



Intensification differentially affects the delivery of multiple ecosystem services in subtropical and temperate grasslands

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ABSTRACT

Intensification, the process of intensifying land management to enhance agricultural goods, results in "intensive" pastures that are planted with productive grasses and fertilized. These intensive pastures provide essential ecosystem services, including forage production for livestock. Understanding the synergies and tradeoffs of pasture intensification on the delivery of services across climatic regions is crucial to shape policies and incentives for better management of natural resources. Here, we investigated how grassland intensification affects key components of provisioning (forage productivity and quality), supporting (plant diversity) and regulating services (CO₂ and CH₄ fluxes) by comparing these services between intensive versus extensive pastures in subtropical and temperate pastures in the USDA Long-term Agroecosystem Research (LTAR) Network sites in Florida and Oklahoma, USA over multiple years. Our results suggest that grassland intensification led to a decrease in measured supporting and regulating services, but increased forage productivity in temperate pastures and forage digestibility in subtropical pastures. Intensification decreased the net CO₂ sink of subtropical pastures while it did not affect the sink capacity of temperate pastures; and it also increased environmental CH₄ emissions from subtropical pastures and reduced CH₄ uptake in temperate pastures. Intensification enhanced the global warming potential associated with C fluxes of pastures in both ecoregions. Our study demonstrates that comparisons of agroecosystems in contrasting ecoregions can reveal important drivers of ecosystem services and general or region-specific opportunities and solutions to maintaining agricultural production and reducing environmental footprints. Further LTAR network-scale comparisons of multiple ecosystem services across croplands and

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grazinglands intensively vs extensively managed are warranted to inform the sustainable intensification of agriculture within US and beyond. Our results highlight that achieving both food security and environmental stewardship will involve the conservation of less intensively managed pastures while adopting sustainable strategies in intensively managed pastures.

1. Introduction

Grasslands are among the most widespread ecosystems in the world providing essential ecosystem provisioning services especially forage for livestock and milk production (Reid et al., 2008) that constitute a significant portion of the global food supply (O'Mara, 2012). Grasslands provide other essential supporting and regulating ecosystem services: maintaining biodiversity, water, nutrient cycling, and greenhouse gases [GHGs] mitigation (White et al., 2000; MEA, 2005; Dass et al., 2018). To meet increased global demand of food and energy for a growing human population, a large portion of global grassland ecosystems are managed intensively (White et al., 2000). Popular practices for intensively managed perennial pastures (hereafter referred to as intensive pastures; see Paudel et al., 2021 for definition) include (i) planting selected, more productive, perennial grass species that are often non-native and predominantly established as a monoculture; (ii) use of agrochemical products (fertilizers, amendments such as liming, manure and biosolids, and in some cases herbicides); and (iii) use of water irrigation and/or drainage (Auclair, 1976; Isselstein et al., 2005).

The management of pastures has global significance for agriculture production, biodiversity conservation, and climate change mitigation (O'Mara, 2012; Boval and Dixon, 2012) because they occupy ~50% of global grasslands (Friedl et al., 2010). Confronting the global challenges of pasture intensification requires comparing trade-offs among ecosystem services beyond forage productivity alone (Foley et al., 2005). More diverse and less-intensively managed mixtures of native pastures (hereafter, extensive pastures; see Bengtsson et al., 2019, Paudel et al., 2021 for definition) could provide food and economic return for ranchers and landowners while reducing negative biological and environmental impacts of management typical of intensive pastures (Hooda et al., 2000; Tilman et al., 2006). Yet, forage quality, livestock weight gain, and milk production may be higher on intensive pastures than on extensive pasture, for example in central Florida (Brown and Kalmbacher, 1998; McClelland et al. unpublished) and in southern Brazil (Dick et al., 2015).

Although information about the delivery of services from intensive and extensive pastures is crucial to inform conversations about biodiversity, greenhouse gas (GHG) mitigation, and sustainable livestock production with policymakers and the public, the research to evaluate these services is limited. The inconclusiveness of results suggest ecosystem services vary with grassland management, local abiotic variables (e.g., soil moisture; Risch and Frank, 2007), regional climatic conditions (temperature and precipitation; Soussana et al., 2004), and landscape edaphic conditions (soil type and elevation). Furthermore, previous studies have frequently focused on only one or two services (Sollenberger et al., 2019), such as diversity (Dauber et al., 2010), productivity (Johnson et al., 2010; Griffith et al., 2011), and C sequestration (Machmuller et al., 2015) without considering the tradeoffs or synergies that can arise when considering multiple ecosystem services.

In this study, our objectives were (i) to evaluate key components of provisioning services (aboveground biomass production and forage nutritive value), supporting services (plant alpha diversity), and regulating services (CO₂ and CH₄ fluxes) from extensive and intensive pastures in subtropical and temperate climates over multiple years, and (ii) to investigate how intensification affected the delivery of multiple ecosystem services across two ecoclimatic regions. We hypothesized that provisioning, supporting, and regulating services would differ between extensive and intensive pastures regardless of ecoclimatic region. We addressed the objectives by focusing our research on subtropical humid

and continental humid (temperate) grasslands at two USDA Long-term Agroecosystem Research (LTAR) network sites. Globally, these two grassland types occupy about 50% of the grassland biome and characterization of how pasture intensification affects multiple ecosystem services at regional and national scales is critical to informing sustainable intensification of agriculture, the challenge of advancing agricultural production while reducing environmental footprints and enhancing non-production agroecosystem services to society (Kleinman et al., 2018; Spiegel et al., 2018). We define pasture intensification as the combination of management practices (selection of grass species, fertilizer and herbicide application, and greater grazing intensity) and landscape factors (elevation and soil type) to increase productivity, and thus we compare services from extensive and intensive pastures as different holistic pasture-types.

2. Material and methods

2.1. Long-term agroecosystem research (LTAR) study sites

This study was carried out at Archbold Biological Station's Buck Island Ranch (BIR) in Lake Placid, Florida (27°09' N, 81°11' W), one part of the ~12,000 ha Archbold-University of Florida LTAR site, and at the United States Department of Agriculture-Agricultural Research Service's Grazinglands Research Laboratory (GRL) in El Reno, Oklahoma (35°33' N, 98°02' W) (Fig. S1). The BIR is a 4290-ha commercial cow-calf ranch that operates as an ecological field station and is a division of Archbold Biological Station. This area has a typical, humid, subtropical climate with strong seasonality (see Chamberlain et al., 2017). The two distinct seasons include a wet season (mid-May through mid-October) and a dry season (late-October through early-May). The area receives mean annual precipitation of ~1300 mm, with an average high summer air temperature of ~33 °C (July-August) and minimum winter temperature of ~11 °C (December-January) for the 1980–2017 period (DayMet database; Thornton et al., 2017). The GRL, a tallgrass prairie that supports year-round cow-calf production in the Southern Great Plains, has a humid continental climate; typical of temperate regions with a mean annual precipitation of ~890 mm and an average maximum summer air temperature of ~33 °C (July-August) and minimum winter temperature of ~ -3 °C (December-January) for the 1980–2017 period (DayMet database; Thornton et al., 2017). Temperature varies considerably throughout the year with hot summers and cold winters. Precipitation varies by year and season but the area tends to receive much of the rainfall from spring through early summer and fall. Both sites are part of the USDA's Long Term Agroecosystem Research network that provides a sophisticated platform for research and development on sustainable agroecosystems across the US (Spiegel et al., 2018). At BIR, provisioning and supporting services were measured in 2014 and 2015; regulating services were measured in 2013, 2014 and 2015. At GRL, provisioning and supporting services were measured in 2014, 2015, 2016 and 2018, and regulating services were measured in 2014, 2015 and 2016.

Pastures at BIR and GRL consist of two main types; intensive and semi-native (extensive) in BIR and intensive and native (extensive) in GRL. At both sites, intensive pastures differ from extensive pastures in how they are managed, how they were established, and plant community structure. At BIR, "extensive" pastures were defined as areas dominated by native grasses with limited cover of a non-native forage grass and no known history of fertilization (Swain et al., 2013). At GRL, "extensive" pastures were less intensively managed pastures dominated by native grasses that received occasional herbicide application. At both

BIR and GRL, we defined intensive pastures as the combination of management practices (selection of grass species, fertilizer and herbicide application, and greater grazing intensity) and landscape factors (elevation and soil type) to increase productivity. At BIR, all measurements were made in one 16-ha area of an intensive pasture and in one 16-ha extensive pasture; at GRL, measurements were made on one 63-ha intensive pasture and one 64-ha extensive pasture.

In subtropical regions of Florida, grazed pastures (hereafter, subtropical pasture) cover > 35% of the total land area of the state (Ramankutty et al., 2008; U.S. Department of Agriculture, 2009). There are several differences between subtropical intensive and extensive pastures, including management, soil type, plant composition, elevation, and hydrology that contribute to the classification of intensive and extensive (Supplementary Table S1). Most of the conversion of native prairies to pastures in Southeastern USA occurred in the 1940's and 1950's (Swain et al., 2013). Before land conversion, dry native prairies were typically on Spodosols and they were at higher elevation on the landscape than native wet prairies (Abrahamson and Hartnett, 1990; Stephenson, 2011). Native rangeland can still be found in Florida including pine flatwoods, dry prairie, wet prairie and marshes. The conversion of dry native prairies and some mesic pine flatwoods to intensive pastures resulted in a mosaic of land uses in Florida in which intensive pastures typically occur on Spodosols in higher and drier areas of the landscape while the wet prairies mostly occur on lower, wetter parts of the landscape (i.e. lower elevation) on Alfisols (Boughton et al., 2010; Swain et al., 2013). Alfisols are similar in hydrology to the typical Spodosols of central Florida, but they hold water slightly longer during wet periods due to their loamy to clayey subsoils (Stephenson, 2011).

In our study, the extensive pastures at BIR occupied lower elevations than the intensive pasture and consisted of several C₄ native and non-native perennial grasses managed without fertilizer applications (Supplementary Table S1). The extensive pasture in this study contained on average 12% bahiagrass, 42% *Andropogon* spp., 40% *Coleataenia longifolia*, along with other forbs and graminoids (Boughton unpublished). Soils under the extensive pastures at BIR are primarily Alfisols, but they include some Spodosols. We collected all measurements for the study in an extensive pasture with sandy loamy Malabar soil (Alfisol) (Supplementary Table S1). In contrast, intensive pastures are regularly fertilized (nitrogen, ~26 kg/ha every 2 years) and limed (~229 kg/ha every 5 years; Swain et al., 2013) and historically received phosphorus fertilizer until 1986; they are more extensively ditched and are better drained, and occur largely on Immokalee sand (Spodosols). All measurements in the intensive pasture occurred in a pasture with fine sandy Spodosol (Supplementary Table S1). During the study period, none of the pastures where measurements were taken received any fertilizer. Intensive pastures predominantly (85% cover on average) consisted of warm season C₄, non-native Bahia grass (*Paspalum notatum* Flueggé) (Swain et al., 2013). With higher elevation, the two-year mean (2013–2014) soil wetness was higher in extensive (37.4% volumetric water content; VWC) than in intensive pasture (30.3% VWC) (Gomez-Casanovas et al., 2018). Both pasture types have been grazed regularly and burned every 2–3 years in winter to manage for forage production and suppress woody plants. For the years studied, intensive pasture was grazed with greater stocking density (1.4 Animal Unit Days/ha; AUD/ha) compared to extensive pasture (0.53 AUD/ha) (Supplementary Table S1). Grazing in both pasture-types was rotational and periods of rest occurred, average rest days for the extensive pastures was 66 days between grazing events and average rest days for intensive pastures was 24 days of rest between grazing events. No herbicides were applied to either the intensive or the extensive pastures at BIR.

Continental humid grasslands (henceforth, temperate pastures), within the south central Great Plains, at GRL were native tallgrass prairie (extensive pasture) dominated by a mixture of native warm season C₄ grasses and the intensive pasture was a monoculture of an introduced warm season grass – Old World Bluestem (*Bothriochloa ischsemum* (L) Keng) (Supplementary Table S1). The extensive and

intensive pastures are located at 414 m above sea level on a gently sloping east and west facing aspects, respectively (Peterson et al., 2018). The soil type for these pastures was Bethany silty clay loam, and the pastures share broadly similar soil physical and chemical properties (Peterson et al., 2018), except the intensive pasture soils are slightly hardpan. Soil moisture between the pastures vary with time of year and weather pattern, but typically average 15–26% VWC in intensive pasture and 18–25% VWC in extensive pasture during forage growth period (Peterson et al., 2018). These grasslands differ in their management (Supplementary Table S1). Intensive pasture is grazed with slightly greater intensity (average stocking density during peak growing season for the year 2015–16 = 0.74 AUD/ha) than extensive pasture (average stocking density for the same period = 0.58 AUD/ha). Baling hay occurs in the intensive pasture as necessary. Similar to BIR, grazing in both pasture-types was also rotational and periods of rest. Extensive pasture was grazed for 30-day periods with 90 days of rest between grazing events. However, intensive pasture experienced grazing at various times of the year depending on forage growth and availability. The intensive pasture was fertilized (89.7 kg/ha urea) annually and treated with picloram + 2,4-D, (Grazon® P + D; Dow AgroSciences, Midland, MI, USA) at a rate of 2339 mL/ha to suppress broadleaf forbs. The extensive pasture historically has never been fertilized but weed suppression occurs as needed with Grazon® P + D (2339 mL/ha) following burning for woody plant control; currently a four-year cycle. The intensive pasture is burned on the same cycle.

2.2. Measurement of provisioning and supporting services

Forage quantity, a provisioning service, was determined by harvesting aboveground live plant biomass for two years (2014, 2015) in subtropical pastures, and four years (2014, 2015, 2016 and 2018) in temperate pastures (Supplementary Table S1). In the subtropical pastures, we used eight randomly placed moveable-exlosures and grazed paired plots per pasture and harvested aboveground live plant material within circular 0.25 m² plots (see, Knapp et al., 2012). In each plot and each year, biomass was measured approximately bi-monthly throughout the year to obtain aboveground net primary productivity (ANPP). ANPP was calculated as $ANPP = \sum ME(T_2) - PP(T_1)$, where ME = exclosures and PP = grazed paired plot. T₁ = time 1 and T₂ = time 2 (McNaughton et al., 1996; Sala and Austin, 2000). Fresh samples were dried to a constant weight at 60 °C for 48 h and weighed to determine dry aboveground biomass.

In the temperate grasslands, in each pasture we laid out four ~400 m long east-west transects that were spaced about 100 m apart to collect biomass data from 2014, 2015, 2016 and 2018 during peak growing season (i.e., June to August). We located three 0.25 m² square plots (~200 m apart) along the transect to capture potential variability within the pasture and these locations remained the same throughout the years. Before we clipped the biomass, cattle were removed from the pasture at least a month in advance.

The nutritive value (percent crude protein, (%CP) and percent in vitro true digestibility (%IVTD) of plant tissue, a provisioning service, was measured at the same pasture sites sampled for biomass. In the subtropical pastures, forage quality was measured by clipping biomass from 12 random points per pasture once a month in 2018, and in temperate pastures it was measured in 2014 and 2015 (Supplementary material S2) from aboveground live plant material concurrent with aboveground biomass collection as described above. Biomass was dried at 60 °C for 48 h and then ground with a Wiley Mill to pass through a 1 cm sieve. In the subtropical pastures, the % CP was determined by measuring N concentration in the harvested plant material. Plant samples at BIR were digested using a modification of the aluminum block digestion procedure of Gallaher et al. (1975) to determine N concentration. Sample weight was 0.25 g, the catalyst used was 1.5 g of 9:1 K₂SO₄:CuSO₄, and digestion was conducted for at least 4 h at 375 °C using 6 mL of H₂SO₄ and 2 mL H₂O₂. Nitrogen in the digested state was

determined by semiautomated colorimetry (Hambleton, 1977). %CP was calculated as N multiplied by 6.25. The %IVTD was determined by a modification of the two-stage technique (Moore and Mott, 1974) for both sites. First, forage samples were incubated with rumen microorganisms for 48 h followed by incubation with acid-pepsin. In temperate grassland, the concentration of N in a harvested plant material was measured using a combustion technique (Sweeney, 1989; Elemental Analyzer, Elementar Vario Max, Elementar Analysensysteme GmbH, Germany). For subtropical grassland, all laboratory analyses were conducted at the Forage Evaluation Support Laboratory of the University of Florida, FL, USA using the recommended protocols for these forage species (<https://agronomy.ifas.ufl.edu/service-labs-and-facilities/forage-evaluation-support-laboratory/>). For temperate grassland, laboratory analyses were performed at Soil, Water, and Forage Analytical Laboratory of Oklahoma State University, OK, USA.

Plant species richness (alpha diversity), a supporting service, was measured using different techniques at each site. At BIR, alpha diversity was measured in 120 random 1 m² circular plots (60 in each of the two study pastures) in July 2014. This sampling strategy was selected to ensure equal sampling across the pasture and to adequately sample heterogeneous vegetation. At GRL, multi-scale modified Whittaker plots following National Ecological Observatory Network (NEON) Terrestrial Observation System (TOS) protocols were used (Barnett, 2014; Thorpe et al., 2016). In July 2018, in the two temperate pasture sites, we randomly established three 20 m × 20 m permanent plots per pasture. Each plot comprised of four 10 m × 10 m subplots and each subplot contains nested subplots: a 1 m × 1 m subplot nested in a 3.16 m × 3.16 m subplot in each of two corners (for detail see Barnett, 2014 and Supplementary Fig. S2 for plot layout). Presence of each individual species was recorded in each 1 m × 1 m nested subplot and the species data were used to determine alpha diversity. The total number of 1 m² plots surveyed for alpha richness at GRL was 48 (24 in each pasture). Although the methodology used across sites differs, species area curves showed that species richness reached an asymptote at each site indicating adequate sampling at each site.

2.3. Measurement of regulating services

At the subtropical and temperate pastures, CO₂ fluxes were measured using the eddy covariance technique. Fluxes of CH₄ were measured using the eddy covariance technique at the subtropical pastures, and using the static chamber method at the temperate pastures (Supplementary Table S1). The eddy covariance data from subtropical pastures were separately reported in Chamberlain et al. (2017) and Gomez-Casanovas et al. (2018). At the subtropical pastures, CO₂ and CH₄ flux measurements were recorded from July 2013 through October 2015 (a total of 28 months). At temperate pastures, CO₂ fluxes were recorded from January 2015 through December 2016 (a total of 22 months) (Supplementary Table S1).

2.3.1. Eddy covariance measurements

At both ecoregions, an eddy covariance tower was installed at the center of each pasture. The eddy covariance tower consisted of a three-dimensional sonic anemometer for measuring wind speed, direction, and virtual temperature, a CO₂/H₂O infrared gas analyzer at both sites. At both temperate pastures, the CO₂ analyzer was an open-path LI-7500, and the sonic anemometer was a CSAT3 (Campbell Scientific Inc., Logan, UT, USA). In subtropical pastures, an enclosed-path LI-7200 (LI-COR Biosciences, Lincoln, NE, USA) and a Young 81000 V (R.M. Young Company, Traverse City, MI, USA) were used to measure fluxes of CO₂ in the extensive pasture, and a LI-7500 and a CSAT3 in intensive pasture. At the subtropical site, both pastures were also equipped with an open-path LI-7700 (LI-COR Biosciences, Lincoln, NE, USA). As detailed below, uncertainty in fluxes due to the use of different instruments was accounted for in the subtropical pastures as previously described (Wang et al., 2013). In general, instrumental errors in CO₂ fluxes due to the use

of an open or an enclosed LICOR gas analyzer, and a CSAT3 or a Young 81000 sonic anemometer have been reported to be low in previous studies (10% or below; Burba et al., 2012; Mauder and Zeeman, 2018; Schmidt et al., 2012).

At both sites, raw data were acquired at 10 Hz. Instruments were always kept at a height 1.34 times the average plant height to minimize occasions when the flux footprint extended beyond the plot's edge (Raupach, 1994). Raw data were processed with EddyPro (LI-COR Biosciences, Lincoln, NE, USA) and data corrections included cross-wind correction of sonic temperature by the firmware (81000 V, R.M. Young Company, Traverse City, MI, USA), lagged covariances between vertical wind velocity and each flux scalar, corrections for air density fluctuations (Webb et al., 1980) and for spectroscopic effects for CH₄ fluxes (Moncrieff et al., 1997; Moncrieff et al., 2004). Low quality, non-representative fluxes as well as fluxes below the u* - threshold (Chamberlain et al., 2017; Gomez-Casanovas et al., 2018) were discarded. The threshold for u* for CO₂ and CH₄ fluxes was 0.1 m s⁻¹ for both, subtropical and temperate pastures. In addition, we discarded fluxes when more than 70% of the half hour flux occurred from an area outside of each pasture site using Hsieh cross-wind-integrated flux footprint model (Hsieh et al., 2000).

Gaps in the half-hour CO₂ flux record were filled using the Eddy covariance gap-filling and flux partitioning online tool (<http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php>; (Reichstein et al., 2005; Wutzler et al., 2018)). This tool fills gaps in CO₂ records using the Look-Up table and Mean diurnal course methods (Wutzler et al., 2018), and partitions CO₂ fluxes into ecosystem respiration (Reco) and gross primary production (GPP). Half-hour CH₄ gaps of < 2.5 h were filled using a linear interpolation, and gaps of > 2.5 h were filled using the mean diurnal variation method (Chamberlain et al., 2016; Dengel et al., 2011). Missing CH₄ and H₂O values for a specific half-hour were replaced by the mean of that specific half-hour of four adjacent days (Dengel et al., 2011). Preliminary trials showed that using this method but increasing the time window for adjacent days up to one month did not affect cumulative annual CH₄ and H₂O sums when climatic conditions remained similar. When cattle were present in the grazed pasture, half-hour CH₄ missing values were filled using values from adjacent days with cattle present. When cattle were not present in the grazed pasture, half-hour CH₄ missing values were filled using values from adjacent days without cattle.

Total uncertainty for each scalar was derived by adding random flux uncertainty to gap-filling uncertainty following (Richardson and Hollinger, 2007) for all sites. In addition, for the subtropical pastures we also added the relative instrumental uncertainty in fluxes to total uncertainty as previously described (Wang et al., 2013) due to the use of different instruments. Random measurement uncertainty in half-hour fluxes was estimated as described previously (Finkelstein and Sims, 2001), and gap-filling uncertainty was calculated by adding random artificial gaps to the records and applying the gap filling algorithm (Reichstein and Beer, 2008). The relative instrumental uncertainty for C fluxes from subtropical pastures was calculated through the determination of the lack of surface energy balance closure as previously proposed (Mauder et al., 2013). In our subtropical sites, the energy balance deficit was between 9% and 30% of the mean (Gomez-Casanovas et al., 2018). We took a conservative approach in this study, and the relative instrumental uncertainty was considered 30% of the CO₂ fluxes. A review by Schmidt et al. (2012), analyzing 84 Ameriflux sites, reported a relative instrumental error derived from using either an open (e.g., LI-7500) or an enclosed (e.g., LI-7200) path gas analyzer of 5%, and an uncertainty of 10% derived from using different sonic anemometers. The uncertainty values reported previously (Schmidt et al., 2012) are well below the 30% uncertainty considered in our study, implying that our approach is rather conservative.

Auxiliary measurements including air temperature, relative humidity, net radiation, photosynthetically active radiation, soil heat flux, soil temperature, moisture, and precipitation were compiled at 30-min

intervals and logged to a CR3000 datalogger (Campbell Scientific, Logan, UT, USA) synchronized to the LI-7200, LI-7500 and LI-7700 as described in (Gomez-Casanovas et al., 2018).

2.3.2. Estimates of soil CH₄ fluxes using static chamber method

At temperate pastures, we used static chamber methods to measure CH₄ fluxes from soil underlying the pastures. These CH₄ measurements were obtained bi-weekly from March through November in 2015 and 2016 (Supplementary Table S2). Stationary chambers were located within 200 m radius of the EC tower in both extensive and intensive pastures. Soil flux static chambers were placed in a serpentine pattern of five replicates. Static chamber bases and chamber tops were made from polyvinyl chloride (PVC). Bases measured 25 cm diameter by 10 cm high (a total volume of 4906.25 cm³) were inserted into the ground to a depth of 5 cm (Hutchinson and Mosier, 1981), one month before sampling.

Static chamber bases were affixed with chambers tops of complementary size equipped with a septa for sampling, vent and rubber gasket to prevent leaks. When the chamber top was placed on the base at time zero, a sample was obtained from the chamber using a 60 mL syringe equipped with a stopcock (Hutchinson and Mosier, 1981). The gas sample was placed in an evacuated 20 mL MicroLiter® crimp top vial (#20–2300, MicroLiter, A Wheaton Company, Millville, New Jersey, USA). This process was repeated for each replicate at time zero, 15, 30 and 45 min post closure. The vials were stored in a cooler until transport to the laboratory for processing on a Shimadzu gas chromatograph, GC-2012, equipped with flame ionization detector (FID), electron capture detector (ECD) and thermal conductivity detector (TCD) (Shimadzu, Kyoto, Japan). CH₄ flux was estimated using the change in gas concentrations in the chamber headspace at minutes 0, 15, 30 and 45, after factoring in chamber size, atmospheric pressure, soil and air temperatures (pre- and post-sampling). Annual fluxes of CH₄ were estimated using the linear interpolation method. Cumulative emissions from each month were then summed to produce the annual flux. The annual flux using linear interpolation has been shown to provide accurate annual estimates of CO₂ and N₂O fluxes from discrete measurements (Mishurov and Kiely, 2011; Gomez-Casanovas et al., 2013) and CH₄ (Pittelkow et al., 2013).

2.3.3. Estimates of CH₄ fluxes from soil derived from the eddy covariance method

In our subtropical pastures, the eddy covariance method measures CH₄ from both soils (i.e. paddocks and ditches) and enteric ruminant fermentation. To investigate how intensification affects CH₄ fluxes from soils we partitioned these fluxes into its sources using an approach as in Gomez-Casanovas et al. (2018). When cattle were present, methane fluxes in the pasture were derived from enteric ruminant fermentation and from soils (i.e. paddock and ditches), and when cattle were not in the pastures, CH₄ fluxes from the eddy covariance were derived from soils. To estimate cumulative CH₄ emission from soil we first estimated emissions from enteric ruminant fermentation using the IPCC Tier 2 methodology, in which emissions from cattle were calculated from estimated energy requirements for metabolic activity of grazers (Chamberlain et al., 2017; Dong et al., 2006; Gomez-Casanovas et al., 2018). Then, CH₄ emissions by enteric ruminant fermentation were subtracted from CH₄ fluxes measured with the eddy covariance method over the same time period to estimate the flux from soil. These data were separately published in Chamberlain et al. (2017) and Gomez-Casanovas et al. (2018).

2.3.4. Global warming potential (GWP) of pastures

Fluxes of GHGs from each pasture were expressed as CO₂ equivalents to calculate the GWP (Bridgham et al., 2013; Neubauer and Megonigal, 2015). For a 100-year time horizon, the GWP for CH₄ fluxes was 28 times greater than CO₂ (Myhre et al., 2013). This calculation does not include N₂O fluxes and therefore refers to the GWP associated with C fluxes.

2.4. Statistical analysis

One way mixed model analysis of variance (mixed model ANOVA) was used to compare aboveground dry biomass (kg ha⁻¹) production between the pasture-types and at each site separately with biomass as a continuous response variable, pasture-type and year as fixed predictor variables, and plot number nested within pasture ID as random variable. Linear mixed models with the random effects (plot # as random effect) was used to assess aboveground dry biomass for each year separately. We used mixed model ANOVA to avoid likely temporal and spatial pseudoreplication. Prior to ANOVA analyses, data were checked for normality and homogeneity with Shapiro-Wilk and Levene's tests, respectively. Whenever necessary, data were square root transformed to achieve normality and homogeneity of variances (Zar, 1999). One-way mixed model ANOVA was used to compare the nutritive value between the pastures-types in each year and at each site separately with nutritive value—% CP and % IVTD as continuous response variables and pasture-type and year as fixed predictor variables, and pasture ID as a random variable. In addition, for each site, we compared overall % CP and % IVTD between the pasture types over the measurement periods using mixed model ANOVA.

We described plant species diversity of each pasture using alpha diversity (number of individuals present in each sampling plot; Whitaker, 1972). One-way mixed model ANOVA was used to compare alpha diversity between the pastures in each year at each site. Differences in cumulative C fluxes between pasture types were evaluated by comparing measured values and their uncertainty (Baldocchi, 2003; Desai et al., 2008; Falge et al., 2001; Reichstein et al., 2005). At temperate grasslands, we used a repeated measures mixed model separately to test the effects of pasture types, time, and their interactions on ecosystem scale CH₄ efflux. Post-hoc comparisons were performed with Tukey HSD multiple comparisons between the pastures and across the months when the results indicated significant overall differences.

Regression analyses were performed between average monthly air temperature and cumulative monthly net ecosystem CO₂ and CH₄ fluxes and between total monthly precipitation and cumulative monthly net ecosystem CO₂ and CH₄ fluxes. Whenever necessary, monthly total CO₂ and CH₄ flux data were square root transformed to achieve normality and homogeneity of variances (Zar, 1999). All statistical analyses were conducted using R statistical software (R Development Core Team, 2017) with significant effects inferred at $\alpha = 0.1$.

3. Results

3.1. Provisioning and supporting services

In subtropical pastures, there was no evidence for a clear effect of intensification on aboveground productivity ($F_{1,18} = 0.12, P = 0.27$) and aboveground biomass did not differ between the pasture-types in both years (Fig. 1a; Supplementary Table S3). In contrast, intensification increased aboveground biomass in temperate grassland across the years studied except in 2015 ($F_{1,92} = 14.16, P < 0.001$) (Fig. 1b; Supplementary Table S3).

Intensification did not consistently influence forage nutritive value. In BIR, percent crude protein (%CP) was not significantly different between the pastures ($F_{1,22} = 0.51, P > 0.1$, Table 1), but in vitro true digestibility (%IVTD) was significantly higher in intensive pasture compared to extensive pasture ($F_{1,22} = 3.297, P = 0.08$). In GRL, %CP was significantly higher in intensive pasture in 2014 ($F_{1,23} = 28.81, P < 0.001$), but it was higher in extensive pasture in 2015 ($F_{1,22} = 28.9, P < 0.001$) (Table 1). Similarly, %IVTD was significantly higher in intensive pasture in 2014 ($F_{1,23} = 16.45, P < 0.001$) and lower in 2015 ($F_{1,22} = 3.03, P = 0.09$) compared to extensive pasture (Table 1). Grassland intensification substantially decreased plant diversity in intensive pastures of both sites (Fig. 2a and Fig. 2b).

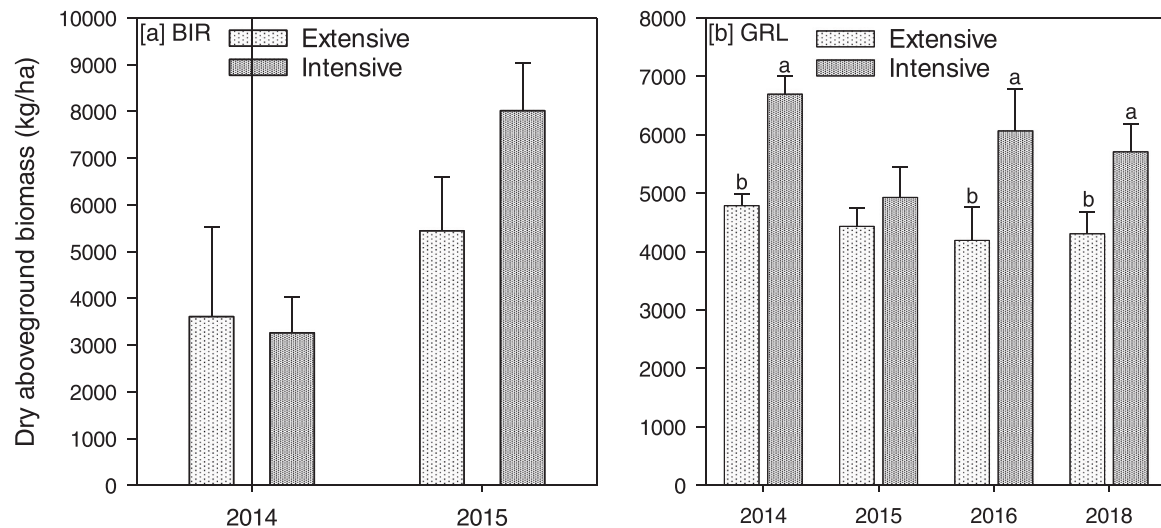


Fig. 1. . Aboveground dry biomass production compared separately for each year (means and standard error) from extensive pastures vs intensive pastures at [a] subtropical grasslands (BIR) and [b] temperate grasslands (GRL) (see Table 1 for statistics). Bars with different letters are significantly different ($P < 0.1$) based on Tukey's HSD test.

Table 1

Annual average forage quality, % crude protein (CP: mean (\pm SE)) and % in vitro true digestibility (IVTD: mean (\pm SE)) of extensive and intensive pastures in subtropical grasslands and extensive and intensive pastures in temperate grasslands. Differences between pastures within each year was indicated by letters a-b and x-y, respectively at sub-tropical and temperate grasslands. Means with the same letter were not significantly different ($\alpha = 0.1$).

Subtropical						Temperate							
Year	CP		ANOVA	IVTD		ANOVA	Year	CP		ANOVA	IVTD		ANOVA
	Extensive	Intensive		Extensive	Intensive			Extensive	Intensive		Extensive	Intensive	
2018	6.21 (\pm 0.57)	5.93 (\pm 0.61)	Pasture: ns*	31.74 (\pm 1.69) a	37.93 (\pm 1.19) b	Pasture: $P = 0.08$	2014	5.32 (\pm 0.19) x	6.81 (\pm 0.20) y	Pasture: $P < 0.001$	52.96 (\pm 1.09) x	59.37 (\pm 1.13) y	Pasture: $P < 0.001$
							2015	6.08 (\pm 0.14) x	4.99 (\pm 0.14) y	Pasture: $P < 0.001$	63.14 (\pm 0.85) x	61.064 (\pm 0.85) y	Pasture: $P = 0.095$
							Overall	5.70 (\pm 0.19)	5.90 (\pm 0.18)	Pasture: ns*	58.0 (\pm 0.83)	60.2 (\pm 0.81)	Pasture: ns*

*Non-significant

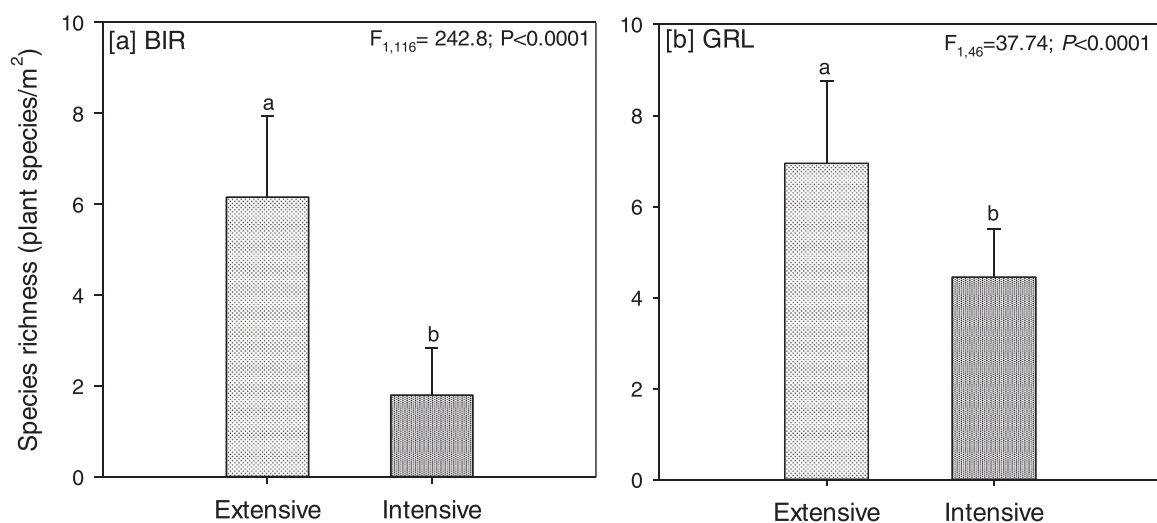


Fig. 2. . Comparison of species richness at 1 m² spatial scale (alpha diversity) (means and standard error) between extensive and intensive pastures at BIR [a] and extensive and intensive pastures at GRL [b]. Bars with different letters are significantly different.

3.2. Regulating services

Overall, intensive management reduced the net CO₂ sink strength of subtropical grassland while it did not affect the sink strength of temperate pasture (Table 2). In the subtropics, extensive pasture was a stronger net sink of CO₂ during the growing season than intensive pasture, and their sink strength was similar during the non-growing season (Supplementary Table S4). In the temperate sites, the net CO₂ sink strength of intensive and extensive pastures was similar during the growing and non-growing seasons (Supplementary Table S4). For both pasture types at both ecoregions, pastures were a stronger net sink of CO₂ during the growing season than during the non-growing season (Supplementary Table S4 and Supplementary Fig. S3b and S3d). In subtropical grasslands, intensification increased GPP and Reco by 1.44-fold and 1.6-fold, respectively (Supplementary Table S5). Intensification did not affect GPP and Reco of temperate grasslands (Supplementary Table S5). Net ecosystem CO₂ uptake increased with increasing precipitation and temperature regardless of pasture types and ecoregions (Supplementary Fig. S4 and Fig. S5).

Overall, intensification increased soil CH₄ emissions from subtropical pastures and decreased net CH₄ uptake fluxes from temperate pastures although its impact on fluxes varied across months and years (Supplementary Fig. S6a and S6b, respectively). In the subtropics, CH₄ emissions were not different in 2013 between intensive and extensive pastures, and they were 7.9-fold and 3.6-fold higher in intensive than in extensive pastures in 2014 and 2015, respectively (Table 3). In temperate pastures, there was a significant interactive effect between pasture type and time on CH₄ emissions (Supplementary Fig. S6b, $F_{17,23} = 17.2$, $P < 0.001$), and intensive pasture consistently was a weaker net sink of CH₄ compared to extensive pasture in both 2015 and 2016 (Table 3).

In subtropical pastures, CH₄ emissions increased with increases in precipitation and temperature (Supplementary Fig. S7), while temperature was the main driver of net CH₄ uptake in temperate intensive pasture (Supplementary Fig. S8d). Changes in temperature and precipitation did not affect net CH₄ uptake from temperate extensive pasture ($P > 0.05$; Supplementary Fig. S8a and Fig. S8c).

Although variable among years, intensification increased the global warming potential (increased GHGs emissions) of subtropical pastures and decreased the GHG sink capacity of temperate pastures (Table 4). In the subtropics, both intensive and extensive pastures were sources of GHG emissions except in 2015 where extensive pasture was neutral (Table 4). In the temperate ecoregion, both grassland types were sinks of GHGs (Table 4).

4. Discussion

Perennial grasslands can support multiple ecosystem services in

Table 2

Cumulative annual carbon dioxide (CO₂) fluxes of extensive and intensive pastures in subtropical grasslands and extensive and intensive pastures in temperate grasslands. The error term refers to total uncertainty derived from the sum of random flux uncertainty, gap-filling uncertainty and systematic uncertainty.

Carbon dioxide (CO ₂) (g CO ₂ -C m ⁻² yr ⁻¹)					
Subtropical			Temperate		
Years	Extensive	Intensive	Years	Extensive	Intensive
2013	-66.50 ± 4.00	-33.29 ± 19.71	2014	-99.54 [± 21.46]	NA
2014	-135.90 ± 6.00	68.65 ± 22.81	2015	-241.99 [± 19.39]	-274.005 [± 13.28]
2015	-201.44 ± 11.00	-156.29 ± 19.81	2016	-52.13 [± 26.26]	-15.96 [± 27.40]
Overall	-134.6 ± 29.50	-40.3 ± 28.30	Overall*	-174.12 ± 16.3	-144.98 ± 15.22

* includes only 2015 and 2016 data

Table 3

Cumulative and overall annual methane (CH₄) fluxes from vegetation and soil under extensive and intensive pastures at subtropical grasslands and mean annual and overall CH₄ fluxes from soil in extensive and intensive pastures at temperate grasslands. At BIR, CH₄ fluxes were measured using the eddy covariance technique and partitioning these fluxes to estimate CH₄ emission from soil. At GRL, CH₄ fluxes were measured using the chamber method.

Methane (CH ₄) (g CH ₄ m ⁻² yr ⁻¹)					
Subtropical			Temperate		
Years	Extensive	Intensive	Years	Extensive	Intensive
2013	13.2 ± 4.6	12.6 ± 4.6	2015	-33.1 ± 10.2	-19.5 ± 4.5
2014	2.27 ± 0.8	17.9 ± 6.4	2016	-49.6 ± 8.0	-23.8 ± 5
2015	3.9 ± 1.3	14.0 ± 5.1			
Overall	4.83 ± 1.6	14.8 ± 3.15	Overall	-41.3 ± 6.5	-21.7 ± 3.3

Table 4

Cumulative yearly greenhouse gas (GHG) equivalent emissions (CO₂ + CO₂ equivalent of CH₄; g CO₂-C m⁻² yr⁻¹) in extensive and intensive pastures in subtropical grasslands and extensive and intensive pastures in temperate grasslands. Fluxes of CO₂ and CH₄ were reported in Tables 2 and 3.

Subtropical			Temperate		
Years	Extensive	Intensive	Years	Extensive	Intensive
2013	364.30 [± 61.23]	470.80 [± 77.82]	2015	-1407.66 [± 126.59]	-1093.65 [± 97.15]
2014	92.09 [± 29.34]	783.21 [± 64.17]	2016	-1492.62 [± 108.30]	-659.68 [± 97.60]
2015	-44.73 [± 25.88]	404.23 [± 53.54]			
Overall	411.66 [± 13.79]	1658.24 [± 20.88]	Overall	-2900.28 [± 50.52]	-1753.33 [± 43.69]

agricultural landscapes (Werling et al., 2014). However, few studies have investigated how land intensification in perennial grasslands influences multiple ecosystem services. We compared a subset of provisioning, supporting, and regulating services across pastures managed intensively and extensively, representing subtropical and temperate perennial pastures at two LTAR sites in Florida and Oklahoma, respectively. Since subtropical and temperate grasslands represent more than 50% of the global grassland biome, these LTAR sites are broadly representative of grassland agroecosystems in their regions (Franzuebbers et al., 2019; Steiner et al., 2019; Coffin et al., 2021; Bean et al., 2021). Our study, therefore, can help understand how intensification affects the delivery of multiple ecosystem services in two of the major grassland types. Our results conform with the understanding that intensification reduces species richness (Beckmann et al., 2019; Wesche et al., 2012). However, intensification did not necessarily result in substantial increased annual forage productivity or forage quality across the study systems. Considering GHGs emitted from pastures without accounting for CH₄ emissions from enteric ruminant fermentation, grassland intensification enhanced the Global Warming Potential (GWP; increased GHG emissions) of subtropical pastures and reduced the GHG sink capacity of temperate pastures associated with C fluxes. These results suggest important ecosystem service tradeoffs resulting from the intensification of perennial grasslands across climate regions. Understanding these tradeoffs is critically important as land use intensification continues to increase globally (Foley et al., 2005; Oenema et al., 2014).

Intensification of perennial grasslands across agricultural landscapes was historically implemented to support economically viable livestock production and rural economic benefits (Beckmann et al., 2019; Spiegel et al., 2018). In our study, intensification increased forage quantity (growing season biomass) substantially in the temperate pastures supporting a positive relationship between agriculture intensification and the production reported elsewhere (Griffith et al., 2011; Chen et al., 2016; Beckmann et al., 2019). However, intensification did not significantly influence annual productivity in subtropical pastures as expected

(Fig. 1). The lack of clear evidence for greater forage production in more intensely managed subtropical pastures may be due to the level of conversion that has occurred in studied extensive pastures as well as management and landscape factors. Both the extensive and intensive pastures at the subtropical study site contained the productive non-native forage grass (*Paspalum notatum*), although there was lower coverage of this grass in extensive pastures (Gomez-Casanovas et al., 2018) and thus they may have statistically comparable productivity due to the presence of this species in both pastures. Furthermore, presence of a diverse mixture of perennial grasses, including productive *P. notatum* likely helped maintain the productivity in extensive pasture through ecological complementarity (Tilman et al., 2006; Picasso et al., 2011). The lack of a significant positive effect of intensification on forage productivity of the subtropical pasture could also be explained by a combination of management and landscape factors. Compared to intensive pastures that were ditched and are better drained as the part of intensification, extensive pastures were located at lower elevation and on soils with higher water holding capacity (Supplementary Table S1) (Chamberlain et al., 2017; Gomez-Casanovas et al., 2018), and hence soils in extensive pasture were wetter than in intensive pastures, alleviating water limitation for plant growth of extensive versus intensive pasture in the subtropics (Wang et al., 2019; Weltzin et al., 2003). Despite lower biomass production, intensive pasture still supported higher stocking density and maintained forage quality compared to extensive pasture, suggesting the importance of intensive pasture on cow-calf production and farm economics (Fales et al., 1995; Macdonald et al., 2008).

At our subtropical site, two-year average estimates of forage quantities were in the high-range of published values (2676–8921 kg DM ha⁻¹; Wallau et al., 2019; Supplementary Table S3). Annual estimates were higher in 2015 than in 2014 possibly as a result of higher precipitation in 2015 than in 2014, particularly in April and July (Gomez-Casanovas et al., 2020). At the temperate site, average biomass production in the intensive pasture was within the range of Niraula et al. (2020) findings (i.e., 5261–8709 kg DM/ha) in the southern Great Plains, USA and the value was significantly higher than that of extensive pasture.

With respect to forage quality, results showed greater forage digestibility (IVTD) in intensive pastures compared to extensive pastures in the subtropical site and in the temperate site in 2014 (Table 1); and since an increase in %IVTD converts to increased livestock gain (Ba et al., 2008) these results support a positive effect of intensification on provisioning services. However, we found no significant difference in % CP between the pastures in our subtropical site, but in the temperate site it varied across years with no clear difference overall. These results highlight the need to evaluate livestock benefits of increased forage quality under intensification against increased management costs associated with fertilizer and other inputs (e.g., lime and herbicide costs of pumping and seepage irrigation, pasture operation, and a comparison of the cost of nutritional supplements for cattle) in intensive versus extensive pastures.

In this study, higher species richness in native/semi-native pastures was not related to measures of forage productivity in either ecoregion. The literature provides contrasting examples of how increases in diversity influence productivity. In some other studies, increases in biodiversity are associated with enhances in productivity (Oehri et al., 2017; Tilman et al., 1997; Tilman and Downing, 1994). For instance, Picasso et al. (2011) reported substantially higher biomass in an extensive grassland compared to a monoculture intensive pasture in the Midwestern, US. However, Frank (2002) found a relatively higher average aboveground biomass in intensive pasture compared to native prairie over three years in Northern Great Plains, USA, and Werling et al. (2014) however reported no differences in biomass production between native and intensive perennial grasslands in the Midwest, US. These contrasting findings suggest that the regional climate as well as local abiotic factors (soil nutrient and moisture) and plant community structure likely impact the effects of diversity on productivity

(García-Palacios et al., 2018; Yang et al., 2018). It is possible that ‘subsidies’ for productivity, such as nitrogen addition in intensive compared to extensive pastures, or dry season irrigation in subtropical intensive pastures, may be important drivers that ameliorate stressful conditions in intensified pastures whereas in extensive pastures only species richness buffer stress. Tilman et al. (2012) showed that nitrogen application rates similar to those applied to our temperate and subtropical intensive pastures increased productivity as much as biodiversity.

Some means of conventional intensification can increase the net CO₂ sink strength of grasslands due to fertilization and irrigation thereby enhancing plant productivity (Conant et al., 2001; Machmuller et al., 2015). However, this was not the case in this study. In the temperate grasslands, intensification did not affect the net CO₂ sink strength of grasslands, suggesting that both GPP and Reco were tightly coupled and resilient to changes in pasture management (Supplementary Table S5). In contrast, intensification of subtropical pasture increased both Reco and GPP, but in relative terms it increased Reco over GPP (Supplementary Table S5), indicating that Reco played an important role in determining the response of the net ecosystem CO₂ exchange to intensification. Thus, intensification could trigger a release of CO₂ from subtropical pastures to the atmosphere. Further, while aboveground peak productivity was not significantly different in intensive and extensive subtropical pastures, soil microbial decomposition was likely higher in intensive than in extensive pasture (Adewopo et al., 2014, 2015), suggesting that the release of CO₂ associated with intensification of subtropical pastures may be explained by increased soil microbial decomposition.

Overall, intensification increased soil (i.e. paddocks and ditches) CH₄ emissions in subtropical pastures and reduced soil CH₄ uptake in temperate pastures (Table 3). The mechanisms explaining this response likely varied with land use type and climate (Le Clec'h et al., 2019). Previous studies indicate that increased grazing intensity and associated nitrogen (N) increase due to urine as well as N application can decrease the uptake of CH₄ or increase CH₄ emissions from soil (Suwanwaree and Robertson, 2005, 2019), and grazing intensity and hence urine deposition was higher in fertilized intensive than in unfertilized extensive pastures at both ecoregions. Consistent with this observation, Mosier et al. (1991) also reported that a long-term N addition in intensive pasture tended to induce CH₄ emission by inhibiting methanotrophy. In addition, at our subtropical site, liming that increases soil pH may have stimulated the predominance of acetoclastic bacteria vs CO₂ reducers enhancing soil CH₄ emissions in intensive pastures compared to extensive pastures as acetoclastic methanogenesis contributes up to 80% to total CH₄ emissions from soils (Bridgham et al., 2013; Ye et al., 2012). Furthermore, in subtropical pastures, a higher number of flooded ditches in intensive than in extensive pasture also helped explain higher CH₄ emissions due to freshwater bodies having higher CH₄ emissions than paddocks (Chamberlain et al., 2015; DeLucia et al., 2019; Gomez-Casanovas et al., 2020).

The livestock sector accounts for ~18% of the total global anthropogenic GHG emission (Steinfeld et al., 2006), and cattle alone account for ~15% of the CH₄ emissions (FAO, 2006). Given that intensification increased the GWP of pastures, particularly in the subtropical region, and because of the large contribution of CH₄ to the GWP, our results suggest that strategies for sustainable intensification (Pretty et al., 2018) should aim to decrease CH₄ emissions from soils. For instance, recent studies suggest that the addition of slag fertilizer can decrease soil CH₄ emissions by 19% in rice paddies with potential to have a similar impact on grasslands (Das et al., 2019; Gomez-Casanovas et al., 2021). Fluxes of CH₄ from enteric ruminant fermentation can also have a large contribution to the annual CH₄ budget, and hence, strategies particularly aimed to reduce CH₄ emissions from enteric ruminant fermentation, such as the addition of legumes in the pastures or in cattle diet (Archimède et al., 2011) and moderate stocking density (Liebig et al., 2010), in both temperate and subtropical regions, will likely enhance

the sustainability of grazed pastures (Herrero et al., 2016).

Agricultural productivity has to almost double by mid-century to meet the increasing demand of products for a rising population (FAO, 2017). However, this cannot come at the expense of losing ecosystem services that will undermine the Earth's capacity to provide goods and services in the long-term (Foley et al., 2005). Our study demonstrated that intensification has detrimental effects on supporting and regulating services and, in some instances, it can have a minimal positive impact on provisioning services. The implications of our findings need to be carefully balanced with information about the influence of intensification on provisioning services related to the water cycle, and regulating services related to insects and pollinators along with knowledge on the impact of this land use on weed distribution, wildlife conservation, recreation, and economic services. Although our study was restricted to two LTAR sites, these grassland sites represent two major grassland types of the grassland biome and demonstrates that comparisons of ecosystem services across agroecosystems in different ecoregions can reveal drivers of ecosystem services and general or region-specific opportunities and solutions to maintaining agricultural production and reducing environmental footprints. Further research utilizing the entire LTAR network could investigate the benefits and costs of intensification on multiple ecosystem services across the continental US through a range of agricultural production systems, spatial and temporal scales, and climates. Our findings also indicate that innovative research on strategies for sustainable intensification (e.g., shifts from conventional to diversifying pasture management, Gomez-Casanovas et al., 2021), are needed to reduce the negative aspects, particularly the supporting and regulating services, of intensification. As the goal of sustainable agricultural intensification is to enhance production, environmental quality, and maintain rural sustainability (Kleinman et al., 2019), policies are needed that provide incentives for farmers to maintain extensive pastures and to incorporate aspirational strategies in intensive pastures (e.g., diversifying intensive pastures with legumes) for multiple ecosystem services.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108398.

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