Pasturelands as natural climate solutions: a socioecological study of tree carbon and beef production trade-offs

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Pasturelands as natural climate solutions: a socioecological study of tree carbon and beef production trade-offs

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A thesis submitted to the Graduate Faculty of

JAMES MADISON UNIVERSITY

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Abstract

Forest restoration is the most effective natural climate solution, with the potential to sequester 37% of the carbon dioxide (CO$_2$) needed to reach the Paris climate mitigation goal. Cattle pastures offer an underutilized opportunity to increase global forest restoration efforts, improve biodiversity, and maximize carbon storage through the adoption of management strategies that prioritize the incorporation of trees into pasturelands. However, remote estimations of tree carbon storage in pastoral systems have never been field-verified and their accuracy is unclear. Furthermore, the effect of increased trees on cattle production is understudied across biomes. Lastly, the restoration potential of these landscapes as a byproduct of tree carbon also remains to be studied. Therefore, the aims of this study were (i) compare past remote tree carbon estimations in pastureland systems to current field estimates to assess their accuracy, (ii) evaluate the effect of increasing tree carbon (MgC ha$^{-1}$) on the pastoral stocking density (AU ha$^{-1}$), (iii) quantify the woody species diversity (H') within pastures, and (iv) compare findings between farms in temperate (n = 26) and tropical (n = 16) ecosystems. To accomplish these goals, two remote datasets of global tree carbon from Harris et al., 2021 and Chapman et al., 2020 were first acquired, while the current pastoral carbon storage in temperate forest ecosystems of Virginia, USA and dry tropical forest ecosystems of Los Santos, Panama was estimated with in-situ plots. Woody plant species were also quantified to determine diversity as a metric of ecological restoration potential within these systems. We also conducted IRB-approved interviews with landowners to better understand their motivations for tree incorporation in their systems. We found that Chapman et al., 2020 significantly overestimated the carbon storage of pasturelands in Los Santos, Panama, while underestimating carbon in Virginia (p < 0.001). There was no
difference in MgC ha\(^{-1}\) between tropical farms and temperate farms, but H’ (p < 0.001) and stocking density (AU ha\(^{-1}\)) were significantly higher in Los Santos, Panama (p = 0.003). Additionally, farms enrolled in conservation programs had lower stocking densities than those that practiced traditional management (p = 0.026), but no significant differences in H’ or MgC ha\(^{-1}\). There was also no effect of MgC ha\(^{-1}\) on stocking density, which suggests that pastures with more trees did not result in a decrease in beef production. Woody species diversity (H’) was positively associated with increasing MgC ha\(^{-1}\) (p < 0.001), in Los Santos, but not in Virginia. Landowners had overall positive perceptions of trees in their systems, but some struggled to incorporate them due to financial and labor-related hurdles. These findings demonstrate the potential for pastures to increase above ground tree carbon and potentially woody species diversity without decreasing beef production. Moreover, such efforts support landscape restoration and offer potentially novel revenue streams for farmers through carbon credit programs. Lastly, we demonstrate the importance of taking a socio-ecological approach to restoration of human-dominated systems.
Introduction

The burning of fossil fuels has resulted in the accumulation of dangerously high levels of greenhouse gas (GHG) emissions in the atmosphere, driving our global climate into a crisis. Carbon dioxide (CO₂) accounts for 80% of emissions and has the highest concentration of any GHG (Lashof & Ahuja, 1990). Under the current conditions, human-induced CO₂ emissions are projected to intensify, exceeding 70 petagrams of carbon (PgC) by the year 2050 (Griscom et al., 2017) (Table 1). This exorbitant amount of carbon could have devastating impacts worldwide, particularly by increasing the warming of the planet. Such changes include environmental consequences, such as drastic climatic shifts and loss of global biodiversity, as well as economic losses of up to 10% global GDP (Ciscar et al., 2019). Consequently, the Paris Climate Agreement outlined a commitment to prevent the average global temperature from warming more than 2 degrees Celsius above industrial levels (IPCC 2016).

In recent years, natural climate solutions have been identified as key climate mitigation tools, with the potential to contribute up to 37% of the mitigation needed to achieve the main goal outlined in the Paris Climate Agreement (Griscom et al., 2017). Natural climate solutions are nature-based carbon sequestration approaches that utilize productive and consistent land management to maximize carbon storage across the environment (Fargione et al., 2018; Griscom et al., 2017). While there are over 20 recognized natural climate solutions, the most productive by far is the restoration of previously forested habitats (Griscom et al., 2017) (Figure 1). Restoration is the re-establishment of previously degraded or destroyed lands and encompasses a wide array of strategies that aim to reverse the impacts of destructive human land uses (Gann et al., 2019). If implemented effectively, restoration efforts could collectively have a maximum
global carbon mitigation potential of 2.7-17.9 PgCO₂e y⁻¹, which is equivalent to the removal of 650 million cars from the roads per year (The Nature Conservancy 2018; Griscom et al., 2017) (Figure 1). Furthermore, forest restoration will also add a host of benefits, including restored biodiversity, additional ecosystem services, such as improved water availability and stable microclimates, and bolstered ecosystem resilience (Aryal et al., 2019; Griscom 2020; Hayek et al., 2021).

**Figure 1.** Climate mitigation potential of various natural climate solutions, with reforestation having the highest contribution. From: The Nature Conservancy (2018).

*Livestock pastures as potential carbon sinks*

Of the many human land use types, clearing for agriculture is the dominant driver of land degradation and deforestation in both temperate and tropical forests (Armenteras et al., 2017; Havlík et al., 2014). Livestock pasturelands are responsible for most of this degradation, accounting for nearly 3,315 million ha of that land, equivalent to roughly 30% of the world’s ice-free surface, as of 2013 (Herrero et al., 2013). Presently, global pastureland coverage has remained stable (Winkler et al., 2021). Despite their extensive land cover, livestock pastures currently store only about 3.87 PgC per hectare, with over
90% of that stored carbon concentrated on less than 10% of the total pastureland area (Chapman et al., 2020; Herrero et al., 2013). In large part, this is due to the low carbon density of pasturelands, which is on average less than 5 megagrams of carbon (MgC) per hectare (Chapman et al., 2020). These virtually “empty” livestock pastures are mostly beef pastures and are estimated to be costing the global community around 152.5 Pg of sequestered carbon per year (Hayek et al., 2021) (Table 1).

**Table 1:** Unit conversions used for measuring carbon stocks. Adapted from: Bartlett et al., 2020 NINA Report 1774b

<table>
<thead>
<tr>
<th>Unit</th>
<th>Meaning</th>
<th>Alternative units</th>
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<td>kg m$^{-2}$</td>
<td>kilogram per square meter</td>
<td>ton per hectare</td>
<td>1 kg m$^{-2}$ = 10 t ha$^{-1}$ (We use Mg ha$^{-1}$)</td>
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However, recent studies have found that despite the current low carbon density, if increased tree restoration efforts, such as silvopasture, are adopted, beef cattle pastures will have a high carbon storage potential (Chapman et al., 2020). With effective and consistent management, nearly 44.5 PgCe y$^{-1}$ could be sequestered on pasturelands, with roughly 530 Tg of this carbon stored in temperate forests and about 31.09 PgC in tropical Latin American forests (Chapman et al., 2020; Chazdon et al., 2016; Wilkens et al., 2021).
Altogether, this could contribute 0.2-7.6% of the total carbon sequestration needed to reach the Paris Climate Agreement goal (Meinshausen et al., 2009).

**Agroforestry**

The management and incorporation of trees within agricultural landscapes encompasses all forms of agroforestry strategies (Feliciano et al., 2018; Nair, 2012; Rosenstock et al., 2019). The prevalence and effectiveness of these strategies are generally dependent on regional economic and socio-ecological factors, though many are shared throughout the globe (Pent, 2020; Rosenstock et al., 2019). In temperate ecosystems, the most common agroforestry methods include riparian buffer zones and wind breaks (Pent, 2020). Other less prevalent methods include lines of trees and alley cropping, which is when crops are interplanted between rows of trees (Wilkens et al., 2021). Conversely, in dry tropical ecosystems, agroforestry is far more common in the form of live fences, gallery forests that line riparian areas, and isolated trees (Griscom 2020). Silvopastoral systems, which implement the planting and management of trees for timber within cattle pastures are also frequently found in the tropics and have been shown to provide substantial carbon storage (López-Santiago et al., 2019). Additionally, silvopastoral systems also provide alternative sources of income and/or food resources, as many of the tropical trees have edible fleshy fruit (Bruck et al., 2019).

Planted or naturally occurring trees each provide significant ecological benefits beyond carbon sequestration as well. Primarily, they serve as vital sources of habitat within an otherwise cleared pastureland (Harvey et al., 2011). These small areas of habitat, especially clustered and fragmented tree formations, allow important seed dispersers, such as bats and birds, to survive in pasturelands, in turn helping tree species
continue to spread and reforestation to take place (Griscom et al., 2007; Uhl et al., 1981). In addition, isolated trees have been shown to have improved seedling success rates under their canopies in livestock pastures (Slocum and Horvitz, 2000). Riparian zones create more habitat for seed dispersers and improve vegetation regrowth, while dually functioning as windbreaks and water quality buffers (Griscom 2020, Griscom et al., 2007; Pettit & Naiman 2007).

The general integration of trees within agricultural landscapes has been shown to substantially increase overall species richness, particularly of native species, which has important implications for the restoration of many threatened ecosystem types that have been converted to pastureland (Aryal et al., 2019). Over time, a broader species and functional range of vegetation, combined with the creation of additional native habitat, leads to higher biodiversity and reforestation potential when compared to unmanaged systems (Griscom, 2020; Torralba et al., 2016). Other environmental benefits provided by added trees include increased soil nutrient, moisture, and carbon levels (Aryal et al., 2019; Hoosbeek et al., 2016). Higher nutrient contents and organic carbon elevate soil quality, which can contribute to pastureland success by supporting more productive forage yields (Pang et al., 2019). Moreover, systems that have increased tree cover also have enhanced, more stable microclimate conditions, including reduced solar radiance, decreased risk of fire, and less fluctuation in temperature (Hooper et al., 2004; Uhl et al., 1982).

Collectively, these benefits help increase cattle resiliency under environmental stressors, such as disease (Hoosbeek et al., 2016). Resiliency can be measured as physical metrics and will be particularly important in a changing climate, as high temperature extremes are only increasing in frequency throughout the globe (Rasmussen et al., 2016).
At any temperature above 80°F, cattle experience significant psychological distress from heat exhaustion, enough to require additional management and intervention, and above 90°F, they can suffer health-related consequences (Hoosbeek et al., 2016). It is likely that collectively, rising temperatures will warrant increasing intervention from cattle farmers, which can be particularly strenuous, financially, and logistically, for many small-holder farms (Hoosbeek et al., 2016). However, due to the benefits that they provide for cattle and farmers alike, sustainable management strategies like agroforestry offer an opportunity to proactively mitigate these potential strains (Vasquez et al., in press; Pent 2020). Such strategies are typically implemented through participation in programs that provide incentives for conservation land management (Kamal et al., 2015).

*Conservation management programs*

Land management programs are typically voluntary agreements established between landowners and governmental organizations or nonprofits that focus on restoring ecosystem functioning in agricultural lands (Kamal et al., 2015; Milder 2007). Specific management strategies and projects vary widely across programs but can include restoration efforts such as tree plantings and land retirement agreements, as well agroforestry projects like home gardens and timber plantations (Milder 2007). The impact of conservation management on widespread environmental change is low because, like the use of agroforestry strategies, adoption is low. Improving the participation in these types of programs globally could help maximize the potential for carbon sequestration within pasturelands, as more farmers would be implementing sustainable management (Chapman et al., 2019). Furthermore, conservation programs offer unique opportunities for collaboration between landowners and scientists. These collaborations may help
facilitate a connection between farmers, scientists, and extension agencies, which can in turn promote adoption of conservation methods more effectively than each component individually (Nettle et al., 2022). While much research has been dedicated to identifying farmer motivations for enrollment from a socio-ecological point of view, less have specifically considered the impact that such programs have on farmer stewardship, management priorities, and their perceptions of the benefits of a healthy ecosystem on their production goals specifically.

**Farmer motivations**

To proactively implement sustainable management practices and improve participation in conservation management programs, the interests of the farmers themselves must be considered (Gosling et al., 2020). Given that small family farmers own over 80% of these vital agricultural lands worldwide, understanding both their motivations and hesitations regarding tree incorporation, as well as prioritizing their involvement in decisions surrounding the implementation of reforestation strategies and sustainable land-use practices are key to maximizing carbon sequestration (FAO 2017; Schneider 2016). Many studies have examined the perception of farmers towards agroforestry practices, reforestation, and the incorporation of trees across the globe (Vasquez et al., in press.; Calle 2020; Gosling et al., 2020; Frey et al., 2016; Lerner et al., 2015; Zahawi et al., 2014). Collectively, they have demonstrated that there is widespread use of trees across agricultural contexts, and for this reason, there may be a path forward towards widespread agroforestry adoption. In general, there are a variety of economic (e.g., diversified revenue from silvicultural products), cultural (e.g., certain tree species can have spiritual value), and agricultural reasons (e.g., improved soil quality) that
farmers include trees in their pastures (Gosling et al., 2020; Garen et al., 2011).

Additionally, many farmers consider the implementation of at least one agroforestry technique as an optimal management scenario for their land (Gosling et al., 2020).

Despite these generally positive perceptions, long-term adoption of agroforestry practices remains low worldwide (Lerner et al., 2015). Likely, this is because many adoption initiatives of agroforestry are supported by short-term financing programs and are not as economically feasible for landowners in the long term, despite such estimations from past economic models (Frey et al., 2013). While initially successful, short term support programs, typically around two years long, can result in a lack of continuation in system maintenance after program support ends (Frey et al., 2013). Additionally, support must be competitive with other payments from large corporations in industrial agriculture for agroforestry to persist as well (Dahlquist et al., 2007). Without sustained management, the landscape will regress to its prior degraded state, reducing carbon storage capacity and facilitating the encroachment of invasive species (Guillerme et al., 2020). However, the underlying motivations that drive farmers to either continue sustainable management practices or return to traditional practices, and the barriers that each face, are not well documented. Therefore, to further restoration efforts and maximize the carbon sequestration potential of pastoral landscapes, investigating these drivers is paramount (Gosling et al., 2020).

**Impacts of tree carbon on pasture production**

One of the main challenges farmers face when considering incorporating additional trees or restoration efforts in their pastures is the potentially hindering effect of trees on the production of their farm (Calle 2020). Pastureland productivity is frequently
measured in terms of forage nutrient (nitrogen, phosphorus, and potassium) content and abundance (Pang et al., 2019; Feldhake et al., 2008). While these metrics can vary amongst pastures in different regions with different forage types, they directly determine the overall cattle yield of the pasture and as a result, farmer earnings (Pang et al., 2019). However, forages require certain environmental conditions, such as high light levels, to optimize growth and maximize productivity (Pent 2020; Pang et al., 2019). In pasturelands that incorporate restoration efforts, these environmental requirements can be compromised, as some studies have found that increasing tree cover reduces the area available for forage growth and limits forage light access (Bruck et al., 2019; Pang et al., 2019). Together, these limitations lower forage productivity and quality, reducing the number of healthy cattle a pasture can support per hectare and potentially decreasing farmer income (Bruck et al., 2019; Pang et al., 2019). Nevertheless, other work on silvopastoral management that looked at total production output, as opposed to individual production units, has found that well-managed tree cover within a pasture can result in higher overall productivity. However, individual productivity for forage or cattle was still reduced. The combined higher overall productivity may be because the biological and material benefits that additional trees provide could supersede any individual reductions (Pent 2020; Fike & Pent 2017). However, this relationship is likely to vary between ecosystems, and requires regionally specific guidance (Pent 2020; Rosenstock et al., 2019). Furthermore, these past studies have solely focused on the presence of tree carbon within pasturelands, not the quantity of the carbon stored on the production area of the farm.

As such, clarifying this relationship between cattle yield and quantity of tree carbon storage across various types of ecosystems could increase the integration of trees
within pastoral systems, and increase the type of land and total area available to be used as pasture, subsequently bolstering the potential carbon sequestration of these ecosystems (Rosenstock et al., 2019). It could also help maximize cattle productivity, resulting in reduced greenhouse gas emissions (Rodríguez-Miranda et al., 2021). Lastly, demonstrating the effects (or lack thereof) of tree carbon on beef production may highlight pasturelands as carbon sinks while preserving the production capacity of the systems, thereby creating a path for pasturelands to be utilized in nationally determined contribution plans (NDC’s). Consideration of pasturelands in NDC’s could also lead to funding opportunities through carbon credit payment programs for farmers and potential reforestation co-benefits (Baumber et al., 2020; Cunningham et al., 2015). However, for such opportunities to occur, estimations of the carbon stored in these systems needs to be further verified (Nair 2012).

Estimating pastoral tree carbon

Numerous studies have focused on calculating and mapping the overall carbon sequestration and forest cover of terrestrial surfaces, including agricultural areas, worldwide, both remotely and in the field (Rosenstock et al., 2019; Fargione et al., 2018; Griscom et al., 2017; Caughlin et al., 2016; Zomer et al., 2016, Caughlin 2013). However, these practices of carbon accounting have historically been dominated by inconsistencies in methodology and hindered by limited data reporting (Nair 2012). In addition, carbon sequestration in agroforestry systems has been particularly difficult to assess, due to management strategies that differ culturally, temporally, and spatially. For example, farmers may remove or add trees into their systems at differing rates, or some farmers may manage trees more intensively than others, which can lead to uneven
quantities of carbon within similar systems. For that reason, agroforestry systems likely do not follow past allometric models, which are equations used to estimate tree carbon based on other tree metrics such as diameter-at-breast-height (DBH), to the same degree of accuracy as other systems (Nair 2012).

As such, the development of a simple, yet effective and clearly defined methodology for aboveground carbon sequestration in various agroforestry systems is needed (Nair 2012). Past remote methodology utilized a grid layer with cells of a large size and relied primarily on low resolution spatial imagery, around 500m. This allowed for course estimates on a broad scale by quantifying carbon storage within each large grid cell, but likely resulted in the misclassification of tree cover and over-yielding of carbon estimations on a finer scale, especially in smaller, family-owned farms (Chapman et al., 2020). However, recent advances in carbon accounting technology and understanding have allowed for new opportunities to develop standardized protocols, particularly for detailed nuances in tree cover (Tarbox et al., 2018). By using higher 30m resolution imagery, a detailed remote assessment of the woody carbon storage of small-holder livestock farms is feasible (Chapman et al., 2020; Tarbox et al., 2018).

While remote methodology is less expensive and less time consuming than other forms of carbon accounting, verification of the remote classification and carbon storage estimates with ground-truthing field measurements is best practice (Tarbox et al., 2018; Boukili et al., 2017; Nair 2012). This is particularly true of agroforestry landscapes and cattle pastures, where less data is available, and the landscape is constantly evolving (Nair 2012). Common field verification methodology typically considers organic soil carbon content and/or uses older allometric equations that require several assumptions of ecological processes such as tree growth rate, which may not always be true, particularly
for intensively managed agroforestry systems (Nair 2012). Nevertheless, more recently developed allometric equations that rely on measurements from trees in urban environments may provide more accuracy for carbon accounting in systems like forested pasturelands that have more open spaces and smaller tree groupings compared to naturally occurring forests, especially for temperate regions (Nair 2012). In addition, other tools, such as the recently developed BIOMASS package in R-Studio, allow for continuous updating of any models used to account for any new findings (Rejou-Mechain et al., 2017). Such novel resources and equations allow for noninvasive carbon measurements and take into consideration variables such as diameter at breast height (dbh) and wood density (McPherson et al., 2016). Therefore, by combining the use of recent high resolution remote carbon storage estimates with ground-truthing measurements in the field, as well as standardized tree grouping categories, a more accurate estimation of carbon storage in pasturelands may be feasible.
Aims and predictions

The overarching goal of this research was to evaluate the relationship between pasture trees and cattle production with a socio-ecological approach across regions and management regimes.

The primary aim of this research was to evaluate the relationship between tree carbon storage (MgC ha$^{-1}$) and the number of cattle a pasture can sustain per hectare of land in both temperate and tropical ecosystems, under two different management regimes (conventional/conservation). We predicted the following:

1. There will be a threshold effect of increasing average tree carbon storage per hectare on cattle production. Further, the quantity of carbon per hectare at the apex of the threshold where cattle production declines, will be greater than the current average tree carbon (MgC ha$^{-1}$) stored on pasturelands, indicating that beef pastures could support more trees than they currently do, without negative impacts on cattle yield.

2. Tropical regions will experience a decline in cattle production at a higher threshold than temperate regions, because of the increased need for trees and shade in these hotter, drier climates.

3. Tropical pasturelands will have a lower stocking density and higher tree carbon storage overall, given historical grazing patterns in the region.

4. Conservation farms will have a higher MgC ha$^{-1}$ before production begins to decline and a higher stocking density than conventional systems.

5. Increasing tree carbon per hectare will positively correlate with woody species diversity, indicating a potential for the recovery of the ecosystem functioning as a byproduct of improving tree carbon.
A second aim of this study was to assess past remote estimations of tree carbon by comparing them to present-day ground-truthed estimations. We predict the following:

1. Field-measured carbon values will be lower than past remote estimations in Los Santos due to its loss of tree cover since 2000. In contrast, given that Rockingham County, VA has experienced a net gain in tree cover since 2000, we predict that the field carbon estimations will be greater than past remote estimations.

2. Of the two remote datasets used in this study (one from 2020 and one from 2000, to be discussed further), we predict that the dataset from 2000 will have the highest overall carbon storage in Los Santos, followed by the dataset from 2020. This pattern will differ for Virginian farms, with the field estimations having the highest values, followed by the 2020 remote dataset and the dataset from 2000.

The final aim of this research was to interview cattle farmers in Virginia, U.S.A and Los Santos, Panama to better understand their perceptions of the benefits and consequences of trees in the pasturelands, as well as to determine barriers to enrolling in programs that assist farmers in incorporating trees into their production systems and prevent them from maintaining the systems once support ends. We predicted that farmer opinion towards trees and wildlife would vary in the two program types, regardless of region, while certain barriers (e.g., cost of implementation, intensity of management, etc.) will be more uniform throughout all those involved in the survey.
Methods

Study regions

This study focused on two ecoregions: Rockingham County in Virginia, USA, and the Pedasi region in the Los Santos province of southern Panama. Located in the valley between the Blue Ridge Mountain and the Shenandoah Mountain, Rockingham County has a temperate climate, dominated by oak-hickory forests (Figure 2). In the summer months, the average temperature is around 72.5°F, but maximum temperatures have exceeded 90°F (NOAA 2022). Temperatures have increased every decade at a rate of 0.2°F (NOAA 2022). At present day, Rockingham County experiences about 18 days above 90°F per year. However, this total is expected to double, with nearly 40 days over 90°F degrees by the year 2080 (Rasmussen et al. 2016). Increasingly frequent temperature extremes will drastically hinder human activity, especially agriculture. In Rockingham County, over 228,542 acres of land are used for agricultural purposes, with most dedicated to livestock production. Accordingly, the county is ranked 3rd in the state for beef production as of 2017 and is home to ~55,000 cattle (NIDIS 2022; USDA 2017). Many of these cattle farms are small holder owned, and less than 200 acres in area (USDA 2017).

The Los Santos province is located on the Azuero Peninsula, on the Pacific coast of Panama (Figure 2). The dominant ecosystem type is the highly endangered, seasonally dry, tropical deciduous forest (Griscom 2020; Olson et al. 2001). On the Azuero, there is a pronounced dry period of roughly half the year, extending from December 7th to May 1st (Nakaegawa et al. 2015). Annual rainfall averages 1600mm, with 100% of precipitation occurring during the wet season (Nakaegawa et al. 2015). The mean annual
temperature is 77°F, with currently over 160 days per year reaching temperatures above 90°F (Rasmussen et al. 2016; Griscom et al. 2011). These extremes are also projected to increase in frequency to 247 days over 90°F by the year 2080 (Rasmussen et al. 2016). The prevailing land use type is also agricultural, primarily cattle pastures (Griscom 2020). As such, land clearing for pastures has furthered the deforestation of dry forests in the region, resulting in a net forest loss rate of 40 hectares per year; the third highest in the globe for all forest types (Hansen et al., 2013). The presiding tree species in pasturelands include *Guazuma ulmifolia* and *Cordia alliodora*, as cattle naturally select for these species due to their easily dispersed seeds and rapid resprouting abilities (Griscom et al. 2009). In contrast, *Calyxophyllum candidissimum* and *Tabebuia rosea* are more frequently prominent in fragmented secondary forest patches throughout the region (Griscom & Ashton 2011).

A total of 42 farms were included in the study. Within each region, roughly half of the farms were enrolled in a conservation-focused land management program, while the others practiced traditional grazing management (Figure 2). Participants from each group were contacted by third-party members affiliated either with a conservation program or agricultural society, and involvement in the study was voluntary. In Virginia, the conservation program treatment was represented by farms participating in the Conservation Reserve and Enhancement Program (CREP) through the Virginia Department of Conservation and Recreations, which provides financial support for farmers who remove cattle access from riparian areas and enhance riparian forests with additional tree plantings (CREP 2023). Traditional Virginia farmers were identified through affiliation with the Virginia Cooperative Extension. In Panama, farms enrolled in
the Environmental Leadership and Training Initiative (ELTI), through the Yale School of Forestry, represented the conservation program treatment group. Like CREP, ELTI enables farmers to implement sustainable management strategies, such as silvopasture, by providing educational and financial resources. ELTI also served as the contact for traditional farms.

**Figure 2.** Partial map of farms (green outline) in Virginia, USA (A) and example of field Virginia field site (B). Partial map of farms in Los Santos, Panama (C) example of Los Santos field site (D). All maps were created with ArcGIS Pro v. 3.0.2 (ESRI, California, USA).
Spatial data acquisition

Farm boundaries for Virginia were extracted from the “Parcels” layer in the Rockingham County GIS database, while a shapefile containing property boundaries for Panama was provided by ELTI (Figure 3A). Stream layers used in tree cover classification were obtained from the Rockingham County GIS database and the Smithsonian Tropical Research Institute for Virginia and Panama, respectively. All layers were projected to the NAD 1983 UTM Zone 17N coordinate system (Figure 3A).

Tree cover classification

The production of all farms was delineated with in-situ ground-truthing and verification from landowners to include only the area where cattle had access (hereafter referred to as “production area”) using a Trimble Geo 7x GPS (Sunnyvale, Ca, USA) and the Avenza Systems iPhone application v. 4.2.2. (Toronto, Canada). For Virginia farms, additional hectares of production land were added to the total area used for each farm, depending on the number of 1000 lb. round, mix-grass hay bales supplemented per year. The mean number of bales produced per hectare was estimated to be seven, based on information from the landowner survey.

Following designation of the total production area, the Grid Index Features tool was used to overlay a 15m x 15m grid across the entirety of each property feature. We then classified every cell within the grid according to its dominant tree cover class (Figure 3B, Table 2). Dominance in mixed plots with both softwood and hardwood trees was assigned based on the majority stem count in Virginia farms (Figure 4). The purpose of such tree cover classification was to obtain the highest level of variation within the
landscape as possible, given that complexity within these systems is highly variable and consistently overlooked in broader scale analyses (Nair 2012). The additional use of the grid cell classification allowed for consistency during remote identification and for in-situ verification to reflect the exact location of each cell.

Figure 3. Workflow diagram for A) production boundary acquisition grid overlay and B) tree cover type classification in ArcGIS Pro.

Figure 4. A) General classifications for isolated, clustered, and fragmented tree cover types, broken down into broadleaf and conifer species for Virginian farms. B.
General classifications of fence line and riparian areas with 15m buffers. C. Lines of trees classification for Virginian farms. D. Plantation classification for Los Santos farms.

Recent imagery from Earth (2022) served as the base map for tree cover classification and had an average resolution of 15cm (Tarbox et al., 2018). To quantify the tree cover types within a landscape, a new feature class was created in ArcGIS Pro for each tree cover class (Figure 3 – 6) and any time that cover type occurred within a grid cell on a farm, a 225m² polygon was hand digitized by tracing over the individual cell with the Snapping tool (Figures 4 & 5).
Figure 5. A) Example of tree cover classifications on a Rockingham County farm and B) a Los Santos farm. Tree classes were initially classified via remote sensing and verified by ground truth analysis. Created with ArcGIS Pro.

Field tree carbon

Field surveys were conducted on each farm to verify tree cover classification and production boundaries and estimate current tree carbon storage and woody species diversity during August 2021- August 2022. Within each farm, two 30m x 30m plots were constructed for each tree cover type present. Plot locations were randomly selected remotely using the Generate Random Points tool in ArcGIS Pro and navigated to in the field using the Avenza iPhone application v. 4.1.1. Then, within each plot, the species and diameter at breast height (DBH, cm) of all woody species greater than 5 cm DBH were recorded.

To determine average tree carbon density per farm, the total tree carbon (KgC) was first calculated for each stem on every tree measured using the following allometric equations for Virginia and Panama (McPherson et al., 2016; Chave et al., 2015) where $E =$ environmental stress at the site location (0.112324, Los Santos only), $\rho =$ species wood density (g cm$^{-3}$), $D =$ diameter at breast height (cm), and $ln =$ log base e. In equations for Virginia, estimates were multiplied by 1.28 to convert to total biomass (aboveground and belowground), and by 0.5 to convert to carbon specifically. Species-specific wood densities were obtained through the Dryad database (Zanne et al., 2009). When species level data was not available, the mean wood density for the genus was used.
Virginia:

1. \[ \text{Broadleaf KgC}_{\text{est}} = (0.0002835 \times (D^{2.310647} \times \rho) \times 1.28 \times 0.5) \]

2. \[ \text{Conifer KgC}_{\text{est}} = (0.0000698 \times D^{2.578027} \times \rho \times 1.28 \times 0.5) \]

Panama:

3. \[ \text{KgC}_{\text{est}} = \exp \left[ -1.803 - 0.976 \ln(p) + 2.673 \ln(D) - 0.0299[(\ln(D))^2] \right] \]

The total KgC per tree was the result of the sum of the total KgC for each stem measured. Then, all trees within a 30 x 30m inventory plot were summed to determine the total KgC/900m². The following equation was used to convert to megagrams of carbon per hectare for both regions.

4. \[ \text{MgC ha}^{-1} \text{ per plot} = \left( 10,000 \times \left( \frac{\text{KgC/900m}^2}{900} \right) \right) \times 1000 \]

The resulting values for all inventory plots were assigned to their respective tree cover classes and averaged for the mean MgC ha\(^{-1}\) in each tree cover type for each farm (Table S2). The one exception was in the case of the Panamanian live fences, which are pollarded continually, and as such, do not reflect standard heightdbh allometry. To account for this variation, mean height was estimated in the field using a subset of randomly selected live fence trees. The field estimate equaled roughly ~6m, on average. The expected height based on the measured DBH was estimated remotely in the “BIOMASS” package in RStudio for each tree (Réjou-Méchain et al., 2017). The percent difference in height between the remote and field estimates was calculated for each tree and averaged ~20% in total. As a result, total KgC per tree in the live fence category was then reduced by 20% to reflect this discrepancy.
The average MgC ha\(^{-1}\) for each tree cover type on a farm was then multiplied by the area (ha) of its respective tree cover type to estimate total MgC. Finally, the area of each tree cover class on the farm was divided by the total area with trees and multiplied by total MgC. All weighted values (MgC) were then totaled and divided by the total production area (ha) to obtain the weight average carbon density (MgC ha\(^{-1}\)) for each farm (Table S3).

**Woody species diversity**

The type and abundance of all woody species greater than 5 cm in diameter was recorded in each plot. The “vegan” package in R-Studio was used to calculate the woody species richness and Shannon Diversity Index (H’) per farm. (Oksanen et al., 2017).

**Stocking density**

We chose stocking density as the metric of cattle yield for this study. Stocking density is typically presented as the number of animal units per unit of land area. Other metrics that are widely used to quantify cattle yield include stocking rate, which dictates the amount of land available per head, and carrying capacity, which is the maximum number of animals a pasture can support safely. However, these are generally estimated using forage information, such as species, dry matter weight, etc., which were beyond the scope of this study.

The total number of cattle per farm, breed, age class, and weight of the cattle were extracted from interviews with landowners. The total head of cattle was converted to animal units (1 AU = one 1,000lb cow, plus calf) to account for variation amongst the
cattle in terms of age, weight, and sex (Table 2) (Yamamoto et al., 2007; Allen et al., 2011).

**Table 2.** Animal unit conversions from USDA National Range and Pasture Handbook (2022)

<table>
<thead>
<tr>
<th>Cattle class</th>
<th>Average weight (lbs.)</th>
<th>AU equivalent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cow + calf</td>
<td>~1,000lbs</td>
<td>1.0</td>
</tr>
<tr>
<td>Bull</td>
<td>~1,200lbs</td>
<td>1.35</td>
</tr>
<tr>
<td>Steers (rearing stage)</td>
<td>~600-800lbs</td>
<td>0.7</td>
</tr>
<tr>
<td>Weaned calves</td>
<td>~400lbs</td>
<td>0.5</td>
</tr>
</tbody>
</table>

Using the following equation, we calculated the stocking density for the farms for a 12-month grazing period. $A = \text{total production area (ha)}$ and $\text{AU} = \text{total animal units}$ (Allen et al., 2011).

$$4 \quad SD = \frac{\text{AU}}{A}$$
Remote estimation comparisons

Two global-scale remote aboveground biomass datasets, Hansen et al. 2002, and Chapman et al, 2020, were used to compare the accuracy of remote estimations to the estimations made in this study using field-collected data (Figure 6). Chapman et al., 2020 consisted of two datasets that estimated the total MgC in pasturelands (TIP) and in croplands (TIC) globally and were used with permission from the authors. The versions of the Hansen et al. 2002 dataset used were in MgC ha\(^{-1}\) for 40N 80W (Virginia) and 10N 090W (Los Santos) and were retrieved from the Global Forest Watch database (GFW).

![Figure 6](image)

**Figure 6.** Example images of A) Global Forest Watch and B) Chapman et al., 2020 rasters in Rockingham County, Virginia farms.

All datasets were downloaded as raster files and projected to the NAD_1983_UTM_17N projection using a nearest neighbor resampling method for discrete data (Figure 7). The *Zonal Statistics as Table* tool was then used to extract statistics for each farm (Figure 7).
Figure 7. Workflow diagram for remote dataset acquisition and carbon estimation for each parcel in ArcGIS Pro.

The mean statistic was used for the TIC/TIP data, which was in MgC, while the sum statistic was used for the GFW data and converted to carbon, because it was in aboveground biomass per ha. The following equations were used to convert the values from each dataset into average MgC ha\(^{-1}\) for each farm, where A = the production area of the farm (ha).

6 Chapman et al., 2020: \(\text{MgC}_{\text{est}} = \frac{\text{TIC}}{A}\)

7 Hansen et al., 2002: \(\text{MgC}_{\text{est}} = \text{GFW} \times 1.28 \times 0.5\)
Landowner interviews

Internal review board (IRB) approved semi-structured interviews were given to all landowners, when possible (Table S4). For certain farms, the properties were rented to outside cattle farmers, who were interviewed jointly with the landowner. For other farms, the renter declined to participate, and no interview was conducted.

All participants were interviewed at the time of ecological data collection on their property. Interviews consisted of a semi-structured series of questions, either in English or Spanish (see Appendix). We used the data collected to gather cattle production specifications for each farm, as well as quantify preferences on and experiences with conservation programs. All interviews took an hour to complete and were conducted from May 2022 – August 2022.

Statistical analyses

All statistical analyses were conducted in R Studio v 4.2.2. Normality of the data was assessed using a Shapiro-Wilks Test (p > 0.05). To evaluate the effect of increasing average MgC ha\(^{-1}\), region, and management types on the stocking density and woody species diversity, Type III generalized linear models were fitted using a ziGamma distribution and logit = link function in the glm2 package in R-Studio (Marschner 2011). The logit-link function confirms that predictor variables differ with the expected response value along a linear gradient (Bolker et al., 2009). All dependent variables were analyzed separately. Type III ANOVA tests were then run using generalized linear models with ziGamma distributions and logit - link functions to test for differences in MgC ha\(^{-1}\), AU, H’, and species richness between regions and management types, using the native stats
package in R-Studio. Significant variables were evaluated using Tukey comparisons of means tests.

A standard Kruskal-Wallis rank sum test was used to test for differences between our field-verified tree carbon data and the two remotely estimated datasets. Significant variations between each dataset were assessed using a Dunn’s test adjusted with the Holm method.

A qualitative components analysis was conducted to code survey responses for questions used in statistical analysis (see supplemental materials). Generally, when questions regarded quantities of benefits and costs, a score was assigned to the respondent based on how many items were listed (1 benefit = 1, etc.). Overall differences between benefits and costs of trees and wildlife, and the number of beneficial and detrimental species listed, were analyzed using a Wilcoxon-Rank Sum test. To compare differences in the above variables between management groups, Type III ANOVA tests were again run using generalized linear models with Poisson distributions and logit-link functions and Tukey’s comparisons of means test was used to analyze significant differences between groups.
Results

Field tree carbon

Mean tree carbon storage (MgC) per hectare (ha) varied from 0.06 to 48.24. There was no significant difference in pastoral MgC ha\(^{-1}\) between Los Santos and Virginia, nor were there any differences between management types (p > 0.05, Table 3, Table S5).

Table 3. Mean ± standard deviation of average tree carbon per ha (MgC ha\(^{-1}\)), woody species diversity (H’), and stocking density (AU ha\(^{-1}\)). C = farms were those that participated in a conservation land management program, NC = farms that did not participate in a conservation land management program. Capital letters indicate significant differences at p < 0.05 for totals in Virginia and Los Santos, regardless of treatment and lowercase letters indicate significant differences between treatments in region at p < 0.05.

<table>
<thead>
<tr>
<th>Region</th>
<th>Virginia</th>
<th>Los Santos</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NC</td>
<td>C</td>
</tr>
<tr>
<td>Treatment</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MgC ha(^{-1})</td>
<td>1.26 ± 1.11(^a)</td>
<td>6.53 ± 13.03(^a)</td>
</tr>
<tr>
<td>AU ha(^{-1})</td>
<td>1.66 ± 0.89(^ab)</td>
<td>1.09 ± 0.38(^b)</td>
</tr>
<tr>
<td>H’</td>
<td>1.12 ± 0.59(^b)</td>
<td>1.16 ± 0.70(^b)</td>
</tr>
</tbody>
</table>
Stocking density

The dominant cattle breed in Virginia was Black Angus (*Bos taurus*) while in Los Santos the dominant breed was Brahman (*Bos taurus indicus*). Overall, stocking density (AU ha\(^{-1}\)) per farm ranged from 0.35 to 5.49 AU ha\(^{-1}\). Stocking density differed significantly between regions, with Los Santos having a higher stocking density than Virginia (\(t = -3.135, p = 0.003, \text{Table 3}\)). Further, farms that were not enrolled in conservation programs had higher stocking densities than those that were enrolled, regardless of region (\(t = 2.317, p = 0.026, \text{Table 3, Table S5}\)).

In contrast to our prediction, there was no effect of increasing MgC ha\(^{-1}\) on the stocking density, regardless of region (\(p > 0.05, \text{Figure 8, Table S6}\)). However, the effect of MgC ha\(^{-1}\) on stocking density did differ significantly between management types, (\(t = 2.325, p = 0.026, \text{Figure 8, Table S6}\)). No interactions between predictor variables were found.

| Richness | 7.727 ± 5.061\(^b\) | 9.786 ± 5.041\(^b\) | 8.88 ± 5.052\(^b\) | 23.500 ± 13.005\(^a\) | 25.000 ± 7.910\(^a\) | 24.25 ± 5.052\(^A\) |
Figure 8. Generalized linear model displaying effect of weighted mean aboveground tree carbon (MgC ha$^{-1}$) on the average stocking density of farms enrolled and not enrolled (traditional management) in conservation programs Los Santos and Virginia.

Woody species diversity

Woody species richness ($t = 6.249$, $p < 0.001$) and diversity was significantly greater on farms in Los Santos than in Virginia ($t = 6.949$, $p < 0.001$, Table S5). However, there was no difference in either richness or $H'$ between management treatments, regardless of region ($p > 0.05$, Table 2, Table S5). As expected, there was also a positive effect of aboveground tree carbon per hectare on species diversity overall ($t = 2.730$, $p = 0.010$), but this effect differed significantly between regions ($t = 3.156$, $p = 0.003$) and was not affected by management type (Table S6). In Los Santos, the effect of
MgC ha\(^{-1}\) on woody species diversity was significant (t = 2.878, p = 0.014), but in Virginia, there was no significant relationship between these two variables, although the trend was positive (Figure 9, Table S6).
**Figure 9.** Generalized linear models displaying the relationship between weighted mean tree carbon (MgC ha\(^{-1}\)) and woody species diversity (H’) in Los Santos, Panama (A) and Virginia, USA (B).

*Remote estimation comparisons*

Overall, estimations between the three datasets varied significantly (\(\chi^2 = 18.21, \text{df } = 2, p = 0.0001\)). Chapman et al., 2020 was significantly higher than our field-verified data (\(z = 3.14, p \text{ adj } = 0.003\)), but was not different from Global Forest Watch (\(z = -0.939, p \text{ adj } = 0.5214\)). Global Forest Watch was also significantly greater than our field-verified data (\(z = -4.074, p \text{ adj } < 0.001\)).

Estimations within regions varied by region as well. In Los Santos, Chapman et al., 2020 had significantly higher estimates than our field-verified data (\(z = 7.331, p \text{ adj } < 0.001\)) and the estimates by Global Forest Watch (\(z = 3.655, p \text{ adj } < 0.001\)). Global Forest Watch was also greater than our field-verified estimations (\(z = -3.675, p \text{ adj } < 0.001\)). In Virginia, there was no difference between estimates derived from Chapman et al., 2020 or our field values (\(z = -1.635, p \text{ adj } = 0.1529\)), but Chapman et al., 2020’s estimate was significantly greater than that by Global Forest Watch (\(z = -4.450, p \text{ adj } < 0.001\)) and the Global Forest Watch estimate was significantly greater than the field estimates (\(z = -2.811, p \text{ adj} = 0.007\)) (Figure 10). The total carbon in pasture (TIP) raster from Chapman et al., 2020 did not yield values for any of the farms included in the study, but the total carbon in cropland (TIC) did. Therefore, all values used in this comparison are from the cropland dataset for Chapman et al., 2020. Aboveground tree carbon density (MgC ha\(^{-1}\)) estimates from both remote studies were greater for each farm than the field collected...
data in Los Santos, but not Virginia (Figures 10). In Virginia, Global Forest Watch (GFW) data was significantly higher (by 79.40%) than Chapman et al., 2020 and the field estimated data (by 69.11%). The field estimates for Virginia exceeded estimates by Chapman et al., 2020 by 33.33%, though this difference was not significant. In Los Santos, the estimates from Chapman et al., significantly exceeded both the field and the GFW estimates by 78.23% and 69.62%, respectively. GFW was significantly greater than the field estimates by 28.37% (Figures 9 & 10).

**Figure 10.** Estimated aboveground tree carbon from three sources: Global Forest Watch (Harris et al., 2021), Chapman et al., 2020, and data from field measurements in this
study. Capital letters indicate significant differences at $p < 0.05$ for carbon estimates in Virginia, while lowercase letters indicate significant differences for measurements within Los Santos at $p < 0.05$.

Landowner perceptions

Across both regions and management types, landowners held a predominantly favorable perspective on the presence of trees and wildlife in their pastures (Tables S5 & S6). They listed a higher number of benefits received by the presence of trees ($W = 817, p < 0.001$) and wildlife ($W = 562.5, p < 0.001$) than costs of the trees and wildlife within their system (Figure 6). Further, most farmers named more tree species that they considered valuable than those they considered detrimental to cattle production ($W = 114, p < 0.001$). The most prominent tree species listed in Virginia as beneficial included *Robinia pseudoacacia*, *Juglans nigra*, and *Quercus* spp., while in Los Santos, the most named beneficial species included *Guazuma ulmifolia*, *Cedrela odorata*, and *Dalbergia retusa*. These species have multiple uses with the potential for economic benefit for farmers, beyond providing shade for the cattle and ecosystem services. *Guazuma ulmifolia* in Los Santos, and *Robinia pseudoacacia* in Virginia are both tree species that cattle can use as additional fodder. *Quercus* spp., *Cedrela odorata*, and *Dalbergia retusa* are all valuable timber species that could be used in silvopastures. Tables S9 and S10 contain a list of all species mentioned by farmers and their various uses.

While there were no differences in farmer responses between regions, farmers enrolled in conservation programs listed more benefits from trees than farmers that were not enrolled in a management program ($z = 0.265, p = 0.035$, Figure 11A). Of these
named benefits, 31.08% were environmental, 29.73% were concerned with supporting cattle welfare, 20.27% were personal benefits, and 18.91% were involved with supplementing income and diversifying revenue. In both Virginia and Los Santos, the most common use for trees was to produce shade; other tree uses included fodder for cattle, timber, and fruit production. There were no differences between the management types with regards to costs of tree presence, or the benefits and costs of wildlife (p > 0.05, Figure 11B).

**Figure 11.** The number of benefits (A) and costs (B) of trees described by farmers in each management group. (* = statistically significant at p < 0.05 using a Wilcoxon Rank Sum test).
Discussion

Tree carbon storage and stocking density

Past research has demonstrated the potential of sustainable land management practices to greatly improve ecosystem functioning in agricultural landscapes and promote resilience in such systems across the globe (Chapman et al., 2020; Griscom et al., 2017). However, for these practices to be widely adopted and the resulting environmental benefits maximized, their effects on the livelihoods of those who use them must be thoroughly considered (Gosling et al., 2020). The present study examined the effects of a typically overlooked metric of climate mitigation in livestock systems - tree carbon - on the production of beef cattle. We show that if a threshold exists at which increasing tree carbon (MgC) per hectare (ha) reduces cattle production, it is greater than the current average MgC ha\(^{-1}\) stored within the beef cattle pastures in Virginia (4.12 MgC ha\(^{-1}\)) and Los Santos (5.11 MgC ha\(^{-1}\)). This, along with the general lack of effect of MgC ha\(^{-1}\) on stocking density, suggests that more MgC ha\(^{-1}\) than the current average can be stored within cattle pastures across temperate and dry tropical regions, without compromising cattle production. Such findings are significant, as they may unlock funding sources from carbon credit and/or ecosystem restoration programs to facilitate the planting of more trees in these landscapes, as well as provide evidence to hesitant farmers that they will not suffer economic consequences that are typically associated with high tree presence in pastures (Baumber et al., 2020).

The exceptions to the aforementioned pattern are the farms enrolled in the ELTI program in Los Santos, which displayed a positive trend between increasing tree carbon and stocking density. While not statistically significant, this trend is likely a reflection of
the specific silvopastoral management within these farms. The active incorporation of
trees into the production systems differs from the Virginia conservation farms (CREP),
which primarily focus on removing cattle access from streams, and have only occasional
tree plantings in that excluded area (Farm Service Agency, 2017). This difference
highlights the potential of specifically combining intensively managed trees within the
pastoral system to positively affect production, as opposed to more passive efforts that do
not interact with the cattle, such as exclusion from certain areas.

The fenced-off riparian areas in Virginia conservation farms were not included in
our tree carbon calculations, as they were not within the agricultural production areas.
Because of this, the Virginia CREP farms lacked any significant differences in
aboveground carbon storage and species diversity from traditionally managed Virginia
farms. However, when considering the entirety of the parcel, regardless of cattle
restriction, the average tree cover, and likely woody species diversity, is likely higher
than traditionally managed farms.

In contrast to those in Virginia, Los Santos farms had a higher stocking density,
which did not align with our predictions, as U.S. farms are typically more productive and
competitive in the market than those in Central America (Dominguez-Escudero, 2015).
Virginia farms also supplemented cattle feed with various types of grain and hay, and
moderate supplementation of cattle feed can increase the stocking rate of the pastures,
while hardly any Los Santos farms included in the study supplemented cattle feed with
additional grain or hay (Beck et al., 2008). However, overgrazing has been historically
more prevalent in Central America than in North America. In Panama specifically, the
current relative area over-grazed exceeds 80%, while in the USA, overgrazing only
accounts for 20-40% of total grazed area (Piipponen et al., 2022). As such, it is likely that overgrazing contributed to the higher stocking densities in Los Santos than in Virginia.

Conversely, there was no significant difference between the average tree carbon stored per hectare in each region. Los Santos did have a higher average carbon storage per hectare than Virginia farms, but the difference was not significant. This does not reflect expected patterns based on past literature, as it has been estimated that the potential in temperate agroforestry systems to sequester aboveground tree carbon is less than that in tropical agroforestry systems (Oelbermann et al, 2004). Additionally, other factors that constrain sequestration, such as wood density, are dependent on latitude and elevation. Lowland tropical regions are known to have a greater average wood density than temperate regions, and as such, a higher carbon storage capacity (Swenson & Enquist, 2007). Therefore, the lack of difference in carbon between regions in our study is likely driven from management extremes. In both regions, there were some farms that had as little as a single tree within the parcel, while there were also farms that had large swaths of secondary forest that covered more than 50% of the total production area. This variation underscores the importance that single landowner decision-making has on the ability of the system to meet its potential restoration capacity.

**Woody species diversity**

Woody species diversity (H') displayed a similar pattern. There was regional variation between H', with significantly higher diversity in Los Santos than in Virginia, but no variation within each region between management types or between management
types overall. Los Santos pasturelands had higher H’ than Virginian pasturelands, reflecting typical species diversity patterns along latitudinal gradients (Stehli et al, 1969). However, it was predicted that farms enrolled in conservation programs would retain higher H’ than those that practiced traditional management within each region. It is possible that because of the prescriptive nature of the management programs in both regions, the number of different species that were provided for plantings was limited. Further, given the relatively young nature of the management programs and the projects they helped implement (< 15 years old in Virginia, < 11 years old in Los Santos), species recovery has likely not reached its maximum potential. In the dry tropical forests of Panama specifically, species recruitment can occur over 10-15 years following abandonment (Griscom & Ashton, 2011). In the eastern United States, this process can take even longer, with a dense shrub layer only developing after 20-30 years and maximum richness after 80 years on post-agricultural land (Flinn & Vellend 2005). The continual management and use of land in this study likely delays the species recovery process in both regions. Moreover, in Virginia, it is likely that the specific type of conservation management practiced by CREP farms also contributed to this lack of variation in diversity between management types in the pasturelands. A common strategy employed by certain CREP projects is to separate sites of cattle production from restoration projects, like riparian tree plantings, which likely hinders the recruitment of planted trees into production sites and prevents species diversity from improving.

Overall H’ was also positively affected by increasing aboveground tree carbon per hectare. Previous research has primarily focused on the positive effect of woody species diversity on carbon stocks, but the observed relationship also depicts the ability of
management for carbon sequestration to improve restoration potential within these systems (Magnano et al., 2023; Mensah et al., 2016). However, this effect was influenced by region, displaying significance in Los Santos, but not Virginia. Diversity levels are higher overall in the tropics, which may have contributed to the presence of a stronger relationship in Los Santos. Additionally, the temperate pasturelands were dominated by *Juniperus virginiana*, which accounted for 68% of all trees inventoried in Virginia farms. *J. virginiana* is an early-successional species that has been historically recognized as a nuisance for cattle management due to its tendency to form dense thickets that hinder forage production more than other tree species, and hinder cattle movement through pastures (Wilson & Schmidt, 1990). Despite this, many farmers in this study stated that they have chosen to leave cedar clusters and fragments in their landscape, because of the shaded spaces they provide without the farmers having to plant additional trees. No single species was as abundant in tropical farms. Nevertheless, the prospective landscape restoration is critical for all pastoral landscapes, but especially for farms in the dry tropical forests of Los Santos, where remaining intact forest is severely threatened (Griscom et al., 2009; Condit 1998).

Remote estimations comparisons

Before management practices can become widespread and opportunities for restoration are maximized, their potential needs to be clearly defined. This study highlights the discrepancy between remotely conducted estimates of aboveground biomass and field-measured values, particularly within small-scale pastoral systems. Both remote studies depicted much higher average carbon storage values than the field
estimated amounts in both regions, but the difference was especially pronounced in Los Santos. In the Pedasi region of Los Santos, estimates made by Chapman et al., in 2020 were consistently higher than those made in 2000 by Harris et al., 2021 and the field estimates collected in 2022. Los Santos experienced a tree cover loss of 7.7% from 2000-2020, which does not align with the significantly higher values found by Chapman et al. (Harris et al., 2021, online at www.globalforestwatch.com). A possible explanation is the misclassification of pastureland as cropland by Chapman et al., due to the stated low resolution of their pastureland dataset (Chapman et al., 2020). When comparing remote studies, assumptions, such as definitions of land cover types, may differ between the datasets, which can lead to uncertainty, and may have resulted in erroneous estimations of carbon within each land cover type (Gilbert et al., 2018; Caughlin 2013).

While pasturelands were also misclassified in Virginia by the Chapman et al. 2020 dataset, the estimates were more reflective of our predictions. The Global Forest Watch estimations in 2000 were the highest, followed by Chapman et al. 2020, and then the field data. However, while this pattern, and global trends, suggest a decline in tree cover since the year 2000, Rockingham, Virginia, has actually experienced a positive 1.1% net change in forest cover (Harris et al., 2021, online at www.globalforestwatch.com). The gains made in the region may not have been specifically within the pastoral boundaries, and given continual agricultural development, tree loss is still likely. Lastly, in both regions, the ways that farmers incorporated trees, especially those that had agroforestry practices, was more detailed than depicted in either remote study. For example, we identified eight categories of tree groupings in farms, and all had a different average MgC ha\(^{-1}\) (Table 1). Our remote protocol even allowed us to
distinguish between evergreen and deciduous species in Virginia, solely from high resolution imagery sourced from Google Earth. The two previous remote studies did not break up tree cover into more specific groups or species, which likely contributed to the uncertainty as well (Chapman et al., 2020). Further, in our study, the resolution we used for the remote component was less than 1m, which allowed us to utilize a detailed classification scheme. Yet, it is also important to note that many publicly available satellite imagery sources, including the Google Earth imagery used in this study, have biases, with higher resolution in western nations, and lower resolution in developing regions (Lesiv et al., 2018).

Farmer perceptions

Responses to the interviews indicate that while farmers have a common sense of stewardship and appreciation of the land, participation in a conservation program fosters a greater recognition of the environmental benefits from trees and wildlife and a more conscious ecological awareness. Hesitancy towards incorporating more trees into farmlands mainly comes from lack of financial support and the required infrastructure and labor needed to maintain high levels of production, which aligns with past surveys amongst farmers (Gosling et al., 2020; Garen et al., 2011). However, unlike past studies, relatively few farmers interviewed expressed concern regarding production trade-offs, such as space available for forage, when considering incorporating trees (Gosling et al., 2020). Moreover, some farmers, in Los Santos in particular, have chosen to keep large swaths of secondary forest within their pastoral landscape, because of a widespread recognition of the importance of such habitat within a threatened ecosystem and its
cultural significance. The values held by farmers and their perceptions of ecologically focused management strategies are critical indicators of the likelihood of maximizing the restoration potential of agricultural landscapes, as they are the final decision-makers for their parcel. These types of non-financial motivations, particularly those associated with environmental conscientiousness have been found in past studies as key characteristics of participants likely to adopt conservation management strategies (Prokopy et al., 2019). Our findings highlight a collective shift in mindset away from conventional management priorities towards a more holistic approach.

**Implications & limitations**

Beef cattle pastures in Los Santos, Panama, and Virginia, USA have the capacity to store more tree carbon within their systems, without compromising cattle production or the livelihoods of those who depend on the land. The incorporation of more trees, whether through agroforestry techniques or natural regeneration, will not only increase the carbon sequestration of the landscape, but also potentially improve woody species diversity and create habitat for wildlife, facilitating the “rewilding” of these systems. Restoration is particularly important in threatened ecosystems, like the dry tropical forests of Panama. In addition, more trees within the system will support sustainable farming practices, especially by improving the welfare of the cattle under increasing stress from a changing climate (Rasmussen et al., 2016). Sustainability is also significant because the profession of cattle ranching is becoming less viable overall for many farmers -- profits can be unpredictable, high-risk, and many simply choose it as a lifestyle over financial benefit (Vasquez et al., *in press*). This sentiment was reflected in our
interview as well, with one farmer explaining, “You can go for a year and just break-even. But I want to raise my kids around cattle. This is my family’s land, and I don’t want to see it grow up to brush.”

Furthermore, carbon sequestration and improved system health may qualify farmers for participation in carbon credit trading programs that could diversify revenue streams and offer financial security (Montagonini & Finney 2011). Other monetary gains from trees include intensifying management within the system to include timber production, fruit trees, and other non-timber forest products (Bruck et al, 2019). Partnerships between farmers, governmental organizations, and nonprofits through land management and conservation programs like the Yale ELTI program in Panama and CREP administered by Virginia’s DCR facilitate the adoption of management techniques that prioritize ecosystem functioning and farm production. Enrollment in such programs also allows farmers to gain access to educational resources and management guidance that bolster stewardship of the environment. To maximize this potential for both the environment and the landowners, it is critical that more research is dedicated to better understanding variations within complex agricultural systems.

Conclusions and future directions

Here, we employed an often-underutilized approach of coupling remote sensing using high-resolution imagery with in-situ field verification to assess MgC ha⁻¹ in fine-scale, heterogeneous landscapes. This allowed us to provide more accurate assessments of current carbon storage within cattle pastures and evaluate the degree of uncertainty in past remote estimations. We have shown not only the potential for beef pastures to store
more tree carbon and promote higher woody species diversity, but also highlighted the discrepancies between past remote sensing estimations and current carbon storage values in these systems.

These findings re-emphasize the need for continual field verification of remote studies. Field studies are often more difficult to implement because of financial constraints and labor/time. However, in systems with a high level of complexity, field verification could improve remote sensing capabilities and contribute to machine-learning efforts that achieve a higher degree of accuracy (Burke et al., 2021). Moreover, long-term field studies are harder to implement, but point-in-time studies, such as this one, allow for a rapid assessment of current data and can still provide the same comparison and inform guidance on a local-scale (Johnson et al., 2022). Further, constraints on field collection may be mediated through self-collection of data on these farms. Programs like Yale’s ELTI promote science-based management practices with specific protocols for data collection, and often teach farmers how to assess various environmental metrics themselves, which may provide an opportunity for more field data (ELTI 2023).

While we found a discrepancy between remote and field collected data, advances in remote technology, such as hyperspectral imagery and LiDAR may help eliminate such issues, especially in mosaic agricultural landscapes. Primarily, they may be able to detect relatively minor gains in carbon accumulations. LiDAR data has been shown to accurately predict height and canopy cover change in tropical agricultural landscapes, while hyperspectral data can be used to predict change in DBH (Caughlin 2013; Caughlin et al., 2016). Collectively, these metrics could be used to assess biomass accumulations
and carbon through allometric equations. However, improved verification of remote
technology applications is needed before it may be applied on a wide-spread scale for
forestry management applications. In agricultural landscapes like pasturelands that have
scattered trees, verification and data collection is more feasible and cost-effective
compared to using a fully forested area.

Agricultural landscapes managed for conservation may also be an ideal setting for
assessing other improvements of remote technology because of the sparse, yet highly
managed and varied tree presence. Past research has found that the accuracy of
hyperspectral imagery could be improved with finer definition of individual tree crowns
(Caughlin et al., 2016). In cattle pastures, and particularly in silvopastures, which have
higher tree cover than conventional farms, individual tree crowns are easily identifiable
using high-resolution imagery, like that used in our study. They also have a variety of
tree cover types that could be used to refine carbon models for more specific species
groupings. This is particularly important for predicting forest succession patterns, as the
way the trees are arranged in pasturelands directs their future succession trajectory
(Zahawi & Augspurger 2016). Moreover, utilizing parcel-scale assessments will also
allow for consideration of individual landowner preferences more closely, a metric that
also improves model accuracy (Caughlin et al., 2016).

Given that landowners are the ultimate decision makers for their systems,
restoration efforts should be approached with their livelihoods as a top priority, and
should complement agricultural goals, rather than conflict with them (Gosling et al.,
2020; Chapman et al., 2019). Combining observational studies with farmer interviews
and partnerships with research and development organizations could also promote
inclusion of farmers in the scientific process and provide insight into factors that drive
decision-making processes and questions that remain to be answered that would facilitate
higher adoption of sustainable management strategies (Nettle et al., 2022).

Lastly, while our findings suggest that more tree carbon can be stored in cattle
pastures without hindering production, it would be worthwhile to determine a theoretical
tipping point. These thresholds may be unique depending on the locality but will better
inform specific management decisions and make the process of implementation more
targeted for farmers. Also, it would be useful to obtain more thorough assessments of
agricultural production through measurements of forage production and nutrient
composition, as well as cattle weight and health. Our estimations of stocking density
were based solely on the quantity of animal units on the land at the time of the study,
which is subject to farmer preference and short-term environmental factors. Obtaining
more thorough estimations of the effects on cattle welfare under increasing tree carbon
would be beneficial for providing additional evidence of the advantages of trees within
the system.

Altogether, this study demonstrates that both ecosystem restoration and successful
agricultural production can be achieved through strategies that balance stewardship,
production, and ecological functioning within a system. Although the threshold at which
tree carbon reduces cattle yield remains to be defined, we show that pasturelands across
temperate and dry tropical regions have the capacity for much tree carbon without
compromising production. Further, our findings emphasize the importance and utility of
taking a socio-ecological approach to climate mitigation research in human-dominated
systems and add to a growing body of evidence that individual landowners are the key
drivers of restoration and sequestration potential in a mosaic agricultural landscape
(Vasquez et al., in press; Hand & Tyndall 2018; Caughlin et al., 2016).
Appendix

Table S1. Tree cover classification definitions for each 15x15m grid square. The majority of conifer vs broadleaf categories for Virginia were determined based on stem count.

<table>
<thead>
<tr>
<th>Tree Class</th>
<th>Description</th>
<th>Tree Class</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isolated broadleaf</td>
<td>$1 - 2$ majority broadleaf trees</td>
<td>Isolated</td>
<td>$1 - 2$ trees</td>
</tr>
<tr>
<td>tree</td>
<td></td>
<td>tree</td>
<td></td>
</tr>
<tr>
<td>Isolated conifer</td>
<td>$1 - 2$ majority conifer trees</td>
<td>Clustered</td>
<td>$3 - 10$ trees</td>
</tr>
<tr>
<td>Conifer cluster</td>
<td>$3 - 10$ majority conifer trees</td>
<td>Live fence</td>
<td>Any cell with over 50% tree cover containing or within 15m of a property line.</td>
</tr>
<tr>
<td>Broadleaf cluster</td>
<td>$3 - 10$ majority broadleaf trees</td>
<td>Riparian</td>
<td>Contains a waterway or is directly adjacent to a cell containing a waterway. Waterways identified using the 1:50K Hydrology Layer for the Republic of Panama from the Smithsonian Tropical Research Institute (2022).</td>
</tr>
<tr>
<td>Broadleaf fragment</td>
<td>&gt;$10$ majority broadleaf trees</td>
<td>Forestry</td>
<td>Determined by using a shapefile of previously classified forestry plantation areas provided by ELTI, 2022.</td>
</tr>
<tr>
<td>Riparian</td>
<td>Any cell with over 50% tree cover containing or within 15m of a waterway. Waterways are identified using the Rockingham County Stream Layer from the Rockingham County GIS database (2022).</td>
<td>plantation</td>
<td></td>
</tr>
<tr>
<td>Fence line</td>
<td>Any cell with over 50% tree cover containing or within 15m of a fence line on the interior of the property.</td>
<td>Secondary</td>
<td>&gt;$10$ trees within a cell</td>
</tr>
<tr>
<td></td>
<td></td>
<td>forest</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>fragment</td>
<td></td>
</tr>
</tbody>
</table>
Table S2. Example calculation of carbon in Mg C ha$^{-1}$ within a single plot (VA, broadleaf species).

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Diameter at breast height (cm) (D)</th>
<th>Wood density (ρ)</th>
<th>KgC est</th>
<th>Total KgC est / 900m$^2$</th>
<th>KgC ha$^{-1}$</th>
<th>MgC ha$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q. alba</td>
<td>11.14</td>
<td>661.8</td>
<td>31.55</td>
<td>263.69</td>
<td>2929.92</td>
<td>2.929</td>
</tr>
<tr>
<td>J. nigra</td>
<td>8.41</td>
<td>587.7</td>
<td>14.60</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>J. nigra</td>
<td>14.96</td>
<td>587.7</td>
<td>55.37</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>J. nigra</td>
<td>13.37</td>
<td>587.7</td>
<td>42.69</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Q. alba</td>
<td>9.24</td>
<td>661.8</td>
<td>20.43</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>J. nigra</td>
<td>13.69</td>
<td>587.7</td>
<td>45.08</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Q. alba</td>
<td>7.13</td>
<td>661.8</td>
<td>11.25</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Formula

\[
\text{Total KgC est} = (0.0002835 \times ((D^{2.310647} \times ρ \times 1.28 \times 0.5)) = \text{sum of each tree’s KgC est in the plot}
\]

\[
\text{KgC ha}^{-1} = ((\text{KgC est} / 900) \times 10000) / 1000
\]
Table S3. Example calculation of MgC ha\(^{-1}\) in a single farm in Los Santos.

<table>
<thead>
<tr>
<th>Farm area (ha)</th>
<th>Plot type</th>
<th>Average MgC ha(^{-1})</th>
<th>Proportion of total production area</th>
<th>Total weighted average MgC ha(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>9.71</td>
<td>Riparian</td>
<td>152.37</td>
<td>0.19</td>
<td>5.70</td>
</tr>
<tr>
<td></td>
<td>Fragment</td>
<td>-</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Live fence</td>
<td>4.79</td>
<td>0.18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Isolated tree</td>
<td>40.54</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cluster</td>
<td>43.68</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Plantation</td>
<td>31.24</td>
<td>0.04</td>
<td></td>
</tr>
</tbody>
</table>
Table S4. Social survey questions used in this study. (JMU IRB approved)

<table>
<thead>
<tr>
<th>Questions</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.  How long have you owned the farm?</td>
</tr>
<tr>
<td>2.  What is your breed of cattle?</td>
</tr>
<tr>
<td>3.  Do you participate in an artificial insemination program that improves cattle genetics?</td>
</tr>
<tr>
<td>4.  How many years have livestock grazed your land?</td>
</tr>
<tr>
<td>5.  What is the size of your farm and beef production area? (U.S. survey acres).</td>
</tr>
<tr>
<td>6.  How many cattle do you raise on average each year? How many calves are born?</td>
</tr>
<tr>
<td>7.  Are the cattle moved to other grazing lands? If so, what are the size (in acres) of those pastures?</td>
</tr>
<tr>
<td>8.  How many months old are the cattle when they are sold?</td>
</tr>
<tr>
<td>9.  Do you know the average weight (or range) of the cattle when sold?</td>
</tr>
<tr>
<td>10. Do you add supplemental food for the cattle? If so, how much approximately? (including # of hay bales in VA).</td>
</tr>
<tr>
<td>11. Do you use ivermectin, vaccinations, or other supplemental vitamins, minerals, and medications?</td>
</tr>
<tr>
<td>12. Do you have a cattle water system?</td>
</tr>
<tr>
<td>13. Do you use herbicides, fertilizers, or pesticides on the land?</td>
</tr>
<tr>
<td>14. What do you see as benefits to adding trees into your production system?</td>
</tr>
<tr>
<td>15. Were there any unanticipated costs to adding trees?</td>
</tr>
<tr>
<td>16. Are there any particular tree species you especially prefer to keep in pastures?</td>
</tr>
<tr>
<td>17. Do you prefer how the trees are arranged on your farm? (i.e., a forest fragment, clusters, along the stream, in lines, isolated, etc.)</td>
</tr>
<tr>
<td>18. What are some barriers to enrolling in restoration/land conservation programs?</td>
</tr>
<tr>
<td>19. Do you see any added benefits/costs to increased wildlife on your property (birds, insects, monkeys, etc.)?</td>
</tr>
<tr>
<td>20. What are the major challenges you face when raising cattle?</td>
</tr>
</tbody>
</table>
21. Do you have any questions for us?

**Table S5.** Estimated ANOVA coefficients from a generalized linear model with ziGamma distribution. Coefficients ($\beta$), standard errors (±SE), Z-values, and $p$-values for differences between regions and treatments for the stocking density (A), MgC ha$^{-1}$ (B), woody species diversity (C), richness (D). No significant interactions were found between predictor variables. Bolded values indicate statistical significance.

<p>| Variable       | Estimate ($\beta$) and Std. Error (±SE) | t-value | Probability ($&gt;|t|)$ |
|----------------|-----------------------------------------|---------|---------------------|
| <strong>(A) Stocking density</strong> |                                        |         |                     |
| (Intercept)    | 0.601 ± 0.051                           | 11.766  | &lt; 0.001             |
| Region         | -0.160 ± 0.051                          | -3.135  | 0.003               |
| Treatment      | 0.119 ± 0.051                           | 2.317   | 0.026               |
| <strong>(B) MgC ha$^{-1}$</strong> |                                      |         |                     |
| (Intercept)    | 0.335 ± 0.087                           | 3.838   | &lt; 0.001             |
| Region         | -1.586 ± 0.087                          | -1.586  | 0.121               |
| Treatment      | -0.152 ± 0.087                          | -1.743  | 0.0897              |
| <strong>(C) $H'$</strong>   |                                        |         |                     |
| (Intercept)    | 1.805 ± 0.096                           | 18.787  | &lt; 0.001             |</p>
<table>
<thead>
<tr>
<th></th>
<th>Estimate 1</th>
<th>Estimate 2</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Region</td>
<td>0.0668 ± 0.096</td>
<td>6.949</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Treatment</td>
<td>-0.023 ± 0.096</td>
<td>-0.469</td>
<td>0.642</td>
</tr>
</tbody>
</table>

(D) **Richness**

<table>
<thead>
<tr>
<th></th>
<th>Estimate 1</th>
<th>Estimate 2</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>16.503 ± 1.24</td>
<td>13.306</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Region</td>
<td>7.747 ± 1.24</td>
<td>6.246</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Treatment</td>
<td>0.089 ± 1.24</td>
<td>-0.113</td>
<td>0.911</td>
</tr>
</tbody>
</table>
Table S6. Estimated GLM coefficients ($\beta$), standard errors (±SE), Z-values, and $p$-values for the stocking density model (A) and woody species diversity model (B). No significant interactions were found between predictor variables.

| Variable     | Estimate (β) and Std. Error (±SE) | t-value | Probability (>|t|) |
|--------------|-----------------------------------|---------|------------------|
| (A) Stocking density |                                   |         |                  |
| (Intercept)  | 0.733 ± 0.097                     | 7.601   | < 0.001          |
| MgC ha$^{-1}$| -0.032 ± 0.025                    | -1.299  | 0.203            |
| Region       | -0.051 ± 0.097                    | -0.531  | 0.599            |
| Treatment    | 0.224 ± 0.097                     | 2.325   | 0.026            |
| (B) $H'$     |                                   |         |                  |
| (Intercept)  | 1.424 ± 0.163                     | 8.731   | < 0.001          |
| MgC ha$^{-1}$| 0.129 ± 0.047                     | 2.730   | 0.010            |
| Region       | 0.515 ± 0.163                     | 3.156   | 0.003            |
| Treatment    | -0.010 ± 0.163                    | -0.061  | 0.095            |
Table S7. Virginia, USA survey responses to select survey questions.

<table>
<thead>
<tr>
<th>Question</th>
<th>Conservation farmers</th>
<th>Non-conservation farmers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree benefits</td>
<td>Shade, wildlife habitat, improved water quality/availability, intrinsic value, timber/firewood, windbreak/shelter for cattle, recreation, overall, better for the environment, fodder, improved cattle health, carbon sequestration, biodiversity, none</td>
<td>None, shade, improved soil nutrients</td>
</tr>
<tr>
<td>Tree costs</td>
<td>High cost, labor needs, upkeep/maintenance required, increase in weeds, die-off, none</td>
<td>High cost</td>
</tr>
<tr>
<td>Preferred species</td>
<td><em>Juglans nigra</em>, <em>Quercus</em> sp., <em>Juniperus virginiana</em>, <em>Robinia pseudoacacia</em>, <em>Diospyros virginiana</em>, <em>Prunus</em> sp., <em>Pinus rigida</em>, <em>Morus</em> sp., <em>Castanea dentata</em>, <em>Platanus occidentalis</em>, <em>Quercus alba</em>, none</td>
<td><em>Juniperus virginiana</em>, none</td>
</tr>
<tr>
<td>Detrimental species</td>
<td><em>Juniperus virginiana</em>, <em>Prunus</em> sp., <em>Robinia pseudoacacia</em>, <em>Toxicodendron vernix</em></td>
<td>None</td>
</tr>
<tr>
<td>Preferred tree arrangement</td>
<td>Clusters, lines</td>
<td>None</td>
</tr>
<tr>
<td>Wildlife benefits</td>
<td>Intrinsic value, recreation, reduced pest presence, aesthetic, biodiversity, none</td>
<td>Intrinsic value, facilitate nutrient turnover, none</td>
</tr>
<tr>
<td>Wildlife costs</td>
<td>None, more ticks, property destruction, predation on livestock</td>
<td>Predation on livestock</td>
</tr>
<tr>
<td>Barriers to enrollment in conserv</td>
<td>High upfront cost, infrastructure, loss of most fertile land, low rental payments, competition</td>
<td>Infrastructure, time, cost</td>
</tr>
<tr>
<td>tion programs</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Challenges in cattle production today

High cost, butchering dates/prices unpredictable, price fluctuations, disease risk, fuel costs

Low prices, butchering dates/prices unpredictable, high cost

Table S8. Los Santos, Panama survey responses to select survey questions.

<table>
<thead>
<tr>
<th>Question</th>
<th>Conservation farmers</th>
<th>Non-conservation farmers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree benefits</td>
<td>Shade, wood, intrinsic value, sustainability, aesthetic, supports streams, better for the environment, improves climate, improves soil retention, windbreak, cattle welfare, fodder, improved quality of meat, passive income</td>
<td>Shade, wood, recreation, fruit, intrinsic value, wildlife habitat, none</td>
</tr>
<tr>
<td>Tree costs</td>
<td>Less area for pasture, sucia (“dirty” pasture), time, tree die-off</td>
<td>Less area for pasture, “sucia”, none</td>
</tr>
<tr>
<td>Preferred species</td>
<td><em>Guazuma ulmifolia, Jatropha curcas, Spondias mombin, Spondias purpurea, Swietenia macrophylla, Pachira quinata, Cedrela odorata, all</em></td>
<td><em>Guazuma ulmifolia, Mangifera indica, Callicophyllum candidissimum, Dalbergia retusa, Enterolobium cyclocarpum, Diphysa americana, Spondias mombin, Gliricidia sepium, Genipa americana, Bursera simaruba, Chrysophyllum cainito, Hura creptians, Pachira quinata, any timber species, none</em></td>
</tr>
<tr>
<td>Detrimental species</td>
<td>None</td>
<td>None</td>
</tr>
<tr>
<td>Preferred tree arrangement</td>
<td>Riparian, live fences, clusters, fragments, none</td>
<td>Clusters, riparian, isolated, none</td>
</tr>
<tr>
<td>Wildlife benefits</td>
<td>Intrinsic value, endangered species conservation, restoration</td>
<td>Intrinsic value</td>
</tr>
</tbody>
</table>
Wildlife costs

Predation on fruit trees

Vampire bats, biting ants

Barriers to enrollment in conservation programs

Tree die-off, system maintenance, lack of programs

None

Challenges in cattle production today

Rotational grazing, challenging landscape, lack of water, lack of shade, maintenance, high cost, high risk, lack of water

Table S9. Beneficial species listed by farmers in Los Santos, in order from most frequently mentioned to least, with the functions they serve in ecological and economic contexts from Griscom & Ashton, 2011.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>Uses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Guazuma ulmifolia</td>
<td>Guacimo</td>
<td>Growth, animals, nursery, NTFP, fodder</td>
</tr>
<tr>
<td>Cedrela odorata</td>
<td>Cedro amargo</td>
<td>Growth, timber</td>
</tr>
<tr>
<td>Dalbergia retusa</td>
<td>Cocobolo</td>
<td>Nitrogen, timber</td>
</tr>
<tr>
<td>Pachira quinata</td>
<td>Cedro espino</td>
<td>Growth, timber</td>
</tr>
<tr>
<td>Cordia alliodora</td>
<td>Laurel</td>
<td>Growth, timber</td>
</tr>
<tr>
<td>Gliricidia sepium</td>
<td>Balo</td>
<td>Nitrogen, growth, timber</td>
</tr>
<tr>
<td>Mangifera indica</td>
<td>Mango</td>
<td>NTFP</td>
</tr>
<tr>
<td>Bursera simaruba</td>
<td>Corotu</td>
<td>Growth, animal, timber, NTFP, LF</td>
</tr>
<tr>
<td>Chrysophyllum cainito</td>
<td>Caimito</td>
<td>-</td>
</tr>
<tr>
<td>Samanea saman</td>
<td>Guachapele</td>
<td>Growth, animal, timber, nurse, nitrogen</td>
</tr>
</tbody>
</table>
**Table S10.** Beneficial species listed by farmers in Virginia, in order from most frequently mentioned to least, with the functions they serve in ecological and economic contexts, modified from Griscom & Aston, 2011.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>Uses</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Juglans nigra</em></td>
<td>Black walnut</td>
<td>Growth, animals, nursery, NTFP, fodder</td>
</tr>
<tr>
<td><em>Quercus alba</em></td>
<td>White oak</td>
<td>Growth, timber</td>
</tr>
<tr>
<td><em>Robinia pseudoacacia</em></td>
<td>Black locust</td>
<td>NTFP, fodder</td>
</tr>
<tr>
<td><em>Juniperus virginiana</em></td>
<td>Eastern red cedar</td>
<td>-</td>
</tr>
<tr>
<td><em>Platanus occidentalis</em></td>
<td>Sycamore</td>
<td>-</td>
</tr>
<tr>
<td><em>Prunus sp.</em></td>
<td>Cherry</td>
<td>Timber</td>
</tr>
<tr>
<td><em>Morus sp.</em></td>
<td>Mulberry</td>
<td>NTFP</td>
</tr>
<tr>
<td><em>Diospyros virginiana</em></td>
<td>Persimmon</td>
<td>Timber, NTFP, animals</td>
</tr>
<tr>
<td><em>Pinus sp.</em></td>
<td>Pine</td>
<td>Timber, NTFP, animals</td>
</tr>
</tbody>
</table>
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