ECOLOGY AND MANAGEMENT OF SOIL CARBON ON RANCHLANDS OF FLORIDA, USA

By

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To all who love and care for the Land
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ECOLOGY AND MANAGEMENT OF SOIL CARBON ON RANCHLANDS OF FLORIDA, USA

By

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There is widespread scientific consensus that anthropogenic climate change poses a serious and growing threat to human civilization, and is already leading to significant deterioration of ecosystem health and function. Globally, pastures and rangelands managed for livestock grazing occupy roughly 25% of ice-free terrestrial land area, account for a similar fraction of global SOC stocks, and play a critical role in food security. Although managed grasslands have historically contributed to global climate change through SOC depletion, improved management can reverse this adverse legacy through soil carbon sequestration (SCS). Unfortunately, our ability to predict, manage and monitor SCS at scale in grazing lands is limited by uncertainty surrounding the impact of large herbivores on the ecosystem processes that regulate SOC. Here I aim to, 1) clarify how grazing impacts belowground carbon allocation, and soil carbon pools across subtropical pasture in south Florida, USA, and 2) test the utility of remote sensing data for informing spatial predictions of SOC stocks. My results show that grazing impacts on root production, a critical component of the carbon cycle, are mediated both by severity of defoliation and plant genetics, suggesting that both grazing patterns and plant composition are important to SOC regulation. Moreover, subsequent work showed that grazed pasture sustains higher root biomass, higher microbial biomass, and higher SOC compared to
pasture under long-term grazing exclusion. Molecular characterization revealed that across both grazed and ungrazed pasture SOC pools are more closely coupled to the greater flux of plant tissue inputs than to stabilization of microbial carbon. Thus, monitoring of root biomass and productivity is central to understanding and predicting SCS. Finally, the best predictor of spatial variations in SOC across a large area of grazed pasture was a long time series of vegetation greenness data obtained from the Landsat 5 satellite, consistent with a close coupling between plant productivity and SOC. Overall, my work shows that grazing can enhance plant productivity, especially root production, and thereby increase SOC pools in subtropical pasture, while also illustrating the importance of developing data and models to account for spatial and temporal variability.
CHAPTER 1
INTRODUCTION

Background

Due to increasing threats to biodiversity and ecosystem function, there is growing urgency to mitigate global climate change through biological carbon sequestration and by reducing fossil carbon emissions (Mann and Gleick 2015). Soil carbon sequestration (SCS), in particular, is a primary candidate for offsetting emissions, particularly in agricultural and grassland/rangeland ecosystems (Lal 2010a). Grasslands occupy close to 40% of ice-free terrestrial land area, sustain livestock critical to global food security and the economic wellbeing of pastoralists (Thornton 2010), and account for a large fraction of the planet’s current soil carbon (Scurlock and Hall 1998). Although many pastures and rangelands have historically contributed to global climate change through losses of soil organic carbon (SOC), there is significant potential to reverse this soil degradation and mitigate both historic and on-going carbon emissions via SCS (Franzluebbers et al. 2000, Soussana et al. 2004, Lal 2004).

Practices such as enhanced nitrogen fertility and improved grazing management have been associated with increased soil carbon over time in grasslands (Conant et al. 2001). However, the drivers that govern SCS in grasslands at large scales are poorly understood (McSherry and Ritchie 2013, Stockmann et al. 2013). For instance, large herbivore grazing (e.g., livestock) is sometimes associated with higher and other times with lower soil carbon pools compared to ungrazed grasslands (McSherry and Ritchie 2013). Although McSherry and Ritchie (2013) quantitatively link soil texture and climate (especially precipitation) to these diverging signals of grazing impacts on SOC via meta-analysis, the underlying mechanisms remain unclear. In general, root productivity may be the primary proximate driver of SCS (Rasse et al. 2005), and total root biomass predicts short-term SCS in experimental grasslands (Fornara and Tilman 2008). However, the impact of
large herbivore grazing on belowground production, and its consequences for SCS remains largely unknown. Overall, we lack a consistent theoretical framework for understanding the biogeochemical impacts of grazing across environments. Consequently, it is my contention that evaluations of the greenhouse gas footprint of ruminant production on pasture and rangeland (Soussana et al. 2010) are therefore necessarily incomplete. Secondly, I believe that current knowledge gaps hinder development and implementation of more effective management practices to sustainably optimize SCS on pasture and rangeland.

The pasture and range management literature has featured a long and spirited debate on the role of livestock grazing management in maintaining ecosystem structure and function in grasslands (Savory 1983, Briske et al. 2014). Although the role of large herbivore grazing in maintaining grassland plant composition is generally accepted (McNaughton 1985, Knapp et al. 1999, Fuhlendorf and Engle 2001), as is the fact that grazing can stimulate higher levels of productivity (Milchunas and Lauenroth 1993), the extent to which domestic livestock grazing can be actively managed to achieve greater plant diversity, productivity and ecosystem function is hotly contested (Briske et al. 2008b, Teague et al. 2013). The resolution to this debate is partially a scientific matter of obtaining greater insight into direct and indirect impacts of grazing on ecosystem processes (McNaughton 1984, Piñeiro et al. 2010), but is also fundamentally a question of how to incorporate scientific data into adaptive management processes that seek simultaneously to fulfill multiple objectives and values (Armitage et al. 2009, Kothmann et al. 2009, Herrick et al. 2012). From an ecosystem science point of view, it is unfortunately rather difficult to quantify the impacts of resulting land management activities because ordinary experimental design principles cannot strictly be followed (Butterfield et al. 2006, Kothmann et al. 2009). Thus, the results of simplistic grazing trials with fixed treatments or, equivalently, comparisons observed in grazed and ungrazed plots,
cannot be directly applied to forecasting the consequences of real-world land management. Moreover, similar complications apply in evaluation of any particular management practice and not just livestock grazing. For these reasons, I maintain that the first step is for ecosystem science to develop the information and knowledge necessary to situate the effects of livestock grazing within process-based model frameworks. Secondly, we must pursue interdisciplinary syntheses to holistically evaluate the ecosystem services coming from pasture and rangelands under active management.

**Overview of Dissertation**

The over-arching theme of my dissertation is developing a greater understanding of the mechanisms and pathways of carbon sequestration in pastures of Florida, USA. Pastureland is regionally critical to development of sustainable agriculture in the Southeast, in particular owing to the ability of well-managed pastures to restore soil carbon and thus soil fertility and moisture holding capacity (Franzluebbers et al. 2000, Franzluebbers 2010). Cattle ranches are a highly significant land use in Florida, where they provide numerous ecosystem services, including prominent roles in regional hydrology, plant and wildlife conservation and represent a significant cultural legacy (Bohlen et al. 2009, Swain et al. 2013). In this dissertation, I address primarily the critical links between grazing, belowground carbon allocation (BCA) and root production, and SOC pools in improved pasture.

In Chapter 1, I examine the impact of various grazing management options on belowground productivity via a factorial field-plot experiment manipulating the elements of defoliation frequency, severity and genotypic identity in a dominant pasture grass of South Florida. The information in this chapter fills critical gaps in our knowledge of how grazing patterns may differentially impact shoot (and forage) production versus root production, and also suggests the role of plant genetics in mediating these responses by contrasting responses across four widely available cultivars.
In Chapter 2, I address the large-scale environmental factors that might regulate SOC in Florida pastures, from soil factors to the history of vegetation productivity as revealed by long-term remote sensing data. Two important themes that emerge are the role of management relevant spatial scale in constraining the scope and nature of SOC predictions, and the importance of temporal scale in assessing the utility of satellite-derived vegetation indices for improving prediction of SOC.

In Chapter 3, I combine a survey of soils from long-term grazing exclosures with an isotope pulse-chase experiment to reveal how pasture grasses allocate carbon belowground in response to long-term grazing pressure, and the impacts on SOC pools. The study is based around untangling the implications of two forms of BCA, turnover of root tissues versus exudation of labile organic compounds, for explaining variations in SOC.

Finally, in Chapter 4 I synthesize historical, economic and sociological information about cattle ranching in Florida to develop a more holistic understanding of the factors that underpin management of these ecosystems. My main question is, what shapes and constrains the potential for large-scale adoption of new management practices? I focus particularly on a water retention program currently administered by the South Florida Water Management District as a case study, and derive relevant lessons for the potential adoption of any kind of carbon market intended to incentivize SCS.
CHAPTER 2
ROOT PRODUCTION IN A SUBTROPICAL GRASSLAND IS MEDIATED BY CULTIVAR
AND DEFOLIATION SEVERITY

Background

Grassland ecosystems occupy more than a fifth of earth’s land area and account for a large proportion of the global SOC stock (Scurlock and Hall 1998, Lal 2010b). However, there is considerable uncertainty in predictions of net ecosystem exchange, and hence carbon sequestration services from grasslands (Gilmanov et al. 2007, Cahill et al. 2009). One significant source of uncertainty is that while large herbivore grazing is known to mediate patterns of plant species composition, diversity, and aboveground primary production (McNaughton 1985, Knapp et al. 1999, Fuhlendorf and Engle 2001), the effects of grazing on belowground processes and soil carbon is less clear (McNaughton et al. 1998, Hamilton and Frank 2001, McSherry and Ritchie 2013, Balogianni et al. 2014). In particular, there are limited field studies where the impact of grazing on root production in grassland systems has been directly measured (e.g., via root ingrowth cores or minirhizotron technology) (but see Ziter and MacDougall 2012, Balogianni et al. 2014). Since belowground production may be the largest component of total NPP for many grasslands (Gill et al. 2002, Hui and Jackson 2006), determining how grazing affects root production will help to predict if and when grassland ecosystems will behave as carbon sinks, and whether grazing is likely to promote or inhibit carbon sequestration services.

Root carbon inputs may constitute a disproportionate amount of the total SOC stock compared with shoot carbon (Rasse et al. 2005), and are especially critical in grassland ecosystems where aboveground tissue is susceptible to frequent removal by fire and grazing (Johnson and Matchett 2001). Current understanding of how grazing affects root production is ambiguous. For example, one temperate mesocosm study showed that intense defoliation inhibited root production and accelerated the loss of SOC (Klumpp et al. 2009), whereas some field studies have documented
greater belowground allocation and root production under grazing (e.g. Hafner et al. 2012 in Tibetan Plateau). Augustine et al. (2011) found that defoliation reduced belowground carbon allocation in one grazing-adapted North American grass species (*Pascopyrum smithii*, Western Wheatgrass) but not in another (*Bouteloa gracilis*, Blue Grama). In general, laboratory and mesocosm studies have found that frequent grazing/defoliation leads to declines in standing root biomass over the long term (Bardgett et al. 1998), whereas a global synthesis of data comparing grazed and ungrazed grasslands found a mix of positive and negative effects on standing root biomass (Milchunas and Lauenroth 1993). Overall, this discordance suggests that variations in plant composition, underlying environmental factors, grazing intensity, or some combination of these factors significantly mediates the effects of grazing on root production.

Grazing effects on belowground production may not only vary based on plant species, but also on the genotypic composition of a grazed stand, given the increasing evidence of the importance of intraspecific variation in driving ecosystem structure and function (Madritch and Hunter 2002, Whitham et al. 2006). In general, some literature suggests that reduced root allocation (and increased shoot allocation) following grazing may represent an evolutionarily adaptive trait for grazing tolerance (Briske and Richards 1995). For instance, Carman (1985) noted that short-leaved genotypes of *Schizachyrium scoparium*, selected from a long-term grazed site, exhibited lower rates of root elongation post-grazing than longer-leaved genotypes from a long-term grazing excluded site. Planted pasture grasses also have been shown to exhibit genotypic variability in shoot and root production in response to grazing (e.g. Dawson et al. 2000). For example, Interrante et al. (2009) observed significantly less plant cover in recently selected, upright-growing *Paspalum notatum* Flüegge (Bahia grass) cultivars in response to severe, frequent defoliation, but did not observe less
cover in the widely naturalized cultivars, suggesting significant intraspecific variability in grazing tolerance and belowground allocation.

Although root production is a critical component of predicting the carbon cycle in grassland ecosystems, it is difficult to monitor or predict over large spatial scales. Thus, regional-scale grassland models have been developed that predict total NPP and/or greenhouse gas exchange on the basis of aboveground canopy characteristics estimated from remote sensing (Houborg and Soegaard 2004, Li et al. 2012, Gu et al. 2013). Similarly, some previous work has sought to predict BNPP on the basis of readily obtained aboveground measurements in both grasslands (Gill et al. 2002) and forests (Chen et al. n.d.). However, given the evidence for potentially significant genotypic and defoliation effects on belowground carbon allocation, it is unclear whether aboveground proxies can ever reliably approximate root production. Thus, to develop improved grassland carbon models, we need more data from grassland systems where genotypic composition and grazing management have been experimentally manipulated, and the relationship between above and belowground allocation quantified.

In this study, we tested the independent and combined roles of defoliation intensity and frequency, and cultivar on root production of a widely adapted pasture grass species of the southeastern United States, Bahiagrass. We conducted our experiment in a common garden setting under realistic conditions of limited soil fertility in order to isolate the role of defoliation intensity and cultivar in belowground production. Consistent with the literature on compensatory growth responses from natural and planted pastures (McNaughton 1983, Parsons et al. 1988), and the literature on genotypic variability (e.g. Dawson et al. 2000) we hypothesized that:

1. Severe defoliation, applied infrequently, would stimulate increases in aboveground primary productivity, but would have neutral effects on root productivity across all cultivars, and

2. Severe defoliation, applied frequently, would significantly suppress shoot and root production across all cultivars, and
3. Widely naturalized, decumbent cultivars would show proportionally greater reductions in root production under severe defoliation compared to the more upright cultivars, reflecting a beneficial adaptation for increased shoot allocation following severe defoliation events, and

4. Despite alterations to belowground allocation on the basis of cultivar and defoliation treatment, shoot production and root production would positively correlate at the plot level reflecting variations in underlying soil factors determining total productivity.

**Materials and Methods**

To evaluate the independent and potential interactive effects of defoliation intensity and plant cultivar on root production, we established 32 3 m x 7 m experimental plots at the University of Florida Range Cattle Research and Education Center, Ona, FL (27°26’ N, 82°55’W) in 2009. The soils were uniform and classified as Pomona fine sand (sandy, siliceous, hyperthermic Ultic Alaquod). First, we seeded plots with one of four *P. notatum* cultivars (Argentine, Pensacola, Tifton-9, and UF-Riata). *Paspalum notatum* is a perennial C4 pasture grass with improved germplasm that was introduced to Florida in the 1920s from South America and constitutes the primary forage for the Florida cow-calf industry (Silveira et al. 2011). Argentine and Pensacola are widely-distributed, naturalized cultivars in Florida with a decumbent growth habit, whereas Tifton-9 and UF-Riata are recently-released cultivars selected for improved agronomic characteristics including more upright growth habits and less photoperiod sensitivity (Interrante et al. 2009, Vendramini et al. 2013). Plots were fully established by the onset of the 2010 summer growing season with complete, uniform plant cover. More details, including soil fertility characteristics can be found in Vendramini et al. (2013). Site weather data for this period were accessed from the Florida Automated Weather Network (FAWN, [http://fawn.ifas.ufl.edu/data/](http://fawn.ifas.ufl.edu/data/)), including temperature, precipitation, and evapotranspiration, and all fell within normal ranges (Table A1).

We initiated defoliation treatments on June 13th 2013 and concluded field sampling 16 weeks later on October 5th 2013. Although we did not measure soil moisture, the soils were all visibly waterlogged from July until the end of the experiment, as is typical in Florida Spodosol soils.
(Silveira et al. 2011). We therefore assumed that plant growth was not limited by water availability during the sampling period, or at the very least that water availability was essentially constant across plots. Each plot (n = 32) was randomly assigned to either a frequent (2 week) or infrequent (4 week) defoliation treatment to simulate grazing. Each plot was divided in half and received two defoliation intensities (a severe defoliation to 5 cm residual height, and a mild defoliation to 15 cm residual height) resulting in n = 64 experimental units (Figure A1). Thus, our design was effectively split-plot with two main-plot treatments (cultivar and defoliation frequency), while our subplot factor was defoliation intensity. Overall, each cultivar X defoliation severity X defoliation frequency treatment was replicated 4 times.

We cut a 0.92-m² quadrat from each subplot during each defoliation treatment with a rotary mower (Sensation Mow-Blo Model 11F4-0) at the target cutting heights: 5 cm for the severe defoliation, 15 cm for the mild defoliation, values chosen based on personal observation (C.H. Wilson, L.E Sollenberger, J.M. Vendramini) to represent the extremes of pasture defoliation under grazing by beef cattle in Florida. To quantify aboveground production, harvested material was oven-dried at 60°C to constant mass and weighed on an analytical scale. During the final harvest, all subplots were harvested at 5 cm. Total aboveground production was determined by summing values for each subplot across all dates including the final harvest. Aboveground production values are presented in g/m² (dry biomass).

To quantify root primary production in response to the defoliation treatments, we installed 2-mm mesh root in-growth cores (Makkonen and Helmisaari 1999) on June 7th, 2013, prior to imposing the defoliation treatments (n = 64). Cores were 7.5 cm diameter x 25 cm deep and constructed of fiberglass mesh. They were installed by first excavating a cylinder of soil with a soil auger to target dimensions, placing the mesh bags into the cylinder so that the upper edge of the bags
was just below the soil surface, and then re-filling the cores with sieved, root-free soil from the same plot. We retrieved the cores at the end of the growing season on October 5th 2013, 16 weeks after installation. The final volume of soil contained in each core was quantified prior to washing the roots free of soil on a 250-uM sieve. Root samples were then oven-dried at 60°C to constant mass and weighed on an analytical scale. To correct for variation in core volume, root biomass was multiplied by a correction factor determined as the inverse of the ratio of each core volume to a reference core (a cylinder of 7.5 cm diameter and 25 cm depth). Finally, we determined that almost all root biomass was contained within the depth we evaluated, thus we multiplied root biomass by a constant (10000/(pi*3.75^2)) to convert our measures to g/m², putting them on an easily interpretable scale.

**Statistical Analysis.** Response variables for analyses were shoot and root production. To analyze among-cultivar variability in response to our treatments, we parameterized a varying-intercept/varying-slope Bayesian hierarchical model that we applied to both of our response variables. In this model, we estimate intercept and slope (i.e., treatment effects) coefficients for each cultivar, where each batch of coefficients is modeled as a draw from a normal distribution with an estimated variance component (Gelman and Hill 2007). We included binary predictor variables using a -0.5/0.5 “effect coding” for our experimentally imposed treatments: lenient (15 cm) and infrequent (4 wk) defoliation were assigned -0.5 values, while frequent (2 wk) and severe (5 cm) defoliation were assigned 0.5 values. Under this coding, the model intercept represents the grand mean, and the coefficients for defoliation severity and frequency represent the main effects of severe and/or frequent defoliation across both levels of the other treatment (see Schabenberger et al. 2000). We also included a term for the interaction of severe and frequent defoliation treatments and a random effect of plot to allow for correlation in observations from the same plot. Our varying-
intercept/varying-slope model therefore included four separate estimates of grand means (one for each cultivar), each of which represents an estimate of performance for that cultivar across all defoliation treatment conditions, and four treatment effect estimates (one for each cultivar) for frequent defoliation, severe defoliation, and their interaction. Since these coefficients were drawn from distributions with estimated variance components, the separate estimates were partially pooled towards their common mean, which also was estimated from the data, a property that built in an automatic correction for multiple comparisons and obviated the need for arbitrary post-hoc adjustments such as the Bonferonni correction (Gelman et al. 2012). Finally, because we observed significant differences in variability among our defoliation treatment groups, we included a model for unequal variances across treatments (Gelman and Hill 2007) to formally test whether defoliation treatments led to differences in plot-plot variability in plant production, and to quantify effects on plant responses.

We display treatment effects graphically by plotting model coefficients grouped by cultivar and centered on the median, and include both a 50% (thick) and a 95% (thin line) confidence interval. These coefficients represent the main effects of treatment or the interaction effect for each cultivar. In addition to the cultivar-level estimates, we also plotted a dashed line that represents the mean effect across all cultivars. Where the 95% confidence intervals do not cross zero, we infer strong confidence in having estimated the sign of a treatment effect correctly (i.e., positive or negative). Likewise, when the 95% confidence intervals for a given cultivar does not cross the dashed line representing the group mean, we infer strong evidence for that particular cultivar differing in response from the other cultivars (Gelman et al. 2012).

We estimated these models in a Bayesian framework using Gibbs Sampling using JAGS (v3.4.0) called from R (v3.1.0) via the “R2jags” package (v0.5-7). Treatment effect parameters were
assigned non-informative normal priors and variance components were assigned conventional uniform priors on the standard deviation scale. For all models we sampled the target (posterior) distribution with four chains of $10^5$ iterations each, discarding the first $2\times10^4$ as burn-in, and thinning by 40. Model convergence was assessed via use of the R-hat < 1.1 criterion (Gelman and Hill 2007) as well as by visual inspection for chain blending and stability.

To understand the relative importance of defoliation treatment and cultivar compared to aboveground production for predicting root production, we refit our varying-intercepts/varying-slopes model (with “lme4” package in R) using only aboveground biomass from each subplot (n=64) as a continuous covariate. We compared the strength of the linear relationship, indexed by coefficient estimates and $R^2$ values, between aboveground and belowground biomass in a univariate model to the estimated relationship in the full model, while accounting for treatment and cultivar identity. Lastly, as recommended by Nakagawa and Schielzeth (2013) and extended by Johnson (2014), we estimated both the conditional and marginal $R^2$ value from our full varying-intercepts/varying-slopes model, which enabled us to partition the respective contributions of our fixed effects (defoliation severity and frequency), and the varying “random” effects (cultivar identity), for explaining root production (see Appendix B for code).

**Results**

**Shoot Production Model**

Average shoot production across all cultivars and treatment combinations in our study was 290 g m$^{-2}$, with the highest values observed in the infrequent severe defoliation treatment, which averaged 384 g m$^{-2}$ (Fig 2-1). Overall we found minimal evidence of variability in shoot production among cultivars across all treatments, although the upright cultivars (‘UF-Riata’ and ‘Tifton-9) had slightly higher production than the decumbent cultivars ‘Argentine’ and ‘Pensacola’ (Fig. 2-2a). Compared to mild defoliation, severe defoliation consistently resulted in greater shoot production
across all cultivars, while frequent defoliation resulted in lower shoot production (Fig 2-2b/c). The overall main effect estimates (in g m\(^{-2}\) and with 2.5% and 97.5% CI) were +82.7 [25.2; 137.2] for severe defoliation and -59.0 [-108.4; -9.9] for frequent defoliation. There was also a significant negative interaction effect, consistent with the pattern that severe but infrequent defoliation maximized shoot production (Fig 2-2d).

**Root Production Model**

We observed an average root production of 224 g m\(^{-2}\), where mild defoliation treatments were the highest with 262 g m\(^{-2}\) averaged across 2 wk and 4 wk defoliation frequencies, compared to severe defoliation with an average of 186 g m\(^{-2}\) (Fig 2-1). Average root production across treatment groups varied significantly by cultivar (Fig 2-2e), from ‘Tifton-9’ with a mean of 185 [150; 221] at the low end to ‘Argentine’ at the high end with a mean of 263 [225; 300], a 42% increase. In contrast to shoot production, severe defoliation inhibited root production compared to mild defoliation (Fig 2-2g), with a main effect of -75 [-136; -11] and minimal variation in response among cultivars. The effects of frequent defoliation and its interaction with severe defoliation were mixed, with nothing of statistical significance, although it appears that the cultivar Argentine may sustain minimally less root production under severe defoliation if applied infrequently (Fig 2-1b, and Fig 2-2h). Sampling variance (on SD scale) was significantly lower in the severe + infrequent defoliation group than in the other treatments, with a mean estimate of 18 compared to the mild + infrequent group with a mean estimate of 107 (Fig A2).

**Root Production Predictions**

The univariate regression between aboveground and belowground biomass revealed a weak (\(R^2 = 0.08\)), but statistically significant relationship (\(p = 0.014\)), where root production was slightly less with greater shoot production (Fig 2-3a). However, this relationship did not exist when we accounted for treatment effects in the full varying-intercept/varying-slope model (Appendix A3:
The full model had a conditional $R^2$ of 0.53 and a marginal $R^2$ of 0.18 (Figure 2-3b), indicating that accounting for cultivar identity triples the model $R^2$.

**Discussion**

Severe defoliation resulted in substantially greater shoot production and lower root production among the *P. notatum* cultivars, while root production but not shoot production was also mediated by among-cultivar variability. Thus, our results suggest that severe defoliation can trigger a tradeoff between aboveground and belowground allocation in managed subtropical pastures.

Contrary to Georgiadis et al. (1989) and Briske and Richards (1995) who suggested that overcompensation is only likely to occur under water limitation, or concomitant fertilization, we found significant enhancement of shoot production in response to severe defoliation under limited fertility and abundant soil water. Compared to mild defoliation, all cultivars exhibited this compensatory aboveground growth response to severe defoliation, but only when defoliation was applied infrequently. However, the severe, but infrequent defoliation treatment that led to aboveground compensatory growth also suppressed root production. Thus, under low-input conditions, manipulating defoliation intensity to enhance forage production could evoke a tradeoff between shoot and root production. Given the substantial literature suggesting the importance of root carbon for maintenance of soil carbon pools (Rasse et al. 2005), these altered allocation patterns may have significant consequences for carbon cycling, and hence soil carbon sequestration services, in managed subtropical pastures.

Our results differ from the short-term responses measured by Ziter and Macdougall (2014) and Hamilton III et al. (2008) where a single defoliation event stimulated root production and root exudation, respectively. This discrepancy suggests that root responses to isolated grazing/defoliation events can strongly differ from season-long responses to grazing regimens where both intensity and frequency of defoliation are expected to mediate plant regrowth strategies (Briske and Richards...
For instance, Thornton and Millard (1996) found that greater severity of defoliation resulted in lower root mass (but greater N uptake per unit of root mass), which is consistent with our findings. On the other hand, Dawson et al. (2000) found that weekly defoliation over a growing season reduced root biomass compared to no defoliation, but infrequent defoliation (every 8 weeks) had no effect. Our ambivalent findings on the role of frequency of defoliation were thus surprising. Although we observed significant suppression of variability of production under our severe + frequent treatment, root production was not markedly lower than in our severe + infrequent treatment, except perhaps for the Argentine cultivar. Overall, it appears that in our system, severity, not frequency, of grazing is the more important determinant of grass root production.

We observed significant overall variability in root production among the grass cultivars. However, it does not appear possible to predict cultivar-level belowground responses to specific grazing regimens based on observations of aboveground compensatory growth responses. As we hypothesized, the cultivars selected for enhanced upright growth habit (Tifton 9, UF-Riata; (Interrante et al. 2009) exhibited less overall root production, especially Tifton 9, compared to the widely naturalized decumbent types (Argentine, Pensacola), especially Argentine. On the other hand, all cultivars responded equally negatively to severe defoliation *per se*, and we observed similar total root production among all cultivars in the severe + frequent defoliation treatment, a scenario reasonably representative of overstocked pastures. These results contradict the theory that more grazing-tolerant genotypes, in our case Argentine and Pensacola, will have lower root production as a consequence of greater post-grazing allocation to shoot regrowth (Briske and Richards 1995, Dawson et al. 2000). Instead, it appears that cultivars simply vary in root growth potential, but that severe defoliation, especially when applied frequently, overwhelms this variability.
Contrary to hypothesis, our study revealed that shoot and root production are decoupled at fine spatial scales, with shoot production explaining only 8% of the total variance in root production. Moreover, this relationship was entirely mediated by responses to defoliation treatments, and was statistically insignificant after accounting for defoliation treatment and cultivar identity. By contrast, defoliation treatment and especially cultivar identity appear to be very important for predicting root production in this system, together accounting for over half the observed variance in root production.

Gill et al. (2002) reported some success in predicting belowground NPP using an algorithm based only on aboveground biomass and climate. However, their model consistently under-predicted root production in more productive sites. Thus, we caution against using aboveground proxies to predict belowground production, even within uniform and homogeneous ecosystems, such as the planted pasture system where we worked. Our results suggest that knowledge of grazing management and cultivar identity (in addition to species-level variations in composition, e.g. Steinbeiss et al. 2008; Tilman et al. 2012) is critical for generating accurate predictions of BNPP. Moreover, half of the variance in belowground production was unexplained, even in our best model, suggesting significant spatial heterogeneity in root system productivity that should be further investigated.

At the large scale, McNaughton (1998) found that grazing intensity is uncorrelated with standing root biomass or productivity in the Serengeti. However, in speciose natural grasslands plant diversity may confer a stabilizing influence on root production (Fornara et al. 2009, Tilman et al. 2012). By contrast, monoculture pasture systems may respond more like mesocosm systems where high defoliation intensity is associated with reduced root biomass (Bardgett et al. 1998). Moreover, since a large proportion of managed grasslands are dominated by single species, variation in root production among cultivars may represent an especially important component of diversity. Grazing management may need to be matched to cultivar-level characteristics to optimize both forage and
root production, and establishment of planted pastures with multiple cultivars or genotypes may be a viable, yet underappreciated, strategy for enhancing functional diversity. For instance, combining upright and decumbent cultivars may introduce beneficial genotypic diversity that could maximize utilization of both above and belowground resources via niche complementarity (Avolio et al. 2011, Chang and Smith 2014). Additionally, cultivar-level variability suggests the potential for ecologists to collaborate with plant breeders to improve the sustainability of grassland agroecosystems by development of improved forage cultivars selected for superior belowground traits.

Overall, our results suggest that intermittent severe defoliation can elicit much greater shoot growth, but have neutral or negative effects on root production. It is possible that a more moderate defoliation intensity than we tested would have led to similar stimulation of aboveground compensation without the negative consequence for root production, a possibility our study was not designed to test. Neither did our study consider impacts of defoliation on rhizome biomass, but we note that our intent was to focus on root production since it appears to be of greater relevance for soil carbon sequestration than other compartments of plant biomass (Rasse et al. 2005). Likewise, it is also possible that the lower fine root production we measured may have been compensated for by greater rhizodeposition/root exudation. However, this seems unlikely given that rates of root exudation generally correlate to fine root surface area (Jones et al. 2009).

Root production is critical for maintaining and increasing soil carbon pools in grassland ecosystems, yet the short and long-term effects of grazing on root production remain variable. In addition to recommending greater future consideration of intraspecific variations in belowground responses to grazing, our work supports the need to perform season-long measures of belowground productivity to obtain reliable estimates of belowground production that can be used to parameterize soil carbon models. Our data suggest that reliance on aboveground proxies is, unfortunately, not

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justified at least for subtropical pastures. In addition, given the limitations of observational and comparative work, we suggest that longer-term field manipulations are necessary to evaluate a suite of grazing management scenarios across plant composition treatments. Such experiments will significantly improve our ability to inform the design and management of grassland agroecosystems for meeting aboveground (forage) production goals while also optimizing belowground production, and thus soil carbon sequestration and other soil carbon mediated ecosystem services such as nutrient retention and water cycling (Lal 2010b).

Figure 2-1. Mean biomass (gm^-2) +/- 1 SE for shoots (white bars) and roots (grey bars). The panels are faceted by treatment combinations: frequency of defoliation on top (4 weeks versus 2 weeks), and intensity of defoliation on right hand side (mild or severe). The x-axis groups responses by cultivar: A = Argentine, P = Pensacola, T9 = Tifton-9, and UF-R = UF-Riata.
Figure 2-2. Coefficient plot of our varying-intercepts/varying-slopes hierarchical regression model for shoot (left column, panels a-d) and root production (right column, panels e-h). Cultivar identity: A = Argentine, P = Pensacola, T9 = Tifton-9, and UF-R = UF-Riata. The decumbent (Argentine, Pensacola) upright (Tifton-9, UF-Riata) cultivars are indicated by square and circle symbols, respectively. Each coefficient is presented as a mean alongside a 50% (thick line) and 95% (thin line) credible interval. In the top row are displayed the estimated means (intercepts) for each cultivar across all treatment groups, for shoots (panel a) and roots (panel e). The next two rows display the estimated main effects (for each cultivar) of both defoliation frequency (panels b and f) and severity (panels c and g). These effect estimates therefore represent the impact of moving from 15cm to 5cm cutting height in the case of severity, or from 4 week to 2 week frequency of defoliation, across both levels of the other treatment. Finally, the last row displays the interaction of frequency and treatment (panels d and h). Negative values indicate a negative interaction between severe X frequent defoliation.
Figure 2-3. Scatterplot of the relationship between shoot (x-axis) and root (y-axis) production a) and predicted versus observed scatterplot using our full varying-intercepts/varying-slopes model that accounts for both defoliation treatments and cultivar identity b). Both the conditional $R^2$ (signified as $R^2_{\text{def + cult}}$ that includes both defoliation treatment and cultivar identity effects), and marginal $R^2_{\text{def}}$ (that includes only defoliation treatment) are shown.
CHAPTER 3
MULTI-DECADAL TIME SERIES OF REMOTELY SENSED VEGETATION IMPROVES PREDICTION OF SOIL CARBON IN A SUBTROPICAL GRASSLAND

Background

Soil carbon sequestration (SCS) is a promising strategy for mitigating global climate change (Lal 2004, 2010b, Stockmann et al. 2013), particularly in managed ecosystems that have suffered soil organic carbon (SOC) losses due to agricultural conversion, land degradation, or overgrazing (Conant et al. 2001, Conant and Paustian 2002a, DeGryze et al. 2004, Rees et al. 2005). However, it is difficult to manage for SCS at meaningful scales because predicting and quantifying SOC outside of experimental plots remains a considerable challenge (Vasques et al. 2010, Eigenbrod et al. 2010, O’Rourke et al. 2015). This difficulty is due in part to the natural heterogeneity in underlying drivers of SOC, especially soil and vegetation properties. Moreover, we have limited knowledge of how these drivers interact at the scale of individual land management units, which is necessary to quantify and incentivize ecosystem services (hereafter “management-relevant spatial scale” Saby et al. 2008, Power 2010, Swain et al. 2013, O’Rourke et al. 2015). Although recent work has emphasized the potential utility of simple measures of plant traits for improving SOC predictions across diverse ecosystems at national scales (Yang et al. 2008, Manning et al. 2015), such work has not explored whether continuous variations in vegetation properties (e.g., green leaf area) improve SOC predictions across more homogeneous management units (e.g., pastures or forest stands). This gap in our current knowledge is critical because efforts by ecosystem scientists and land managers to promote SCS ultimately rely on development of cost effective and efficient methods for predicting and quantifying SOC at management-relevant scales.

Across the largest spatial scales (i.e., bioregions or continents), climatic factors, especially mean annual temperature (MAT) and mean annual precipitation (MAP), are assumed to dominate SOC dynamics through their combined effects on vegetation productivity, microbial metabolism,
and rates of soil weathering (Jenny 1961, Chapin et al. 2012). Landscape-scale variations in soil properties, such as clay content, mineralogy, and pH, also exert control over plant composition, microbial activity, and the potential for stabilization of carbon (Burke et al. 1989, Conant and Paustian 2002b, Cotrufo et al. 2013). These mechanisms are reflected in basic ecosystem process models (e.g., CENTURY, Parton et al. 1993, Bolker et al. 1998, Evans et al. 2011) that are used to predict SOC across regional or continental gradients (Burke et al. 1989, Schimel et al. 1994). For agricultural land managers seeking to enhance SCS as part of a portfolio of ecosystem services (Chapin III 2009), understanding factors leading to variations in SOC stocks at the scale of their working landscapes is vital for designing proper monitoring protocols and to spatially target interventions. At management-relevant scales, ranging from 10s to 1000s of hectares, climatic variables such as MAT and MAP are essentially constant, so variations in SOC are largely due to the interaction of vegetative (e.g., productivity and composition, Conant et al. 2001), topographic and edaphic (e.g., soil texture, soil moisture and pH, Kemmitt et al. 2006) factors. In general, predicting SOC within homogenous landscapes should be more difficult than predicting SOC across heterogeneous areas with significant variation in edaphic and climatic factors. Thus, the best predictive models for SOC at management-relevant scales should emerge by combining two types of information: 1) soil properties that predict variations in soil capacity to stabilize carbon and constrain microbial decomposition (Davidson and Janssens 2006), and 2) vegetation data on plant productivity and composition within and across management units (i.e., pastures, forest stands).

Remotely sensed vegetation indices may be an efficient method for providing data to improve SOC predictions at management-relevant scales. Recent advances in the accessibility of pre-processed remote sensing data (e.g., Google Earth Engine, Moore and Hansen 2011) have greatly increased the practicality of extracting long time series of vegetation data for specific sites.
These multi-decadal time series of remotely sensed vegetation data include well-validated greenness indices, such as the Normalized Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI), which reflect the biomass and productivity of vegetation (Hill et al. 2004, Gu et al. 2013, Cook and Pau 2013). In an Australian pastureland, Hill et al. (2004) utilized satellite-derived NDVI to parameterize simple light-use-efficiency models that accurately predicted pasture growth rate ($R^2 \sim 0.7$). However, thus far the use of EVI and NDVI to predict SOC has been limited to simple data summaries over brief time periods of only one or two years (e.g., Yang et al. 2008, Vasques et al. 2010), which is far too short for any plant-driven biophysical process to substantially alter total SOC stocks (Smith 2004). Thus, any predictive power from snapshot summaries must derive from one of two sources: a) discriminating coarse variations in vegetation composition such as grassland from forest, or b) autocorrelation originating from a process whereby higher SOC consistently leads to higher greenness. By contrast, scientists and land managers seeking to understand and predict SOC within management units characterized by relatively homogeneous vegetation cover need to know: a) whether variations in vegetative greenness correlate with variations in underlying SOC, and b) whether any correlation between greenness and SOC is stable and consistent across time or if there is significant inter-annual variability. Analyzing multi-decadal time series of vegetation indices is an ideal way to disentangle these possibilities.

To test the utility of remote sensing derived vegetation indices for predicting SOC, we posed three specific questions: 1) What is the explanatory power of a two-year summary of EVI data relative to a multi-decadal time series for predicting SOC?; 2) What is the importance of EVI data for predicting SOC relative to edaphic factors?; and 3) How does the predictive value of EVI change at different soil depths? We hypothesized that average EVI would be positively correlated with measured SOC pools, and that this association would be stronger when averaged over longer time
periods. Moreover, in line with the mounting evidence that SOC storage is controlled by different factors at different depths (Silveira et al. 2014a) and because above and belowground plant inputs are concentrated near the surface, we hypothesized that the relative importance of plant productivity as a driver of SOC variability would be greater at shallower soil depth.

**Methods**

**Study Site**

Our study site was a 4300 ha commercial cattle operation, Buck Island Ranch (BIR), located in Lake Placid, FL, USA just north of Lake Okeechobee. Pastureland and native rangeland are dominant land uses in the northern Everglades watershed, provide numerous ecosystem services, including livestock production, wildlife habitat conservation, and maintaining cultural legacy, and represent relatively benign, low-input agricultural management (Swain et al. 2007). Like most commercial cattle ranches in the watershed, BIR maintains both planted (“improved”) pasture, dominated by *Paspalum notatum* Fluegge (Bahiagrass), and “semi-native” pasture, consisting of a mixture of native warm-season wet and dry prairie species and some introduced pasture grasses. Improved pasture is utilized far more intensively for livestock grazing than semi-native pasture, supplying several times more usable forage on a per area basis, and accordingly is fertilized (at a low rate) and limed regularly to improve the quantity and quality of forage (Silveira et al. 2011). The soil series at BIR are mostly from Spodosol and Entisol orders, and are uniformly coarse-textured with the clay+silt fraction accounting for 2-3% of total mineral mass and a range of sand grades accounting for the remainder (Silveira et al. 2014b). There is no significant stone content. Here we focused on SOC in improved pastures given their agronomic relevance (i.e., there is ~1m ha of planted “improved” pasture in Florida, Bohlen et al. 2009), thus our scope of inference is limited to this particular land-use type.
Soil Organic Carbon Sampling

In July 2014, we sampled 57 plots distributed across 2000 hectares of improved pasture at BIR (Fig 3-1). Our focus was on SOC sequestration in improved pasture, thus we focused our sampling on upland pasture and specifically avoided wetlands and tree hammocks. Plots were identified with stratified random sampling in GIS software (ESRI 2009. ArcGIS Desktop 9.3.1, Redlands, CA: Environmental Systems Research Institute) with a minimum spacing of 150 m. To quantify SOC concentration and soil bulk density, we collected one 0-15 cm soil sample from each plot using a hammer core (AMS 5.08 cm x 15.24 cm Signature SCS Complete/354.26) and computed SOC stock for 0-15 cm. To separately analyze SOC concentration from 0-5 cm and 5-15 cm depth fractions, while also averaging over fine-scale variability in soil properties, 12 subsamples were collected from a circle of 5 m radius using a narrow gauge soil auger (AMS Soil Step Probe 83 cm/401.4), and divided into 0-5 cm and 5-15 cm depth fractions. The 12 subsamples for each depth fraction were bulked together in the field.

Soils were oven-dried at 60 °C prior to being passed through a 2 mm sieve to remove plant litter. Essentially no stones were found. A subsample from each soil sample was prepared for %C/%N analysis by grinding for 15 minutes in a Spex SamplePrep Mill, and was then sent to the University of Florida’s (UF) Light Stable Isotopes Lab for analysis on a Carlo Erba NA1500 CNS Elemental Analyzer (EA). Separate subsamples were sent to the UF IFAS Analytical Laboratories for measurements of pH, and Mehlich III extractable Ca, K, Mg, and P.

For the 0-15 cm soil sample we converted the SOC concentration from the EA to a measure of SOC mass by using the bulk density measured from each core. We then standardized the resulting SOC stock estimate to units of kg m⁻², according to the following formula:

$$\text{SOC Stock} = \text{SOC} \left(\frac{g}{100g}\right) \times \text{BD} \left(\frac{g}{cm^3}\right) \times \left(100^2 \frac{cm^2}{m^2} \times 15 \text{ cm}\right) \times \left(\frac{1kg}{1000g}\right)$$  \hspace{1cm} (3-1)
Acquisition of GIS Data

To obtain LiDAR surface elevation data, BIR was flown on April 13, 2006, with 36 flight lines covering 72 km². Each flight line was 10.55 km long. Data were collected using an Optech 1233 Airborne Laser Terrain Mapper (http://www.optech.ca/) mounted on a twin-engine Cessna 337. The LiDAR data were used to produce a DEM (Digital Elevation Map) which we used for topographic measurements (more detail in Appendix 3-1).

To gain insight into variations in pasture productivity and biomass, for each sampled point (n = 57) we extracted time series of EVI, a widely-used vegetation index, on a 32-day interval at 30m pixel resolution from January 1st 1984 to December 31st 2011. Each time series was composed of cloud and shadow masked, atmospherically corrected Surface Reflectance data processed by the USGS using the Landsat Ecosystem Disturbance Adaptive Processing System (Masek et al. 2006) from Landsat 5’s TM multi-spectral sensor using Google Earth Engine (https://earthengine.google.com/ and discussion in supplementary information for Hansen et al. 2013). The open-access Landsat archive has a global extent and images dating back to 1972 (Wulder et al. 2016). Earth Engine is a cloud computing platform designed for rapid processing of large remote sensing datasets through a distributed computing architecture. The EVI data points were calculated as follows (following Huete et al. 2002):

\[
\text{EVI} = 2.5 \times \frac{B4 - B3}{B4 + 6 \times B3 - 7.5 \times B1 + 1}
\]  

(3-2)

Here, B4 corresponds to the Near Infrared band, B3 represents the Red band, and B1 represents the Blue band. EVI values are therefore dimensionless quantities constrained to be between 0 and 1 in practice. Whereas the better-known NDVI exhibits a non-linear saturating response with increased leaf area index (LAI) above 2-3, the EVI index greatly reduces the saturating response present in
NDVI so that more information can be retrieved from high biomass or high LAI vegetation (Huete et al. 2002). For instance, EVI was found to correlate linearly with pasture LAI/biomass up to LAI ~ 5 (the entire tested range) by Houborg and Soegaard (2004).

**Statistical Analysis**

To fully leverage the information contained in the EVI time series’, we first decomposed each time series record (n=57) into two components: a linear temporal trend from 1984-2012, which represents whether the EVI was trending higher or lower, and a periodic component representing the amplitude of the seasonal phenology, using a simplified form of Fourier analysis based on Bradley et al. (2007) (further details in Appendix 3-2). However, analysis showed that only the linear components of the EVI time series were useful in predicting SOC, and only when the intercept (starting value) and trend were taken in combination, which is a formulation that is mathematically similar to simply taking the mean of the entire time series. In particular, there was no benefit to knowing the particular trend *per se*; the average value sustained was critical, not whether EVI increased or decreased over time. Thus, for subsequent analyses we only used the simple arithmetic mean of the entire time series record.

To isolate the predictive value of summarizing a long time-series of EVI data compared to using only the most recent two years, we first compared the model fit (using $R^2$) between these two predictors. Then, since we had previously ruled out temporal trends, seasonal phenology or variance *per se* as important aspects of our long EVI time series, we investigated whether all dates in the time series contributed equally to predictive power, or if there was significant variation in contribution among dates. To accomplish this task, we performed a simple exploratory analysis where we plotted $R^2$ from a univariate regression model predicting surface SOC concentrations (0-5cm) (n = 57) with mean EVI (n =57) derived by taking the mean for each year in the time series (n = 28). To estimate whether high $R^2$ observations within any given year were likely to arise from chance sampling
variation, we performed a simple Monte Carlo analysis to randomly generate $10^5$ vectors of $n = 57$ EVI observations within the range of EVI we observed in this study system, fitted univariate least squares regression models between the random vectors and our observed SOC stock, and plotted resulting sampling distribution of $R^2$ values (see Appendix S3).

Next, we compared the relative importance of EVI to the other environmental covariates in the context of a multivariate regression across all responses. Other environmental predictors included elevation (from LiDAR-derived DEM), soil pH, and Mehlich III extractable P, K, Ca, and Mg. Note that silt+clay content, as noted above in study site description, is uniformly low across our sampled points ($n = 57$), and thus we did not include data on soil mineralogy. To simplify comparison among factors, we combined the information contained in the Mehlich III soil audit by taking the arithmetic mean of the standardized values for each element (Appendix C4), but we also analyzed calcium separately due to its potential role in SOC stabilization processes (i.e., due to cation bridging, Stockmann et al. 2013). Thus, our candidate predictors included: mean EVI, elevation, soil pH, Ca, and Soil Fertility Index. Prior to analysis we standardized all predictor variables by dividing by two standard deviations and centering around the mean so that we could interpret coefficients on the same scale (Gelman 2008). Each coefficient was read as the impact on the response variable of moving from a typical low to a typical high value for that predictor. By contrast, response variables were standardized to have mean zero and unit standard deviation, and therefore each regression coefficient could be interpreted as the effect size of that predictor in units of standard deviations of the response. The purpose of standardizing both predictor and response variables was to enable relative importance comparisons of each predictor both within models (i.e., compared to other predictors) and across models where the original scale of responses could differ. We present the results of these models in the form of coefficient plots, which show the point
estimate from least squares regression surrounded by 50 and 95% CIs. Additionally, each coefficient plot also displays the constrained point estimate from the LASSO regression (explained below), and we provide R² model fit summaries from both the unconstrained (least squares) and constrained (LASSO) models, with the latter computed based on out-of-sample predictions that correct for overfitting.

To perform predictive model selection among these candidate variables, we implemented LASSO (least absolute shrinkage and selection operator) regression (Tibshirani 2011). LASSO constrains the sum of coefficients in a linear regression to be less than or equal to a constant tuning parameter, a form of penalization that reduces estimates of small and/or noisy effects, sometimes all the way to zero (thus eliminating that covariate, Tibshirani 1996). We used cross-validation to set the tuning parameter for our LASSO regression models using the R package ‘glmnet’ (Friedman et al. 2010). We overlaid the LASSO point estimates onto the unpenalized least squares coefficient plots. Next, we validated the predictive contribution of our time-series EVI measure by performing LASSO regression on models with and without the EVI predictor and comparing the out-of-sample predictive performance using leave-one-out cross-validation (LOOCV). Specifically, we iteratively re-fit a LASSO regression model, each time holding out a single data-point to predict with the re-fitted model (N=57), and then computed a LOOCV-R² metric for each model. In this way, we validated the predictive value of multi-decadal time-series EVI on SOC stock estimation and compared its contribution to quantifying surface SOC versus SOC contained in lower horizons.

**Results**

Observed SOC stock (0 - 15 cm) ranged widely from 1.78 kg C m⁻² to 6.34 kg C m⁻², with a mean value of 4.27 kg C m⁻² (sample CV = 27%) (Fig. 3-1). Surface SOC concentrations (0-5cm) were even more variable, ranging from 1.04-6.34%, while deeper SOC concentrations (5-15cm) were between 0.63% and 2.55%.
Averaging across the N=57 sampled plots, the EVI data captured fluctuations in seasonal phenology between 0.14 and 0.71 (Fig.3-2a). Across the 1984 to 2011 time series, plots varied substantially in both estimated intercepts and slopes, indicating variations in temporal trends (Fig.2b), and also differed in the amplitude of seasonal EVI (Fig. 3-2c). However, only the combination of linear terms was statistically significant for predicting SOC, and was equivalent to simply taking the arithmetic mean of the entire time series (Appendix C1). Overall, mean EVI across the 28-year record varied between 0.35 and 0.44. Measured soil fertility parameters varied widely among the sampled points; for instance, in the 0-15 cm cores pH was between 4.08-6.70 and P was between 4.13 and 38.57 ppm.

In univariate regressions with soil carbon as a response variable, R² values of models with mean EVI from a short time interval (2 most recent years) were uniformly low, with R² values of 0.03 (0-15 cm SOC stock), 0.04 (0-5 cm SOC concentration), and 0.04 (5-15 cm SOC concentration). In contrast, for mean EVI derived from the whole 28-year time series, R² varied between 0.24 (0-5 cm SOC concentration) and 0.31 (0-15 cm SOC stock, with P < 0.0001 for all models) (Fig. 3-3a,c,e versus b,d,f).

Relative importance of different dates in the EVI time series varied dramatically (Fig.3- 4ab). One year showed an R² of 0.35, comparable to the mean of the entire record, while several other years were very low (practically zero), and many were in-between (Fig. 3-4). However, exclusion of the high R² year did not significantly impact predictive value of the rest of the time series (i.e., mean EVI was still a strong predictor). Moreover, our multiple observations of years with R² > 0.1 are extremely unlikely to have resulted by chance variation (i.e., P << 0.00001, appendix C3). Comparing EVI (mean of 28-year period) to our suite of other environmental covariates for predicting soil C revealed differences across responses (i.e., between 0-15 cm SOC stock, 0-5 cm
SOC concentration and 5-15 cm SOC concentration). For explaining variations in the SOC stock (0-15 cm, Fig. 3-5a), EVI and extractable-Ca concentration were both significant positive predictors and appeared to be of similar importance (i.e., coefficient estimates were similar at around 0.9 as were 95% CI coverage), while the other predictors were ambiguous (95% CI crossed zero), and LASSO shrunk their coefficients to zero. Thus, moving from a low to a high value for both EVI and Ca corresponded to a positive effect of about 0.9 standard deviations in SOC stock. For surface SOC concentration (Fig. 3-5b), EVI, elevation, and calcium, and soil fertility were all retained by LASSO, and EVI was clearly most important. Higher values of EVI, Ca, and fertility positively correlated to greater SOC concentration, while higher elevations corresponded to lower SOC concentration. By contrast, in the 5-15 cm depth fraction (Fig. 3-5c), EVI was still statistically significant but had a smaller estimated effect size (0.5) than Ca availability (1.35) and was similar to pH in importance. In that model, LASSO shrunk pH to zero but retained both EVI and Ca.

Comparing cross-validated $R^2$ among our selected models with and without EVI, we found that inclusion of EVI enhanced the (out-of-sample) model fit for both the SOC stock (0-15cm), and the surface SOC concentration by 17% and 7% of variance explained, respectively (Fig. 3-6 a-d). These improvements corresponded to relative improvements of 74% and 21% in $R^2$, respectively. By comparison, inclusion of EVI alongside pH and Ca in the 5-15 cm model only marginally increased out-of-sample model performance (Fig. 3-6 e-f). Overall, our LASSO models explained between 40-46% of variance under leave-one-out cross-validation.

**Discussion**

Across grazed subtropical pastures we found that a long time series of vegetation greenness data significantly enhanced predictions of SOC stocks. EVI was a crucial predictor for total SOC stocks because its addition to our model improved the out-of-sample predictive fit by 74% relative to a model containing only elevation and edaphic factors. Moreover, EVI was more important than
elevation and edaphic factors in explaining surface SOC concentrations (0-5 cm), and played a greater role in improving the out-of-sample predictive fit for surface SOC compared to deeper SOC (5-15 cm). In contrast, a short time interval of EVI (2-year mean) failed to deliver any discernable predictive power (contrary to Yang et al. 2008 but consistent with Vasques et al. 2010). The significant improvements in predictive power arising from the use of a long time-series of remote sensing data demonstrates that across a relatively homogeneous landscape significant spatial variation in SOC stocks can be related to variations in long term vegetation greenness. Finally, when we quantified the relative predictive value of different dates across the entire time series, we found that the coupling of EVI and SOC stocks was highly stochastic across time. In total, our results demonstrate the value of leveraging recent computational advances to acquire and process long time series remote sensing data for the purposes of improving ecosystem SOC predictions.

As we hypothesized, EVI was a stronger predictor of surface SOC than deeper SOC, and a different suite of factors best predicted surface compared to deeper SOC. A stronger coupling between pasture EVI and surface SOC concentrations could arise for at least two, non-exclusive reasons: 1) higher EVI implying a greater rate of plant litter inputs, which concentrate in the upper 5 cm of soil, or 2) upper 5 cm SOC/SON stocks being more significant for predicting nutrient mineralization and hence grass production than deeper stocks. Moreover, both processes could be reinforced in a positive feedback cycle. Targeted experimental fieldwork clearly would be necessary to disentangle these causal pathways. For instance, ion-exchange resin membranes (Durán et al. 2013) could be deployed across the landscape to assess whether net mineralization of N and P related to total SOC stocks or pasture production and consequent spectral properties. Despite less predictive power with greater depth, mean EVI was equivalent to Ca as the most important predictor
of total measured SOC stocks in the 0-15 cm fraction, suggesting great potential utility in estimating variation in SOC across management relevant scales (10’s-1000’s of hectares).

Aside from EVI, the best predictors for surface SOC pools were elevation and Ca, while for deeper SOC pools, soil-extractable Ca appeared to be of over-riding importance. The importance of elevation at shallow but not deeper depths is likely related to soil water distribution given that we observed development of a muck horizon in low-lying wet pastures. By contrast, at depth, higher pH values predicted lower SOC (although LASSO shrunk the pH coefficient to zero), whereas higher Ca was positively associated with SOC at both depths, a contrast that is somewhat counter-intuitive. Soil pH has many well-known effects on microbial activity and function, and lower pH can inhibit microbial decomposition of SOC (Kemmitt et al. 2006). The consistent and strong importance of Ca for all responses, but particularly for 5-15 cm SOC, is striking. Since this relationship only existed for calcium and not for any other of the cations or for phosphorus, autocorrelation between SOC stocks and cation/anion-exchange capacity alone seems unlikely to drive the observed relationship. Rather, it may be that Ca plays an underappreciated role in stabilizing SOC in these soils through mineral-organic complexation (Fornara et al. 2010, Clarholm et al. 2015, Keiluweit et al. 2015), a possibility that deserves to be tested experimentally.

In this ecosystem, we found evidence of significant inter-annual variability in the coupling of vegetation phenology and SOC pools. EVI from some years in isolation delivered almost the same predictive power as the time series as a whole, whereas EVI from others years had almost no correlation. A primary utility of long time series is to smooth out any sampling effects that could arise from using only a single or few years of data as a composite measure. For instance, if we had averaged over an arbitrary 4-year time window with, for example, years 11-14 of the time series, our predictive power would be extremely low, whereas years 21-24 would deliver excellent predictions.
The source of inter-annual variability in this system is unknown, but perhaps relates to climatic factors (e.g., duration and intensity of drought) or complex interactions of climate with landscape processes such as grazing and fire. Future work should investigate the generality of patterns within and across land-uses in grazing landscapes. In the meantime, given the stochasticity in EVI-SOC relationships, we encourage further research to develop and analyze multi-decadal time series as a best practice. Fortunately, the advent of Google Earth Engine and cloud computing make the difference in difficulty between acquiring, for example, 5 years and 30 years of data, essentially trivial.

The correlation between EVI and SOC stocks could be due to higher primary productivity (indexed by EVI) driving higher SOC stocks, or higher SOC stocks driving greater productivity, or both. The high predictive power of certain individual years in our EVI time series (e.g., years 11-14) favors the latter possibility. Although the survey design of the present study precludes definitive disentanglement of these causal pathways, note that for the purpose of predicting SOC, both causal pathways should strengthen a positive association between EVI and SOC. Another major challenge in using satellite-derived vegetation indices to link vegetation and SOC pools is that recent empirical and theoretical work suggests that SOC may primarily originate from root system production and turnover (Rasse et al. 2005). However, the relationship between green leaf area and root production in grazed grasslands is complex, especially over short timescales where defoliation due to grazing or haying temporarily removes green leaf area and potentially alters root:shoot allocation patterns (Briske and Richards 1995, Dawson et al. 2000). Thus, future work will require more extensive experimentation to understand how vegetation indices may relate to variations in above/belowground allocation patterns.
Leave-one-out cross-validation verified that a long time series of EVI is a powerful predictor of total SOC stock and surface SOC pools in this ecosystem. Likewise, penalized regression via LASSO (Tibshirani 1996, Friedman et al. 2010) retained EVI as a predictor across all depths. We suggest that these findings have at least two practical implications for predicting SOC at management relevant scales. Most obviously, future work with geostatistical models (e.g., Vasques et al. 2010) should acquire the longest time-series possible for EVI and/or NDVI for use as a spatial covariate, rather than continue to utilize only short time interval summaries of 1 or 2 years. However, in assessing the overall (out-of-sample) fit of our best model it was clear that some significant sources of variation were unexplained. While there are no meaningful variations in climate or clay+silt content across our study site, it is worth noting that our best proxy of soil moisture (LiDAR elevation) is not perfect, in large part because ranch water management (i.e., drainage and sub-surface irrigation, Swain et al. 2013) can occasionally over-ride elevation in determining soil moisture at this site. More importantly, just as previous work has incorporated remote sensing derived vegetation indices into models of plant and pasture production (e.g. Hill et al. 2004), we suggest that future work could improve estimates of SOC by utilizing these unprecedented datasets to parameterize ecosystem carbon models (e.g. CENTURY Parton et al. 1993, or a more modern microbially-driven model such as MIMICS, Wieder et al. 2014) to estimate variability in SOC across space and evaluate differential spatio-temporal trends. For example, given a model and field data linking EVI/NDVI to plant productivity, a spatially-explicit process-based SOC model could be run using 40 years of variable input rates (i.e., net primary production) across the study site(s) of interest as predicted by the EVI/productivity model in each individual Landsat pixel. A spatially-resolved hydrological model also could be included to better constrain variable rates of decomposition across the landscape. We argue that integration of spectral data into process models is
a promising path toward generating more accurate predictive surfaces of SOC at management-relevant spatial scales.

Based on our results, we encourage greater integration of vegetation spectral data into ranch management. First, given the robust link between greenness metrics and pasture productivity (e.g. Hill et al. 2004), EVI maps such as we present in Figure 1 could provide insight into spatial patterns of productivity across large management operations. Understanding spatial variations in EVI could enable managers of pastoral systems to target grazing in more productive areas and apply appropriate management to areas with less production, an application of “precision agriculture” concepts that are more often deployed in higher-value commodity production (e.g., Lee and Ehsani 2015). Second, as ecosystem scientists improve our mechanistic understanding of the linkages between productivity and SOC stocks in these systems, similar spatially-explicit renderings of EVI data could prove useful for monitoring and predicting future SOC. If confirmed by subsequent experimental investigation, our finding that calcium availability is an independent driver of SOC suggests that increased fertilization with this element (e.g., via lime or gypsum applications) may be a cost-effective approach to enhancing SCS in addition to providing other agronomic benefits (e.g., pH amelioration). Although the observational design of our present work precludes strict estimation of causal effects, we note that the soils in the upper ranges of soil-extractable Ca were associated with 0.75 standard deviation higher SOC stocks, representing an additional 10 tons of C per hectare.

Overall, we found strong evidence that remote sensing of long-term vegetation EVI can be critical for predicting SOC. In contrast to previous work, these data did not enhance predictive power by discriminating coarse vegetation types (as in large landscape transects such as Yang et al. 2008), but instead reflect deeper relationships between pasture green leaf area and SOC. The relationship between EVI and SOC appears to have a high degree of inter-annual variability, a
finding that calls for investigation. Nevertheless, remote sensing of vegetation can help scale predictions of SOC from plots to management-relevant units. Accordingly, we call for deeper and more extensive testing of the utility of long time series of remotely sensed vegetation indices for predicting SOC stocks across various ecosystems. These improvements in efficient SOC estimation may help promote adaptive management of grazing lands to optimize SCS in parallel with other ecosystem services such as biodiversity maintenance and livestock production.

Figure 3-1. Map showing spatial layout of soil sampling plots. Dot sizes are proportional to observed size of measured SOC stock (in units of kg C m$^{-2}$ in 0-15cm depth fraction), ranging from 1.78 kg C m$^{-2}$ to 6.34 kg C m$^{-2}$. Background map contains mean EVI, with lighter yellow colors indicating higher EVI, and darker blue colors indicating lower EVI (ranging from 0.34 to 0.42). Note that the distinct patches of dark blue represent either wetlands or tree hammocks, both of which we deliberately avoided in our soil sampling where we focused on planted pasture.
Figure 3-2. Analysis of EVI time series from soil sampling plots. a) Spatial average of EVI for all 57 plots across the time series. b) Linear temporal trends for each plot, and c) Estimated seasonal phenology for each point from first order Fourier Series expansion.
Figure 3-3. Assessing univariate regression models in terms of model fit ($R^2$), for SOC stock 0-15cm (a,b), SOC concentration 0-5 cm (c,d), and SOC concentration 5-15 cm (e,f), comparing a snapshot approach to EVI (simple mean of the most recent 2 years), versus taking mean of the full (28 year) time-series.

Figure 3-4. Exploratory analysis of inter-annual stochasticity in relationship between mean EVI and SOC measured in 2014. Plot of model fit ($R^2$) using each year’s EVI summary to predict surface SOC concentration.
Figure 3-5. Coefficient plot from multiple regression models comparing the relative importance of weighted mean EVI (0-28 years) to our other landscape (elevation), and edaphic (soil pH, P, K, Ca, and Mg) variables for SOC stock 0-15 cm a), SOC concentration 0-5 cm b), and SOC concentration 5-15 cm c). Predictors were all standardized to same scale prior to analysis, and coefficients represent estimates of effect size in units of standard deviation of the response variable. We report point estimates with a black dot surrounded by 50% (solid lines) and 95% (dashed lines) confidence intervals resulting from ordinary least squares regression. Coefficients with 95% CI that do not overlap zero can be considered statistically-significant. In addition, we overlay red squares to indicate the point estimates obtained by using the LASSO to shrink the estimates for covariates with limited predictive power. Finally, we report both adjusted $R^2$ from our multiple regression models estimated via least squares (upper left corner) and out-of-sample $R^2$ from the LASSO regression, which corrects for over-fitting rampant with unconstrained least squares regression.
Specifically, we compared predictive power for models with and without our weighted EVI predictor, for 0-15 cm SOC stock (a,b), 0-5 cm SOC concentration (c,d), and 5-15 cm SOC concentration (e,f). Predictions were generated via leave-one-out cross-validation. We assess the contribution of EVI as a predictor based on improvements in the cross-validated model fit metric ($R^2$). Conversely, over-fitting would be indicated by a decline in cross-validated $R^2$. 

Figure 3-6. Out-of-sample predictive model assessment for LASSO models developed above.
CHAPTER 4
GRAZING ENHANCES BELOWGROUND CARBON ALLOCATION, MICROBIAL BIOMASS
AND SOIL CARBON IN A SUBTROPICAL GRASSLAND

Background

Due to rising concern about anthropogenic climate change (Mann & Gleick, 2015), there is increasing demand for greenhouse gas mitigation services from agricultural land, especially soil carbon sequestration (Lal, 2010; American Carbon Registry, 2014). Globally, pastures and rangelands occupy more than 22% of ice-free terrestrial land area and account for a similar fraction of total soil organic carbon (SOC, Scurlock & Hall, 1998; Ramankutty et al., 2008), but they also contribute substantially to atmospheric carbon pools through loss of SOC (Lal, 2004; Foley et al., 2011). Strategic management of pastures and rangelands can enhance sequestration of SOC (Conant et al., 2001), reverse historic declines, and potentially offset a significant portion of fossil carbon emissions. Although there is robust literature on the role of large herbivores in shaping grassland plant composition, structure, and productivity (McNaughton, 1984; McNaughton et al., 1997; Fuhlendorf & Engle, 2001; Fuhlendorf et al., 2012), there remains considerable uncertainty about how large grazers affect belowground carbon allocation (McNaughton et al., 1998; Derner et al., 2006; Augustine et al., 2011), and SOC stocks (McSherry & Ritchie, 2013).

Across various ecosystems, grazing has been associated with higher, lower, and no difference in SOC compared to ungrazed areas (Milchunas & Lauenroth, 1993; Derner et al., 1997, 2006). Despite the vigorous debate over how best to manage livestock grazing to achieve both ecological and economic sustainability and profitability (Provenza, 2008; Kothmann et al., 2009; Teague et al., 2011, 2013; Bestelmeyer & Briske, 2012), there are surprisingly few studies on the long-term impacts of grazing on SOC. In a meta-analysis of grassland SOC studies with controlled grazing/no-grazing treatments, McSherry and Ritchie (2013) identified several patterns that help account for conflicting results on grazing-SOC relationships. Somewhat contrary to an earlier hypothesis that
grazing effects on grassland SOC may only be positive where precipitation is low (Derner & Schuman, 2007). McSherry and Ritchie (2013) found an interaction with precipitation and soil texture whereby higher precipitation on coarse-textured soils was associated with a positive effect of grazers on SOC. By contrast, higher precipitation on fine-textured soils was associated with losses of SOC under grazing. In general, C4 grasslands appear to sequester SOC in response to grazing whereas C3 grasslands lose SOC (Derner et al., 1997, 2006; McSherry & Ritchie, 2013), with grazing-driven shifts in plant composition to more C4 grasses often credited for cases where grazing has increased SOC (Derner et al., 2006; Piñeiro et al., 2010). However, the mechanisms underlying these patterns are unclear, making it difficult to generalize grazing-SOC patterns globally, especially to understudied tropical and subtropical grasslands (McSherry and Ritchie 2013). Additionally, lack of mechanistic insight precludes development of effective grazing management strategies across a range of environments to optimize SOC.

Grazing may influence SOC directly via effects on plant carbon allocation and soil resource availability, and indirectly via effects on long-term plant community composition (Piñeiro et al., 2010). In the short term, root carbon allocation is often lower under grazing in favor of rapid re-establishment of photosynthetic tissue (Briske & Richards, 1995; Dawson et al., 2000), but the long-term effects of grazing on belowground biomass vary considerably (Milchunas & Lauenroth, 1993; Bardgett et al., 1998; Hafner et al., 2012). As such, root biomass may be critical for sustaining SOC (Rasse et al., 2005), especially in grasslands where aboveground tissue is lost to grazing or fire.

Grazing may also influence the partitioning of root C allocation between synthesis of new root tissue and loss of C through fine root exudation. Fine root exudation can increase in the hours and days following grazing/defoliation (Hamilton & Frank, 2001; Hamilton III et al., 2008; Augustine et al., 2011), however long-term implications of grazing for fine root exudation are unknown. In general,
the degree to which long-term grazing effects can be attributed to plant composition shifts (McSherry & Ritchie, 2013), plant carbon assimilation, belowground carbon allocation (BCA), or soil microbial processing is unclear.

Grazing effects on SOC depend on plant carbon allocation, and also interactions between carbon inputs, soil microbes, and the soil mineral matrix. Traditional models of SOC turnover emphasize the importance of biochemically recalcitrant fractions of litter for accumulation of SOC, whereas recent attention has focused on the role of labile carbon inputs in stimulating microbial growth and contribution to long-term pools of SOC (Schmidt et al., 2011; Bradford et al., 2013; Cotrufo et al., 2013). Considerable evidence suggests that the physically protected SOC pool is dominated by simple organic molecules, and is not composed of the complex supra-molecular structures previously thought responsible for long-term stabilization of SOC (Kleber et al., 2007; Prescott, 2010; Schmidt et al., 2011; Stockmann et al., 2013). Thus, a large proportion of stabilized SOC may consist of microbial products that accumulate during litter decomposition (Grandy & Neff, 2008), or that result from direct input of labile carbon in the form of fine root exudates (Jones et al., 2009; Paterson et al., 2009; Strickland et al., 2012; Bradford et al., 2013). Moreover, labile carbon inputs stimulate microbial growth more efficiently compared to more recalcitrant litter, and hence should optimize SOC accumulation by virtue of greater microbial necromass entering into stabilizing associations with the soil mineral matrix (Cotrufo et al., 2013; Kallenbach et al., 2015). These complex interactions among recalcitrant/labile carbon inputs, microbes, and physical versus biochemical protection of SOC have been formalized into recent process-based computational models for predicting SOC, such as the MIcontral-MInderal-Carbon-Stabilization model (Wieder et al., 2014). Although the importance of microbial carbon in regulating SOC in agricultural systems
has received some attention (Kallenbach et al., 2015), studies that specifically evaluate grazing impacts on SOC in light of recent findings are needed.

Here, we assessed the effects of grazing on overall BCA, allocation to root tissue versus exudates, microbial biomass, and SOC pools across a system of long-term grazing exclosures and nearby ungrazed plots in a subtropical pasture system in Florida, USA. We combine an in situ $^{13}$C-CO$_2$ pulse-chase experiment to resolve patterns of carbon allocation within plants and soil microbes, with soil surveys inside and outside of grazing exclosures to quantify SOC pools and characterize their isotopic and molecular composition. We focus specifically on the role of lignin as a proxy for plant-tissue inputs in contributing to SOC (Thevenot et al., 2010). The soils in this study were extremely sandy (~ 97%), similar to the vast majority of pastureland in south central Florida (Silveira et al., 2011), thus, we expected low capacity to physically stabilize SOC (Six et al., 2002; Stockmann et al., 2013). On the other hand, recent work on similar soils in south Florida has shown that the mineral-associated SOC fraction constitutes a disproportionate fraction of the total SOC, despite clay and silt accounting for only a few percent of mineral mass (Silveira et al., 2014). As such, it is possible that variations in microbial carbon sequestration could explain variations in SOC responses to grazing.

We framed our investigations around testing two general pathways by which grazing may impact SOC pools, and we infer the impact of grazing by comparing grazed pasture to adjacent pasture inside long-term grazing exclosures. Given previous observations that cattle grazing enhances microbial biomass in these systems (Wang et al., 2006), we hypothesized that grazing stimulates allocation of carbon into the rhizosphere, especially in the form of fine root exudates, at least partially accounting for greater microbial biomass. Therefore, we speculated that grazing-induced changes in this pathway of labile carbon input could lead ultimately to greater accumulation
of microbial necromass in these soils, thus promoting SOC accumulation over the long term (hereafter the “exudate-microbe pathway”). By contrast, grazing effects on SOC may be best accounted for by impacts on fine root biomass and turnover, given the substantial evidence that root litter inputs are conserved in SOC more effectively than shoot litter (Rasse et al., 2005). Thus, if grazing promotes root system production, hence root litter deposition, we hypothesized that this effect would be associated with larger SOC pools, and vice versa (the “root litter pathway”). Critically, neither pathway requires that total NPP be greater in response to grazing (McNaughton, 1983; Briske & Richards, 1995), only that grazing induce alterations in absolute root system biomass or exudation patterns.

Methods

Study Site

This study was conducted at the MacArthur Agroecology Research Center (MAERC) located in Lake Placid Florida, USA just north of Lake Okeechobee (lat 27°09’N; long 81°12’W). MAERC operates a full-scale commercial cow-calf ranch (~3000 head) in order to study ecological aspects of cattle ranching, a dominant land use in the Northern Everglades watershed (Bohlen et al. 2009, Silveira et al. 2011). Average annual precipitation is around 1.3 m, mostly falling in the summer rain season (May-October). Mean annual temperature is 24°C. MAERC combines both planted Bahiagrass (P. notatum Fluegge) pastures and semi-native pastures, although here we focus on the planted pasture due to their greater agronomic and regional relevance. Like on most ranches in S. Florida, the soils are mostly from Spodosol and Entisol orders and are uniformly coarse-textured with clay+silt fraction accounting for 2-3% of total mineral mass while various grades of sand account for the remainder (i.e. no significant stone content) (Silveira et al. 2014b).
Overview of Field Studies

To study the impacts of grazing, we analyzed plant, microbial and soil responses to grazing exclusion across long-term 10 m x 10 m grazing exclosures at MAERC. Four exclosures were established in a paired-plot design in Bahiagrass pastures in 2002, and have since undergone various pathways of plant succession, with large consequences for plant and soil carbon pools (Julia Maki, unpublished data). In three out of the four exclosures, sufficient Bahiagrass remained inside to randomly sample for soil properties while holding plant composition constant (i.e. comparing soil under Bahiagrass inside the exclosure to soil under Bahiagrass outside exclosures in grazed patches). At the site of one of the exclosures, sufficient Bahiagrass remained to permit a full-scale replicated field experiment to resolve variations in carbon allocation above and belowground using stable isotope $^{13}$C pulse-chase methodology (as in e.g. Hafner et al. 2012). Thus, to test our hypotheses about the impact of grazing on BCA and SOC stocks in the context of subtropical pasture at MAERC, we combined two field studies, a background survey of soils in each of the three exclosures, and a replicated pulse-chase experiment at one exclosure.

Background Soil Survey

To obtain information about the impacts of grazing exclusion on SOC and soil organic nitrogen (SON) stocks across sites we randomly sampled three locations inside and outside of each exclosure to a depth of 5 cm using a hammer core (AMS 5.08 cm x 15.24 cm Signature SCS Complete/354.26). Soils were oven-dried, sieved (2 mm), and analyzed for %C/N, d$^{13}$C/d$^{15}$N, and total lignin phenols (more details below).

Pulse-Chase Experiment

At the site of one exclosure, we randomly located 4 1-m$^2$ plots inside and outside the grazing exclosure to conduct a $^{13}$C-CO$_2$ pulse-labeling experiment. The purpose was to measure how long-term grazing exclusion impacted the allocation of carbon between above and belowground plant
tissues, while simultaneously quantifying fine root exudate recovery in the microbial biomass. Specifically, we tested whether grazing resulted in greater absolute and/or proportional allocation of carbon into root tissue or fine root exudates, while also testing whether grazing affected fine root exudation independently of its effects on root system biomass.

Pulse-labeling occurred over a two week period in early September 2016. For each pulse-labeling event, we installed a wooden frame base, fitted with a forged steel cladding that was trenched 5 cm into the soil to prevent gas exchange from outside the plot. A 1m³ plexiglass chamber was placed on the base and all seams were sealed using a combination of pipe insulation foam and duct tape to ensure no air infiltration. The chamber was fitted with a closed-loop air conditioning system to maintain ambient temperature inside the chamber and humidity low enough to prevent condensation and fogging of chamber walls (to maximize available PAR, more details of chamber design and operation in Appendix C1).

**Pulse Methods**

Each labeling event lasted a total of three hours. We introduced 430 mg of $^{13}$C-C as CO$_2$ by reacting 3 g of 99% $^{13}$C-NAHCO$_3$ with 10% acetic acid and flushing the CO$_2$ into the chamber through plastic tubing (Bev-A Line Tubing, United States Plastic Corp., Lima, OH) using a vacuum pump. To generate a more consistent supply of $^{13}$C-CO$_2$ to during each run, we split the 3 g into two 1.5 g doses and added the second dose after 1.5 hours. We monitored $^{12}$C-CO$_2$ levels inside the chamber as a proxy for photosynthesis and respiration with an EGM-3 environmental gas monitor (PP Systems, Cambridge, MA), while PAR was tracked with an ACCUPAR LP-80 photosynthetically active radiation (PAR) meter (Decagon Device Inc., Pullman, WA, USA).

**Chase Methods**

Immediately after each pulse, we sampled aboveground biomass to quantify initial label uptake due to photosynthesis. Then, for each plot, we performed successive harvests of plants and
soils at 2 days, 7 days and 32 days post-pulse, separately resolving shoots, rhizomes, roots, and soils. For the 2 day and 7 day harvest, we included two replicates per plot, and then harvested one final replicate at 32 days due to space constraints. For shoots, we harvested 7.5-cm X 100-cm swaths to average over as much spatial heterogeneity as possible. Likewise, for belowground pools, each replicate consisted of four cores taken to 5-cm depth along each harvested swath and then combined into one aggregate sample. Shoots were immediately placed in an oven to dry at 60°C, while field moist soils were sieved to separate roots and rhizomes from soil. Roots and rhizomes were then rinsed and placed in oven at 60°C to dry until constant mass. After weighing, all plant samples were homogenized in a Wiley mill (Mini Wiley Mill, Thomas Scientific, NJ) prior to analysis.

After wet sieving, the soil was divided into two samples. One half was sent to the Strickland Laboratory at Virginia Tech University for extraction of microbial biomass. The other half was dried to constant mass at 60°C. At the end of the experiment, all oven-dried soil samples from each plot were aggregated, and re-sampled prior to analysis. Thus, we have 4 replicates inside and outside the grazing exclosure. Note that each pooled sample is expected to represent its plot well as an aggregation across 20 soil cores in an area of only 1m². After drying to constant mass, soils were homogenized in a ball mill (Win-L-Bug, Dentsply) prior to analysis. Samples were then analyzed for the same soil parameters as in the background survey: %C/N, d¹³C/d¹⁵N, and lignin phenols.

For all plant and soil samples, we analyzed %C/N and d¹³C/d¹⁵N with a Carlo Erba NA1500 CNS Elemental Analyzer (EA) coupled to a Thermo Finnigan DeltaPlus XL ratio mass spectrometer at the University of Florida stable isotope laboratory.

¹³C Label Computations

To quantify patterns of carbon allocation between shoots, roots, rhizomes and microbes we combined measured masses of carbon with their delta values to generate a measure of “¹³C label”,
i.e. a quantification of label mass recovery in each pool. First, we converted all delta values into atom %, as:

\[
\text{atom} \% = R_{std} \left( \frac{\delta^{13}C_{samp}}{1000} + 1 \right) / \left( 1 + R_{std} \left( \frac{\delta^{13}C_{samp}}{1000} + 1 \right) \right)
\]  

(4-1)

Then, we multiplied the observed mass of carbon in a pool by the difference between the atom % in the enriched pool and the atom % of a background, un-enriched pool as follows:

\[
^{13}\text{C label} = C_{\text{pool}} \cdot (\text{atom}\%_{\text{labeled}} - \text{atom}\%_{\text{background}})
\]  

(4-2)

This metric of \(^{13}\text{C label}\) allows us to quantify patterns of carbon allocation within plants and between plants and microbes, and naturally accounts for variation in biomass carbon observed in various pools.

**Microbial Biomass and Isotope Quantification**

We measured microbial biomass using the modified slurry chloroform fumigation and extraction (sCFE) method (Fierer and Schimel 2002, 2003). To determine microbial biomass carbon and delta \(^{13}\text{C}\), we lyophilized (i.e. freeze-dried) fumigated and unfumigated extracts, and analyzed their %C and d\(^{13}\text{C}\) with a Carlo Erba NA1500 CNS Elemental Analyzer (EA) coupled to a Thermo Finnigan DeltaPlus XL ratio mass spectrometer at the University of Florida stable isotope laboratory. As usual, we compute the mass of microbial C using the difference between fumigated and unfumigated samples. To deconvolute the isotopic signature of the microbial biomass pool from the total extractable pool we used the mass-balance equation from Dijkstra et al. (2006),

\[
\delta^{13}C_{\text{mic}} = \left( \delta^{13}C_{\text{fum}} \cdot C_{\text{fum}} - \delta^{13}C_{\text{ex}} \cdot C_{\text{ex}} \right) / C_{\text{mic}}
\]  

(4-3)

where \(C_{\text{fum}}\) represents the mass of C measured in the fumigated samples (including both microbial biomass and extractable carbon, i.e. DOC), and \(C_{\text{ex}}\) is the extractable carbon. After computing the \(\delta^{13}\text{C}\) for microbial biomass, we converted to atom % using equation 1 and estimated isotopic enrichment due to pulse-labeling with equation 2.
Quantification of Exudation

Root exudation of recent photoassimilates in graminoids is a rapid process, normally reaching a maximum within 12-24 hours (Johnson et al. 2002, Kuzyakov and Gavrichkova 2010, Bradford et al. 2012, Kaiser et al. 2015). Thus, we consider recovery of label $^{13}$C at 48 hours our best index of exudation rates in pulse-labeled plots. However, observed $^{13}$C label is a significant underestimate of true exudation rates because chloroform fumigation-extraction is known to be only about 50% efficient at extracting microbial C (e.g. correction factor in Bradford et al. 2012), and because we cannot account for variations in microbial growth yield efficiency (GYE i.e. fraction of exudates incorporated into microbial cells rather than lost to respiration, generally estimated around 0.6 for glucose Thiet et al. 2006, Blagodatskaya et al. 2014). Thus, we assume that GYE = 0.6 in all plots.

Because our goal was to study fine root exudation after long-term grazing removal, we first present and analyze our calculated $^{13}$C label recovery in microbes. We then estimate total exudation as

$$C_{\text{exudate}} = ^{13}C_{\text{label}} \times (1/0.5) \times (1/0.65)$$

and compute proportion of BCA of exudates as,

$$\text{Exudate}_{\text{frac}} = C_{\text{exudate}}/(C_{\text{root}} + C_{\text{exudate}})$$

Soil Lignin Extraction

We extracted lignin-phenols from all soil samples using CuO and analyzed using gas chromatography in the Bianchi Laboratory at the University of Florida (Hedges and Ertel 1982, see Shields et al. 2016 for more details). All three major families of lignin phenols (vannilyl, syringyl and cinnamyl, VSC) were quantified and normalized both to unit dry mass of soil ($VSC_{\text{soil}}$) and to 100mg-OC (carbon-normalized lignin or $VSC_{\text{OC}}$). Regressing SOC concentration against $VSC_{\text{soil}}$ informs on the extent to which variations in SOC concentration are coupled to input and retention of plant tissues, whereas $VSC_{\text{OC}}$ is used to infer variations in the relative importance of plant inputs in
sustaining observed SOC pools between our treatments. Moreover, comparing VSCoc between plants and soils indexes the degree to which non-plant (i.e. microbial) sources are likely contributing to the SOC. Finally, we examine Ad:Alv (acid-aldehyde ratio of the vannillyl family), which reflects decomposition status of the lignin and provides additional information on the balance between input and decomposition rates across our treatments (Jex et al. 2014). Finally, we analyzed lignin in pooled samples of plant tissue, separately resolving shoots, roots and rhizomes from both grazed and excluded plots. Since lignin phenols are extracted from the most recalcitrant fraction of plant litter, differences in the carbon-normalized lignin concentrations between plant tissue sources and soils can inform on the overall contribution of decomposed plant litter versus microbial sources in the bulk SOC.

**Statistical Analysis**

**Plant and microbial pools**

To estimate the effect of grazing exclusion on plant and microbial biomass pools in the pulse-chase plots, we parameterized Bayesian general linear mixed effects (i.e. hierarchical) models. We modeled all responses with a normal sampling distribution. We constrained the mean of the sampling distribution to be a function of both a (fixed) treatment indicator for grazing treatment (i.e. grazed/un-grazed), and also included varying intercepts for both harvest day and plot, to account for the spatial and temporal structure of observations (Gelman and Hill 2007). Moreover, to better account for any systematic differences between the plots inside and outside the exclosure we let both data-level (i.e. sampling distribution) and plot-level variance components differ based on treatment (i.e. grazing indicator) (Gelman and Hill 2007). In practice, this strategy allows the variation both among and within plots to systematically vary inside versus outside the exclosure, facilitating more accurate and efficient estimation of our main treatment effect. In addition to gains in statistical efficiency, this specification also accounts for the possibility that plots inside the exclosure may vary
as a function of several unmeasured/unknown covariates beyond the simple presence/absence of grazing. For the binary (0/1) treatment indicator, we assigned the reference 0 value to the grazed plots, and 1 for the exclosure treatment. Our coefficient for treatment effect therefore represents the estimated effect of grazing exclosure, and we thus infer the effect of grazing by the effect of its removal from the system. Furthermore, each response variable was estimated twice—first on its original scale of measurement, and second after standardization onto a unit normal scale to facilitate inter-comparison of treatment effects among various response variables.

All coefficients were assigned weakly informative priors to improve computational efficiency and stabilize inference (e.g. Gelman et al. 2008). For the treatment coefficients, we set the prior scale based on observed scale (SD) of data multiplied by 5 (for the intercept, i.e. baseline) or 2.5 (for the effect), both of which constrain estimation to the same order of magnitude but are relatively uninformative within that range. For the hierarchical effects, we set the hyper-prior for scale based on the observed data scale, but within a fat-tailed Student T distribution with 4 degrees of freedom, which allows for large deviations from the prior where supported by data. Finally, the components of the sampling model variance were assigned Normal(0,5) priors which are effectively uninformative over the entire conceivable range of values for sampling variance.

In statistical notation, our basic model has the following form:

\[
y | \beta_0, \beta_g, \omega_0, \omega_1, \eta_{\text{day}}, \eta_{\text{plot}} \sim \text{Normal}(\beta_0 + \beta_g \times \text{EXC} + \eta_{\text{day}} + \eta_{\text{plot}}, e^{\omega_0 + \omega_1 \times \text{EXC}})
\]

\[
\eta_{\text{day}} | \sigma_{\text{day}} \sim \text{Student}_T(0, \sigma_{\text{day}}) \tag{4-6}
\]

\[
\eta_{\text{plot}} | \sigma_{\text{plot-g}}, \sigma_{\text{plot-e}} \sim \text{Student}_T(0, \sigma_{\text{plot-g}}, \sigma_{\text{plot-e}})
\]

\[
\sigma_{\text{day}} \sim \text{Student}_T(0, \pi_{\text{day}})
\]

\[
\sigma_{\text{plot-g}}, \sigma_{\text{plot-e}} \sim \text{Student}_T(0, \pi_{\text{plot}})
\]

\[
\beta_0 \sim \text{Normal}(0, \pi_{\text{int}})
\]
\[ \beta_1 \sim Normal(0, \pi_g) \]
\[ \omega_0 \sim Normal(0, 5) \]
\[ \omega_1 \sim Normal(0, 5) \]

where \( y \) is our response variable, \( \beta_0 \) is the model intercept (i.e. reference value of the grazed treatment), \( \beta_g \) is the coefficient for treatment effect (of exclosure), EXC is the 0/1 indicator for Exclosure, \( \eta_{day} \) are the random effects of harvest day (post-pulse), \( \eta_{plot} \) are the random effects of plot identity, \( \{ \omega_0, \omega_1 \} \) are the coefficients for sampling variance model (constrained to be positive via the log-link), \( \sigma_{day} \) and \( \sigma_{plot} \) are the variance components for the random effects of day and plot with hyper-priors \( \pi_{day}, \pi_{plot}, \) and \( \pi_{int} \) and \( \pi_{g} \) are priors for treatment effects.

We report both standardized and unstandardized estimates of treatment effects using the posterior mean calculated from 8000 MCMC samples, along with their standard errors and 95% uncertainty intervals (Appendix C-3 and Table 1).

**Fine root exudates**

To better understand the long-term effects of grazing on fine root exudation, we tested our estimates of exudation (based on \(^{13}\)C label' in the microbes 48 hours post-pulse) with a linear mixed effects model that included both a treatment indicator (for exclosure) and measured root biomass C as a continuous covariate. We fit this linear mixed effects model using the “lme4” (v1.1-12) package in R (v.3.3.2). We present fitted regression line and \( R^2 \) from these models.

**Soil properties**

We modified the Bayesian GLMM model described above to combine and analyze the soil data collected from both the pulse-chase plots and from the background survey of three exclosures. We added an indicator to identify whether the observed data-point was collected during the background survey, or as part of the pulse-chase experiment, eliminated the inapplicable random
effects of day and plot, added a random effect of site, and modified the sampling variance to also account for variations between background survey and pulse-chase plots, where the latter should have lower sampling variability due to averaging over many cores per plot.

All models were estimated using Hamiltonian Monte Carlo programmed in the Stan language (Carpenter et al. 2017) linked to R (v. 3.3.2, R Core Team) via the ‘rstan’ package (v.2.14.1). For each model we ran 4 chains of 2000 iterations each, except for the plant and microbial responses where we increased chain-length to 4000. In both cases, our target was to achieve effective sample size (Neff) > 1000 for all estimands of interest. All chains were monitored for convergence via use of the R_hat < 1.01 statistic, and absence of computational pathologies via the diagnostics built into Stan, and visual inspection of chains.

**Results**

**Plant Carbon**

We found a substantially larger pool (+75%) of shoot biomass C inside the grazing exclosure, 92.2 g m\(^{-2}\) compared to 52.9 g m\(^{-2}\) (Fig 4-1a). Despite this substantial difference in photosynthetic canopy, average shoot delta \(^{13}\)C post-pulse did not differ significantly (Fig 4-1b), although total label uptake trended higher for the exclosure plots (Fig 4-1c).

By contrast, plots inside the exclosure exhibited much lower root biomass C (-72%) of 279 g m\(^{-2}\) compared to 80 g m\(^{-2}\) (Fig 4-1d). Thus, overall root:shoot ratios are lower under grazing exclusion (1.2 compared to 5.3), a clearly substantial shift in plant biomass allocation priorities. Although root delta \(^{13}\)C values were not significantly different between grazed and excluded plots (Fig 4-1e), total label \(^{13}\)C enrichment was much greater in grazed plots where estimated recovery was 11.9 mg m\(^{-2}\) compared to 1.6 mg m\(^{-2}\) for excluded plots (Fig 4-1f).
**Microbial Carbon**

Microbial biomass C was twice as large in grazed plots compared to excluded plots, 0.37 mg g\(^{-1}\) versus 0.16 mg g\(^{-1}\) and was fairly consistent over the harvest dates (Fig 4-1g). We observed a spike in delta \(^{13}\)C at the two-day harvest, which was particularly evident in the grazed plots (Fig 4-1h). Additionally, grazed plots showed a larger enrichment of +8.4 permill compared to a smaller enrichment of +3.7 permill for exclosure plots. Thus, average \(^{13}\)C enrichment of the microbes in grazed plots was much larger (1.3 mg m\(^{-2}\) versus 0.2 mg m\(^{-2}\)) (Fig 4-1i).

**Exudation**

Our estimates of exudation varied from 4.91 mg m\(^{-2}\) in the grazed plots to 0.88 mg m\(^{-2}\) in the excluded plots. However, we found that root biomass was the stronger predictor of estimated exudation, and the treatment indicator was statistically insignificant after controlling for root biomass. Root biomass C explained 79% of the variance in exudation estimates (Fig 4-2a), while allocation of carbon into root tissue was highly correlated with exudation estimates (r = 0.82, Fig 4-2b). Overall, exudation estimates represented 40-50% of label recovery in roots (11.9 vs 4.91 mg m\(^{-2}\)), thus exudates may account for 25-30% of total C allocated into root systems.

**Soil Carbon and Nitrogen**

After pooling across both the background survey of three exclosures, and the plots included in the pulse-chase experiment, we found significantly less SOC (6.7% versus 8.5%) and SON (0.4% versus 0.5%) in the ungrazed plots (Table 4-1). Given consistent bulk density estimates inside and outside the exclosure this equates to ~ 22% lower SOC/SON stock after 15 years of grazing exclusion. At the same time, the delta \(^{13}\)C signature was more depleted in excluded plots (-2.73 versus -1.29 compared to plant and microbial reference value of -13.5), while the delta \(^{15}\)N was heavier (+2.05 versus +1.83) (Table 4-1).
Soil Lignin Markers

As a proportion of SOC (i.e. C-normalized) total lignin phenols were lower in the exclusion plots (4.26% versus 4.83%) (Table 1). The lower VS\textsubscript{SOC} in exclosure soils was consistent across all three major groups of phenols (vannilyl, syringyl and cinnamyl). By comparison plant source material was highly enriched in lignin with values ranging from 7.2-10.6%. Overall, lignin-phenol concentration (on a soil weight basis) explained nearly 93% of the variation in SOC concentration (Fig 3). At the same time, acid:aldehyde (i.e. Ad:Al\textsubscript{v}) ratios were significantly higher in the exclosure plots, although the effect size was small (0.53 compared to 0.59; Table 1).

Discussion

Our \textit{in situ} \textsuperscript{13}C pulse labeling of subtropical pasture revealed that long-term grazing exclusion resulted in significantly lower allocation of carbon to both new root tissue and fine root exudation. Lower carbon allocation into and through roots was associated with substantially less standing root biomass, microbial biomass, and lower SOC/SON stocks across a system of long-term grazing exclosures. Moreover, molecular characterization of soils revealed that SOC/SON stocks were closely coupled to plant tissue inputs across both grazed and excluded plots. Additionally, the higher proportional contribution of lignin to SOC with grazing suggests that a large fraction of the greater SOC pools was plant-derived. Thus, our results are consistent with the hypothesis that higher rates of root litter deposition account for the higher SOC observed under grazing in this system. Although we found that grazed plots had enhanced rates of fine root exudation, this pathway of carbon input appears to scale quite closely with standing root biomass, and does not appear to be the primary reason for increased SOC under grazing. Taken together, these results suggest that grazing C4 pasture grasses can promote root system production and turnover and thereby higher SOC/SON stocks.
We found little support for the hypothesis that labile carbon inputs (e.g. fine root exudates) play a unique role in mediating the impact of grazing on SOC through their effects on accumulation of microbial carbon. The impacts of grazing-stimulated fine root exudation depend crucially on the processes regulating SOC turnover in these grassland systems. In turn, SOC turnover is a function of complex interactions between microbial populations, organic substrates and the soil mineral matrix (Cotrufo et al. 2013, Wieder et al. 2014). Despite finding that grazed plots sustain more than twice the microbial biomass as excluded plots (consistent with previous data from other pastures at MAERC, Wang et al. 2006), the 28% larger SOC stock in the grazed plots contained roughly 13% more lignin per unit SOC. This strongly argues that much of the increase in SOC derives from plant tissue inputs (Thevenot et al. 2010), and thus is likely to be found more in particulate form rather than in stabilizing mineral-associations (Cotrufo et al. 2013). Additionally, across both grazed and excluded plots, lignin phenol concentration explained nearly 93% of the variance in SOC concentration. Although this molecular characterization of the SOC cannot by itself discriminate between various functional fractions of SOC, or inform on their relative turnover rates, it does strongly suggest that increased stabilization of microbial necromass (Kallenbach et al. 2015) is unlikely to be a primary mechanism underlying grazing-associated increases in SOC in this system.

Grazing dramatically alters plant carbon allocation in this system. Grazed plots allocated over 5X the C into root systems, and sustained a standing biomass stock more than 3X as large as excluded plots, resulting in a 4-fold amplification of root:shoot ratios. Consistent with Hafner et al. (2012), we also found significantly enhanced rates of rapid belowground assimilate allocation in grazed plots compared to long-term un-grazed plots. We also found that the overall flux of carbon as fine root exudates may represent as much as 25% of the total carbon allocated into the root systems, thus representing a quantitatively significant fraction of total soil C inputs. Previous literature has
documented increases in fine root exudation as a short-term (scale of days) response to grazing (Hamilton and Frank 2001, Hamilton III et al. 2008, Augustine et al. 2011), and suggested an adaptive role for this response as a nutrient acquisition strategy. While we did not test short-term responses to defoliation, our study strongly suggests that fine root exudation is more closely coupled to fine root biomass than to grazing status over long timeframes. Also, unlike the findings reported by Hafner et al. (2012), we observed a stark contrast in exudation rates even after controlling for plant species composition, comparing nearly monotypic stands inside and outside of a long-term grazing exclosure. This strengthens the conclusion that grazing per se is responsible for radically shifting plant carbon allocation priorities, with long-term consequences for ecosystem function including greater stocks of SOC and SON. Clearly, long-term impacts of grazing can occur in absence of significant plant composition shifts (Piñeiro et al. 2010), and our study suggests that grazing effects on SOC in C4 grasslands cannot necessarily be explained by simply increasing the proportion of C4 plants as has been suggested in some places (Derner et al. 2006, McSherry and Ritchie 2013).

Overall, our measured SOC concentrations (5-16%) are quite high, likely reflecting a combination of very high input rates and environmental constraints to microbial decomposition (Davidson and Janssens 2006) due to water-logging (i.e. anaerobiosis) during the summer wet season. On the other hand, our lignin decomposition status (Ad:Al) at 0.55 is in the middle range of what is expected for grasslands and croplands (Thevenot et al. 2010), suggesting that decomposition rates are not too seriously impeded. Given the generally accepted relationship between particle size fraction distribution and capacity to physically stabilize labile organic molecules such as microbial products (Grandy and Neff 2008, Wieder et al. 2014, Kallenbach et al. 2015), it would stand to reason that our coarse-textured soils (>97% sand) should contain little stabilized microbial
necromass, and that plant inputs should be predominantly represented in the SOC stock. Thus it is not surprising that our soil lignin concentrations are quite high, and are consistent with other sands (Thevenot et al. 2010). However, our soil lignin concentrations are less than half the concentration observed in plant source pools in both treatments. Given that the lignin fraction is the most recalcitrant and selectively preserved pool of plant tissue during decomposition (Six et al. 2002, Thevenot et al. 2010), this suggests a large mass of non-plant-sourced (i.e. microbial) C is contributing to SOC in our system. Whether this microbial carbon originates from root exudate flux (Bradford et al. 2012), or from the microbial decomposition of plant tissues (Grandy and Neff 2008) is unclear. However, based on our findings, both sources of microbial carbon will be highly collinear with observed root biomass.

Although we observed significant impacts of grazing on BCA and SOC pools, future work will be needed to gain greater mechanistic insight into the processes regulating SOC turnover, and thus long-term implications of grazing for carbon sequestration. For instance, our findings support that plant tissue inputs account for a disproportionate fraction of the increase in SOC under grazing, but we do not have data to link this increase to any particular fraction of SOC (von Lützow et al. 2007, Moni et al. 2012). It is possible that particulate forms of SOC have increased, while the absolute concentration of mineral-associated C is similar due to saturation of physical-protection capacity in these coarse sandy soils. Thus, given a larger capacity to stabilize microbial necromass, it is possible that grazing would be associated with an even greater SOC stock. On the other hand, grazing-stimulated increases in exudation could accelerate microbial access to mineral C (e.g. via organic acid release Keiluweit et al. 2015), leading to SOC loss via ‘priming effects’ (Cheng 2009, Strickland et al. 2010, Blagodatsky et al. 2010, Cheng et al. 2014). To resolve these possibilities, we recommend that longer-term in situ $^{13}$C pulse-chase experiments be done using combinations of
labeled litter and model exudates (e.g. Strickland et al. 2012) to trace the fate and transformation of these carbon inputs through various SOC pools and to test for priming effects across meaningful environmental gradients (e.g. plant composition, soil moisture).

Our results have potentially profound implications for more effective stewardship of SOC and carbon sequestration services (Chapin et al. 2009, Swain et al. 2013) in subtropical grazing lands. First, they suggest that plant productivity is indeed a key control-point in the SOC cycle, consistent with previous remote-sensing based findings in this ecosystem (Wilson et al. n.d.). Second, it appears that grazing managers should focus attention on routine monitoring of fine root biomass. At least for coarse-textured soils under C4 pasture, we suggest that management of SOC stocks ultimately devolves into a relatively straightforward task of optimizing root system health and proliferation. Although we did not test for variations in plant composition or grazing pressure, we suggest that their effects on SOC will be readily predictable based on observations of root systems, a conclusion in accord with Derner and Schuman (2007).

Large herbivore grazing can clearly increase belowground carbon allocation and SOC pools in C4 subtropical pasture, irrespective of impacts on plant community composition. Although microbial carbon appears to constitute a large fraction of the total SOC, the flux of substrate to sustain microbial growth, whether as fine root exudates or deposition of root litter, is tied directly to overall root biomass, and hence is expected to be collinear with plant tissue inputs. Accordingly, molecular characterization of our soils revealed an overall close coupling of plant inputs and SOC, and suggested a larger role for plant inputs in sustaining the increased SOC pools observed with grazing. Future work is needed to define functional pools of carbon in this ecosystem, quantify turnover rates and to better assess the role of microbial biomass in regulating SOC accumulation or loss. Nevertheless, it is clear from our current results that large herbivore grazing is critical in
maintaining belowground carbon stocks in subtropical pasture, a role that needs to be considered very carefully in evaluating their impact on global change and potential to contribute to greenhouse gas mitigation via soil carbon sequestration.
Table 4.1. Model results for all responses included in study, on original scale. The columns under Treatment represent the means and standard errors (in parentheses) marginalized across all dates for each treatment condition. Model coefficients (representing estimates of difference in means) are reported under Effect column with mean, standard error, and 95% uncertainty interval. The last column represents a simple computation of % effect size of Exclosure from the Grazed baseline. N.S. = not significant. Diff = % scale inappropriate.

<table>
<thead>
<tr>
<th>Pool</th>
<th>Measure</th>
<th>Treatment</th>
<th>Effect Mean (SE) [95% interval]</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Grazed</td>
<td>Exclosure</td>
<td></td>
</tr>
<tr>
<td>Shoots</td>
<td>Mass C (gm⁻²)</td>
<td>52.9 (18.2)</td>
<td>92.2 (23.1)</td>
<td>39.7(15.9) [7.2;70.7]</td>
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<td></td>
<td>Δ13C (ppt)</td>
<td>68.3 (25.1)</td>
<td>47.2 (24.2)</td>
<td>-21.1(14.6) [-49.7; 8.3]</td>
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<td>13C Label (mg m⁻²)</td>
<td>45.2 (18.5)</td>
<td>60.9 (21.8)</td>
<td>15.7(14.0) [-12.0;42.9]</td>
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<tr>
<td></td>
<td>Mass C (gm⁻²)</td>
<td>279.3 (67.0)</td>
<td>79.6 (46.8)</td>
<td>-199.7(63.7) [-335.8; -78.3]</td>
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<tr>
<td>Roots</td>
<td>Δ13C (ppt)</td>
<td>4.0 (1.5)</td>
<td>1.2 (1.5)</td>
<td>-2.8(1.9) [-6.6; 1.1]</td>
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<td>13C Label (mg m⁻²)</td>
<td>11.9 (2.7)</td>
<td>1.6 (2.2)</td>
<td>-10.2(3.1) [-16.3;4.0]</td>
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<td>Mass C (mg g⁻¹)</td>
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<td>0.16 (0.04)</td>
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<td>Δ13C (ppt relative to -13.5)</td>
<td>+8.4 (2.2)</td>
<td>+3.7 (2.3)</td>
<td>-4.8(1.7) [-8.1; -1.2]</td>
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<td>C (%)</td>
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<td>6.7 (1.5)</td>
<td>-1.8 (0.9) [-3.67; -0.04]</td>
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<tr>
<td></td>
<td>N (%)</td>
<td>0.52 (0.08)</td>
<td>0.40 (0.08)</td>
<td>-0.12 (0.05) [-0.22; -0.03]</td>
</tr>
<tr>
<td></td>
<td>Δ13C (ppt relative to -13.5)</td>
<td>-1.29 (0.18)</td>
<td>-2.73 (0.27)</td>
<td>-1.44(0.22) [-1.86; -0.97]</td>
</tr>
<tr>
<td></td>
<td>Δ15N</td>
<td>1.83 (0.34)</td>
<td>2.05 (0.36)</td>
<td>0.21 (0.12) [-0.03; 0.45]</td>
</tr>
<tr>
<td></td>
<td>C-Normal Lignin (%)</td>
<td>4.83 (0.36)</td>
<td>4.26 (0.38)</td>
<td>-0.57 (0.23) [-1.02; -0.12]</td>
</tr>
<tr>
<td></td>
<td>Ad:Al(v)</td>
<td>0.53 (0.02)</td>
<td>0.59 (0.02)</td>
<td>0.05 (0.01) [0.03; 0.08]</td>
</tr>
</tbody>
</table>
Figure 4-1. Measured biomass carbon pool size, delta $^{13}$C, and computed mass of $^{13}$C label for shoots (a-c), roots (d-f), and microbes (g-i) across all harvest dates of the pulse-chase experiment.
Figure 4-2. Regression of $^{13}$C label in microbes at 48 hours (index of exudation) versus a) root biomass carbon pools, and b) $^{13}$C label in root biomass. Circles represent soils collected inside grazing exclosure, whereas triangles are from grazed plots.
Figure 4-3. Regression of SOC concentration (mg g⁻¹) versus lignin phenol concentration (mg g⁻¹) on a dry soil weight basis. Triangles represent samples collected from individual cores as part of the background survey of three long-term grazing exclosures, whereas circles represent pooled samples from the 1 m² plots included in the pulse-chase experiment.
CHAPTER 5
SOCIAL-ECOLOGICAL ANALYSIS OF SOUTH FLORIDA RANCHLANDS: HISTORY, ECONOMICS AND ECOSYSTEM SERVICES

Introduction

Cattle ranches have a long and colorful role in the history of Florida. Cattle ranches are a dominant land use in south and central Florida and provide numerous important ecosystem services. These services include the provisioning of food, maintenance of biodiversity, landscape connectivity, water storage and potentially carbon sequestration (Shrestha et al. 2004, Swain et al. 2007, Bohlen et al. 2009). A number of ecological and management factors mediate the provision of these ecosystem services. For instance, cattle grazing management can contribute positively to maintaining habitat heterogeneity for avian species (Willcox et al. 2010). On the other hand, ranch management decisions are constrained by connection to out-of-state market cycles (Marsh 2003) and other economic considerations (Arthington et al. 2007, Willcox et al. 2010).

In order to grapple with the complexity of land management decisions in the real-world, various theoretical approaches have been devised that attempt to couple ecological dynamics and human behavior (Peterson 2000, Iii 2009). The resilience model posits that human-ecological systems fluctuate systematically in their susceptibility to disturbance. As a system matures, interactions between various human and ecological processes become stronger, producing internal structure and organization. Although initially resilient to perturbation, this very structure and organization makes the system progressively more vulnerable. At some point, the system goes into a crisis (collapse). When this occurs, reorganization along new lines is possible (Peterson 2000).

A central thesis in this paper is that south Florida ranchlands are human-ecological systems that couple external (non-local) market dynamics to ecosystem processes and human livelihoods in Florida. Access to those markets, as well as their internal dynamics, has thus been a crucial driver of ecosystem management and consequent services. Past fluctuations in markets have lead to profound
reorganizations of cattle ranching in Florida, with many economic and ecological consequences. I propose that the current move towards monetizing ecosystem services is potentially a similar kind of market fluctuation. The extent to which this new type of market may alter land-use and management decisions is obviously unclear, but history suggests that it could be quite significant. I will delineate the present social-ecological context in which this dynamic may unfold. Although the focus of my personal scientific work is the interactions between cattle grazing and ecological processes, it is vital to situate ranch management variables inside this larger social-ecological context.

A Brief History of Ranching in Florida

Beginnings

When Ponce de Leon, Hernando de Soto, and other Spanish *conquistadores* began to explore Florida in the mid-1500s, they brought livestock with them as food, including cattle and pigs, as well as their horses for transportation (Yarlett 1985). It is likely that these animals periodically escaped and may have formed viable wild populations. Additionally, North Florida was the seat of a relatively large Spanish ranching complex in the mid 1600s, involving Andalusian cattle from the Mediterranean (Arnade 1961). Although Spanish control of Florida had declined considerably by the early 1700’s, their cattle persisted. Descendants of these various introductions formed viable wild populations, leading later to the particularly well-adapted “Florida Scrub Cow” (Otto 1984, Yarlett 1985).

At the same time, these cattle were maintained by Lower Creek Indian groups (Seminoles) who had replaced the mostly extinct Timicuan tribes (Covington 1968). The Seminole ranching culture, famously described by William Bartram in the late 1700s (Bartram 1794), was centered in North Central Florida around the Alachua Savanna, now Payne’s Prairie. This part of Florida was endowed with a heterogeneous landscape of Longleaf Pine (*Pinus palustris*) savanna in the uplands, rich oak and magnolia hammocks in more mesic and nutrient-rich sites, and numerous grassy

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savannas. According to Bartram’s (1794) descriptions, the Seminole cattle and horses were small but sleek and in good condition. This suggests that the natural resources of the region at that time could support at least a modest number of well-adapted cattle.

The outcome of the Seminole Wars fought by the US government in the early 1800s, and ending finally in the 1840s, was that the Seminole and their cattle were pushed further south, below present-day Ocala (Sievers et al. 1985, Riordan 1996). Although pastureland for cattle and horses remains an important land use in north Florida, the largest cattle operations have been found in south-central Florida since the 1850s. Therefore, cattle ranching has played a larger role in shaping south-central Florida’s ecosystems and their services.

**Frontier Ranching in Florida**

Frontier ranching, including open range grazing, persisted in Florida until a state legislative act in 1949 required cattle to be fenced into defined property boundaries. Thus, although the mythos of the open range in the American West is better known, the open range endured longer in Florida than anywhere else in the United States. Although there is much uncertainty, the basic pattern of open range ranching in Florida has been described in the literature notably by Mealor and Prunty (1976), and by Otto (1984, 1986).

The basic cultural pattern of frontier ranching in Florida, as in much of the Southeastern United States, derives ultimately from Anglo-Saxon roots (Otto 1986). Cattle herders in the English Isles grazed the commons (i.e. without property boundaries and fencing) and similarly tended to be concentrated in harsh environments, ill suited to annual cropping. They fired the land annually during winter to stimulate more nutritious re-growth for their stock, used dogs to assist in herding, and penned lactating cows and their calves at night for safety. The so-called “Cracker” frontiersman brought these pastoral practices into the Southern Coastal Plain. As the frontier advanced into South
Florida, this basic pattern persisted and many of its elements survive intact to the present day (Mealor and Prunty 1976, Otto 1984).

The settlement pattern in South Florida was sparse. For instance, in 1850 Hillsborough County had a total population of around 2,400 residents, but was home to nearly 20,000 cattle (Otto 1983). Generally, the cattlemen homesteaded relatively small tracts (32.4 to 65 ha), but their cattle might range over dozens or even hundreds of square kilometers. The homestead tract provided food for the family, with the aid of manure from penned cattle, but would have been totally inadequate to support sufficient cattle, since each head required roughly 20 acres of the native range to supply adequate forage (Mealor and Prunty 1976).

Throughout the whole frontier period, from around 1850 to 1949, South Florida cattle ranchers were dependent on foreign markets (Mealor and Prunty 1976). Except for a period of time during the Civil War (Yarlett 1985), when Florida supplied beef to the Confederacy, Cuba was the principal market for the range cattle produced in the flatwoods and prairies of South Florida. The quality of meat from these range cattle was generally poor by domestic standards, however the enthusiastic market in Cuba kept the livelihood of Florida cattlemen intact until the 1920s and 30s (Mealor and Prunty 1976).

In agronomic terms, range cattle production was extensive, low-input and generally low-cost. Cattle foraged through a heterogeneous environment, were provided no supplemental feed or veterinary care, and largely behaved as semi-wild animals. Ecologically, range cattle production was well suited to the Florida environment. As a whole, the region consisted of a mix of pine flatwoods, freshwater marshes, prairies, and mesic oak hammocks. The cattle utilized all of these types of habitats, in various sequences during the seasonal cycle (Otto 1983, Tanner et al. 1984). The practice of annual burning was compatible with the native pyrogenic ecosystems. Native grasses, especially
Wiregrass (*Aristida stricta*) and various Bluestems (*Andropogon* spp.), respond well to frequent burning and are tolerant of grazing (Yarlett and Roush 1970, Lewis and Hart 1972, Roush and Yarlett 1973).

When the markets for range cattle in Cuba dried-up, largely due to competition from Venezuela, this land-use system underwent a profound crisis and subsequent transformation. In order to compete in the domestic market, it was necessary to bring in improved beef genetics, primarily bulls of Brahman lineage, to cross with the Florida Scrub Cow (Yarlett 1985). In turn, maintaining these generally larger animals required the establishment of “improved pastures” and the elimination of cattle tick fever via a coordinated campaign of dipping livestock in arsenic (Mealor and Prunty 1976). Both campaigns were successful and the result was a dramatic transformation of the cattle industry in Florida, and the ecosystems that host it. Cattle ranching in Florida switched from being an extremely extensive, zero-input land use, to operating in more intensively modified agroecosystems. It was found that a combination of planted pasture – often complemented by drainage and fertility management — and native range not only could sustain higher quality beef animals, but also a much higher stocking rate and calving percentage (Lewis and McCormick 1971, Hughes 1974), two central drivers of ranch profitability (Arthington et al. 2007).

From a social-ecological systems point of view, the history of ranching in Florida can be seen as having undergone a relatively sudden and swift transition from one stable state to another. The central driver of this transition was the drying up of one non-local market (Cuba) and the concerted entry into another non-local market (Midwestern feedlot beef production). The technical hurdles (cattle genetics and disease) were rapidly overcome in the face of this economic pressure. In my social-ecological description of contemporary cattle ranching in South Florida, I argue that external
market pressures continue to be a key variable in determining land use and, hence, ecosystem services.

**Contemporary Cattle Ranching in South Florida**

Since the 1950s cattle ranching has remained a dominant land use in south Florida. Presently, the state hosts about 1 million head of cow-calf units on about 2.1 million ha of pasture and rangeland (USDA-NASS 2007). In turn, this land-use is concentrated in south-central Florida, especially in the Lake Okeechobee watershed, which alone hosts 40% of the state’s cattle population on 65% of its total land area (Shrestha and Alavalapati 2004). For context, a full 80% of cattle production is located in south and central Florida (Silveira et al. 2011). Although the proportion of this acreage in native rangeland has declined over the years, it is still an important resource both agronomically and ecologically (Bohlen et al. 2009, Boughton et al. 2010).

In terms of land tenure and occupation, south Florida ranchlands are extensive and dominated by a relatively few land holders. Following an evident power-law distribution (i.e. Pareto Law), 98% of Florida ranches are classified as small, while the 2% classified as large are primarily in central and south Florida (see figure 1), but comprise 75% of the land area in cattle ranching and own roughly half of the total state cattle population (Shrestha and Alavalapati 2004). This pattern of ownership is consistent with the distribution of wealth in contemporary Western capitalist societies (Drăgulescu and Yakovenko 2001). Moreover, this economic pattern suggests that political clout should be concentrated in a small elite of large ranchers, a conclusion consistent with my personal observations and experiences in these systems. Under current socio-political arrangements, strategies to enhance ecosystem resilience, and to foster increased provision of desired ecosystem services in this region, need to gain acceptance amongst large, private landowners (Swain et al. 2007, Bohlen et al. 2009). As we will see later, this pattern of ownership has profound implications for the necessary
framework and operation of any market-based system for monetizing and incentivizing improved ecosystem management activities.

**Cow-Calf Ranch Economics**

Since most Florida ranches are cow-calf enterprises (Bohlen et al. 2009), the economics of the Florida cattle industry is principally determined by prices for feeder cattle in the Midwestern feedlots, and the variable costs associated with cattle production in this state. From the standpoint of ranchers who have either inherited their land and capital infrastructure or have already purchased it, evaluating the profitability of various alternative agricultural enterprises is generally best done by a gross margin analysis (Upton 1964). In essence, the variable costs associated with production are deducted from the revenue generated from a particular enterprise. Over time, both the revenues from feeder calf sales and the variable costs of production tend to vary cyclically, tracking a multitude of other variables, including fossil energy costs.

The most significant variable cost in cow-calf ranches nationally (Miller et al. 2001) and in Florida (L.O. Lollis, pers.comm., December 18th, 2012 and Swain et al. 2013) is feed. In Florida, supplemental feeding is generally done over winter and into spring to improve performance of animals grazing dormant pasture or range, and to meet the needs of lactating animals for protein and energy (Swain et al. 2007). In terms of improving gross margins, controlling feed costs is the most critical control point in cow-calf ranch economics. In recent years, despite relatively high prices for feeder calves, high input costs associated with feed (corn silage, urea-molasses slurry) and fertilizer (chemical N) have constrained Florida ranch profitability (L.O. Lollis, pers.comm., December 18th, 2012). This insight should motivate the development of integrated strategies for ranch and cattle management. If grazing or land management practices can be implemented that reduce feed costs and simultaneously enhance the provisioning of ecosystem services, that would be a rare but clear example of developing a concrete win-win strategy in these human-ecological systems.
Ecosystem Services from South Florida Ranchlands

South Florida ranchlands provide numerous ecosystem services, including habitat for species such as the Crested Caracara (*Caracara cheriway*), White-tailed Deer (*Odocoileus virginianus*), Florida Black Bear (*Ursus americanus floridanus*) and Panther (*Puma concolor*), a relatively friendly landscape-level agricultural matrix (Perfecto and Vandermeer 2010, Tscharntke et al. 2012), conservation of a diverse array of plant and avian species (Willcox et al. 2010), significant potential for water retention (Bohlen et al. 2009), carbon sequestration via silvopasture (Shrestha and Alavalapati 2004, Haile et al. 2008) or possibly via soil carbon sequestration through improved grassland management (Conant et al. 2001). Other services provided include various aspects of cultural conservation, and provision of recreational space for hunting. The diversity of services provided mirrors the heterogeneity of the landscape itself and the ecosystems involved. In the rest of this chapter, I will focus on two, water retention and carbon sequestration, and then conclude with a synthesis of lessons learned and a look to the future.

Managing for Water Retention

Perhaps the best-documented experiment in incentivizing ecosystem service provision is the Florida Ranchlands Environmental Services Project (FRESP). Developed initially as a collaboration between the World Wildlife Fund (WWF), Archbold Biological Station (ABS), and the South Florida Water Management District (SFWMD), FRESP was an innovative payment for environmental services (PES) scheme (Bohlen et al. 2009) that has now become operationalized by SFWMD as the Northern Everglades Payment for Ecosystem Services (NE-PES) program. The principal goal of NE-PES (and its predecessor FRESP) is to reduce the peak flows of water into Lake Okeechobee during the wet season, by retaining the water on the ranchlands that comprise ~33% of its watershed (Shabman et al. 2013). In turn, the quantity and quality of water flowing into Lake Okeechobee plays a crucial role in maintaining the health of the Everglades, supports
agriculture in the Everglades Agricultural Area, sustains a vibrant sport fishing industry, and plays a crucial role in water supply for densely populated metropolitan areas of South Florida (Bohlen et al. 2009).

The basic premise of the NE-PES program is that landowners enhance the capacity of their landscapes to retain water, and thus mitigate flow of water into regional drainage canals during rain events. In turn, this reduces water load going into Lake Okeechobee, a positive environmental service. Although the original FRESP project assessed a variety of land management activities to achieve this goal (Bohlen et al. 2009), the SFWMD broadly classifies the services into either water retention or nutrient removal (Shabman et al. 2013). In addition to helping regulate the water level in Lake Okeechobee, expanding water retention capacity in the Northern Everglades likely reduces phosphorous loading (P-loading), a serious concern throughout the Everglades, because less will be transported off of pastures by surface or subsurface drainage (Swain et al. 2013). Both outcomes contribute to the overall goal of reducing the total maximum daily loading of P into Lake Okeechobee by 75%, and (Bohlen et al., 2009).

Although the initial pilot program involved predetermined ranch partners, SFWMD has operationalized the PES using a “reverse auction” bidding system (Horne 2011, Shabman et al. 2013). Ranches enter into a fixed-term contract (10 years) agreeing to provide a certain amount of water retention through implementation of WMA(s) on a defined area of land, e.g. via installation of a riser-board system in drainage culverts. This water retention surface is estimated via use of a hydrological model that was developed during the FRESP pilot project phase, the Potential Water Retention Model (PRWM) (Florida Ranchlands Environmental Services Project (FRESP) 2012). The PWRM calculates the environmental service as the difference between the baseline water retention and the new potential service given implementation of WMAs. In turn, the SFWMD
compensates ranchers for the capital costs associated with design and construction of WMAs, and then pays an agreed quantity annually for the service, provided proper documentation of monitoring is submitted. Preliminary results suggest that the potential for water storage can be high and is technically feasible (Bohlen et al. 2009). For instance, at Buck Island Ranch (BIR), one of the ranches in the pilot project, the storage potential is estimated to be roughly 0.45 acre-feet per acre.

The overall goal for the NE-PES is to make a substantial contribution to the goal of establishing 450,000 acre-feet of distributed storage across the Northern Everglades, at a price that is competitive with the cost of constructing reservoirs (Horne 2011, Timothy and Jankie 2014). According to the 2014 SFWMD audit, the average annualized cost to the district (hence South Florida taxpayers) per acre-foot of storage in a reservoir project is $167.84, whereas the average cost of the existing NE-PES contracts on private lands is $103.10, and on public lands is a mere $8.02. Thus, the NE-PES program with cattle ranchers appears to be cost-effective compared to water storage in reservoirs, but costs an order of magnitude more than projects implementing comparable WMAs on public lands. This cost discrepancy, along with evidence of lobbying being used to secure a very large contract for a politically well-connected company, Alico, Inc., has generated some controversy in the popular press (Pittman 2015). Notably, Pittman (2015) quotes Sarah Lynch, one of the initial framers of the FRESP project, as effectively saying that the contract system is not working as intended to foster improved environmental services and economic livelihood for a wide range of landowners in the northern Everglades.

The goal of the FRESP collaboration, and by extension the NE-PES program, was to develop a market-like process for enhancing ecosystem service provision (Bohlen et al. 2009, Lynch and Shabman 2011, Shabman et al. 2013). However, it is difficult to find evidence that the program, as currently constituted, is actually lowering costs through any kind of competitive bidding dynamics.
As it is, to achieve 450,000 acre-feet of annual retention on private lands, would cost the district on the order of $45 million annually, or $450 million over the course of 10 years. By comparison, the fiscal year 2017-2018 budget request for the entirety of the SFWMD is $659.1 million (South Florida Water Management District 2017). Fully funding the water retention on private lands north of Lake Okeechobee would thus require a 6.8% increase in the SFWMD operating budget, an unlikely proposition given the current political environment. Although it is tempting to conclude that the SFWMD should simply pursue cheaper water retention options on public lands (at ~ $10/acre-foot) there is little evidence that sufficient land area is available to achieve the target. Another pathway to lower costs would be to inject more actual competition into the price negotiations for acre-foot of retention service. Of course, achieving this competition requires a large pool of interested potential “sellers” of water retention service. Instead of awarding fewer larger contracts to the most politically connected actors (i.e. “crony capitalism”), the SFWMD should prioritize expanding market access to as many ranchers as possible.

Despite persistence of significant obstacles to scaling up, the NE-PES plan may represent the beginning of a durable and potentially lucrative new market for cattle ranchers in south Florida. Given the low profit margins achieved by conventional cow-calf production in South Florida (Arthington et al. 2007), payments on the order of $100/acre-foot of water retention represent a desirable agricultural enterprise, especially when capital (or fixed) costs are also covered by the SFWMD. For example, the average annual net revenue per brood cow at BIR is $50 (leading to a net revenue of around $150,000 from calf sales, (Swain et al. 2013), but the annual value of the NE-PES water retention contract is $173,600 (Timothy and Jankie 2014), and a newly added NE-PES nutrient removal contract is worth $131,500. These programs are therefore tripling the bottom-line for this particular ranch. Even if a more competitive bidding process were to lower the price to $50/acre-
foot, the contract at BIR would still be extremely valuable. Future work should analyze the potential size of this market through a more detailed geographic analysis of property ownership and land suitability for various types of WMA projects. One limitation to achieving the intended scope may be that enrollment in a program such as this is only really tempting for large landholders. A small rancher with a 100-acre project proposal that achieves 50 acre-feet of storage is unlikely to find the overhead and opportunity cost of enrolling worth the $5000 in annual payments.

From a social-ecological systems perspective the NE-PES program may yet prove to be a powerful strategic intervention during a period of environmental and economic crisis (Olsson et al. 2006), where concerns about water quality and quantity for the Everglades are coalescing with increasing pressure on ranchers to sell land into private development (Bohlen et al. 2009). If the target goal of 450,000 acre-feet of storage is met on private ranchlands, there will be a profound transformation of the landscape in the Northern Everglades. For instance, retention rates at BIR (roughly 2/5 acre-foot per acre) would have to be deployed over nearly all regional pastureland. The consequences of this significant re-hydration of the landscape are hard to predict, but may involve moderate declines in agricultural productivity and higher disease burdens in addition to beneficial environmental impacts (Swain et al. 2013). Whether this transformation will unfold on the same spatiotemporal scale as the transformation from frontier ranching remains to be seen. One crucial difference is that Florida ranchers are not, in this case, fighting to survive as cattle ranchers at a basic level. Rather, the decision is likely to be made based on a variety of factors, including current profit margins raising and selling feeder calves. Overall, the stability and profitability of engaging this emerging market for ecosystem services remain to be seen.

Managing for Soil Carbon Sequestration

Another possible ecosystem service from grazing lands is carbon sequestration. The definition and goal of carbon sequestration is to remove carbon from the atmospheric pool and
deposit it into a relatively stable sink (UNFCCC). In grassland ecosystems, the soil organic carbon pool is the most promising sink for carbon in part because woody biomass accumulation does not occur (by definition) and aboveground litter pools are susceptible to frequent loss via fire (Schuman et al. 2002, Soussana et al. 2004). Increasing the pool of carbon in the soil generally requires managing the ecosystem for higher net primary productivity (NPP), increasing the fraction of carbon allocated belowground, or both (Rasse et al. 2005, Rees et al. 2005). However, accumulation of SOC is ultimately limited by the mean residence time of added C\(^1\) The stability and mean residence time of soil carbon is related to a number of factors, including physical occlusion inside aggregate structure (Six et al. 2000); the size, activity and diversity of microbial populations (Fontaine & Barot, 2005; Six, Frey, Thiet, & Batten, 2006); and the availability of high-energy substrates for microbial metabolism (Fontaine et al. 2007).

In the grassland context we can define two basic approaches to monitoring and verifying carbon sequestration: longitudinal SOC sampling (at appropriate spatial and temporal scales), and integrated GHG flux monitoring via Eddy Covariance technology. There are advantages and disadvantages to both approaches. Briefly, eddy covariance technology quantifies net ecosystem exchange (NEE) of greenhouse gases (e.g. CO\(_2\), CH\(_4\) and N\(_2\)O) between the ecosystem and the atmosphere, where NEE is customarily designated as negative when fluxes into the ecosystem dominate fluxes out of the ecosystem. NEE of CO\(_2\) can be partitioned into gross primary production (GPP) and ecosystem respiration (R\(_{eco}\)), itself the combination of autotrophic and heterotrophic respiration. A necessary but not sufficient condition for an ecosystem to be sequestering carbon is that the NEE must be negative over some sufficient time interval. However, NEE cannot account for movement of carbon within soils (e.g. via percolation, (Brady and Weil 1996), and, more

\(^1\) Indeed the equilibrium solution for SOC in a first-order model is input*MRT
importantly, only ever represents a record over a given time interval for a given sampling location. Upscaled NEE estimates must therefore adequately account for spatial and temporal variability (Oren et al. 2006, Belshe et al. 2012). By contrast, longitudinal soil sampling can more readily account for spatial variations across heterogeneous landscapes, but appropriate sampling design to monitor ongoing SOC accumulation is a non-trivial task (Conant and Paustian 2002b, Saby et al. 2008, Viscarra Rossel et al. 2014).

Actual data on either SOC or NEE in Florida pastureland is scarce. Although various projects have reported SOC values measured in the course of specific experiments (Dubeux et al. 2006, Wang et al. 2006, Silveira et al. 2014b), and general values of SOC associated with various soil orders found on Florida ranches is referenced in (Swain et al. 2013), the work reported in Chapter 2 of this dissertation (published as Wilson et al. 2017) is the first attempt I am aware of to specifically study spatial variations in pasture SOC. At the time of this writing, I am also unaware of any project to systematically monitor SOC over time in order to quantify SCS. Moreover, the first NEE dataset has just been published (Chamberlain et al. 2017), containing integrated flux data for CO$_2$ and CH$_4$ over a two year period (2013-2015) from a planted pasture at BIR. Their data suggest that this pasture was a net carbon sink for both years (sequestering 163 +/- 54 g CO$_2$-C m$^{-2}$ and 75 +/- 51 g CO$_2$-C m$^{-2}$ respectively). However, after accounting for the 100-yr global warming power (GWP) of methane, according to IPCC methodology, the strong release of methane from pasture soil (which apparently considerably exceeds methane from enteric fermentation by livestock, (Chamberlain et al. 2015) converts this ecosystem into a net GHG source (emitting around 500 g CO$_2$-eq C m$^{-2}$ both years). Interestingly, estimating the ruminant contribution to the CH$_4$ flux based on Chamberlain, Boughton, & Sparks (2015) at around 25%, the net GHG footprint would be approximately 0 (or carbon neutral) if pasture soils themselves did not contribute significant methane.
Ultimately, as argued in chapters 2 and 3 of this dissertation, upscaled estimates of carbon sequestration will require understanding how carbon fluxes in Florida pastureland respond to variations in major landscape drivers (e.g. grazing, fire, flooding, nutrient inputs) and interactions with vegetative composition, productivity and edaphic factors (e.g. soil texture, elevation and microtopography). Prior studies in other grassland ecosystems have identified a variety of factors that may promote SCS including functional diversity, species richness (Fornara and Tilman 2008, Steinbeiss et al. 2008), proper grazing management and fertilization (Conant et al. 2001). Although semi-native pastures are generally quite diverse (Willcox et al. 2010), improved pastures tend to be monocultures, and thus we might expect them to contain less SOC ceteris paribus. However, in practice the distribution of planted/improved pastures compared to semi-native pastures is non-random with respect to underlying soil characteristics. Additionally, management tends to be far more intensive in planted pastures (e.g. higher fertilizer application rates). N-fertilization may improve soil carbon accumulation in some agroecosystems (Conant et al. 2001), but has been shown to decrease soil carbon (despite higher aboveground productivity) in some natural ecosystems (Mack et al. 2004) and may be a factor in observed soil carbon loss in some temperate pastoral agroecosystems (Schipper et al. 2007). However, Silveira et al. (2014b) found that more intensively grazed and N-fertilized P. notatum pasture in South Florida contained larger SOC stocks than native wiregrass rangeland on equivalent soils. Finally, the impact of grazing in planted pasture appears to be positive for SOC. In chapter 3 of this dissertation, I marshal considerable evidence that grazing exclusion leads to a ~30% loss of SOC from the topsoil of planted pastures at BIR.

Overall, it is difficult to assign any a priori estimate to potential for SCS services in Florida ranchlands before rigorous monitoring of soil carbon and ecosystem carbon exchange data are available from a much larger number of sites. Based on synthesis and review of experience with SCS
in a variety of systems (Conant et al. 2001, Conant and Paustian 2002b, Lal 2004, 2010b, Stockmann et al. 2013), I would estimate the potential to sequester an additional 250-1000 kg C ha\(^{-1}\) yr\(^{-1}\) for around 10-30 years based on simultaneous adoption of improved grazing management and incorporation of perennial and annual reseeding legumes into Florida pastures. Assuming that this entire increase can be mapped one-to-one into carbon offset credits, this increase would be worth $3.40-$13.57 ha\(^{-1}\) in California’s currently mandatory cap-and-trade carbon market (“California Cap-and-Trade Program Summary of Joint Auction Settlement Prices and Results” 2017). Drawing on the lessons of the NE-PES project, it is probably infeasible to develop a payment scheme based on annual service provision given the high likelihood of inter-annual variability in carbon sink strength (e.g. Chamberlain et al. 2017), which could relate to a variety of factors well outside rancher control. Rather, given a particular management practice that has been shown to enhance SOC accumulation, payments will need to be based on expected return averaged over some longer time period, perhaps 5 or 10 years. Clearly, quantification of service provision will need very careful thought and delineation.

More broadly, market-based mechanisms to incentivize SCS must grapple with several critical issues. First, the sequestration must verifiably occur over a time-scale that is meaningful for the goal of mitigating climate change (i.e. achieve practical permanence) and furthermore gains in one system must not come at the expense of losses in another (leakage) (Richards and Andersson 2001, Stickler et al. 2009). Given that the mean residence time of CO\(_2\) in the atmosphere is on the order of 100’s of years (IPCC 2013), it makes sense to establish this timeline as a reference. But this instantly poses problems for SCS in topsoil, especially in tropical regions where mean residence time is unlikely to exceed 40-70 years (ŠantRůčková et al. 2000). Second, the actual definition of the sequestration service hinges crucially on the concept of additionality (Richards and Andersson
Additionality identifies the service as the difference between the increase in some ecosystem stock (say carbon) given implementation of a specific incentive policy versus what would have happened without it (i.e. counter-factual scenario). In the case of water retention, the NE-PES program resolves this question by paying ranchers based on parameterizing the PWR model given implementation of a new WMA, and assumes, quite reasonably, that ranchers would not be inundating potentially productive pastureland in the absence of payments. However, most of the practices that increase SOC in grasslands also improve agronomic productivity in one way or another (Conant et al. 2001). Clearly, the baseline or reference scenario needs very careful delineation.

The American Carbon Registry (ACR), a leading source of third-party verification of carbon credits for California’s statewide market, has recently implemented the rangeland compost protocol, the first protocol in the United States for generating carbon credits based on SCS in rangelands (American Carbon Registry 2014). The compost addition protocol arose out of a collaboration between the Marin County Carbon Project, and the lab of Whendee Silver at UC Davis. In essence, protocol is based on a pilot project conducted at two ranches in Marin County, CA, which found that a one-time application of compost lead to increases in SOC above and beyond that contained in the organic amendment (Ryals et al. 2014). This effect was attributed to differential enhancement of NPP compared to heterotrophic respiration (Ryals and Silver 2013, Ryals et al. 2016), and suggested that organic matter amendments on rangelands might generally strengthen their capacity to act as carbon sinks. Based on these findings, the ACR formalized a monitoring and verification protocol that can be fulfilled based on empirical longitudinal SOC monitoring, or via use of a field-tested process-based model (PBM). The compost protocol also generates carbon credits based on diversion
of organic material from waste streams that would otherwise contribute substantial GHG (American Carbon Registry 2014, Ryals et al. 2014).

Overall, I am reasonably satisfied that this protocol does not incur negative leakage (sensu Richards and Andersson 2001), however I am concerned both about permanence and with some aspects of additionality. Specifically, although PBMs can be relied upon to retroactively fit observed SOC, scientific consensus on long-term (i.e. multi-decadal or longer) SOC trajectories given global change is conflicted (Wieder et al. 2013, 2015, Luo et al. 2016, 2017). Also, future land-uses could jeopardize sequestered SOC (i.e. conversion from grassland into annual tillage cropping). From the standpoint of additionality, practices with desirable co-benefits (such as enhanced agricultural productivity), ironically become harder to justify. For policy-makers, the goal is to not spend money incentivizing a practice that is already cost-effective and likely to succeed without the incentive policy in place. On the other hand, given the generally risk-averse nature of agricultural producers, incentive policies can make a lot of sense as a way to jump-start experimentation and adoption of innovative practices.

Managing for Ecosystem Services in the Real World

Ultimately, managing for ecosystem services is a complex endeavor. Ecosystems provide a wide variety of important services, and there is always a risk that a monomaniacal focus on just one aspect or another could lead to detrimental impacts on other aspects of ecosystem function. For instance, full optimization of primary productivity within any given season (say to maximize subsequent crop yields) generally involves heavy fertilization, irrigation, and rigorous selection of the most responsive plant species and genotypes, a set of practices that severely degrade biodiversity, enhance GHG emissions, and lead to depletion of freshwater supplies. Moreover, ecosystem response to management interventions is always at least somewhat uncertain. Outside of mathematical models, grassland ecosystems do not generally exist near any kind of equilibrium, and
indeed may have many alternative stable states (Briske et al. 2008a). Even when alternative states are known precisely, their boundaries could theoretically be quite complex, even fractal, undermining any ability to forecast changes in response to even minor stochastic variations (Vandermeer 2004). More prosaically, ecosystem managers in semi-arid to arid grassland systems must contend with significant and essentially unpredictable inter-annual variations in precipitation (Ellis and Swift 1988, Westoby et al. 1989). Managing for ecosystem services in any ecosystem is therefore an exercise in both creativity and adaptability.

The academic community has developed a rich literature in the discussion of how to affect change within complex social-ecological systems. Perhaps most relevant to grazing lands is the framework of adaptive management (Kothmann et al. 2009). The key insight of adaptive management is that real world land management is best formulated as an iterative process: define a holistic goal encompassing desired environmental and economic outcomes (Butterfield et al. 2006, Herrick et al. 2012), derive manageable objectives and monitoring protocols, implement both management and monitoring practices, adapt management practices based on monitoring, and then repeat the whole cycle (Kothmann et al. 2009). The genius of the adaptive management cycle is that it entirely sidesteps the need to derive a precise, quantitative understanding of ecosystem dynamics in order to move towards desired goals. The real world is allowed to enter into the process via continuous monitoring which forms a feedback cycle. Adaptive management has shown great success at the level of individual producers seeking to optimize their financial viability and steward ecological resources under their direct control (Gerrish 2004, Provenza 2008, Kothmann et al. 2009, Teague et al. 2011). However, the provision of ecosystem services inherently involves a challenge to define and manage processes that cross property boundaries (i.e. are multi-scale), and generally involve multiple stakeholders with potential conflicts of value and interest. In this context, emphasis
on ‘adaptive co-management’ is most appropriate, and involves the art and science of analyzing institutions, fostering collaboration and ensuring adaptive cycles of management, monitoring and feedback (i.e. learning, Armitage et al. 2009).

From the standpoint of adaptive co-management, the FRESP and subsequent NE-PES collaboration is a relative success story. As discussed in Bohlen et al. (2009), and Lynch and Shabman (2011), the initial FRESP project was a multi-stakeholder collaboration that underwent many rounds of management implementation, monitoring, and revision of policies for both, building tremendous support for the program along the way. My main criticism is at the level of defining an appropriate objective for the holistic goal of building out 450,000+ acre-feet of new water retention service in the northern Everglades. In particular, I see no evidence that the reverse-auction bidding market hosted by SFWMD has sufficient funds given the current rate of ~$100/acre-foot-annum, and can find no evidence of a plan to inject sufficiently competitive dynamics to bring the price down and/or broaden the base of participants substantially (Lynch and Shabman 2011, Timothy and Jankie 2014, South Florida Water Management District 2017).

The potential design and operation of a carbon market for selling offsets generated by improved ranch management activities will need to incorporate the myriad lessons from adaptive management and the FRESP/NE-PES program. Defining relevant management practices and developing reliable protocols to document their impacts is only the first of many challenges. Given a satisfactory arrangement with buyers of carbon offsets, ranchers will need to manage the provision of carbon services against any trade-offs with other ecosystem services (Swain et al. 2013). For instance, although conflicts between SCS and agronomic productivity are unlikely, the GHG footprint of water retention practices will need somehow to be accounted for to ensure that carbon offsets being sold from a ranch are not simply ‘robbing Peter to pay Paul’. Thankfully, initial
analyses suggest that enhanced soil methane efflux due to water retention practices are likely inconsequential at current market prices (Chamberlain et al. 2017).

A Look to the Future

Given what we know about the social-ecological systems in south Florida ranchlands, can we predict how ranchers are likely to respond to market-based incentives to enhance provisioning of various ecosystem services? It is tempting to conclude that ranchers will simply maximize their marginal utility, in accordance with conventional economic theory. By this line of reasoning, it will be a simple matter of calibrating economic payoffs for ecosystem services so that they more than offset the opportunity costs of engaging in them (e.g. lost revenue from cow-calf operations, time, energy, etc.). However, this kind of prediction has obvious flaws. Ranchers in south Florida are generally risk averse (L. Sollenberger, pers.comm., December 8th, 2012) and attach a high value to their cultural legacy and values (Swain et al. 2007). Thus, factors influencing the perception of stability and reliability in these markets are likely to enter into land-management decisions as much as assessments of marginal economic utility at any given time.

In the end, cattle ranches in south Florida are complex enterprises balancing social, economic and ecological variables. Much more work remains to be done to delineate the social and political variables that determine land management practices. In particular, many more ethnographic and sociological studies are needed. Shresta et al. (2004) identified south Florida ranchers as politically conservative and influenced by centrist opinion leaders. Additionally, ranchers tend to have a somewhat adversarial relationship to government agencies. Although south Florida ranchers often participate in Conservation Easement programs (Bohlen et al. 2009), they are unlikely to voluntarily cede significant sovereignty in land management decision-making. In light of these considerations, the relative success of FRESP/NE-PES, a multi-agency interdisciplinary project, is noteworthy.
The historical transition from frontier ranching to modern practices was driven largely by external factors that provoked a deep crisis in the structure of open-range ranching. Recent increases in input prices may or may not represent a similarly abrupt disruption of the human-ecological system. Although there are too many contingencies to generate confident predictions, some increase in pressure to provide ecosystem services is likely to coincide with rising input prices over the long term as fossil energy supplies become more expensive (Provenza 2008). Given current socio-political arrangements, the resulting modifications in land management, and therefore regional ecology, are likely to be heterogeneous and represent the sum of individualistic responses and adaptations to changing conditions rather than a coordinated regional strategy (i.e. full co-management).
CHAPTER 6 CONCLUSIONS

Soil carbon sequestration (SCS) in pastures and rangelands is a promising strategy to mitigate greenhouse gas (GHG) emissions and thus combat the growing threat posed by climate change. However, the ecosystem processes regulating soil organic carbon (SOC) in grazing lands require greater elucidation. Prior to the research reported in this dissertation, very few data existed on how grazing impacts plant allocation of carbon belowground, in the form of root production and exudation, in subtropical or tropical pasture (discussed in chapters 1 and 3). Additionally, the data in Chapter 3 on SOC pool size and composition under long-term grazing or grazing-exclusion are novel contributions to the subtropical grassland literature. These studies proved useful in at least two respects, first in providing data to quantitatively constrain estimates of key carbon fluxes, and second to test key hypotheses concerning the short and long-term effects of grazing on plant growth and carbon allocation. Naturally, this research has also raised new questions and suggested future research directions. Below, I briefly summarize the key conclusions from each chapter, and then discuss my vision of the next steps.

In Chapter 1, we saw that grazing cannot be understood along a single axis of intensity, and that plant growth responses to grazing are mediated by cultivar identity (i.e. genotype). Across four cultivars of *P. notatum*, defoliation severity rather than frequency induces significant modifications of productivity both above and belowground. Severe defoliation triggers over-yielding of shoots when applied infrequently (i.e. grazing optimization), while reducing root production whether applied frequently or infrequently. However, the extent of reduction in root production varies by cultivar. Notably, it does not appear that there is any particular correlation between productivity observed aboveground and that which occurs belowground at the spatial scale of these experimental plots (2.5 X 5 m). Future work needs to examine root production responses across environmental
gradients and under realistic variations in plant composition and grazing pattern. In particular, I would like to see greater attention to quantification of root production at operational scales, given more realistic grazing practices in terms of timing, intensity and duration.

During the research reported in Chapter 2 we found that two factors were of over-riding importance in predicting spatial variations in SOC across a working cattle ranch in S. Florida: history of vegetation greenness (quantified by the Enhanced Vegetation Index, EVI) as measured by the Landsat 5 satellite, and soil calcium as measured in a Mehlich III soil audit. Surprisingly, knowledge of soil series was not useful, and micro-elevation (from LiDAR) was only marginally useful in constraining surface but not deeper SOC. This research is the first to link spatial variations in SOC to a long time series of EVI from a single land use type (improved pasture). By contrast, earlier work has utilized satellite-derived greenness indices to help improve SOC predictions arguably by discriminating coarse variations in vegetative cover (e.g. distinguishing between forests and grasslands). In order to advance our ability to predict variations in SOC across spatial scales relevant to ranch management, I argue that satellite records of vegetation greenness could be used to drive variations in carbon inputs in computational models such as CENTURY or MIMICS.

In Chapter 3, we quantified fine root exudation, an understudied yet significant component of soil carbon input, alongside plant, microbial and soil carbon pools inside and outside of long term grazing exclosures. We found that grazed plots sustain a far larger root biomass, and correspondingly much greater rates of exudation, higher microbial biomass, and higher SOC. Despite the larger flux of labile carbon into the soil in the form of root exudates, and the greater microbial biomass, we found no evidence that accumulation of microbial forms of carbon explain the higher SOC seen under grazing. In fact, the SOC pools under grazing contained a greater proportion of lignin phenols, a marker of plant tissue inputs, suggesting that it is the turnover of the
larger root biomass that promotes greater SOC. Taken together with the findings of Chapters 1 and 2, I believe that these results greatly strengthen the case for the centrality of root system production in regulating grassland SOC. Unfortunately, direct measurement of root biomass or production is logistically challenging and difficult to scale. Thus, an important open research question is whether satellite-derived remote sensing data can be used effectively to constrain estimates of root biomass or belowground carbon allocation more generally. Given the role of root system in supplying water and nutrients for rapid re-growth, I suggest that a detailed examination of vegetation indices obtained during stress conditions (e.g. drought) is a logical starting point.

The social-ecological synthesis developed in Chapter 4 concludes that large-scale shifts in the grazing ecosystems of south Florida have occurred before, and can easily occur again given appropriate market signals. The current payment for ecosystem services (PES) system administered by the South Florida Water Management District (SFWMD) to increase water retention north of Lake Okeechobee is a useful starting point in considering how to promote SCS via a market-based program. However, the operation of any carbon market will require significantly more work to develop reasonably accurate, scalable protocols to predict and monitor SCS. One unique challenge of SCS is that the “service” only accrues with relatively permanent changes to SOC pools, whereas the service of water retention is naturally defined on an annual basis. Thus, calculation of ‘carbon offset’ credits requires accounting for uncertainty not only about what has already happened (i.e. uncertainty in monitoring of on-going SCS), but also what will happen in the foreseeable future (i.e. the fate of sequestered carbon). In my opinion, this requires significant advances in both basic ecosystem science, to develop improved and scalable SOC models closely coupled to efficient monitoring protocols, and also in economic models, to account for risk and uncertainty in SOC trajectories in the pricing of offsets.
## APPENDIX A
### ADDITIONAL INFORMATION ON FIELD EXPERIMENT AT ONA REC (ONA, FL)

<table>
<thead>
<tr>
<th>Block 4</th>
<th>Block 3</th>
<th>Block 2</th>
<th>Block 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>R (2wk)</td>
<td>T9 (2wk)</td>
<td>P (2wk)</td>
<td>A (4wk)</td>
</tr>
<tr>
<td>Severe</td>
<td></td>
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<tr>
<td>Mild</td>
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<tr>
<td>A (4wk)</td>
<td>R (4wk)</td>
<td>A (2wk)</td>
<td>P (4wk)</td>
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<tr>
<td>Mild</td>
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<tr>
<td>Severe</td>
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<td></td>
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<tr>
<td>P (4wk)</td>
<td>A (2wk)</td>
<td>T9 (4wk)</td>
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<td>Mild</td>
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<td>Severe</td>
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<td>T9 (4wk)</td>
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<td>R (2wk)</td>
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<td>Severe</td>
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<tr>
<td>Mild</td>
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</tbody>
</table>

Figure A-1. Diagram showing the layout of plots. North is top of the page. Legend: Defoliation severity- Red = Severe Defoliation (5 cm), Blue = Lenient Defoliation (15 cm). Defoliation frequency - 2wk = Defoliated every 2 weeks, 4wk = Defoliated every 4 weeks. Bahia cultivar identity - A = Argentine, P = Pensacola, T9 = Tifton 9, R = UF-Riata.
Table A-1. Meteorological Data from our study site, Ona Range Cattle Research and Education Center. Accessed from the Florida Automated Weather Network (FAWN), http://fawn.ifas.ufl.edu/.

<table>
<thead>
<tr>
<th>Period</th>
<th>Temp Avg (F)</th>
<th>Rel. Humid. Avg.</th>
<th>Precip. Total (in)</th>
<th>ET avg (in, daily)</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 2013</td>
<td>78.6</td>
<td>86</td>
<td>9.7</td>
<td>0.15</td>
</tr>
<tr>
<td>July 2013</td>
<td>78.5</td>
<td>88</td>
<td>10.4</td>
<td>0.15</td>
</tr>
<tr>
<td>August 2013</td>
<td>80.3</td>
<td>86</td>
<td>7.4</td>
<td>0.16</td>
</tr>
<tr>
<td>September 2013</td>
<td>78.4</td>
<td>87</td>
<td>7.3</td>
<td>0.13</td>
</tr>
</tbody>
</table>

Figure A-2. Figure showing the estimated sampling variance across the four treatment groups for each of our responses (shoot and root production). Bars represent median estimates of variance, on the standard deviation (SD) scale, and error bars represent end-points of the 95% credible intervals. It is clear that the severe-2wk defoliation treatment (simulating intensive grazing) leads to a dramatic suppression of variability for both shoot and root production. These results suggest that grazing may have impacts on heterogeneity of plant production at meter scales in addition to impacts on the overall magnitude of plant responses.
APPENDIX B
R CODE

Analysis of conditional and marginal $R^2$ for chapter 2. First is the univariate regression between shoot and root production, showing a weak but statistically significant relationship.

```
lm(formula = root_std ~ shoot_std, data = dat_lmer)
   coef.est  coef.se
(Intercept)  0.00     0.12
shoot_std  -0.31     0.12
---
 n = 64, k = 2
residual sd = 0.96, R-Squared = 0.09
```

Next is the full model used also to decompose contributions to $R^2$ as recommended by Nakagawa and Schielzeth (2013):

```
lmer(formula = rootmass ~ abovemass + Freq * Resid + (1 + Freq * Resid | Cults) + (1 | Plots), data = dat_lmer)
   coef.est      coef.se
(Intercept)     281.85       57.25
abovemass  -0.07        0.17
Freq2        -5.72       46.36
Resid2       -91.40       42.66
Freq2:Resid2   41.60     58.66
Error terms:
   Groups   Name         Std.Dev. Corr
   Plots    (Intercept)   0.00
   Cults    (Intercept)  73.68
               Freq2        80.22       -0.76
               Resid2       70.43       -0.98       0.87
               Freq2:Resid2 93.01        0.99       -0.82       -1.00
               Residual    65.32
---
number of obs: 64, groups: Plots, 32; Cults, 4
AIC = 728.9, DIC = 757.6
deviance = 726.3
```

# Code for computing conditional and marginal $R^2$ values
## Credit for code goes to supplemental material provided by (Johnson 2014)

```
X <- model.matrix(full_mod)
n <- nrow(X)
Beta <- fixef(full_mod)
Sf <- var(X %*% Beta)
```
Sigma.list <- VarCorr(full_mod)
Sl <-
  sum(
    sapply(Sigma.list,
      function(Sigma)
        {
          Z <- X[,rownames(Sigma)]
          sum(diag(Z %*% Sigma %*% t(Z))/n
        }))
    ))
Se <- attr(Sigma.list, "sc")^2
Sd <- 0
total.var <- Sf + Sl + Se + Sd
Rsq.m <- Sf / total.var # marginal R^2 is 0.18
Rsq.c <- (Sf + Sl) / total.var # conditional R^2 is 0.53
APPENDIX C
ADDITIONAL INFORMATION FOR EVI-SOC PROJECT AT MACARTHUR AGROECOLOGY RESEARCH CENTER

Additional Detail on LiDAR

Two GPS reference station locations were used during the survey, a high-accuracy bench NGS monument (A518) and an FDOT CORS station OKCB. After navigation processing (KARS software) calibration and laser point processing (REALM processing suite), Terrasolid’s TerraScan was used to classify the last return LiDAR points and generate a “bare-earth” dataset.

Analysis of Periodic Components in EVI Time Series

We estimated these components for each time series via Ordinary Least Squares (OLS) regression, with the following statistical model:

\[ Y_{j,i} = B_0 + B_1 \cdot \text{Day}_i + B_2 \cdot \sin(2\pi \frac{\text{Day}_i}{365}) + B_3 \cdot \cos(2\pi \frac{\text{Day}_i}{365}) + B_4 \cdot \sin(2\pi \frac{\text{Day}_i}{182}) + B_5 \cdot \cos(2\pi \frac{\text{Day}_i}{182}) + B_6 \cdot \sin(2\pi \frac{\text{Day}_i}{91}) + B_7 \cdot \cos(2\pi \frac{\text{Day}_i}{91}) + \epsilon_i \]

\[ \epsilon_i \sim \text{Normal}(0, \sigma) \]  

for \( j = 1-57 \) time series, and \( i = 1-426 \) EVI sample dates, where \( B_0 \) represents the estimated intercept (starting value) for each time series, \( B_1 \) is the slope of the linear temporal trend over time, and \( B_3 - B_7 \) represent the estimated Fourier coefficients for the annual and seasonal periodic behavior. Thus, our model is in effect summarizing the information contained in 426 EVI samples to 7 estimated coefficients. We then tested the value of these four coefficients for predicting SOC across each of our measured responses (SOC stock 0-15 cm, SOC concentration 0-5 cm, SOC concentration 5-15 cm), by OLS regression of the form:
\[ Y_{k,j} = \sum_{m=1}^{m=7} B_{k,m} + \varepsilon_{k,j} \]  
\[ \varepsilon_{k,j} \sim \text{Normal}(0, \sigma) \]  

for \( k = 1-3 \) responses, and \( j= 1-57 \) sample points. Since we found that the linear trend coefficients (i.e. \( B_0 \) and \( B_1 \)) were the only significant predictors, and only when taken together, we decided to opt for the simpler approach of simply using the arithmetic mean of the time series record at each point (which is mathematically extremely similar).

**Monte Carlo Simulation**

This shows that the high correlation of many dates in our EVI time series, and the time series as a whole, with observed SOC, is astronomically unlikely to have arisen simply by chance sampling variation. See also supplemental R code file for computation of binomial test p-value.

![Figure C-1. Plot of Monte Carlo simulation of R2 values relating randomly drawn vectors of EVI observations to our SOC response](image-url)
Computation of Soil Fertility Index

Rather than include coefficients for each cation and phosphorous separately, we elected to condense their information into a single measure. Although a variety of options could be pursued, we chose the simplest possible, which was to take the average of their standardized values. For each nutrient element, the raw data values represent concentrations (i.e. ppm) measured via a Mehlich III soil audit. We standardize the concentrations by subtracting the mean (centering on zero) and dividing by one standard deviation, so that each response is distributed as a normal random variable with mean zero and unit standard deviation. The index is then, simply:

$$\frac{1}{4} \sum (Ca_{std} + Mg_{std} + K_{std} + P_{std})$$

(C-3)

By construction, this index includes the information about calcium which we also analyze separately, inducing an autocorrelation between these two predictors. However, we are entirely unconcerned by this correlation for two reasons: 1) when analyzed separately, Ca is the only nutrient element that shows a statistically significant relationship with SOC, and 2) the Lasso procedure, implemented in our multiple regression model, is known to exert a strong selection pressure on autocorrelated variables, retaining one and rejecting the other. It consistently rejects Soil Fertility Index while retaining Ca as a strong predictor, which verifies that the other nutrient elements do not add useful predictive information.
APPENDIX D
ADDITIONAL INFORMATION FOR ISOTOPE PULSE-CHASE EXPERIMENT

Pulse Labeling Chamber Design and Operation

The pulse-labeling chamber was constructed out of \( \frac{1}{4} \)" plexiglass, custom cut into correct dimensions. Aluminum angle siding was attached along all joints using furniture screws and sealed along all seams with high-performance caulk. Two pairs of furniture handles were attached along the upper edge, flush with aluminum siding to prevent cracking. The base was constructed out of wood with a forged steel cladding welded in place along the lower edge, with 7cm of overhang. We ground out as sharp an edge as practical along the base to facilitate insertion into the soil.

Figure D-1. Photograph of pulse-chase experiment in progress inside the grazing exclosure on September 10th, 2016. Photograph credit to the author, Chris H. Wilson.
Heat Pump System for 1-m³ Plexiglass Field Chamber for Isotope Pulse-Labeling

Materials

-Small automotive radiator core (Napa Auto Parts, Ford Focus)
- HVAC register box
- Foam board insulation
- Plastic Tubing
- PVC quick couplers, adaptors, etc.
- Pipe Foam Insulation for tubing
- Large insulated cooler
- 12V DC cooling fan (rated to 200 cfm)
- 12V DC digital thermostat and temperature controller
- 12 V DC submersible water pump
- Adjustable DC motor speed controller
- Electrical on/off switch
- Surplus #16-18 wire and spade terminals

System Design

The goal of this cooling system is to transfer heat energy from the chamber atmosphere into a cooler full of ice water. Heat exchange is accomplished by circulating chamber air through the automotive radiator core, fed by a continuous loop of ice-cold water circulating from the insulated cooler outside the chamber. The automotive radiator core is mounted inside the HVAC register box with a fan immediately behind it. The fan-core assembly has an air intake placed at a 90-degree angle, and the entire assembly is mounted at a slight upward angle (pointed towards center-top of chamber on opposite side) in order to create a circular air mixing cell inside the chamber. Placement of the radiator inside the register box and use of reflective duct work (made from board insulation) minimizes direct heat gain into the cooling system from solar radiation. The entire assembly was mounted into the chamber using aluminum angle pieces and large zip ties.

The automotive radiator tubes are connected via plastic tubing to ice water stored in the cooler outside the chamber. The plastic tubing is run through precisely matched holes drilled into the plexiglass chamber with specialized drill bits, and PVC quick connect couplings enable rapid connection and disconnection of the chamber and cooler tubing. The cooler has holes drilled in it on
opposite sides. On one side, a 12V DC pump (powered off battery) is submerged and this is the source of water circulating into the radiator; on the other side water is returned to ice bath from the radiator core (having gained a little bit of heat). All exposed tubes are first covered in pipe foam insulation, and then taped with reflective HVAC tape to minimize heat gain via direct insolation.

To monitor temperature, a thermostat probe is mounted inside the air return duct, and is thereby shielded from direct sunlight and measures the temperature of air before passing over radiator core heat exchanging coils. Both the fan and the submerged pump are also wired into the digital thermostat controller. The thermostat is programmed to maintain a certain temperature and can run in both heating and cooling mode. In addition to setting target temperature, the “temperature span” is also set, i.e. the deviation in temperature required to trigger thermostat, which in this case is what switches both the fan and pump to ‘On’. The speed of the 12V fan is controlled using the DC motor speed controller (which is basically a voltage gate). This is important because when solar radiation is low due to time of day or clouds, heat gain can be very slow. Under those conditions, running the system at full power results in short-cycling, where motors will be switching on/off too frequently, thus causing premature wear and tear and preventing effective dehumidification.

**Results**

Indoor testing revealed that this system could maintain a 20F temperature differential front-to-back, which is the same standard used for residential HVAC systems. Run at full power, it could maintain an ambient-matched temperature in the chambers up to PAR readings ~ 2100 PPFD. Around 2200 PPFD, temperature would VERY slowly start to climb, but that kind of PAR is rarely encountered even in S. Florida. This basically means that the system has around 1 KW of cooling power.

In practice, a large cooler full of ice water could last for several hours of operation in the sun in S. Florida (with intermittent clouds), with ambient temperatures in the mid 90’s and extremely
high relative humidity. Extremely high humidity would cause condensation and fogging of chamber walls during the time required to set up, but the cooling system would de-fog the plexiglass after ~5 minutes of full-speed operation, while lowering temperatures to below ambient. Pulse labeling would be initiated when temperature levels re-equilibrated to ambient.

Figure D-2. Plot of standardized grazing ‘effect sizes’ across responses. Each coefficient represents impact on the scale of standard deviations in the response in terms of mean estimate (circle), 50% and 95% uncertainty intervals (thick and thin lines respectively).
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BIOGRAPHICAL SKETCH

Chris Wilson grew up in Ann Arbor, MI, a proud college town kid with a love of the outdoors and an ardent ethic of environmentalism. He developed a passion for all things food production late in high school, and nurtured this interest during his undergraduate education at the New College of Florida, where he received his B.A. in Ecology in 2009. His studies included biology, environmental studies, applied mathematics, and agriculture, aided by a brief stint as an exchange student at the University of Massachusetts in Amherst, MA. His baccalaureate thesis reviewed the ecological foundations for integrated pest management on organic vegetable farms. Subsequently, he completed a research internship at Macarthur Agroecology Research Station (Lake Placid, FL) studying impacts of grazing on native grass growth and microbial biomass, and later gained experience with cutting-edge methods for sustainable grassfed beef production on pasture. He entered University of Florida in fall 2012 on a Graduate School Alumni Fellowship, and advanced to candidacy in spring 2015. He received a National Science Foundation Doctoral Dissertation Improvement Grant in 2015, to support the research reported in Chapter 3 and is proud to be co-PI on another USDA grant.

His primary goal is to participate as a scientist in improving and redesigning agroecosystems to foster production of more healthful food, economic justice for farmers, and enhance ecosystem health and integrity. Throughout, he has drawn inspiration from a passage by the late, great Richard Levins: “my political commitment requires that I question the relevance of my work. In one of Brecht’s poems he says, ‘Truly we live in a terrible time…when to talk about trees is almost a crime because it is a kind of silence about injustice.’ Brecht was of course wrong about trees: nowadays when we talk of trees we are not ignoring injustice. But he was also right that scholarship that is indifferent to human suffering is immoral.”