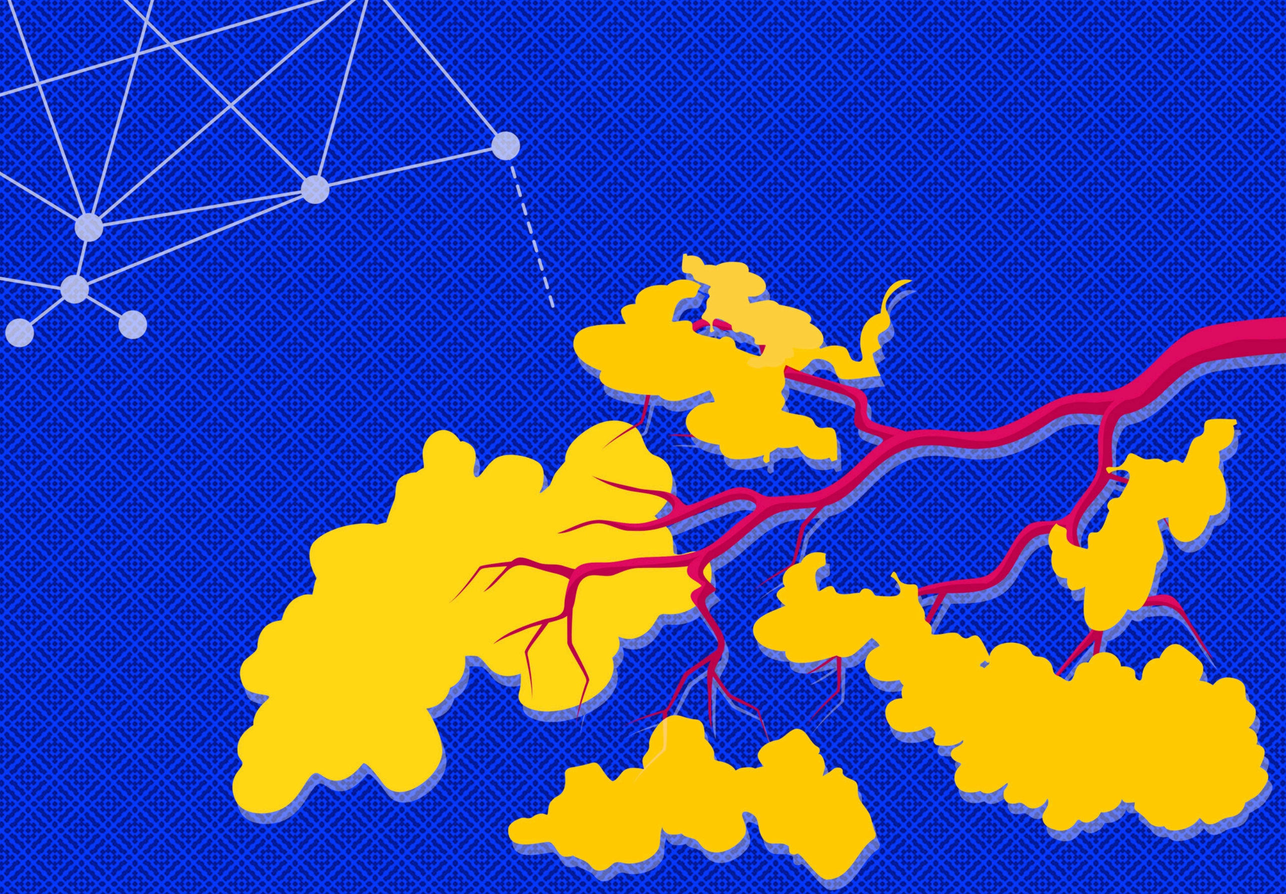

Resilience of dry tropical rangelands:

How native palms and trees mediate the effects of seasonal droughts

Ivan R. Hernández Salmerón

Propositions

1. Native trees and palms increase forage availability and reduce cattle thermal stress during dry conditions.
   (this thesis)
2. Retaining native palms and trees in pastures reflects a holistic understanding of socio-ecological systems.
   (this thesis)
3. Bridging ecological understanding and conservation goals requires scientific communication in indigenous and native languages.
4. Science advances more by cooperation than by competition.
5. Educational and research institutions should grant PhD candidates the same benefits, rights and obligations regardless of their funding sources.
6. Governmental grants for studying abroad, that do not support reincorporation to local labor market, are a great source of brain drain.
7. Positive feedback initiates big changes: from personal mindsets to biosphere conditions.
8. Recognizing the benefits of diversity in both nature and society is necessary for peace and prosperity for people and the planet.

Propositions belonging to the thesis, entitled

Resilience of dry tropical rangelands: How native palms and trees mediate the effects of seasonal droughts.

Ivan Raniero Hernández Salmerón
Wageningen, 22 October 2021

Resilience of dry tropical rangelands:

How native palms and trees mediate the effects of seasonal droughts

Ivan Raniero Hernández Salmerón

Thesis committee

Promotor:
Dr M. Holmgren Urba
Associate professor, Wildlife Ecology and Conservation Group
Wageningen University & Research

Co-promotor
Dr F.J. Solorio Sánchez
Associate professor, Faculty of Veterinary Medicine and Animal Science
Universidad Autónoma de Yucatán, México.

Other members
Prof. Dr F.J.J.M Bongers, Wageningen University & Research
Prof. Dr P.A. Tittonell, University of Groningen
Dr K.E. Barry, University of Utrecht
Dr H.H.E. van Zanten, Wageningen University

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Resilience of dry tropical rangelands:

How native palms and trees mediate the effects of seasonal droughts

Ivan Raniero Hernández Salmerón

Thesis
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A mi ma, mi pa y Julie,
por ser mi soporte y guías.

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Chapter 1

Introduction

1.1 Socio-ecological networks in livestock rangelands

Livestock rangelands cover approximately 30% of the ice-free surface of Earth and have a substantial impact on the world's climate, water, land and biodiversity resources (Steinfeld *et al.* 2006). Rangelands differ in structure and composition from practically treeless pastures to landscapes with scattered trees or woody plant patches within a matrix of grasses (Fig. 1.1). Trees, grasses, cows and wildlife coexist in these agroecosystems often creating complex networks with various types of interactions.

Fig. 1.1. Livestock rangelands during the growing season a) with scattered woody plants (Yucatán, México). b) with no tree cover (Wageningen, the Netherlands).

At least two types of networks can be identified in cattle rangelands: social and ecological (Fig. 1.2). Social networks include rangers who are in direct contact with cattle but also the managers, landowners, consumers, sellers, among many more actors that interact directly or indirectly in the production chain of cattle products. Ecological networks involve all kinds of organisms that interact in the agroecosystem: crops, remaining native trees in pastures and in the surrounding forest, wild and domestic animals, soil microorganisms, etc.

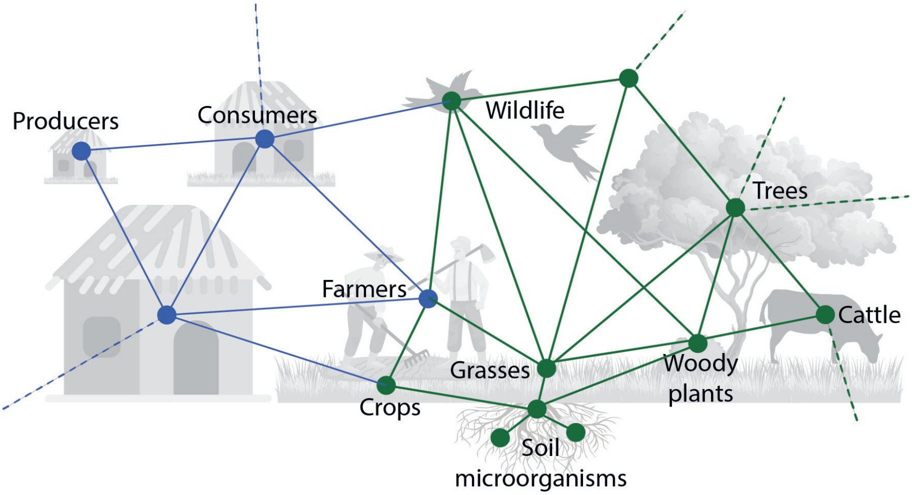

Fig. 1.2. Networks within networks. In cattle farms, organisms of different species (including humans), interact directly or indirectly with each other. Social (blue) and ecological (green) networks are intertwined in cattle farms and are connected with external networks through the exchange of individuals, energy and resources.

These networks are complex, communicate with one another and share resources across their boundaries to determine the resources available to livestock and wild species (Scholes & Archer 1997; Treydte *et al.* 2007; Harvey *et al.* 2011; Costa *et al.* 2016) and therefore, ultimately shaping food security (Vira *et al.* 2015), ecosystem services (MEA 2005) and nature conservation (Harvey *et al.* 2008). Networks are able to adapt to external stressors (e.g. global warming, altered precipitation regimes, increase frequency of extreme events, market fluctuations, etc.) but their adaptability can be compromised when the pressure of stressors is too high.

1.2 The feedback loop: livestock farming – deforestation - global warming

Socio-ecological networks in cattle rangelands are severely threatened by global warming. Higher temperatures and erratic rains resulting from climate change accentuate existing problems in livestock systems, and are expected to compromise pasture and cattle productivity worldwide (Lobell & Gourdji 2012; Field 2014). At the same time, livestock farming is expanding to respond to increases in human population, socio-economic growth and the maintenance of meat eating habits, contributing significantly to global warming and threatening forests across the global tropics (Miles *et al.* 2006b; Blackie *et al.* 2014a). This massive forest conversion into mostly treeless pastures and crop fields has altered the existing social and ecological networks by decreasing biodiversity and carbon sequestration, increasing soil erosion and greenhouse emissions, and altering vegetation-climate feedbacks and biogeochemical cycles (Harrison & Bruna 1999a) (Fig. 1.3).

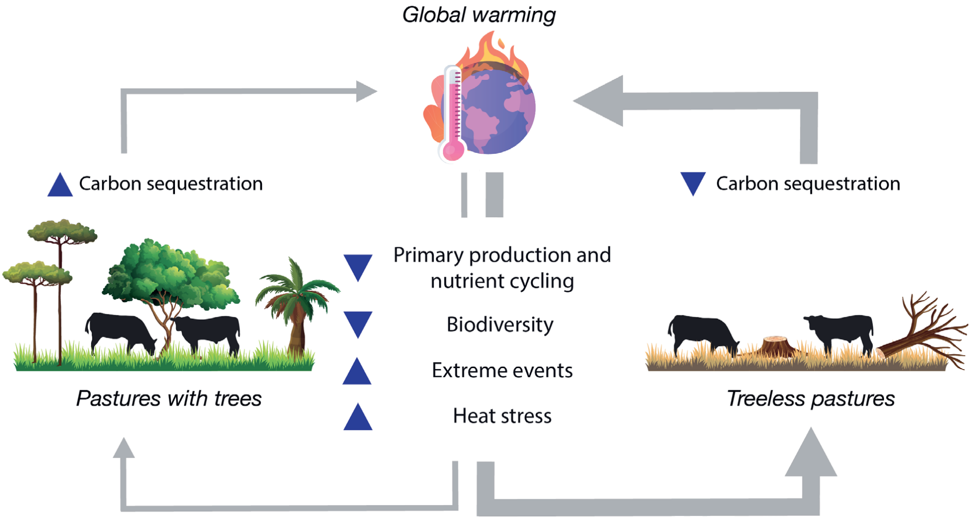

Fig. 1.3. Schematic overview of the feedback loop between livestock pastures with a diversity of scattered trees and pastures without trees. The width of the arrows indicate the relative magnitude of the effects on the feedback loop between pastures and global warming.

One of the biggest challenges for farmers and researchers is to develop more climate-resilient livestock systems. Resilience is the capacity of a system to maintain its organizational structure and be able to recover from perturbations (Holling 1996; MEA 2005). Therefore, resilient livestock systems to global warming must be able to maintain productivity despite increases in temperature and altered patterns of precipitation, while also contributing to biodiversity conservation.

Increasing tree cover in rangelands could contribute to ameliorate the impacts of climate change on pasture and cattle productivity (Murgueitio *et al.* 2011b; Altieri *et al.* 2015; Solorio *et al.* 2017) while having positive effects on biodiversity conservation. Tree shade improves forage in the understory herbaceous layer, allows for animal thermoregulation under stressful weather conditions and serves as habitat to species involved in ecological networks and biogeochemical cycles that maintain the functioning of rangelands. By providing habitat to wild species, trees could also facilitate their movement and connection across landscapes fostering genetic diversity and migration.

1.3 Effects of scattered trees on cattle rangelands

In many tropical and subtropical rural areas, local farmers usually retain some disperse trees within their grazing paddocks (Manning *et al.* 2006; Bernardi *et al.* 2016). Farmers actively select trees for various purposes and often recognize their economic and ecological value (Harvey *et al.* 2011). Yet, there is a strong need for understanding how farmers manage on-farm tree cover and how these decisions impact the effects trees have on the ecological networks on cattle rangelands.

The presence of trees can alter the productivity of grasses in natural systems, such as savannas (Scholes & Archer 1997). Early work on tree-grass interactions emphasized competitive effects and promoted a view on production systems where grasses would benefit from treeless landscapes (Walter & Burnett 1971; Walker & Noy-Meir 1982; Walker & Salt 2012). This emphasis on negative interactions between trees and grasses was softened in the nineties by the appreciation of positive effects of trees on grass productivity under abiotic stress conditions, such as droughts and heatwaves or poor soil fertility (Belsky 1994; Holmgren *et al.* 1997; Scholes & Archer 1997; Valladares *et al.* 2016). While there is a vast literature on the effects of trees on grasses in natural ecosystems such as savannas (Blaser *et al.* 2013; Dohn *et al.* 2013) and woodlands (Jackson & Ash 1998; Barbier *et al.* 2008), the debate on the overall effects of trees on grasses in productive systems persists. Much uncertainty still exists about the desirable levels of tree canopy density and the environmental conditions under which trees may have positive, negative or neutral effects (Treydte *et al.* 2007; Moustakas *et al.* 2013; Bernardi *et al.* 2016).

Trees can ameliorate abiotic stress through several mechanisms above and belowground that facilitate grass growth and improve grass quality (Solorio *et al.* 2017; Jose & Dollinger 2019a). Trees reduce air temperature and soil water evaporation (Murgueitio et al., 2011; L. B. Lopes et al., 2016; Jose and Dollinger, 2019; Deniz et al., 2020), increase soil water holding capacity (Bosi et al., 2019), improve soil structure (Vazquez et al., 2020) and, sometimes, also translocate deeper soil water to grasses through hydraulic lift (Gyenge et al., 2002; Pollock et al., 2009). Tree-grass facilitative interactions are more common as abiotic stress increases. However, this general pattern differs across systems and species depending on environmental conditions, functional traits (e.g. root depth and canopy architecture) and interactions with other organisms.

By modifying environmental factors and soil characteristic, trees can also have profound effects on the microbial communities in the rhizosphere of grasses (Berg and Smalla, 2009), and consequently, on pasture productivity. The rhizosphere is a complex and largely unknown ecosystem within a narrow zone of only a few millimeters surrounding the plant roots (Reinhold-Hurek *et al.* 2015). Usually consisting of plant-growth promoting bacteria, the rhizosphere microbiota contribute to plant growth by enhancing nutrient availability through nitrogen fixation (Sarabia et al., 2020), organic matter accumulation and higher decomposition rates (Peri et al., 2008). These microbes also provide protection from pathogens by inducing the plant systemic resistance or through the synthesis of antibiotics (Lugtenberg and Kamilova, 2009; Glick, 2012), and can contribute to counteracting abiotic stressors, such as drought or soil salinity (Glick, 2014; Ferjani et al., 2015; Soussi et al., 2016). It is well known that the rhizosphere composition differs between plant species, suggesting that plants may regulate the composition of their rhizosphere to improve plant fitness (Shi et al., 2011; Berendsen et al., 2012; Zhalnina et al., 2018). Characterizing genetic and functional diversity of grass rhizosphere bacterial communities can contribute to understand ecological networks to better manage productive systems.

Trees not only improve forage for cattle but also enhance their welfare by allowing for behavioral thermoregulation (Broom *et al.* 2013). As heat-stress increases, bovines spend more energy to maintain their thermal equilibrium, which decreases growth rates (West 2003) and therefore reduces milk and meat production (Kadzere *et al.* 2002). One of the most simple adaptation strategies to ameliorate animal heat stress is the provision of shade (Muller *et al.* 1994; Valtorta *et al.* 1997; Tuyttens *et al.* 2015) which is highly used by livestock as ambient air temperature and solar radiation increase (Kendall *et al.* 2006; Tucker *et al.* 2008). Other factors such as wind speed and relative humidity also influence the perception of heat stress and therefore influence animal behavior and movement across open and shady microsites in agricultural landscapes. Forecasting early heat stress risk and understanding the overall effects of trees on livestock behavior can limit the negative impacts of weather conditions on cow welfare and identify ways of adapting production systems to environmental stresses (Herbut *et al.* 2018b).

1.4 Unravelling seasonal effects of trees on cattle rangelands, from global to landscape scale

Trees play a major role in the ecological networks of cattle rangelands as their interactions can determine the resources available to livestock and wild species (Scholes & Archer 1997; Treydte *et al.* 2007; Harvey *et al.* 2011; Costa *et al.* 2016), biodiversity conservation (Harvey *et al.* 2008) and other ecosystem services (MEA 2005). Understanding the overall effects of trees on grass productivity and on livestock behavior under contrasting environmental conditions, as well as the mechanisms behind these processes, is of major importance as it may contribute to ameliorate the impacts of warmer climates on livestock systems.

In the following chapters, I and different teams of collaborators reviewed the existing literature on the global effects of trees on grasses and carried out field assessments in neotropical cattle farms to assess the effects of trees on the resilience of dry cattle rangelands to droughts (Fig. 1.4). I made a distinction between several functional groups of trees (i.e. palms, N_2 fixing trees and Non-N_2-fixing trees) because their differences in root depth (Rivest *et al.* 2013), soil organic matter and carbon (Binkley 2005), and canopy architecture could all lead to different effects on cattle rangelands.

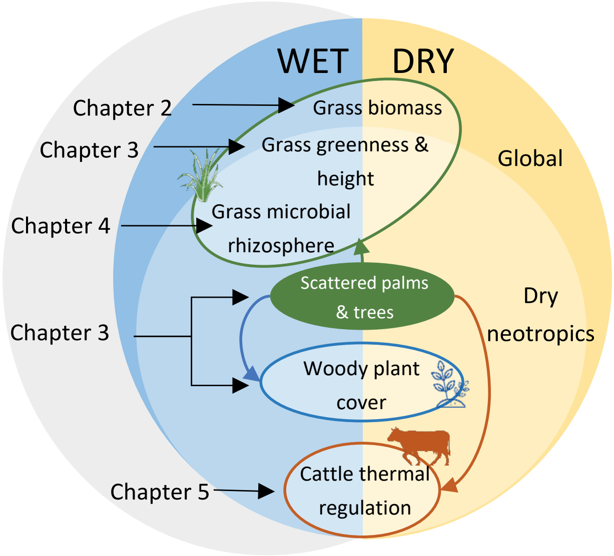

Fig. 1.4 Schematic overview of the effects of trees assessed during the dry and the wet seasons in cattle rangelands in the dry neotropics and globally.

In **chapter 2**, I perform a global meta-analysis to evaluate the effects of tree cover on grass biomass 1) along environmental gradients in tropical and temperate pastures, 2) during contrasting seasons, and 3) at different levels of canopy density. Based on the results of this chapter, I specifically aim at understanding the effects of both scattered palms and trees on several organisms that may influence productivity in dry neotropical rangelands in **chapters 3-5**. Because these studies were performed in the field, we move from a global level to a landscape level.

In **chapter 3**, I study tree composition of dry cattle pastures of Yucatán, México and assess the effects of palms, N_2-fixing trees and non-N_2-fixing trees on microsite environmental conditions, bare soil cover, and the performance of woody plants and grasses in their understory during the dry and wet seasons. In addition to assessing the effects of different canopy types on the performance of grasses, I also analyze their effect on the impact of droughts and the recovery afterwards.

In **chapter 4**, I explore the interactions between palms and the soil microbial community to further understand the mechanisms behind palm-grass facilitation observed in **chapter 3**. I assess the influence of palm tree overstory on the microbial community structure of the grass rhizosphere in a cattle farm in Yucatán, México. Based on the massive sequencing of the 16S rRNA gene, I analyze the diversity of bacterial species of the grass rhizosphere in the understory of the highly abundant palm tree *Sabal* spp. and in the open pastures exempt from any palm tree. I contrast these two microenvironments with the rhizobiome of a legume tree *Acacia* spp., which is also abundant in the sampled farm, and harbours intrinsic, well-known, relations with nitrogen-fixing bacteria (Hoque et al., 2011), and compare all rhizosphere samples to the bulk soil microbial composition.

In **chapter 5**, I determine cow heat stress risk during the dry and wet seasons in dry tropical pastures. Based on behavioral observations, I assess the response of cattle behavior along a gradient of abiotic stress and analyze how heat stress risk influences cattle tree shade utilization (i.e. palm and tree shade).

Finally, in **chapter 6**, I synthesize the results of the previous chapters and discuss their contribution to increasing our understanding on the resilience of dry cattle rangelands. I discuss the implications to develop more climate-resilient livestock systems and address some challenges for future research as well as some limitations of my dissertation.

By studying the interactions between some of the organisms coexisting in the ecological network of cattle rangelands, this dissertation sheds light on how trees can contribute to increase the resilience of dry tropical rangelands to seasonal droughts. This knowledge could help us develop more sustainable and resilient livestock systems to global warming that maintain productivity while also contributing to biodiversity conservation.

Chapter 2

Sparse tree cover increases grass biomass in dry pastures.

This chapter is based on:

Hernández-Salmerón, I. R. and Holmgren, M. (*submitted*). Sparse tree cover increases grass biomass in dry pastures.

Abstract

The effects of tree cover on the productivity of livestock rangelands are hotly debated. We assessed the experiences of having trees on livestock pastures worldwide. Trees facilitate grass biomass during dry seasons, especially in the tropics and dry regions. These positive effects are more likely to occur at intermediate levels of evapotranspiration and irradiance. We suggest that integrating trees in pastures might increase resilience of current livestock production systems to drier and warmer conditions.

2.1 Introduction

Livestock rangelands expand through tropical and temperate regions covering approximately 25% of our planet (Steinfeld *et al.* 2006). They differ in structure and composition from practically treeless pastures to landscapes with scattered trees or woody plant patches within a matrix of grasses. How trees and grasses interact has fascinated rangers, ecologists, and conservationists alike because the outcome determines the resources available to livestock and wild species (Scholes & Archer 1997; Treydte *et al.* 2007; Harvey *et al.* 2011; Costa *et al.* 2016) and therefore food security (Vira *et al.* 2015), ecosystem services (MEA 2005) and nature conservation (Harvey *et al.* 2008). Tree-grass interactions have enormous implications for the management of rangelands under climate change and the conservation of biodiversity. Increasing tree cover in rangelands could contribute to ameliorate the impacts of higher temperatures, and erratic rains as climate change progresses (Murgueitio *et al.* 2011b; Altieri *et al.* 2015; Solorio *et al.* 2017). This climate change adaptation strategy in productive systems could also have positive effects on biodiversity conservation as increasing the cover of native trees in livestock pastures could maintain ecological networks and facilitate the movement and connection of wild species across landscapes fostering genetic diversity and migration. However, the management of multifunctional landscapes aiming to promote win-win solutions that combine sustainable production with nature conservation and climate change mitigation remains challenging (Bustamante *et al.* 2014; Mbow *et al.* 2014).

Early work on tree-grass interactions emphasized competitive effects and promoted a view on production systems where grasses would benefit from treeless landscapes (Walter & Burnett 1971; Walker & Noy-Meir 1982; Walker & Salt 2012). Young trees and grasses usually compete for water and soil resources, but as trees become taller and reach deeper soil layers, competition for soil resources becomes less relevant for trees and light competition more relevant for grasses (Bazzaz 1979; Smith & Huston 1990). This emphasis on negative interactions was softened in the nineties by the appreciation of positive effects of trees on grass productivity under abiotic stress conditions, such as droughts and heatwaves or poor soil fertility (Belsky 1994; Holmgren *et al.* 1997; Scholes & Archer 1997; Valladares *et al.* 2016).

While there is a vast literature on the effects of trees on grasses in natural ecosystems such as savannas (Blaser *et al.* 2013; Dohn *et al.* 2013) and woodlands (Jackson & Ash 1998; Barbier *et al.* 2008), the debate on the overall effects of trees on grasses in productive systems persists, especially on the desirable levels of tree canopy density and the environmental conditions under which trees may have positive, negative or neutral effects (Treydte *et al.* 2007; Moustakas *et al.* 2013; Bernardi *et al.* 2016). Previous synthesis of the published literature have found tree facilitation on grasses to be stronger under N_2-fixing trees and in dry environments (Rivest *et al.* 2013; Mazía *et al.* 2016). We build upon these studies to systematically evaluate the effects of trees on grasses 1) during contrasting seasons, 2) along expanded environmental gradients in tropical and temperate pastures and 3) at different levels of canopy density. We report, for the first time, the contrasting seasonal effects of trees on productive systems around the globe and show that trees have stronger positive effects on grass yields under intermediate levels of abiotic stress. These findings contribute to promote win-win solutions in current livestock production systems with focus on climate change mitigation, food security and sustainability.

2.2 Results

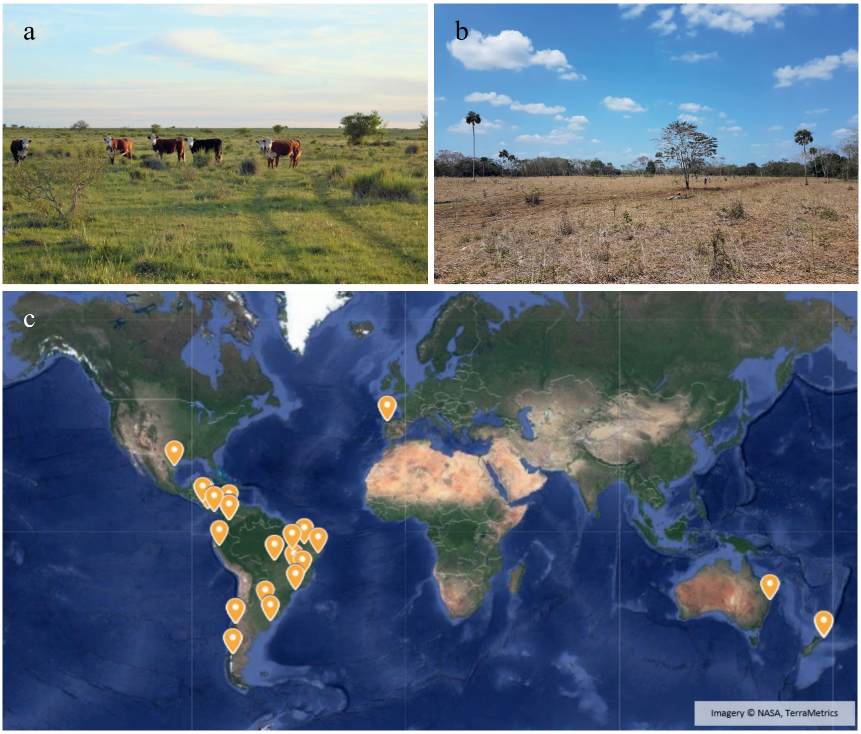

Fig. 2.1 (a) Temperate pastures in Durazno, Uruguay during the dry season. (b) Dry tropical pastures in Yucatán, México during the dry season. (c) Worldwide locations of studies. Studies from the same site are represented by a single dot.

2.2.1 Tree cover effects vary between seasons and biomes.

We identified 174 studies from 33 publications that assessed grass biomass under contrasting seasons and levels of tree cover across seven biomes (Supplementary Fig. 2.1). About 61% were conducted in the tropics and 39% in temperate regions (Fig. 2.1).

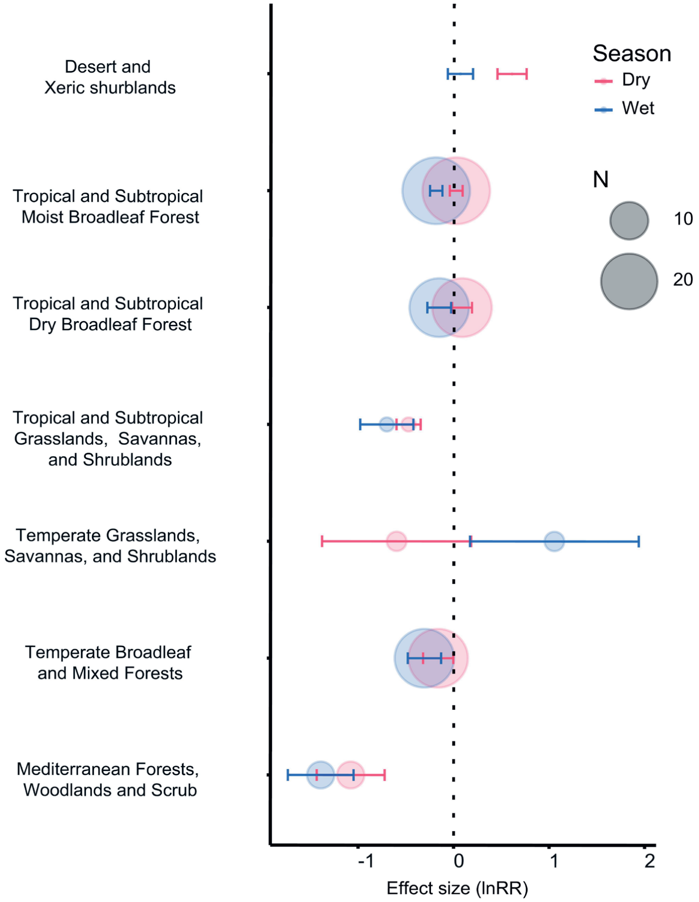

Fig. 2.2. Tree effects on grass biomass in the dry and wet seasons across biomes. Facilitative effects are stronger in Desert and Xeric biomes and Tropical and subtropical biomes where C4 grasses occur, especially during the dry season. Tree effects vary in the temperate biomes: facilitation occurs in grasslands where C4 grasses dominate; in temperate forests mostly neutral to negative effects are observed. Dotted lines indicate zero effect sizes. 174 studies were identified of which 61% were conducted in the tropics and 39% in temperate regions. Point size indicates the sample size.

The effect of tree cover on grass biomass varied between biomes, seasons and C3/C4 grass species ($p < 0.0001$, Fig. 2.2, Supplementary Fig. 2.2 & 2.5). We found the largest tree facilitative effects in the Desert and Xeric shrublands, especially during the dry season. In tropical and subtropical biomes, we found mostly tree facilitative effects on C4 grasses during the dry season. Also in the Mediterranean, tree facilitative effects, for the dominant C3 grasses, were higher during the dry season than during the wet season. In contrast, in temperate regions the effects varied per biome; in temperate grasslands, savannas and shrublands, tree facilitative effects on C4 grass species occurred only during the wet season; while in broadleaf forests we found neutral effects on C3 grasses during both seasons and higher facilitative effects on C4 grass species during the dry season.

2.2.2 Tree cover effects depend on rainfall, temperature and irradiance

The positive effects of trees on grass biomass for C3 and C4 grasses peak at intermediate levels of daily evapotranspiration (4 and 5 mm for C3 and C4 grasses, respectively) and become negative at both ends of the evapotranspiration gradient (Fig. 2.3a). We grouped the biomes in two major regions: tropical and temperate, and did not find differences between them.

When analyzing the contribution of rainfall and temperature separately, we found contrasting patterns on the role of trees on grass biomass along these climatic gradients. The effects of trees on both C3 and C4 grasses became increasingly negative as seasonal rainfall increases ($p < 0.005$, Fig. 2.3b), especially for C3 species ($p < 0.0001$), in both tropical and temperate regions. While we found only negative effects on C3 grass species along the whole gradient of precipitation, we observed neutral to slightly positive effects on C4 grasses when monthly precipitation drops below ~50 mm.

The nonlinear patterns of how trees and grasses interact are mostly explained by temperature. In the tropics, the effects of trees on C4 grass biomass are mostly neutral at intermediate maximum daily temperatures (~35°C) and become negative at both colder and hotter ends of the temperature gradient (Fig. 2.3c). Also in temperate regions, trees have neutral effects on C3 grasses at intermediate temperature (~27 °C) that become negative at both ends of the gradient of maximum daily temperature. In temperate regions, trees have positive effects on C4 grasses as conditions become warmer than ~32°C (Fig. 2.3d).

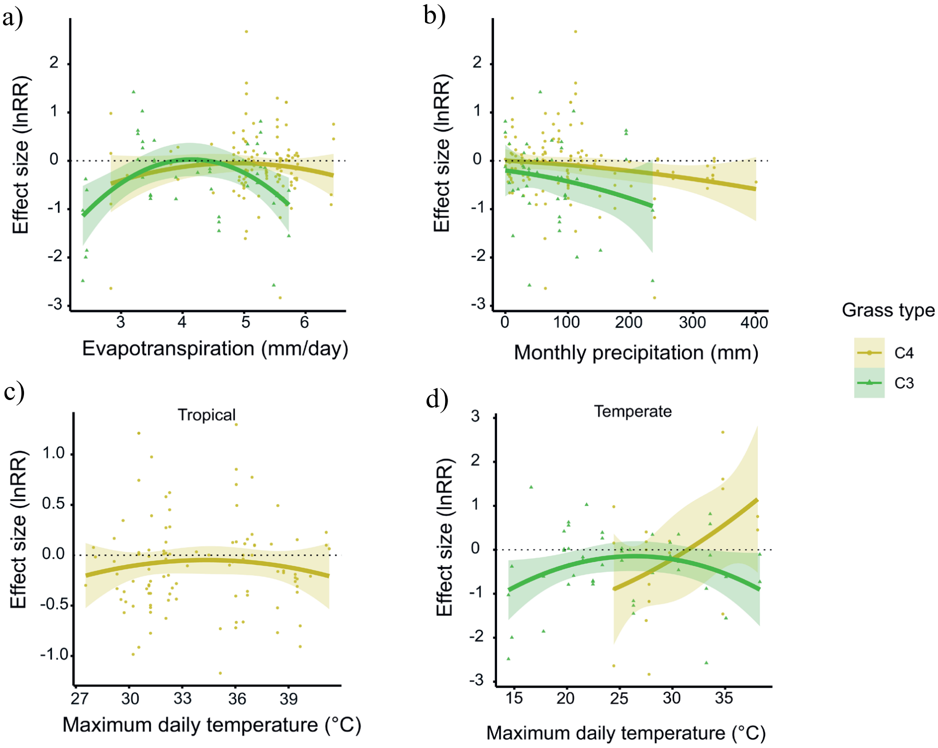

Fig. 2.3. Tree effects on C3 and C4 grass biomass along gradients of (**a**) evapotranspiration, (**b**) monthly precipitation and maximum daily temperature in tropical (**c**) and temperate regions (**d**). Dotted lines indicate zero effect sizes.

Tree cover density determines the levels of irradiance received by grasses. Overall, we found that the positive effect of trees on grass biomass peaks at roughly 60-80% of irradiance and becomes negative at lower or higher irradiance levels (Supplementary Fig. 2.3). This facilitative effect tends to be higher under N_2 fixing trees than under Non-N_2 fixing trees although it is not significantly different ($p = 0.5$). The response of grasses to the irradiance levels are strongly dependent on the rainfall season and the grass type. C4 grasses respond negatively to lower irradiance levels especially during the rainy season. In contrast, C3 grasses are facilitated by intermediate levels of irradiance both in the dry and wet seasons (Fig. 2.4).

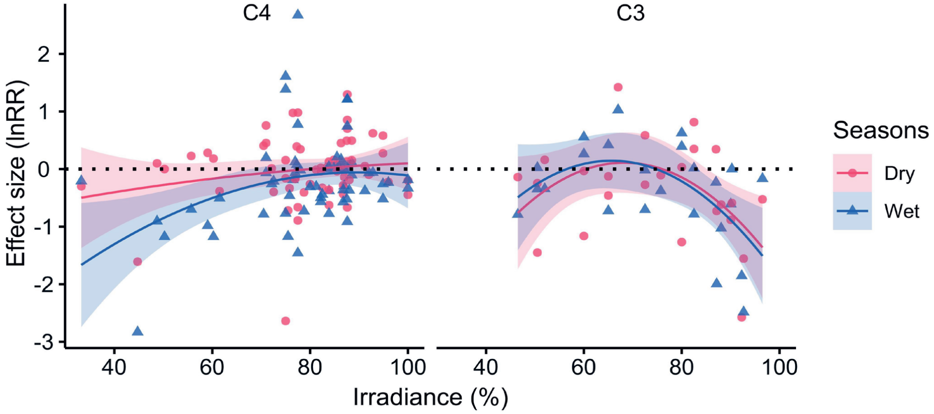

Fig. 2.4. Tree effects on C3 and C4 grass biomass along the irradiance gradient in the dry and wet seasons. Dotted lines indicate zero effect sizes.

2.3 Discussion

Here we report for the first time the contrasting seasonal effects of trees on productive systems around the globe. Our meta-analysis shows that the effects of trees on grass biomass have been studied more often in tropical and subtropical pastures than in temperate pastures. Overall, our results indicate that positive effects of trees on grasses: 1) are higher during seasonal droughts, especially on C4 grasses in tropical pastures and 2) peak at intermediate levels of evapotranspiration, temperature and irradiance, and at low levels of precipitation. These findings show that water, temperature and light, are key resources for grass growth and their interactions can shape the nature of tree-grass interactions in a wide range of productive ecosystems.

2.3.1 Facilitation is higher during seasonal droughts in the tropics.

This meta-analysis shows that trees increase grass biomass in pastures during seasonal droughts and that these effects are stronger in tropical pastures where C4 grasses dominate, than in temperate pastures where C3 grasses are more common. The higher tree facilitative effects during droughts on C4 grasses can result from a combination of mechanisms that ameliorate abiotic stress. Although C4 grasses have been widely promoted across tropical productive systems (Edwards *et al.* 2010) for being highly tolerant to water stress and high temperatures (Chaves *et al.* 2003), they still benefit strongly from the shade of trees. During seasonal droughts in the dry tropics, when temperature and evapotranspiration increase sharply, the canopy of trees ameliorates environmental stress by reducing temperature and mediating irradiance levels even for highly tolerant C4 grasses.

In temperate regions, we found mostly, but not exclusively, neutral to negative effects of tree cover on grass biomass. C3 grasses occur more often in temperate regions and have a higher tolerance and photosynthetic capacity in colder temperatures (Brown 1982; Gardner *et al.* 2017). Interestingly, the only positive effect of trees we found in temperate regions was described for open temperate savanna, specifically on C4 grasses during the wet season. This is very contrasting to the facilitative effects for C4 grasses in the tropical pastures which occur mostly in the dry season. Temperate savannas are open biomes with high levels of irradiance which in combination with high water availability are less stressful for grasses. However, the wet season often corresponds with the coldest period of the year. In such open biomes, trees might ameliorate temperature in an opposite direction than in the tropics. While in the tropics abiotic amelioration implies a reduction in high temperature levels, in the temperate pastures, amelioration may be related to an increase in temperature under the tree canopy (Zellweger *et al.* 2019), creating a warmer microclimate that would benefit C4 grasses during wet and cold seasons.

2.3.2 Facilitation tends to peak at intermediate abiotic stress

We found a shift from neutral effects to negative effects of trees on grasses as monthly precipitation increases. Previous meta-analyses on the effect of trees on grass biomass in natural savannas also found stronger facilitation at drier places(Moustakas *et al.* 2013) or with decreasing annual precipitation (Dohn *et al.* 2013).

Our meta-analysis also revealed non-linear patterns of tree facilitative effects on grasses. These effects peak at intermediate levels of evapotranspiration, temperature and irradiance and can be lost at very low or high levels. Tree cover plays a key role in the interplay between positive and negative effects. In plant communities, the shade of neighboring plants is expected to increasingly ameliorate drought stress as conditions become drier (Bertness & Callaway 1994), although these facilitative effects may be lost under extremely stressful conditions (Holmgren & Scheffer 2010; Soliveres *et al.* 2015; Zhang *et al.* 2018). These non-linear effects of shade and drought have been found in meta-analyses of plant performance in field and experimental conditions (Holmgren *et al.* 2012) as well as in agroforests (Blaser *et al.* 2018). We now found comparable results for productive livestock pastures.

Although there was a tendency for N_2-fixing trees to have slightly higher facilitative effects than Non-N_2-fixing trees on grass biomass, we did not find significant differences between these two tree functional groups. N_2-fixing trees have been reported previously to increase pasture yields as drought pressure increases abiotic stress on livestock grazing systems (Rivest *et al.* 2013). Palm trees are highly abundant in tropical livestock pastures where farmers preserve them for their multipurpose value (Martínez-Ballesté *et al.* 2008; Macía *et al.* 2011), however, their effect on grasses is still poorly known compared to other groups of trees that have been studied more in detail. We found only one publication where the effects of palm trees on livestock pastures have been reported. Field experiments and long-term observational studies are needed to understand the effects of palm trees on grasses and determine whether they can contribute to increasing resilience to drought in livestock pastures.

We compared studies from seven different biomes that varied in time, period of the year of sampling, duration, and research methodology. Despite this variation, we identified higher facilitative effects of trees on grasses during seasonal droughts, especially in the tropical biomes where C4 grasses dominate and to a lesser degree in the temperate pastures. We showed that these effects are not only strongly related to the available levels of precipitation but also to temperature and irradiance. Understanding the effect of trees is crucial for managing and transforming current livestock production systems into multifunctional landscapes with increased resilience to seasonal droughts around the globe. We encourage the integration of trees with intermediate canopy density (i.e. ~20-40%) in drier and warmer pastures, especially in the tropics where trees have positive and neutral effects on grass biomass. Positive and neutral effects of trees on grass biomass imply that trees can be used in productive pastures to ameliorate abiotic weather conditions favoring, or at least not compromising grass yields, while also contributing to other ecosystem services such as biodiversity conservation, carbon sequestration, habitat provision, construction materials, etc.

2.3.3 Challenges ahead

Our understanding of how trees influence the functioning of productive pasture systems is still fragmented. The existing literature has focused on identifying the effects of different types of trees according to their functional traits such as N_2-fixation or deciduousness (Rivest *et al.* 2013; Mazía *et al.* 2016) but we lack holistic assessments of the direct and indirect effects of tree diversity on livestock productivity. One major challenge is to widely assess how tree diversity affects both grass and animal production and how these effects can be translated into economic benefits for farmers while considering multiple ecosystem services at meaningful temporal scales.

Most of the studies we identified were carried out in the neotropics, especially in Latin America, which may reflect different cultural traditions in either how farmers perceive the separation between productive versus natural landscapes or how scientists study them in different regions around the world. We encourage researchers to bridge across scientific disciplines to expand the knowledge of tree-grass interactions in agroecosystems and multifunctional landscapes across environmental gradients and cultures. Merging the existing traditional knowledge from farmers with the ecological theory developed in natural and productive systems could facilitate generating effective strategies for sustainable productive systems that can contribute to biodiversity conservation and be better adapted to changing climate conditions.

2.4 Methods

2.4.1 Paper selection

We searched for studies that evaluated grass performance (i.e. dry matter) under two contrasting seasons and two or more levels of tree cover. Searches were conducted in Web of Science (1945-2020) using the following keywords: “shade” OR “light” OR “irradiance” OR “shelter” OR “tree*” OR “canop*” OR “crown” OR “sun*” OR “arbol” OR “cobertura arborea” OR “luz” OR “irradiaci?n” OR “protecci?n” OR “sombra” OR “dosel arbo*” ; “drought” OR “water” OR “precipitation” OR “wet” OR “humid” OR “dissecat*” OR “arid*” OR “irrigat*” OR “dry” OR “rain*” OR “microclimat*” OR “temperat*” OR “sequia” OR “desecaci?n” OR “agua” OR “precipitaci?n” OR “humed*” OR “irrigaci?n” OR “seco” OR “microclima” OR “temperature”; “grass” OR “forage” OR “fodder” OR “grass” OR “pasture” OR “animal producti*” OR “producti*” OR “herbs” OR “herbace*” OR “forraje” OR “pasto” OR “hierba” OR “pastizal*” OR “leche” OR “carne” OR “pastura”; “pasture” OR “S?lvo-pastor*” OR “Agro-s?lvo-pastor*” OR “Agros?lvopastor*” OR “livestock” OR “wood* pasture*” OR “wood* grassland” OR “wood* rangeland” OR “ranching land” OR “pastureland” OR “ganado” OR “ganader*” OR “vaca” OR “cattle” OR “s?lvopastor*”. We chose dry matter as it was the most commonly used indicator of forage biomass. We registered the levels of tree cover and expressed it in a percentage scale of irradiance where 100% would represent the irradiance that reaches and open microsite (i.e. 0% of tree cover). This relative scale is adequate to compare the response of species that naturally occur under different ranges of light availability (Holmgren *et al.* 2012). We decided not to include studies that reported grass performance at only one season or one level of tree cover because we wanted to explicitly assess season-tree cover interactions. We screened publications for studies that included grass responses within the same calendar year or continuous year, specific location or coordinates where the study was carried out, and period in time when the measures were taken. We only considered studies conducted in the field and with natural tree shade.

The search from 5,135 papers yielded 174 studies from 33 suitable publications (Supplementary Fig. 2.1). When publications involved several grass species or irradiance levels, each species and each irradiance level was treated as a separate study. We decided to include several studies from the same paper because, although it tends to reduce the overall heterogeneity in effect sizes, excluding multiple results from a paper can underestimate effect sizes (Gurevitch & Hedges 1999; Karst *et al.* 2008).

2.4.2 Data collection

Mean values of grass dry matter were collected from text and tables in the main publication and/or supplementary information. We used WebPlotDigitizer (Rohatgi 2020) to extract mean and standard error values from figures when raw data was not provided. If not provided, standard deviations were back calculated from standard errors and sample sizes (SD = SE × $\sqrt{n}$). When there were multiple studies within the same publication, we calculated several means (i.e. one per study), pairing the different levels of tree cover with the one with the lowest tree cover (highest irradiance). Some publications reported multiple responses under the same levels of tree cover within the same season, thus we averaged those responses to one value per tree cover level and season.

For each record in our dataset, we converted the grass dry matter mean to kg/ha/d and classified the grass species as C3 or C4. We registered the location, country and biome where the study took place. We obtained evapotranspiration (mm/day), monthly precipitation (mm) and maximum daily temperature (°C) based on the period of time of the records and coordinates, and distinguished between dry and wet seasons. Environmental data was obtained using the R package *climatrends* (de Sousa *et al.* 2020). The literature search workflow is presented in Supplementary Fig. 2.1.

2.4.3 Effect Size Calculations

Following identification, means (X), standard deviations (SDs), and sample sizes (n) were extracted from the published studies. If not reported, these statistics were derived from other metrics. We conducted a meta-analysis to assess the effects of tree cover and season on grass biomass following (Koricheva *et al.* 2013). For each study, we calculated the effect size using the natural log of the response ratio [ln (RR)] and its associated variance ($v_{\ln\mathrm{RR}}$). The estimate of ln (RR) and for each study is based on *X*, SDs, and replicate numbers for control and treatments (Hedges *et al.* 1999). Positive ln (RR) values indicate facilitative effects and negative values indicate net competitive effects of tree cover on grass biomass.

We used the *escalc* and *rma.mv* functions in the *metafor* package in R 4.0.3 (R Core Team 2020) to calculate the ln (RR) and to perform the statistical analysis. To address the question of how tree cover influences the response of grasses under contrasting seasons, we performed several multivariate meta-analysis models with random effects. We first analyzed whether the effect of tree cover differs between seasons and C3/C4 species across the different biomes. We used the ln (RR) for tree cover as the response variable, and the Seasons, biome and C3/C4 species as predictors (with interactions: Seasons * C3/C4). We assessed the effects of tree cover along environmental gradients of evapotranspiration, monthly precipitation, maximum, daily temperature and irradiance. We grouped biomes into two major regions: Temperate (i.e. Temperate, Mediterranean and Desert biomes) and Tropical (i.e. Tropical and subtropical biomes). Mediterranean and desert biomes were grouped in the Temperate region based on their mean annual precipitation and mean annual temperature. We fitted meta-regression models with evapotranspiration, major region and C3/C4 species as predictors (with interactions Evapotranspiration*C3/4 and major region*C3/4). Both linear and quadratic regressions were fit and the best model chosen using the Akaike Information Criterion corrected for small sample sizes ($\mathrm{AIC_c}$).The same models were fitted replacing evapotranspiration for maximum daily temperature and monthly precipitation separately. Lastly, we analyzed the type of response of the effect of tree cover to irradiance and tree type (i.e. functional group) with Irradiance, Tree type, Seasons and C3/C4 species as predictors (with interactions Irradiance*Seasons, Irradiance * Tree type and C3/4*Seasons). In all the models we included the Study nested within the Paper as random factors.

Acknowledgments

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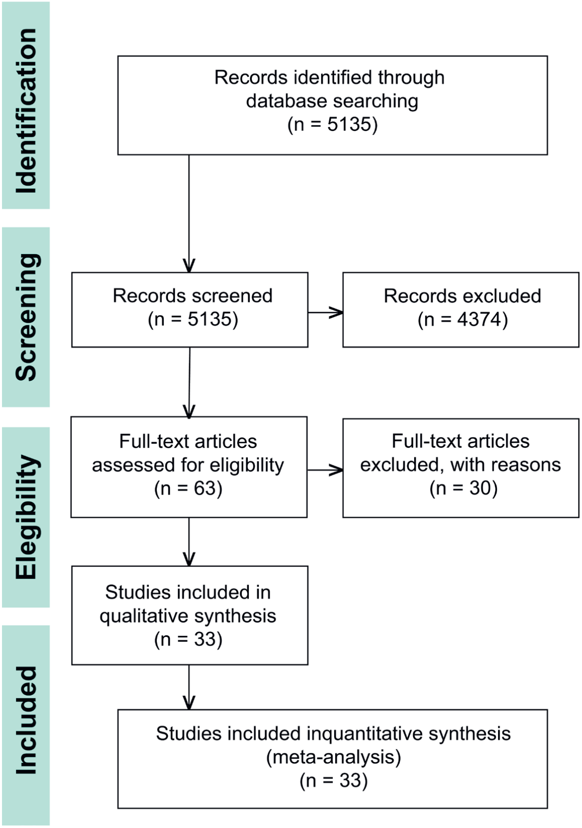
Author Contributions

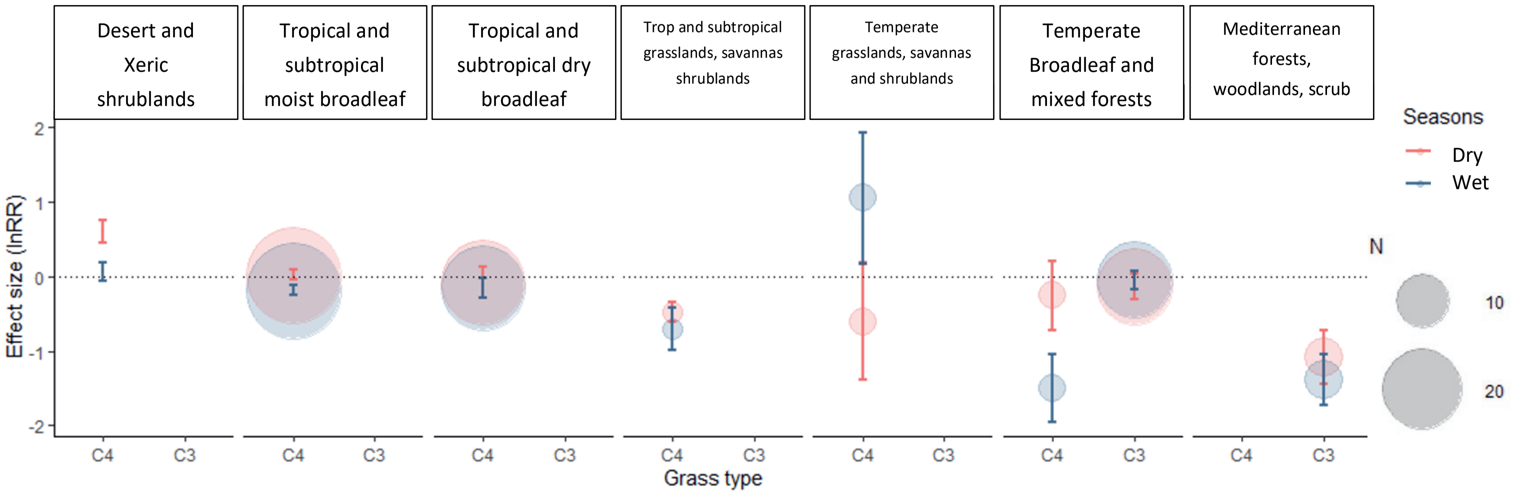
IRHS and MH conceived the ideas, designed the study, analysed and interpreted the results and wrote the manuscript. IRHS screened all potential papers, extracted the data and prepared the figures.

Supplementary Information

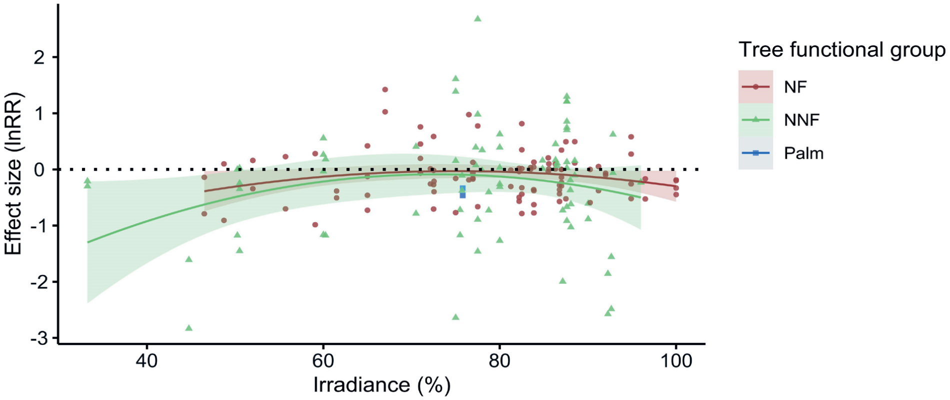
Supplementary Fig. 2.1. Flow diagram for the selection of manuscripts.



Supplementary Fig. 2.2. Comparison of tree effects on C3 and C4 grass biomass in different biomes between studies in the dry and wet seasons. 174 studies from 33 publications were identified and distributed as follows: 56 the Tropical and Subtropical Moist Broadleaf Forest, 44 in the Tropical and Subtropical Dry Broadleaf Forest, 44 in the Temperate Broadleaf and Mixed Forest, 12 in the Mediterranean forests, Woodlands and Scrub, 8 in the Temperate Grasslands, Savannas, and Shrublands, 6 in the Tropical and Subtropical Grasslands, Savannas, and Shrublands and 4 in the Desert and Xeric shrublands. Facilitative effects are stronger in Desert and Xeric biomes and Tropical and subtropical biomes where C4 grasses occur, especially during the dry season. Tree effects vary in the temperate biomes: facilitation occurs in grasslands where C4 grasses dominate; in temperate forests mostly neutral to negative effects are observed. Dotted lines indicate zero effect sizes. Point size indicates the sample size.



Supplementary Fig. 2.3. Tree effects on C3 and C4 grass biomass along irradiance gradient between studies.



Supplementary 2.4. Multivariate meta-analysis models of environmental factors on tree cover effects. Best models with the lowest AICc were used for the prediction of the effect of trees on grass biomass.

Model	AICc
Evapotranspiration	
ETo* C3_4 + C3_4*major_biome + ETo*major_biome	1567.7
ETo2* C3_4 + C3_4*major_biome + ETo2*major_biome	1139.1
Monthly precipitation	
C3_4*major_biome + C3_4*Monthly_precip	2152.9
C3_4*major_biome + C3_4*Monthly_precip2	1982.8
Maximum daily temperature	
maxDT* C3_4 + C3_4*major_biome + maxDT*major_biome	2178.7
maxDT2* C3_4 + C3_4*major_biome + maxDT2*major_biome	1931.8
Irradiance	
Irradiance*Seasons + Seasons*C3_4 + Tree_type	1197.2
Irradiance2*Seasons + Seasons*C3_4 + Tree_type	1196.6

Supplementary 2.5. Results of the multivariate meta-analysis models on tree cover effects, showing the performance of the best models and estimates for environmental factors included in the best models.

Model				
Evapotranspiration (N=174, AICc = 1139.1)	Estimate	Standard Error	z-value	p-value
intrcpt	0.741	2.4688	0.3002	0.7641
poly(ETo, degree = 2, raw = TRUE)1	-0.3171	0.8783	-0.361	0.7181
poly(ETo, degree = 2, raw = TRUE)2	0.029	0.0779	0.3721	0.7098
C3_4C3	12.4908	1.389	8.9925	<.0001
major_biomeTemperate	-2.4528	2.7852	-0.8807	0.3785
poly(ETo, degree = 2, raw = TRUE)1:C3_4C3	-5.7896	0.5763	-10.046	<.0001
poly(ETo, degree = 2, raw = TRUE)2:C3_4C3	0.6336	0.0599	10.5774	<.0001
poly(ETo, degree = 2, raw = TRUE)1:major_biomeTemperate	0.8419	1.0262	0.8204	0.412
poly(ETo, degree = 2, raw = TRUE)2:major_biomeTemperate	-0.0725	0.0941	-0.7705	0.441
Monthly precipitation (N=174, AICc = 1982.8)				
Intrcpt	-0.1591	0.1159	-1.3721	0.17
poly(Monthly_precip, degree = 2, raw = TRUE)1	0.0019	0.0002	9.5629	<.0001
poly(Monthly_precip, degree = 2, raw = TRUE)2	0	0	-9.2445	<.0001
C3_4C3	0.481	0.3712	1.2959	0.195
major_biomeTemperate	-0.2299	0.3176	-0.7239	0.4691
poly(Monthly_precip, degree = 2, raw = TRUE)1:C3_4C3	-0.0164	0.0019	-8.5981	<.0001
poly(Monthly_precip, degree = 2, raw = TRUE)2:C3_4C3	0.0001	0	10.605	<.0001
Maximum daily temperature (N=174, AICc = 1931.8)				
intrcpt	7.021	0.7324	9.5869	<.0001
poly(maxDT, degree = 2, raw = TRUE)1	-0.4397	0.0437	-10.0628	<.0001
poly(maxDT, degree = 2, raw = TRUE)2	0.0067	0.0007	10.1606	<.0001
C3_4C3	12.2184	3.6573	3.3408	0.0008
major_biomeTemperate	-8.4393	3.645	-2.3153	0.0206
poly(maxDT, degree = 2, raw = TRUE)1:C3_4C3	-0.9408	0.2321	-4.0532	<.0001
poly(maxDT, degree = 2, raw = TRUE)2:C3_4C3	0.0174	0.0036	4.776	<.0001
poly(maxDT, degree = 2, raw = TRUE)1:major_biomeTempera	0.4798	0.2269	2.1145	0.0345
poly(maxDT, degree = 2, raw = TRUE)2:major_biomeTempera	-0.0068	0.0034	-1.9688	0.049
Irradiance (N = 174, AICc = 1196.6)				
intrcpt	-3.2025	1.4403	-2.2236	0.0262
poly(Irradiance, degree = 2, raw = TRUE)1	0.0966	0.0404	2.3895	0.0169
poly(Irradiance, degree = 2, raw = TRUE)2	-0.0007	0.0003	-2.4395	0.0147
SeasonsWet_F	-1.5053	0.2495	-6.0338	<.0001
C3_4C3	-0.6747	0.2224	-3.0332	0.0024

Tree_typeNNF	-0.1796	0.1682	-1.0676	0.2857
Tree_typePalm	-0.4792	0.6215	-0.7711	0.4406
poly(Irradiance, degree = 2, raw = TRUE)1:SeasonsWet_F	0.0201	0.0059	3.3911	0.0007
poly(Irradiance, degree = 2, raw = TRUE)2:SeasonsWet_F	0	0	-1.1639	0.2445
SeasonsWet_F:C3_4C3	0.9396	0.0267	35.1922	<.0001

Chapter 3

Native palms and trees mediate drought impacts on dry neotropical pastures

This chapter is based on:

Hernández-Salmerón, I. R., Delconte, V., van Hoeflaken, J., Solorio- Sánchez & Holmgren, M. (under revision). Native palms and trees mediate drought impacts on dry neotropical pastures.

Abstract

Dry forests are the most threatened biome across the global tropics. Despite their massive conversion into agricultural landscapes, local farmers often retain disperse trees and palms within grazing paddocks. Understanding how farmers manage on-farm tree cover in the dry neotropics, and how these decisions impact the environmental and productive functions of pastures is key for biodiversity conservation and the development of climate-resilient production systems.

We studied tree composition of 23 dry cattle pastures of Yucatan, Mexico. We assessed the effects of palms, N_2-fixing trees and non-N_2-fixing trees on microsite environmental conditions, bare soil cover, and the performance of grasses and woody plants in their understory during the dry and wet seasons of 2018 and 2019.

We found that 45% of the regional pool of tree species of the native dry forest of Yucatan is conserved in the pastures. Palms were the most abundant overstory functional group with a relative abundance of 45%, followed by N_2-fixing trees and non-N_2-fixing trees with 33% and 22%.

Palms and trees ameliorated the impact of seasonal drought on grasses but slowed down their recovery during the wet season. They had overall higher positive effects on grass greenness and height than N_2-fixing trees and non-N_2-fixing trees and these effects were higher during the driest season. Palms also had lower bare soil than trees. Woody plants tended to increase in the understory of all functional groups as the canopies of palms and trees became denser.

Synthesis and applications

Climate warming and the alteration of precipitation regimes are expected to compromise pasture and cattle productivity worldwide. Our results show that fostering the maintenance of a diversity of native palms and trees has positive effects on the functioning of cattle pastures, especially during dry periods. A larger appreciation and understanding of the facilitative effects of remnant palms and trees on pastures during droughts may help developing more climate-resilient livestock systems that maintain productivity while contributing also to biodiversity conservation.

3.1 Introduction

Dry forests are the most threatened biome across the global tropics (Miles *et al.* 2006b; Blackie *et al.* 2014a). Massive dry forest conversion into mostly treeless pastures and crop fields has decreased biodiversity, altered vegetation-climate feedbacks and biogeochemical cycles (Harrison & Bruna 1999a; MEA 2005) and diminished the positive contribution trees can have on farm productivity and livestock well-being (Harvey *et al.* 2011).

Nevertheless, in many tropical and subtropical rural areas, local farmers usually retain some disperse trees within their grazing paddocks (Manning *et al.* 2006; Bernardi *et al.* 2016). Farmers actively select trees for various purposes and often recognize their economic and ecological value (Harvey *et al.* 2011). Trees may be crucial to maintain pasture productivity and facilitate their climate change adaptation to drought and heatwaves (Murgueitio *et al.* 2011b; Altieri *et al.* 2015) and their loss may result in undesirable changes in ecological systems (Manning *et al.* 2006).Trees can ameliorate abiotic stress through several mechanisms that facilitate grass growth, improve grass quality (Solorio *et al.* 2017; Jose & Dollinger 2019a) and enhance cattle welfare by providing forage and allowing for behavioral thermoregulation (Broom *et al.* 2013).

Despite the recognition of positive effects of trees on grass and livestock productivity, much debate remains on the levels of tree cover desirable (Augustine *et al.* 2011; Veldman *et al.* 2015), the mechanisms behind (Dohn *et al.* 2013) and the species (Harvey *et al.* 2011) and environmental conditions (Rivest *et al.* 2013) under which trees may have positive, negative or neutral effects on livestock rangelands.

Our current understanding on positive interactions between plants in natural ecosystems can guide our search for mechanisms and generalizations in agropastoral systems. Plant facilitation results as the net outcome of an interplay between positive and negative effects between plants both above and belowground. Facilitative interactions are more common as abiotic stress increases, but this general pattern differs across systems and species depending on environmental conditions and the functional traits of interacting species. Several theoretical models and meta-analysis indicate that plant facilitation peaks at intermediate levels of stress and is outweighed by competition under extreme stressful conditions and very low levels of resources (Holmgren *et al.* 2012; Valladares *et al.* 2016; Guignabert *et al.* 2020). Indeed, based on what has been learnt on facilitative interactions, we suspect scattered trees can facilitate understory grasses growth in dry tropical cattle rangelands during dry seasons, but the responses may vary among tree species and be lost during extreme drought.

There is a strong need for understanding how farmers in the dry neotropics make decisions to manage on-farm tree cover and how these decisions impact the effects trees have on the environmental and on the productive functions of pastures. A better understanding on how existing on-farm tree cover modifies pasture productivity is critical for designing sustainable livestock systems that incorporate dispersed trees or palms for climate-resilient and biodiversity conservation purposes.

Here we assess the effects of dispersed native trees and palms within dry pasturelands of southeast Mexico. We aim at understanding a) what is the species composition of scattered trees and palms in dry cattle pastures, b) how native trees and palms affect the understory during different levels of precipitation, and c) how trees and palms influence the impact of droughts on grasses and their recovery rates during rainy seasons.

3.2 Materials and methods

3.2.1 Study Region

The study was conducted in cattle farms, within the municipality of Tizimín, Yucatán, in the southeast of Mexico (Fig 3.1). The climate is warm sub-humid (Köppen & Geiger 1930) with marked dry (November to May) and wet seasons (June to October). Mean annual precipitation is 1263 mm (392 mm in the dry season; 871 mm in the wet season), and mean annual temperature is 26ºC (min. 19 ºC, max. 42 ºC), (period 1969-2016; (SMN 2020). Interannual variability in weather conditions is high and partly explained by El Niño Southern Oscillation (Philander 1983). The region is very flat with elevations ranging between 10-40 m.a.s.l. Soils are classified as leptosols (Estrada-Medina *et al.* 2013). Thin layers of unfertile topsoil cover bare rock at most sites, with soil depth generally not exceeding 30 cm.

Dry tropical forests cover about 75% of the state of Yucatan (INEGI 2017). However, they are being rapidly converted into cattle rangelands, planted with C4 exotic grasses (Bonilla-Moheno & Aide 2020). Cattle pastures are often surrounded by tropical dry secondary forests and some have a sparse tree cover of native trees.

3.2.3 Sampling design

We selected 23 actively used cattle pastures between 2.5 – 5 ha each, representing a gradient of native tree cover density (Supplementary 3.1). These pastures belonged to

6 farms with no irrigation and similar rotation system and cattle stocking rates (0.5 livestock unit/ha). The most common cattle breeds were mixed race (*Bos indicus x Boss taurus*) raised for breeding stock. This type of livestock production systems with low input of resources and dependent on seasonal rainfall is very common across the dry neotropics (Harrington & Tow 2011). The pastures were dominated by *Brachiaria brizantha, Cynodon plectostachyus* and *Megathyrsus maximus* (cover ≥ 70%).

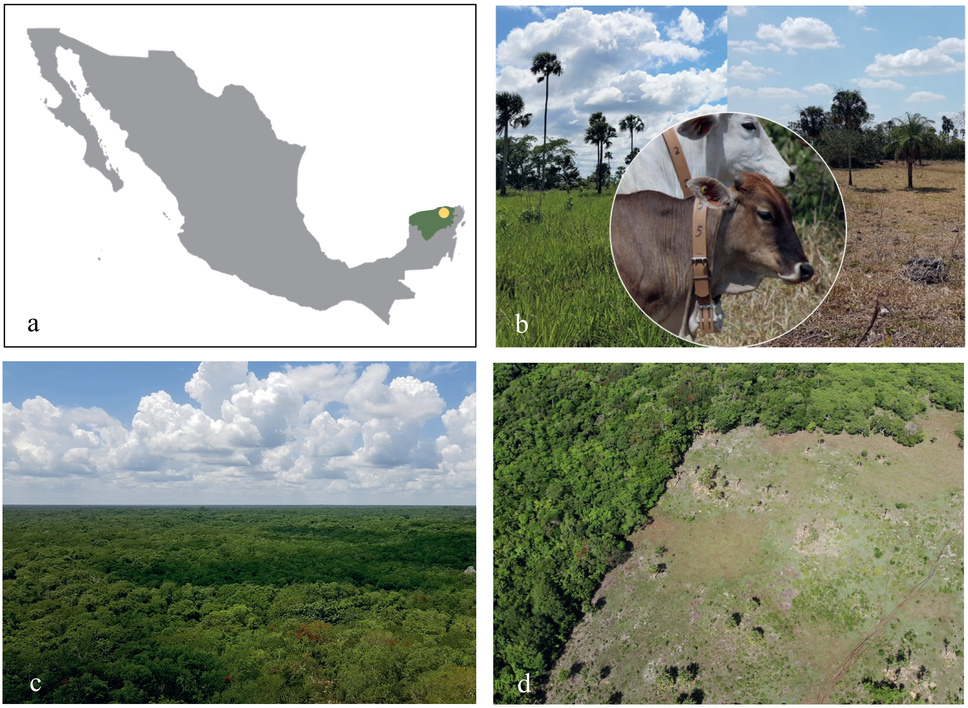


Fig. 3.1. a) Study location in Yucatan, Mexico. b) Overview of pastures during the dry and wet season. c) Tropical dry forests during the rainy season. d) Forest conversion to pasturelands with remaining scattered palms and trees.

3.2.3 Data collection

3.2.3.1 Tree diversity

Between February and March 2018, we characterized tree cover by counting and identifying all woody stems with DBH ≥ 5 cm found along five parallel transects of 4 x 50 m, separated at least 30 m from each other and evenly distributed across each pasture. We measured tree canopy density at breast height in three points along each transect using a Forestry Suppliers, Inc Spherical Convex Densiometer, and the 15 points were averaged to estimate total tree canopy density per pasture. Each individual tree or palm was identified to the species level using local knowledge and botanical collections (Universidad Autónoma de Yucatán, México). We classified tree cover into three functional groups, Palms, N_2-fixing trees (NF), and non-N_2-fixing trees (NNF) because their differences in root depth (Rivest *et al.* 2013), soil organic matter and carbon (Binkley 2005), and canopy architecture could all lead to different effects on grass productivity. Palms usually have more superficial root systems and smaller canopies than most trees.

3.2.3.2 Tree understory

To monitor tree understory during dry and wet seasons, we selected 10 trees and palms of the most abundant species in each pasture for a subset of 12 pastures (n = 120). We aimed for dispersed solitary individuals with DBH > 10 cm and measured their canopy density, canopy diameter, height, and DBH. Tree canopy density was measured periodically during each sampling between 2018 and 2019.

Under each tree or palm canopy, we established a 1-m^2 permanent plot and a paired plot in the open grassland at one tree canopy distance, both plots facing north from the tree stem. We monitored the changes in the herbaceous layer in 120 plots under trees and 120 paired plots in the adjacent open grassland once every month (30 - 35 days) during the dry (March, April, May) and the wet (July, August, September) seasons of 2018 and 2019. In each plot, we used a 1-m^2 quadrat with intersections every 20 cm to estimate the percent cover of green grass (i.e. green tones, flexible), dry grass (i.e. yellow to brown tones, crunchy), woody plants (shrubs and tree seedlings) and bare soil. Grass height was measured at the center of the plot.

3.2.3.3 Environmental conditions

We registered microsite environmental conditions and calculated the difference between conditions in the understory of palms and trees and the open grassland at the peak of every season. Samples were taken in all pastures within 2 weeks, always at the center of the plots, first below the tree canopy and 5 min later in the paired plot in open grassland. We measured soil moisture and soil temperature at the top 10 cm with the IMKO HD2 hand-held meter and the sensor with integrated TDR electronics Trime®-PICO 32; we also recorded light irradiance and air temperature every minute for 5 min using a HOBO® pendant Data Logger UA-002-64. Throughout the whole duration of this study, we recorded hourly air temperature and relative humidity with two dataloggers HOBO® U23-001 permanently placed in a pole at 4 m height in the open pastures at San Jose and Xhoppel farms. Finally, we obtained seasonal precipitation data using the R package *climatrends* (de Sousa *et al.* 2020).

3.2.3.4 Soil nutrients

We analyzed organic carbon, phosphorus, calcium, potassium and magnesium content in a subsample of 60 plots. We selected the most abundant species of each overstory functional group (i.e. Palm: *Sabal* sp., N_2-fixing tree: *Acacia pennatula,* non-N_2-fixing tree: *Coccoloba spicata*) and sampled 15 individuals of each group and 15 plots in the open at the end of the dry season 2019. Samples were evenly distributed when possible across 15 paddocks. A soil sample of 100 g was collected from the upper 10 cm soil within each plot using a soil core or a small shovel when soil was too rocky. Soil samples were stored in sealed plastic bags, dried for at least 48 hours at 55 °C and sieved (mesh-width 2 mm). All laboratory analyses were conducted at Universidad Autónoma de Yucatán (Supplementary 3.1).

3.2.4 Statistical analysis

3.2.4.1 Effects of the overstory canopy on the understory

We assessed the effects of trees and palms on the understory as the difference between the performance under the tree or palm canopy and the paired open plot. This overstory canopy effect index ($OCE = Performance_{open} - Performance_{undertree}$) ranges from -100% to 100%, being 0 when there is no difference between the response variable under the canopy and its paired plot outside the canopy. We assessed the overstory canopy effect on grass greenness, grass height, woody plants cover and bare soil during each season. To have one overall estimator of the response variable for every season, we averaged the three monthly monitoring conducted during the season. We used linear mixed models with overstory functional group (i.e. palms, N_2-fixing trees and non-N_2-fixing trees) and season (i.e. dry, wet) as fixed factors, and tree species and plot as random factors; plot was nested within pasture, and pasture nested within farm. We included the overstory traits of trees and palms (i.e. canopy density, canopy diameter, height and DBH) and microsite environmental conditions (i.e. soil moisture, soil temperature, air temperature and light irradiance) as covariates using a backward selection and the AIC criteria.

3.2.4.2 Effects of the community overstory canopy on the grass layer.

To assess the overall community effect of palms, N_2-fixing trees and non-N_2-fixing trees on grass, we considered their relative abundance and average effect on each pasture to calculate the community overstory canopy effect (COCE = OCE * relative abundance$_{\text{func group}}$). We assessed the overstory canopy effect on grass greenness, grass height, woody plants cover and bare soil during each season We assessed the community overstory canopy effects on grass greenness and grass height. Each response variable was analyzed using linear mixed models with functional group (palms, N_2-fixing trees and non-N_2-fixing trees) and season (dry, wet) as fixed factors and tree species and plot as random factors; plot was nested within pasture, and pasture nested within farms. We included the overstory tree and palm traits and environmental conditions that had a significant effect on the OCE (different for each response variable, Supplementary 3.6) as covariates.

3.2.4.3 Drought impact and recovery rate

We used the impact and recovery rates as proxies for ecological resilience to drought. The dry season impact was calculated as the difference between the pre-disturbance state and the state at the time of the peak impact (i.e. the change in grass greenness percent between wet season 2018 and dry season 2019, $I = \bar{x}_{\text{greenness}\cdot\text{wet}\cdot 2018} - \bar{x}_{\text{greenness}\cdot\text{dry}\cdot 2019}$). The recovery rates were quantified by the change of grass condition per unit time after the dry season (i.e. the change in grass greenness per day after each dry season in 2018 and 2019, $RR = \bar{x}_{\text{green}\cdot\text{wet}} - \bar{x}_{\text{green}\cdot\text{dry}}$ / days of recovery). During the sampling period, we experienced one transition from wet to dry season, and two transitions from dry to wet season, therefore, we calculated one impact and two recovery rates.

To assess the effects of the overstory tree functional group on how the dry season impacted grass greenness and its recovery afterwards, we used linear models with overstory functional group (i.e. palms, N_2-fixing trees and non-N_2-fixing trees) as fixed factor.

We used R (R Core Team 2020) with lme4 (Bates *et al.* 2014) to perform linear and linear mixed models.

3.3 Results

3.3.1 Tree diversity in pastures

Overstory canopy density in cattle pastures ranged between 0 to 30%. In total, we found 167 individuals belonging to 35 species of palms and trees. Palms was the most abundant group with a relative abundance of 45% (15% of all overstory species), followed by N_2-fixing trees with 33% relative abundance (46% of all species) and non-N_2-fixing trees with 22% of all individuals (39% of all species) (Fig. 3.2b). The most abundant species were the palms *Sabal yapa* and *S. mexicana* (Guano), the N_2-fixing tree *A. pennatula* and the non-N_2-fixing tree *C. spicata.* The most abundant families were Arecaceae (dominated by the genus *Sabal)*, and Fabaceae (well represented by the genera *Acacia, Lysiloma* and *Piscidia)*.

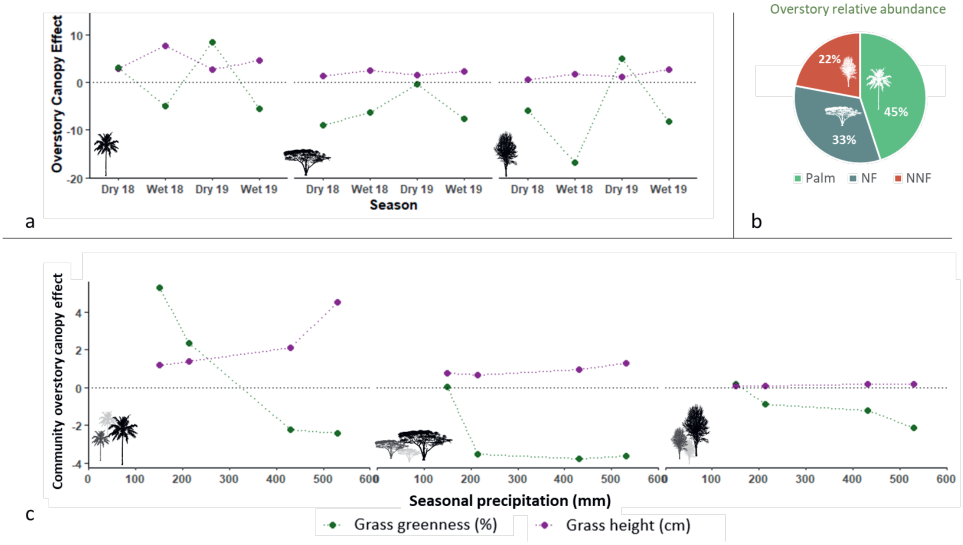


Fig. 3.2. a) Overstory canopy effect on grass greenness and grass height. b) Relative abundance of overstory functional groups in pastures. c) Community overstory canopy effect of palms, N_2-fixing trees and non-N_2-fixing trees on grass greenness and grass height along a rainfall gradient. Precipitation corresponds to total accumulated per season during monitoring period.

3.3.2 Overstory canopy effects on the understory.

Palms and trees had strong effects on grasses, shrubs and bare soil. These effects varied in direction and intensity as a function of the overstory functional type, the palm or tree canopy density and the season (Supplementary 3.5).

Palms had an overall higher positive effect on grass greenness and height than trees (Figs. 2 and 3). Grasses were greener under the canopy of palms than in adjacent open pastures during the dry seasons ($p=0.02$) and they were also taller ($p=0.02$) especially in rainy seasons (Fig. 3.2a). These effects were maintained at the community level when we consider the higher relative abundance of palms compared to trees ($p<0.01$, Fig. 3.2c, Supplementary 3.6). The facilitative effect of palms on grass greenness depended also on the density of their canopy as positive effects were lost under palm canopies denser than 40% (Fig. 3.3a).

N_2-fixing trees had a negative effect on grass greenness compared to adjacent open pastures ($p=0.02$, Fig. 3.2). Only during the most severe dry season, with 100 mm of rainfall, we observed neutral effects of N_2-fixing trees on grass greenness (Fig. 3.2a). As with palms, the effects of N_2-fixing trees depended on the density of their canopies ($p<0.001$). The negative effect of N_2-fixing trees on grass greenness was clearly visible at canopy density higher than 30% (Fig. 3.3a). The effect of N_2-fixing trees on grass height varied with the season ($p<0.01$), being neutral during the dry seasons and positive during the wet seasons (Figs. 2a). These effects were maintained at the community level when we consider the relative abundance N_2-fixing trees (Fig. 3.2c, Supplementary 3.6).

Non-N_2-fixing trees had mostly negative effects on grass greenness except under the driest season when grass was equally green in the open pasture than under the tree shade ($p=0.02$). Non-N_2-fixing trees also had neutral effects on grass height regardless of the season ($p=0.02$, Fig. 3.2c).

Palms, N_2-fixing trees and non-N_2-fixing trees had all higher woody plant cover under their canopies than in adjacent open pastures. Woody plant cover was rather similar under the different overstory types ($p>0.05$) and slightly tended to increase as the canopies of palms, N_2 and Non-N_2 fixing trees became denser (Fig. 3.3c). With denser canopies, all overstory functional groups also had higher bare soil in their understory. N_2- and non-N_2-fixing trees had more bare soil in the understory compared to palms ($p<0.01$, Fig. 3.3d).

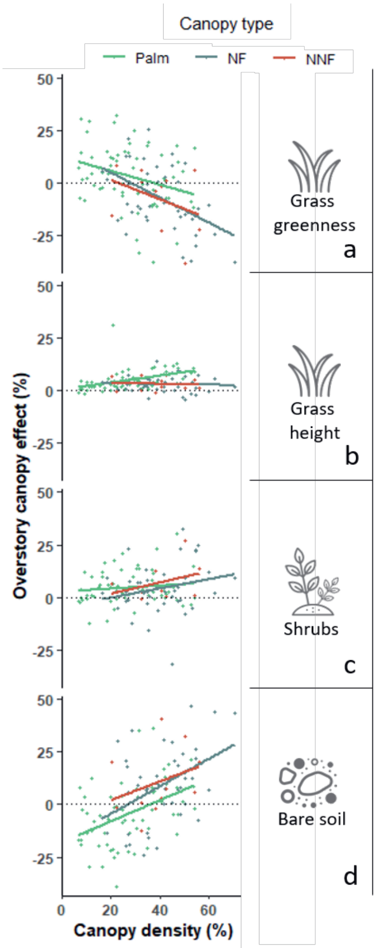


Fig. 3.3. Canopy density effects of palms, N_2-fixing trees and non-N_2-fixing trees on a) grass greenness, b) grass height, c) shrub cover and d) bare soil cover.

3.3.3 Overstory density canopy effects on environmental conditions and soil nutrients

Throughout the year, palms had a more constant, and a less dense canopy than trees (i.e. 29% palms, 42% non-N_2-fixing trees and 44% N_2-fixing trees). During the dry season, palms retained their canopy whereas most trees tended to lose their leaves (i.e. Δ canopy density = -2% palms, -15% non-N_2-fixing trees and -12% N_2-fixing trees compared to wet season). At the onset of the wet season, trees leaved out and this is reflected in stronger amelioration of irradiance under their canopies during the wet season (Irradiance = - 29% palms, -54% non-N_2-fixing trees and -50% N_2-fixing trees compared to the open grassland).

Irradiance levels and air temperature dropped by roughly 50% and 3°C under the canopies of trees and palms whereas soil temperature remained comparable to levels in open grassland (Supplementary 3.1). All the functional overstory groups reduced irradiance stronger during the wet than during the dry season ($p<0.01$) but N_2-fixing trees tended to reduce irradiance during the wet season more strongly than palms and non-N_2-fixing trees (Supplementary 3.4 and 3.8). Contrastingly, the effects on soil moisture varied with the functional group and the season ($p<0.01$). Palms and non-N_2-fixing trees had a neutral effect during the dry and wet seasons. N_2-fixing trees also had a neutral effect during the dry season but a negative effect during the wet season, reducing soil moisture compared to the open grassland (Supplementary 3.4).

Palms and trees had diverse effects on soil nutrients (Supplementary 3.1). Under palms and non-N_2-fixing trees, soils were richer in C and P ($p=0.01$ and $p<0.001$) content compared to the open grasslands, but not in Ca, K and Mg content. None of the soil nutrients assessed differed between soils under N_2-fixing trees and adjacent open grasslands.

3.3.4 Drought impact and recovery rates afterwards.

Palms and trees ameliorated seasonal drought impact on grasses ($p<0.001$, Supplementary 3.7). Grass greenness was higher in grasses growing under the canopy of palms than in grasses growing under the canopy of trees, both during and after the dry seasons (Fig. 3.4a). During the severe dry season of 2019 (characterized by a drop of 100 mm from average), the reduction in greenness was lower for grasses growing under palms and trees than in the open grassland but not different among the functional groups (Fig 4b). However, during the subsequent rainy season, grasses growing in open grasslands recovered their greenness faster than those growing under trees and palms ($p<0.001$, Fig 4c, Supplementary 3.7). Overall, grass recovery rates slowed down with the severity of the dry season. After the severe dry season of 2019, grass greenness recovered more slowly under the shade of trees and especially under the shade of palms.

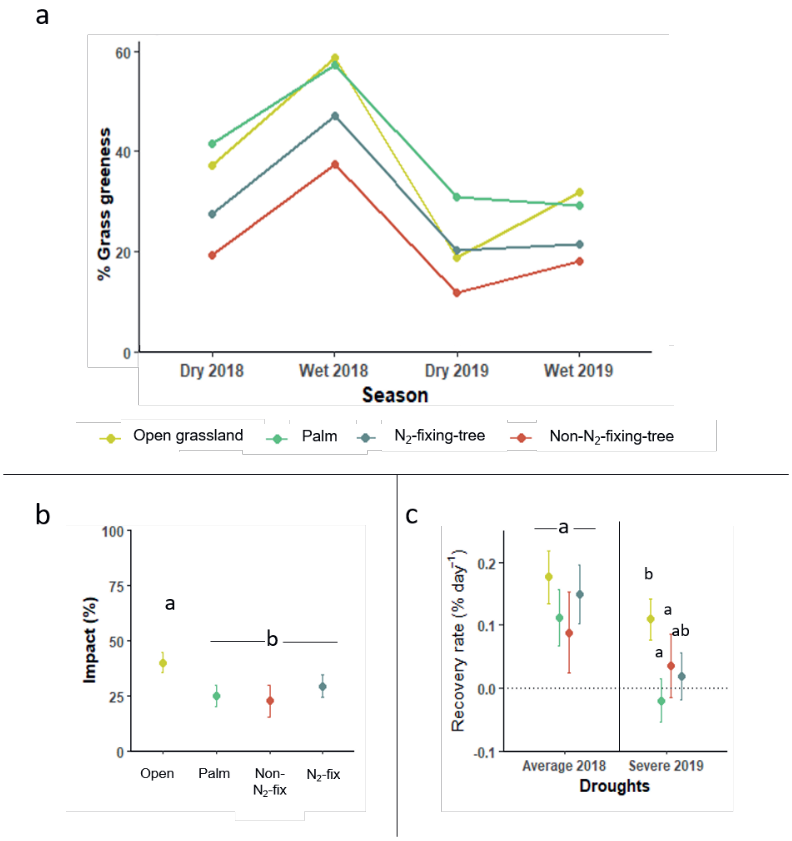


Fig. 3.4. a) Grass greenness percent under different overstory canopy types during dry and wet seasons in 2018 and 2019. b) Impact of a severe drought (2019) on the greenness of grasses growing under the different canopy types. c) Recovery rates of grass greenness after droughts in 2018 and 2019.

3.4 Discussion

3.4.1 Palms and trees mediate the effects of droughts

Our detailed monitoring of the effects of palms and trees on the functioning of dry cattle pastures shows that their facilitative effects on grasses are enhanced during drought. The positive effect of palms increased, and the negative effects of N_2-fixing and non-

N_2-fixing trees decreased during the driest season. Overall, our results indicate that 1) overstory functional groups determine the relationships between drought intensity and tree-pasture interactions in cattle pastures; 2) within overstory functional groups, the effects on the understory depend on canopy density; and 3) the overstory maintains grass greenness when water is scarce reducing the impact of prolonged droughts.

3.4.1.1 Overstory functional groups determine the relationships between drought intensity and tree-pasture interactions in cattle pastures

Palms facilitated grass greenness and height more strongly than trees. Palms also had lower bare cover under their canopies than trees and facilitated the recruitment of woody plants below their canopy. These overall positive effects of palms on cattle pastures can result from the combination of above and belowground abiotic amelioration while maintaining irradiance levels sufficiently high for grasses. Throughout the year, palms have a more constant, and a less dense canopy than trees. Palms increase total organic carbon and uniformly distribute radicular exudates that maintain organic matter in the upper soil (Leite *et al.* 2013). Also diazotrophic bacteria and other N_2-fixing bacteria associated to palms can potentially contribute to soil nutrients (Reis *et al.* 2000). In general, N_2-fixing trees had the lowest positive effects on grass greenness in both dry and wet seasons. Although N_2-fixing trees can potentially supply nitrogen to grasses, they also have dense canopies and the strongest reductions of soil moisture, especially at the onset of the wet season when they are leafing out (Supplementary 3.4). It is plausible to think that there may be a trade-off between abiotic amelioration (i.e. transpiration demands and nutrient levels) and lower irradiance levels under the overstory canopy, particularly N_2-fixing trees.

Our results show that the relative importance of the facilitative effects of overstory trees on dry tropical pastures depends on the interactions and characteristics of the benefactor trees and the overall environmental conditions, probably as the result of trade-offs in resource levels under the canopy compared to open conditions. Meta-analysis and recent literature on the effects of shade and drought on plant performance in field and experimental conditions (Holmgren *et al.* 2012; Stahlheber & D'Antonio 2014) and some productive systems (Caldeira *et al.* 2014; Cooper *et al.* 2014) show that facilitative interactions tend to be non-linear and drop at lower levels of irradiance.

3.4.1.2 Within overstory functional groups, the effects on the understory depend on canopy density

Overstory canopy density plays a key role in the interplay between facilitative and competitive effects. We found facilitative effects on grasses at low canopy densities and increasing facilitative effects on shrubs and tree seedling recruitment as canopies became denser. Below the denser canopies, the amount of bare soil also tended to increase. As canopy density increases, not only light levels may drop below optimal for C4 grasses but also competition for soil water may increase as woody plant cover increases under denser tree canopies. Indeed, vegetation surveys in semi-arid regions have demonstrated that trees facilitate directly understory plants by increasing the habitat for the less adapted species and, indirectly, by affecting their competitive outcomes (Soliveres *et al.* 2011).

The effects of tree canopy density on the understory are complex and seasonally dependent. In dry seasonal systems, deciduous and semi-deciduous trees drop their leaves as a synchronized strategy to escape water stress and increase reproductive success during the dry months (Eamus 1999). Therefore, the potentially ameliorating effect of the overstory canopy on air temperature and the transpiration demands of the understory plants are reduced in the dry season when understory plants may need it the most. The implications will depend on the physiological characteristics of the understory plants. More drought-tolerant and light-demanding species may benefit the most from overstory tree species with low canopy density during the dry season. We found facilitative effects on the C4 grasses mostly under the low canopy density of palms than under the deeper canopies of non-N_2-fixing trees and N_2-fixing trees. These exotic C4 grass species are very tolerant to water stress and able to keep a positive photosynthetic capacity at high temperatures and low water availability (Chaves *et al.* 2003). That is one of the reasons why they have been promoted across tropical natural and productive systems (Edwards *et al.* 2010).

Cattle behavior may also play an important role in the observed patterns of tree-grass interactions. During hot and dry periods, palms and trees increased or maintained grass greenness under their canopy and provided shade that can alleviate the negative effects of heat stress on cattle (Broom *et al.* 2013). Both factors can attract a higher concentration of cattle grazing, ruminating or resting and partly explain the higher proportion of bare soil under the shade of trees compared to palms (Supplementary 3.3).

3.4.1.3 The overstory maintains grass greenness when water is scarce reducing the impact of prolonged droughts.

We found that palms and trees reduce the impact of droughts on pasture productivity. Canopy shade becomes extremely valuable in dry periods by providing cooler microsites compared to the adjacent grasslands. This results in higher green grass cover under the overstory than in the open grasslands. On the contrary, we found that palms and trees slow down grass recovery at the onset of the rainy season, especially after the most severe drought. Grass greening recovery responds and progresses faster in open pastures where light is not limiting.

Interestingly, although palms had the overall largest positive effects on pastures by increasing grass greenness during dry periods and grass height along the whole year, grasses failed to recover under palms after the severe drought of 2019. In contrast, grasses recovered faster under the N_2- and non-N_2-fixing trees despite the overall neutral to negative effects we had monitored earlier. These seemingly puzzling patterns may be explained by a combination of factors including microclimate conditions under the canopy, root depth of trees and the abundance of grasses under the canopy of palms and trees.

Palms have shallower root systems, which may result in higher soil moisture competition with grasses during the dry season. Palms also have smaller canopies that allow higher irradiance levels in the understory that can contribute to higher rates of soil water evaporation and understory plant transpiration demands. Indeed, we recorded lower levels of soil moisture under palms than under trees during the dry seasons (Supplementary 3.4). Also, the lower grass abundance under N_2 and non-N_2-fixing trees compared to palms may result in lower competition for resources and therefore a faster grass recovery after a severe drought.

These results point towards opposite contributions of palms and trees on pasture resilience. While palms have overall positive effects on grass greenness and grass height during most of the year, trees may offer pockets of green grass after severe dry seasons. Future field experiments combined with continual monitoring are needed to assess the relative importance of the direct and indirect effects trees and palms have on microclimate, nutrient levels, cattle behavior and woody plant competition to explain the direction and magnitude of their interactions with grasses in productive cattle pastures.

3.4.2 Building resilience of tropical pastures: Towards reconciling biodiversity conservation and climate change adaptation.

Scattered palms and trees in pasturelands provide important conservation opportunities in their own. We found a wide diversity of palm and tree species of the native dry forest of Yucatan conserved in the cattle pastures (i.e. 45% of the regional pool of tree species; (Hernandez-Ramirez & Garcia-Mendez 2015).

Palms are the most abundant species in pastures and their positive effects we carefully documented contribute to understand why farmers may be motivated to conserve palms over other dry forest tree species in their pastures. Despite their widespread occurrence across the neotropics and their highly diversified local uses (Araújo & Lopes 2012), the effects of palms on grasses in productive landscapes may have been widely overlooked. Attention has focused on the economic benefits of palms with worldwide importance (Barfod *et al.* 2015), and there have been some mostly anecdotally references to possible positive effects of palms on pastures (Calle *et al.* 2017). Our study contributes to understand the role of native palms in neotropical productive systems and the mechanisms explaining their facilitative effects on grasses during droughts demonstrating that palms have an overall positive effect on pasture productivity in the dry tropics.

Whether farmers perceive the positive effects of palms or not on grasses, it is clear they do not consider them as a threat and maintain them in pastures. It is less obvious though, why native trees remain in pastures given their mostly competitive effects with grasses. Farmers may counterbalance the negative effects of trees on grasses by considering the provision of different ecosystem services such as provision of diverse forage and shelter for livestock and other animal species under their dense canopies (Murgueitio *et al.* 2011b; Broom *et al.* 2013), even when they do not profit directly. Farmer's choices of retaining native trees may not aim at maximizing grass yields but rather may reflect a deeper and holistic understanding of the resilience, adaptability and transformability of their social-ecological systems and livelihoods (Walker *et al.* 2004).

Our findings demonstrate that even in productive systems designed to tolerate high levels of abiotic stress such as dry tropical C4 pastures, native palms and trees play a fundamental role in their resilience to drought. Removing whole functional groups of species can make ecosystems more vulnerable to environmental changes that previously could be buffered, compromising their resilience and capacity to maintain the provision of ecosystem services (Folke *et al.* 2004). Our results indicate that integrating native trees and palms in productive pastures may help mitigating the loss of biodiversity (Harvey *et al.* 2011) while increasing the resilience and adaptation of productive systems to drought, heat and increasing variability in rainfall patterns and weather extremes (Murgueitio *et al.* 2011b; Matocha *et al.* 2012b).

There is much understanding about the management and restoration of pastures in the wet tropics but less is known about the dry tropics (Griscom & Ashton 2011). Considering the rapid expansion of pasturelands for livestock farming throughout Mexico and other tropical regions (Wassenaar *et al.* 2007; Bonilla-Moheno & Aide 2020), replacement of dry forests by pasture lands may continue to advance in the future. Our results show that fostering the maintenance of a diversity of native trees and palms has positive effects for the functioning of cattle pastures especially during dry periods. These positive effects of trees and palms on pastures may become increasingly important to maintain cattle pastures and their provisioning services as climate warming progresses. A larger appreciation and better understanding of the facilitative effects of remnant palms and trees on pastures may help developing more sustainable livestock management systems that maintain productivity while contributing also to biodiversity conservation. Transforming current visions of cattle pastures from treeless landscapes to systems with larger native tree cover will take time (Holmgren & Scheffer 2017) but this study provides clear evidence that this transformation can build resilience of agricultural landscapes in the dry tropics to the challenges of the future.

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Author Contributions

I.R.H.S. and M.H. conceived the ideas, designed the study, analyzed and interpreted the results and wrote the manuscript. I.R.H.S., J.v.H and V.D. collected and analyzed data. F.J.S.S. contributed to data collection and interpretation. All authors revised the manuscript. The authors declare no conflicts of interest.

Supplementary information

Supplementary 3.1. Palm and tree characteristics, environmental variables and soil nutrients measured during the field surveys.

	Open			**Palm**			**N_2 fixer tree**			**No - N_2 fixer tree**		
Tree characteristics												
n	120			63			43			11		
Canopy density (%)	2.18	±	0.26	29.62	±	1.78	44.40	±	2.05	42.35	±	4.18
Dry season	2.21	±	0.25	28.55	±	1.72	39.69	±	2.03	35.43	±	3.29
Wet season	2.07	±	0.32	30.68	±	1.95	51.90	±	2.33	49.78	±	5.65
Canopy diameter (m)	NA	NA	NA	3.56	±	0.08	7.61	±	0.66	4.69	±	0.70
DBH (cm)	NA	NA	NA	20.33	±	1.87	39.44	±	6.58	13.69	±	3.22
Height (m)	NA	NA	NA	17.24	±	0.79	19.18	±	1.55	15.27	±	2.42
Environmental variables*												
Soil moisture* (%)	16.53	±	0.29	-0.07	±	0.45	-0.38	±	0.51	0.70	±	0.86
Soil belowground temperature* (°C)	35.36	±	0.24	0.31	±	0.31	0.32	±	0.24	0.56	±	0.81
Soil aboveground temperature* (°C)	39.95	±	0.42	-1.20	±	0.54	-1.81	±	0.70	-2.77	±	1.64
Light intensity* (lux)	101156	±	5329	-46149	±	7382	-61489	±	8207	-78641	±	18201
Light intensity* (%)				-22.77	±	6.85	-44.27	±	5.41	-49.44	±	13.11

Soil nutrients$^+$	14	18	15	14	Anova	K-W
Calcium (Cmol(+)/Kg)	38.22 ± 6.33	18.53 ± 1.52	29.81 ± 5.46	20.76 ± 1.18		0.398
Carbon (%)	9.46 ± 0.42	11.97 ± 0.82	9.50 ± 0.70	12.44 ± 0.87	0.01	
Magnesium (Cmol(+)/Kg)	25.39 ± 2.53	32.53 ± 2.25	28.23 ± 2.52	32.14 ± 1.94	0.10	
Phosphorus (mg/Kg)	4.74 ± 2.09	14.05 ± 1.80	6.97 ± 1.64	11.48 ± 1.56		0.0007
Potassium (Cmol(+)/Kg)	0.35 ± 0.02	0.38 ± 0.03	0.44 ± 0.08	0.42 ± 0.05		0.94

Mean values ± standard error.

*Values for Palm, N_2 fixer tree and No – N_2 fixer tree express the difference with the open plots in absolute values.

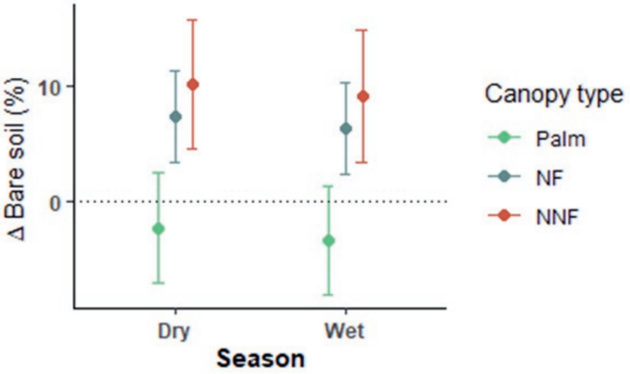
[1] We run Anova or Kruskal-Wallis tests to analyze the effect of ovestory functional groups on soil nutrient contents. The corresponding p-values are reported.

+ Determination of soil organic carbon was based on the Walkley & Black method (Walkley & Black 1934) and of phosphorus on the Olsen method (Olsen & Sommers 1982). Calcium and Potassium were determined using a Photoelectric flame photometer and Magnesium was determined by titration with EDTA - disodium-dihydrogen-ethylenediaminetetraacetate (Tucker & Kurtz 1961). Total nitrogen was not determined because lack of adequate storage capacities and transport could cause nitrogen significant changes.

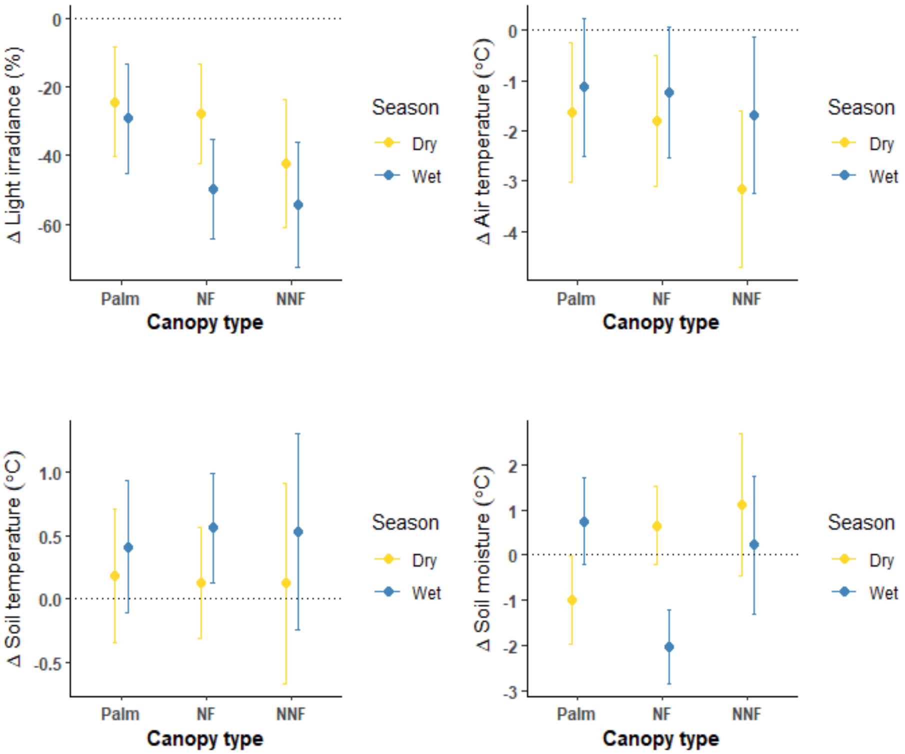
Supplementary 3.2. Characteristics and coordinates of the livestock farms studied in Yucatan, Mexico.

Farm Pasture	**Pasture size (ha)**	**Tree canopy density (%) in pasture**	**Latitude**	**Longitude**
San Jose				
11	2.83	15.69	21.22317	-87.9414
12	3.17	20.89	21.22399	-87.9399
13	3.46	4.24	21.22467	-87.944
14	2.48	6.56	21.22439	-87.9469
15	2.19	18.68	21.22421	-87.9455
Josué				
21	2.22	5.83	21.23194	-87.9512
Eduardo				
31	3.03	29.25	21.22647	-87.9492
Santa Cruz				
41	2.82	4.24	21.15069	-87.9114
42	3.07	3.47	21.14937	-87.9122
43	2.61	0.95	21.14782	-87.9126
Xhoppel				
51	4.46	14.18	21.1131	-87.7992
52	4.34	0.36	21.10709	-87.8022
53	4.53	0.71	21.10474	-87.8022
54	4.55	3.89	21.10242	-87.8022
55	3.83	1.93	21.09797	-87.8022
56	3.70	4.90	21.10752	-87.7949
57	4.40	3.92	21.10762	-87.792
58	4.67	18.70	21.11094	-87.7992
59	4.60	7.88	21.10752	-87.7895
510	3.88	5.05	21.10763	-87.7873
512	4.92	1.82	21.10935	-87.7893
La Escalera				
61	2.76	16.94	21.15461	-87.8096
62	3.77	21.74	21.15	-87.81
Average	**3.49**	**14.18**		

Supplementary 3.3. Difference in bare soil percent between the open grasslands and the understory of palms and trees during the dry and the wet seasons. Positive values indicate an increase in bare soil in the understory of trees and palms compared to the adjacent grassland.



Supplementary 3.4. Difference in the environmental variables between the open grasslands and palms and trees during dry and wet seasons. Negative values indicate reduction and positive values indicate increase.



Supplementary 3.5. Results of the mixed linear models of the functional group and season factors and the environmental covariates on the understory response variables.

Predictors	*Sum Sq*	*Mean Sq*	*Num DF*	*DenDF*	*F value*	*Pr(>F)*	
Grass greenness (N = 1191)							
Season (all)	19193.21	6397.7379	3	1103.60	13.461	0.000	***
Functional group	2364.196	1182.0979	2	120.549	2.48725	0.087	
Canopy density	4760.35	4760.3499	1	677.575	10.0162	0.002	*
Dif. light irradiance	3224.425	3224.4254	1	879.423	6.78451	0.009	*
Season (all):Functional group	7167.308	1194.55143	6	1094.11	2.51345	0.020	*
Grass height (N = 999)							
Season (all)	728.8998	242.966617	3	907.927	4.77001	0.003	*
Functional group	402.4545	201.227253	2	88.6755	3.95056	0.023	*
Tree height	388.9285	388.928552	1	88.5627	7.63559	0.007	*
Canopy diameter	340.5002	340.500277	1	93.7870	6.68482	0.011	*
Season (all):Functional group	588.9170	98.1528458	6	910.111	1.92697	0.074	
Woody plant cover (N = 1191)							
Functional group	230.7144	115.357202	2	117.546	0.57026	0.567	
Canopy density	127.2871	127.287152	1	968.200	0.62923	0.428	
Bare soil (N=1191)							
Functional group	5882.7	2941.33	2	117.33	5.9316	0.00351	*
Season (2)	299.1	299.06	1	1117.41	0.6031	0.43756	
Canopy_density	1287.5	1287.51	1	991.23	2.5964	0.10742	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Supplementary 3.6. Results of the mixed linear models of the functional group and season factors and the environmental covariates on the understory response variables at the community level.

Predictors	*Sum Sq*	*Mean Sq*	*NumDF*	*DenDF*	*F value*	*Pr(>F)*	
Community effect on grass greenness (N = 1191)							
Season (all)	1287.62	429.207	3	1105.23	5.28012	0.001	**
Functional group	321.944	160.972	2	121.220	1.98028	0.142	
Canopy density	573.619	573.619	1	722.450	7.05667	0.008	*
Dif. light irradiance	468.460	468.460	1	887.011	5.76301	0.017	*
Season (all):Functional group	1407.28	234.548	6	1094.61	2.88541	0.009	*
Community effect on grass height (N = 999)							
Season (all)	102.397	34.1325	3	907.698	4.31598	0.005	*
Functional group	118.156	59.0779	2	89.8460	7.47029	0.001	**
Tree height	69.9563	69.9563	1	109.862	8.84583	0.004	*
Canopy diameter	46.0519	46.0519	1	103.028	5.82317	0.018	*
Season (all):Functional group	153.048	25.5081	6	910.094	3.22544	0.004	*
Community effect on woody plant cover (N = 1191)							
Functional group	88.35793	44.17897	2	115.2985	1.526272	0.222	
Canopy density	19.97552	19.97552	1	979.1117	0.690104	0.406	
Community effect on bare soil (N=1191)							
Functional group	808.7122	404.3561	2	116.942	5.119286	0.007391	*
Canopy_dens	93.411	93.411	1	1013.674	1.182615	0.277083	
Season	22.32021	22.32021	1	1117.025	0.282581	0.59512	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Supplementary 3.7. Results of the linear models of the functional group factor on the impact and recovery rates during and after droughts 2018 and 2019.

Predictors	*Sum Sq*	*Mean Sq*	*NumDF*	*DenDF*	*F value*	*Pr(>F)*	
Impact 2019 (N=237)							
Functional group	11659.24	3886.415	3	184.8388	12.16648	0.000	***
Recovery rate 2018 (N= 172)							
Functional group	0.155326	0.051775	3	136.1447	2.950806	0.035	*
Recovery rate 2019 (N= 237)							
Functional group	0.74712	0.24904	3	195.5545	15.65318	0.000	***

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Supplementary 3.8. Results of the mixed linear models of the functional group and season factors on the environmental variables.

Predictors	*Sum Sq*	*Mean Sq*	*NumDF*	*DenDF*	*F value*	*Pr(>F)*	
Δ Light irradiance (N = 436)							
Functional group	4449.834	2224.917	2	110.3179	1.770331	0.175079	
Season	10364.21	10364.21	1	318.095	8.246638	0.004357	**
Functional group:Season	7009.817	3504.908	2	318.8116	2.7888	0.062996	
Δ Air temperature (N= 436)							
Functional group	5.208014	2.604007	2	107.5369	0.570293	0.56706	
Season	45.31554	45.31554	1	319.411	9.924363	0.001785	**
Functional group:Season	8.204736	4.102368	2	320.0761	0.898442	0.408228	
Δ Soil temperature (N=427)							
Functional group	0.083722	0.041861	2	102.7472	0.007083	0.992942	
Season	7.76879	7.76879	1	305.0906	1.314562	0.252469	
Functional group:Season	1.021948	0.510974	2	305.287	0.086462	0.917193	
Δ Soil moisture (N = 427)							
Functional group	60.21941	30.1097	2	115.4585	0.77399	0.463547	
Season	23.34761	23.34761	1	327.8574	0.600165	0.439073	
Functional group:Season	465.7404	232.8702	2	327.6233	5.98608	0.002797	**

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Chapter 4

Palm trees increase microbial diversity of grass rhizosphere in dry tropical pastures

This chapter is based on:

Hernández-Salmerón, I. R., Holmgren, M., Moreno-Hagelsieb, G., Olmedo- Álvarez, G. & Hernández-Salmerón, J. E. (*submitted*). Palm trees increase microbial diversity of grass rhizosphere in dry tropical pastures.

Abstract

Tropical dry forests are rapidly being converted into mostly treeless pastures. Nevertheless, in many tropical and subtropical areas, farmers retain native trees and palms for various purposes, often recognizing their economic and ecological values. In dry environments, trees can have positive effects on grass productivity through above and belowground mechanisms. The interactions between trees and soil microbial communities are essential for plant defense and soil nutrient availability and acquisition. Palm trees are the most common overstory tree functional group in dry tropical pastures. The purpose of this study is to determine how the overstory of palm trees influences the microbial communities in dry cattle pastures. We analyzed soil samples collected from the grass rhizosphere growing under the palm tree and from the surrounding areas of exposed grasses. In order to have a broader comparative reference, bulk soil and Acacia sp. rhizosphere were also analyzed. After DNA isolation and 16S rRNA gene sequencing, a total of 10,900 OTUs were referenced against the Silva database. We found higher soil microbial richness, diversity and dominance in the grass rhizosphere under palms, which suggests a positive effect in the microbiome structure. An enrichment of Proteobacteriota and Bacteroidota was observed in the grass rhizosphere growing under palm trees. Firmicutes were less abundant in the grass rhizosphere compared to Acacia and bulk soil. Functions related to plant-growth promotion were similar in grass and Acacia rhizospheres. This is the first report suggesting that soil microbiomes in dry tropical grasslands are influenced by palm trees, providing evidence for the advantage of maintaining palm trees in dry tropical pastures.

4.1 Introduction

The rhizosphere is a complex and largely unknown ecosystem within a narrow zone of only a few millimeters surrounding plant roots. It is influenced by the release of plant-derived organic exudates and mucilage (Mendes *et al.* 2013; Philippot *et al.* 2013). Rhizosphere microbiota, usually constituted of plant-growth promoting bacteria (PGPB), contribute to plant growth by enhancing nutrient acquisition from insoluble mineral compounds, nutrients such as phosphorus, iron, sulfur and nitrogen. These microbes also provide protection from pathogens either by inducing the plant systemic resistance, or directly through the synthesis of antibiotics (Lugtenberg & Kamilova 2009; Glick 2012). Microbial communities directly interact with the host plant as a result of long ongoing co-evolution (Berg *et al.* 2016). It has been well documented that the rhizosphere composition differs between plant species, since rhizodeposits can be species-specific and act as attractants for a specific group of microorganisms, suggesting that plants may regulate the composition of their rhizosphere to improve plant fitness (Shi *et al.* 2011) (Berendsen *et al.* 2012) (Zhalnina *et al.* 2018). However, environmental factors, soil characteristic (e.g. pH, humidity, oxygen, nutrients) and other microbial compounds have profound effects on microbial community structure (Berg & Smalla 2009).

Rhizosphere bacterial communities can be particularly abundant when compared, in relative terms, to soil bulk density. They usually display higher densities and increased microbial activity, while richness and evenness are often affected too (Lopes *et al.* 2016). Bacteria play important ecological roles in carbon, nitrogen and phosphorus cycles, nutrient acquisition, and recycling. Bacterial species can contribute to counteracting abiotic stressors such as drought or soil salinity, by protecting the roots from dryness or by producing metabolites that help maintain nutrient and hormone homeostasis in the plant (Glick 2014; Ferjani *et al.* 2015; Soussi *et al.* 2016). The adaptation of plants to environmental stressors is indeed, partly, a result of the structure of the rhizobiome. Characterizing genetic and functional diversity of soil bacterial communities is fundamental to better understand and manage ecosystem processes in both natural and productive systems.

Globally, tropical dry forests are the most threatened terrestrial biome by intensive land use (Miles *et al.* 2006a; Blackie *et al.* 2014b). They are being rapidly converted into livestock pastures and agricultural land altering biodiversity, vegetation-climate feedbacks, and biogeochemical cycles (Andren 1994; Harrison & Bruna 1999b; MEA 2005). Yet, local farmers in tropical rural areas usually retain some native trees and palms in their lands because they provide multiple ecosystem services (Harvey & Haber

1998; Angelsen *et al.* 2014; Reed *et al.* 2017). Trees are crucial to maintain pasture productivity and facilitate their adaptation to climate change (Murgueitio *et al.* 2011a; Matocha *et al.* 2012a; Altieri *et al.* 2015). They can facilitate grass growth and improve grass quality by reducing air temperature and soil water evaporation (Murgueitio *et al.* 2011a) (Lopes *et al.* 2016) (Jose & Dollinger 2019b) (Deniz *et al.* 2020), increasing soil water holding capacity (Bosi *et al.* 2019), improving soil structure (Vazquez *et al.* 2020) and, sometimes, also translocating deeper soil water to grasses through hydraulic lift (Gyenge *et al.* 2002; Pollock *et al.* 2009). Furthermore, trees can improve soil nutrient availability through higher decomposition rates by their associated microorganisms (Peri *et al.* 2008), nitrogen fixation (Sarabia *et al.* 2020) and organic matter accumulation. In fact, positive effects of trees on grasses have been reported in dry environments, mostly under N_2 fixing trees (Rivest *et al.* 2013; Mazía *et al.* 2016). Recent observations in cattle farms in the dry tropics found that palms also have higher positive effects on grass greenness and height during dry periods, which highlights the importance of palms, as they are the most abundant trees in this landscape with a relative abundance of 45% compared to N2-fixing trees with 33%, and non-N2-fixing trees with 22% of all individuals (Hernández-Salmerón and Holmgren, submitted). These results have motivated us to study the effect of the tree overstory (i.e., tree canopy) on a microecosystem governed by microorganisms interacting with plant roots. Thus, in this study we explore the link between the above-ground ecological services and the rhizosphere microbiome structure. We hypothesized that tree overstory influence the microbial community structure of the grass rhizosphere. Based in the massive sequencing of the 16S rRNA gene, we analyzed the diversity of bacterial species of the grass rhizosphere in the understory of the highly abundant palm tree *Sabal* spp. and open pasture areas exempt from any palm tree. To contrast these two microenvironments, we also analyzed the rhizobiome of a legume tree *Acacia* spp., which is also abundant in the sampled farm, and harbours intrinsic relations with nitrogen-fixing bacteria (Hoque *et al.* 2011). All rhizosphere samples were also compared to the bulk soil microbial composition.

4.2 Materials and Methods

4.2.1 Study site description and samples collection

This study was performed in the cattle farm San José, located in the municipality of Tizimín (21.22399, -87.9399), Yucatán, in southeast México (Fig. 4.1). The climate in this region is warm sub-humid (Köppen & Geiger 1930), with marked dry and wet seasons (November to May and June to October). The mean annual precipitation is 1263 mm, with a mean annual temperature is 26ºC (min. 19 ºC, max. 42 ºC), being May the hottest month (27.9ºC), and January the coldest (21.9 ºC) (SMN 2020). The region is practically flat, with elevations ranging between 10-40 m.a.s.l. Soils are generally dark brown or red, shallow, very rocky, and not very fertile, classified as leptosols (Estrada-Medina *et al.* 2013). Thin layers of topsoil cover bare rock at most sites, with soil depth generally not exceeding 30 cm. Cattle pastures are often surrounded by tropical dry secondary forests and tend to have a sparse tree cover of native trees used for different purposes by local people. The pastures have been planted with exotic C4 grasses, especially *Brachiaria brizantha, Cynodon plectostachyus, and Megathyrsus maximus.*

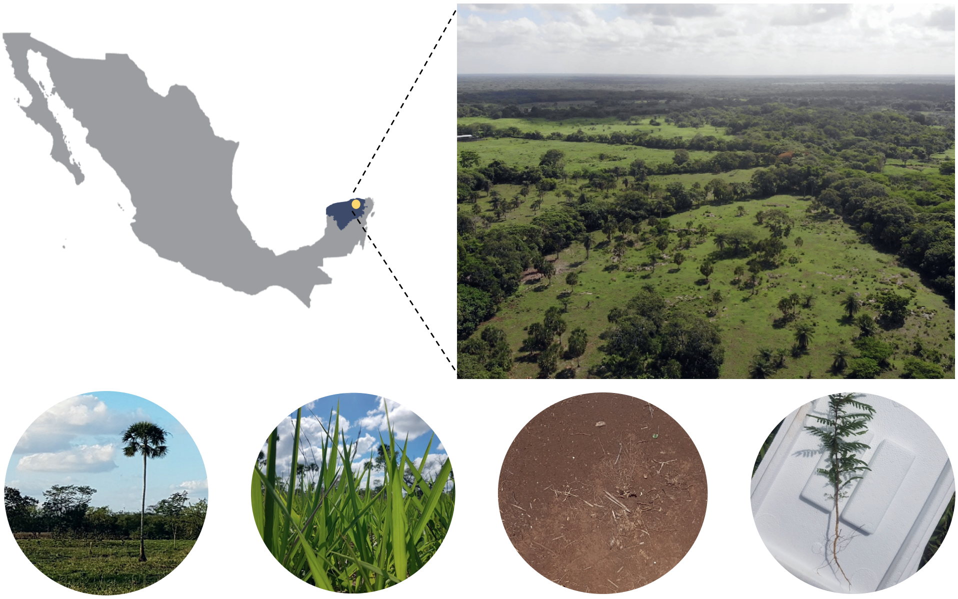


Fig. 4.1. Location and aerial view of the study system in Yucatán, México. Samples were collected from the grass rhizosphere growing under palm trees and from open pastures and compared to rhizosphere from bulk soil and *Acacia* sp. as references.

Soil properties were measured before sampling. Phosphorus, calcium, magnesium and potassium content were analyzed in composite samples from the grass in the open and under the palm in May 2019. In each of the two microsites, five soil samples of 100 g were collected and pooled from the upper 10 cm using a soil core or a small shovel if the soil was too rocky. The soil sample was stored in a sealed plastic bag, dried for at least 48 hours at 55 °C and sieved (mesh width 2 mm). Determination of soil organic carbon was based on the Walkley & Black method (Walkley & Black 1934), while phosphorus was determined by the Olsen method (Olsen & Sommers 1982). Calcium and Potassium were determined using a Photoelectric flame photometer; Magnesium was determined by titration with EDTA - disodium-dihydrogen-ethylenediaminetetraacetate (Tucker & Kurtz 1961). Total nitrogen was not determined because lack of adequate storage capacities and transport could cause significant changes (Nelson & Bremner 1972). Laboratory analysis was conducted at Universidad Autónoma de Yucatán.

For microbiome data, we sampled four microsites: 1) grass rhizosphere in open pasture, 2) grass rhizosphere under the canopy of *Sabal* palm trees, collected 1 m away from the tree trunk, 3) *Acacia* spp. rhizosphere, obtained from a 30 cm high young plant, due to the ease of digging the soil and manipulating the roots, and 4) bulk soil, collected a few meters away from any plant with a sterile spatula at a depth of ~20 cm. The grass rhizosphere was sampled as follows: root systems were excavated at least 10 cm and up to ~20 cm under the base of the plant. The roots were shaken to collect only the adhered soil and poured into separate 500 g sterile sealed bags and frozen on dry ice immediately after collection. We collected five replicate samples for each microsite condition at the end of the rainy season (October 2019). Samples were transported to the laboratory and preserved at -20 °C until DNA was isolated.

4.2.2 DNA extraction and sequencing

Metagenomic DNA was extracted from 1 g of each of the soil samples using the QiagenÒ DNeasy Power Soil Kit, following the manufacturer instructions. Purified DNA samples were quantified and prepared to 30 hg/hl before sequencing. The V3-V4 region of the 16S rRNA gene was amplified using primers 341F (5´ CCTACGGGNGGCWGCAG 3´) and 785R (5´ GGACTACHVGGGTATCTAATCC 3´), showing high performance for the amplification of bacterial sequences, as described in (Takahashi *et al.* 2014) . Libraries were obtained following protocols from IluminaÒ Miseq^{TM} (2 x 300 bp), with approximate 30 K reads per sample. Sequencing services were provided by the Laboratory of Genomics Services, Irapuato, México (http://langebio.cinvestav.mx/labsergen).

4.2.3 Bioinformatics processing

The amplified reads were quality checked using the dada2 program (Callahan *et al.* 2016). Reads of >30 higher quality were later analyzed using the mothur software package v.1.44.3 (Schloss *et al.* 2009). Sequences were de-noised, that is, ambiguous base calls and homopolymers exceeding 8 bp were removed. Sequences were aligned using the Silva reference alignment (Quast *et al.* 2013). Chimeric sequences were removed using vsearch (v2.13.3) (Rognes *et al.* 2016), also implemented in mothur. The clean sequences were clustered at 97% identity to obtain Operational Taxonomic Units (OTUs). For the taxonomy assignment we used Silva v138, using a Naïve Bayes classifier with $\geq$ 80% confidence scores (Wang *et al.* 2007). After removing low abundance OTUs and normalizing to account for differences in read depth, we rarefied at the minimum sequence number per sample (21,094 sequences). The rarefied set of sequences was exclusively used for alpha diversity estimations. Chloroplast and mitochondrial sequences were removed from the OTU table.

4.2.4 Data analysis

Microbial diversity analysis and plots were performed using phyloseq and ggplot2 (McMurdie & Holmes 2013; Wickham 2016), implemented in R version 4.0.3 (R Core Team 2020). Alpha diversity estimations (Shannon - H' and Richness - S') were performed using the phyloseq package and the differences for the diversity indexes between samples were assessed through the non-parametric two-tailed Kruskal-Wallis test. Comparisons between microbial communities of all samples were visualized through beta diversity measures using a non-metric dimensional scaling (NMDS) with Bray Curtis dissimilarities. To test the ordinations, a multivariate analysis of molecular variance (AMOVA), based on a traditional analysis of variance, was calculated in mothur (Anderson 2001). To evaluate differences in the abundance of microbial communities between all the samples and functions, Generalized Linear Model tests were performed using the stats package. To explore the possible functions associated to plant growth, we obtained the genomic metadata from PATRIC database (https://www.patricbrc.org) (Davis *et al.* 2020) and searched all genera related to any of the Plant-Growth-Promoting Bacteria (PGPB) activities, we also complemented with an exhaustive literature search to assign all possible functions to our OTUs.

4.3 Results

4.3.1 General sequencing analysis

A total of 20 soil DNA samples were sequenced to learn about the influence of tree cover on the grass rhizobiome. A total of 1,649,430 reads were generated, which were paired-end into 824,727 sequences. These raw sequences were filtered leaving 552,032 unique sequences, which were clustered into 104,985 distinct 97% identity OTUs. A total of 85 archaeal OTUs were identified (0.08% of the sequences) and removed. We only kept OTUs for bacteria, finding none for chloroplasts or mitochondria. The final data set included 104,900 OTUs representing 42 distinct bacterial phyla and a total of 551,574 sequences, from which the top 100 most abundant taxa and relative abundances were obtained.

4.3.2 Bacterial diversity of soil and rhizosphere microbial communities

Alpha diversity estimations showed few variations of microbial composition within each of the studied sites (Fig. 4.2). However, the grass rhizosphere under the palm tree was found to be significantly more diverse and included many more dominant species than the rest of the samples (Shannon and Simpson diversity index; Kruskal-Wallis, $p < 0.05$, Appendix A). Increased species richness was also observed in grass-palm rhizosphere compared to the rest of the samples. The observed species richness, and the estimations by Chao1 showed similarities between *Acacia*, grass and bulk soil, while the grass-palm associated rhizosphere was also higher, though not significantly different (Fig. 4.2). This means that the rhizosphere of grass laying under the palm tree showed higher OTU diversity, while there is an even pool of species richness.

To determine differences in community structure, we analyzed beta diversity through a non-metric dimensional scaling (NMDS) with Bray Curtis dissimilarities. The analysis of molecular variance showed significant differences among group compositions, at the OTU level, between all four samples ($p= 0.001$, AMOVA; Fig. 4.3, Appendix B). The overall composition of bacterial communities varied among the samples. Again, the grass rhizosphere microbiome collected under a palm tree appeared significantly dissimilar to the rest of the samples ($p = 0.001$ AMOVA); while those for grass, *Acacia* and bulk soil pairwise comparisons showed more commonalities (Fig. 4.3).

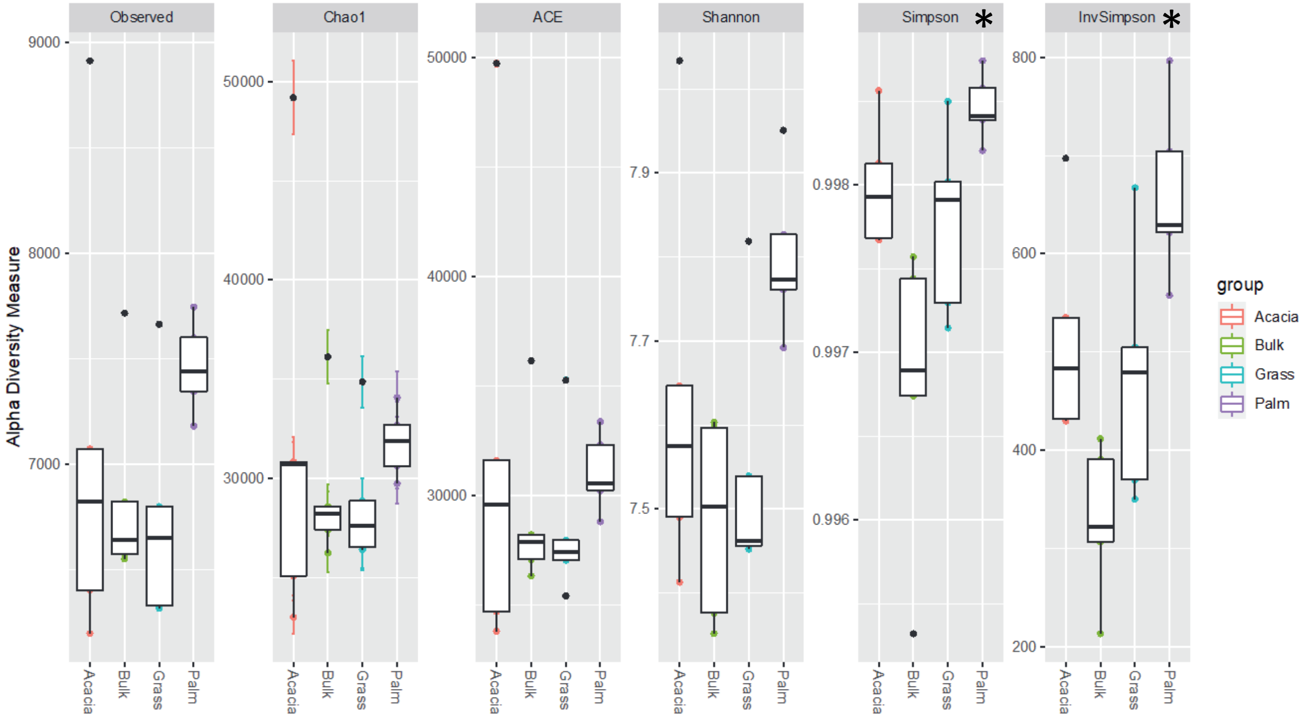


Fig. 4.2. Richness and alpha diversity estimates at OTU level of the four exploratory groups of samples. Asterisks on top of each boxplot denote statistically significant difference. Grass rhizosphere under the palm tree displayed higher richness, dominance and diversity.

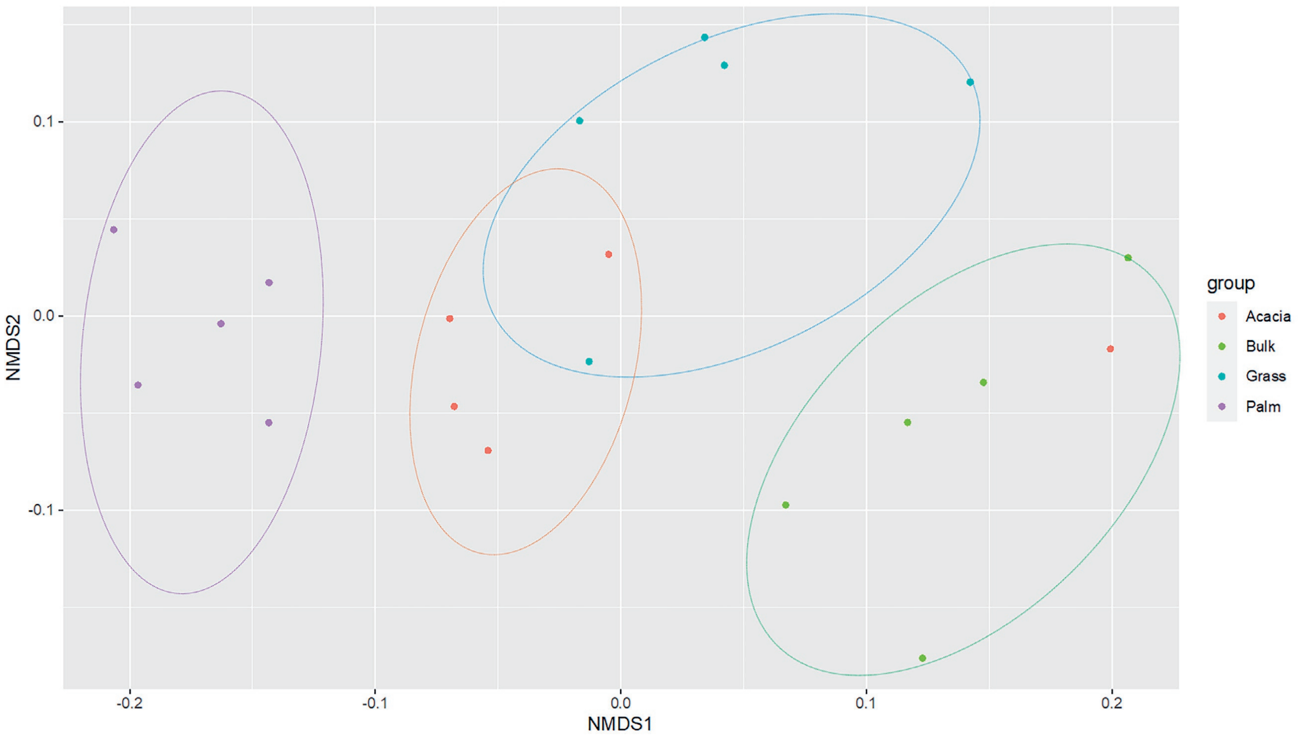


Fig. 4.3. NMDS ordination at OUT level with Bray Curtis dissimilarity. Grass rhizosphere microbiome under a palm appeared significantly dissimilar to the rest of the samples.

Fig. 4.4 shows an in-depth analysis of the composition of the top main phyla for each of the four samples. Relative abundances of the top 100 OTUs, by abundance, were obtained and assessed at the three higher taxonomical levels: phylum, class and order. The most abundant phyla corresponded to thirteen representatives, accounting for 28.9% (159,680 sequences) of the total OTUs detected. Overall, we found that the microbiome diversity was dominated, at the phylum level, by Actinobacteriota, Proteobacteria, Acidobacteriota, Verrucomicrobiota and Firmicutes, accounting for 24.9% of the total sequences detected (Fig. 4.4a). From the 42 bacterial phyla identified, 33 were present in the four samples, while only three were exclusively found in the open grass sample (Synergistota, Rs-K70_termite_group and Cloacimonadota), and one in the *Acacia* rhizosphere (Zixibacteria). At the class level, the most abundant taxa comprised Alphaproteobacteria, Thermoleophilia, Gammaproteobacteria, Blastocatellia and Verrucomicrobiae, accounting for 15.5% of the total OTUs (Fig. 4.4b). Finally, the most abundant orders were represented by Rhizobiales, Gaiellales, Vicinamibacterales and Gemmatimonadales, accounting for 7.4% of the total OTUs detected. The main differences in microbiome composition and diversity observed primarily in the grass-palm rhizosphere support our initial hypothesis that the presence of a tree might influence microbial community structure. Thus, such differences were further addressed.

4.3.3 Shifts in microbiome composition in the grass rhizosphere under the influence of palm trees

The grass rhizosphere under the palm showed differences in microbial composition, with a general enrichment of Bacteroidota and Proteobacteria, and a considerable depletion in Firmicutes (Fig. 4.4a). At class level, an increased abundance in Gammaproteobacteria and Bacteroidia was also observed for the palm grass rhizosphere, while a notorious decrease in Bacilli, Blastocatellia and Rubrobacteria were detected (Fig. 4.4b). Grass rhizosphere contained less unclassified bacteria, while Acacia and grass-palm rhizospheres showed more abundances. When compared to bulk soil, grass-palm rhizosphere showed a reduction of Acidobacteria (particularly Blastocatellia class), Actinobacteria (including Thermoleophilia and Rubrobacter classes) and Firmicutes. The variation in the remaining taxa was very minor. Actinobacteriota appeared as the most abundant phylum in the four communities studied, though it was notably higher in the bulk soil compared to the rhizospheres (Fig. 4.4a).

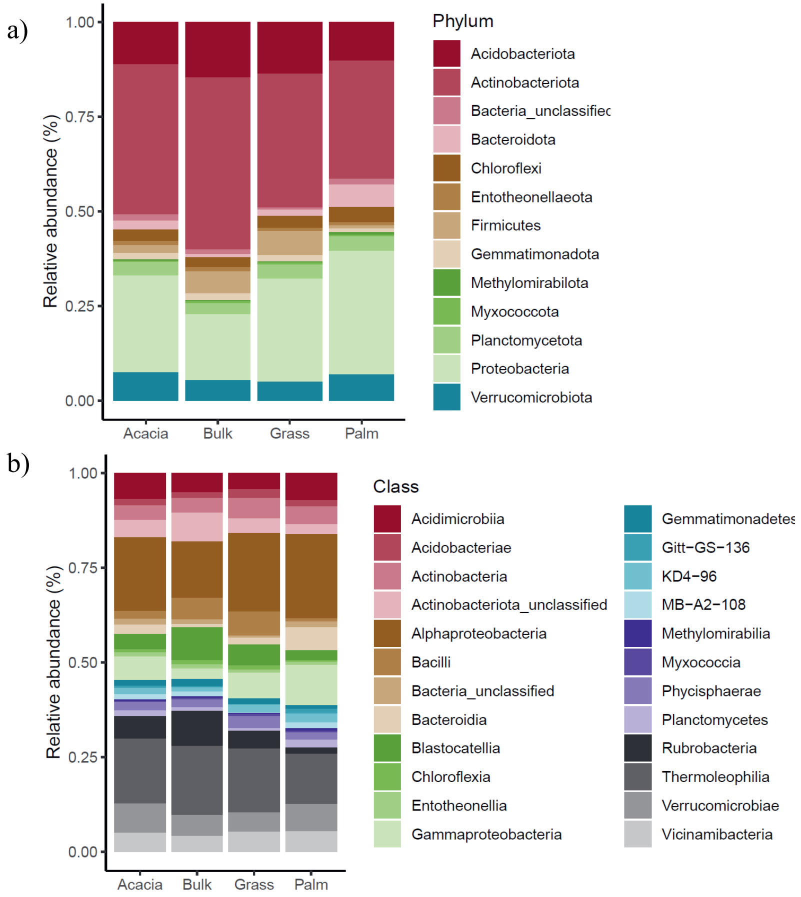


Fig. 4.4. Microbiome structure among rhizosphere samples and bulk soil. Relative abundances are summarized for the five samples of each group, displayed at Phylum (a) and Class level (b).

4.3.4 Possible microbial activities associated to plant-growth promotion

We used an exhaustive literature research and the genomic metadata retrieved from the PATRIC database to relate the identified genera with a known plant host-microbial function, such as plant-growth promoting activities, nitrogen fixation (Nfix), drought tolerance, and biocontrol functions. We identified a total 3,142 unique OTUs (50,145 sequences) pertaining to taxa that have been described as having one or more of the PGPB functions. These sequences accounted for 9.1 % of the total dataset (Fig. 4.5a). A summary of OTUs associated with PGPB activities is shown in Fig. 4.5b. Taxa associated to PGPB traits were more abundant in the rhizosphere of grasses growing in the open pasture than in the rhizosphere of the understory of palms and in the rhizobiome of Acacia (Fig. 4.5a). Nfix was the most abundant function in the four environments. Moreover, drought tolerance was the second most abundant function in open grasses unlike those from the understory, and, also, less abundant in bulk soil. Taxa associated to biocontrol were noticeably less abundant in bulk soil. OTUs associated to drought tolerance, Nfix, biocontrol and other PGPB functions appeared to be less abundant in the bulk soil, as well as in the rhizobiome of Acacia and palms, than in the rhizosphere of grasses growing in the open pasture (GLM, $p < 0.0001$). However, pairwise comparisons did not reveal significant differences (GLM, $p > 0.05$, Appendix C).

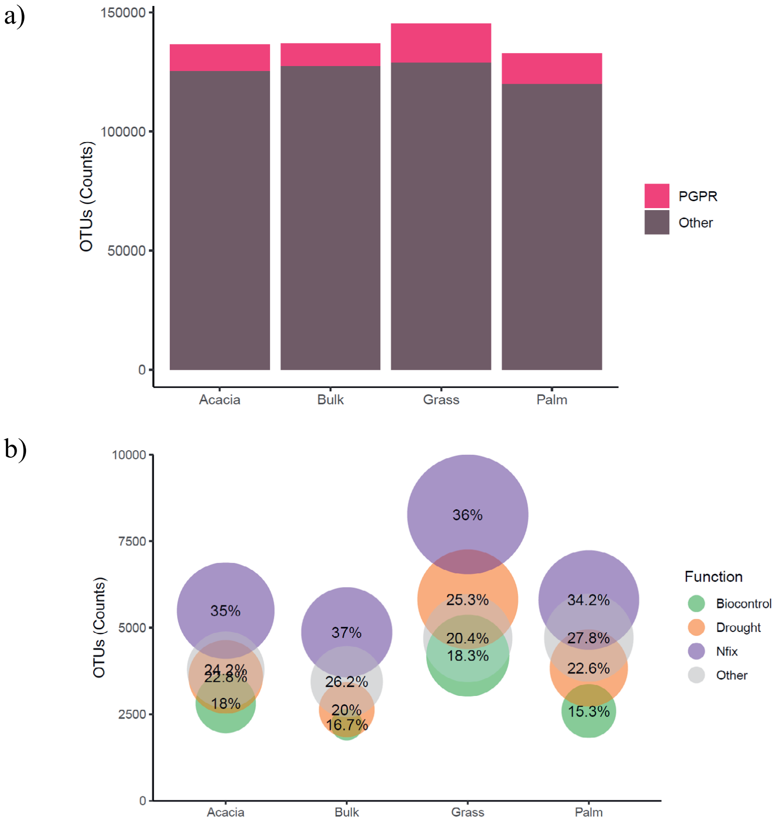


Fig. 4.5. OTUs associated to plant-growth promoting functions. Nitrogen fixation is the most abundant activity in all four samples, while drought tolerance function appeared to be more prevalent in the open grass rhizosphere. a) Proportion of OTUs with a PGPB assigned function. b) Plant-growth-promoting associated functions illustrated with circles of different colors and size, percentages of OTUs associated to any plant-growth promoting function appear within each circle.

4.4 Discussion

4.4.1 Grass microbiome of dry tropical forests

We explored the microbial diversity of grasses in dry rangelands under two different growing conditions, exposed grasses and understory grasses, specifically, associated with the *Sabal* palms, the most abundant overstory trees in these pastures. Plant-associated microbiomes have been widely studied in diverse environments across the globe, mostly in crop plants (i.e., maize, wheat, and rice). These are usually studied within monospecific crop systems and compared to diversity from bulk soil (Fang *et al.* 2011; Peiffer *et al.* 2013; Ding *et al.* 2019). Non-crop species, particularly grass plants, have been rarely studied and the information about their root microbiome is very scarce (Naylor *et al.* 2017). To our knowledge, this study is one of the few to characterize grass root-associated microbiomes and perhaps the first to assess the influence of tree cover in the microbial community structure from the grass rhizosphere.

Previous works have attempted to integrate the data for bacterial diversity associated with different soils worldwide. (Delgado-Baquerizo *et al.* 2018) observed that only 2% of bacterial phylotypes dominated almost half of the soil communities analyzed. The eight most abundant phylotypes described by (Delgado-Baquerizo *et al.* 2018), were also the most abundant bacterial phyla we observed in this work (Fig. 4.4). The graphical analyses of both open grass and palm grass rhizospheres, show similarities in bacterial composition. Overall, phyla composition was parallel in the grass and palm rhizospheres, though they exhibited significant differences in abundances. The main variations consisted of an increase of Proteobacteria (particularly Gammaproteobacteria) and Bacteroidota (Bacteroidia class) and a notable depletion of Firmicutes in the rhizosphere of grass under the palm (Fig. 4.4a).

The most contrasting environment in this study is that of bulk soil, where microbes would be expected not to be influenced by rhizosphere exudates. When comparing the two grass rhizospheres with the bulk soil, we observed that *Actinobacteria* were more abundant in the bulk soil, while an increased abundance of *Proteobacteria* prevailed in grasses. This is in agreement with what has been observed in other soil studies, that show Alphaproteobacteria, Betaproteobacteria and Gammaproteobacteria (all from the proteobacterial phylum) to dominate in the rhizosphere of soil (Fierer *et al.* 2007). In particular, we observed Alphaprotobacteria to be lower in bulk soil, compared to soil associated to plants. This same pattern was observed by (Thomson *et al.* 2010) in an upland grassland soil. Furthermore, we observed that in bulk soil, Acidobacteria abundance decreased while Blastocatellia sequences increased, we only found this similar pattern for tundra soils lacking vegetation (Ivanova *et al.* 2020).

Since few studies have been carried out in similar environments, we presented a description of the microbial structure of grass rhizosphere in dry tropical pastures. Members of the main classes of Proteobacteria, Alpha and Gammaproteobacteria, have been recognized in diverse rhizospheres, including those of maize (Peiffer *et al.* 2013), coffee (Caldwell *et al.* 2015), sugar beet (Mendes *et al.* 2011), rice (Ding *et al.* 2019), temperate grasses (Singh *et al.* 2007; Vieira *et al.* 2020), and, as identified in our results, tropical grasses and *Acacia* rhizosphere.

Unlike other rhizosphere environments that have identified an enrichment of Actinobacteria, this bacterial group appeared to be less abundant in the grass and the *Acacia* rhizobiome compared to the bulk soil. However, it has been reported to be highly abundant in drought soils due to the presence of spore-forming microorganisms (Soussi *et al.* 2016; Naylor *et al.* 2017). Similarly, enrichment in Bacteroidota has been widely documented in plant-associated microbiomes, including grasslands. In our study, a notable increase in the class Bacteroidia was seen in grasses in the understory of palms, while open grasses presented similar abundances to the *Acacia* rhizosphere and bulk soil (Cao *et al.* 2017; Vieira *et al.* 2020).

Furthermore, shifts at the order level suggested that Bacillales, Blastocatelliales, Rubrobacteriales and Thermoleophiliales occurred in larger abundance in the exposed grass rhizosphere, than under the palm, while Rhizobiales and Chitinophagales were more abundant in the grass rhizosphere under palm compared to the exposed grass rhizosphere. Rhizobiales is the most abundant order in the palm rhizosphere and second most abundant in the grass rhizosphere. According to research conducted by (Erlacher *et al.* 2015), Rhizobiales are critical for supplying nutrients to surrounding plants as well as for nitrogen fixation. More recently, species from the order Chitinophagales have been described in grasslands and forest soils playing important roles in metabolizing b-glucan, therefore making sugars available as nutrients for other species (Cao *et al.* 2017; Mckee *et al.* 2019). These data suggest that having a large number of Rhizobiales and Chitinophagales is important for the survival of surrounding plants, and a symbiotic relationship between the bacteria and grasses.

The observed relative abundances showed an outright shift in Bacillales from the rhizosphere of grasses in the understory. The principal members of this group include *Bacillus* sp. and *Paenibacillus* sp. as common inhabitants of the rhizosphere (Santiago *et al.* 2016; Hashem *et al.* 2019). The genus *Bacillus* represents one of the best well-known models to explore the genetic functions related with plant-growth promotion (Ryu *et al.* 2003; Yi *et al.* 2016; Fan *et al.* 2018), especially those related with biological control through the production of metabolites that inhibit infection by phytopathogenic fungi (Yangui *et al.* 2008; Huang *et al.* 2012; Passera *et al.* 2017), and insects (Fang *et al.* 2011). *Bacillus* species are considered as excellent biocontrol agents widely used in the production of biological pesticides (Vinodkumar *et al.* 2017), as well as bacterial inoculants to stimulate plant growth (Bashan *et al.* 2014; du Jardin 2015). However, bacteria from other taxa, mainly several Gammaproteobacteria from the *Pseudomonas* genus, have also been described as growth-promoting, and to particularly function in disease control (Hernández-Salmerón *et al.* 2016; Naik *et al.* 2019).

Although Firmicutes was not amongst the top ten most abundant *phyla* for the four samples explored, it is important to note that it is even less significant in the rhizosphere of grasses under the palm. Thus, it would be interesting to study in greater detail the ecological conditions why such an abundant and common group in the rhizosphere was not identified among the dominant *phyla* in our study sites. A possible scenario involves the edaphological conditions, since the soil nutrients analyzed were found below the optimum level for crop yield (P, Ca, Mg and Ca; Appendix D), making nutrients less available for some microorganisms, and thus contributing to shaping the rhizosphere microbiome (Santoyo *et al.* 2017). Another possible factor relies on the plant genotype, as root exudates play an important role in recruiting the microbiota interacting with the roots of plants (Chaparro *et al.* 2013; Walker *et al.* 2014; de Vries & Wallenstein 2017). More effort has to be made to explore plant-associated microbiomes structure and dynamics under arid/dry conditions.

4.4.2 Beneficial plant-microorganism interactions: growth and stress resilience

To have a general insight of the possible functions present in the grass rhizosphere, we identified the genera previously documented as PGPB. The rhizosphere of grass hosted a greater abundance of PGPB than the rhizosphere of grasses under the palm and *Acacia* trees, however, the rhizobiome of the latter two remained similar. *Acacia* is well-known for its intrinsic relations with nitrogen-fixing bacteria, and these interactions have been less studied in the roots of grasses interacting with palms (Ferreira et al., 1995 and 1997 in (Reis *et al.* 2000). Nutrient supply appears as the most abundant function provided by PGPB, though important data might be obtained from those drought-related functions, which is relevant for studying plant-growth promoting microorganisms with drought resilience capacities (Soussi *et al.* 2016). On the other hand, a lower abundance was found for biocontrol-related functions in all samples. This suggests that the presence of a tree affects the abundance of PGPB in grasses but not the type of interactions. Microorganisms from the rhizosphere represent a huge repertoire of genetic functions with potential to produce beneficial bioproducts for agrosystems, without negative effects for human health and the agrosystem itself. One of the hopes of these type of studies is to go beyond enumeration and identification of taxa, to actually predict function. This is not trivial given that some organisms identified in soils, are not active. Furthermore, given the microdiversity that exists at species level, some functions known to be encoded in a given strain, might be absent in another. A recent study found that functional groups of active microbes in rhizosphere soil are correlated with the measured enzyme activities (Wahdan *et al.* 2021), which suggests that the studies directed at identifying microorganisms from the rhizosphere is a great resource for the discovery of new taxa with application towards a sustainable agriculture.

Our overall results suggest that the presence of the palm tree allows for the establishment of a greater diversity of microorganisms favoring the growth of the host plant in the pastures of dry tropical forests. Considering that only near to 10% of the OTUs were assigned to any PGP activity, we encourage further research on the identification of new plant-growth promoting microorganisms and biocontrol agents with promising applications in grassland agroecosystems and assess their contribution to the resilience of productive systems to the diverse challenges facing the climate change.

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Authors contributions

These authors contributed equally: Ivan R. Hernández-Salmerón and Julie E. Hernández-Salmerón. IRHS, JEHS and MH conceived the ideas and designed the study. IRHS collected field samples. GOA analyzed soil samples. JEHS and GMH processed the sequences. All authors analyzed and interpreted the results and wrote the manuscript. IRHS and JEHS prepared the figures.

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Appendices

Appendix A. Results of the non-parametric Kruskal-Wallis tests for the alpha diversity indexes and their pairwise comparisons between the four microsites.

Kruskal-Wallis tests alpha diversity

Diversity index	Kruskal-Wallis chi-squared	df	p-value
Observed	4.8171	3	0.1857
Chao1	2.7257	3	0.4359
ACE	2.7943	3	0.4244
Shannon	7.6857	3	0.0529
Simpson	12.44	3	0.0060

Pairwise comparisons using wilcoxon rank sum exact

Observed

	Acacia	**Bulk**	**Grass**
Bulk	1.000	-	-
Grass	0.690	0.690	-
Palm	0.151	0.095	0.095

Chao1

	Acacia	**Bulk**	**Grass**
Bulk	1.00	-	-
Grass	1.00	1.00	-
Palm	0.55	0.15	0.15

ACE

	Acacia	**Bulk**	**Grass**
Bulk	1.00	-	-
Grass	1.00	0.69	-
Palm	0.55	0.15	0.15

Shannon

	Acacia	**Bulk**	**Grass**
Bulk	0.0079	-	-
Grass	0.5476	0.0952	-
Palm	0.0556	0.0079	0.0556

Simpson

	Acacia	**Bulk**	**Grass**
Bulk	0.0079	-	-
Grass	0.5476	0.0952	-
Palm	0.0556	0.0079	0.0556

Appendix B. Results of multivariate analysis of molecular variance (AMOVA), showing the pairwise comparison between microbial communities.

AMOVA

Pairwise comparison	p-value
Acacia-Bulk-Grass-Palm	<0.001*
Acacia-Bulk	0.054
Acacia-Grass	0.032
Acacia-Palm	<0.001*
Bulk-Grass	0.014
Bulk-Palm	<0.001*
Grass-Palm	0.007*

Appendix C. Results of the Generalized linear models and pairwise comparisons on the differences in the abundance of microbial communities and plant-growth promoting functions between all the samples.

Generalized linear model

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	514.60	54.30	9.478	2.38e-14 ***
Bulk	-126.50	58.04	-2.179	0.032532 *
Grass	365.45	58.04	6.296	2.04e-08 ***
Palm	63.45	58.04	1.093	0.277934
Drought	202.95	58.04	3.496	0.000806 ***
Nfix	631.40	58.04	10.878	< 2e-16 ***
Other	241.85	58.04	4.167	8.38e-05 ***

Signif. Codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Generalized linear model pairwise comparisons, adjusted by “Tukey”

Pairwise comparison	estimate	SE	df	z.ratio	p.value
acacia Biocontrol – bulk Biocontrol	126.5	58.0	Inf	2.179	0.7120
acacia Biocontrol – grass Biocontrol	-365.4	58.0	Inf	-6.296	<.0001
acacia Biocontrol – palm Biocontrol	-63.5	58.0	Inf	-1.093	0.9994
bulk Biocontrol – grass Biocontrol	-491.9	58.0	Inf	-8.475	<.0001
bulk Biocontrol – palm Biocontrol	-189.9	58.0	Inf	-3.272	0.0801
grass Biocontrol – palm Biocontrol	302.0	58.0	Inf	5.203	<.0001
acacia Drought – bulk Drought	126.5	58.0	Inf	2.179	0.7120
acacia Drought – grass Drought	-365.4	58.0	Inf	-6.296	<.0001
acacia Drought – palm Drought	-63.5	58.0	Inf	-1.093	0.9994
bulk Drought – grass Drought	-491.9	58.0	Inf	-8.475	<.0001

bulk Drought – palm Drought	-189.9	58.0	Inf	-3.272	0.0801
grass Drought – palm Drought	302.0	58.0	Inf	5.203	<.0001
acacia Nfix – bulk Nfix	126.5	58.0	Inf	2.179	0.7120
acacia Nfix – grass Nfix	-365.4	58.0	Inf	-6.296	<.0001
acacia Nfix – palm Nfix	-63.5	58.0	Inf	-1.093	0.9994
bulk Nfix – grass Nfix	-491.9	58.0	Inf	-8.475	<.0001
bulk Nfix – palm Nfix	-189.9	58.0	Inf	-3.272	0.0801
grass Nfix – palm Nfix	302.0	58.0	Inf	5.203	<.0001
acacia Other – bulk Other	126.5	58.0	Inf	2.179	0.7120
acacia Other – grass Other	-365.4	58.0	Inf	-6.296	<.0001
acacia Other – palm Other	-63.5	58.0	Inf	-1.093	0.9994
bulk Other – grass Other	-491.9	58.0	Inf	-8.475	<.0001
bulk Other – palm Other	-189.9	58.0	Inf	-3.272	0.0801
grass Other – palm Other	302.0	58.0	Inf	5.203	<.0001

Appendix D. Soil properties of the composite sample under palm trees and open grassland.

Canopy type	P (mg/Kg)	Ca(Cmol(+)/Kg)	Mg(Cmol(+)/Kg)	K (Cmol(+)/Kg)
Palm	29.12	22.21	57.5	0.25
Open	10.19	21.26	31.5	0.46

Chapter 5

Too hot to graze: cattle refuge under trees as heat stress increases in dry tropical rangelands

This chapter is based on:

Hernández-Salmerón, I. R., Landwier, M., de Knegt, H. J., Solorio- Sánchez, F. J. & Holmgren, M. (submitted). Too hot to graze: cattle refuge under trees as heat stress increases in dry tropical rangelands.

Abstract

Cattle productivity is expected to be compromised worldwide with global warming and changes in precipitation patterns. Cattle heat stress often occur with direct continuous exposure to solar radiation and high temperatures without shade, resulting in reduced growth rates and therefore, low meat and milk production. Livestock benefits from the use of tree shade in humid and sub-humid tropical areas, yet, the effects of trees on cattle behavior and welfare in the dry tropics remain debated as previous studies have reported positive and negative effects. Understanding the overall effects of trees on livestock under contrasting environmental conditions is of major importance as it may contribute to develop production systems that ameliorate the impacts of warmer climates and that conserve biodiversity. We studied the effects of weather variables on heat stress risk in cattle in dry tropical pastures under contrasting environmental conditions during the dry and wet seasons to understand how heat stress risk influences cattle tree shade utilization and behavior. Our observations indicate that cows actively seek dense tree cover, especially during the wet season when the environmental heat stress is higher. These results highlight the importance of tree shade for cow thermal regulation in seasonally dry tropical regions and contribute to identify ways of adapting production systems to environmental stresses.

5.1 Introduction

Global warming and changes in precipitation regimes are expected to compromise pasture and cattle productivity worldwide (Lobell & Gourdji 2012; Field 2014). As heat stress increases, bovines spend more energy to maintain their thermal equilibrium, which decreases growth rates (West 2003) and therefore reduces production of milk and meat (Kadzere *et al.* 2002). Heat stress in cattle often occurs with a combination of environmental conditions, with direct continuous exposure to high intensity solar radiation, high ambient temperature, and high air humidity (Hahn 1999; Das *et al.* 2016) . However, other environmental factors such as wind speed and precipitation may also contribute to ameliorate heat stress (da Silva & Maia 2012) and therefore influence animal behavior and movement across open and shady microsites in agricultural landscapes.

One of the simplest adaptation strategies to ameliorate animal heat stress is the provision of shade (Muller *et al.* 1994; Valtorta *et al.* 1997; Tuyttens *et al.* 2015). In tropical rural areas, farmers generally retain dispersed trees within pastures as sources of shade, fodder, timber, firewood and other resources (Cajas-Giron & Sinclair 2001; Harvey *et al.* 2011). Among this diversity of trees in pastures, native palms are the most abundant species. Palms provide a lower degree of protection from solar radiation than trees but facilitate grass growth and greenness more strongly as palms canopies are less dense than those of trees (Hernandez-Salmeron *et al.*, submitted). Given that the degree of protection from solar radiation is an important feature on the design of effective shade availability for cattle (Tucker *et al.* 2008), it is relevant to understand how cattle uses the shade of different types of trees as an strategy to cope with heat stress.

Livestock animals are heat challenged during the summer months in temperate regions and most of the time in tropical and subtropical regions. It is well known that livestock benefits from the use of tree shade under hot ambient air temperature and solar radiation conditions (Kendall *et al.* 2006; Tucker *et al.* 2008) in the humid (Geraldo *et al.* 2012; Álvarez *et al.* 2021) and sub-humid tropical regions (Souza *et al.* 2010; Carnevalli *et al.* 2019a). Yet, the effects of trees on cattle behavior and welfare in the dry tropics remain contested as previous studies have reported both positive (Mello *et al.* 2016; Mancera *et al.* 2018) and negative effects (Ainsworth *et al.* 2012). Furthermore, these effects may also differ between seasons due to the large rainfall variability within and between years in the tropics (Holmgren *et al.* 2013).

Forecasting early heat stress risk can contribute to contain the negative impacts of weather conditions on cow welfare and identify ways of adapting production systems to environmental stresses (Herbut *et al.* 2018b). Here, we study the effects of weather on heat stress risk for cattle in dry tropical pastures, characterized by having strongly marked dry and wet seasons. Dry and wet seasons in the dry tropics are warm but differ in the levels of humidity and cloud cover associated to contrasting rainfall levels. Dry seasons are rain-free periods with lower relative humidity and higher solar radiation levels, while wet seasons are periods with heavy rainfall (1 to 3 m of rain during 2-6 months), higher relative humidity and lower solar radiation (Janzen 1988). We aim at understanding how heat stress risk influences cattle tree shade utilization and behavior. We expect cattle to use tree shade more often when weather conditions increase thermal stress and we expect cattle to select the shade of trees more often than the shade of palms as their canopy is more dense. Understanding the overall effects of trees on livestock under contrasting environmental conditions is of major importance as it may contribute to ameliorate the impacts of warmer climates and improve productivity on current livestock systems.

5.2 Materials and methods

5.2.1 Study Region

The study was conducted in cattle farms within the municipality of Tizimín, Yucatán, in southeast Mexico (Fig. 5.1). These cattle rangelands have a sparse tree cover of native trees and palm species from the surrounding dry forests (Supplementary 5.1). The pastures are planted with C4 exotic grasses (Bonilla-Moheno & Aide 2020) *Brachiaria brizantha*, *Cynodon plectostachyus* and *Megathyrsus maximus* (cover ≥ 70%).

The climate is warm sub-humid (Köppen & Geiger 1930) with marked dry (November to May) and wet seasons (June to October). Mean annual precipitation is 1263 mm (392 mm in the dry season; 871 mm in the wet season), and mean annual temperature is 26 ºC (min. 19 ºC, max. 42 ºC), (period 1969-2016; (SMN 2020). Interannual variability in weather conditions is high and partly explained by El Niño Southern Oscillation (Philander 1983). The region is very flat with elevations ranging between 10 - 40 m.a.s.l. Soils are classified as leptosols (Estrada-Medina *et al.* 2013) and are characterized by thin layers of unfertile topsoil covering calcareous bare rock.

Fig. 5.1. Study location in Yucatán, Mexico. Cattle standing under the shade of a tree on during the wet season.

5.2.2 Sampling design

We selected 11 actively used cattle pastures between 2.5 – 5 ha each with different levels of native tree cover density (Supplementary 5.1). The pastures belonged to the farms San José and Xhoppel with similar cattle stocking rates (0.5 livestock unit ha^{-1}) in rotational grazing system. The most common cattle breeds were mixed race (*Bos indicus x Boss taurus*) raised for breeding stock. This type of livestock production systems with low input of resources and dependent on seasonal rainfall is very common across the dry neotropics (Harrington & Tow 2011).

5.2.3 Data collection

Between February and March 2018, we characterized tree cover by counting and identifying all woody stems with DBH ≥ 5 cm found along five parallel transects of 4 x 50 m separated at least 30 m from each other and evenly distributed across each pasture. We identified each individual to the species level using local knowledge and botanical collections (Universidad Autónoma de Yucatán, México). We measured tree canopy area (m) covered by each individual tree. We classified trees into two functional groups, palms and trees because their differences in canopy architecture, root depth (Rivest *et al.* 2013) and effects on soil organic matter (Binkley 2005), could all lead to different effects on grass productivity and the levels of shade provided to cattle.

5.2.4 Behavioral observations

We observed the behavior of groups of cattle during the dry (March, April, May) and wet (July, August, September) seasons of 2018 and 2019. We recorded cow behavior every 15 min from 8:00-16:00, for 40 days. We recorded individual cow behavior (classified as grazing, browsing, ruminating and idling) and location in relation to tree canopy (classified as under canopy or in the open grassland). For a subset of days, during the second year, we further recorded the canopy animal location as: under a palm or under a tree. To reduce perturbations to the animal behavior, we maintained at least 150 m distance and allowed 15 min for animals to adapt to human presence prior to registering the observations with the use of binoculars.

Air temperature and relative humidity were recorder hourly with two HOBO® U23-001 dataloggers permanently placed on a pole at 4 m height in the open pastures at San Jose and Xhoppel farms. Wind speed (km/h) was recorded at the time of each observation (i.e. every 15 min or every hour) with the Skywatch ® Meteos anemometer in the open pasture. We obtained monthly solar radiation data from the *Global Solar Atlas 2.0* (World Bank Group 2021).

5.2.5 Data analysis

For each group observation, we calculated the proportion of animals performing each type of behavior (i.e. grazing, browsing, ruminating and idling) at each of the two locations in relation to trees (i.e. under tree canopy or in the open grassland). Using proportions standardizes field observations and allows for comparisons since cattle group sizes generally differ between observations, pastures and years.

To assess the effect of tree canopy and season on cattle behavior, we used independent linear mixed models (LMMs) for each type of behavior, with Season and Tree location (i.e. under canopy and open) as fixed factors, and paddock number and year as random factors. We included the environmental conditions (i.e. air temperature, relative air humidity, wind speed and solar radiation) as covariates using a backward selection and the AIC criteria.

We also assessed the response of cattle behavior along a gradient of abiotic stress. We used the Comprehensive Climate Index (CCI) to predict and determine animal heat stress risk (Mader *et al.* 2010). The CCI computes an index for the animal perceived temperature via ambient temperature and includes corrections due to relative humidity, wind speed and solar radiation. This allows assessing the temperature effect as perceived by the cow under the combination of these different abiotic conditions (Herbut *et al.* 2018a).

We analyzed the effects of tree canopy and season on foraging (i.e. grazing + browsing) and not foraging behavior (i.e. idling + ruminating) using LMMs with Season and Tree location as fixed factors, paddock number, and year as random factors and environmental variables along with the CCI as covariates. LMMs were performed using the package lmerTest in R version 4.0.5 (R Core Team, 2020).

For the subset data of the second year, we further assessed if cattle actively choose for a particular type of tree canopy (i.e. tree, palm, open). We used a χ^2 test in R version 4.0.5 (R Core Team, 2020) to assess if there was any significant difference between the observed proportions of animals under these three microsites and the expected proportions per canopy type based on the landscape. To calculate the expected proportions of the landscape covered by palms and trees, we first calculated the total area covered by either palms or trees (by multiplying their averaged individual area times their density) and later calculated the proportions of the area (1 ha) covered per canopy type. The expected proportion of the open landscape was calculated as the difference between the total area (1 ha) and the expected proportions of the landscape covered by palms and trees.

5.3 Results

5.3.1 Use of tree canopy by cattle in dry and wet seasons

Overall, we recorded 57% of the animals in the open grassland, 39% under the canopy of trees and 4% under the canopy of palms (Fig. 5.2a). The observed proportions of animals under each canopy type differed from the expected proportions based on the area covered per each canopy type in the paddocks (i.e. open: 90%, trees: 7%, palms: 3%. χ^2, $p<0.0001$, Supplementary 5.2 and 5.3).

The relative use of shade by cattle differed between dry and wet seasons (Fig. 5.2b). During the dry season, we found a higher proportion of animals in the open grassland than under the canopy of palms and trees. This shifted during the wet season when a higher proportion of animals were found under the shade than in the open grassland. The type of behavior displayed by cattle in the shade differed from the behavior displayed in the open grassland (Fig. 5.2b). During both seasons, the proportion of animals grazing was higher in the open grassland than under shade of palms and trees. The shade was used mostly for ruminating and idling and this shade was less dense under the palm than under the trees (with values of 18% and ~25% respectively, Supplementary 5.2).

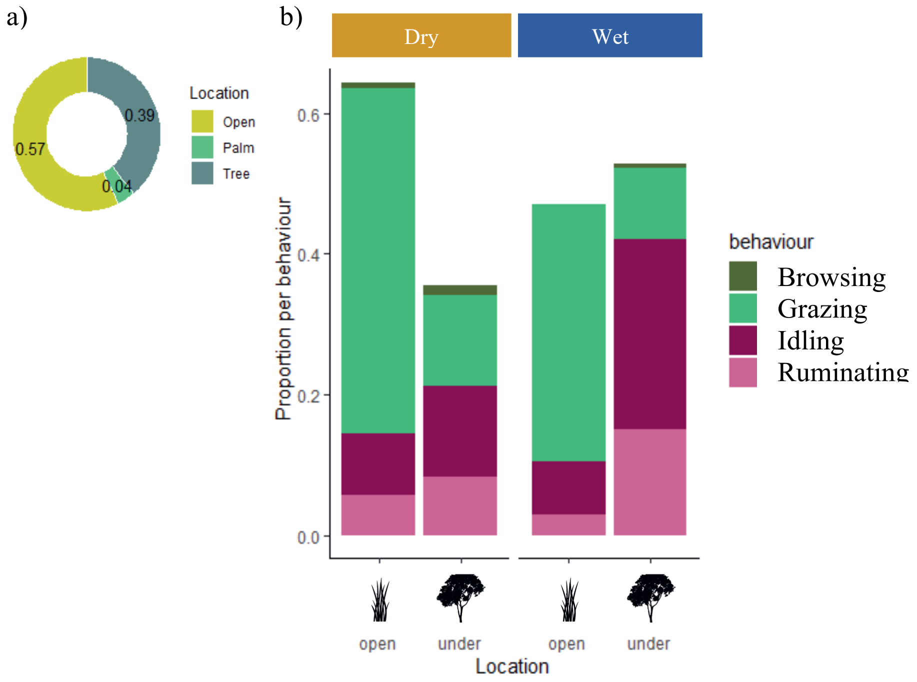

Fig. 5.2. a) Proportions of cows found in the open grassland, under the canopy of palms and under the canopy of trees. b) Proportion of cows browsing, grazing, idling and ruminating in open grassland or under the shade of trees or palms during the dry and wet seasons of 2018 and 2019.

5.3.2 Effect of weather conditions and CCI on cattle behavior

We recorded very similar mean air temperatures between the dry and the wet seasons, with daily average values of 30.7 °C and 30.0 °C, respectively. Relative humidity was higher during the wet season than during the dry season, with values of 59 % and 71 %, respectively. Solar radiation and wind speed were higher during the dry than the wet season, with values of 480 Wh/m^2 and 427 Wh/m^2, and 4.3 km/h and 3.2 km/h, respectively.

The Comprehensive Climate Index (CCI) ranged between ~30 – 50, peaking at around noon and decreasing in the morning and afternoon. Overall, CCI was higher during the wet season than during the dry season (Fig. 5.3).

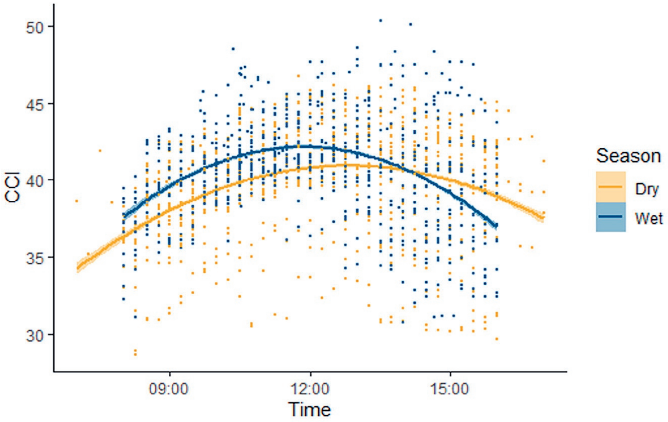

Fig. 5.3. Comprehensive Climate Index (CCI) along the day during the dry and the wet seasons.

The CCI affected cattle behavior. Foraging behavior (i.e. grazing and browsing) tended to decrease as CCI increased, especially in the open grassland during the dry season. Not foraging behavior (i.e. idling and ruminating) increased under the shade as CCI increased. Cattle sought shade at about CCI > 30 during the wet season and CCI ~32 during the dry season (Fig. 5.4).

Cattle behavior under the shade differed between seasons. During the wet season, non-foraging behavior was always more common than foraging behavior. During the dry season, non-foraging behavior was more common than foraging behavior only at CCI > ~40 (i.e. ~32 °C) but below this value, foraging behavior was more common than non-foraging behavior .

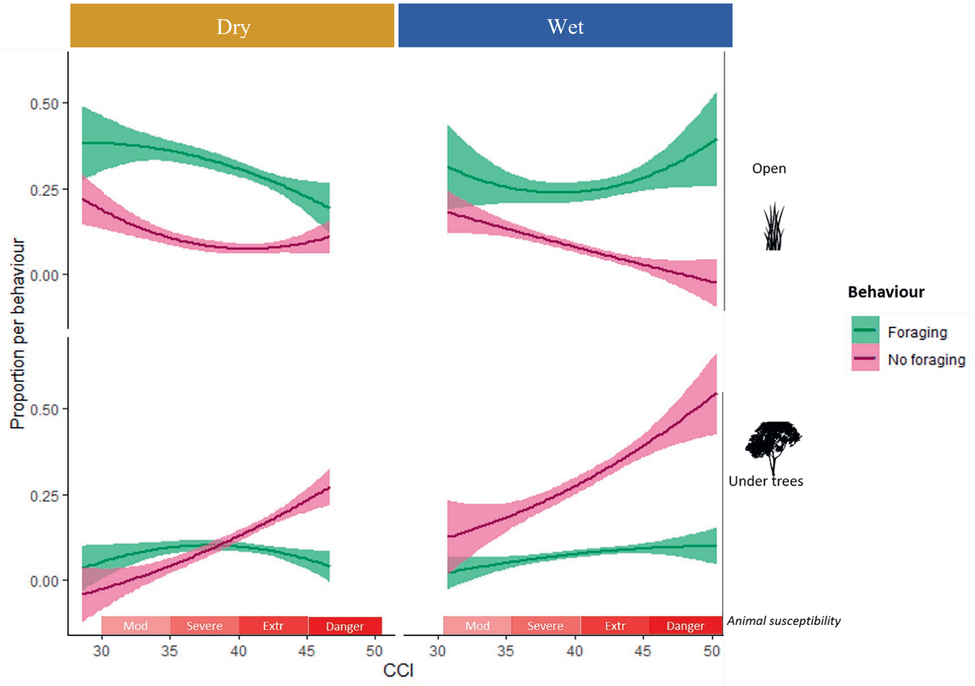

Fig. 5.4. Proportion of animals foraging (i.e. grazing and browsing) and not foraging (i.e. ruminating and idling) in the open grassland or under the shade of trees and palms, along a gradient of environmental heat-stress (CCI) during the dry and wet seasons of 2018 and 2019. Threshold values of heat stress among cows based on CCI (Mader *et al.* 2010) are indicated in red.

5.4 Discussion

Our observations on cattle behavior during two years indicate that cows seek dense tree cover, especially during the wet season when the environmental heat stress is higher. Our results showed that animals actively selected (i.e. used disproportionally) the denser shade of trees rather than the shade of palms in response to increased heat stress. Seeking shade can incur high costs on cattle survival and reproduction as animals can miss opportunities to forage or care for offspring (Cunningham *et al.* 2021). Providing shade thus, may reduce the high costs of missed opportunities and allow animals to engage in important activities for their survival.

We found that heat stress is higher during the wet season, however, our results suggest that animals are exposed to heat stress during both seasons in dry tropical pastures. We detected medium to high levels of abiotic stress (CCI > 30) in the pastures which is considered as moderate-to-dangerous for cattle and capable of causing death as it increases further (Mader *et al.* 2010). Furthermore, we recorded mean temperatures (~30 °C) that exceeded the 25 - 27 °C values that indicate heat stress for multiple Bos taurus breeds (Council 1981; Scharf *et al.* 2010). Noticeably, cows sought shade before air temperatures reached heat stress values (i.e. ~23 °C). As heat stress increased, the difference between the proportions of animals grazing and not grazing under the canopies increased as well. These results highlight the importance of tree shade for cow thermal regulation in dry tropical regions.

Additionally, next to using shade as a behavioral response to minimize heat stress, cattle also modify their foraging behavior (Zähner *et al.* 2004; Valente *et al.* 2015; Alves *et al.* 2020). During the dry season, foraging occurs mostly when CCI is the lowest, which corresponds to the coolest hours of the day (i.e. early morning and late afternoon, Fig. 5.3). This decrease in foraging behavior as CCI increases was only observed during the dry season although CCI was overall higher during the wet season. Because radiation is higher during the dry than during the wet season, it is plausible to think that animals may perceive high levels of irradiance as stressing and prefer to avoid foraging under very warm conditions. Thus, radiation plays also an important role on how cattle perceive and behave under heat stress.

Strategies to save energy and to cope with heat stress were more common during the wet season, when CCI was higher, compared to the dry season. Rumination and idling increase with CCI, but only under shade, which is in agreement with previous research that showed increases in rumination and idleness time under shade and as environmental stress increases (Shultz 1984; Blackshaw & Blackshaw 1994; Carnevalli *et al.* 2019b).

Relative humidity seems to have a stronger influence on the CCI than irradiance does, as we found that CCI was higher during the wet season (when relative humidity was higher) than during the dry season (when irradiance was higher). High relative humidity compromises evaporative cooling, an effective mechanism for animal cooling as air temperature rises (West 2003), making it difficult for cattle to cool down during the wet season. Although air temperature has the strongest influence on cattle behavior, relative humidity and solar radiation also contribute to explaining cattle behavior under contrasting seasons as they determine the exchange of heat between an animal's body and its surroundings (da Silva & Maia 2012).

We demonstrated that cattle seek dense tree shade more often during the wet season than during the dry season. Our results provide evidence that maintaining scattered trees in pasture systems benefit livestock well-being by providing cooler areas for resting and ruminating under stressful weather conditions. However, the role of tree cover goes beyond ameliorating cattle heat stress and having positive effects on animal welfare and productivity. Increasing tree cover can improve the resources available to livestock and wild species as well (Scholes & Archer 1997; Treydte *et al.* 2007) (Hernandez-Salmeron 2021, submitted), contribute to the greenhouse gas emissions by removing carbon from the atmosphere and stocking biomass and soil (de Figueiredo *et al.* 2017), and have positive effects on biodiversity conservation (Harvey *et al.* 2008) among other ecosystem services (MEA 2005).

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Authors contributions

IRHS and MH conceived the ideas, designed the study and wrote the manuscript. IRHS performed cattle observations and prepared the figures. IRHS, ML and MH analyzed the data. All authors revised the manuscript.

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Supplementary Information

Supplementary 5.1. Farm and pasture characteristics.

Farm Pasture	**Pasture size (ha)**	**Tree canopy density (%) in pasture**	**Latitude**	**Longitude**
San Jose				
11	2.83	15.69	21.22317	-87.9414
12	3.17	20.89	21.22399	-87.9399
13	3.46	4.24	21.22467	-87.944
14	2.48	6.56	21.22439	-87.9469
15	2.19	18.68	21.22421	-87.9455
Xhoppel				
52	4.34	0.36	21.10709	-87.8022
53	4.53	0.71	21.10474	-87.8022
54	4.55	3.89	21.10242	-87.8022
57	4.40	3.92	21.10762	-87.792
58	4.67	18.70	21.11094	-87.7992
512	4.92	1.82	21.10935	-87.7893

Supplementary 5.2. Expected proportions and tree inventory of pastures.

Functional group / Species	# Ind	Rel. abund. of total	Rel. abund. of ident.	Can. Dens. (%)	Can. Diam. (m)	Density (ind/ha)	Ind area	area / ha	% area occupied of total tree cover	% area occupied ha = Expected proportions
Palms	**59.0**	**0.35**	**0.45**	**18.2**	**3.5**	**25.7**	**9.9**	**253**	**0.3**	**0.03**
Acrocomia mexicana	5.0	0.03	0.04	29.9	4.0	2.2				
Sabal spp.	54.0	0.32	0.41	17.1	3.5	23.5				
N_2 - fixer tree	**44.0**	**0.26**	**0.33**	**27.5**	**6.4**	**19.1**	**32**	**615**	**0.6**	**0.06**
Acacia collinsi	1.0	0.01	0.01	1.8	1.5	0.4				
Acacia pennatula	17.0	0.10	0.13	26.4	5.0	7.4				
Enterolobium cyclocarpum	3.0	0.02	0.02	13.2	4.2	1.3				
Gliricidia sepium	3.0	0.02	0.02	2.4	2.2	1.3				
Lysiloma latisiliquum	7.0	0.04	0.05	49.2	12.9	3.0				
Piscidia piscipula	13.0	0.08	0.10	28.4	6.7	5.7				
No N_2 - fixer tree	**29.0**	**0.17**	**0.22**	**21.6**	**3.2**	**12.6**	**8.0**	**100**	**0.1**	**0.01**
Annona squamosa	2.0	0.01	0.02	39.3	5.0	0.9				
Bursera	2.0	0.01	0.02	5.6	3.3	0.9				
Byrsonima crassifolia	4.0	0.02	0.03	54.1	5.1	1.7				
Coccoloba spicata	15.0	0.09	0.11	12.6	1.9	6.5				
Vitex gaumeri	6.0	0.04	0.05	21.9	4.4	2.6				
Unknown	**35.0**	**0.21**		**20.4**	**3.1**	**15.2**	**7.8**	**118**	**1.0**	**0.01**
3	1.0	0.01		44.3	3.0	0.4				
21	2.0	0.01		21.4	4.5	0.9				
34	2.0	0.01		41.5	5.5	0.9				
36	5.0	0.03		13.5	3.8	2.2				
42	1.0	0.01		0.5	4.0	0.4				
43	1.0	0.01		2.6	1.5	0.4				

44	1.0	0.01		11.7	8.0	0.4
47	1.0	0.01		82.8	4.0	0.4
48	1.0	0.01		62.9	2.0	0.4
53	1.0	0.01		22.7	2.5	0.4
56	1.0	0.01		0.3	1.5	0.4
59	5.0	0.03		23.3	2.1	2.2
60	1.0	0.01		24.7	1.5	0.4
bec / sinanche	1.0	0.01		3.9	2.0	0.4
Gimnopodium floribundum	1.0	0.01		0.3	2.0	0.4
Paw	1.0	0.01		26.8	3.0	0.4
Ponbonché, poponxé	1.0	0.01		5.2	2.0	0.4
Roble	1.0	0.01		0.3	0.5	0.4
Sachabin	4.0	0.02		27.1	5.1	0.4
Yax habin	1.0	0.01		8.6	1.5	1.7
Yaxek	1.0	0.01		0.0	1.0	0.4
?	1.0	0.01		0.0	0.0	0.4
Grand Total	**167.0**	**1.0**	**1.0**	**21.7**	**4.2**	**72.6**

Supplementary 5.3. Chi-squared test for given probabilities

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data:  cattle

X-squared = 194.54, df = 2, p-value < 2.2e-16
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Chapter 6

Synthesis

6.1 Introduction

At all scales of nature, we find living systems nesting within other living systems – networks within networks. In cattle rangelands, complex social and ecological networks communicate with one another and share resources across their boundaries. These networks are able to adapt but their stability is currently being threatened by global warming. Trees in pastures could maintain the connectivity and stability of ecological networks and contribute to ameliorate the impacts of droughts with climate change on pasture and cattle productivity (Murgueitio *et al.* 2011b; Altieri *et al.* 2015; Solorio *et al.* 2017).

While much of the literature has investigated the effects of trees on grasses in natural ecosystems such as savannas (Blaser *et al.* 2013; Dohn *et al.* 2013) and woodlands (Jackson & Ash 1998; Barbier *et al.* 2008) , the overall effects of trees on grasses in productive systems are still being debated. Previous studies have reported positive, negative or neutral effects of trees on productive systems throughout the year (Treydte *et al.* 2007; Moustakas *et al.* 2013; Bernardi *et al.* 2016), and have analyzed these effects on dry and wet regions. Due to the large rainfall variability within and between years in the tropics (Holmgren *et al.* 2013), the effects of trees may differ as well between dry and wet seasons within the same system.

In this thesis I aimed at understanding the interactions between different types of trees and other species coexisting in cattle rangelands. From a holistic perspective, I give attention to the effects of trees on 1) grass productivity, 2) biodiversity conservation and 3) cattle thermoregulation in dry tropical rangelands considering seasonal weather variability. In this chapter, I will first summarize the findings of each of my research chapters in relation to the three or either of these three aspects (section 6.2). **Chapter 2** reveals that sparse tree cover increases grass biomass in dry pastures worldwide. **Chapter 3** highlights the importance of maintaining palms and trees to enhance woody plant recruitment and highlights the relevance of palms on the facilitation of grass productivity. **Chapter 4** provides evidence of the importance of maintaining palms in pastures to increase microbial diversity of grass rhizosphere that may facilitate pasture productivity. **Chapter 5** highlights the importance of tree shade for cattle for cow thermal regulation to enhance cattle welfare. The summary of the findings of each chapter is followed by a discussion on the contribution of trees in the dynamics of ecological networks in tropical dry cattle rangelands with a view to increase our understanding on their resilience to droughts (section 6.3). As part of the discussion I will mention the implications of my results, further research and implications and finalize with the conclusions of this dissertation (section 6.4).

6.2 Findings

6.2.1 Sparse tree cover increases grass biomass in dry pastures worldwide

Tree facilitation on grasses is known to be stronger in dry productive systems (Rivest *et al.* 2013; Mazía *et al.* 2016) and natural dry ecosystems such as savannas (Dohn *et al.* 2013; Moustakas *et al.* 2013). These studies assessed the differential role of trees across space (dry and wet systems). In **chapter 2**, I built upon these studies by studying the differential role of trees across time within a same system (dry and wet seasons). I reported, for the first time, the contrasting seasonal effects of trees on productive systems and suggested that positive effects of trees on grass yields: 1) peak at intermediate levels of evapotranspiration and temperature, and low levels of precipitation, 2) are higher during seasonal droughts, especially on C4 grasses in tropical pastures, and 3) peak at intermediate levels of canopy density. These findings show that water, temperature and light are key resources for grass growth and interactions of these resources can shape the nature of tree-grass interactions in a wide range of productive ecosystems.

In my meta-analysis, I distinguished between different functional groups of trees (i.e. palms, N_2-fixing trees and Non N_2-fixing trees). Tree characteristics such as canopy architecture, root depth (Rivest *et al.* 2013), soil organic matter and carbon (Binkley 2005) could affect above and belowground conditions differently and lead to different effects on grass productivity. I did not find significant differences on the effects of trees on grass yields between the three functional groups. However, I observed that the effects of palms have been poorly studied compared to the other groups of trees despite their widespread occurrence in tropical livestock pastures and their highly diversified local uses (Martínez-Ballesté *et al.* 2008; Macía *et al.* 2011; Araújo & Lopes 2012). In **chapters 3-5** I specifically aimed at understanding the effects of both scattered palms and trees in dry neotropical rangelands, where facilitation is stronger during dry seasons.

6.2.2 Palms facilitate pasture productivity while trees provide refuge for cattle. Both, palms and trees, facilitate woody plant recruitment

In many tropical and subtropical rural areas, local farmers usually retain some disperse trees within their grazing lands after forest clearing (Manning *et al.* 2006; Bernardi *et al.* 2016). These trees are actively selected because of their economic and ecological value (Harvey *et al.* 2011) and play major roles in the stability of the ecological network of cattle rangelands. Their shade can ameliorate abiotic environmental stress, improving grass growth and quality (Solorio *et al.* 2017; Jose & Dollinger 2019a) and enhancing cattle welfare by providing forage and allowing for behavioral thermoregulation (Broom *et al.* 2013). Characterizing existing tree diversity and composition in cattle farms is a priority for further understanding the effects of trees on the environmental and on the productive functions of pastures.

In **chapter 3**, I explored the species composition of scattered palms and trees (i.e. N_2-fixing trees and non-N_2-fixing trees) in dry cattle pastures of Yucatán, México, and assessed their effects on the performance of grasses and woody plants in their understory during dry and wet seasons. I found that 45% of the regional pool of tree species of the surrounding native dry forest is conserved in pastures. Of this wide diversity, palms was the most abundant group with a relative abundance of 45%, followed by N_2-fixing trees and non-N_2-fixing trees with 33% and 22%. The presence of palms and trees ameliorated the impact of seasonal drought on grass greenness but slowed down its recovery during the rainy season. Both palms and trees facilitated the recruitment of woody plants below their canopies. Furthermore, palms had overall higher positive effects on grass greenness and height than trees, especially during the driest season.

My findings in **chapter 3** highlighted the importance of palms for grass productivity in cattle farms in the dry tropics, as they are the most abundant arboreal species and had the highest positive effects. These overall positive effects can result from the combination of above and belowground abiotic amelioration. The intermediate canopy density of palms ameliorates environmental stress aboveground while maintaining irradiance levels sufficiently high for C4 grasses to grow well.

In **chapter 4,** I explored the interactions between palms and the soil microbial community to further understand the mechanisms behind palm-grass facilitation observed in **chapter 3.** Based on the massive sequencing of the 16S rRNA gene, I assessed the influence of palm tree overstory on the microbial community structure of the grass rhizosphere in a cattle farm in Yucatán, México. I found that soil microbial richness, diversity and dominance is higher in the grass rhizosphere under palms, which suggests a positive effect of the palms in the microbiome structure. Few studies have associated palms to diazotrophic and other N_2-fixing bacteria that can potentially contribute to soil nutrients (Reis *et al.* 2000), increase total organic carbon and contribute to maintain organic matter in the upper soil (Leite *et al.* 2013). **Chapter 4** provides evidence, for the first time, of the advantage of maintaining palm trees as part of the ecological networks of dry tropical grasslands as they influence the grass rhizosphere microbiome.

In **chapter 5**, I aimed at understanding the effects of palms and tree shade on cattle behavior and determined cow heat stress during the dry and wet seasons in dry tropical pastures. Our observations indicate that cows actively seek dense tree cover, especially during the wet season when the environmental heat stress is higher. This highlights the importance of tree shade for cow thermal regulation in dry tropical regions as shade may reduce the high costs of missed opportunities (e.g. to forage or care for offspring), allowing animals to engage in important activities for their survival.

6.3 Discussion

6.3.1 Conserving native palms and trees in pastures reflects a holistic understanding of the socio-ecological systems

My findings point towards complementary contributions of the diverse scattered palms and trees on paddock productivity as a whole. It is plausible to think that farmers perceive the benefits of palms in their farmlands as they clearly select and maintain them in their pastures. Palms offer pockets of green grass during droughts (**chapter 3**) and allow for the establishment of a greater diversity of soil microorganisms that promote plant growth (**chapter 4**). It is less obvious why farmers maintain native trees in pastures given the mostly competitive effects with grasses (**chapter 3**). Farmers may counterbalance the negative effects of trees on grasses by considering the provision of other ecosystem services. Trees offer pockets of green grass after severe seasonal droughts and facilitate the recruitment of woody plants below their canopy (**chapter 3**). Trees also provide deep shade for cattle to refugee and cool down when heat stress increases, reducing energy costs and improving their well-being (**chapter 5**). The observed facilitative effects of palms and trees during the dry and the wet seasons in dry neotropical rangelands are visualized in Fig. 6.1.

Farmer's choices for retaining native palms and trees may not aim at maximizing grass yields but rather may reflect a deeper and holistic understanding of their socio-ecological systems. Trees help mitigating the loss of biodiversity (Harvey *et al.* 2011) and increasing the resilience and adaptation of productive systems to drought, heat and increasing variability in rainfall patterns and weather extremes (Murgueitio *et al.* 2011b; Matocha *et al.* 2012b). The positive effects of trees and palms on pastures may become increasingly important to maintain productivity in cattle pastures and their provisioning services as climate warming progresses. Removing whole functional groups of species can make ecosystems more vulnerable to environmental changes that previously could be buffered, compromising their resilience and capacity to maintain the provision of ecosystem services (Folke *et al.* 2004).

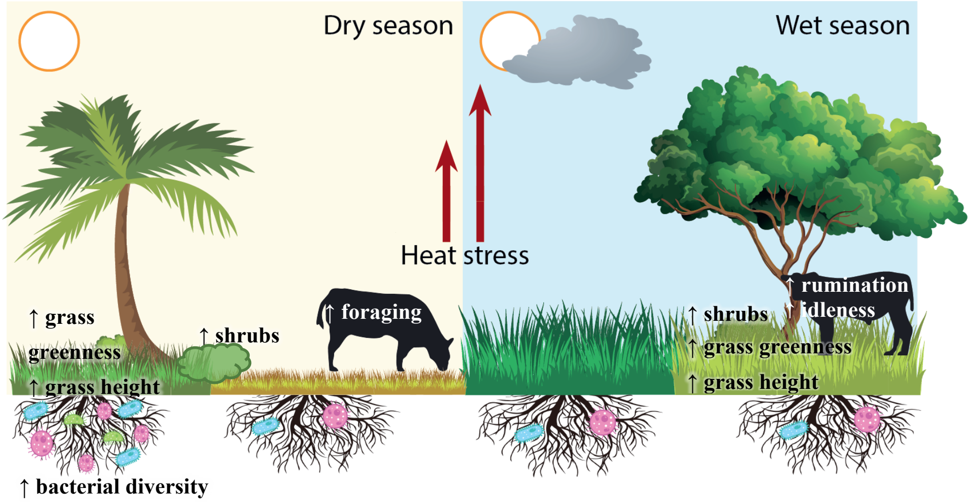

Fig. 6.1. Facilitative effects of palms and trees in dry neotropical rangelands during the dry and wet season. Arrows pointing upwards indicate an increase and downwards indicate a decrease.

6.3.2 Win-win for pasture productivity and biodiversity conservation at intermediate tree canopy density

Throughout this dissertation, trees have been characterized simply by their cover. Tree cover plays a key role in the interplay between positive and negative effects and is involved in a series of feedbacks in the ecological network of cattle rangelands. In plant communities, the shade of neighboring plants is expected to increasingly ameliorate abiotic stress as conditions become drier (Bertness & Callaway 1994), although these facilitative effects on other plants may be lost under extremely stressful conditions (Holmgren & Scheffer 2010; Soliveres *et al.* 2015; Zhang *et al.* 2018). These non-linear effects of shade and drought have been found in meta-analyses of plant performance in field and experimental conditions (Holmgren *et al.* 2012) as well as in agroforests (Blaser *et al.* 2018). I now found comparable results for productive livestock systems where I noted that the facilitative effects on grass yields (**chapter 2**) and grass greenness (**chapter 3**) peak at intermediate levels of tree canopy density (Fig. 6.2).

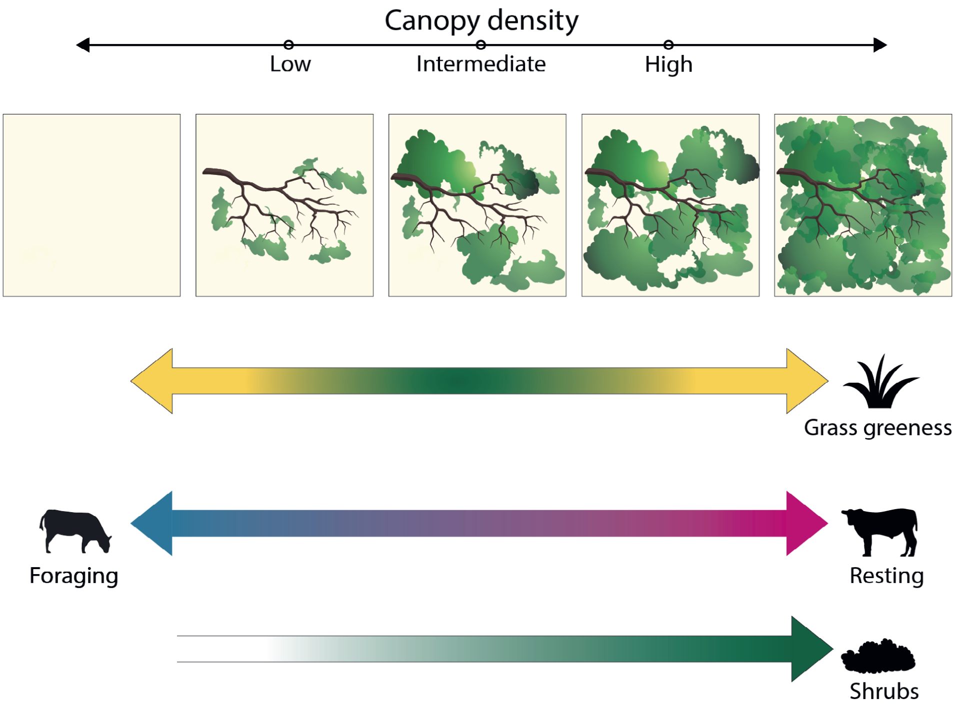

Fig. 6.2. Effects of canopy density on grass greenness, cattle behavior and woody plant cover. Intermediate levels of canopy density maximize grass greenness while still providing shade for cattle to rest and ruminate, and for other woody plants to establish.

My results suggest that intermediate levels of tree canopy density are a win-win scenario for pasture productivity and biodiversity conservation. At intermediate levels of tree canopy density, grass productivity during droughts is maximized (**chapters 2** and **3**), woody plants (i.e. shrubs, tree seedlings and samplings) can establish in the understory (**chapter 3**) and cattle can refuge under shade when heat-stress increases (**chapter 5**). Fig. 6.2 shows the overall effects of canopy density on grass productivity, cattle behavior and woody plant cover.

6.3.3 Palms: an overlooked, dominant, multi-use tree in tropical pastures

Despite the widespread occurrence of palms across the neotropics and their highly diversified local uses (Araújo & Lopes 2012), their effects on grasses in productive landscapes may have been widely overlooked. The positive effects of palms I carefully documented contribute to understand why farmers may be motivated to conserve them over other dry forest tree species in their pastures. Until now, attention has focused on the economic benefits of palms with worldwide importance (Barfod *et al.* 2015), and there have been some mostly anecdotal references to possible positive effects of palms on pastures (Calle *et al.* 2017). This study contributes to understanding the role of native palms in the socio-ecological networks in neotropical productive systems. We demonstrate that palms have overall positive effects on grasses, woody plants, cattle behavior and bacterial diversity in the rhizosphere of grasses that will ultimately reflect into positive effects on pasture productivity and nature conservation in the dry tropics.

6.3.4 Implications of results, further research and limitations

Near-term actions are needed to mitigate the impact of climate warming, reverse land degradation and stop biodiversity loss caused by intensive industrialized production systems. Strategies should aim at increasing the complexity of the social and ecological networks on productive systems as this will ultimately increase the resilience of food systems to different perturbations (i.e. global warming, hurricanes, floods, market fluctuations, etc). My dissertation provides more insight in the dynamics of the ecological networks of cattle farms and contributes to promote win-win solutions for nature and society in current livestock production systems around the globe.

I encourage to increase complexity in livestock production systems by integrating and maintaining a diversity of scattered palms and trees in pastures. Increasing complexity is desirable as it diversifies the positive effects with social and ecological benefits. Scattered trees may contribute to more resilient livelihoods for smallholders that may benefit directly from increases in pasture productivity during droughts and by obtaining food resources and construction materials. They also contribute to biodiversity conservation by increasing connectivity in fragmented landscapes and facilitating the recruitment of other native species from the surrounding forest. Lastly trees provide shade that may reduce the high costs related to missed opportunities with behavioral changes as global temperatures increase with climate change.

Additionally to increasing tree cover, I encourage to actively manage on-farm tree cover to maintain intermediate levels of canopy density (~20-40%). By maintaining intermediate levels of canopy density, palms and trees facilitate grasses and provide shade for cattle thermoregulation while still contributing to the conservation of native species by recruiting woody plants in their understory.

The perceptions on the role of trees by farmers seem to be contrasting in different parts of the world. Most of the studies on the effect of trees on grasses in productive systems have been carried out in the neotropics (**chapter 2**) where small-scale farmers already recognize more benefits from trees (e.g. shade, benefits on water and wildlife, etc.) than conventional and large scale farmers do (Teixeira *et al.* 2018). This recognition of the positive effects of trees on cattle rangelands in Latin America may not be arbitrary. Trees have been present in neotropical landscapes for centuries, some of them figuring as sacred in the cosmology of antique pre-Columbian cultures and with diverse uses (Kufer *et al.* 2006; Knowlton & Vail 2010). Recognizing and merging the traditional indigenous knowledge of trees with the existing ecological theory developed in natural and productive systems could facilitate the transition to agroecological practices. The knowledge of the benefits of trees on cattle rangelands in Latin America can open the path on how to adapt rangelands to climate warming in other regions around the globe. I pledge researchers to bridge across scientific disciplines to expand this knowledge in agroecosystems and multifunctional landscapes across environmental gradients and cultures around the globe to generate effective strategies for sustainable productive systems to be better adapted to changing climate conditions.

Finally, although I unraveled several facilitative effects of native palms and trees on pasture productivity, animal welfare and biodiversity conservation in neotropical cattle farms, this dissertation has some limitations that should be acknowledged. First, the field surveys were carried out in the southeast of Mexico, and even when we aimed at the maximum number of paddocks to collect the data, extending the geographic range to other latitudes within the tropics would be advisable. Nonetheless, carrying out the studies in Mexico had advantages as well, as we could select farms with similar management type. Yet, the rotation system and grazing pressure sometimes differed among farms, possibly introducing some noise in the data collected. To reduce this noise, it would have been desirable to have farms with the exact same management type which is rather difficult when there is no payment back to the farmers. Moreover, we assessed the effects of trees on pasture productivity but did not assess directly their effects on cattle productivity. Further studies are needed to assess how trees could influence cattle productivity in terms of, for example, weight gain or number of offspring per year. Lastly, assessing farmers perceptions on tree cover is needed, as their management decisions may not necessarily be determined on ecological or cultural reasoning but most of the time may be influenced by economic reasons that directly influence the dynamics of social-ecological networks.

6.4 Conclusions

Scattered native palms and trees play a crucial role in the socio-ecological networks of cattle rangelands by improving pasture productivity during droughts, enhancing cattle welfare and conserving biodiversity. Farmer’s choices for retaining native palms and trees may reflect a holistic understanding of the resilience, adaptability and transformability of their socio-ecological systems and livelihoods (Walker *et al.* 2004). Understanding the networks’ dynamics on tropical cattle dry rangelands brings us one step closer to developing resilient livestock systems that maintain productivity and contribute to conserve biodiversity as global warming progresses.

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Summary

English

Resilience of dry tropical rangelands: How native palms and trees mediate the effects of seasonal droughts.

Cattle rangelands cover more than one quarter of the ice-free surface of Earth and have a big impact on the world´s climate, water, land and biodiversity resources. Livestock farming keeps expanding in response to increases in human population, socio-economic growth and the maintenance of meat eating habits, threatening forests across the global tropics and contributing significantly to global warming. At the same time, the higher temperatures and erratic rains resulting from climate change accentuate existing problems in livestock systems, and are expected to compromise pasture and cattle productivity. There is a strong need for more sustainable and resilient livestock systems to global warming that maintain productivity while also contributing to biodiversity conservation.

Increasing tree cover in rangelands could maintain the existing ecological networks and contribute to ameliorate the impacts of global warming on pasture and cattle productivity while having positive effects on biodiversity. By studying the interactions between trees and some of the organisms coexisting on cattle rangelands, this dissertation sheds light on how trees can contribute to increase the resilience of dry tropical rangelands to seasonal droughts. This knowledge could help us develop more sustainable and resilient livestock systems to global warming that maintain productivity while also contributing to biodiversity conservation.

Throughout this dissertation, I and different teams of collaborators reviewed the existing literature worldwide and carried out field campaigns in dry tropical rangelands to assess the effects of trees on the resilience of dry cattle rangelands to droughts. We gave special attention to the effects of trees on 1) grass productivity, 2) biodiversity conservation and 3) cattle thermoregulation in dry tropical rangelands considering seasonal weather variability.

In **chapter 2**, we performed a global meta-analysis to evaluate the effects of tree cover on grass biomass 1) along environmental gradients in tropical and temperate pastures, 2) during contrasting seasons, and 3) at different levels of canopy density. We concluded that the facilitative effects of trees on grass biomass are the strongest in

neotropical pastures during dry seasons. Moreover, these facilitative effects are more likely to occur at intermediate levels of evapotranspiration and irradiance. We noticed that the effects have been poorly studied for palms compared to the other groups of trees despite their widespread occurrence in tropical livestock pastures and their highly diversified local uses. Based on these results, we specifically aimed at understanding the effects of both scattered palms and trees on several organisms that may influence productivity in dry neotropical rangelands. Because these studies were performed in the field, we moved from a global level to a landscape level in **chapters 3-5.**

In **chapter 3**, we studied tree composition of dry cattle pastures of Yucatán, México and assessed the effects of palms, N_2-fixing trees and non-N_2-fixing trees on microsite environmental conditions, bare soil cover, and the performance of woody plants and grasses in their understory during the dry and wet seasons. In addition to assessing the effects of different canopy types on the performance of grasses, we also analyzed their effect on the impact of droughts and the recovery afterwards. We found that nearly half of the tree species of the surrounding native dry forests are conserved in the pastures. These palms and trees facilitate the recruitment of other woody plants below their canopies and ameliorated the impact of seasonal drought on grass greenness but slowed down its recovery afterwards. Of the different types of trees we studied, palms had overall higher positive effects on grass greenness and height than trees, especially during the driest season. Our findings highlighted the importance of palms for grass productivity in cattle farms in the dry tropics, as they are the most abundant arboreal species and had higher positive effects than trees.

In **chapter 4**, we explored the interactions between palms and the soil microbial community to further understand the mechanisms behind palm-grass facilitation observed in **chapter 3**. We assessed the influence of palm tree overstory on the microbial community structure of the grass rhizosphere in a cattle farm in Yucatán, México. Based on the massive sequencing of the 16S rRNA gene, we analyzed the diversity of bacterial species of the grass rhizosphere in the understory of the highly abundant palm tree *Sabal* spp. and in the open pastures exempt from any palm tree. We contrasted these two microenvironments with the rhizobiome of a legume tree *Acacia* spp., which is also abundant in the sampled farm, and harbours intrinsic, well-known, relations with nitrogen-fixing bacteria, and compared all rhizosphere samples to the bulk soil microbial composition. We found that soil microbial richness, diversity and dominance is higher in the grass rhizosphere under palms than in the other microenvironments which suggests a positive effect of the palms in the microbial community. Our novel findings provide evidence for the advantage of maintaining palm trees in dry tropical pastures as they allow for the establishment of a greater diversity of microorganisms that favor grass growth.

In **chapter 5**, we determined cow heat stress during the dry and wet seasons in dry tropical pastures and analyzed the effects of palms and tree shade on cattle behavior, based on behavioral observations in the field. Our observations indicated that cows actively seek dense tree shade, especially during the wet season when the environmental heat stress is higher. These findings highlight the importance of tree shade for cow thermal regulation in dry tropical regions and contribute to identify ways of adapting production systems to environmental stresses.

Finally, in **chapter 6**, I synthesize the results of the previous chapters and discuss their contribution to increasing our understanding on the resilience of dry cattle rangelands. I argued that farmer´s choices for conserving native palms and trees in pastures may reflect a deeper and holistic understanding of the social-ecological systems. Moreover, I suggested that intermediate levels of tree canopy density are a win-win scenario for pasture productivity and biodiversity conservation; at intermediate levels of tree canopy density, grass productivity is maximized during droughts, cattle can refuge under the shade when heat-stress increases and woody plant can establish in the understory. I also called attention on the poorly studied effects of palms on grasses in neotropical rangelands and emphasized on their positive effects on pasture productivity and nature conservation in the dry tropics. I encouraged to integrate and maintain a diversity of scattered palms and trees in pastures and to actively manage on-farm tree cover to maintain intermediate levels of tree canopy density to maximize and diversify the observed facilitative effects of palms and trees on cattle rangelands. Lastly I pledged researchers to bridge across scientific disciplines to expand the traditional indigenous knowledge in agroecosystems and multifunctional landscapes across environmental gradients and cultures around the globe to generate effective strategies for sustainable productive systems to be better adapted to changing climate conditions.

Understanding the interactions within the ecological networks of tropical cattle dry rangelands brings us one step closer to developing resilient livestock systems that maintain productivity and conserve biodiversity as global warming progresses.

Spanish

Resiliencia de pastizales tropicales secos: Como las palmas y árboles nativos median los efectos de la sequía estacional.

Los pastizales ganaderos cubren más de un cuarto de la superficie de la Tierra libre de hielo y tienen un gran impacto en el clima, agua, suelo y biodiversidad mundial. La ganadería sigue extendiéndose en respuesta al incremento de la población humana, del crecimiento socio-económico y del mantenimiento de los hábitos del consumo de carne, amenazando los bosques alrededor de los trópicos y contribuyendo significativamente al calentamiento global. Al mismo tiempo, las altas temperaturas y lluvias erráticas resultantes del cambio climático acentúan los problemas existentes en los sistemas ganaderos, y se espera que comprometan la productividad ganadera y de pastos. Hay una fuerte necesidad por desarrollar sistemas ganaderos más sustentables y resilientes al cambio climático que mantengan la productividad al mismo tiempo que contribuyan a la conservación de la biodiversidad.

Incrementar la cobertura arbórea en pastizales podría mantener las redes ecológicas existentes y contribuir a aminorar los impactos del calentamiento global en la productividad ganadera y de pastos. Al mismo tiempo, también podría tener efectos positivos en la biodiversidad. Por medio del estudio de las interacciones entre árboles y algunos de los organismos que coexisten en los pastizales ganaderos, esta tesis doctoral muestra cómo los árboles pueden contribuir a incrementar la resiliencia de pastizales tropicales secos al calentamiento global para mantener productividad y contribuir a la conservación de la biodiversidad.

A lo largo de esta disertación, yo y diferentes equipos de colaboradores revisamos la literatura existente en el mundo y llevamos a cabo campañas en el campo en los pastizales tropicales secos para estudiar los efectos de los árboles en la resiliencia de los pastizales ganaderos a la sequía. Especialmente nos enfocamos en entender los efectos de los árboles en 1) la productividad de pastos, 2) la conservación de la biodiversidad y 3) la termorregulación del ganado en pastizales tropicales secos, considerando la variabilidad climática estacional.

En el **capítulo 2**, llevamos a cabo un meta-análisis global para evaluar los efectos de la cobertura arbórea en la biomasa de pastos 1) a lo largo de gradientes ambientales en pastizales tropicales y templados, 2) durante estaciones contrastantes, y 3) a diferentes niveles de densidad del dosel arbóreo. Concluimos que los efectos facilitadores de árboles en la biomasa de pastos son más fuertes en pastizales neotropicales durante la temporada de secas. Además, estos efectos facilitadores son mas propensos a ocurrir a niveles intermedios de evapotranspiración y luz. Observamos que estos efectos han sido poco estudiados para las palmas en comparación con los otros grupos de árboles, a pesar de su extensa ocurrencia en pastizales ganaderos tropicales y de sus usos locales altamente diversificados. Basados en estos resultados, específicamente nos enfocamos en entender los efectos de palmas y árboles en diferentes organismos que podrían influir en la productividad de pastizales neotropicales secos. Debido a que estos estudios se llevaron a cabo en el campo, en los **capítulos 3-5** nos movemos de una escala global a una escala de paisaje.

En el **capítulo 3**, estudiamos la composición arbórea en los pastizales ganaderos secos de Yucatán, México. Evaluamos los efectos de palmas, árboles asociados con la fijación de N_2 y árboles no asociados con la fijación de N_2 en las condiciones ambientales, cobertura de suelo desnudo y en el desempeño de plantas maderables y pastos bajo el árbol durante la temporada de lluvias y de secas. Adicionalmente de evaluar los efectos de los diferentes tipos de dosel arbóreo en el desempeño de pastos, también analizamos su efecto en el impacto de la sequías y en la recuperación después de la sequía. Encontramos que cerca de la mitad de las especies arbóreas del bosque seco nativo adyacente son conservadas en los pastizales. Estas palmas y árboles facilitaron el reclutamiento de otras especies maderables de plantas bajo su dosel y aminoraron el impacto de la sequía estacional en el verdor del pasto pero lentificaron su recuperación después de la sequía. De los diferentes tipos de árboles que estudiamos, las palmas tuvieron, en general, efectos positivos más altos que los árboles en el verdor y en la altura del pasto, especialmente durante la temporada más seca. Nuestros hallazgos realzan la importancia de las palmas para la productividad de pastos en granjas ganaderas en los trópicos secos, no solo porque tuvieron los efectos positivos más altos, sino también porque son las especies arbóreas más abundantes en estos sistemas.

En el **capítulo 4**, exploramos las interacciones entre palmas y la comunidad microbiana del suelo para entender más a detalle los mecanismos detrás de la facilitación palma – pastos observados en el **capítulo 3**. Evaluamos la influencia del dosel de la palma en la estructura de la comunidad microbiana de la rizósfera de pastos en una granja ganadera en Yucatán, México. Basados en la secuenciación masiva del gen 16S ARNr, analizamos la diversidad de especies de bacterias en la rizósfera del pasto bajo el dosel de la altamente abundante palma *Sabal* spp. y en la rizosfera del pasto creciendo a cielo abierto. Contrastamos estos dos microambientes con el rizobioma de un árbol de leguminosa *Acacia* spp., el cual es también muy abundante en la granja muestreada, y mantiene relaciones intrínsecas con bacterias fijadoras de nitrógeno. Todas las muestras de la rizósfera fueron comparadas con la composición microbiana del suelo desnudo.

Encontramos que la riqueza, diversidad y dominancia microbiana son más altas en la rizósfera del pasto bajo las palmas que en los otros microambientes, lo cual sugiere que hay un efecto positivo de las palmas en la comunidad bacteriana. Estos novedosos hallazgos proporcionan evidencia de la ventaja de mantener palmas en pastizales tropicales secos ya que permiten el establecimiento de una mayor diversidad de microorganismos que promueven el crecimiento de pastos.

En el **capítulo 5,** determinamos el estrés térmico del ganado durante las temporadas secas y de lluvias en pastizales tropicales secos. Analizamos el efecto de la sombra de los árboles y palmas en el comportamiento del ganado basándonos en observaciones directas en el campo. Nuestros resultados indicaron que el ganado activamente busca la sombra densa de los árboles, especialmente durante la temporada de lluvias cuando el estrés térmico ambiental es mayor. Estas observaciones demuestran la importancia de la sombra de árboles para la regulación térmica del ganado en regiones del trópico seco y contribuyen a identificar maneras para adaptar los sistemas de producción al estrés ambiental.

Finalmente, en el **capítulo 6**, sintetizo los resultados de los capítulos previos y discuto su contribución para incrementar nuestro conocimiento en la resiliencia de pastizales ganaderos secos. Argumento que las decisiones de los ganaderos para conservar palmas y árboles nativos en sus pastizales podrían reflejar un conocimiento más profundo y holístico de los sistemas socio-ecológicos. Además, sugerí que los niveles intermedios de densidad del dosel arbóreo representan un escenario de ganar-ganar para la productividad de los pastizales y la conservación de la biodiversidad. A niveles intermedios de densidad del dosel arbóreo, la productividad del pasto es maximizada durante las sequías, el ganado se puede refugiar bajo la sombra cuando el estrés térmico aumenta y las plantas maderables se pueden establecer bajo el dosel. También llamé la atención en los efectos poco estudiados de las palmas sobre los pastos en los pastizales neotropicales y enfaticé en sus efectos positivos para la productividad de pastos y la conservación de la naturaleza en los trópicos secos. Alenté a integrar y mantener una diversidad de palmas y árboles dispersos en potreros y a activamente manejar la cobertura arbórea para mantener niveles intermedios y maximizar y diversificar los efectos facilitadores observados de palmas y árboles en sistemas ganaderos. Finalmente, hago un llamado a los investigadores para unir puentes entre las disciplinas científicas para expandir el conocimiento indígena tradicional de los agroecosistemas y paisajes multifuncionales en diferentes gradientes ambientales y culturas alrededor del mundo con la finalidad de generar estrategias efectivas y desarrollar sistemas de producción sustentables que estén mejor adaptados a las cambiantes condiciones climáticas.

Entender las interacciones dentro de las redes ecológicas de los pastizales ganaderos tropicales secos nos acerca un paso más al desarrollo de sistemas ganaderos resilientes que mantengan la productividad y conserven la biodiversidad a medida que el calentamiento global avanza.

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About the author

Ivan Raniero Hernández Salmerón was born in Morelia, Mexico on August 15th, 1989. He grew up in the city but his holiday playground was in the remote town of Cuauhlotitlan, Guerrero. There, he enjoyed being surrounded by wildlife, climbing trees, riding his grandpa´s donkey and horses or just swimming at the river with his cousins. During his childhood, he joined the Scouts group and discovered his passion for nature and outdoor activities. The beauty of nature drew him to study his bachelor in Biology, at Universidad Michoacana de San Nicolás de Hidalgo, in 2007. During his last semester, he became an exchange student at Universidad de Sevilla, Spain where he found out his second biggest passion: travelling. After graduating, he had his first encounter with the rewarding and exciting world of teaching as he became an English and a Science teacher. In 2014, Ivan´s passion for nature and travelling took him to the Netherlands, where he studied a Master degree in Forest and Nature Conservation at Wageningen University (WUR, with a scholarship from the National Council and Technology of Mexico, CONACYT). During his MSc program, he investigated the effects of elevation in the phylogenetic diversity of fungi in the mountains of Borneo. Additionally, he conducted an experimental study in Uruguay to understand the mechanisms behind tree recruitment in the extensive temperate grasslands. Ivan always had the conviction to do a PhD, and in 2017, he joined the Wildlife Ecology and Conservation Group at WUR. His project focused on understanding how native palms and trees mediate the effects of seasonal droughts in dry tropical rangelands. Again, he managed to combine travelling and nature conservation and spent a couple of years doing (hard) fieldwork in the stunning warm tropical pastures of Yucatán, México. The nature of his research is strongly connected to the fields of plant ecology, dry forests ecology and tree-grass interactions. He has also a strong interest on Agroecology as a science, a movement and a practice. Ivan is currently designing an agroecological farm with his family in México, always having nature conservation in his mind and aiming to connect to his roots.

Publications

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Other publications

Gómez-Reyes, V. M., Hernández-Salmerón, I. R., Terrón-Alfonso, A., & Guevara-Guerrero, G. (2012). Taxonomic study on Elaphomyces spp. (Ascomycota, Eurotiales, Elaphomycetaceae) from Michoacan, Mexico. *Revista mexicana de micología*, **36**, 57-82.

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Affiliation of co-authors

Wildlife Ecology and Conservation Group, Wageningen University & Research, NL

- Ivan Raniero Hernández-Salmerón
- Milena Holmgren
- Henrik J. de Knegt
- Valentina Delconte
- Maxime Landwier
- Jannes van Hoeflaken

Faculty of Veterinary Medicine and Animal Science, Universidad Autónoma de Yucatán, México.

- Francisco J. Solorio-Sánchez

Department of Biology, Wilfrid Laurier University, Canada

- Julie E. Hernández-Salmerón
- Gabriel Moreno-Hagelsieb

Department of Genetic Engineering, Centro de Estudios Avanzados del I.P.N., Mexico

- Gabriela Olmedo-Álvarez

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Resilience of semiarid cattle drylands to drought

Post-graduate courses (6.6 ECTS)

- Training week on agroecology; Agrotopia (2017)
- International course on agroecology and ecological restoration: sustainable resilient agro-landscapes; SOCLA, Elti, El Hatico Natural Reserve, CIPAV, Ganadería sostenible Colombia(2017)
- Uncertainty propagation in spatial environmental modelling; PE&RC and SENSE (2018)
- Introducción a Data Science: Programación Estadística con R; UNAM, Coursera online (2018)
- Tidy data transformation and visualization with R tidyverse and ggplot; PE&RC (2020)

Laboratory training and working visits (4 ECTS)

- Tree cover effect on grass biomass; Tropical Agricultural Research and Higher Education Center (CATIE) (2017)

Competence strengthening / skills courses (2.1 ECTS)

- Scientific writing; Wageningen in to Languages (2017)
- Reviewing a scientific paper; Wageningen Graduate Schools (2019)

- Scientific publishing; Wageningen Graduate Schools (2021)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)

- PE&RC Day: preventing the end of the world, how science can save the planet (2017)
- PE&RC First years weekend (2017)
- PE&RC Day: the social network of nature (2018)

Discussion groups / local seminars or scientific meetings (4.5 ECTS)

- International dairy nutrition symposium: new perspectives on transition cow management (2017)
- International dairy nutrition symposium: nutrition and health from dairy calf to heifer (2019)
- Current themes in ecology: biodiversity in crisis, perspectives on how to bend the curve (2019)
- Wageningen evolution & ecology seminar (2020-2021)
- Netherlands annual ecology meeting (2021)

International symposia, workshops and conferences (6.6 ECTS)

- 1st Mexican congress on agroecology: influence of native palms and trees on the productivity of tropical pastures; Chiapas, Mexico (2019)
- Ecological society of America annual meeting: fostering native palms and trees to increase resilience of cattle rangelands to drought; online, USA (2021)
- Dry forest symposium: native palms and trees mediate drought impacts on dry neotropical pastures; Online (2021)

Committee work (1 ECTS)

- Founder and board member of MEXA association (Mexican association); Wageningen (2020)

Lecturing / supervision of practical's / tutorials (1 ECTS)

- Trends in forest and nature conservation (2021)

BSc/MSc thesis Supervision (7.5 ECTS)

- BSc: The effect of trees on grass productivity in tropical grasslands
- MSc: Palms and trees in neotropical pastures: assessing their ecological benefits on grass productivity
- BSc: Cattle behaviour and use of tree cover during wet and dry seasons in dry tropical pastures of Yucatán, Mexico

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