tree	Fruit	6		1	Forests/Pastures
Escoba Amarilla	*Sida acuta*	Grass	Leaf	5	1		Pastures
Gmelina	*Gmelina arborea*	Tree	Fruit	5			Domesticated
Gmelina	*Gmelina arborea*	Tree	Leaf	5			Domesticated
Picapica	*Mucuna urens*	Liana	Leaf	5			Scrubland
Amapola	*Malvaviscus arboreus*	Shrub	Leaf	4			Forests/Scrubland
Aromo	*Acacia farnesiana*	Shrub	Leaf	4	1		Pastures/Scrubland
Cortez amarillo	*Handroanthus ochraceus*	Tree	Flower	4			Forests/Scrubland

Cattle was said to be little selective on what plant species to browse: 71% of the farmers that place cattle in forests and expressed themselves on the matter (n=24) estimated that "cattle would eat anything in its reach when it is hungry enough" and that it would mostly eat shrubs, climbing plants and understory grasses, leaving the forest understory "clean". Few ranchers knew names of understory plants that were not trees. A common answer was "Cows eat everything, but who knows the name of all those plants". It is interesting to note that a forest in the ranching lexicon refers mainly to the canopy layer rather than to a multi-layer ecosystem. In certain cases, this definition allowed farmers to affirm, within the same sentence, not to have intervened the forest at all and to have eliminated forest understory to plant pastures. The understory layer was often referred to as "*charral*" or scrub, the same term with a negative connotation used for unkempt pastures where shrubs and weeds overtake pasture. This lexical discrepancy clearly highlighted the little interest lent by farmers to understory vegetation and hence the lack of general knowledge on the matter.

Farmers were more divided on the subject of tree regeneration. If some assured that cattle would not damage tree saplings, some indicated that cattle preferred only a few species, while others said that there was no selection from cattle and that anything would be eaten. This division is evidenced as dry forest trees typically not growing in pastures were rarely mentioned as preferred by cattle or were categorized as avoided by it in the same measure, leaving unclear the effect of cattle on tree regeneration.

Another divisive subject was whether or not cattle would eat leaf litter. Out of farmers who expressed themselves on the matter, 68% (n=25) affirmed having seen cattle eat leaf litter, while the rest would say they have not seen cattle eating litter. This divergence could depend on many factors such as forest structure, type of supplement and amount of dry matter in supplements or remnant in pasture, or unprecise observations from ranchers, but this matter cannot be answered by this study.

Potentially harmful plants identified were usually eaten by cattle, and required actions in herd and farm management. Again, many of those plants were marginal in forests, and were found mostly in pastures. *Mansoa hymenea* and *Petiveria alliacea*, which do grow in forests, spoiled cow's milk with a strong garlic smell and taste, and were a deterrent to forest browsing for dairy producers. As mentioned previously, some producers cleared their forests and pastures of toxic plants by hand, but for most occurrences of cattle death following plant ingestion was too low to justify such demanding management practice. *Samanea saman* and *Enterolobium cyclocarpum* seeds were widely mentioned as abortive, but less than expected, as the abortifacient properties of those seeds are part of the region's empirical knowledge about trees, according to talks with locals, specialists, MAG and SINAC employees, although little studied by literature. This is due to the fact that while cattle eat fallen fruits from those trees, few farmers had experienced cattle miscarriage following ingestion. As explained by two farmers who did experience said effects on their herd, – and subsequently avoided letting cattle browse in areas with high concentration of those species – those effects only appeared when excessive consumption happened, e.g. when a tree fell down, allowing cows to feed entirely on those seeds.

Table 5 - Harmful plants browsed by cattle and their alleged effect on cattle's health according to farmers. Number of time mentioned are reported for plants considered by farmers as eaten by cattle (E), avoided (A) or harmful to the animal (H).

Common name	Scientific name	Life form	Part	E	A	H	Alleged Effect
Josmeca/Ajillo	*Mansoa hymenaea*	Liana	Leaf	13		13	Spoils milk
Cenízaro	*Samanea saman*	Tree	Fruit	20		10	Abortive
Escoba morada	*Melochia pyramidata*	Grass	Leaf	8		8	Paralysis and death
Guanacaste	*Enterolobium cyclocarpum*	Tree	Fruit	23		5	Abortive
Zorrillo	*Petiveria alliacea*	Shrub	Leaf	3	1	3	Spoils milk
Piñuela	*Bromelia pinguin*	Bromeliaceae	Leaf	3	3	2	Obstructs digestive tract
Cinco Negritos	*Lantana camara*	Grass	Leaf	1		1	Toxic
Hoja Chigua	*Tetracera volubilis*	Liana	Leaf		2	1	Toxic
Jícaro	*Crescentia* sp.	Tree	Fruit	3		1	Obstructs digestive tract
Jobo	*Spondia mombin*	Tree	Fruit	6		1	Makes animal skinny
Mango	*Mangifera indica*	Tree	Fruit	7		1	Deadly if stuck in rumen

3.6 Limitations of this study

The round of interviews with farmers from Liberia county was initially designed to be a simple preliminary field reconnaissance to select farms for a research project aiming to study the impact of cattle on the ecological integrity and flammability of the forest. Facing the lack of literature available, we decided that a first step was to understand and describe the practice of dry season forest browsing before studying its impacts. As this study was mostly exploratory and used a preliminary survey more than a full-fledged research project, we are conscious that the data might lack the level of detail in farm management strategies required for an in-depth analysis of the economic and management constraints that affect farmers' decision to allow their cows to move into a forest patch to browse. We are also conscious of the limited statistical power provided by the number of interviews, when the sheer diversity of management strategies, farm structures and owners' socio-economic situations made building a coherent typology impossible without a much larger number of interviews. However, within the area covered (Figure 1), most of the existing farms were interviewed, and in this sense, this survey is closer to a census than a sample of farms in the surveyed area.

Despite those admitted flaws, we deemed the results of these interviews worth to be communicated, as an exploratory basis for further research, a first documentation of an ignored but locally important practice, as well as an exhortation to scientists and agronomists to consider forests as a part of a farm's management unit.

4 Conclusions

This exploratory study on the dry season forest browsing practice highlighted some important conclusions that will help understand the state of cattle ranching in the dry regions of Costa Rica and Central America, and the reasons for maintaining this practice in dry season farm management. Farmers of the Liberia county are facing a challenging situation as droughts and market pressure force them to find low-cost alternatives for cattle supplementation. Fire is a recurrent disturbance in farms, and although it used to be a management tool with pasture burns, it reportedly occurs mostly due to factors exogenous to farm management, and can be devastating for pastures and forests. Frequent cattle theft also obligates farmers to keep a tighter surveillance of their herd.

Browsing in forests is considered by farmers as a central part of summer supplementation for cattle and is used in the majority of interviewed farms. It remains a free form of supplementation which can improve cattle's ability to cope with the heat stress and lack of food experienced during the dry season. Dry season browsing was the most common type of supplementation in farms, mostly used in breeding and backgrounding ranches, although some dairy and beef fattening farms relied on this practice. No supplementation profiles could be found, and supplementation types were extremely variable from one farm to another. A more detailed research, with a larger number of farms and including supplementation type and quantity fed to each group of animals is needed to understand the relationship between forest browsing and other supplementation practices. However, this lack of success in grouping farms based on supplementation types highlights the complexity of farm management in Liberia county and in the dry regions of Central America in general, and the necessity for researchers to understand the situation of each farm based on their available resources and objectives without generalizing.

We, however, found some slight differences in supplementation fed to animals between extensive farms in the plains of the county, compared to farms on the slopes of the Volcanic Cordillera, which were more oriented towards subsistence agriculture. Farms in the mountains tended to use more fodder banks and silage than farms in the plains, possibly due to a common irrigation project, better soil conditions or a stronger presence of technical assistance entities such as the MAG. Browsing in forests was not associated with other types of supplementation.

The benefits of using forests for browsing listed by farmers were mostly related to animal well-being, and drawbacks associated to this practice were mostly the complications included in farm management. We conclude that the decision to use this practice or not could be due to the farmers' choice to favor an efficient farm management over animal welfare or vice versa, based on personal decision, familiarity with this practice or farm management constraints. Browsing in forests could lower supplementation costs, but increase other management costs. Due to the increased market pressure, farmers are intensifying the management of their farms. Forest browsing could be abandoned progressively to allow for more controlled practices, but more frequent droughts and increasing costs of supplementation could also lead to farmers relying more heavily on low-cost alternatives like this practice. In a conversation that took place at the end of the dry season with one farmer that had said initially that his goal was to improve his pastures to not depend on forest browsing, he admitted having realized how important the forest had been for his herd during the driest months and that his original statement had been unrealistic, given the increasing harshness of dry seasons. Another farmer had opened a patch of forest for cows for this particular summer. These experiences show that climate change can delay the transition of farms to more intensive practices, and that cattle browsing might stay a prominent way for farmers to deal with droughts in the region.

A topic which remained unclear was the ecological impact of cattle on forests, which was deemed positive by some farmers, and negative by others. Farmer's knowledge about behavior of cattle in forests and its impact on it is limited and often restricted to behavior observed at forests' edge or in pastures. This subject is also scarcely studied by scientific literature and needs an experimental ecological study to assess the impact of cattle on the structure, diversity and composition of a secondary dry forest, comparing forests in farms with secondary forests in neighboring protected areas, for example. If it is established that cattle do not affect forests in a significant way, this practice would be a great example of ecosystem-based adaptation and could be improved and integrated by local policy-makers into a local climate change mitigation plan for the years to come.

Would the impact of cattle be deemed negative for the ecosystem services provided by the forests, better dry-season preparedness needs to be encouraged by local entities by fostering other types of low-cost alternatives. The implementation of silage and fodder banks in all farms could help reduce farmers' dependence on forest, but the cost of establishing and maintaining a fodder bank can be prohibitive, in particular with beef cattle farms, which are dominant in this landscape and do not have the regular cash flow of a dairy farm. In any case, this practice is part of the cattle ranching culture of the study area and possibly all of Central America's dry areas, and should be considered in any further research regarding farm management or climate change adaptation.

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Chapter II: Comparison of composition and diversity of protected and unprotected seasonally dry tropical forests in the cattle ranching landscape of Liberia county, Guanacaste, Costa Rica.

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Abstract:

Seasonally Dry Tropical Forests (SDTFs) are growing back in Costa Rica after a heavy deforestation period, but only a small part of them is under formal conservation status. Most secondary forests in the Guanacaste province are located in cattle ranches, and are regularly disturbed by fire, as well as the local practice of using forests as a dry season supplementation for cattle, where cows browse in those forests and find shelter from the harsh dry season conditions. We sampled four secondary forests of the same age in farms under different levels of fire and browse pressure, and compared them to a forest in a protected area in terms of taxonomical composition and ecological diversity, at three different forest strata, using principally a cluster analysis, indicator species and a Non-Metric Multidimensional Scaling (NMDS).

Canopy composition and diversity did not differ between protected and unprotected forests, although fire was an influencing factor of canopy composition. Fire was also a discriminating factor for shrubs and saplings, showing different responses in composition to this disturbance, while browsing was the only discriminating factor between floor vegetation clusters. A Mantel correlation analysis returned a significant correlation between all forest strata, while the associations between clusters of the different strata of the forest were variable and not always significant, despite some strong trends. We conclude that, although fire and cattle browsing might have an effect on forests, these are not the main factors that influence forest composition and diversity in SDTFs of this landscape, which could be abiotic factors. Moreover, this study suggests that SDTFs are more resilient to cattle browsing than to fire. We suggest that this practice does not negatively impact forest integrity and can even preserve it, while maintaining local livelihoods. However, a more thorough experiment with a tighter control on all covariables is recommended to confirm these findings.

Key words: Anthropogenic effects on forests, Seasonally dry tropical forests, Ecological diversity, Composition, Cattle ranching, Climate change, Protected areas.

Resumen:

El bosque seco tropical (Bs-T) volvió a crecer en Costa Rica después de una intensa etapa de deforestación, pero solo una baja proporción de esos bosques se encuentra bajo un régimen de conservación formal. La mayoría de los Bs-T secundarios en Costa Rica se ubica en fincas ganaderas, donde es regularmente perturbado por incendios y por la presencia de ganado, que se lleva comúnmente al bosque para ramonear hojas y tolerar en la sombra el clima hostil de la temporada seca. En este estudio se muestreó tres estratos de vegetación (dosel, sotobosque y suelo) en cuatro parches de bosque secundario seco tropical en Liberia, Costa Rica, de edad similar y bajo diferentes niveles de disturbio debido al ramoneo del ganado e incendios. Estos se compararon con un bosque protegido en términos de diversidad ecológica y composición taxonómica. Se usaron principalmente un análisis de conglomerados, especies indicadoras y un Escalamiento No-Métrico Multidimensional (NMDS).

La composición y diversidad del dosel no difirió entre bosques protegidos y no protegidos, aunque el fuego haya sido un factor discriminante de la composición al nivel del sotobosque, mostrando especies indicadoras cuyas respuestas al disturbio varían en función de la ocurrencia de incendios. La composición de la vegetación del suelo varió en función al ramoneo. Un análisis de correlación de Mantel mostró una correlación significativa entre la composición de cada estrato, mientras las asociaciones entre conglomerados de los varios estratos del bosque eran variables y a veces no significativas, aunque se destacaron tendencias fuertes de asociación. Se concluye que, aunque el fuego y el ramoneo puedan tener un efecto en bosques secos, esos no son los factores de mayor influencia sobre su composición y diversidad. Esos factores pueden ser de origen abiótico. Además, los resultados sugieren que los Bs-T son más resilientes al ramoneo que a incendios. Sugerimos que esa práctica no tiene impactos mayores sobre la integridad ecológica del Bs-T, y podría hasta preservarlo, mientras apoya a los medios de vida locales. Sin embargo, un experimento más detallado y con un mayor control de covariables abióticas se recomienda para confirmar esas conclusiones.

Palabras claves: Efectos antropogénicos sobre el bosque, Bosque seco tropical, Diversidad ecológica, Composición, Ganadería, Cambio climático, Áreas protegidas.

1 Introduction

Seasonally dry tropical forests (SDTFs) are among the most threatened ecosystems on earth due mostly to agricultural conversion (Janzen 1988, Maass 1995, Sánchez-Azofeifa et al. 2005), but still they remain severely underrepresented internationally in conservation areas. In particular, Central American SDTFs are estimated to be under formal protection status at a proportion of 4.5% (de Albuquerque et al. 2015) to 5.7% (Miles et al. 2006) of their total extent. There are virtually no large extent of primary dry forests left in the sub-continent, and the World Wildlife Fund (WWF) describes the Central American SDTFs ecoregion defined by Olson et al. (2001) as “Patches scattered through Central America”. However, despite having been heavily deforested until the late 1970s by an increase in beef cattle production driven by international incentives, Central American SDTFs are growing back today (Arroyo-Mora et al. 2005, Aide et al. 2012, Redo et al. 2012), and particularly in the Guanacaste northwest region of Costa Rica (Arroyo-Mora et al. 2005), our study area. These dry forest ecosystems are hence conformed in majority of patches of secondary forest scattered through a landscape where the land belongs to private hands rather than government-owned protected areas. In Costa Rica, despite the strict legislation issued by the government via the 1996 Forest Law prohibiting land use change (Asamblea Legislativa de Costa Rica 1996), forests in private farms experience many disturbances on a regular basis, such as fire and cattle browsing (Janzen 1988, Stern et al. 2002, Quesada and Stoner 2004, Miles et al. 2006).

Cattle ranching is a common agricultural activity in the dry regions of Central America (FAO and ACF 2012), and pastures in Guanacaste correspond to more than 27% of the province's area (INEC 2014), while forests in those same farms represented 19% of Guanacaste territory, or 201,752 ha in 2014. Guanacaste province is considered as part of the Central American Dry Corridor, a climatic adaptation priority area which combines both climatic and socio-economic variables to locate areas of major climatic vulnerability for agricultural populations (FAO and ACF 2012, Quesada-Hernández et al. 2019). Cattle ranching is an activity less affected by seasonal droughts than crops, but prolonged droughts often can be disastrous for farmers, as many cows have died during the driest years (FAO 2017, Ravelo et al. 2016). As a response, farmers traditionally use patches of secondary forests in their farms to provide shade and supplementation to cattle during the driest months.

A set of semi-structured exploratory interviews was conducted by Godinot (unpublished data) to characterize the practice, where 70% of interviewed farmers were using forests in their farms as a refuge for cattle at some point in the dry season. The presence of cattle in forests has been widely criticized for affecting negatively understory regeneration (Stern et al. 2002, Quesada and Stoner 2004, Etchebarne and Brazeiro 2016) and forest structure (Belsky and Blumenthal 1997, Relva and Veblen 1998) by browsing and trampling, although not all sources agree on livestock impacts on sapling survival. Another disturbance common to cattle ranching landscapes is fire. Fire usually starts in pastures due to agricultural practices (Janzen 1988), by accident or criminal intent (Godinot, unpublished data), and spreads further into forests. Fire has been shown to affect plant communities by favoring fire-resistant species, characterized by thick bark and other fire-resistance traits (Poorter et al. 2014, Brando et al. 2012), or fire tolerant species that have strong resprouting or mending abilities (Otterstrom et al. 2006), in addition to killing smaller stems (Balch et al. 2013). Moreover, repeated fires, as it happens in many farms in the studied landscape, are known to have cumulative effects on tree mortality, as Cochrane and Schulze (1999) have shown.

Dry forests have long been underrepresented in scientific literature, even though the latest decades have shown an increased interest in this ecosystem, with many studies dissecting the taxonomic and functional composition of dry forests and their particular successional patterns characterized by the dominance of species with a resource conservative profile in early succession stages (Kalacska et al. 2004, Powers and Tiffin 2010, Gillespie et al. 2000, between others, and sources from Derroire et al. 2016).

However, most of the studies conducted in SDTFs took place in protected areas. In Costa Rican dry forests, most of those studies were conducted either in Palo Verde or Santa Rosa national parks. Experimental setups are easier to build within protected areas, where better monitoring and information are available than in private farms. However, despite the ability to study and control variables that have proved of importance in dry forests successional patterns, such as edaphic conditions (Powers et al. 2009) or land use history (Ferguson et al. 2003), it proves more difficult to understand the impact of browsing and fire disturbances that have affected secondary SDTFs on private land from the first year of succession onwards. We decided to study various scenarios of fire and cattle disturbance in several strata of secondary forests of the same age in private farms, to answer our first questions: What is the structure and composition of forests in private farms, and do they differ from the structure and composition of protected SDTFs?

Additionally, as we characterize several strata of dry forests in this study from the canopy stratum to the shrub, tree regeneration and grasses in the understory and forest floor level, we will try to understand the relationship between those strata, in search of a correlation between overstory vegetation types and understory vegetation. This relationship has been studied mostly in temperate and boreal forests (Strong 2011, Dölle et al. 2017) but little in the dry forests of Central America. Of course, the seed rain from established and remnant trees influence the woody regeneration (Derroire et al. 2016). Moreover, higher availability of light in most deciduous or less dense parts of forests can rise a denser and more diverse understory vegetation, although a closed canopy can facilitate seedling survival during the dry season (Gerhardt 1996, Maestre et al. 2009, Derroire et al. 2016). However, we want to assess if understory composition will be systematically dependent on the overstory vegetation of SDTFs, or rather to the disturbance factors that regularly affect the understory of those forests, as grazing and fire are disturbances that occur at floor level.

2 Materials and methods

2.1 Study area

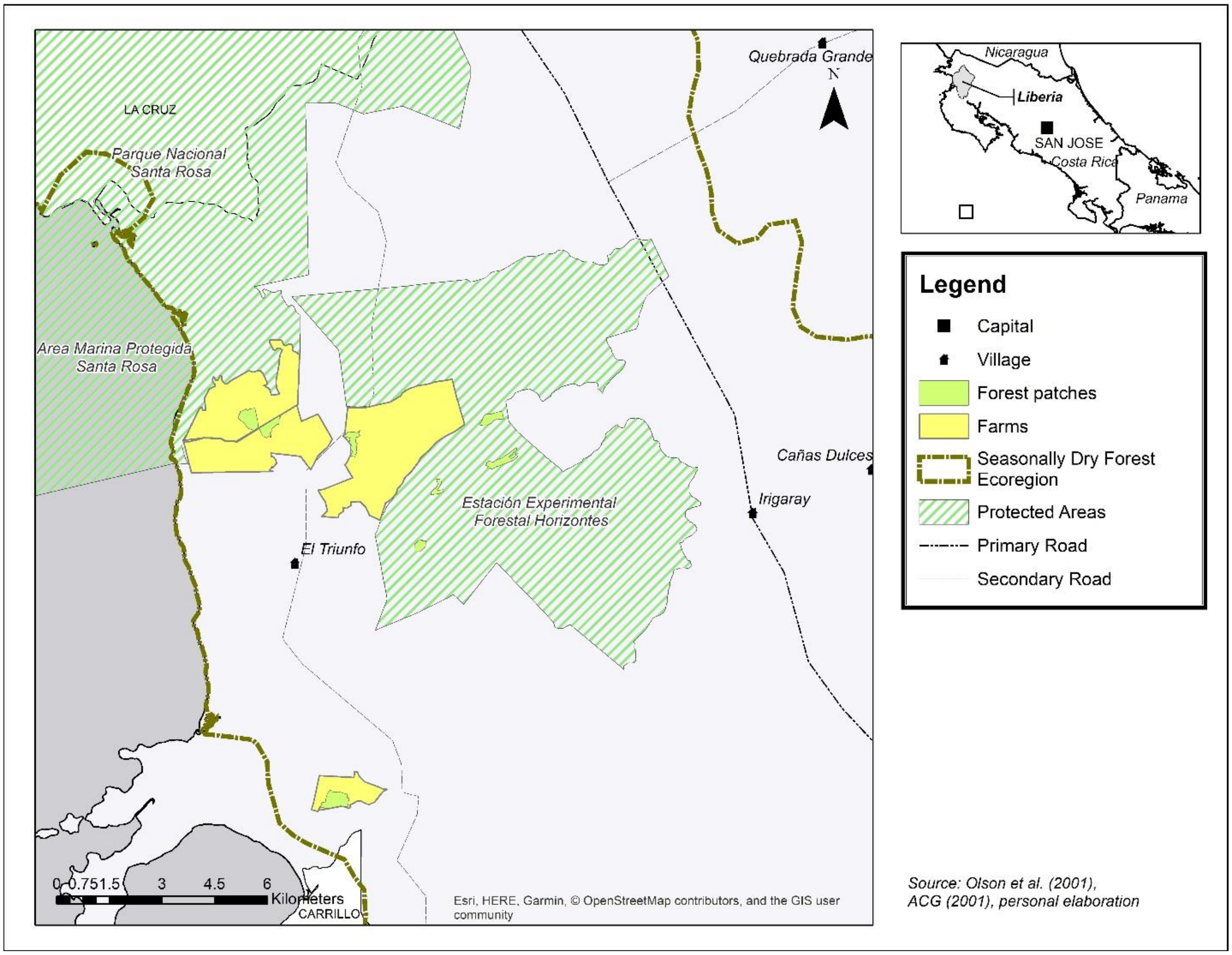
This study was carried out in the coastal plains of Liberia county, Guanacaste Province, Costa Rica, within the Horizontes Forest Experimental Station (Estación Experimental Forestal Horizontes, EEFH) and in four forests located in private cattle ranches in the landscape surrounding the EEFH (Figure 1). This landscape falls under the management of the Guanacaste Conservation Area (Área de Conservación Guanacaste, ACG), a Costa Rican conservation unit managed by the national Ministry of Environment (MINAE). The area is part of the Mesoamerican Dry Corridor, considered as a region where marked dry seasons and climate change threaten rural livelihoods and food security in areas depending on agriculture as the main source of income for a significant part of the population (FAO and ACF 2012). The EEFH is a 7,317-ha protected area with a unique status in Costa Rica, which allows forest management and sylvicultural experimentation within its boundaries to develop climate resilient solutions for a productive forest landscape rather than pure conservation. The landscape surrounding the EEFH is composed of extensive cattle ranches with small surfaces of crops, mostly rice, grains and sugar cane. Liberia County has a strongly seasonal climate, with a dry season (<100mm of precipitation per month) from December through May. Most of the county's lowlands have a tropical dry sub-humid climate with a period of light to moderate excess of precipitation. Average annual rainfall is 1,600mm, September being the rainiest month (346.3 mm) and January the driest (1.3 mm) (IMN 2013). Temperatures range from 19.2°C to 37.7°C in April and from 18.9°C to 33.4°C in November, with a relative humidity ranging from 60.5% to 86.1% in March and October respectively (IMN 2013).

Soils are mostly Inceptisols over a shallow layer of brittle volcanic rocks in the plains, among which are interspersed many patches of clayey deep soils with low water absorption capacity (Bergoeing 2017). Restoration initiatives on those clayey soils can be challenging as natural succession can be extremely slow or stopped altogether, leaving abandoned pastures in the first stage of succession for decades, as it is the case in several parts of the EEFH (Werden et al. 2018).

Forests of the area are mostly secondary seasonally dry tropical forests (SDTF), as defined by Sánchez-Azofeifa et al. (2005), with a high proportion of dry season-deciduous species and species of the Fabaceae family (Kalacska et al. 2004, Murphy and Lugo 1995), as it is the case for most of dry forests (Gei et al. 2018). These forests are for the most part heavily disturbed, as fire, agricultural clearings and habitat fragmentation in general are common in the region (Maass 1995, Miles et al. 2006) despite their illegality. Fire in particular has been a major concern for local conservation authorities, as pasture burns and voluntary or accidental wildfires have damaged thousands of hectares of forests in private farms as well as protected areas in the previous decades. As a response, most protected areas of the ACG rely on a small fire intervention unit which operates in those areas as well as in the surrounding farms, and promotes a limited or responsible use of fire in farm management. The 2019 dry season followed a rainy season that had been extremely low in precipitation, and was expected by local firemen to be particularly destructive. However, during this season no pasture or major forest fires were reported in the surrounding of the EEFH, showing the effectiveness of farmer outreach and early fire intervention in preventing fires.

A wave of deforestation took place in the province during the second half of the 20th century with the fast development of extensive cattle ranching, boosted by national development incentives and international meat prices (Arroyo-Mora et al. 2005). The Costa Rican golden age of beef cattle ended in the late 1970s, with a drop in meat prices and the end of those incentives, triggering a return of least productive cleared areas to forest (Arroyo-Mora et al. 2005, Redo et al. 2012). As a consequence, most dry forests today in Guanacaste province and Liberia county are relatively young secondary forests. The EEFH itself used to be a cattle farm until its donation to the state by one of the most extensive haciendas of the country, with most of its area being pastures, although some of the land was used for rice and sorghum crops (Cabrera 2007).

Figure 5 - Map of the study area



2.2 Data collection

Sampling was performed during the months of April and May 2019 in 29 plots of 400m^2 (20mx20m), distributed in 4 private farms and in the EEFH. Patches of secondary forests with a size ranging from 14.2 to 29.5 ha were selected based on a set of 43 interviews performed in the months of November and December 2018 to determine the age and use of forests in cattle ranches of the Liberia county (Godinot, unpublished data). The selection particularly focused on fire frequency and the use of forests by cattle during the dry season for browsing as a form of supplementation, which are the main disturbances occurring historically in this landscape. Forests in farms were selected following several scenarios of cattle and fire disturbance, ranging from the absence of fire or browsing from cattle (EEFH) to heavy browsing/no fire and medium browsing /frequent fires, shown by Table 1. Forests age ranged from 30 to 40 years, according to farm owners and confirmed by expert opinion. The selected definition of forests followed the one provided by the Costa Rican law (REDD/CCAD-SINAC 2015), with a few exceptions. Forests could not be plantations, and could not be cleared manually of understory vegetation, or planted with pastures.

Some parts of forests that had been heavily degraded by fire, according to farmers. These areas, although they were still considered as forests by farmers, were not retained for sampling, as those had a very low canopy cover and a dense floor vegetation made of spiny or stinging plants that made sampling unsafe and tedious, in addition to not being representative of a closed canopy multi-layer forest ecosystem. Hence, the sites sampled were "healthy" forests, with a relatively high tree cover, and it is important noting that the studied effect of fire on tree composition and diversity in unprotected forests, or the absence of it, is only valid for those forests that were burnt with relatively low frequencies, as fire had heavily degraded the areas not sampled. We visited 377 ha of forests during a preliminary sampling, and only 172 ha of those were deemed usable for sampling, which suggests that this study might underestimate the effects of fire on the Guanacaste dry forests landscape. Photographs of the types of vegetation avoided are available in Appendix II. Similarly, sampled patches of forests needed to have a certain size to be sampled, in order to avoid edge effect. As a consequence, selected patches of forests were located in extensive farms that were above the average farm size in Guanacaste, and browse effect might be underestimated compared to smaller farms where forests represent a smaller proportion of farmland, where forests experienced a heavier animal load than in those larger forests.

Table 6 - Sampled forests and available preliminary information obtained from farmers on fire frequency and browse intensity in the sampled forest patches. Fire frequency is shown as years that pass between two fire disturbances. Animal stocking is described as live weight (1 adult cow = 450kg) per hectare of forest sampled, weighted by the time passed in forests during the year.

Forest	Cattle live weight/ha/year (kg)	Average fire frequency (years, approx.)
EEFH	0	30
Castañeda	227	1-2
Roble	102	5
Laguna	625	10
Madroño	272	15

Although the information from Table 1 was valid for forests as a whole, most forest fires in the region tend to start from pastures (Janzen 1988), and plots located closer to pastures might have been more burnt than further plots in the same forest. Additionally, cattle repartition and effect on forest depends on cattle's supplementation, forest proximity from water, and many other variables (Roath and Krueger 1982). This happened in the case of the EEFH, which was theoretically not burnt since the instauration of its protected status in 1987, where trees in some plots showed burn scars and where deer browsed some plots to a small extent. As a result, these forest-wide numbers were indicative and not directly applicable to plots. Moreover, browsing by deer, tapir or other large herbivores was present in the EEFH and other forests, and the values reported in Table 1 do not account for browsing by those animals. Response variables of proportion of individuals showing fire damage and proportion of floor vegetation browsed by cattle were used as proxies to estimate fire and browsing intensity in plots.

Five plots were located in each of the private farms, in one forest patch per farm. Nine plots were located along four patches ranging from 6.3 to 16 ha distributed within the whole forested area of the EEFH. The EEFH was considered as one forest for the sake of this study. Plots were placed randomly within each forest, with only the following restrictions: plots were located at more than 30m from forest edge (including forest roads and trails) to avoid edge effect, on a slope no greater than 30% and at least at 50m from streams and rivers. Randomly placed plots were located at a minimum of 70m from each other. Three stratums of the forest were sampled. In each 20x20m plot, all trees ≥5cm diameter at breast height (dbh, 1.3 m) were sampled, as well as all lianas with a ≥2cm dbh (see Gerwing et al. 2006 for details about dbh measurements in lianas).

For each stem, collected variables were taxonomic identification, dbh, estimated height, estimated height of first furcation, alive/dead status, presence of damages between 0-2m height caused by fire or other reason, presence of resprouts, presence of branch tips between 0-2m height, signs of browsing on branches/resprouts. This stratum will be referred to in the document as the “Canopy” stratum. Two 5mx5m subplots were nested in each plot, located at Northeast and Southwest corners, where all woody plants with a height ≥150cm and < 5 cm dbh were sampled, including taxonomic identification, dbh, estimated height, estimated height of first furcation, alive/dead status, presence of branch tips between 0-2m height, signs of browse. This stratum was called the “shrubs and saplings” stratum. In the same plots, all plants between 30-150cm height were counted by species, counting as well the number of plants showing signs of browsing, and will be referred as the “Floor” stratum. Taxonomic identification was performed by the parataxonomists Roberto Espinoza, (Santa Rosa National Park, SINAC) and Vicente Herra (CATIE), via field observation and photographic identification.

2.3 Statistical analysis

All floristic analyses were performed with the software Qeco (Di Rienzo et al. 2010), and statistical comparisons were performed with the statistical software Infostat (Di Rienzo et al. 2018), using specialized community ecology libraries and functions in R (R Core Team 2018).

Forests were first compared using species rarefaction curves, then with a set of ecological diversity indexes on each sampled stratum, including Species density (S) Shannon (H’), Simpson (D), and Pielou’s Evenness (J’) Indexes. For the main plots of 400m2, the analysis was carried both with and without lianas with a simple analysis of variance (ANOVA) between forests, in order to assess the impact of liana diversity on general species diversity within each forest. A comparison of the proportion of liana species in species richness per forest was also performed with ANOVA. Fisher’s LSD test was used for comparisons of means. When comparing proportions (e.g. proportion of floor vegetation eaten by cattle), those were transformed to the arc sine of their square root to normalize their distribution and compare them via a classic ANOVA. However, original proportions were maintained in tables for a better interpretability.

A Non-Metric Multidimensional Scaling ordination (NMDS) was then performed on the species abundance matrix for the main 400m2 plots to better represent graphically the relationships between plots and the species that influenced the most the variability in plot taxonomic composition. The NMDS analysis was carried out in Qeco using the R MASS library (Venables and Ripley 2002) and the isoMDS function, with a maximum of 30 randomized starting points and the Bray-Curtis distance measure. Only species that had appeared in a minimum of two plots were used in this analysis, to avoid an over-contribution of rare species in plot distribution on the axis, as recommended by Greig-Smith (1983). The Hellinger transformation was applied to the data to lower the effect of low and high extremes in species abundance (Legendre and Gallagher 2001).

A cluster analysis using Ward minimum variance method and a Bray-Curtis distance measure was run to group plots by species composition (Legendre and Legendre 2006). The cluster analysis was carried out separately on all three sampled strata of the forest. For each 20 m x 20 m plot, the two 5 m x 5 m subplots were pooled together to represent a single 50m2 sampled area. Significance of all cluster groupings was tested via an analysis of similarities (ANOSIM), using the "anosim" function of the Vegan R package (Oksanen et al. 2018), with a Šidák correction for multiple comparisons. An ANOVA was carried out to compare mean values of diversity indices between clusters.

For each cluster and for each stratum separately, indicator species were identified via the 'multipatt' fuction of the Indicspecies R package (De Cáceres et al. 2010, based on the work of Dufrêne and Legendre (1997) integrated in Qeco). Indicator species were selected based on the criteria of their index value ($\geq$0.5), and the p-value associated to it ($p \leq 0.05$).

Finally, in order to determine if the forest understory vegetation depended on plot's canopy composition or on other factors, e.g. grazing intensity or fire frequency, a comparison was made between strata using a Mantel correlation test; for each forest stratum, a distance matrix was computed between plots, based on their coordinates in the spatial representation provided by the NMDS ordination. Distance matrices were then compared between strata to provide a correlation coefficient between matrices, establishing whether or not plots had consistently the same distances between each other, regardless of the forest stratum studied.

Clusters were then compared across strata using contingency tables. The goal of this comparison was to verify if a plot whose canopy composition belonged to any given cluster X, with Y indicator species, would consistently have an understory vegetation belonging to the same understory cluster X_2 with indicator species Y_2, or if the understory clusters were uncorrelated with canopy clusters. Contingency was tested with Pearson and Maximum likelihood Chi-squared tests, to measure the association error rate, with their respective p-values, as well as with Cramer and Pearson contingency coefficients, which are merely a transformation of the Chi-squared value into a 0 to 1 scale.

3 Results

3.1 General floristic composition

Within the total of 29 plots of 400m2 (total area 11,600m2), 1171 individuals were sampled for trees with ≥ 5cm dbh and lianas ≥2cm dbh, belonging to 126 species, of which 99 species (922 individuals) were dicot trees and 27 species (249 individuals) were lianas. Of those, only 10 individuals belonging to 5 unknown species remained unidentified, or less than 1% of all canopy stratum individuals. Two individuals of *Lysiloma* sp. were identified at genus level. Most common liana families were Bignoniaceae (52% of liana individuals/9 species), Malphigiaceae (18% of liana individuals/3 species) and Sapindaceae (10% of liana individuals/3 species). Tree families most represented were Fabaceae (17% of tree individuals/24 species), Malvaceae (16% of tree individuals/7 species) and Rubiaceae (8% of tree individuals/9 species). In the fifty-eight 25m2 subplots of each main plot (total area 1450 m^2), the total number of woody plants ≥150cm height and <5 cm dbh reached 629 individuals, including 386 individuals of trees and shrubs distributed in 77 species, and 243 lianas (35 species). Three species remained unidentified while two were identified at genus level, for a total of 2.5% of individuals not identified to species level. Liana families most encountered were Bignoniaceae (42% of liana individuals/11 species), Malphigiaceae (14% of liana individuals/2 species) and Sapindaceae (9% of liana individuals/2 species). Common trees and shrubs families encountered were Fabaceae (20% of tree individuals/10 species), Malvaceae (11% of individuals/7 species), and Salicaceae (10% of tree individuals/5 species, 4 of which belonging to the *Casearia* genus). The number of woody species as well as non-woody plants in the same subplots <150cm was 4454 individuals of 185 species, of which 11 species remained unidentified while 9 species were identified at genus level, representing 2.7% of all individuals lacking full identification. Most common families in this stratum were Poaceae (18% of individuals/2 species, only 1 individual not being *Lasciasis sorghoidea*), Bignoniaceae (16% of individuals/13 species of trees and lianas), Malphigiaceae and Acanthaceae (6.5% of individuals each, respectively 6 and 3 species).

The twenty most common canopy tree and liana species in the landscape are presented in Table 2.

Table 7 - Twenty most common canopy species in the studied landscape.

Taxon	Family	Life form	Number of individuals
Guazuma ulmifolia	Malvaceae	Tree	62
Luehea speciosa	Malvaceae	Tree	55
Cochlospermum vitifolium	Bixaceae	Tree	52
Cordia alliodora	Boraginaceae	Tree	48
Heteropterys laurifolia	Malpighiaceae	Liana	43
Casearia sylvestris	Salicaceae	Tree	42
Handroanthus ochraceus	Bignoniaceae	Tree	42
Melloa quadrivalvis	Bignoniaceae	Liana	41

Xylophragma seemannianum	Bignoniaceae	Liana	41
Chomelia spinosa	Rubiaceae	Tree	37
Pisonia macranthocarpa	Nyctaginaceae	Tree	31
Sebastiania pavoniana	Euphorbiaceae	Tree	22
Machaerium biovulatum	Fabaceae	Tree	22
Gliricidia sepium	Fabaceae	Tree	22
Stemmadenia pubescens	Apocynaceae	Tree	21
Spondias mombin	Anacardiaceae	Tree	21
Amphilophium paniculatum	Bignoniaceae	Liana	21
Ateleia herbert-smithii	Fabaceae/Papilionoideae	Tree	20
Cupania guatemalensis	Sapindaceae	Tree	20
Byrsonima crassifolia	Malpighiaceae	Tree	19

3.2 Secondary forest composition and its variation

3.2.1 Grouping of taxonomical composition types per stratum

The cluster analysis provided a 3-group classification for each stratum of the forest where it was performed. The dendrograms are presented in Annex 1. Indicator species for these clusters are listed in Table 3, and represented graphically in Figure 2. The genus of the two first indicator species per cluster were used to name those.

For the canopy stratum, the three identified cluster types were the following: Spondias-Casearia, Guazuma-Serjania and Chomelia-Heteropterys. An ANOSIM between clusters returned a significant Šidák corrected p-value of 0.003 for all comparisons. The Spondias-Casearia cluster was composed mostly of plots from the Castañeda and Rincón del Roble forests, while the Chomelia-Heteropterys cluster was made of plots from the Laguna and Madroño forests. The Guazuma-Serjania cluster was an intermediate cluster, with plots from most of forests. Plots from the EEFH were equally distributed in all clusters, with three plots per cluster.

The shrubs/saplings stratum was separated in three clusters, which composition was proved different by an ANOSIM returning corrected p-values of 0.003. The first cluster, Tetracera-Xylophragma, was the most common with 14 plots, belonging to forests but the Laguna patch. This cluster was composed mostly of plots from the EEFH (6) and the Rincón del Roble (5) forests. The Heteropterys-Vachellia cluster included 8 plots, 4 from Rincón del Roble and 4 from Laguna forests. The last cluster, Cupania-Casearia, was made of three EEFH plots, three Castañeda and one Laguna forests plots.

For the forest floor stratum, the cluster classification separated plots in three groups, given statistical significance by an ANOSIM that returned corrected p-values of 0.003, as for other strata of forests. The first cluster was highly dominated by the herbaceous species *Lasciasis sorghoidea*, which accounted for 39.3% of all individuals reported and was the only indicator species in this cluster. This group was composed of 11 plots from all forests, only one plot belonging to the Laguna forest. The second cluster, named Ruellia-Melanthera, was made of four plots from the Laguna forest, three plots from the Madroño forest and three plots from the Rincón del Roble forest. The last cluster, Cupania-Smilax, included mostly plots from the EEFH (6), as well as Castañeda forest (2).

3.2.2 Ordination of plots based on their taxonomical composition

The NMDS analysis was performed on both trees and lianas in the main plot for the Canopy stratum. It provided a three-dimensional representation which explained a total of 84% of total variation, of which 38%, 26% and 21% were represented by dimensions 1, 2 and 3, respectively. Reported stress value was 14.06. The graphic representation of plots and indicator species found by cluster and IVS analysis showed no clear distinction between sampled forests (Figure 2a, b). This was due to the wide range of composition covered by each of the studied forests, with many sites showing plots located across each dimension, reflecting a patchiness typical of seasonally dry forests and witnessed in the field. In particular, as hinted by the cluster analysis, plots located in the EEFH protected forest overlapped with all forests in private farms. There seemed to be a distinction between the group formed by Castañeda and Rincón del Roble forests and the group formed by Laguna and Madroño forest on Axis 1 and 2, but not on Axis 3. An ANOSIM between forests returned insignificant results, showing that community composition was more variable within forests than between them. Clusters were strongly separated by Axis 1 and 2, while Spondias-Casearia and Guazuma-Serjania clusters were almost completely overlapped on Axis 3. Indicator species and their respective code on the NMDS representation are the following, also summarized in Table 3:

Indicator species for the Spondias-Casearia cluster were Spondias mombin (Anacardiaceae, tree, SPOMOM), Casearia sylvestris (Salicaceae, tree or shrub, CASSYL) and Bixa urucurana (Bixaceae, small tree, BIXURU). The Guazuma-Serjania cluster was characterized by Guazuma ulmifolia (Malvaceae, tree, GUAULM), Serjania schiedeana (Sapindaceae, liana, SERSCH), Stemmadenia pubescens (Apocynaceae, tree, STEPUB) and Mansoa hymenaea (Bignoniaceae, liana, MANHYM). The Chomelia-Herteropterys cluster had the most distinctive species, with Chomelia spinosa (Rubiaceae, small tree, CHOSPI), Heteropterys laurifolia (Malpighiaceae, liana or shrub, HETLAU), Machaerium biovulatum (Fabaceae, tree, MACBIO), Luehea speciosa (Malvaceae, tree, LUESPE), Semialarium mexicanum (Celastraceae, small tree, SEMMEX), Diospyros salicifolia (Ebenaceae, small tree, DIOSAL), and Gliricidia sepium (Fabaceae, tree, GLISEP).

Another NMDS analysis on the shrubs/saplings stratum returned a three-dimensional solution explaining 70% of variance (28%, 23% and 19% for Axis 1,2 and 3 respectively), with a stress value of 17.49. Clusters were mostly separated by Axis 1 and 2, as the Heteropterys-Vachellia cluster was overlapping on both other clusters on Axis 3 (Figure 2c, d). Again, no clear separation between forests jumped to the eye. The Castañeda, Rincon del Roble and EEFH forests were negatively correlated with Axis 1 and separated from the Laguna forest, but the Madroño forest covered the whole range of the axis. Separation of forests on the other axis only differentiated the Madroño forest from the Castañeda forest, on Axis 2, while Axis 3 separated very little of the different forests.

Indicator species for the Tetracera-Xylophragma cluster were lianas: Xylophragma seemannianum (Bignoniaceae, XYLSEE) and Tetracera volubilis (Dilleniaceae, TETVOL). The Heteropterys-Vachellia cluster was mostly composed of Heteropterys laurifolia (Malpighiaceae, liana or shrub, HETLAU), Bonellia nervosa (Primulaceae, small tree, BONNER) and Vachellia collinsii (Fabaceae, small tree, VACCOL). The Cupania-Casearia cluster was characterized by Cupania guatemalensis (Sapindaceae, tree or shrub, CUPGUA), Casearia sylvestris (Salicaceae, tree or shrub, CASSYL) and Bixa urucurana (Bixaceae, small tree, BIXURU).

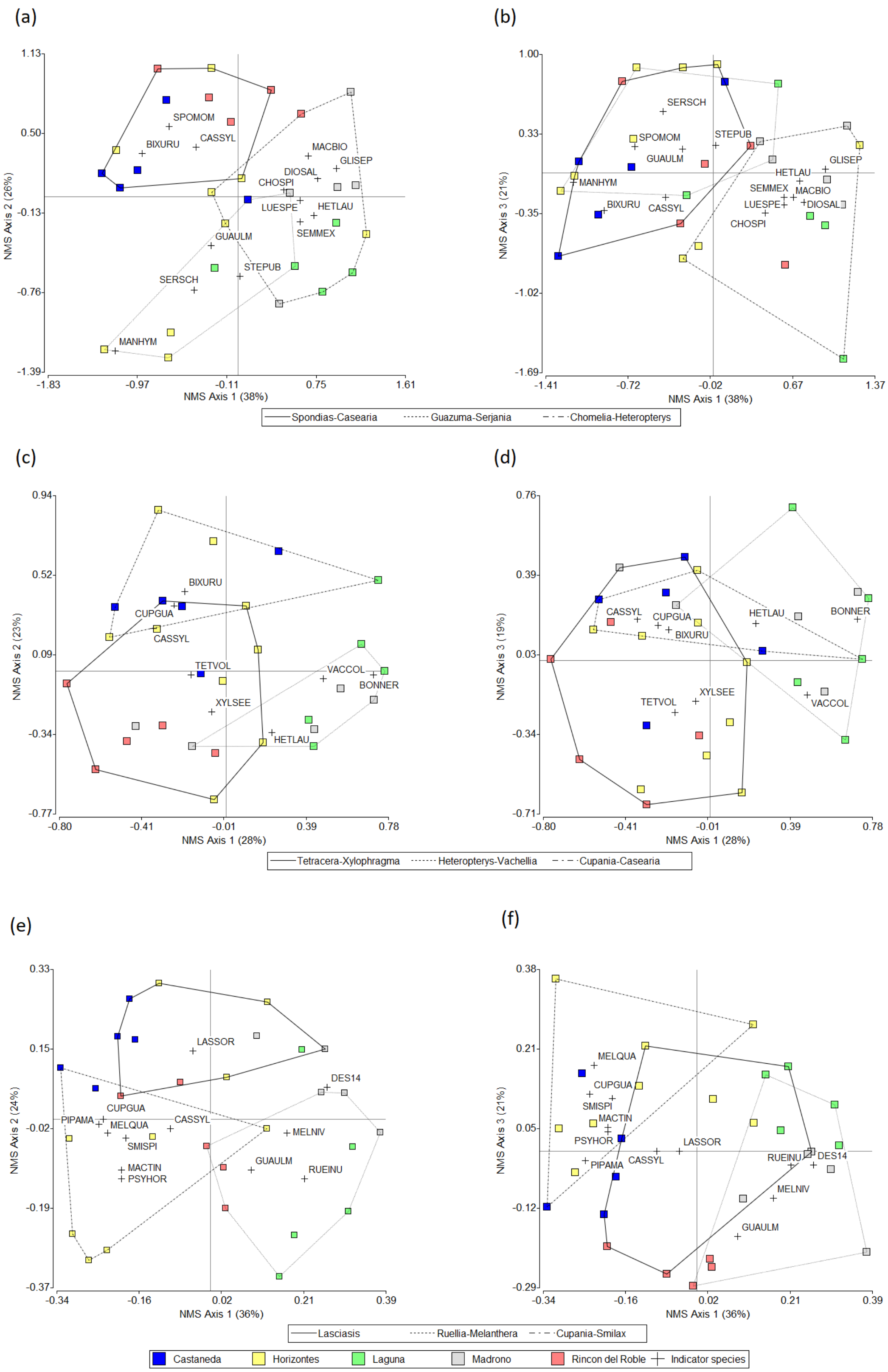
The NMDS analysis of the Floor stratum returned once again an ordination in 3 dimensions (Figure 2e, f), with a stress value of 14.52. Axis 1, 2 and 3 represented 36%, 24% and 21% of variation respectively, for a total of 81% of explained variability. The graphical representation allowed to distinguish a clearer separation between forests than in other forest strata, separating Laguna and Madroño forests from the bulk of the other forests along Axis 1, but not in other dimensions. Clusters were clearly separated on all three axis and did not overlap in a strong manner.

The Lasciasis cluster was widely dominated by Lasciasis sorghoidea, a wild grass (Poaceae, LASSOR) common to Central American dry forests. The Ruellia-Melanthera cluster was composed of Ruellia inundata (Acanthaceae, herbaceous, RUEINU), Melanthera nivea (Asteraceae, herbaceous, MELNIV), Guazuma ulmifolia (Malvaceae, tree, GUAULM) and an unknown shrub species from the Malvaceae family (DES14). Cupania guatemalensis (Sapindaceae, tree or shrub, CUPGUA), Smilax spinosa (Smilaceae, liana, SMISPI), Maclura tinctoria (Moraceae, tree, MACTIN), Piper amalago (Piperaceae, shrub, PIPAMA), Psychotria horizontalis (Rubiaceae, herbaceous, PSYHOR), Casearia sylvestris (Salicaceae, small tree or shrub, CASSYL) and Melloa quadrivalvis (Bignoniaceae, liana, MELQUA) were indicator species for the Cupania-Smilax cluster.

Table 8 - Summary table of indicator species per forest stratum and per cluster, with IVS index and related p-value

	SPECIES	IVS	P	SPECIES	IVS	P	SPECIES	IVS	P
	Cluster 1 (n = 11)			***Cluster 2 (n = 7)***			***Cluster 3 (n = 11)***		
CANOPY	*Spondias mombin*	0.92	<0.001	*Guazuma ulmifolia*	0.87	<0.001	*Chomelia spinosa*	0.84	<0.001
	Casearia sylvestris	0.66	0.05	*Serjania schiedeana*	0.72	0.01	*Heteropterys laurifolia*	0.81	<0.001
	Bixa urucurana	0.62	0.03	*Stemmadenia pubescens*	0.64	0.04	*Machaerium biovulatum*	0.76	<0.001
				Mansoa hymenaea	0.53	0.05	*Luehea speciosa*	0.71	0.03
							Semialarium mexicanum	0.7	0.02
							Diospyros salicifolia	0.69	0.01
							Gliricidia sepium	0.65	0.02
	Cluster A (n = 14)			***Cluster B (n = 8)***			***Cluster C (n = 7)***		
SHRUBS AND SAPLINGS	*Tetracera volubilis*	0.76	<0.001	*Heteropterys laurifolia*	0.86	<0.001	*Cupania guatemalensis*	0.9	<0.001
	Xylophragma seemannianum	0.75	0.01	*Vachellia collinsii*	0.77	0.01	*Casearia sylvestris*	0.7	0.01
				Bonellia nervosa	0.67	0.02	*Bixa urucurana*	0.65	0.01
	Cluster I (n = 11)			***Cluster II (n = 10)***			***Cluster III (n = 8)***		
FLOOR	*Lasciasis sorghoidea*	0.91	<0.001	Ruellia inundata	0.97	<0.001	Cupania guatemalensis	0.84	<0.001
				Melanthera nivea	0.93	<0.001	Smilax spinosa	0.73	0.02
				Guazuma ulmifolia	0.55	0.04	Maclura tinctoria	0.72	0.01
				Desc. 14	0.55	0.05	Piper amalago	0.7	0.02
							Psychotria horizontalis	0.65	0.01
							Casearia sylvestris	0.65	0.05
							Melloa quadrivalvis	0.63	0.04

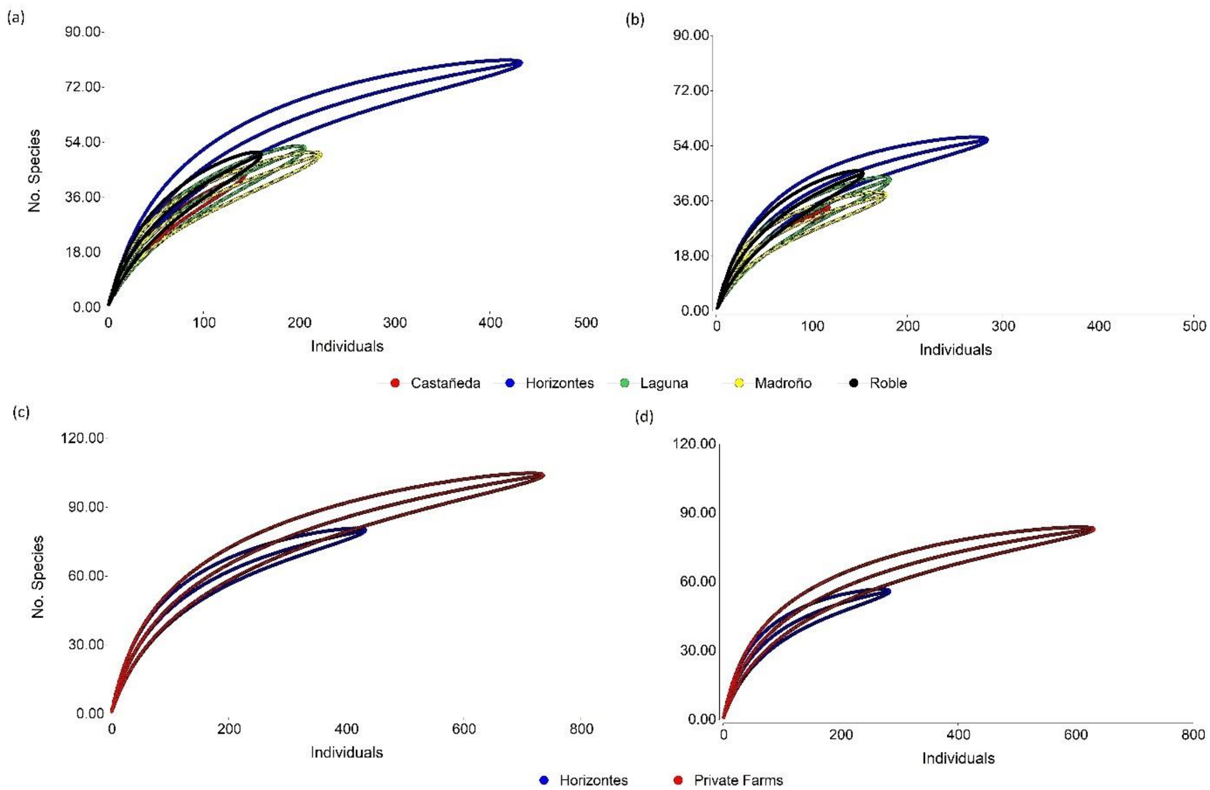
Figure 6 - NMDS Representation of plots, clusters and indicator species in a three-dimensional space, for Canopy stratum (a,b), Shrubs/saplings stratum (c,d) and Floor stratum (e,f). Cluster names are indicated under each stratum's graphs.



3.3 *Alpha diversity*

Species rarefaction curves for trees indicated that the EEFH showed a higher apparent diversity than unprotected forests, as represented in Figure 3. However, when grouping together unprotected forests in farms vs. the EEFH, the latter appeared less diverse. The removal of lianas reduced differences when keeping all forests separate (Fig. 2 a, b), but increased the difference between private forests as a group vs. EEFH forest (Fig. 2 c, d). However, none of those rarefaction curves reached an asymptote and must be interpreted with caution.

Figure 7 - Species rarefaction curves for canopy vegetation all forests (a and b) and unprotected forests in farms (c and d) with (a and c) and without lianas (b and d).



The difference in mean alpha diversity and density of individuals was not significant between forests (Table 4). Individuals density per plot was highly variable. After removing lianas from the count of individuals per plots, differences in average densities remained non-significant, but the EEFH experienced a 34.4% decrease in average density of individuals and a 28.6% decrease in species richness per plot, while other forests experienced a lesser decrease. Other diversity indexes experienced changes in minor proportions. No statistical significance for any index was either found when grouping all unprotected forests in a pool and comparing them to the EEFH.

Table 9 - Individuals density and diversity indices comparison between forests, with and without lianas

Composition	***Forest***	***N***	***Density (SE)***	***S (SE)***	***Evenness (SE)***	***Shannon (SE)***	***Simpson (SE)***
With lianas	Castañeda	5	29 (6.44)	15.8 (2.24)	0.92 (0.02)	2.51 (0.15)	0.89 (0.02)
	EEFH	9	48.11 (4.8)	18.22 (1.67)	0.89 (0.02)	2.55 (0.11)	0.89 (0.02)
	Laguna	5	41.4 (6.44)	17.4 (2.24)	0.85 (0.02)	2.43 (0.15)	0.86 (0.02)
	Madroño	5	44.6 (6.44)	18.2 (2.24)	0.91 (0.02)	2.63 (0.15)	0.91 (0.02)
	Roble	5	32.2 (6.44)	16.4 (2.24)	0.92 (0.02)	2.55 (0.15)	0.9 (0.02)
p-value (ANOVA)			*0.1349*	*0.8943*	*0.2474*	*0.9109*	*0.6411*
Without lianas	Castañeda	5	23.6 (4.49)	11.6 (1.83)	0.92 (0.02)	2.19 (0.16)	0.86 (0.03)
	EEFH	9	31.56 (3.35)	13 (1.36)	0.9 (0.02)	2.25 (0.12)	0.86 (0.02)
	Laguna	5	36.4 (4.49)	14.8 (1.83)	0.85 (0.02)	2.28 (0.16)	0.84 (0.03)
	Madroño	5	35.6 (4.49)	14 (1.83)	0.91 (0.02)	2.38 (0.16)	0.88 (0.03)
	Roble	5	30.8 (4.49)	15.2 (1.83)	0.92 (0.02)	2.48 (0.16)	0.89 (0.03)
p-value (ANOVA)			*0.3036*	*0.6264*	*0.1506*	*0.7042*	*0.6287*

No mean comparison was done on any of the variables, as the general p-value for each ANOVA indicated no effect of forest on the variables. Hence, no letter was attributed to reported values.

Lianas contributed the most to the EEFH species richness, while representing a minority within the total diversity and number of individuals of other forests like Rincón del Roble, as shown in Table 5. Liana species density (Liana S), proportion of species richness per plot (Liana P) and number of lianas as a proportion of the total number of individuals per plot (Liana P-ind) ranked consistently highest in the EEFH. Liana P-ind was highest in the EEFH, followed by the Madroño and Castañeda forests, which had more liana individuals than the Rincón del Roble forest. The Laguna forest was similar to both Madroño, Castañeda and Rincó del Roble forests. Liana species density S was highest in EEFH, with only Castañeda and Madroño forests reaching a similar species density. Liana P was highest in the EEFH and Castañeda forest, while the Madroño forest was similar but also related to Laguna forest, which had a significantly lesser proportion of liana species in its plots. Rincón del Roble was consistently the forest with lowest values.

Table 10 - Comparison of the effect of liana diversity on total diversity in plots for all forests, based on total liana species density(Liana S), proportion of liana diversity in species pool (Liana P) and proportion of lianas as part of the total number of individuals (Liana P-ind), for canopy individuals.

Forest	**Liana S (SE)**	**Liana P (SE)**	**Liana P-ind (SE)**	**Total Ind (SE)**
Castañeda	4.2 (0.83)$_{ab}$	0.28 (0.04)$_{a}$	0.19 (0.04)$_{b}$	29 (6.44)
EEFH	5.11 (0.61)$_{a}$	0.28 (0.03)$_{a}$	0.33 (0.03)$_{a}$	48.11 (4.8)
Laguna	2.6 (0.83)$_{bc}$	0.13 (0.04)$_{bc}$	0.11 (0.04)$_{bc}$	41.4 (6.44)
Madroño	4 (0.83)$_{ab}$	0.22 (0.04)$_{ab}$	0.20 (0.04)$_{b}$	44.6 (6.44)
Roble	1.2 (0.83)$_{c}$	0.07 (0.04)$_{c}$	0.04 (0.04)$_{c}$	32.2 (6.44)
p-value	*0.0105*	*0.0016*	*<0.0001*	*0.1349*

Values with a shared letter in the same column are not statistically different (p>0.05).

A run of diversity indexes on Canopy clusters returned significant results on individual density per plot. Proportion of individuals with burn damages was very significant for this forest stratum, the Spondias-Casearia cluster being the most burnt, including mostly plots from forests with high fire frequency, despite including three plots from the EEFH, of which two however had stems with burn damages, although to a lower extent.

In comparing clusters from the shrubs/saplings stratum, the Tetracera-Xylophragma cluster was consistently the highest ranked cluster in terms of diversity indexes, as shown in Table 6. Heteropterys-Vachellia and Cupania-Casearia clusters only differed in terms of Evenness, where composition of Heteropterys-Vachellia cluster was significantly less equally distributed in plots than other clusters. Burnt trees in plots showed significant differences for this stratum, although the separation between clusters was not clear, and percentage of floor vegetation eaten was not a strong separator between clusters at this level.

Comparison of diversity indexes for all plants <150cm height in plots clustered in the three goups returned non-significant differences in density of individuals, species richness and Shannon index. The Lasciasis cluster had a less even composition than other clusters, with significantly lower Simpson and Evenness indexes, which was due to the strong dominance of *Lasciasis sorghoidea.* At this level of the forest, only cattle disturbance was a significant separator, with the cluster Ruellia-Melanthera being the most browsed cluster. This cluster displayed *Guazuma ulmifolia* regeneration as an indicator species, whose fruit is known to be favored by cattle as a dry season source of energy and heavily dispersed by it via manure (Janzen 1982).

Table 11 - Diversity indexes, density of individuals, number of adult stems with signs of burn (Burnt) and proportion of floor vegetation eaten by cattle (Eaten) comparison for all clusters.

		n	Density (SE)	S (SE)	Evenness (SE)	Shannon (SE)	Simpson (SE)	Burnt (SE)	Eaten (SE)
Canopy	Spondias-Casearia	11	32.45 (3.67)b	16.55 (1.40)a	0.92 (0.02)a	2.56 (0.10)a	0.90 (0.02)a	0.47 (0.07)a	0.45 (0.07)a
	Guazuma-Serjania	7	33.14 (4.60)b	15.71 (1.76)a	0.91 (0.02)ab	2.47 (0.12)a	0.89 (0.02)a	0.19 (0.09)b	0.45 (0.07)a
	Chomelia-Heteropterys	11	52.73 (3.67)a	19.18 (1.40)a	0.87 (0.02)b	2.56 (0.10)a	0.89 (0.02)a	0.06 (0.07)b	0.33 (0.09)a
	p-value		*0.0009*	*0.2536*	*0.1091*	*0.8035*	*0.8268*	*0.0009*	*0.5388*
Shrubs/ Saplings	Tetracera-Xylophragma	14	24.79 (2.74)a	13.64 (0.93)a	0.94 (0.02)a	2.43 (0.11)a	0.90 (0.03)a	0.36 (0.07)a	0.36 (0.05)b
	Heteropterys-Vachellia	8	20.13 (3.63)a	8.75 (1.23)b	0.81 (0.03)b	1.69 (0.15)b	0.71 (0.03)b	0.02 (0.09)b	0.56 (0.08)a
	Cupania-Casearia	7	17.29 (3.88)a	9.00 (1.32)b	0.90 (0.03)a	1.91 (0.16)b	0.80 (0.04)b	0.26 (0.10)ab	0.38 (0.08)ab
	p-value		*0.2705*	*0.0042*	*0.0068*	*0.0009*	*0.0012*	*0.0233*	*0.1218*
Floor	Lasciasis	11	160.18 (14.64)a	28.18 (3.02)a	0.69 (0.03)b	2.27 (0.14)a	0.79 (0.03)b	0.27 (0.09)a	0.51 (0.05)a
	Ruellia-Melanthera	10	152.50 (17.16)a	29.10 (3.16)a	0.80 (0.03)a	2.66 (0.15)a	0.88 (0.03)a	0.24 (0.09)a	0.54 (0.05)a
	Cupania-Smilax	8	147.20 (15.35)a	29.75 (3.54)a	0.81 (0.03)a	2.71 (0.17)a	0.89 (0.03)a	0.22 (0.10)a	0.16 (0.06)b
	p-value		*0.828*	*0.9428*	*0.0103*	*0.0976*	*0.0222*	*0.9473*	*0.0001*

Values with a shared letter in the same column and stratum are not statistically different (p>0.05).

3.4 *Correlations between forest strata*

Mantel correlations between distance matrices returned highly significant results, with the highest correlation reaching a 38% (p<0.0001) between canopy and floor vegetation composition (Table 7). Canopy and shrubs/saplings vegetation were also correlated at 22% (p=0.001), as well as understory vs. forest floor vegetation (31% correlation, p=0.001).

Table 12 - Mantel correlations between distance matrices between plots calculated for each forest stratum NMDS axis coordinates. The single asterisk represents p=0.001 and the double asterisk p<0.0001.

Mantel Correlation	Canopy	Shrubs/Saplings
Canopy	1	
Shrubs/saplings	0.22*	1
Floor	0.38**	0.31*

Correlation between vegetation in all strata was relatively strong, but did not provide further description of the taxonomic associations between canopy, shrubs/saplings and floor strata. We used contingency tables between clusters previously established per stratum to determine a more direct correlation between the respective indicator species belonging to clusters of each forest stratum. Refer to Table 3 for indicator species per cluster. A synthesis of cluster attribution per forest represented in Table 11 allows identification of the most common cluster combination between forest strata and to distinguish patterns of composition.

The first contingency table comparing canopy and understory strata showed significant results, with a Pearson $\chi 2$ value of 12.47 (p=0.0142) and a contingency coefficient of 0.55 (Table 8). Eight of eleven plots (73%) from Canopy Spondias-Casearia cluster had an understory composition belonging to shrub/saplings Tetracera-Xylophragma cluster, while the rest belonged to the Cupania-Casearia cluster. Four of seven plots in Canopy Guazuma-Serjania cluster belonged to the shrub/sapling Tetracera-Xylophragma cluster as well, but the classification error was high. Finally, seven of eleven plots (64%) in the Canopy Chomelia-Heteropterys cluster belonged to understory Cluster Heteropterys-Vachellia, while the four leftover plots were distributed equally between Tetracera-Xylophragma and Cupania-Casearia clusters. Shrub/saplings cluster Cupania-Casearia was found in all canopy clusters.

Table 13a and b - Contingency table between clusters of canopy and understory vegetation strata, with significance indicators.

Indicator	Value	df	p
Chi Squared Pearson	12.47	4	0.0142
Chi Squared MV-G2	14.66	4	0.0055
Conting. Coef.Cramer	0.38		
Conting. Coef. Pearson	0.55		

Shrub-saplings/Canopy	Spondias-Casearia	Guazuma-Serjania	Chomelia-Heteropterys	Total
Tetracera-Xylophragma	0.73 (8)	0.57 (4)	0.18 (2)	0.48 (14)
Heteropterys-Vachellia	0.00	0.14 (1)	0.64 (7)	0.28 (8)
Cupania-Casearia	0.27 (3)	0.29 (2)	0.18 (2)	0.24 (7)
Total	1.00 (11)	1.00 (7)	1.00 (11)	1.00 (29)

Association between understory and floor vegetation clusters returned insignificant results (Table 9), contrasting with the Mantel correlations shown in table 8. Pearson's $\chi 2$ was 8.40, with a p-value of 0.0779, despite some strong contingencies between Canopy cluster Spondias-Casearia and Floor cluster Lasciasis (64%) and Canopy cluster Guazuma-Serjania and Floor cluster Cupania-Smilax (57%).

Table 14a and b - Contingency table between clusters of canopy and floor vegetation strata, with significance indicators.

Indicator	Value	df	p
Chi Squared Pearson	8.40	4	0.0779
Chi Squared MV-G2	7.99	4	0.0918
Conting. Coef.Cramer	0.31		
Conting. Coef. Pearson	0.47		

Floor/Canopy	Spondias-Casearia	Guazuma-Serjania	Chomelia-Heteropterys	Total
Lasciasis	0.64 (7)	0.14 (1)	0.27 (3)	0.38 (11)
Ruellia-Melanthera	0.18 (2)	0.29 (2)	0.55 (6)	0.34 (10)
Cupania-Smilax	0.18 (2)	0.57 (4)	0.18 (2)	0.28 (8)
Total	1.00 (11)	1.00 (7)	1.00 (11)	1.00 (29)

The correlation between understory and floor vegetation clusters was significant with a Pearson's $\chi 2$ value of 10.81 and p=0.0288, with a Pearson contingency coefficient of 0.52. If association between clusters was not random, it was not consistent either, with unclear patterns of association (see Table 10). The strongest association was between shrubs/saplings cluster Heteropterys-Vachellia and floor cluster Ruellia-Melanthera, with six plots of eight (75%) belonging to both clusters, followed by the association between clusters Cupania-Casearia and Floor cluster Cupania-Smilax, with four of seven plots (57%) associated. All other combinations had a strong classification error.

Table 15a and b - Contingency table between clusters of understory and floor vegetation strata, with significance indicators.

Indicator	Valor	df	p
Chi Cuadrado Pearson	10.81	4	0.0288
Chi Cuadrado MV-G2	11.88	4	0.0183
Coef.Conting.Cramer	0.35		
Coef.Conting.Pearson	0.52		

Floor/Shrubs-Saplings	Tetracera-Xylophragma	Heteropterys-Vachellia	Cupania-Casearia	Total
Lasciasis	0.50 (7)	0.25 (2)	0.29 (2)	0.38 (11)
Ruellia-Melanthera	0.21 (3)	0.75 (6)	0.14 (1)	0.34 (10)
Cupania-Smilax	0.29 (4)	0.00	0.57 (4)	0.28 (8)
Total	1.00 (14)	1.00 (8)	1.00 (7)	1.00 (9)

Table 16a and b - Cluster attribution to plots in forests for each forest stratum. Numbers represent the clusters, colors were chosen arbitrarily to better represent correspondence between clusters. Refer to table 11b for the correspondence between number and cluster name.

Clusters	Castañeda Burnt/Browsed					EEFH Little burnt/No browse									Laguna Little burnt/heavily browsed					Madroño Little burnt/Browsed					Roble Burnt - Browsed				
Canopy	1	1	1	2	1	2	2	3	1	2	3	3	1	1	3	2	3	3	2	3	3	3	3	2	1	1	3	1	1
Shrubs/saplings	1	1	3	3	3	1	1	1	1	1	3	3	1	3	2	3	2	2	2	2	2	2	2	1	1	1	1	1	1
Floor	1	1	1	3	3	3	3	1	3	3	3	3	1	1	2	2	1	2	2	2	1	2	2	1	1	2	2	1	2

Clusters	1	2	3
Canopy	Spondias-Casearia	Guazuma-Serjania	Chomelia-Heteropterys
Shrubs/saplings	Tetracera-Xylophragma	Heteropterys-Vachellia	Cupania-Casearia
Floor	Lasciasis	Ruellia-Melanthera	Cupania-Smilax

4 Discussion

4.1 Composition

General forest composition was dominated by trees of the Fabaceae family, in accordance with most research performed on SDTFs (Gillespie et al. 2000, Gei et al. 2018), which had a lower number of individuals for each species than Malvaceae, with a certain dominance however of the *Lonchocarpus* genus, *Gliricidia sepium* and *Machaerium biovulatum*. The most common tree found in the landscape was *Guazuma ulmifolia*, known for being dispersed by cattle and a usual tree in pastures. As all studied forests were previously pastures, it is not surprising that this tree species was dominant in its mature state, even in the EEFH protected forest. The study of liana composition revealed a strong dominance of Bignoniaceae. This pattern of tree and liana composition was reproduced in other strata of the forest, with the exception of the Salicaceae family inclusion in the understory, of which most individuals belonged to the *Casearia* genus, and in particular *Casearia sylvestris*. This species is known for being a strong root resprouter (Imatomi et al. 2014) and was never browsed by cattle, which provides a strong advantage to face the fire and browsing disturbances in SDTFs. At the floor vegetation level, the grass species *Lasciasis sorghoidea* was the most found, and was steadily browsed by cattle, as well as by other herbivores in the EEFH.

The NDMS analysis revealed little differences in composition between the EEFH and other forests, as plots from the EEFH covered the whole range of composition for all dimensions of the canopy stratum. Plots from the EEFH were also well distributed within the ordinations for Shrubs/saplings and Floor strata, although there was more apparent correspondence between the EEFH forest and the Rincón del Roble and Castañeda forest. This result suggests that, at least for canopy vegetation, the most studied by literature (see Chapman and Chapman 1990, Kalacska et al. 2004, Powers et al. 2009, for example), forests in unprotected areas are comparable in composition with protected forests in this landscape, which suggests that the frequent disturbances of browsing and fire do not have a major impact on Costa Rican SDTFs composition, strengthening the results of research led in protected SDTFs. However, a more intensive sampling is recommended to confirm this finding.

The cluster analysis at canopy level returned three groups, which were distinguished by the number of trees with burn scars in a plot. The most burnt cluster was characterized by *Casearia sylvestris* (Salicaceae) and *Bixa urucurana* (Bixaceae), the latter having the same resprouting ability and low palatability as the first, as well as *Spondias mombin* (Anacardiaceae), a tree species with thick bark, which according to Pinard and Huffman (1997) is extremely resistant to fire. Many individuals of this species showed char from recent fires, but were not damaged at all by it. This composition suggests that fire indeed had an effect on the composition of some plots, that were mostly found in burnt plots, including some in the EEFH. The Guazuma-Serjania cluster was found at almost all sites, and the dominance of *Guazuma ulmifolia* might be an indicator of the previous cattle ranching land use. An interesting contrast with this species' dominance in the higher stratum of the forest is the small number of saplings and seedlings found from this species, which were located in the most browsed plots. This could indicate that, although early succession from a pasture land use in all forests favored the presence of *G. ulmifolia*, only a continuous use by cattle, which favors the dispersion of *G. ulmifolia* seeds, would allow the continuity of this dominance in time. Canopy cluster Chomelia-Heteropterys was found almost exclusively in the least burnt forests, and had the highest number of indicator species, which shows that this cluster had many species that were proper to it and were almost not found in more burnt forests, possibly due to a lack of resistance to fire, although no literature was found regarding the survival strategies of those species.

The shrubs/saplings stratum had indicator species that had developed some kind of resistance strategy to cattle and fire. There is no fire resistance strategy known to tropical liana species in general or to the lianas *Tetracera volubilis* and *Xylophragma semannianum*, which were the two indicator species for the most burnt cluster at this level. However, research has shown that disturbances favored the survival of liana seedlings, although large lianas were more typical of low-disturbance environments (Balch et al. 2011, Pinard et al. 1999, Campbell et al. 2018, Umaña et al. 2019), which can be an explanation for the dominance of liana species in the understory of those plots. The Cupania-Casearia cluster indicator species were all observed with green leaves during the dry season, were left untouched by cattle and were root resprouters with multiple stems, although those species, undisturbed, were seen growing as a tall single-stemmed individual. Their presence in this intermediate burn cluster could explain how an intermediate disturbance favors the development of those species that do not experience cattle herbivory.

The Heteropterys-Vachellia cluster was the least burnt, and was dominated by deciduous liana species *Heteropterys laurifolia*, the inverse phenology (growing leaves during the dry season) shrub species *Bonellia nervosa*, as well as the myrmecophile species *Vachellia collinsii* (Fabaceae-mimosoideae), which deserves a special mention: this species hosts *Pseudomyrmex* ants, which protect the tree against competition ad herbivores in exchange for food provided by the plant's Beltian bodies and the shelter of their hollow thorns (Janzen 1967). Ants remove all the vegetation surrounding the tree in a perfect circle, which in early succession is a strong advantage against fire. However, Janzen (1967) notes that in a more mature forest, where litter comes from deciduous trees above, ants cannot remove all branches and leaf litter from those trees, and a fire can easily kill the stem. The resulting potential inability for this species to cope with fire in a forest might explain its absence in other more burnt clusters.

It is interesting to note that none of those indicator species were browsed by cattle, possibly due to deciduousness, thorns, tough or unpalatable/toxic leaves, be it in the protected forest of the EEFH or the browsed forests in farms. This could be due to several reasons that are left to determine, but the EEFH forest is in direct contact with forests in farms that can be influenced by cattle, and it has been shown that secondary succession is greatly influenced by the surrounding matrix by seed dispersal (Santiago-García et al. 2019, van Breugel et al. 2019). In addition, plants that dominate forest understory in SDTFs have developed insect herbivores resistance or avoidance mechanisms to respond to the strong insect herbivory typical to SDTFs (Coley and Barone 1996, Janzen 1981), which could also provide resistance to large mammal herbivory, such as tough leaves or a high concentration of secondary metabolites (Coley et al. 1985, Pérez-Harguindeguy et al. 2013). Janzen (1982) also notes that SDTF composition could have been influenced by now extinct large herbivore species.

At floor level, the Lasciasis and Ruellia-Melanthera clusters, dominated respectively by the Poaceae *Lasciasis sorghoidea* and broad-leaved herbs, were the most browsed by cattle. It is hard to determine the causality of this relationship, i.e. if cattle browsed those plots more because those plants were present or if those plants were the only ones able to withstand the animal loading. However, the Cupania-Smilax cluster can offer the beginning of an answer to this question. This vegetation type was almost exclusively found in the EEFH station, where some species such as *Piper amalago* (Piperaceae, shrub or small tree) were browsed by deer, under low intensity. This vegetation type was found in two plots of the Castañeda burnt and browsed forest, where it was also browsed by cattle to the same extent as plots in other clusters. This could indicate that high intensity cattle browsing on the long term could possibly suppress this vegetation type. Fire was not a discriminating factor between clusters, maybe due to the shorter life cycle of herbaceous vegetation.

4.2 Diversity

No difference in diversity indexes was found at canopy level, between each forest or between the EEFH vs. other sites. However, the proportion of adult lianas within each forest varied greatly, and did not follow the fire intensity pattern. The EEFH forest ranked first in liana species density per plot, proportion of lianas in species density per plot, and proportion of lianas in the number of individuals per plot. However, the two most burnt forests of Rincón del Roble and Castañeda showed inverse patterns. The Castañeda site, the most frequently burnt according to farmers, was closer to the EEFH forest in terms of liana abundance and diversity, while the Rincón del Roble forest had almost no adult lianas. This might be due to the intensity of fire rather than fire frequency, or it might mean that neither fire, browsing nor the protected/unprotected status were significant factors influencing the presence of lianas.

When grouped in composition clusters, the only significantly different indicators for canopy clusters were density of individuals and number of stems presenting damages due to fire, the densest cluster being the least burnt. However, the Guazuma-Serjania cluster, equally least burnt, had significantly less individuals per plot, which suggests that fire was possibly not the only factor influencing the density of individuals.

Clusters in the shrubs/saplings stratum were differentiated by species density, Shannon index, Simpson index, Evenness index and proportion of canopy individuals with signs of burns. The most burnt cluster, Tetracera-Xylophragma, had the highest species density and Shannon index, as well as the lowest Simpson dominance index. Species evenness was lowest in the

Heteropterys-Vachellia cluster, the least burnt. This pattern is in concordance with the intermediate disturbance hypothesis, which states that a disturbance in forests "resets" the competition process of this forest, allowing new species to grow in the disturbed areas without being smothered by dominant vegetation (Connell 1978)**.** However, this evenness tends to be short-lived, as species with competitive advantages will progressively gain back their dominance in the disturbed area (Connell 1978). A study of post-fire understory composition and diversity recovery in SDTFs does not exist yet to the extent of our knowledge, and it is needed.

Clusters of the floor stratum were only different in terms of dominance, evenness and browsing, where the Lasciasis cluster was strongly dominated by the Poaceae *Lasciasis sorghoidea.* Poaceae have a strong capacity to tolerate herbivory and were found in the most browsed cluster, along with the Ruellia-Melanthera cluster, which main two indicator species *Ruellia inundata* (Acanthaceae) and *Melanthera nivea* (Asteraceae) were heavily browsed.

4.3 Correlation between forest strata

The Mantel correlation test highlighted a relatively strong correlation between all forest strata, the highest being a 0.38 correlation between Canopy and Floor vegetation. However, the contingency tables testing for association between clusters did not return a significant relationship between these two strata (p=0.0779). This is not a real contradiction, as clusters simplify forest composition into analyzable categories that do not represent exactly the composition gradient found in plots. The Mantel correlation test was also based on distance matrices provided by the NMDS analysis that did not represent 100% of the variability. The study of vegetation requires simplifications, and each of those tests provided interesting insights on the structural dynamics of SDTFs.

The Mantel correlation test highlights that there is a strong influence of the dominant canopy vegetation on other strata studied. We can hence expect to find a certain type of floor vegetation under a certain type of canopy composition. As canopy composition did not differ significantly between protected and unprotected secondary forests, we conclude that there is a strong probability that all types of understory and floor composition might be found in the Costa Rican SDTFs landscape, regardless of protection status.

However, the relationships between clusters paint a slightly different picture. When looking at the contingency tables between strata and to the synthesis provided by Table 11, we can see that although some trends are present, there is no exact composition pattern. The most common association (5 plots) was between Canopy cluster Spondias-Casearia, Shrubs/saplings cluster Tetracera-Xylophragma and Floor cluster Lasciasis. This association was found in one plot within the EEFH, but mostly in forests disturbed by fire. The presence of this association in the EEFH could be a singularity, or fire could also not be a main factor influencing this association. The other most found association (5 plots) was between the Chomelia-Heteropterys Canopy cluster, Heteropterys-Vachellia cluster and Ruellia-Melanthera cluster. This association was found in the least burnt forests, but not in the EEFH. All other associations were rarer, showing that there was no exact correlation between canopy clusters and other strata, which could be due to a stochastic effect or to the different levels of disturbance of fire and browse between forests.

Table 11 paints a picture that the NMDS analysis and the separate analysis of clusters for each stratum had only hinted: the Laguna and Madroño forests had very similar compositions, which was in turn different from the other three forests. These two forests were almost adjacent to each other, although located in different farms and under very different animal loading. The absence of recurrent fire within the EEFH also provided a very different composition for shrubs/saplings and floor vegetation than in those two sites. The composition of the forests thus might not have been determined entirely by browsing or fire, but rather by abiotic factors or structural properties, such as canopy cover and canopy deciduousness, which was not studied in this research, as sampling took place during the beginning of the rainy season, which provoked a drastic increase in cover throughout the sampling period. Browsing and fire have both been recurring disturbances in SDTFs since the arrival of cattle ranching in the study area centuries ago, and it is possible that the composition of all forests of the landscape has been filtered to favor species resilient to those disturbances, long before the creation of protected areas. This could explain the little difference found in composition and the diversity found between protected and unprotected areas.

However, forests heavily degraded by fire are common within this landscape and the forests in this study might have experienced a lower fire frequency than most forested areas in the region, allowing them to conserve a closed canopy structure. To better control the effects of soil conditions (Powers et al. 2009, van Breugel et al. 2019), water availability or differences in composition due to geographical dispersal limitations (Chain-Guadarrama et al. 2012), we recommend reproducing this study in the framework of an experimental design, for example closing a part of a forest to browsing and monitor possible switches in forest composition in all strata.

5 Conclusions

This research paper explored the relationships in composition and ecological diversity between protected and unprotected SDTFs that were subject to fire and cattle browsing disturbances. Few differences in composition or diversity were encountered between the protected and unprotected forest, at canopy level. There were rather several types of vegetation which were widespread through the landscape and were partially associated to disturbance by fire. The protected forest included all types of vegetation, which suggests that secondary succession in dry forests was not impacted by protection status. Understory and floor strata vegetation types were less distributed between forests, but this difference might be only partially due to the effect of fire, and possibly related to factors not measured in this study, as clustering placed the EEFH forest understory composition closer to the most burnt forests. However, we believe that disturbed forests in this study had been less subject to fire than a great part of SDTFs in the studied landscape, where fire had done heavy damages to forest structure. We suggest additional work on the extensive patches of degraded forests found in the landscape via chronological analysis of satellite images to better understand the degradation process by frequent fire in SDTFs. Lianas formed a greater part of the protected forest diversity, although some disturbed forests presented a similar abundance and diversity of lianas than the EEFH.

The similarity in canopy composition and diversity in protected or unprotected forests suggests that the disturbances caused by cattle and fire are not, or not anymore, a major influence on forests. Browsing did not appear to be a significant influence factor in the long term. This research makes a case for more controlled experiments in the Central American SDTFs to determine the effect of browsing on those forests, as the long-terms dynamics of browsing on SDTFs are still little understood. The current disdain for the use of cattle browsing in forests is based on little research, and does not take into account the notion of animal loading and browsing intensity. As this practice affects a great part of the SDTFs in Costa Rica and possibly Central America, it is paramount to further study this practice with the objective of determining a threshold value of animal loading where forest structure and composition would start differing strongly from forests in protected areas.

Browsing by cattle and previously by extinct large herbivores might have shaped the SDTFs of Guanacaste long time ago to be resilient. The same filtering process might have taken place with fire, which has been a pasture management and forest conversion tool since cattle ranching arrived in the region. Hence, secondary forests growing today in or out of protected areas might be already different from what they were centuries ago, and might be adapted to both of those disturbances, explaining the little difference found between protected and unprotected areas.

However, as fire was a discriminating factor between canopy and understory cluster, we conclude that fire has a stronger impact on forests ecological integrity than browsing by cattle, confirmed by the extensive areas of forests that had been degraded to wooded scrublands where sampling was impossible. It is paramount that forests in farms maintain their ecological integrity to provide landscape connectivity to plant and animal populations of the region and to contribute to the livelihoods of local populations, which is another incentive for forest conservation and restauration. If browsing by cattle in forest understory helps to control fire intensity like it has done for *Hyparrhenia rufa* pastures, this practice should not be fought by the conservation community, if it can increase forests resistance to fire. Some literature mentions that better fire control practices are preferable to the use of cattle, but the occurrence of fire in this landscape has many sources and cannot be reduced to zero. A reasonable animal load in SDTFs could maintain forest integrity, as it was the case in the studied forests, while contributing to cattle well-being and fire control.

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Additional Results: Sampled forests and the state of forests in Guanacaste.

An extensive pre-sampling in three forests in which cattle was introduced for dry season supplementation showed that a significant portion of these areas were avoided by cattle and were extremely impractical for understory sampling, due to the botanical composition of this stratum. These open areas had a very low density of adult tree individuals, that could meet the definition of forests according to FAO and other sources (Chazdon et al. 2016), but did not provide the tree coverage that could allow a forest ecosystem to develop, resembling a scrubland or wooded savanna. Understory in those areas was in general composed of tall stands of dry *Melanthera nivea*, *Triumfetta lappula*, *Vachellia tenuifolia* and *Mucuna pruriens*, between others, almost all plants showcasing heavy spinescence or stinging fruits or leaves, making sampling of those areas extremely tedious and unsafe (See Appendix II II for pictures of this vegetation). Moreover, cattle passed through the dry and lignified vegetation of those shrub areas without stopping or browsing, finding neither shade nor food among the sunburnt understory vegetation. Signs of damages from fire and verification with farmers confirmed that those areas were degraded parts of forests that had been heavily and repeatedly damaged by fire. Moreover, as the effect of cattle on understory composition was a variable of interest in this study, we selected areas where cattle would browse.

The restricted proportion of usable forest in this sampling brings us to question some figures regarding forest coverage in this landscape. Farmers in five of the visited farms had claimed to own a combined area of 1727 ha of forest, representing around 58% of farm area. Visited patches indicated to us by farmers as being forest covered 372ha, while only 177ha were usable for sampling. There might be a linguistic detail at the origin of this discrepancy: farmers often referred to uncultivated areas of land as “monte” or mountain in English, and this notion often overlaps the concept of forest in vernacular Spanish, resulting in the inclusion of shrubland and savanna within the definition of forest.

In comparison to the reality observed in the field, figures from the Costa Rican Agricultural census of 2014 indicate that forests cover 30.6% of farms in Guanacaste. This census uses the definition proposed by the FAO, where any non-cultivated area larger than 0.5ha and with trees >5m height and 10% tree cover or with the potential to reach such figures is considered as forest (Chazdon et al. 2016). However, these areas are rather in a degradation process, as farmers indicated that those areas had been regularly burnt. It is possible that those areas can return to conditions that allow for the development of a forest ecosystem, but it is important to note that the optimistic forest cover estimates from the 2014 agricultural census and for example the incredible forest recovery in the Chorotega studied by Arroyo-Mora et al. (2005) do not take into account the quality and state of disturbance of growing secondary forests in the region. Moreover, the dense and dry understory is very susceptible to fire, which puts these degraded areas at more risk of further disturbance. As these areas are covered by plants browsed by cattle when green, inclusion of cattle in these areas during the growing season could facilitate tree regeneration and diminish risk of consecutive fire, in the same way described by Janzen (1988) regarding the role of cattle in controlling growth of *Hyparrhenia rufa* in the region.

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Appendices

Appendix I: Interview sheet

Nombre del encuestado: ____

Finca: ____________________________

Fecha_____/_____/_____/

Contacto: ________________________

Buenos días. Mi nombre es Florent Godinot. Soy estudiante del CATIE de Turrialba y estoy aquí con el objetivo de entrevistarle, para conocer su finca, el bosque que tiene y su hato. Esta información me va a servir para mi tesis de maestría, que tiene como objetivo de ver si el ramoneo del ganado en bosques lo hace más o menos inflamable. Para eso necesito saber cómo la gente de aquí maneja su ganado en verano, y como hace uso del bosque. Esta entrevista puede durar alrededor de 30 minutos. Su participación en esta conversación es totalmente voluntaria, si no desea participar o si existe alguna pregunta que no desea contestar puede decírmelo sin ningún problema. Si en algún momento se incomoda y no quiere continuar, por favor me lo hace saber. Su respuesta es anónima, esta será estudiada en conjunto y no se analizará en particular. En caso de que mi pregunta no sea clara o desee una explicación adicional no dude en preguntarme. Durante la entrevista estaré tomando notas y fotografías para no perder la información y poder analizarla, quiero contar con su autorización. Quiero estar seguros de que ha quedado claro que está participando en esta entrevista de manera voluntaria.

1. Cuénteme la historia de su finca y descríbamela.
    a. ¿Cuántas hectáreas tiene esa finca?
    b. ¿A qué actividades se dedica la finca?
    c. ¿Cuántas hectáreas de pastura tiene la finca?
    d. ¿Qué tipo de pasto tiene?

    e. ¿Hay un pasto dominante?
    f. ¿Cuántas hectáreas de bosque tiene la finca?
    g. ¿Qué usos de la tierra tiene? ¿En qué superficie?
2. Descríbame su hato ganadero.
    a. ¿Cuánto ganado tiene?
    b. ¿De qué raza?
    c. ¿A qué tipo de producción sirve su ganado?
    d. ¿Cuántas vacas de cada categoría tiene? (vacas secas, en ordeno, novillas, etc.)
    e. ¿Cuánto varía el hato en el año?
3. ¿Cómo maneja su finca en el verano?
    a. ¿Cuáles estrategias utiliza usted en su finca para asegurar la disponibilidad de alimento de sus animales en época seca?
    b. ¿ Cómo las pasturas satisfacen las necesidades de las vacas en verano?
    c. ¿De qué otra manera suplementa su ganado en verano?
4. ¿Si pone su ganado en el bosque, cuánto tiempo al año lo deja?
    a. ¿Lo pone cada año?
    b. ¿Queda siempre el mismo tiempo o depende del año?
    c. ¿Qué hace que usted decida poner o no el ganado en el bosque?
5. ¿ Cómo maneja su ganado en el bosque?
    a. ¿Cuánto tiempo al día lo deja?
    b. ¿Lo deja suelto o lo tiene en lotes de bosque con cercas?
    c. ¿Lo estabula en la noche?
    d. ¿Quién va al bosque con el ganado?
6. ¿Qué come el ganado en el bosque?
    a. ¿Cuáles son las plantas preferidas del ganado?
    b. ¿Cuáles plantas evita?
    c. ¿Cuándo las come?
    d. ¿En el bosque, qué come el ganado además de hojas verdes? (frutos, corteza, etc…)
    e. ¿Cuáles especies son malas para el ganado?
7. ¿Dónde se queda el ganado en el bosque?

   a. ¿Hay lugares preferidos por el ganado en el bosque?
   b. ¿Cómo se desplaza el ganado en el bosque?
   c. Explíqueme cómo se distribuye el hato en el bosque.
8. Descríbame y cuénteme la historia de su bosque que tiene en su finca
   a. ¿Qué edad tiene este bosque?
   b. ¿Se regeneró solo o usted plantó especies? ¿Cuáles?
   c. ¿Qué especies se encuentran más?
   d. ¿Es un bosque de muchos árboles grandes o de arbustivas?
9. Hábleme de los otros animales se encuentran en el bosque.
   a. ¿Cuáles animales?
   b. ¿Cuáles son los que más hay y cuáles son los que hay menos?
   c. ¿Qué significan para usted y su finca estos animales?
10. ¿Qué otros usos se hacen del bosque?
   a. ¿Aprovecha madera? ¿Cuáles especies?
   b. ¿Busca frutas? ¿Cuáles especies?
   c. ¿Busca forraje para ganado? ¿Cuáles especies?
   d. ¿Busca leña? ¿Cuáles especies?
11. ¿ Cómo manejan el fuego en su finca?
   a. ¿Usted usa el fuego en el manejo de su finca?
   b. ¿A qué época del año?
   c. ¿Con qué objetivo?
   d. ¿Con qué frecuencia y en cuántos lotes lo hace?
   e. ¿Cuál es el origen de los incendios no controlados?
   f. ¿Usa unas técnicas de control del fuego?
   g. ¿Ha sido incendiado su bosque en los últimos años?
12. ¿Qué piensa que son los lados positivos y negativos de meter su ganado al bosque, y cómo influye en su decisión de hacerlo?
13. ¿Tiene alguna pregunta o algún comentario adicional que le gustaría hacer para que uno entienda mejor cómo maneja su ganado en temporada seca?
14. ¿A usted le gustaría que venga a hacer un muestreo en su bosque para mi proyecto? (detallar el muestreo)

Appendix II: Examples of types of vegetation indicated as forest that were discarded from sampling.

Appendix III: Complete list of plants mentioned by farmers, in alphabetical order. Scientific name associated by Roberto Espinoza, parataxonomist for the ACG.

Common name	Scientific name	Life form	Part	E	A	H	Grows in
Abejón	*Senna pallida*	Weed	Leaf	1	2		Pastures
Almendro	*Andira inermis* or *Terminalia catapa*	Tree	Fruit		1		Forests/Domesticated
Amapola	*Malvaviscus arboreus*	Shrub	Leaf	4			Forests/Scrubland
Aromo	*Acacia farnesiana*	Shrub	Leaf	4	1		Pastures
Batatilla	*Ipomoea trifida*	Liana	Leaf	7			Pastures
Bejuco de fuego	*Desmodium sp.*	Liana	Leaf		1		Scrubland and open forests
Bejuco engordador	*Calopogonium mucunoides*	Liana	Leaf	16			Pastures/Forests edges
Cana silvestre	*Lasciasis sorghoidea*	Grass	Leaf	2			Scrubland and open forests
Canelo	*Ocotea Veraguense*	Tree	Leaf		1		Forests
Caoba	*Swietenia humilis/macrophylla*	Tree	Leaf	1			Forests
Carao	*Cassia grandis*	Tree	Fruit	1	2		Forests/Pastures
Casco de venado	*Bauhinia ungulata*	Shrub	Leaf		1		Pastures and open forests
Cedro amargo	*Cedrela odorata*	Tree	Leaf	1	1		Forests
Cenízaro	*Samanea saman*	Tree	Fruit	20		10	Forests/Pastures
Chaperno	*Lonchocarpus spp.*	Tree	Leaf	3			Forests and open areas
Cinco Negritos	*Lantana camara*	Weed	Leaf	1		2	Pastures
Cocobolo	*Dalbergia retusa*	Tree	Leaf	1	1		Forests
Contenete	*Acacia tenuifolia*	Shrub	Leaf		1		Scrubland
Cornizuelo	*Vachellia collinsii*	Tree	Leaf		5		Forests/pastures
Cortez amarillo	*Handroanthus ochraceus*	Tree	Flower	4			Forests/Scrubland
Cortez amarillo	*Handroanthus ochraceus*	Tree	Leaf		1		Forests/Pastures
Cortez negro	*Handroanthus impetiginosus*	Tree	Leaf		1		Forests/scrubland
Coyol	*Acrocomia aculeata*	Palm	Fruit	6			Pastures/Scrubland/Forests
Cucharilla	*Amphilophium paniculatum*	Liana	Leaf	1	2		Pastures/Open forests
Cucharilla	*Amphilophium paniculatum*	Shrub	Fruit	1	2		Pastures/Open forests
Encino	*Quercus oleoides*	Tree	Fruit	6			Pastures/Forests
Encino	*Quercus oleoides*	Tree	Leaf		4		Forests/Pastures

Common name	Scientific name	Life form	Part	E	A	H	Grows in
Escoba Amarilla	*Sida acuta*	Weed	Leaf	5	1		Pastures
Escoba Lucia	*Sida rhombifolia*	Weed	Leaf	1			Pastures and scrubland
Escoba morada	*Melochia villosa*	Weed	Leaf	10		10	Pastures
Espavel	*Anacardium excelsum*	Tree	Leaf		1		Forests
Flor Amarilla	*Baltimora erecta*	Weed	Flower	1			Pastures and scrubland
Fruta de pava	*Eugenia hiraefolia*	Tree	Fruit	2	1		Forests
Girasol silvestre	*Tithonia diversifolia*	Weed	Leaf	1			Semi-Domesticated/Open areas
Gmelina	*Gmelina arborea*	Tree	Fruit	5			Domesticated
Gmelina	*Gmelina arborea*	Tree	Leaf	5			Domesticated
Guácharo	*Semialiarium mexicanum*	Tree	Leaf		1		Forests/Scrubland/Pastures
Guachipelín	*Diphysa americana*	Tree	Leaf	2			Pastures and open areas
Guácimo	*Guazuma ulmifolia*	Tree	Fruit	33			Pastures/Forests
Guácimo	*Guazuma ulmifolia*	Tree	Leaf	20	1		Pastures/Forests
Guaitil	*Genipa americana*	Tree	Fruit	2	1		Pastures/Open forests
Guanacaste	*Enterolobium cyclocarpum*	Tree	Fruit	23		5	Forests/Pastures
Guanacaste	*Enterolobium cyclocarpum*	Tree	Leaf	3			Pastures/Forests
Guapinol	*Hymenea courbaril*	Tree	Leaf		1		Forests
Guayaba	*Psidium guajava*	Tree	Fruit	2			Domesticated
Guayacán real	*Guaiacum sanctum*	Tree	Leaf	1	1		Forests
Higuerilla	*Ricinus communis*	Liana	Leaf	1			River banks
Hoja ancha	*Piper sp.*	Weed	Leaf	1			Shaded forests
Hoja Chigua	*Tetracera volubilis*	Liana	Leaf		2	1	Forests/Pastures
Huesillo	*Casearia sp?*	Shrub	Leaf	1			Forests
Jícaro	*Crescentia sp.*	Tree	Fruit	3		1	Early succession/Pastures
Jícaro	*Crescentia sp.*	Tree	Leaf	4			Pastures/Domesticated
Jobo	*Spondia mombin*	Tree	Fruit	6		1	Forests/Pastures
Jocote	*Spondia purpurea*	Tree	Fruit	2			Domesticated/Wild var. in Forests/Pastures
Jozmeca/Ajillo	*Mansoa hymenaea*	Liana	Leaf	13		13	Forests/Pastures
Kudzu tropical	*Pueraria phaseoloides*	Weed	Leaf	1			Domesticated
Laurel	*Cordia alliodora*	Tree	Leaf	2	1		Forests/Pastures
Madero negro	*Gliricidia sepium*	Tree	Leaf	19	1		Pastures

Common name	Scientific name	Life form	Part	E	A	H	Grows in
Madroño	*Calycophyllum candidissimum*	Tree	Leaf		1		Forests/scrubland
Malacaguite	*Chomelia spinosa*	Shrub	Leaf	2			Forests/Open areas
Malva	*Unknown.*	?	Leaf		1		Pastures
Mangle salado/blanco	*Conocarpus erectus*	Tree	Leaf	1			Mangroves
Mango	*Mangifera indica*	Tree	Fruit	7		1	Domesticated
Mango	*Mangifera indica*	Tree	Leaf	2	1		Domesticated
Manteco	*Trichilia americana*	Tree	Leaf		1		Forests and open areas
Manzana Rosa	*Syzygium jambos*	Tree	Fruit	1			Domesticated
Marañón	*Anacardium occidentale*	Tree	Fruit	2			Domesticated
Matapalo	*Ficus sp.*	Tree	Leaf		1		Forests
Melón silvestre	*Agonandra macrocarpa*	Tree	Fruit	3			Forests
Mora	*Maclura tinctoria*	Tree	Leaf		1		Open forests/Scrubland/Pastures
Moringa	*Moringa oleifera*	Tree	Leaf	2			Domesticated
Mostrenco	*Prosopis culiflora*	Tree	Leaf		1		Beaches
Mozote	*Triumfetta lappula*	Shrub	Leaf	2			Scrubland
Nance	*Byrsonima crassifolia*	Tree	Fruit	1			Pastures/Open forests
Nance	*Byrsonima crassifolia*	Tree	Leaf		1		Pastures/Open forests
Níspero	*Manilkara chicle*	Tree	Fruit	1			Forests
Ojo de buey	*Mucuna pruriens*	Liana	Leaf	1			Forests
Ojoche	*Brosimum alicastrum*	Tree	Fruit	4			Forests
Ortiga	*Urera baccifera*	Weed	Leaf		1		Pastures/scrubland/forests
Pansa de burro	*Oplismenus burmannii*	Grass	Leaf	1			Forests
Papa miel	*Combretum farinosum*	Shrub	Leaf	1			Pastures/Forests
Pata de venado	*Bauhinia ungulata*	Shrub	Leaf	4			Pastures and open forests
Picapica	*Mucuna urens*	Liana	Leaf	5			Scrubland
Pichi chivo	*Solanum candidum*	Weed	Fruit	1			Pastures/Forest edges
Piñuela	*Bromelia pinguin*	Bromeliaceae	Leaf	3	3	2	Open forests
Poroporo	*Cochlospermum vitifolium*	Tree	Leaf	2			Early succession, Pastures and Scrubland
Poroporo	*Cochlospermum vitifolium*	Tree	Flower	1			Pastures/Scrubland/Early succession
Quiebra machete	*Calliandra sp. or Combretum sp.*	?	Leaf		1		Pastures
Roble sabana	*Handroanthus rosea*	Tree	Flower	1			Pastures

Common name	Scientific name	Life form	Part	E	A	H	Grows in
Tamarindo	*Tamarindus indica*	Tree	Fruit	1			Domesticated
Teca	*Tectona grandis*	Tree	Fruit		1		Domesticated
Tempisque	*Sideroxylon capiri*	Tree	Fruit	3			Forests
Totolquelite	*Melanthera nivea*	Weed	Leaf	2			Scrubland
Uña de gato	*Sphinga platyloba*	Liana	Leaf		1		Pastures
Viborana	*Asclepia curassavica*	Weed	Leaf			1	Pastures
Zarza	*Mimosa pigra*	Weed	Leaf	1	1		Forests
Zorrillo	*Petiveria alliacea*	Shrub	Leaf	3	1	3	Pastures and forest gaps