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Effects of Cogongrass Invasion on Soil Biota and Nutrient Loads in a Longleaf Pine Savanna

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by

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ABSTRACT

The longleaf pine (*Pinus palustris*) ecosystem, characterized by its namesake pine species and diverse community of understory vegetation, is a hotspot of biodiversity in the southeastern United States. The longleaf pine savanna is differentiated from other longleaf systems through the combination its unique assemblage of herbaceous understory vegetation, wide-open canopy, and distinct hydrogeological composition. Longleaf pine ecosystems, including savannas, are facing significant decline from their historic range due to anthropogenic interference including fire suppression, habitat fragmentation, deforestation, and the introduction of invasive species such as cogongrass (*Imperita cylindrica*).

Cogongrass, a nonnative grass species introduced to the US in the 1920s, poses a significant threat to longleaf pine savannas. Its rapid spread and competitive soil nutrient uptake allow cogongrass to disrupt ecosystem composition by altering the natural fire regime, changing the makeup of the soil biota, and, ultimately, outcompeting native plant species within longleaf pine ecosystems.

This study aimed to investigate the impact of cogongrass invasion on the soil fungal biomass and the carbon and nitrogen availability within the soil in a longleaf pine savanna. Soil samples were collected both from patches of cogongrass and cogongrass-free areas within a longleaf pine savanna to be analyzed for ergosterol content and carbon and nitrogen levels as measures of fungal biomass and nutrient availability within the soil, respectively. Although an equipment malfunction prevented the analysis of ergosterol samples, and thus, an assessment of fungal biomass, analysis of soil carbon

and nitrogen content displayed an increase in carbon and nitrogen within cogongrass patches compared to soils free of cogongrass.

Keywords: longleaf pine savanna, cogongrass, carbon:nitrogen, soil biota, invasive species

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

LIST OF ABBREVIATIONS

C	Carbon
HPLC	High-Performance Liquid Chromatography
ID	Identification
InCG	Inside Cogongrass
LT	Lake Thoreau
N	Nitrogen
OuCG	Outside Cogongrass
PVC	Polyvinyl Chloride

CHAPTER I: Introduction

The longleaf pine ecosystem is one characterized by an abundance of longleaf pine trees, *Pinus palustris*, dispersed among an understory of native tall grasses and short shrubs (Aschenbach et al. 2010). While the pines lend the ecosystem its title, they are not paramount to its ecological significance—rather, the complex interactions between the pines, the landscape, the robust assemblage of understory vegetation, and the vast array of animals specialized for life among the longleaf pines make this ecosystem a hotspot for biodiversity.

Longleaf pine savannas differ from other longleaf systems, such as montane or sandhill habitats, in their composition. Generally occurring at lower elevations than other longleaf habitats, longleaf pine savannas are found in regions with level, silty, relatively poorly draining soils (Oswalt et al. 2012). As such, they are often closely associated with perched water tables and occur near, and sometimes among, bogs and other wetland habitats, though they are known to dry out in the event of a persistent drought (Peet and Allard 1993). The soils are typically acidic and low in nutrients, lending this habitat to its rich diversity of specially adapted understory vegetation, including several species of carnivorous plants and orchids (Peet and Allard 1993). By definition, savanna canopies are open, allowing more light to reach the understory here than in the other longleaf systems, making this habitat especially rich in grasses, small shrubs, and herbaceous flowering plants (Oswalt et al. 2012).

As with all longleaf pine ecosystems, a regular fire regime is required to maintain productivity in longleaf pine savannas (White and Harley 2016). In savannas, the prevalence of grasses and herbaceous species that results from the open canopy provides

a continuous mat of fine fuels that support the occurrence of low-severity ground-level fires at regular intervals, usually every one to two growing seasons (Hopkins et al. 2023). The benefits of these frequent fires create a positive feedback loop—the combustion of organic materials in the leaf litter replenishes the nutrients in the soil, promoting the rapid regrowth of the herbaceous understory, which aids in excluding succession by woody species that would interfere with the success of the herbaceous understory if given the opportunity to grow, and restoring the fuel load that will support the next fire (Hopkins et al. 2023). Disruption of this delicate balance has contributed to the rapid decline seen in longleaf pine savannas in the last century.

Before its exploitation for lumber by European settlers upon their arrival to the New World, longleaf pine ecosystems dominated the coastal plain of the southeastern United States and are estimated to have occupied roughly 92 million acres of land spanning from modern-day Texas to Virginia (Frost 1993). In the past five centuries, anthropogenic interference including, but not limited to, exploitation for tar, turpentine, and lumber, fire suppression, agricultural clearing, habitat fragmentation, and the introduction of nonnative species accounts for an estimated 97% reduction of the longleaf pine ecosystem from its former range (Frost 1993). The loss of longleaf pine habitats has resulted in significant ecological and economic repercussions, as this ecosystem acts as both a hotspot for biodiversity and a source of highly sought-after lumber (Oswalt et al. 2012).

Perhaps one of the most detrimental instances of human interference on longleaf pine ecosystem stability was the introduction of cogongrass to the United States. Cogongrass, *Imperata cylindrica*, is a perennial, rhizomous, C_4 grass species native to

parts of Asia and East Africa (Dozier et al. 1998; Estrada and Flory 2015). It was first introduced to the United States by accident as packing material in parcels sent from Japan to the port of Mobile, Alabama in 1912 before being planted intentionally in Texas, Mississippi, Alabama, and Florida in the 1920s as livestock forage, where it reproduced and spread rapidly, quickly taking over many forested ecosystems in this region, including longleaf pine savanna habitats (Estrada and Flory 2015).

Cogongrass jeopardizes the survival of longleaf pine savannas in several regards. As a nonnative plant, it threatens the biodiversity of the ecosystems it invades by outcompeting the native species for resources (Dozier 1998). Cogongrass is a highly robust, competitive grass species that is capable of rapid spread through clonal reproduction (Yager et al. 2010). Its rhizomes (underground stems) allow it to survive below the soil in harsh conditions, including fires, and its rapid tiller (aboveground stem) resurgence allows it to bounce back efficiently when reduced to soil level by flames or other attempts at mechanical control (Yager et al. 2010). This combination of traits allows cogongrass to displace native vegetation, especially in the critical post-burn period during which the native grasses and herbaceous species typically replenish themselves in longleaf pine savannas (Yager et al. 2010). The resulting disruption to the understory vegetative assemblage results in changes to the natural fire regime, as the increased fuel load attributed to the rapid expansion of cogongrass causes fires to burn more intensely than those occurring in areas inhabited by the native grass species (Yager et al. 2010). This creates a snowball effect wherein cogongrass outcompetes native species, making fires more severe, which further alters vegetative distributions and encourages the cogongrass infestation to expand, ultimately impacting longleaf pine savannas at the

ecosystem level (Yager et al. 2010). While this pattern of disruption by the invasive grass is relatively understood, less is known about the impacts of cogongrass on longleaf pine savannas at the soil composition level.

An estimated 90% of terrestrial plant species, including those native to longleaf pine savannas, exhibit important symbiotic relationships between their roots and specialized fungi in the soil known as mycorrhizae (Parniske 2008, Smith and Smith 2012). Mycorrhizal interactions within plant roots are imperative to plant success as they aid in the plants' ability to take up vital nutrients from the soil (Smith and Smith 2012). Different species of plants have different nutritional needs and are therefore associated with different species and arrangements of fungal symbiotes. Of the plant species that exhibit mycorrhizal interactions, about 6% possess ectomycorrhizal fungi, which describes species of fungal symbiotes whose hyphae do not enter the cell walls of the host plant's roots (Dong 2018). Ectomycorrhizal fungi are diverse, belonging to multiple phyla and typically associating with woody species of host plants, including longleaf pines (Phillips et al. 2013). Ectomycorrhizal fungi take up nitrogen in its organic form, allowing them to access nutrients inaccessible to other symbiotes (Phillips et al. 2013). The other 94% of plant species who exhibit mycorrhizal interactions possess arbuscular mycorrhizal fungi, which describes species of fungi whose hyphae penetrate the cell walls of the host plant's roots (Dong 2018). All arbuscular mycorrhizal fungi belong to phylum Glomeromycota and can be found in association with herbaceous or woody host plants, though they are most commonly associated with grasses, including cogongrass (Parniske 2008, Phillips et al. 2013). Arbuscular mycorrhizal fungi primarily take up nitrogen in its inorganic form following its assimilation by saprophytic microbes, though

they are also capable of utilizing nitrogen in its organic form (Dong 2018, Phillips et al. 2013).

Because different species of plants form relationships with different species of mycorrhizal fungi, changes in the dominant plant species within an ecosystem, such as the introduction of a nonnative species, can result in changes to the makeup of the fungal communities within the soil (Zubek et al. 2016). Changes to the soil biota composition, in turn, impact the nutrient availability within the soil. Two of the most crucial components of soil fertility are total organic carbon and nitrogen, with the ratio between the two playing a significant role in maintaining plant nutrition and metabolic function (Zheng 2009). Nitrogen is considered an essential nutrient for plants as it is a primary component in many vital biomolecules including chlorophyll, proteins, and nucleotides (Moreau et al. 2019). While nitrogen is abundant atmospherically in its inert form, it is unusable to the majority of plant species in this gaseous state, who instead require that it be nitrified into organic molecules, such as amino acids, or assimilated into soil-soluble inorganic forms, such as nitrate or ammonium (Ortigosa et al. 2020). These usable organic and inorganic forms of nitrogen are not readily available in the soil, meaning nitrogen is also the primary limiting nutrient for plant growth (Ortigosa et al. 2020).

In order for plants to take up and use nitrogen, it must first be processed by N-cycling microbes within the soil, which convert various nitrogenous compounds into plant accessible forms (Moreau et al. 2019). This processing and transferal of nutrients between microbes and plants is the result of complex mutualistic relationships formed between plant roots and members the soil biota, including mycorrhizal symbiosis (Fellbaum et al. 2012). Mycorrhizal symbiosis consists of an association between the

roots of a plant and fungi, wherein the fungal component facilitates the uptake and assimilation of nitrogen into an accessible form, which it transfers to the plant in exchange for plant-processed carbon (Fellbaum et al. 2012, Parniske 2008). Therefore, the uptake, processing, and transfer of nitrogen from the fungal symbiote to the host plant is influenced by the amount of carbon made available to the fungus, where increased carbon availability, a condition correlated with increased vegetative productivity often seen in invasive species, is associated with increased uptake of nitrogen by fungal hyphae (Fellbaum et al. 2012).

In an effort to better understand the impact of cogongrass invasion on native plant communities, this study sought to compare the fungal biomass and carbon and nitrogen contents of soils among and outside of patches of invasive cogongrass in a longleaf pine savanna. It was hypothesized that, compared to areas not infested with cogongrass, soils within patches of cogongrass would exhibit an increase in fungal biomass, while the C:N ratio would be reduced.

CHAPTER II: Methods

Soil Sample Collection

Fieldwork for this study was conducted in October of 2023 at The University of Southern Mississippi's Lake Thoreau Environmental Center in Lamar County, Mississippi. Prior to experimentation, two areas with established patches of cogongrass were identified, both within the Longleaf Preserve section of the Lake Thoreau property near the Golden Eagle Trail Complex. At each site, 10 soil cores were taken within the patches of cogongrass, at least 1 meter in from the outer bound of the patch, with cores taken in a zig-zag pattern randomly dispersed throughout the patch. Another 10 cores were then taken outside of the patch, at least 3 meters away from the outer bound of the cogongrass patch. Soil samples were collected using a 1-1/8″ × 12″ nickel plated, slotted soil probe (AMS, Inc., American Falls ID). Soil cores were collected in butyrate plastic liners (1″ × 12″, AMS, Inc., American Falls ID) and then capped and labeled with the location (LT), site ID (1 for frog pond, 2 for bike trail), cogongrass status (InCG/OuCG), sample number (1–10), and date of collection. For both sites, collection of highly disturbed, bottomland, and trail soils was avoided. Cores were put on ice immediately after collection and placed in the freezer until analysis.

Soil Sample Analysis

Prior to processing, the frozen soil cores were allowed to thaw in the refrigerator overnight to soften. Using a segment of PVC pipe about twice the length and the same diameter as the soil core liners, the top 10 cm of soil was extruded from each liner. The 10 cm segment of soil was cut in half lengthwise and each half was placed in its own

Whirl-Pak bag (Whirl-Pak, Pleasant Prairie, WI) labeled with the collection site ID, the cogongrass status, and the sample number. Soil cores being processed were always kept on ice, and processed Whirl-Pak bags were placed in the freezer as quickly as possible. This process was repeated for all 40 soil cores.

Samples were then opened and processed in a lyophilizer until they were fully dry, at least 24 hours. Immediately after drying, samples were homogenized by crushing the soil within the bag using a rubber mallet to gently pat the bag against the workbench. Once homogenized, 200 mg of each sample was measured into individual 50 mL plastic centrifuge tubes using a balance. These tubes were labeled with the information on the Whirl-Pak bag as well as the precise mass of sample material added to the tube. To each tube was added 10 mL of "solution 1," made by adding 16g of potassium hydroxide to 2L of methanol, was added to each tube, and the tubes were left to sit in the freezer overnight before moving to the next step.

Ergosterol was extracted from the samples using pentane separation. Four spikes, which are standards made with a known amount of analyte added to the sample dilutant to increase the accuracy and validity of test results, were made to be processed with the samples by adding 10 µL of ergosterol and 10 mL of solution 1 to each of four 50 mL plastic centrifuge tubes, labeled as spikes 1–4. Samples were then digested 8–11 at a time, in addition to a spike for each set, for 30 minutes in an 80℃ circulating water bath. They were allowed to cool to room temperature before 3 mL of double distilled water was added to each tube. Next, 10 mL of pentane was added to each centrifuge tube using a glass serological pipette. Each tube was then vortexed for 30 seconds. Once settled, the organic top layer was pipetted off into conical bottom ergosterol tubes labeled 1–44. The

organic layer was dried using a nitrogen evaporator. This process was conducted twice more from the pentane addition step, adding 10 mL of pentane for the second round, and reducing to 5 mL of pentane for the third round. Once the samples fully dried in the evaporator following the final round of extraction, a 500 µL Hamilton syringe was used to add 500 µL of methanol to each conical tube. Each tube was then vortexed for 30 seconds before spending five minutes in an ultrasonic water bath. Then, the samples were centrifuged for 10 minutes in a clinical centrifuge set to 2000 rpm. The resulting solution was pipetted into labeled vials and processed through a high-performance liquid chromatography (HPLC) system (Shimadzu10A-vp Series, Columbia, Maryland). A spreadsheet was used to keep track of all tube and corresponding sample labels in addition to date of extraction.

In addition to ergosterol extraction, an encapsulation was performed on each lyophilized sample to measure the C:N content of the soil. Using a small scoop, 20 mg of soil from each Whirl-Pak bag was measured using a balance and packaged into 8 × 5 mm tin capsules. Once filled, the capsules were sealed by pinching the top of the capsule until closed using a clean pair of forceps, being careful to avoid squeezing the sediment at the bottom. With the addition of a second pair of forceps, the top corners of each capsule were held, then folded inward to make a ‘Z’ shape. The top of the capsule was then folded down twice, forming a small ball. Each ball was checked for punctures before being placed in a labeled 96 well polystyrene assay plate. The same methods were used to create a set of 4 atropine standards at 0.25 mg, 0.50 mg, 0.75 mg, and 1.00 mg. A spreadsheet was used to keep track of all sample labels, weights, encapsulation dates, and corresponding well plate locations. Each tin capsule was analyzed using a Carbon

Nitrogen Elemental Analyzer as well as quality controls for every 10 samples and four standards per sample set analyzed.

Data Analysis

Carbon (% C) and nitrogen (% N) data were analyzed separately using *t*-tests with cogongrass as the main effect. Results were considered significant at $\alpha \leq 0.05$. Analyses were conducted using JMP software version 17.2.0 (JMP Statistical Discovery, LLC, Cary, NC).

CHAPTER III: Results

Soil Carbon

Mean soil carbon (% C) was 23.4% greater in soil collected from cogongrass (1.79 ± 0.15, Table 1) than soil not invaded by cogongrass (1.37 ± 0.15, Table 1) although this difference was not significant (P=0.054; Figure 1).

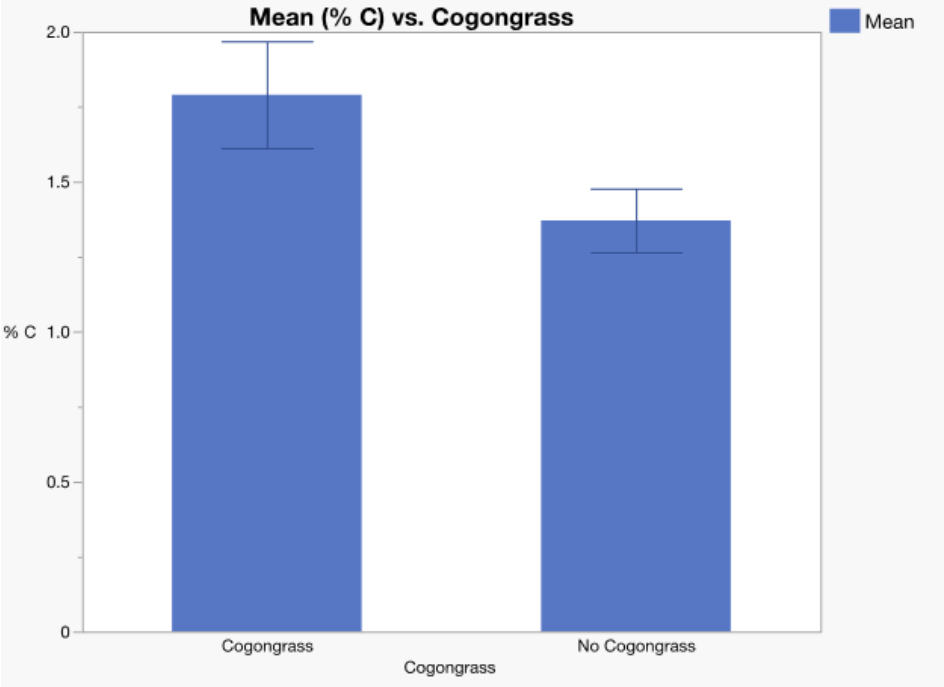

Figure 1. Soil % C in cogongrass-infested soil and normal soil (P=0.054). Bars represent 1 ± SE.

Level	Number	Mean	Std Error
Cogongrass	20	1.79000	0.14886
No Cogongrass	20	1.37100	0.14886

Table 1. Mean % C in cogongrass-infested soil and normal soil**.** N = 20.

Soil Nitrogen

Mean soil nitrogen (% N) was 26.7% greater in soil collected from cogongrass (0.060 ± 0.006) than soil not invaded by cogongrass (0.044 ± 0.006) although this difference was not significant (P=0.068).

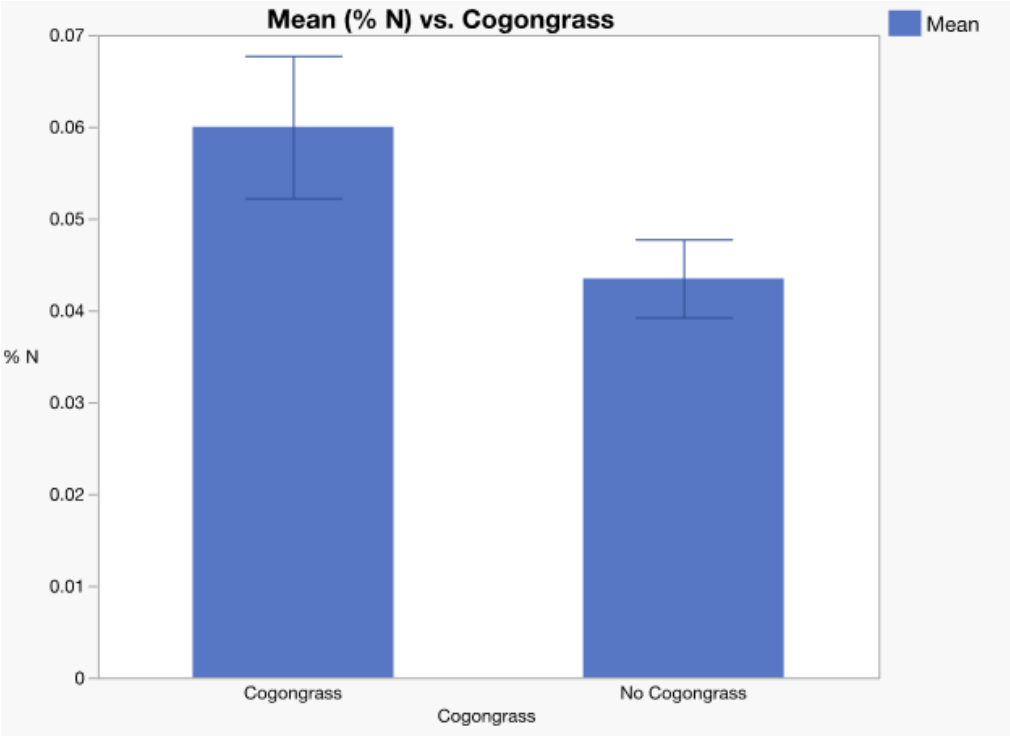

Figure 2. Soil % N in cogongrass-infested soil and normal soil (P=0.068). Bars represent 1 ± SE.

Level	Number	Mean	Std Error
Cogongrass	20	0.060000	0.00621
No Cogongrass	20	0.043500	0.00621

Table 2. Mean % N in cogongrass-infested soil and normal soil**.** N = 20.

Ergosterol

The HPLC auto sampler malfunctioned and ergosterol samples were not able to be analyzed by the completion of this thesis.

CHAPTER IV: Discussion

When an invasive plant takes root in a new habitat, its impacts on the ecosystem structure are not limited to competition for space and other resources at the surface level. Invasive plants are also known to alter the soil composition of the habitats they invade, primarily through changes to the composition and functionality of soil biota (Zhang et al. 2019). Soil biota, consisting of all root-associated organisms and their consumers, is heavily influenced by the vegetative assemblage of the plant community it inhabits, and vice versa (Wardle et al. 2004). This dynamic is the result of the variance in quality and quantity of resources returned to the soil by different species of plants within a community, which determines the suitability of different soils for the maintenance of specific soil biota (Wardle et al. 2004). Maintenance of native soil biota assemblages is important because these organisms directly influence the transfer of resources between and among plants and decomposers. When an invasive plant species becomes prevalent in an ecosystem, it can alter the soil biota there not only by using and releasing resources differently than a native species would, but also through the release of allelopathic compounds into the rhizosphere that may negatively affect the soil biota typically associated with native plant species, thereby obstructing the typical flow of nutrients and further encouraging the expansion of the invasive plant species to the detriment of native plant species (Wardle et al. 2004, Zhang et al. 2019).

Competition between plant species at the mycorrhizal level is one possible explanation for the success of invasive grass species like cogongrass. Previous studies have found that cogongrass invasion can negatively impact the mycorrhizal communities of native longleaf pine savanna vegetative species through the release of allelopathic

rhizochemicals, suggesting that competition between native and invasive species may be as prevalent in the soil as it is on the surface (Hagan et al. 2013). Through allelopathic interference, cogongrass stunts the growth of native plant species by incapacitating their mycorrhizal symbiotes, reducing their ability to take up nitrogen and other nutrients required for growth (Hagan et al. 2013). All the while, the rapid expansion of clonal grasses combined with their dual nitrogen-uptake capable arbuscular mycorrhizae allows these invasive species to monopolize the consumption of nutrients in the soil, further starving the native species (Hagan et al. 2013). In a study on the effects of cogongrass on loblolly pine (*Pinus taeda*) stands above and below the soil surface, researchers found that stands of loblolly pine inundated with cogongrass saw a reduction in ectomycorrhizal colonization among the pine roots and a reduction in both vegetative and microbial diversity compared to plots without cogongrass (Trautwig et al. 2017).

For this study, an analysis and comparison of the ergosterol content in cogongrass-infested and cogongrass-free soils was intended to serve as an indicator of soil biota quantity, with a hypothesized increase in ergosterol concentration expected to accompany cogongrass, as the increase in vegetative biomass associated with cogongrass would result in an increased presence of mycorrhizal fungi. Unfortunately, an equipment malfunction prevented us from completing our analysis of soil ergosterol content.

The C:N ratio of an ecosystem can be predicted, to an extent, by the makeup of said ecosystem's plant community. Studies have found that different vegetative assemblages are associated with different litter types, which can impact the C:N ratio of the soil by determining the rate of decomposition by the soil biota in addition to the variance in rate of nutrient uptake and productivity across plant species (Getino-Álvarez

et al. 2023, Wood et al. 1992). In general, increasing the density of pine species in an ecosystem, thus increasing the prevalence of pine-derived litter in the soil, increases the C:N ratio of the soil (Getino-Álvarez et al. 2023). However, the addition of an invasive species can also impact the C:N ratio of soils in an ecosystem, with the trend across most studies indicating that the introduction of an invasive species will typically decrease soil C:N (Liao et al. 2008). This is because the increase in vegetative and mycorrhizal biomass associated with a successful invader typically increases productivity within an ecosystem, thus increasing carbon availability, which allows for an increase in nitrogen fixation by nitrifying microbes (Liao et al. 2008). While both carbon and nitrogen stocks are generally increased by an invasive species, the disproportionate rise in soil nitrogen due to increased nitrogen fixation compared to the moderate increase in carbon output results in an expected net reduction in the C:N ratio.

Our results are somewhat consistent with most of the literature in that both soil % C and % N were greater in cogongrass-infested patches compared to normal soils. However, the difference in C:N between cogongrass conditions was not statistically significant in our study, likely due to a similar rate of increase across both elements.

Future studies should further examine the effects of cogongrass invasion on soil microbes. Although we were unable to analyze our samples for ergosterol, an earlier study found that mycorrhizae were less abundant in cogongrass-infested soils in loblolly pine plantations (Trautwig et al. 2017). Little is known, however, regarding the effects of cogongrass on microbial diversity. The allelopathic nature of cogongrass has been shown to alter the plant community in pine understories (Hagan et al., 2013). We predict that

these allelochemicals will have a similar effect on both fungal and bacterial communities in cogongrass-infested soils.

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