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RESEARCH ARTICLE

Cropland functional diversity increases ecosystem services supply in watersheds of the Rio de la Plata Grasslands

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Abstract

Context Implementing heterogeneous rural landscapes with high agricultural diversity and a substantial proportion of natural habitats has been proposed to ensure food production while reducing negative impacts on ecosystem services. However, evidence of an increased supply of ecosystem services (ES) in more heterogeneous landscapes remains limited, with no consensus.

Objectives To evaluate the effect of the spatial cropland system's diversity and landscape configuration on indicators of the supply of ES in agricultural landscapes of the Rio de la Plata Grasslands region.

Methods We analyzed the relationship between indicators of ES supply and the heterogeneity of 1121 microwatersheds. We assessed the Ecosystem Services Supply Index (ESSI), the Hydrological Yield (HY), and the Absorbed Photosynthetically Active Radiation (APAR) in agricultural areas. We calculated the average grassland patch area, the structural and functional cropland diversity, the cropland percentage, and the grasslands' juxtaposition to assess landscape heterogeneity.

Results Microwatersheds with higher cropland functional diversity showed higher values for indicators of ES supply. They were positively related to the ESSI and APAR, and negatively with HY, indicating positive effects on Carbon gains and water regulation processes. In contrast, grasslands' juxtaposition had opposite effects to those of cropland functional diversity, so the spatial segregation of grasslands favored the ES supply.

Conclusions Functional cropland diversification and the segregation of natural grasslands improved proxies of ES and counteracted the negative effects of cropland amount. These findings contribute to the design of multifunctional landscapes and suggest that cropland functional diversity and grassland configuration should be considered in food production systems aimed at preserving ES supply.

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Introduction

Land use changes for productive purposes represent one of the most critical dimensions of global change, both in terms of the area occupied and their impact on biodiversity (Newbold et al. 2015), the climate system (Houghton et al. 2012), and various ecosystem functions and services (Richardson et al. 2023). Over the past few decades, there has been an acceleration in the replacement of natural vegetation covers with low-complexity production systems, where land covers became less diverse over time and space, relying more on fossil fuel-based subsidies and external inputs (e.g., fertilizers and herbicides) (Bommarco et al. 2013). While this process of agricultural intensification has contributed to increased agricultural yields, it has also led to negative environmental impacts such as the depletion of limited resources, the generation of pollutants, and the loss and fragmentation of natural habitats (Foley et al. 2005; West et al. 2014). Recently, the implementation of heterogeneous rural landscapes with high agricultural diversity and a substantial proportion of natural vegetation areas has been proposed as an alternative to ensure food production while minimizing the impact on ecosystem services supply (Bommarco et al. 2013; Kremen and Merenlender 2018; Garibaldi et al. 2019).

Landscape multifunctionality involves managing land uses to provide goods and services, maintain biodiversity, and ensure ecosystem integrity (Mastrángelo et al. 2014; Kremen and Merenlender 2018). Assessing the influence of landscape design on the supply of ecosystem services (hereafter referred to as ES) is crucial for their effective implementation (Paruelo and Sierra 2023). The ES framework includes ecosystem structural and functional attributes that support human life and social well-being (Fisher et al. 2009). These services encompass provisioning, supporting, and regulating services such as water supply, food provision, carbon sequestration, nutrient cycling, and soil erosion control (Fisher et al. 2009; Haines-Young and Potschin 2010; de Groot et al. 2010). Haines-Young and Potschin (2010) proposed a "cascade model", where the ES supply is based on the ecosystems' structure and processes that yield *intermediate services* (functions such as primary productivity and evapotranspiration), leading to *final services* (e.g. hydrological regulation, carbon sequestration, forage) for human benefits (e.g. food, climate regulation and flood mitigation). ES bundles arise from similar responses to ecological processes or change drivers, often resulting in trade-offs between regulating and provisioning ES (Bennett et al. 2009; Raudsepp-Hearne et al. 2010). Landscape multifunctionality management seeks to optimize land use and land cover interactions to concurrently supply diverse ES (Bommarco et al. 2013; Kremen and Merenlander 2018; Jeanneret et al. 2021).

Several studies have assessed the environmental and productive impacts of crop diversification at the paddock level (Kremen and miles 2012, Kremen et al. 2012; Tamburini et al. 2020; Cassman and Grassini 2020). However, recent findings highlight the key influence of landscape heterogeneity on food production, biodiversity, and ES (Duarte et al. 2018; Sousa et al. 2019; Sanchez et al. 2022; Priyadarshana et al. 2024). This heterogeneity can be described in terms of their composition (e.g. diversity and proportion occupied by different land uses and land covers) and spatial configuration (e.g. average patch size, shape, patch density, fragmentation, and juxtaposition) (Fahrig et al. 2011). It has been proposed that more heterogeneous landscapes promote higher biodiversity and ecosystem functioning by providing more resources for diverse species and facilitating flows between adjacent ecosystems (Tscharntke et al. 2012; Cardinale et al. 2012; Bommarco et al. 2013; Metzger et al. 2021; Assis et al. 2023; Boesing et al. 2024). ES depend on the functional traits of species at the community or ecosystem level and on the different land use and land cover types at the landscape level (Kremen 2005; Loreau and de Mazancourt 2013). Therefore, more diverse ecosystems and landscapes are expected to offer a wider range of ES and high resilience to disturbances. However, evidence of increased provision of ES in more heterogeneous and diverse landscapes remains limited, without reaching a consensus (Duarte et al. 2018; Rieb and Bennett 2020; Alignier et al. 2020; Beillouin et al. 2021; Metzger et al. 2021).

Management practices for designing multifunctional landscapes are based on diversifying land uses and covers across different spatial and temporal scales

(Kremen and miles 2012, Kremen et al. 2012; Manning et al. 2018). The goal is to increase land use diversity and integrate natural habitats to promote biodiversity and processes such as pollination, pest control, and carbon sequestration (Bommarco et al. 2013; Schipanski 2014; Sanchez et al. 2022). This diversification, along with the conservation of natural habitats, could ensure the provision of ES without compromising agricultural productivity. However, the findings so far are variable and contingent upon the context and the evaluated ES (Tamburini et al. 2020; Frei et al. 2020; Botzas-Coluni et al. 2021; Nelson and Burchfield 2021).

Widely used models for estimating ES, at the landscape level, generally rely on weighting the area occupied by each land use or human activity with fixed factors related to ES provision (Paruelo et al. 2016). These factors are associated with a punctual estimation of the relationship between ecosystem processes and different land uses (Viglizzo et al. 2006; Laterra et al. 2012; Sharp et al. 2015). However, these models limit the possibility of finding trade-offs and/or conditions that promote synergies among different ES, such as food production, carbon sequestration, or water regulation. This limitation arises because they do not account for the variability associated with differences in the functioning of each land cover type; for example, grasslands or forests with varying levels of degradation and agriculture with different management practices (Qiu and Turner 2013; Lavorel et al. 2017; Frei et al. 2018; Rieb and Bennet 2020). Recently, the use of remote sensing data for estimating ecosystem processes and functions has increased significantly (Pettorelli et al. 2005; Ayanu et al. 2012; Paruelo et al. 2016; Haas 2024). This spatially explicit information allows the estimation of key ecosystem functions and processes related to the supply of various ES consistently and cost-effectively (Paruelo 2008). Remotely sensed information enables analyses of how landscape composition and configuration influence the supply of multiple ES.

Most of the evidence for the influence of agricultural diversity on landscape multifunctionality comes from studies in the Northern Hemisphere, where there is a longer history of transforming natural covers into agricultural areas (Birkhofer et al. 2018; Rieb and Bennett 2020; Jeanneret et al. 2021). In contrast, evidence from southern South America, where significant land use changes have occurred in recent decades (Graesser et al. 2022) and are expected to increase (Lambin et al. 2013; Cassman and Grassini 2020), remains limited (Goldenberg et al. 2022). The Río de la Plata Grasslands, the largest grassland region in South America (including Uruguay and part of eastern Argentina and southern Brazil) (Soriano 1992), have undergone significant transformations toward agricultural and forestry uses (Baldi et al. 2006; Jobbágy et al. 2006; Paruelo et al. 2006; Baldi and Paruelo 2008; Vega et al. 2009; Baeza and Paruelo 2020; Baeza et al. 2022). However, this transformation was not uniform across the entire region. Agricultural expansion and its associated intensification through continuous farming systems were more pronounced in particular subregions such as the Rolling Pampas in Argentina (Baeza and Paruelo 2020). In the early twenty-first century, agricultural intensification expanded to the southwest and southern central subregions of Uruguay (Baeza et al. 2022). Additionally, land use regulation policies differ among countries. In Uruguay, land use and management plans, including crop and pasture rotations, must be presented and approved in advance by the Agriculture Ministry (Resolutions N° 0074/2013 and N° 397/018). In contrast, Argentina and Brazil lack such regulatory policies for grassland ecosystems. These differences, in addition to other factors, such as soil type, topography, and historical land use, created gradients of cropland diversity and grassland configuration (Baeza and Paruelo 2020). Biophysical (climate, soil and geomorphology) and regulatory diversity provide an opportunity to evaluate the effect of landscape heterogeneity on agricultural production and the supply of ES. Understanding these aspects is essential for planning land use strategies for ensuring that food production has a reduced environmental impact (Assis et al. 2023).

The studies that assessed the influence of agricultural intensification on ES in the Río de la Plata Grasslands were limited to regional levels (Viglizzo et al. 2011; Villarino et al. 2014, 2019; Modernel et al. 2016; Paruelo et al. 2022; Rositano et al. 2022; Gallego et al. 2023) or within specific delimited areas (Barral and Maceira 2012; Baldassini et al. 2024). Generally, these studies applied fixed factors related to ES provision for each land use and land cover category evaluated, which prevented an assessment of variability within each cover type (Cardinale et al. 2012; Lavorel et al. 2017). Landscape heterogeneity was not adequately considered in most of these analyses. Goldenberg et al. (2022) recently reported no effects of the natural cover proportion and edge density on agricultural yield. The authors suggest that this lack of influence on landscape metrics could be due to the masking impacts caused by high external inputs in agricultural management. Nevertheless, the inclusion of other landscape characteristics, such as landscape matrix heterogeneity (cropland diversity and the intermixing of natural areas with agriculture), would provide additional insights into the influence of landscape on agricultural productivity (Turner and Chapin 2005; Tscharntke et al. 2012; Turner and Gardner 2015b; Metzger et al. 2021; Sánchez et al. 2022).

This study aimed to evaluate the effect of the spatial diversity of cropland systems and landscape configuration on indicators of ES supply in agricultural landscapes in the Río de la Plata Grasslands region. We hypothesize that cropland spatial diversity and heterogeneity in grassland configuration promote a simultaneous increase in the supply of intermediate ES because the functional diversity exhibited by different cropping systems, in addition to the spatial intermixing of natural grasslands, provides distinct key functions for ES production (Turner and Chapin 2005; Turner and Gardner 2015a). Thus, we expect that landscapes having higher cropland diversity and more adjacency between grasslands and other land uses and covers will show a higher value for indicators of intermediate ES supply.

Methods

Study area

We selected regions within the Río de la Plata Grasslands that included a cropland system diversity gradient and exhibited variations in topography that allow the identification of watersheds. This selection resulted in nine regions that corresponded to the Rolling Pampas and Mesopotamic Pampas in Argentina (Soriano 1992), as well as the Western Sediment Basin, the Crystalline Shield, the Basaltic Region, the Santa Lucía Graben, the Eastern Hills, the Lagoon Merin, and the Gondwanic Sediment Basin in Uruguay (Panario et al. 2014) (Fig. 1). In the Argentine regions, the original vegetation physiognomy corresponds to a mesophytic pseudosteppe with low or no tree presence in the Rolling Pampas, and a megathermic grassland with gallery forests in the Mesopotamian Pampas (Oyarzabal et al. 2018). The soils in these areas are primarily deep Argiudolls with well-differentiated horizons, good drainage, and high organic matter content, providing high fertility (Rubio et al. 2019). In the Uruguayan regions, geomorphological and edaphic heterogeneity increases. The predominant Molisols coexist with Alfisols, Inceptisols, Oxisols, Vertisols, and Ultisols toward the North and East, and with Entisols toward the West, resulting in more diverse grassland communities than those of the Argentine Pampas (Oyarzabal et al. 2020). The physiognomy of grasslands in Uruguay is divided into dense grasslands occurring on deep soils, and sparse grasslands occurring on shallow soils (Lezama et al. 2019). The climate in the region is temperate, with an average annual temperature of 14 °C in the south and 18 °C in the north, and the median annual precipitation ranges from 1100 mm in the west (Argentinian regions) (Rubio et al. 2019) to 1350 mm in the east (Uruguayan regions) (INUMET 2024).

Historically, livestock grazing over grasslands and sown pastures was the predominant activity in the Río de la Plata Grasslands region. Annual crops were part of rotations with pastures (Hall et al. 1992; Paruelo et al. 2006). In recent decades, the region has experienced an expansion and intensification of croplands, beginning in the western part of the region (the Argentine Pampas) and subsequently moving eastward into the corresponding regions in Uruguay. In Uruguay, in addition to cropland expansion, tree plantations have increased sharply since the beginning of the century (Jobbágy et al. 2006; Baeza and Paruelo 2020; Baeza et al. 2022). Despite the advancements in monocultures, agricultural-livestock systems and crop rotations are still important in the region and are associated with land use regulation policies and cultural practices (Baeza and Paruelo 2020). In recent years, the area occupied by cover crops has increased (Álvarez et al. 2017; Pinto et al. 2017). As a result, there exists a gradient of agricultural intensification within the study area (Baeza and Paruelo 2020; Baeza et al. 2022).

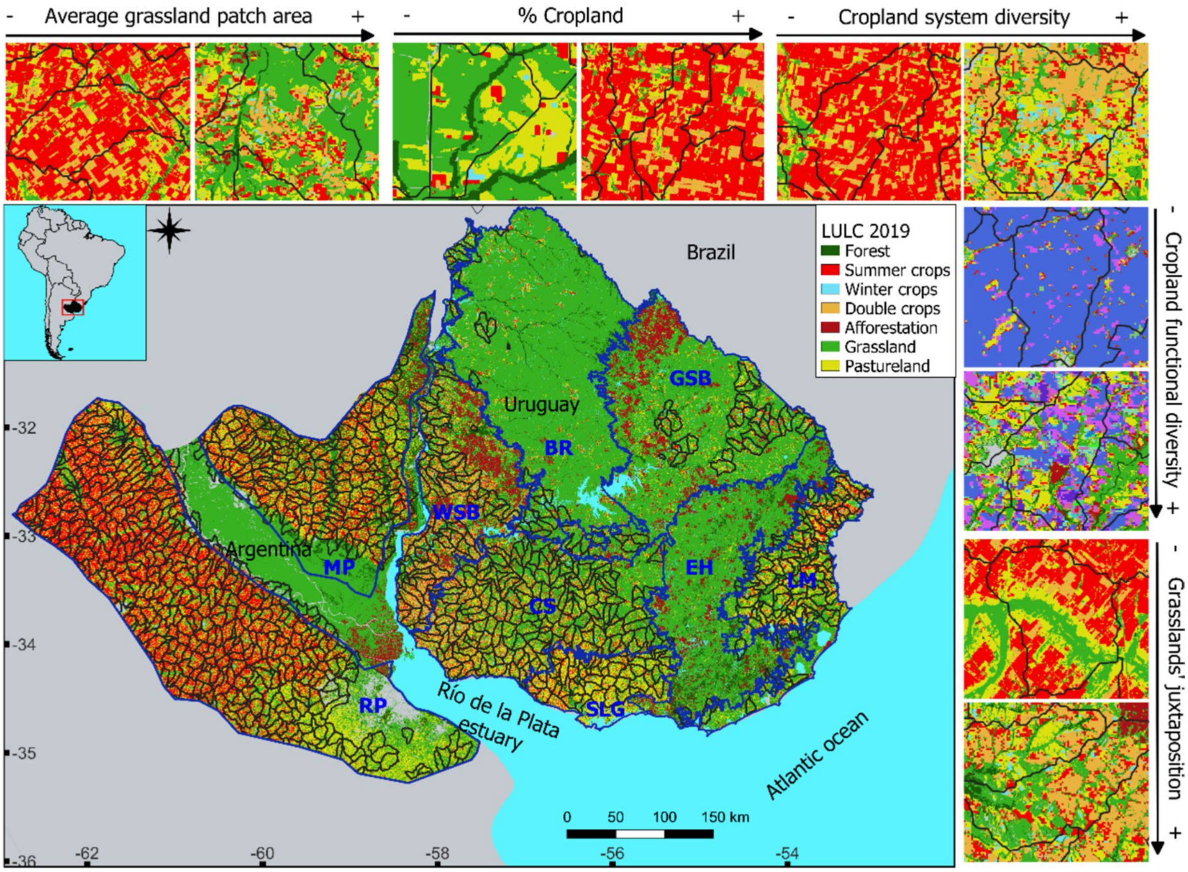

Fig. 1 Study area, microwatersheds selected and landscape metrics calculated. The central part of the figure represents the delimited study area within the Rio de la Plata Grasslands region. The area is subdivided into nine regions, each represented in blue and labeled as follows: *RP* Rolling Pampa, *MP* Mesopotamic Pampa, *WSB* Western Sediment Basin, *BR* Basaltic Region, *CS* Crystalline Shield, *SLG* Santa Lucía Graben, *EH* Eastern Hills, *LM* Lagoon Merin Graben, *GSB* Gondwanic Sediment Basin. Agricultural landscapes (microwatersheds), which are the unit of analysis (n = 1121), are shown in black. The color map in the background represents land uses and land covers (LULC) for the year 2019, including forests, afforestation, summer crops, winter crops, double crops, pastures, and grasslands. LULC was derived from the combination of the MapBiomas Pampa classification and land use maps developed by Baeza and Paruelo (2020) for the Uruguayan portion and from the National Cropland Map (de Abelleyra et al. 2020) for the Argentine portion. The insets at the top and to the right are examples of landscapes with contrasting landscape indices values. The inset at the top left of the central map shows South America with a red rectangle indicating the relative position of the study area on the continent

Selection of agricultural landscapes and data acquisition

The unit of analysis was a landscape whose boundaries corresponded to a hydrological microwatershed. Agricultural microwatersheds were chosen within the nine regions of the study area. Microwatersheds (level 11) were obtained from the "HydroSHEDS" product, which employs digital elevation models to delineate hydrographic polygons at various levels (Lehner and Grill 2013). The Level 11 microwatershed proved suitable for describing landscape metrics variability following the landscape size determination procedure outlined by Pasher et al. (2013). Given that our analysis focuses on landscapes with agricultural uses, we specifically selected microwatersheds with at least 25% agricultural cover (croplands and pastures) and less than 10% of tree plantations. We excluded tree plantations from the analysis because they differ significantly in terms of functionality from herbaceous cover types. Thus, including tree plantations would reduce the variability in ecosystem service indicators between herbaceous covers and limit our ability to describe differences in agricultural food production systems accurately. For microwatershed selection, we calculated the proportion occupied by the "agricultural" and "tree plantations" classes in each microwatershed using the Collection 3 of the land use and land cover (LULC) map from the MapBiomas Pampa initiative (Baeza et al. 2022) for the year 2019. As a result of this selection process, we obtained 1121 agricultural microwatersheds for the study area (Fig. 1).

The landscape metrics calculated for each selected microwatershed (Table 1 and Fig. 1) included the average grassland patch area (AGPA), cropland percentage (%Crop), cropland system diversity (CropDiv), cropland functional diversity (CropFuncDiv), and grasslands' juxtaposition (Jux). These metrics were chosen because they describe heterogeneity in composition (AGPA, %Crop, CropDiv), functioning (CropFuncDiv) and spatial configuration (Jux) within the landscapes. These aspects allow us to evaluate the hypothesis of this study and have been identified as the main factors influencing ES provision in prior research (Duarte et al. 2018; Metzger et al. 2021; Boesing et al. 2024). The AGPA was obtained by summing the area of each grassland patch and dividing it by the total number of grassland patches in the landscape. It is a measure of the natural habitat amount of a landscape (Fahrig 2013). The %Crop was determined using the same procedure applied for landscape selection. It ranges from 0 to 100% and reflects the amount of croplands through the landscape. Grasslands' juxtaposition was calculated based on the relationship between the sum of grassland edges adjacent to other land covers and the total edge length of the landscape (Table 1). It varies from 0 to 100 where values close to 0 indicate a segregated spatial arrangement of grasslands with less adjacency with other covers, while values close to 100 indicate an interspersed spatial arrangement of grasslands with other covers (Turner and Gardner 2015b). Landscape metrics were computed using the "landscapemetrics" package (Hesselbarth et al. 2019) available in the R environment (R Core Team 2021).

To assess the diversity of the cropland systems (CropDiv), we remapped the "farming" class from the MapBiomas Pampa classification (Baeza et al. 2022) into summer crops, winter crops, and double cropping (Fig. 1). This remapping process was based on combining the "farming" class from MapBiomas Pampa with a land use map developed by Baeza and Paruelo (2020) for the Uruguayan portion, and the National Cropland Map (de Abelleyra et al. 2020) for the Argentine portion of the study area during the 2018–2019 growing season (Fig. S1, Online Resource 1). Consequently, only areas where farming classes overlapped in the map superposition were remapped into one of the three mentioned cropland systems, based on their alignment with the conceptually higher-resolution map.

To calculate agricultural functional diversity (CropFuncDiv), we defined and mapped the Ecosystem Functional Types (EFTs), which represent land cover types that share similar dynamics in terms of material and energy transfers with the environment (Paruelo et al. 2001; Alcaraz Segura et al. 2006; Cazorla et al. 2021; Gallego et al. 2024; Bagnato et al. 2024). The EFTs resulted from combining three

Table 1 Landscape metrics, the formula and units of the calculations. A_i and A_t are the patch and landscape area respectively. N_t is the number of patches in the landscape. e_{ik} is the total edge amount between grassland i and use k, m is the number of classes (uses and covers) present in the landscape, and pi is the proportion of use or cover i in the landscape

Landscape metric	Formula	Units
Average grassland patch area	$AGPA = \frac{\sum_{i=1}^{n} A_i}{N_t}$	Hectares
Cropland percentage	$\%Crop = 100\frac{\sum_{i=1}^{n} A_i}{A_t}$	%
Structural & functional cropland diversity (Shannon–Wiener index)	$CropDiv = -\sum_{i=1}^{n} p_i ln p_i$	No units
Grasslands' juxtaposition	$Jux = \frac{-\sum_{k=1}^{m}\left[\left(\frac{e_{ik}}{\sum_{k=1}^{m} e_{ik}}\right) ln\left(\frac{e_{ik}}{\sum_{k=1}^{m} e_{ik}}\right)\right]}{ln(m-1)}100$	%

attributes of annual Normalized Difference Vegetation Index (NDVI) dynamics: annual mean, intra-annual variation, and date of maximum. For this, we used the MOD13Q1 product of the MODIS sensor aboard the Terra satellite (https://lpdaac.usgs.gov/products/mod13q1v061/), which has a spatial resolution of 5.3 hectares and a temporal resolution of 16 days. Pixel values affected by clouds, shadows, and aerosols were filtered using the quality band (QA). Quartiles for the annual mean and the coefficient of variation of the NDVI were obtained, and the season with the maximum NDVI (summer, autumn, winter and spring) was extracted from each pixel in the land cover map for the 2018–2019 growing season. Then, the pixels were classified by assigning a combination of values from these quartiles and the season of maximum NDVI attributes obtaining 64 potential classes. For instance, an EFT might be defined by a high annual mean NDVI, substantial intra-annual variation, and a season in which the maximum NDVI occurs in summer. Noncropland areas were then masked to obtain EFTs for cropland cover types exclusively. Both, the cropland system diversity (CropDiv) and the cropland functional diversity (cropland EFTs, CropFuncDiv) were calculated using the Shannon–Wiener diversity index (Table 1).

Ecosystem services estimation

Three indicators related to the provision of ES were estimated for each selected agricultural microwatershed: the Ecosystem Services Supply Index (ESSI, Paruelo et al. 2016; Staiano et al. 2021), the Hydrological Yield (HY, Gallego et al. 2023), and the Absorbed Photosynthetically Active Radiation (APAR, Monteith 1972). The ESSI is an indicator related to ecosystem supporting and regulating services based on the annual dynamics of carbon gains in ecosystems (Paruelo et al. 2016; Storkey et al. 2024). It showed a high correlation with soil organic carbon content (Paruelo et al. 2016; Staiano et al. 2021; Baldassini et al. 2023; Segura et al. 2024), a key aspect in the provision of regulation services such as atmospheric carbon sequestration and soil structure and fertility. The ESSI captures a bundle of ES, is positively correlated with avian biodiversity (Paruelo et al. 2016; Weyland et al. 2019) and descriptors of the different aspects of water regulation (Paruelo et al. 2016; Baldassini et al. 2024). HY is defined as the fraction of water that leaves a basin in liquid form (Jobbágy et al. 2013; Gallego et al. 2023). It is an indicator of water provision and regulation depending on whether a water surplus is generated or not (Jobbágy et al. 2021). It is a key process in providing irrigation water for agriculture, human water supply, water bodies functioning, and flood regulation, among other purposes (Salemi et al. 2012; Jobbágy et al. 2021). The APAR is directly proportional to the net aboveground primary productivity of vegetation (Monteith 1972), a key determinant of both regulating and provisioning services in grasslands, pastures, and crops (Caviglia et al. 2004; Piñeiro et al. 2006; Grigera et al. 2007; Guido et al. 2014; Baldassini et al. 2018). The three indicators were averaged at the microwatershed level for the 2018–2019 growing season. Annual mean precipitation values for the 2018–2019 growing season were 1290 and 1380 mm for the Argentinian and Uruguayan Río de la Plata Grasslands, respectively (CHIRPS; Funk et al. 2015). These values were similar to the median precipitation values for the Argentinian regions (1100 mm, Rubio et al. 2019) and the Uruguayan regions (1350 mm, INUMET 2024) of the Río de la Plata Grasslands.

The ESSI of agricultural covers (i.e. grasslands, pastures, and crops) was estimated by multiplying the average of the Normalized Difference Vegetation Index (NDVIp, estimator of annual production) with the complement of the intra-annual coefficient of variation of the NDVI (1-NDVIcv, seasonality of production) (Table 2). Higher ESSI values occur when a system is more productive and when its production is less seasonal (less variable within the year) (Paruelo et al. 2016; Staiano et al. 2021). The NDVI values for the July 2018 to June 2019 period were obtained from the MOD13Q1 product of the MODIS sensor aboard the Terra satellite. Pixel values affected by clouds, shadows, and aerosols were filtered using the quality band (QA). Only pixels covering at least 95% of the grasslands, pastures, and agricultural covers were considered. We anticipate that the ESSI will rise in response to larger grassland patch areas (AGPA), greater diversity in cropland systems (CropDiv), increased functional diversity within croplands (CropFuncDiv), and juxtaposition of grasslands (Jux) (Table 2). This expectation is rooted in the idea that landscape heterogeneity fosters complementation and compensation processes (Benton et al. 2003; Turner and Chapin 2005; Tsharntke et al. 2012; Turner and

Table 2 Indicators of ecosystem services, the formula for their estimation and expected direction of the effects of landscape metrics. NDVI is the Normalized Differential Vegetation Index, SW is the initial (t−1) soil water content, PP is total daily (t) precipitation, RET is the daily Real Evapotranspiration and SWC is the Soil Water Storage Capacity. APAR is the Absorbed Photosynthetically Active Radiation, fPAR is the fraction of the Photosynthetically Active Radiation intercepted by green vegetation and PARi is the incident Photosynthetically Active Radiation. The expected directions of the landscape metrics effects are indicated with +, = or − for average grassland patch area (AGPA), cropland percentage (%Crop), cropland system diversity (CropDiv), cropland functional diversity (CropFuncDiv) and grassland juxtaposition (Jux)

Indicator	Ecosystem service	Estimation	Expected direction of the landscape metrics effects
ESSI	Supporting & Regulating services related to carbon dynamics	$ESSI = NDVI_{mean}(1 - NDVI_{cv})$	AGPA(+), %Crop(−), CropDiv(+), CropFuncDiv(+), Jux(+)
HY	Hydrological Yield	$HY = \frac{mean(SW_{t-1}+PP_t-RET_t-SWC)}{meanPP}$	AGPA(−), %Crop(+), CropDiv(−), CropFuncDiv(−), Jux(−)
APAR	Food provision	$APAR\left(\frac{MJ}{m^2 16days^{-1}}\right) = fPAR * PAR_i$	AGPA(+), %Crop(=), CropDiv(+), CropFuncDiv(+), Jux(+)

Gardner 2015a). Specifically, when diverse land uses and land covers interact, they enhance carbon gains and landscape productivity stability given their distinct seasonal dynamics (Cazorla et al. 2021; Gallego et al. 2024; Bagnato et al. 2024). Conversely, the cropland percentage (%Crop) reduces the ESSI by increasing productivity variability at the landscape level (Paruelo et al. 2016; Staiano et al. 2021).

We estimated the HY as the portion of annual precipitation exceeding the soil's water storage capacity, calculated from a water balance that considers precipitation, evapotranspiration, and soil storage capacity (Gallego et al. 2023) (Table 2). Precipitation data were sourced from the "Climate Hazards Group InfraRed Precipitation with Station" (CHIRPS; Funk et al. 2015). This product provides daily precipitation estimates (mm/day) with a spatial resolution of $0.05° \times 0.05°$ (approximately 5×5 km^2). Evapotranspiration data were obtained from the MOD16A2 product (Collection 6) (Mu et al. 2011), which integrates MODIS sensor data with "Modern-Era Retrospective Analysis for Research and Applications" (MERRA, Rienecker et al. 2011) climatic reanalysis. The MOD16A2 product generates composites with total real evapotranspiration (RET) for 8-day periods at 500-m resolution (Running et al. 2017). This product showed better performance in capturing seasonal variations in land covers RET than other satellite-based RET products (Gallego et al. 2023). The soil storage values for Argentina were based on the estimates of Gusmerotti and Mercau (2022) for different soil textures obtained from Schulz et al. (2023). For Uruguay, we used the soil available water capacity product of Hengl and Gupta (2019). The HY for the 2018–2019 growing season was computed daily and then summed annually and expressed as a proportion of the total precipitation. We expect HY to be reduced by AGPA and Jux (Table 2) because grasslands have higher evapotranspiration rates than croplands (Gallego et al. 2023). Both CropDiv and CropFuncDiv would also reduce HY because different crops have varying water consumption patterns. Conversely, %Crop will augment HY because water consumption decreases after the growing season, causing the precipitated water to flow out (Jobbágy et al. 2013).

The APAR was calculated by multiplying the incident photosynthetically active radiation (PARi) by the fraction of that radiation intercepted by green vegetation (fPAR; Table 2) (Monteith 1972). To obtain PARi, values of shortwave incident radiation from the Global Land Data Assimilation System (GLDAS; Rodell et al. 2004) product were used. For the calculation of the fPAR, the Enhanced Vegetation Index (EVI) from the MOD13Q1 product of the MODIS sensor was used, and estimators of a linear model relating the EVI to the fPAR calibrated for herbaceous vegetation in the region of interest were applied (Irisarri et al. 2018). The APAR was calculated for grassland, pasture, and cropland classes, considering only pixels occupied by these three cover types in at least 95%. For this, we masked woody and non-vegetated coverages and then averaged the APAR values of herbaceous covers (grasslands, pastures and croplands) for each microwatershed. We expect the APAR to increase with AGPA, CropDiv, CropFuncDiv and Jux because of the spillover of processes, resources and organisms that are fostered in a diverse and heterogeneous landscape matrix and benefit agricultural production (Tsharntke et al. 2012; Kremen and Merenlender 2018; Garibaldi et al. 2019). Conversely, the %Crop will neither increase nor decrease the APAR because of the increase in productivity that crops would have (Modernel et al. 2016; Baldassini et al. 2024) will be compensated by the increase in the seasonality of productivity related to fallow periods (Volante et al. 2012; Baldassini et al. 2024).

Both satellite image processing and the estimation of ecosystem service indicators (ESSI, HY, and APAR) were conducted in the Google Earth Engine environment (Gorelick et al. 2017).

Statistical analysis

We used a Mixed Linear Model with a hierarchical structure (Harrison et al. 2018) to analyze the relationship between each ES indicator (i.e. ESSI, HY, and APAR) and landscape metrics calculated at the microwatershed level, considering them fixed effects. The nine regions were included as random effects. A model was formulated for each evaluated ES with the following structure:

$$Y_i = \beta_{0j[i]} + \beta_1 * AGPA_i + \beta_2 * \%Crop_i + \beta_3 * CropDiv_i + \beta_4 * CropFuncDiv_i + \beta_5 * Jux_i + \varepsilon_i$$

$$\beta_{0j[i]} \sim N\left(\mu_{\beta_0}, \sigma^2\right)$$

where Y_i corresponds to the mean of each ES indicator and $\beta 0_{j[i]}$ is the intercept parameter of each region j containing each basin i (random effect). β_1, β_2, β_3, β_4, and β_5 are the parameters of the slopes (fixed effects) of the variables average grassland patch area (AGPA), cropland proportion (%Crop), cropland system diversity (CropDiv), cropland functional diversity (CropFuncDiv), and grasslands' juxtaposition (Jux), respectively. εi represents the unexplained variation at the watershed level. A Gaussian distribution was considered for the observations and intercepts after verifying that the quantiles of the residuals of each model had a good fit with the quantiles of a Gaussian distribution (qq-plot analysis). A visual exploration analysis of scatterplots of the residual values against the fitted values, and of the residual values against each predictor variable for each model did not show any patterns. This suggests homogeneity of variances of the fitted models (Zuur et al. 2010).

All the models were fitted using the "lmer" function from the "lme4" package (Bates et al. 2015) in RStudio (R Core Team 2021). All predictor variables were standardized to ensure that their effects were comparable. Pearson correlations among predictor variables were less than 0.7 (Fig. S2) which suggested the absence of multicollinearity (Dormann et al. 2013). Additionally, the variance inflation factor (VIF) of the models was calculated, yielding values less than 2, thus confirming the absence of multicollinearity (Fox and Weisberg 2019). The parameters and their 95% confidence intervals for the fixed effects were estimated by the parametric bootstrap method (Booth 1995) performing 1000 simulations. The R^2 for mixed models (Nakagawa and Schielzeth 2013) was obtained using the "r.squaredGLMM" function from the "MuMIn" library (Barton 2023). This function estimates a marginal R^2, corresponding to the variance explained by the predictor variables included in the model, and a conditional R^2, corresponding to the variance explained by the entire model (predictor variables plus random effects) (Nakagawa and Schielzeth 2013). The "glmm.hp" function from the library of the same name (Lai et al. 2022) was used to obtain the individual contribution of each predictor variable to the marginal R^2, i.e., the percentage of variance associated with fixed effects explained by each predictor variable included in the model.

Finally, we conducted a comparative analysis of ES supply across the nine regions. To achieve this, we scaled the ES indicators within a range of values from 0 to 1. Specifically, we calculated the difference between each microwatershed ES value and the minimum value, and then divided it by the range (the difference between the maximum and minimum values) for each ES indicator. The 5th percentile (p5) and 95th percentile (p95) of each indicator across all microwatersheds were considered the minimum and maximum values, respectively, to avoid outliers. To visualize the ES supply levels among the regions, we generated "flower plots". In these plots, each petal represents the median supply level of an ES indicator. Additionally, we calculated the 25th percentile (p25) and 75th percentile (p75) to represent the variability around the median ES supply level. We complemented this analysis by conducting a correlation analysis between each ES indicator to identify the trade-offs and synergies in each region (Online resource 3).

Results

The landscape indices exhibited wide variability among the regions within the study area. There was a longitudinal gradient, from microwatersheds with more crop areas, smaller grassland patches, and less diverse cropland systems in the West, to microwatersheds with a lower proportion of crops, larger grassland areas, and higher cropland system diversity in the East (Fig. 2). The median grassland area was 6 ha in the landscapes of the Rolling and Mesopotamian Pampas, reaching 151 ha in the landscapes of the Basaltic Region. The median proportion of cropland in the landscape was 12% in the Basaltic Region and the Gondwanic Sediment Basin, increasing to 60% in the Rolling Pampa. Regarding the diversity of the cropland systems, the median was 0.5 in the Rolling Pampa and 0.8 in the Western Sediment Basin and the Crystalline Shield (Fig. 2). In contrast, the cropland functional diversity and grassland juxtaposition exhibited lower values at the western and eastern extremes of the study area. The median cropland functional diversity was 0.8 in the Rolling Pampa, 1.95 in the Merin Lagoon Graben and the Mesopotamian Pampa and reached a value of 2.2 in the Crystalline Shield. The median grassland juxtaposition was 44 and 52% in the Merin Lagoon Graben and the Rolling Pampa,

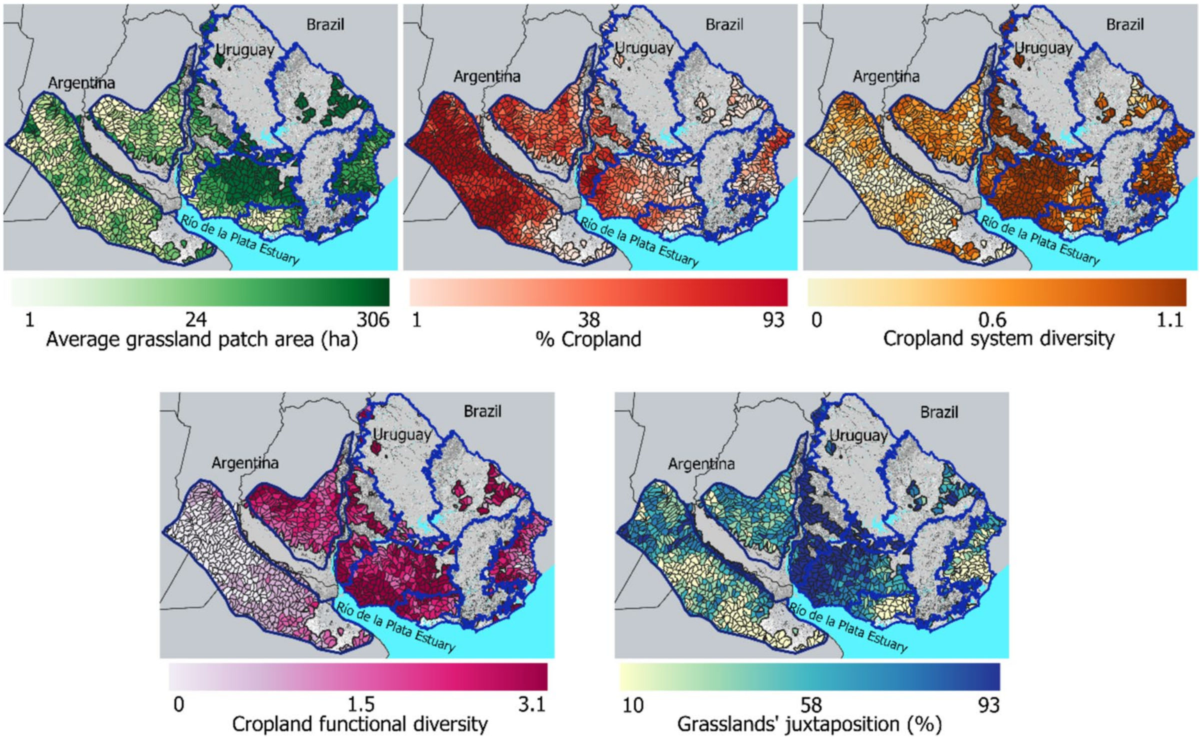

Fig. 2 Landscape metrics values for the agricultural microwatersheds. From the top left to the bottom right the following maps are shown: (1) Average grassland patch area, which represents the average area of grassland patches from the smallest (1 ha) in yellow to the largest (306 ha) in dark green. (2) Cropland percentage, which shows the proportion of cropland within each basin from lowest (1%) in white to the largest (93%) in red. (3) Cropland system diversity, which represents the Shannon–Wiener index for cropland systems from lowest (0) in white to highest (1.1) in dark brown. (4) Cropland functional diversity, which shows the Shannon–Wiener index for cropland ecosystem functional types from lowest (0) in white to the highest (3.1) in purple. (5) Grasslands' juxtaposition, which depicts the adjacency of grasslands to other land uses and covers, and is represented from less juxtaposed (10%) by yellow to more juxtaposed (93%) in dark blue

respectively, reaching a value of 80% in the Western Sediment Basin (Fig. 2).

The indicators of ecosystem services supply (ES) exhibited variation across different regions. The Basaltic Region showed intermediate to high levels for ES supply proxies, with median scaled values of 0.9, 0.7, and 0.6 for the Ecosystem Services Supply Index (ESSI), Hydrological Yield (HY), and Absorbed Photosynthetic Active Radiation (APAR), respectively (Fig. 3). In contrast, the Rolling Pampa region had intermediate to low levels of ES supply proxies, with an ESSI and APAR below 0.5 and HY

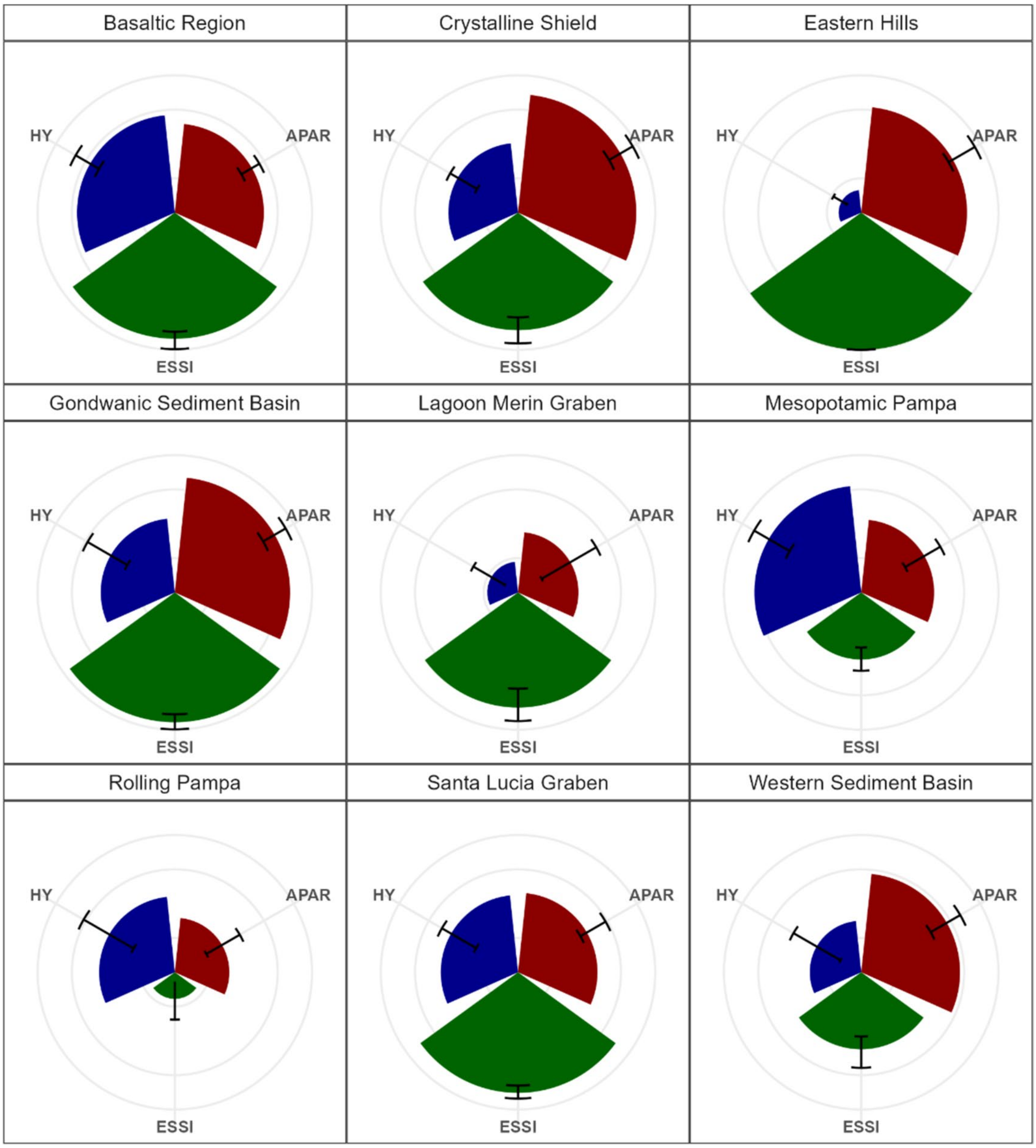

Fig. 3 Flower plots showing the scaled values of the ecosystem service indicators for each region. The median value for each ecosystem service indicator is represented by the length of the flower petal and the error bars show the 25th and 75th percentiles. The scaled values range from 0 at the center to 1 at the periphery of each flower, where the circumferences correspond to 0.25, 0.75 and 1.0 values. The Hydrological Yield (HY), Absorbed Photosynthetically Active Radiation (APAR) and Ecosystem Services Supply Index (ESSI) are represented by blue, red and green petals, respectively

of 0.55 (Fig. 3). The ESSI consistently had higher median values, exceeding 0.75 across most regions within Uruguay (Fig. 3). Following the ESSI, the APAR exhibited median values above 0.75 in three Uruguayan regions. The APAR was equal to the ESSI in the Crystalline Shield (0.86) but surpassed it in the Western Sediment Basin (APAR = 0.72, ESSI = 0.56) and the Mesopotamic and Rolling pampas (APAR = 0.53, ESSI = 0.48; and APAR = 0.4, ESSI = 0.2, respectively). Moreover, HY reached median scaled values of approximately 0.75 only in the Mesopotamic Pampa and the Basaltic Region. Interestingly, in the Mesopotamic and Rolling pampas of Argentina, HY surpassed the median ESSI and APAR values (Fig. 3, for ES values in their original units, refer to Table S3).

The variation in indicators of ES supply corresponded to their distinct correlations across the regions. Most of the Pearson correlations were weak ($r < 0.7$), but the ESSI and APAR showed positive associations in the Lagoon Merin Graben ($r = 0.88$), Mesopotamic Pampa ($r = 0.75$) and Crystalline Shield ($r = 0.7$) (Fig. S3.4, S3.5 and S3.7). Conversely, HY exhibited a negative correlation with APAR, but only in the Rolling Pampa ($r = -0.7$, Fig. S3.8). ESSI and HY displayed weak correlations with different signs across regions (Fig. S3.1–S3.9).

The mean ESSI decreased with increasing cropland proportion in the microwatershed, with a slope of − 0.046 and with increasing juxtaposition of grasslands (slope = − 0.01) (Fig. 4). However, it augmented with the increase in the functional diversity of agriculture with a slope of 0.023 (Fig. 4). Neither the average grassland patch area nor the diversity of cropland systems significantly influenced the ESSI (Fig. 4). The model explained 87% of the variability in the ESSI, 70% of which was associated with the composition and spatial configuration landscape variables (fixed effects). The most influential variable in the model was the cropland proportion (59.6%),

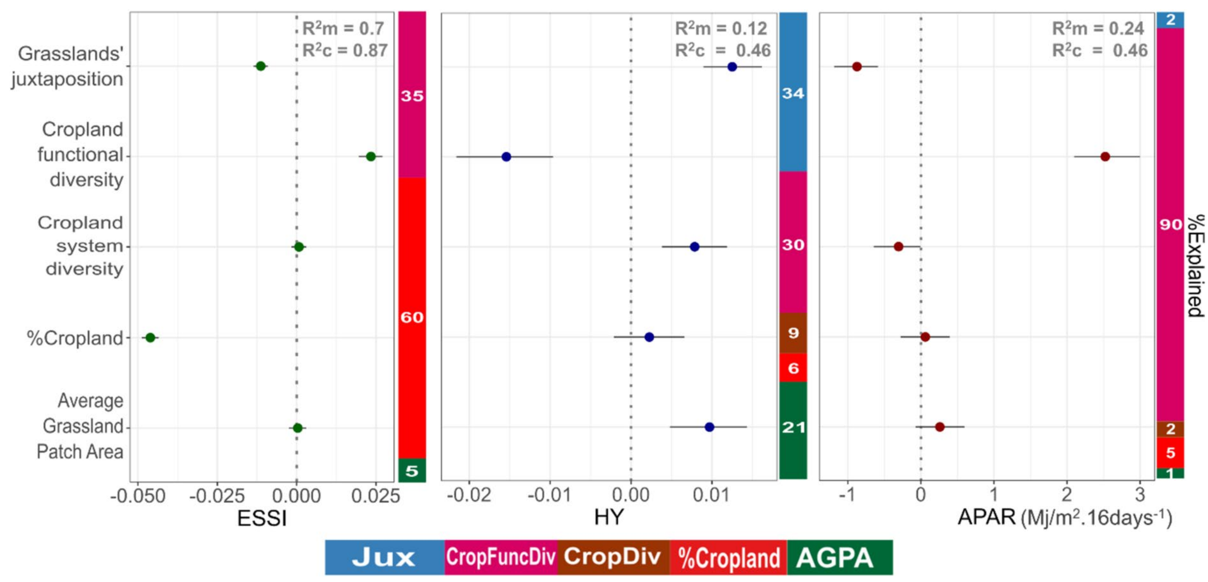

Fig. 4 Coefficients from the models relating Ecosystem Services (ES) indicators to landscape heterogeneity. From left to right coefficients for the Ecosystem Services Supply Index (ESSI, green points), Hydrological Yield (HY, blue points) and Absorbed Photosynthetically Active Radiation (APAR, red points) with the 95% confidence intervals bars are shown. The vertical axis shows the landscape metrics included as predictor variables (fixed effects), and the horizontal axis indicates the ES indicators analyzed. At the top right in each plot the marginal R^2, which quantifies the variability explained by the fixed effects, and the conditional R^2 related to the variability explained by the entire model (fixed + random effects) are shown. The color columns on the right in each plot show the individual contributions (%) of each predictor variable to the variability related to the fixed effects (marginal R^2): green represents the average grassland patch size, red represents the cropland percentage, brown represents the cropland system diversity, pink represents the cropland functional diversity and light blue represents the grasslands' juxtaposition individual contributions. A legend shows the colors assigned to each explanatory variable at the bottom of the figure

followed by cropland functional diversity (35.4%) (Fig. 4).

The mean HY increased with increasing the grasslands' juxtaposition (slope = 0.012), average grassland patch area (0.01), and cropland system diversity (0.007) (Fig. 4). In contrast, cropland functional diversity decreased HY (− 0.015). The percentage of agriculture did not have a significant effect on this variable. The model explained 46% of the variation in HY, of which only 12% was associated with fixed effects (Fig. 4). Grasslands' juxtaposition explained 34% of the variability associated with fixed effects, followed by cropland functional diversity (30%), average grassland patch area (21%), cropland system diversity (9%), and cropland proportion (6%) (Fig. 4).

The mean APAR of agricultural and pastoral covers increased with cropland functional diversity (slope = 2.52 MJ/m^2*16 days) and decreased with grasslands' juxtaposition (− 0.87 MJ/m^2*16 days) and with cropland system diversity (− 0.3 MJ/m^2*16 days) (Fig. 4). In contrast, there were no significant effects from the average grassland patch area or the percentage of cropland in the landscape (Fig. 4). The model explained 46% of the total variability in the APAR, with the fixed effects explaining 24%. Ninety percent of the variability related to the fixed effects was associated with cropland functional diversity (Fig. 4).

Discussion

Cropland system diversity, functioning and grassland spatial configuration had significant effects on indicators of the supply of ecosystem services (ES) in microwatersheds of the Rio de la Plata Grasslands region. Specifically, microwatersheds with higher cropland functional diversity showed higher values of the indicators of the ES supply, as evidenced by the positive effects on the Ecosystem Services Supply Index (ESSI) and absorbed radiation (APAR), and the negative effect on Hydrological Yield (HY) which, in turn, is related to water regulation. Cropland functional diversity explained a considerable proportion of the variability in the three ES indicators evaluated, contributing more than most descriptors of landscape composition and spatial configuration. The positive effect of cropland functional diversity on the ESSI contrasted with the negative effect of cropland proportion, indicating that functional diversification may partially mitigate the negative impacts of extensive croplands on ES supply. Contrary to our expectations, the juxtaposition of grasslands with other land uses diminished ESSI and APAR, suggesting that these indicators benefit from a segregated grassland configuration (Boesing et al. 2024). Our results revealed substantial variability in cropland systems and functional diversity, and the amount and spatial configuration of natural grasslands across landscapes in the Río de la Plata Grasslands. This variability led to differences in the indicator values for key intermediate ES supply. Regions such as the Basaltic Region and Crystalline Shield in Uruguay, which have higher cropland functional diversity and extensive grassland areas, are likely to have a higher supply of ES.

The diversity of cropland functional types was positively correlated with cropland system diversity (r = 0.55), indicating that greater compositional diversity in croplands leads to greater functional diversity. However, both variables had opposite effects on HY and APAR, and cropland functional diversity had a significant effect on the ESSI while cropland system diversity did not. Additionally, in comparison to cropland system diversity, cropland functional diversity explained a greater proportion of the variation in the three ES indicators evaluated. Previous studies have shown that models incorporating the diversity of functional traits of ES providers (species, land uses and land covers) are more precise at predicting ES supply than models based on species identity and land cover (Lavorel et al. 2011), thus providing greater biophysical realism (Cardinale et al. 2012; Lavorel et al. 2017). Indeed, previous works considering cropland diversity based on crop types found a greater influence of spatial configuration compared to a low or negligible impact of crop diversity (Alignier et al. 2020; Botzas-Coluni et al. 2021). Our estimation of cropland functional diversity presented a wider range of variation (0 to 3.08) compared to cropland system diversity (0 to 1.08) due to the additional functional differences derived from varying crop cycle lengths, different genotypes, the use of service crops, and varying sowing dates. Moreover, cropping system heterogeneity can be masked in land use classifications (e.g. Baeza et al. 2020 or MapBiomas Pampa); for example, "double cropping" may include both two commercial crops and a service crop followed by a commercial crop. This likely led to an underestimation of the effect of cropland diversity on ES supply indicators when estimated from fixed classes.

Recent evidence suggests a positive but variable effect of cropland diversity on provisioning, supporting and regulating ES (Tamburini et al. 2020; Frei et al. 2020; Botzas-Coluni et al. 2021; Nelson and Burchfield 2021). Proposals to diversify cropping systems and increase landscape heterogeneity aim to ensure sustainable food production, based on hypotheses that landscape composition modulates biodiversity and ecosystem functioning (Benton et al. 2003; Turner and Chapin 2005; Tscharntke et al. 2012; Turner and Gardner 2015a; Boesing et al. 2024). These hypotheses generalize patterns found at the community or ecosystem level, where ecosystem functioning, and stability are related to complementary (different species providing different functions) and compensatory (one species compensating for another) mechanisms (Kiessling et al. 2005; Kremen 2005; Tilman et al. 2006; Isbell et al. 2017; Loreau and de Mazancourt 2013). At the landscape level, land uses and land covers can be viewed as ES providers due to their diverse functional traits according to the species sown and the natural covers present (Paruelo et al. 2001; Alcaraz-Segura et al. 2006; Schipanski 2014; Cazorla et al. 2021). Our results align with recent evidence showing that high provisioning and regulating ES supplies occurred in regions with both large natural areas and high functional cropland diversity (Qiu and Turner 2013; Duarte et al. 2018; Sousa et al. 2019; Sanchez et al. 2022; Priyadarshana et al. 2024).

Agricultural expansion across the Río de la Plata Grasslands has led to the loss of regulating and supporting ES, as shown by previous studies (Viglizzo et al. 2011; Barral and Maceira 2012; Villarino et al. 2014, 2019; Modernel et al. 2016; Paruelo et al. 2022, 2024; Rositano et al. 2022; Baldassini et al. 2024; Gallego et al. 2024). Our study goes one step further by showing that landscape functional heterogeneity would increase ES supply. Previous work found no significant effects of landscape heterogeneity (the proportion of natural grasslands and their edge density) on cropland yields in the Chaco-Pampean plain of Argentina (Goldenberg et al. 2022). Our findings suggest that cropland functional diversity should be considered when analyzing ecosystem services in rural landscapes. Even though we did not estimate agricultural yields, we found that radiation absorption in cropland and pastures (necessary for obtaining yields) was positively related to cropland functional diversity. Also, cropland functional diversity positively influenced indicators of the supply of regulating ES related to water and carbon dynamics (Paruelo et al. 2016; Staiano et al. 2021). As far as we know, this is the first study that evaluated the influence of cropland functional diversity on ES supply indicators over such an extensive area and at the catchment level.

Addressing cropland diversity from the abundance and presence of Ecosystem Functional Types (EFTs) allows the removal of the restriction imposed by the lack of regional maps that spatially identify different crop types and practices (Jeanneret et al. 2021). The low conceptual resolution of the land use and land cover maps used in our study (Fig. S1) did not allow us to differentiate between cropping types across the study area (Baldassini et al. 2024), limiting the analysis of structural cropland diversity. Additionally, the absence of high-resolution spatial and conceptual land use and cover maps over an extended period, during which significant agricultural transformations occurred (1990-present), hindered the assessment of the influence of temporal cropland diversity and various cropland-livestock rotations on ES provision. Future updates to land use and cover maps from ongoing regional initiatives, such as MapBiomas Pampa (Baeza et al. 2022; https://pampa.mapbiomas.org/), will address these limitations, as demonstrated for other South American regions (Souza et al. 2020).

Describing both grassland edge density and adjacency to other uses is important for analyzing landscape configuration influence on ES supply (Mitchell et al. 2015; Eigenbrod 2016; Boesing et al. 2024). Boesing et al. (2024) hypothesized that ecosystem services (ES) would be influenced by landscape configuration when the local and landscape-level use intensities align (either both high or both low) in their effect on ES supply. This alignment supports ES supply by promoting optimal conditions at both levels, where high intensities at both scales may boost production services, while low intensities can enhance regulating and supporting services. In these situations, a segregated landscape configuration of high and low-intensity land uses and covers is recommended to support the supply of multiple ES (Boesing et al.

2024). Our findings, showing a negative effect of grassland juxtaposition on indicators of ES, align with this hypothesis, but further research is needed to confirm whether local management intensity mirrors landscape-level effects (Boesing et al. 2024). Grasslands' juxtaposition could benefit cropland productivity and carbon dynamics by providing pollinators and natural enemies for pest control at the local level (Tsharntke et al. 2012; Kremen and Merenlender 2018; Garibaldi et al. 2019). Also, the influence of field borders on ES depends on the surrounding natural and semi-natural areas, which enhance pollinator and natural enemy spillover (Martin et al. 2019). However, these borders are also exposed to negative effects from agrochemical drift and agriculture machinery (Aguiar et al. 2023). Our results suggest that cropland functional diversity should also be considered in these analyses, as regions with high functional diversity could provide more resources and could interact with grassland edges for pollination and pest control.

The results of our study provide relevant information for designing multifunctional landscapes that maximize food production while enhancing environmental performance in the Rio de la Plata Grassland region. The inclusion of agricultural microwatersheds in Argentina and Uruguay, which have differing land use regulation policies, allowed us to evaluate the impact of landscape heterogeneity on agricultural production and ES provision. In Uruguay, mandatory cropland and agricultural rotations (resolutions No. 0074/2013 and No. 397/018) promote the multifunctionality of agricultural landscapes through spatial diversification. These policies manifested in more heterogeneous agricultural landscapes in regions within Uruguay, which had a higher simultaneous supply of key intermediate ES than did the analyzed regions from Argentina. Ensuring compliance with such regulations and adopting similar diversification strategies in other countries could effectively increase food production without compromising ecosystem functioning (Kremen and Merenlender 2018; Garibaldi et al. 2019). Our findings could inform rural land-use planning processes that aim to balance food production with environmental sustainability (Bommarco et al. 2013; Uphoff 2014; Wezel et al. 2015).

Conclusion

Designing productive systems that ensure food production while maintaining the provision of multiple ecosystem services involves managing the diversity of land uses and land covers at the landscape level to sustain the structures and processes that provide these services. Our evidence indicates that promoting the functional diversification of croplands (different functional types of crops) along with the conservation of natural areas at the landscape level could be an effective way to enhance the environmental performance (through enhancing ES supply) of food production systems. Future research should incorporate the functional dimension of agriculture, and the temporal diversity presented by various agricultural rotations for a more precise evaluation of ecosystem service provision in multifunctional landscapes.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Gonzalo Camba Sans, Pablo Baldassini, Federico Gallego and José Paruelo. The first draft of the manuscript was written by Gonzalo Camba Sans and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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