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Diversified vegetation types on rangelands promote multiple soil-based ecosystem services

Hannah Waterhouse[1,2] | Felipe Aburto[3] | Gordon Rees[2,4] | Deirdre E. Griffin-LaHue[2,5] | Wilson B. Salls[2] | Devin A. Rippner[2,6] | Zhiyuan Tian[7,2] | Kate Scow[2] | Anthony T. O'Geen[2]

[1]Department of Environmental Sciences, Policy and Management, University of California at Berkeley, Berkeley, California, USA

[2]Department of Land, Air, and Water Resources, University of California at Davis, Davis, California, USA

[3]Pedology and Soil Biogeochemistry Laboratory, Department of Soil and Crop Sciences, Texas A&M University, College Station, Texas, USA

[4]Department of Natural Resources Management and Environmental Sciences, California Polytechnic State University, San Luis Obispo, California, USA

[5]Department of Crop and Soil Sciences, Washington State University, Mount Vernon, Washington, USA

[6]United States Department of Agriculture, Agricultural Research Service-Horticultural Crops Production and Genetic Improvement Research Unit, Prosser, Washington, USA

[7]State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing, China

Correspondence
Hannah Waterhouse, Environmental Science, Policy, and Management, UC Berkeley, Mulford Hall, 130 Hilgard Way, Berkeley, CA 94720, USA.
Email: hawaterh@ucsc.edu

Abstract

Rangelands have the potential to be provisioners of ecosystem services, including livestock products, carbon storage and greenhouse gas regulation, water and nutrient cycling, wildlife habitat, and biodiversity. Due to their vast extent and landscape heterogeneity, the degree to which different ecological components of rangelands contribute to ecosystem services can be varied. Soils are the foundation of rangeland health and associated ecosystem services. While many studies have examined the effect of grazing intensity on rangeland ecosystem services, few studies have looked at the broader rangeland landscape and how managing varying vegetation types can influence soil-based ecosystem services. In this study, a suite of physical, chemical, and biological soil health indicators were measured in various vegetation types found within a working cattle ranch, including coastal live oak woodlands, coastal scrublands, annual grassland, and restored native perennial grassland. Based on the measured soil health indicators, results from this study show scrubland significantly diverges from other vegetation types, having higher water infiltration and plant available water, carbon stocks, and a more diverse microbial community that drives more dynamic cycling of carbon and nitrogen. Strategically maintaining scrubland on unproductive, highly erosive slopes downgradient of highly productive grassland areas could maintain forage production while protecting water quality and increasing carbon storage. These results highlight the relevance of holistically evaluating rangeland operations to assess soil function and ecosystem services and the potential risks and co-benefits of varying vegetation types. Ultimately, process-based linkages described here may provide a working example of how to manage ranches as functional mosaics of strategically maintained vegetation types.

KEYWORDS

carbon sequestration, ecosystem services, emergent properties rangelands, nutrient cycling, soil health, water resources

1 | INTRODUCTION

Rangelands are traditionally considered providers of livestock products. However, more recently, the provisioning of other related ecosystem services on rangelands has been highlighted (Byrnes et al., 2018; Havstad et al., 2007) due to their vast extent and landscape heterogeneity. For example, healthy rangelands can regulate flooding and greenhouse gas (GHG) production, sequester carbon, provide water and nutrients, and support wildlife habitat, biodiversity, and pollination services. In addition, they have intrinsic spiritual and recreational values to the surrounding communities (Havstad et al., 2007; Ryals et al., 2014). On the other hand, degraded rangeland can produce relevant disservices, including the introduction of invasive species, habitat loss and fragmentation, GHG emissions, increased water runoff, and thus, decreased water storage and increased non-point source pollution, and soil erosion (Dangal et al., 2020; Rippner et al., 2015; Swain et al., 2013).

Soils are the foundation of rangeland health and the ecosystem services rangelands provide. While many studies have been conducted examining the impact of grazing intensity on soil health and the resulting ecosystem services, including carbon sequestration, biodiversity, and water quality and storage (Conant & Paustian, 2002; Gravuer et al., 2019; Hiernaux et al., 1999; Soussana & Lemaire, 2014; Z. Wang et al., 2016), few studies have looked at soil health indicators in different vegetation components and the contribution of these vegetation components to ecosystem services provided by the broader rangeland landscape (e.g., Derner et al., 2018; Eastburn et al., 2017; Fuhlendorf et al., 2012). Following the NRCS-USDA definition, we consider soil health as the continued capacity of soil to function as an ecosystem, within the limits of its inherent properties, to support plant, animal, and human health, including the provisioning of ecosystem services such as producing fuel, food, and fiber, regulating water quality and the climate, sustaining biodiversity, and supporting nutrient cycling (NRCS, 2023).

There is increased interest in measuring soil health status, a topic that has been largely explored in cropland systems, with less research conducted in rangeland systems (Brown & Herrick, 2016; Derner et al., 2018). Yet there is recognition that there is large potential, especially on degraded lands, to increase rangeland resilience to environmental change and increase ecosystem provisioning of rangeland systems via soil health management; however, more research is needed to understand how to leverage soil health to achieve these desired goals (Derner et al., 2018). Indeed, refocusing management to address ecological processes (water and nutrient cycling, productivity, wildlife habitat) instead of prescriptive one size fits all management actions could provide land managers with a deeper understanding of how a change in design or management of their system affects the functioning of their system (adaptive management) and how to improve upon this functioning with further experimentation (Hodbod et al., 2016). This understanding could lead to increased advocacy for incentivization payment schemes for the provisioning of ecosystem services on the ranch that benefit the broader society (Hodbod et al., 2016). Thus, what kinds of soil-based ecosystem services result from managing for a mosaic of vegetation types on a ranch?

The four soil health principles—(1) maximize plant diversity, (2) minimize disturbance, (3) maintain soil cover, (4) maintain the period of active plant growth—were developed concerning cropland management and the connection to beneficial soil ecological functioning in these systems. Yet, these principles may not translate to rangeland systems, and more research is needed on the applicability of these principles to rangeland systems (Derner et al., 2018). To assess the sustainability of a rangeland system, the ecosystem service provisioning of multiple vegetation types found within these landscapes must be determined. Indeed, plant species diversity and the effect on soil microbial biomass, respiration, and decomposition on grazing lands have been studied (Bardgett & Shine, 1999; Stephan et al., 2000; van der Heijden et al., 2008), but understanding the broader soil ecosystem provisioning potential of a rangeland's mosaic of heterogenous vegetation is lacking. Managing for a range of vegetation types within a rangeland system, when possible, will not only directly affect soil properties within the vegetation type itself but affect the ecosystem functioning of the ranch as a whole. However, little is known about the direction and magnitude in which soil properties vary across vegetation types and how these variations influence the provisioning of ecosystem services in rangeland systems.

Soil health researchers have placed great efforts in developing soil indicators that are sensitive to land management, predominantly in cropping systems, and, ideally, correlated with ecosystem service outcomes to ensure the long-term sustainability of agroecosystems (Derner et al., 2018; Wade et al., 2022). Typical indicators measured in different soil health assessment protocols and included in this study are aggregate stability, saturated hydraulic conductivity, water holding capacity (WHC), total carbon (C), permanganate oxidizable carbon (POXC), dissolved organic carbon (DOC), total nitrogen (N), ammonium, nitrate, dissolved organic nitrogen, and pH (Andrews et al., 2004; Moebius-Clune et al., 2017). The benefits of improving soil health are manifest in increased infiltration or saturated hydraulic conductivity leading to reduced erosion, increasing the WHC of soils to reduce water limitation, and increasing carbon sequestration to mitigate GHG emissions (Derner et al., 2018; Doran, 2002). While biological indicators have not historically been included in soil health assessments due to the complexity involved in measurement, recognizing the fundamental control microorganisms exert over many ecosystem functions, such as decomposition of organic matter, aggregation, and nutrient cycling, this study included determination of the microbial community using phospholipid fatty acid analysis, abundances of bacteria capable of denitrification and nitrification, and the relative abundances of fungi and bacteria. Many soil health assessment protocols now recognize the need to assess soils variably, considering their inherent properties. Thus, controlling for soil type, understanding the impact of vegetation type on soil health, and how managing heterogeneous landscapes can contribute to ecosystem provisioning at the ranch scale are needed to better understand the trade-offs and synergies of managing for multiple outcomes beyond food production. Eastburn et al. (2017) evaluated soil health indicators across grassland, oak savanna, and woodland vegetation states within a Sierra Foothill rangeland setting. Carbon storage and infiltration rates were highest in the woodland vegetation state compared to the other two. Using a state and transition model framework, they found that while annual revenue losses from foregone forage production would result from a conversion from a grassland state to an oak woodland state, incentivized conservation efforts via payments for ecosystem services by restoring strategic parts of the ranch (e.g., steep erosive hillslopes) could help offset production losses.

Managing rangelands for multiple outcomes is a growing practice in the Western United States. Rangeland comprises 40% of California's land surface (http://ucanr.edu/sites/RangelandES/), providing a significant opportunity for the state's working lands to contribute to ecosystem services. Traditionally, as Hodbod et al. (2016) note, agricultural systems have attempted to reduce variability inherent in these complex systems to increase predictability in productivity, yet in the process, have increased their vulnerability (i.e., large storms increasing runoff and nutrient losses). As Fuhlendorf et al. (2012) assert, "the full suite of ecosystem services valued by society will only benefit by management for heterogeneity, which implies that there is no one goal for management and that landscape-level planning is crucial." As interest in both soil health and carbon sequestration increase, as evidenced in certain policy mechanisms such as the California Department of Food and Agriculture's Healthy Soils Initiative as well as various climate policies (Novick et al., 2022), measuring the ecosystem services from heterogeneous landscapes, especially for vegetation types that do not directly maximize productivity, will be crucial for scoping the full co-benefits and potential tradeoffs/risk of managing for or maintaining diverse vegetation. Recognizing the importance of individual ecosystem services each vegetation type contributes to the overall ecosystem services the ranch provides to society is paramount given the increasing pressure to develop rangelands for either commercial development, thereby increasing net GHG emissions and impervious surfaces leading to runoff, or more water-intensive uses, such as vineyards (Biggs & Huntsinger, 2021; Fairbairn et al., 2021).

A growing group of California landowners has adopted new management practices that can effectively achieve multiple outcomes, including economic output and environmental sustainability. Our study site, TomKat Ranch, is one example where landowners have modified their land management from an intensified livestock-only focused rangeland to a system where differing vegetation types are managed to pursue multiple ecosystem service outcomes. Specific ecosystem service outcomes include forage production, carbon sequestration, increased bird habitat and biodiversity, and improved water quality and storage. Management strategies implemented starting in 2011 on Tomkat Ranch include maintaining areas of high production on naturalized annual grasslands, transitioning annual grassland areas to native perennial grassland to encourage carbon sequestration and optimize nutrient cycling, adaptive grazing of cattle to reduce stress on vegetation and preserve wildlife, maintaining a mosaic of dense scrubland for wildlife habitat, and preserving their iconic oak woodlands to prevent water quality degradation via erosion and sedimentation. The main vegetation types on this ranch are coastal live oak woodlands, coastal scrublands, naturalized annual grassland, and restored native perennial grassland. Previous work has tried to assess ecosystem multifunctionality at a landscape scale by building diversity indexes of different biodiversity components and linking them to simulated ecosystem function (e.g., Hautier et al., 2018; Zirbel et al., 2019). As shown by Le Provost et al. (2023), the provisioning of belowground ecosystem services seems to be more strongly determined by abiotic factors (i.e., wetness index) and management land use decision (i.e., tillage) at the field and plot level. Thus, assessing indicators of soil ecosystem services across the mosaic of vegetation types at this scale is relevant to better determine how soil functionality links to land use decisions at the ranch scale. This study aims to assess soil ecosystem functionality by looking at a suite of soil health indicators directly related to ecosystem services (carbon sequestration, water regulation, nutrient cycling, and biodiversity) within vegetation types across a sustainably managed rangeland in California.

2 | METHODS

2.1 | Site description

The study was carried out in California's Central Coast located south of the San Francisco Bay Area, with soils mapped predominantly as Cayucos clay and clay loam (Fine, montmorillonitic, thermic, Typic Haploxererts, under current classification) (Soil Survey Staff, 2014) (Table 1). TomKat Ranch (https://tomkatranch.org/) is a cow-calf operation (a permanent herd) of approximately 100–150 heads on 728 ha in Pescadero, CA (Henneman et al., 2014; Weverka et al., 2023). Like other coastal rangelands in California, the area is composed of a mosaic of different vegetation types, including riparian vegetation, grasslands, coastal scrub, and oak woodlands. The elevation ranges from 12 to 380 m. The site experiences a Mediterranean climate characterized by cool, wet winters and mild, dry summers, with low overcast skies and fog most of the year, especially during the summer months. The average annual precipitation predominantly falls as rain or fog and amounts to 750 mm (29.5 in.) (Henneman et al., 2014).

The ranch managers have designed strategies with the goal of restoring land that was previously degraded due to excessive grazing and past farming via prescribed grazing techniques such as reducing the stocking rate, managing the timing of grazing, and duration of rest. Managers intentionally keep certain areas in place to provide other ecosystem services not supplied by managed grasslands. To that end, land is maintained in four main vegetation types tied to the most prevalent ecological communities of the ranch: annual grasslands (Grass), restored native perennial grasslands (Perennial), coastal scrub (Scrub), and oak woodlands (Oak) (Figure 1). Grass makes up 305 ha of the ranch, Perennial 9 ha, Scrub 228 ha, and Oak 31 ha. Restored perennial grasslands were achieved using planned grazing focusing the timing and intensity of grazing to reduce annual grasses and

TABLE 1 General description of each vegetation type included in this study including current use, the plant community, and the soil classification.

Vegetation type	Current use	Plant community	USDA soil classification, elevation, aspect, and approximate sampling location
Grass	Pasture for beef production	Mainly naturalized annual grasses (*Bromus* spp.; *Brachypodium* spp; *Avena* spp) and some areas with exotic and native perennial grasses (*Stipa pulchra*, *Danthonia californica*, *Phalaris aquatica*).	Typic Haploxererts, 142 m, S40E, 37°15′29.13″ N, 122°21′19.37″ W
Perennial	Excluded area, converted 3 years earlier from pasture	Purple needle grass (*Stipa pulchra*), creeping wildrye (*Leymus triticoides*).	Typic Haploxererts, 44 m, S50W, 37°15′29.99″ N, 122°21′49.67″ W
Scrub	Biodiversity, water, erosion control and carbon sequestration	Coyote brush (*Baccharis pilularis*), poison oak (*Toxicodendron diversilobum*), California sage (*Salvia columbariae*), coffeeberry (*Rhamnus californica*), toyon (*Heteromeles arbutifolia*), ceonothus (*Ceanothus* spp.), flowering currant (*Ribes sanguineum*), lizardtail (*Eriophyllum staechadifolium*), California blackberry (*Rubus ursinus*), sticky monkeyflower (*Mimulus aurantiacus*), oceanspray (*Holodiscus discolor*), mugwort (*Artemisia douglasiana*)	Typic Haploxererts, 140 m, S80E, 37°15′29.02″ N, 122°21′19.98″ W
Oak	Component of pasture, wildlife, aesthetic	Coast live oak (*Quercus agrifolia*), toyon, redberry (*Rhamnus crocea*), common manzanita (*Arctostaphylos manzanita*), poison oak[a], ceonothus[a], coffee berry[a].	Typic Haploxererts, 146 m, S30E, 37°15′35.53″ N, 122°21′18.1″ W

[a]See taxonomic name in state above.

maximize perennial grass growth and seeding (Henneman et al., 2014). The typical composition of plant communities in these vegetation types is given in Table 1. Grazing occurs on both the annual and perennial grasslands, further management information can be found in Henneman et al. (2014) including stocking rates and frequency of rotation through paddocks. The oak woodland is also utilized by cattle primarily for shade. Coastal scrub occurs most often on steep slopes and in gullies and was too dense for cattle to access.

2.2 | Soil sampling

Using satellite imagery and map information, we delineated areas of the ranch according to vegetation types of Grass, Perennial, Scrub, or Oak (Figure 1). Three random points were located within each vegetation type for soil sampling in nearby areas (within a 100 m radius) at locations with consistent aspect (west facing) and hillslope position (summit position) and sampling was conducted over a 48 h period in September of 2013. However, as there was only one restored perennial location at the time, we were unable to control for aspect in this site location and it was south facing. Multiple sampling approaches were used to meet the needs of specific methods to characterize various physical, chemical, and microbiological soil health indicators. Bulk soil samples were collected at each point using an open bucket auger collecting samples from 0 to 100 cm at 25 cm depth intervals for physical and chemical analyses. Additional bulk soil material was collected at each point by excavating shallow pits to 25 cm to collect materials at a finer resolution of 0–5 and 5–25 cm. Specifics of sampling approaches are included with each method below. Additionally, one soil pit was excavated to bedrock in each of the vegetation types for descriptive purposes, details of which can be found in Supplementary Information.

2.3 | Soil health physical indicators

Physical soil health indicators evaluated were particle size distribution (PSD), bulk density (BD), wet aggregate stability, saturated hydraulic conductivity (K_{sat}), erodibility index, and WHC. All variables were measured from 0 to 25 cm from bucket auger replicate samples, except where otherwise noted.

The hydrometer sedimentation method was used to determine PSD after organic matter removal with sodium hypochlorite and dispersion with sodium hexametaphosphate (Soil Survey Staff, 2004). BD was measured for surface horizons by cores using a BD hammer (Soil Survey Staff, 2004). Wet aggregate stability was evaluated at

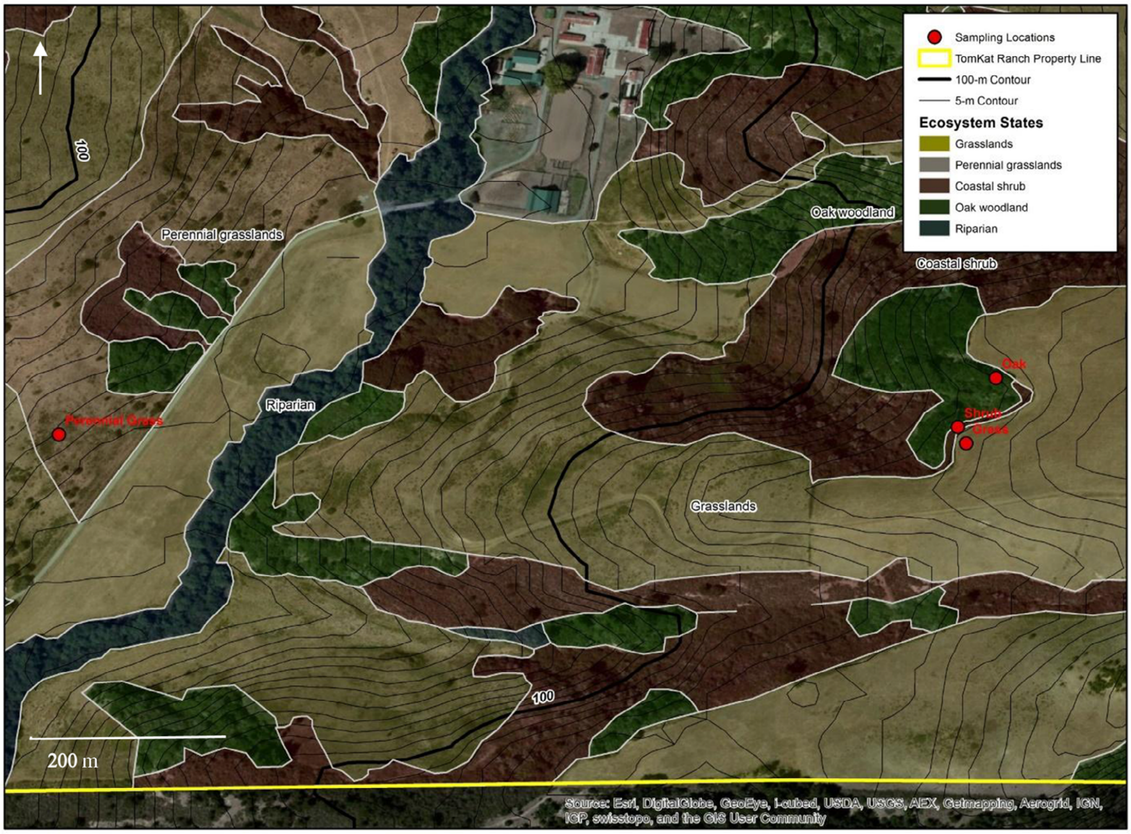


FIGURE 1 General map of the studied area showing the separation of vegetation types as defined by ranch management and soil sampling site locations (red points). Source of map layers display in the map. [Colour figure can be viewed at wileyonlinelibrary.com]

two depths, 0–5 cm and 5–25 cm, on air-dry aggregates between 1 and 2 mm in size and reported as a weighted average of the two depths (Soil Survey Staff, 2004). Results were corrected for sand grains >0.5 mm and expressed as the weight percentage of the original sample remaining on the sieve after treatment.

Laboratory measurements of K_{sat} were carried out following the methodology described by Klute (1965) from four cores sampled within the upper 7.6 cm of the mineral soil from each vegetation type ($n = 16$).

In order to assess vulnerability to erosion of each site, the soil erodibility factor (K-factor), was calculated using the updated universal soil loss equation (USLE) based on the work of Wischmeier and Smith (1978) (Blanco & Lal, 2008). The K-factor is calculated using values for soil texture, organic matter content, surface structure class, and permeability class (estimated using K_{sat} of surface horizons). Since PSD analysis was run in duplicate for each sample replicate, we averaged duplicate values for each replicate before calculating the K-factor. We then calculated the average K-factor for each replicate.

WHC and plant available water (PAW) were estimated using van Genuchten hydraulic parameters (1980). To estimate van Genuchten parameters, we used the regression equation developed by Wösten et al. (1999), which requires percent silt and clay, BD, and organic matter as inputs.

2.4 | Soil health chemical indicators

Soil chemical parameters measured for each replicate bucket auger sampling point include total C, POXC, water extractable DOC, N, total dissolved N (TDN), nitrate-N, ammonium-N, and pH. Total C, N, and POXC were measured down to 100 cm, while all other soil chemical variables were measured at 0–5 and 5–25 cm depth intervals, and values reported as a weighted mean across both depth intervals to be able to compare to other variables sampled at 25 cm increments. Soil organic matter functional groups were analyzed on one replicate sample from 0 to 5 and 5 to 25 cm, taken from the shallow pits, and the methods are reported in Table S1.

Total C and N contents were obtained by combusting air-dried samples ground to 80 mesh in a Costech ECS-4010 CHNSO Elemental Analyzer. POXC was analyzed according to methods outlined by Weil et al. (2003), with modifications described in Wade et al. (2020). DOC was determined for 0–5 cm and 5–25 cm depths by UV-persulfate oxidation after suspension in 1:8 ratio with water, shaking, and vacuum extraction. The carbon stock was calculated as the product of total C content, BD, and layer thickness.

TDN was determined in a water suspension by persulfate digestion (Valderrama, 1981) followed by colorimetric determination of nitrate produced (Doane & Horwath, 2003). Nitrate (NO_3^-) and ammonium (NH_4^+) were extracted from 10 g of soil added in the field to polypropylene tubes containing 40 mL of 2 M KCl. Samples were shaken for 45 minutes on a reciprocating shaker, centrifuged at 2000 rpm, and the supernatant was separated from solids. Samples were then analyzed for NH_4^+-N and NO_3^--N colorimetrically by protocols described by Verdouw et al. (1978) and Doane and Horwath (2003), respectively.

Soil pH was determined using a 1:1 ratio of water to soil and shaken for 15 min on a reciprocal shaker, allowed to settle for 15 min and supernatant analyzed with a pH electrode (Thomas, 1996).

2.5 | Soil health biological indicators (microbial communities)

Using sterilized equipment, soil samples were collected from 0 to 25 cm in three random points per vegetation type. Each sample was sieved to 2 mm and homogenized. From each sample, three representative subsamples were frozen at −20°C. One set of frozen soil subsamples was used for DNA extraction and quantitative PCR (qPCR). Another set of subsamples was frozen at −80°C and then freeze-dried for phospholipid fatty acid (PLFA) analysis. PLFA analysis and profiling were performed by Microbial ID, Inc. (Newark, DE) according to methods detailed in Buyer and Sasser (2012). Lipid profiles as well as relative abundances of lipids associated with specific microbial groups were analyzed.

For qPCR analysis, DNA was extracted in triplicate from 0.25-g subsamples using the PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA) according to manufacturer's instructions. DNA concentrations of the extracts were determined using a Qubit fluorometer and Quant-iT dsDNA HS Assay Kits (Invitrogen, Carlsbad, CA).

To estimate abundances of total bacteria and bacteria capable of denitrification and nitrification, DNA extracts were analyzed for copy numbers of the bacterial 16S rDNA gene, denitrification genes *nirK*, *nirS*, and *nosZ*, as well as *amoA* (subunit A of the ammonia monooxygenase gene). Primers used for detection of *nirK*, *nirS*, *nosZ*, *amoA*, bacterial 16S detection can be found in Table S2. All qPCR assays were run in triplicate for each extract on 25 µL aliquots containing 1X SYBR GreenER qPCR SuperMix (Life Technologies, Grand Island, NY), 500 nM of forward and reverse primers, and 5 µL of DNA extract. Standard curves were generated with each qPCR run (R^2 >0.99) using serial dilutions of cloned gene fragment standards with known gene copy numbers. All reactions were run on an Applied Biosystems Prism 7300 Real-Time PCR System (Applied Biosystems, Foster City, CA). Reaction conditions for all assays are listed in Table S2. After each assay, a melting curve analysis was performed to confirm that only the desired product was obtained.

Abundances of total bacteria and each N cycling bacterial group were estimated as normalized gene copies per gram of dry soil. Functional genes *nirK* and *nirS* encode for nitrite reductase while *nosZ* encodes for nitrous oxide (N_2O) reductase. Therefore, we estimated changes in abundances of producers and reducers of N_2O, and thus the potential for N_2O to be released from soil, based on calculated ratios of these gene copy numbers (Pereira et al., 2015).

2.6 | Soil pit characterization data

Soil description and classification of soil profiles were performed at each vegetation type following Schoeneberger et al. (2013) and Soil Survey Staff (2014), respectively. Various additional parameters were measured for each genetic horizon, including phosphorus (P) sorption, Olsen-P, potassium (K) fixation, and exchangeable K. As these pits were not replicated within vegetation type, results are not included in statistical analyses. However, methods and data down to 25 cm are included as Table S1.

2.7 | Statistical analysis

All statistical analyses were conducted in R (R Core Team, 2018). Statistical tests conducted include analysis of variance (ANOVA) (R Core Team, 2018) and Tukey means separation tests for means comparison between vegetation types using the *agricolae* package (de Mendiburu, 2017). Assumptions for ANOVA, including normality of residuals and homogeneity of variance, were tested using the Shapiro–Wilk test (R Core Team, 2018) and the Levene's test (J. Fox & Weisberg, 2011), respectively. All figures were created using the R package *ggplot2* (Wickham, 2016).

Lipid profiles were analyzed through redundancy analysis (RDA) using the *vegan* package (Oksanen et al., 2019). All lipid data were Hellinger transformed before analysis, and lipids that were present in less than 25% of samples were removed. Soil environmental variables were included to test relationships between lipid profiles and soil properties. Explanatory soil variables were included initially based on hypothesized relevant properties and were selected for the model to minimize variance inflation factors (VIF <5). Significance of explanatory environmental properties and canonical axes was tested with permutation tests (10,000 permutations).

Spider plots in Figure 8 were created by normalizing each variable using the maximum and minimum values across vegetation types and plotting in R using the radarchart function from the *fmsb* package (Nakazawa, 2022). The multifunctionality index was created by averaging across each variable within each ecosystem service category. However, as nitrous oxide potential is considered an ecosystem disservice, this variable was first inverted prior to taking the average across variables.

3 | RESULTS

3.1 | Physical indicators of soil health

Most soil physical properties were very similar between vegetation types. Surface soil textures were categorized as clay in Perennial and Oak, clay loam in Scrub, and silty clay loam in Grass (Table 2). Mean

TABLE 2 Soil physical properties from 0 to 25 cm depth across each vegetation type.

Vegetation type	Soil texture classification	Sand (%)	Silt (%)	Clay (%)	Porosity (%)	Bulk density (g/cm^3)
Grass	Silty clay loam	19.9 ± 0.8 (b)	44.8 ± 2.3 (a)	35.3 ± 1.6 (b)	53.21 (a)	1.26 ± 0.05 (a)
Perennial	Clay	12.2 ± 0.8 (c)	31.5 ± 2.2 (b)	56.3 ± 2.4 (a)	59.40 (a)	1.08 ± 0.20 (ab)
Scrub	Clay loam	23.2 ± 2.1 (b)	45.0 ± 3.5 (a)	31.9 ± 5.3 (b)	65.10 (a)	0.90 ± 0.10 (b)
Oak	Clay	29.8 ± 2.6 (a)	29.5 ± 1.7 (b)	40.8 ± 3.9 (b)	55.61 (a)	1.18 ± 0.11 (a)

Vegetation type	Aggregate stability (%)	K Sat[a] (cm/min)	Water holding capacity (cm^3/cm^3)	Plant available water (cm^3/cm^3)	Erodibility index
Grass	75 ± 9 (a)	0.95 ± 1.21 (a)	0.38 ± 0 (bc)	0.13 ± 0 (d)	0.38 ± 0.02 (a)
Perennial	83 ± 1 (a)	2.11 ± 0.82 (a)	0.39 ± 0 (ab)	0.17 ± 0 (b)	0.32 ± 0.03 (a)
Scrub	89 ± 2 (a)	7.25 ± 4.57 (a)	0.41 ± 0.02 (a)	0.21 ± 0 (a)	0.31 ± 0.05 (a)
Oak	82 ± 11 (a)	5.45 ± 5.12 (a)	0.36 ± 0.01 (c)	0.15 ± 0 (c)	0.29 ± 0.03 (a)

Note: Mean and standard errors shown. Differing letters represent significant differences $p < 0.05$ ($n = 3$/vegetation type).
[a]Saturated hydraulic conductivity.

clay contents of soil horizons within a profile ranged from 32% to 56% across all sites, but the perennial site displayed a significantly higher surface clay content compared to the other vegetation types. Aggregate stability, porosity, K_{sat}, and erodibility did not significantly differ across vegetation types ($p > 0.05$). However, differences were found for BD, WHC, and PAW (Table 2). Grass and Oak had significantly higher BD (1.26 g/cm^3 and 1.18 g/cm^3) compared to Scrub (0.90 g/cm^3), with no significant difference between Grass, Oak, and Perennial (1.08 g/cm^3). Scrub had significantly higher WHC (0.41 cm^3/cm^3) compared to Oak (0.36 cm^3/cm^3) and Grass (0.38 cm^3/cm^3), with no significant differences between Scrub versus Perennial (0.39 cm^3/cm^3), Perennial versus Grass, and Grass versus Oak. Similarly, Scrub had the highest PAW (0.21 cm^3/cm^3) compared with all other vegetation types, while Grass (0.13 cm^3/cm^3) had the lowest.

3.2 | Chemical indicators of soil health

Most soil chemical properties were similar between vegetation types from 0 to 25 cm depth but different below 25 cm. pH was moderately acidic and fell into a narrow range from a low of 5.5 for Oak to a high of 5.9 for Perennial, with no significant differences across vegetation types (Table 3). Mean total C concentrations in the top 25 cm ranged from 2.56% to 3.51% and decreased with depth, with concentrations ranging from 0.21% in the Grass to 1.30% in the Scrub at 75–100 cm depth (Figure 2). Total N decreased similarly with depth in each vegetation type. In the top 25 cm, mean total N ranged from 0.28% in the Perennial to 0.32% in the Scrub, whilst at 100 cm depth, mean total N ranged from 0.10% in the Oak to 0.20% in the Scrub (Figure 3).

In the top 25 cm, no significant differences in total C across vegetation types were found. However, below 25 cm, Scrub (2.02%) and Perennial (1.41%) had significantly higher total C concentrations compared to Grass (0.55%), with no difference between Oak (0.75%) and Perennial (Figure 4a). In the top 25 cm, POXC did not significantly differ across vegetation types; however, similar to total C, differences in POXC between vegetation types existed below 25 cm. Scrub (328.94 mg C/kg soil) and Perennial (242.77 mg C/kg soil) had the highest POXC, while Oak (139.63 mg C/kg soil) and Grass (83.17 mg C/kg soil) had lower POXC below 25 cm (Figure 4b). The depth-weighted ratio of aromatic-C to aliphatic-C was higher for Scrub and Perennial compared to Oak and Grass (Table S1). Water extractable dissolved organic carbon (DOC) was highest in Oak (670.99 mg C/kg soil) compared to Perennial (253.25 mg C/kg soil) and Grass (216.41 mg C/kg soil) sites, with no difference between Oak and Scrub (403.50 mg C/kg soil) and no difference between Scrub and Perennial or Grass in the top 25 cm (Table 3).

Total N did not significantly differ across vegetation types in the top 25 cm; however, below this depth, mean total N was highest in Scrub (0.26%) and Perennial (0.21%) sites, while Oak (0.18%) and Grass (0.17%) had the lowest total N (Figure 5). Similarly, TDN in the top 25 cm significantly differed across vegetation types in the following order; Oak (46.53 mg N/kg soil) > Scrub (27.39 mg N/kg soil) > Grass (22.42 mg N/kg soil) > Perennial (19.49 mg N/kg soil) (Table 3). Ammonium-N and NO_3^--N did not significantly differ between vegetation types in the top 25 cm (Table 3). However, NH_4^+ showed a decreasing trend from Oak (6.41 mg N/kg soil), to Grass (5.99 mg N/kg soil), to Scrub (3.29 mg N/kg soil), with the lowest concentrations found in Perennial (3.07 mg N/kg soil). Nitrate was highest in Grass (5.84 mg N/kg soil) sites, followed by Perennial (4.51 mg N/kg soil), Scrub (2.61 mg N/kg soil), and Oak (0.81 mg N/kg soil).

3.3 | Biological indicators of soil health

qPCR analysis showed that bacterial N cycling and 16S gene copy numbers within the microbial community differed by vegetation type (Figure 6). Total 16S bacterial rDNA copy numbers were highest in

TABLE 3 Soil Chemical properties from 0 to 25 cm depth across each vegetation type.

Vegetation type	pH	Total carbon (%)	POX carbon (mg/kg)	Dissolved organic carbon (mg/kg)	Total nitrogen (%)	Total dissolved nitrogen (mg/kg)	Ammonium (mg/kg)	Nitrate (mg/kg)
Grass	5.71 ± 0.23 (a)	2.56 ± 0.15 (a)	419.33 ± 24.50 (a)	216.41 ± 21.76 (b)	0.29 ± 0.01 (a)	22.42 ± 1.09 (b)	5.99 ± 0.79 (a)	5.84 ± 0.62 (a)
Perennial	5.90 ± 0.14 (a)	2.69 ± 0.44 (a)	427.00 ± 51.22 (a)	253.25 ± 74.26 (b)	0.28 ± 0.03 (a)	19.49 ± 1.04 (b)	3.07 ± 1.03 (a)	4.51 ± 1.99 (a)
Scrub	5.60 ± 0.13 (a)	3.51 ± 0.68 (a)	523.67 ± 55.52 (a)	403.5 ± 46.77 (ab)	0.32 ± 0.04 (a)	27.39 ± 1.28 (ab)	3.29 ± 2.48 (a)	2.61 ± 3.56 (a)
Oak	5.47 ± 0.69 (a)	3.10 ± 0.34 (a)	467.00 ± 14.11 (a)	670.99 ± 189.28 (a)	0.30 ± 0.02 (a)	46.53 ± 1.55 (a)	6.41 ± 4.03 (a)	0.81 ± 1.19 (a)

Note: Mean and standard errors shown. Differing letters represent significant differences with $p < 0.05$ ($n = 3$/vegetation type).

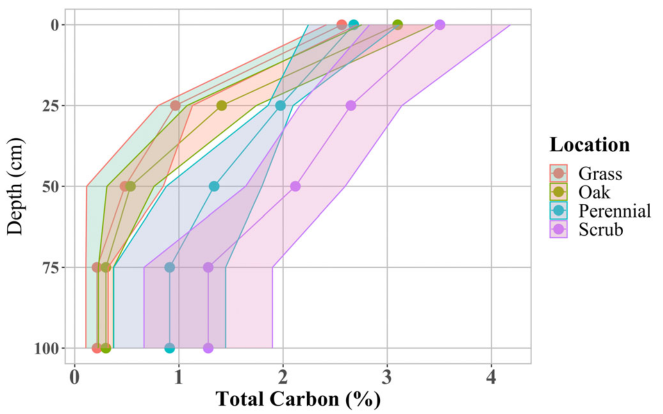


FIGURE 2 Total carbon (C) (%) with depth (0–100 cm) across vegetation types. Vertical lines represent means and shaded region represents standard deviation (n = 3/vegetation type per depth). [Colour figure can be viewed at wileyonlinelibrary.com]

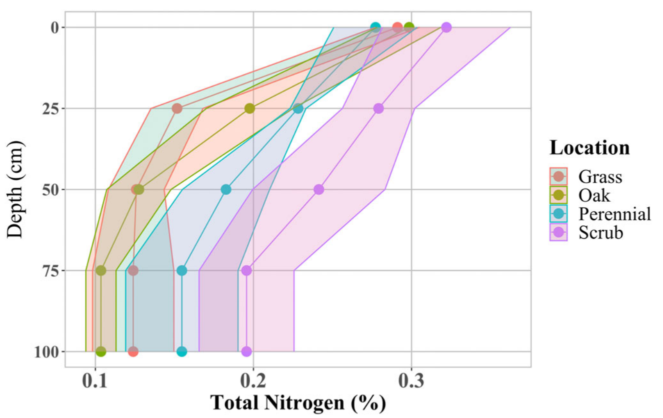


FIGURE 3 Total nitrogen (%) with depth (0–100 cm) across vegetation types. Vertical lines represent means and shaded region represents standard deviation. (n = 3/vegetation type per depth). [Colour figure can be viewed at wileyonlinelibrary.com]

Scrub and lowest in Oak (p = 0.039). However, bacterial *amoA* and *nirK* + *nirS* copy numbers were highest in Oak and Scrub and lowest in Grass and Perennial (*amoA*: p = 0.004; *nirK* + *nirS*: p = 0.044). Though *nosZ* was lowest in Grass, it did not differ significantly between systems (p = 0.135). However, ratios of *nirK* + *nirS*:*nosZ*, an indicator of N_2O production potential, were significantly higher in Grass than in Perennial and were intermediate in Oak and Scrub (p = 0.018).

PLFA analysis showed that relative abundances of microbial groups associated with specific lipids differed between vegetation types and, for some biomarkers, Grass and Perennial vegetation types were more similar, while Oak and Scrub were more alike (Table 4, Figure 7). For example, Oak and Scrub had higher relative abundances of Gram-negative bacteria (p = 0.008), while Grass and Perennial had higher relative abundances of Gram-positive bacteria (p = 0.008) (Table 4). While total biomass did not statistically differ between vegetation types (p = 0.119), Grass had the lowest (98.77 ng/g), while

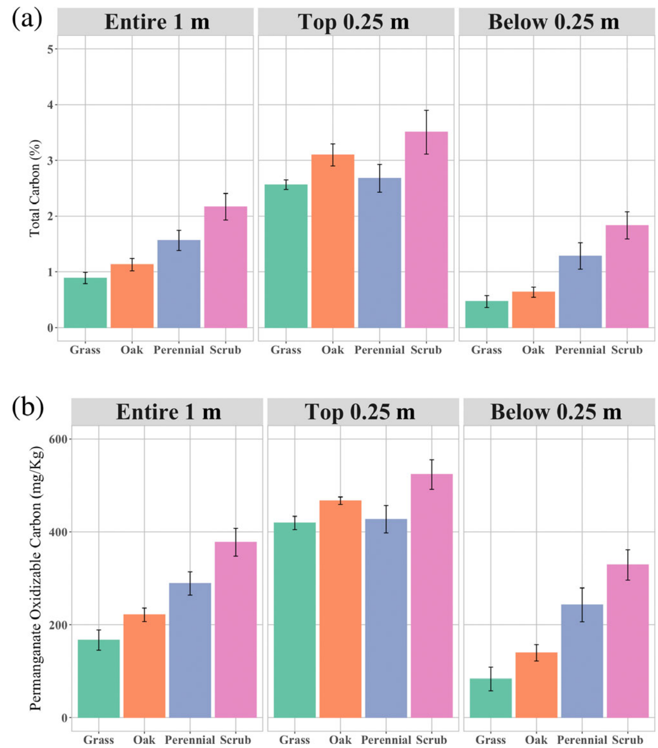


FIGURE 4 (A) Mean total carbon (%) and (B) mean permanganate oxidizable carbon (POXC) across the entire 1 m profile, in the top 25 cm and below 25 cm across vegetation types. Error bars represent standard errors (n = 3/vegetation type per depth). Differing letters represent significant differences (p < 0.05). [Colour figure can be viewed at wileyonlinelibrary.com]

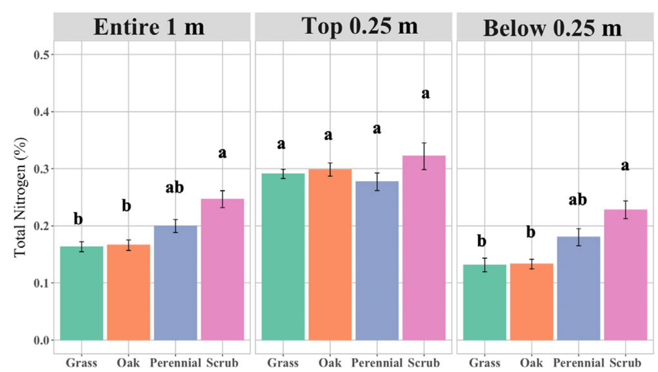


FIGURE 5 Mean total nitrogen (%) across the entire 1 m profile, in the top 25 cm and below 25 cm across vegetation types. Error bars represent standard deviation (n = 3/vegetation type per depth). Differing letters represent significant differences (p < 0.05). [Colour figure can be viewed at wileyonlinelibrary.com]

Scrub (146.26 ng/g) had the highest, with Oak (144.68 ng/g) and Perennial (120.69 ng/g) having relatively intermediate amounts (Table 4). Scrub had the highest relative abundance of lipids associated with eukaryotic organisms, followed by Grass, with Perennial and Oak having the lowest (p = 0.015). Fungal:bacterial ratios (p = 0.763) and relative abundances of fungi (p = 0.548) and actinomycetes (p = 0.131) did not differ significantly between vegetation types.

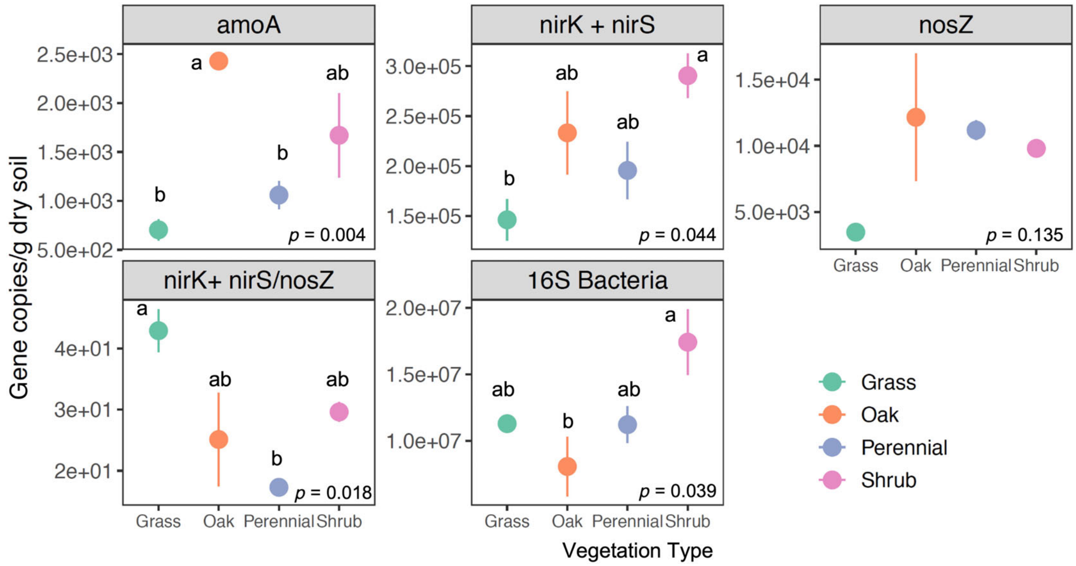


FIGURE 6 Gene copy numbers of key nitrogen cycling genes and 16S bacterial rDNA from qPCR analysis. Points represent the mean for each vegetation type and error bars are standard errors ($n = 3$). Different letters indicate significant differences based on Tukey honest significant difference ($p < 0.05$). [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Total PLFA biomass and relative abundances of lipid biomarkers across each vegetation type from 0 to 25 cm.

Vegetation type	Total PLFA biomass ng/g soil	Gram-negative mol%	Gram-positive mol%	Eukaryotes mol%	Actinomycetes mol%	Fungal: bacterial ratio
Grass	98.8 ± 3.0 (a)	36.8 ± 0.4 (b)	32.7 ± 0.3 (a)	2.5 ± 0.2 (ab)	15.1 ± 0.1 (a)	0.132 ± 0.004 (a)
Perennial	120.7 ± 6.4 (a)	37.4 ± 0.6 (b)	31.8 ± 0.1 (ab)	1.7 ± 0.01 (b)	15.3 ± 0.4 (a)	0.138 ± 0.008 (a)
Scrub	146.3 ± 18.7 (a)	41.3 ± 1.7 (ab)	28.6 ± 0.8 (c)	2.8 ± 0.4 (a)	13.7 ± 0.4 (a)	0.146 ± 0.024 (a)
Oak	144.7 ± 19.0 (a)	43.2 ± 1.0 (a)	29.4 ± 1.0 (bc)	1.6 ± 0.2 (b)	14.0 ± 0.8 (a)	0.127 ± 0.008 (a)

Note: Mean and standard errors shown. Differing letters represent significant differences with $p < 0.05$ ($n = 3$/vegetation type).

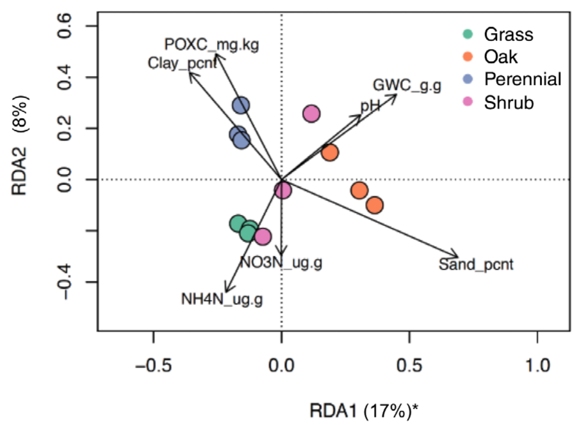
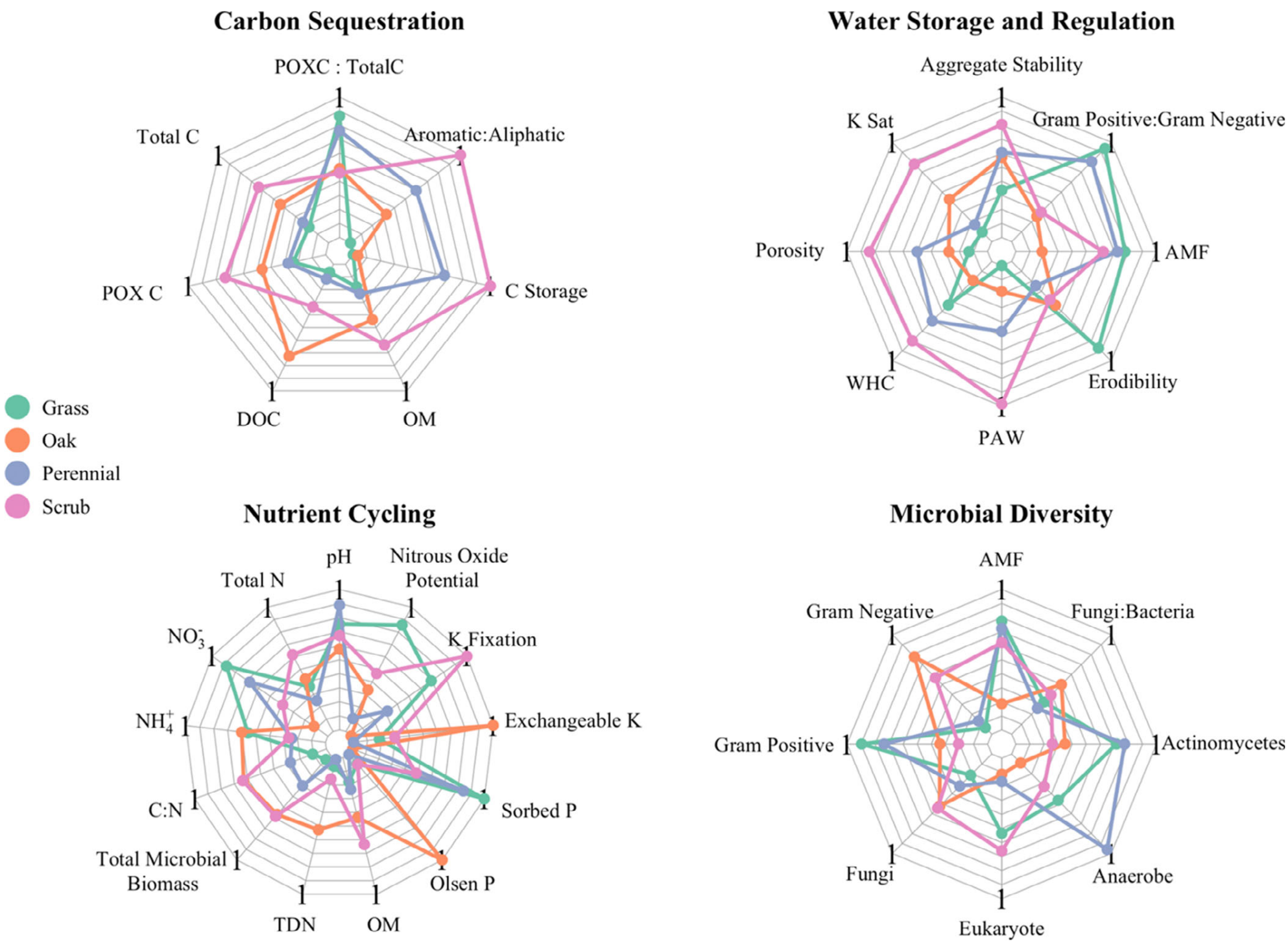


FIGURE 7 Redundancy analysis (RDA) of PLFA lipid profile data from Grass, Perennial, Oak, and Shrub vegetation types, constrained by soil environmental variables, which were selected to maximize variation explained while minimizing the variance inflation factor (VIF). Axes 1 and 2 represent 17% and 8% of the total variation (unbiased estimates), respectively, with the whole model explaining 33.4% of the variation (adjusted R^2). An asterisk on the RDA1 axis indicates that this axis was significant in permutation tests at $p < 0.10$. [Colour figure can be viewed at wileyonlinelibrary.com]

RDA showed that the lipid profile of Oak diverged from Grass and Perennial vegetation types along the primary RDA axis, which explained 16.9% of the variation (unbiased estimate; $p = 0.0713$; Figure 7). Samples from Perennial and Grass systems diverged from one another along the secondary RDA axis, which explained an additional 8% of the variation. Divergence of lipid profiles was correlated with gravimetric water content (GWC) ($p = 0.0470$), POXC ($p = 0.0483$), and clay percentage ($p = 0.0852$), based on permutation tests. Samples from the Scrub system were intermediate between Oak and Grass/Perennial and had more between-sample variability in lipid profiles than other systems. The adjusted R^2 of the RDA model was 0.334.

3.4 | Soil functions link to multiple ecosystem services

The various soil health indicator dimensions across each vegetation type within each ecosystem service category can be visualized using spider plots (Figure 8). In the carbon sequestration and water storage



Vegetation type	Multifunctionality Index
Grass	0.31
Oak	0.41
Perennial	0.37
Scrub	0.58

FIGURE 8 Multiple ecosystem service outcomes normalized from 0-1 by the maximum and minimum values for each variable class across vegetation types. Potassium and phosphorus variables were analyzed on only one replicate from the soil pits, total C and N here represent mean values down to 1 meter, all other variables are from 0-25cm. The multifunctionality index averages the normalized values across each indicator and ecosystem service except for the nitrous oxide potential which was inverted before taking the average to indicate that this is an ecosystem disservice. [Colour figure can be viewed at wileyonlinelibrary.com]

and regulation categories, it becomes clear that Scrub has higher ecosystem provision values than the other vegetation types. However, for nutrient cycling, Oak and Scrub were somewhat similar, especially for total microbial biomass, soil C:N ratios, and low amounts of nitrate, while the grass had higher amounts of nitrate. Similarly, in the Microbial Diversity category, Perennial and Grass had higher abundances of Gram-Positive and AMF. To better understand how each vegetation type contributes to overall ecosystem services, a multifunctionality index was created based on all the ecosystem functions included in this study (Figure 8). This index shows that Scrub had the highest overall ecosystem service provisioning (0.58) out of all vegetation types, followed by Oak (0.41) > Perennial (0.37) > Grass (0.31).

4 | DISCUSSION

On the Central Coast of California, climate, geology, soil type, and land-use history influence the heterogenous structure of rangeland vegetation. This mosaic of vegetation interacts in a cross-habitat manner to influence emergent properties of the ranch as a whole (i.e., net

GHG fluxes, erosion, water regulation) (Felipe-Lucia et al., 2022; W. W. Fox et al., 2009; Gilbert & Henry, 2015). For example, maintaining Scrub, with high infiltration rates on steep slopes, serves as natural buffer strips downgradient of more intensively utilized Grass areas. This vegetative association maintains forage production while protecting water quality for the benefit of the ranch and the broader watershed. In this scenario, sediment and pathogens have the potential to be transported within Grass (field scale) but maintained within the ranch as a whole (catchment scale), and thus, the vegetation mosaic demonstrates the potential to reduce non-point source pollution. Given the increasing interest in rangelands to provide multiple ecosystem services, we examine the potential of managing for landscape heterogeneity and the beneficial (or not) emergent properties that result from interacting effects of varying vegetation types on ecosystem functioning.

4.1 | Carbon cycling

Interestingly, we did not find significant differences in total C (%) in the top 25 cm among vegetation types, but C significantly differed at greater depths (Figure 4a). As a result, C stocks down to 1 m were almost twice as high in Scrub (379.08 ton C/ha) and Perennial (315.95 ton C/ha) than Oak (212.33 ton C/ha) and Grass (199.59 ton C/ha) (Figure 8). Given the differing proportions of hectarage of each of the vegetation types on the ranch enumerated in the methods section, Scrub is a large sink of C on this ranch, yet expanding it without careful consideration could lead to land being taken out of production, as well as increased fire risk. However, if Perennial acreage were to expand, this likely could lead to an increase in both productive feeding/grazing hectarage and a large C sink. Rangeland plant species that are deep-rooted, such as Scrub and Perennial, can increase C inputs to deeper depths and, in some cases, are more effective at increasing C storage than managing grazing intensity (Whitehead, 2020). Furthermore, C stored at deeper depths is generally more protected via association with metal oxides and clay minerals from microbial decomposition and its subsequent loss of CO_2 as microbial activity tends to decrease with depth (Rumpel et al., 2015). Given that the Perennial vegetation type had only been established for 3 years before sampling, it is less likely that the aforementioned was the main driver of increased total C in this vegetation type and more likely is a legacy effect as a result of a higher clay % and particle surface area across all horizons, which contributed to the higher C concentrations via enhanced mineral-organic interaction.

POXC was also significantly higher in the Scrub than in Oak and Grass when considering the entire 1-m profile (Figure 4b). POXC has been proposed as a critical soil health indicator and represents a relatively processed, moderately stable, yet potentially biologically active C fraction sensitive to management (Culman et al., 2012; Morrow et al., 2016). Previous work by Tirol-Padre and Ladha (2004) showed that POXC was positively correlated to sample lignin content. This is in part supported by Scrub having the highest ratio of aromatic-C to aliphatic-C of any of the vegetation types. Given that Scrub acts as a natural buffer, it is likely that C increases in this vegetation type due to C sediment deposition (Berhe et al., 2007). In addition to higher total C and POXC, Scrub also had lower BD and higher PAW, allowing it to support plant productivity and sustain C inputs for sequestration, which could be important for predicted drier conditions in the future (Table 2; Warter et al., 2021).

When examining other C-related variables, Grass displayed the lowest total C, aromatic to aliphatic ratio, DOC production, and POXC concentrations (Figure 8). These indicators suggest that C cycling within Grass is less dynamic as a smaller amount of C seems to be actively cycling, which can also be seen in its lower microbial biomass (although not significantly different from the other vegetation types) and changes in microbial community structure (see Section 4.3). Petrie et al. (2014) showed that scrublands maintain higher C assimilation under arid conditions and, as a result, are a higher C sink than C4-dominated grassland in a desert environment. Similarly, across terrestrial biomes in China, scrublands display the largest C density (Ge et al., 2020). The latter highlights the relevance of maintaining these vegetation types as a critical component of rangeland ecosystems for storing large amounts of C and substantially mitigating GHG emissions from ranch operations. However, while the Grass did have lower amounts of C stored, it must be noted that in fire-prone areas, such as California, grasslands have been shown to be more resilient in their ability to store carbon at the ecosystem level compared to woody habitats since the majority of their carbon is stored belowground (Biggs & Huntsinger, 2021). To maintain (if not increase) grazable lands, reduce fire risk and the resulting GHG while increasing C storage, expanding Perennial vegetation types could increase co-benefits and reduce risks, as well as minimize tradeoffs in productivity while still supplying ecosystem services beyond food provisioning (Eastburn et al., 2018).

4.2 | Water cycling and erosion control

In California, where the frequency of droughts and flooding is expected to increase, the 16 million hectares of rangeland are essential for water provisioning and water quality regulation (Huntsinger & Oviedo, 2014). The way in which vegetation structure and dynamics vary within rangelands will influence the partitioning of hydrologic processes across surface water flow, runoff, groundwater recharge/stream base flow, evaporation, and transpiration (Havstad et al., 2007) and, in turn, affect the distribution, provisioning, and quality of water. At the landscape/regional scale, groundwater recharge is a particularly important hydrologic process in California, where 61% of precipitation is lost to evapotranspiration (ET), and where many watersheds throughout the state, including within the Central Coast, rely on groundwater to meet their drinking and irrigation needs (DWR, 2014). While no statistical differences were found between vegetation types, the Grass site had the lowest K_{sat}, while the Scrub had the highest K_{sat} (Table 2). Thus, Scrub has the potential to infiltrate and recharge water more efficiently compared to the other three vegetation types (Figure 8). Prior studies have shown that infiltration under Scrub vegetation types is higher than in grassland-dominated areas due to increased carbon accumulation, root activity, and soil fauna which can, in turn, increase groundwater recharge (Briske, 2017). However, recharge within Scrub could be limited due to several mechanisms: woody plants, depending on the species composition, can increase the potential ET relative to grasslands as they do not have a dormant period and generally have lower albedo and higher air turbulence within the canopy, they can access water stored in deeper layers, and canopy interception of rainfall is higher compared to grasslands (Bonan, 2008; Briske, 2017; Donohue et al., 2007; Owens et al., 2006). Further studies are needed to capture the annual water balance of different vegetation types and how vegetation composition, edaphic factors, climate, and management interactions affect the hydrology of these systems.

At the pasture and ranch scales, increasing infiltration, in addition to increasing water storage, helps recharge aquifers and abate surface runoff and erosion, the latter of which is particularly important for productivity, as rangelands are often found on nutrient-poor soils (Havstad et al., 2007). At the hillslope scale, retaining areas of higher infiltration, such as that of Scrub or Oak, can create sinks for overland flow, a process known as runoff-run-on, which results in pathogen, sediment, and nutrient capture. Greater effective precipitation (capture of run-on) increases biomass growth in Scrub patches, and thus, increases carbon accumulation on these landscapes (Bergkamp, 1998; Ludwig et al., 2005; Wilcox et al., 2003). Thus, to take advantage of these cross-habitat benefits, maintaining Scrub vegetation on steep rangeland areas where erosion rates are high and productivity is low could enhance ecosystem services at the ranch scale.

Erosion is a dynamic and complex process that depends on a myriad of terrain attributes, rainfall erosivity and biophysical factors, including human activities. While heavy grazing activity can directly impact soil erodibility as excessive livestock utilization can decrease cover and increase soil compaction, decreasing porosity, WHC, and infiltration, light, and moderate grazing management do not differ significantly from their un-grazed counterparts in California (Salls et al., 2018; Zhou et al., 2010). Here, we calculated the USLE's erodibility factor (K) to assess how soils in the four vegetation types differ in their susceptibility to erosion (Sadeghi et al., 2007; Zhou et al., 2010). The K factor considers texture, organic matter, structure, and permeability as the main soil characteristics determining erodibility. Opposite to what has been reported previously, we found no apparent differences in soil erodibility between vegetation types (Table 2). It is important to consider that our approximation focused only on the intrinsic soil susceptibility to erosion as a relative comparison of soil properties influencing K within each vegetation type. We did not consider the effect of the other factors determining actual erosion rates—topography, plant cover and structure, and management (included in the LS, C and P factors of the USLE model). Thus, it could be that the actual erosion rates are different between vegetation types, particularly since the LS and C factors vary substantially between them. The fact that Grass did not significantly increase erodibility could also be considered an indicator of light to moderate grazing management and the area not being overgrazed (Salls et al., 2018).

4.3 | Maintaining biodiversity and nutrient cycling

Vegetation types structured microbial communities via their influence on soil environmental variables such as water availability and C and nutrient inputs (i.e., form, type, quantity, and quality of C resources) (Figure 7). While total microbial biomass, as estimated by total lipid concentrations, did not significantly differ across vegetation types, higher abundances of genes involved in N cycling, including *amoA*, *nirK*, and *nirS*, were found in Scrub and Oak compared to the other vegetation types, with Grass having the lowest (Figures 6 and 8). Concomitantly, Scrub, and to a degree, Oak and Perennial, had the highest total C, total N, and POXC contents, indicating more dynamic C and nutrient cycling occurring in this vegetation type (Figure 8) (Ouyang et al., 2019). Many studies have found that soil nutrients including total C and total N are positively correlated with higher microbial abundances of N cycling genes (Hallin et al., 2009; Ouyang et al., 2019; Q. Wang et al., 2018; Xue et al., 2018). Recent studies have highlighted the significance of microbial biomass and microbial inputs to C accumulation and stabilization, indicating the potential importance of maintaining the Scrub for C sequestration in rangeland systems in semi-arid climates (Kallenbach et al., 2015; Liang et al., 2017; Rumpel et al., 2015). Contrastingly, Grass has the potential of counteracting the gains in C sequestration by Scrub, as it had not only the lowest stores of C, but also the highest N_2O-producing potential, as evidenced by the high ratio of *nirK*+*nirS*:*nosZ* genes (Figure 8). This demonstrates the potential for complex trade-offs that exist within a ranching enterprise. To minimize these tradeoffs, and maximize co-benefits, expanding the hectarage of Perennial could increase C sequestration of the ranch as a whole, without necessarily foregoing productivity as would be the case for increasing Scrub. While a full GHG accounting was beyond the scope of this study, it is conceivable that an optimal state of maintaining naturalized grassland for forage productivity, while maintaining scrubland on non-productive or highly erosive areas could achieve multiple goals of productivity, reduced erosion, and net GHG sinks.

Relative abundances of microbial groups, determined by PLFA, also varied by vegetation type (Table 4). GWC was a key factor in explaining the differences in microbial community composition (Figure 7). The ratio of Gram-positive to Gram-negative bacteria was higher in the drier Grass and Perennial vegetation types compared to the wetter Oak and Scrub (Figure 8). A higher ratio of Gram-positive to Gram-negative bacteria has been proposed as an indicator of the microbial community's ability to withstand drought (de Vries & Shade, 2013). The increase in the relative higher abundance of Gram-positive bacteria to Gram-negative bacteria under soil moisture limitation is attributed to the differences in cell wall thickness (Harris, 1981) and the ability to sporulate under drought conditions (Bérard et al., 2011). An increase in the ratio of Gram-positive to Gram-negative has been shown to influence biogeochemical cycles of C and N (Acosta-Martínez et al., 2014; Fuchslueger et al., 2013, 2016). For example, in drought-affected soils oligotrophic Gram-positive bacteria were found to dominate and tended to use inorganic N to produce enzymes that degrade more complex organic compounds, whereas under moist soil conditions, copiotrophic Gram-negative bacteria dominated and degraded more labile carbon and organic nitrogen, especially from plant root exudates (Naylor & Coleman-Derr, 2017). Within this framework, during drought, the Scrub and Oak could be important for maintaining C storage, while more complex C molecules are being decomposed in the Grass and Perennial vegetation types. However, as noted above, fire could complicate C sequestration outcomes of the whole ranch given the varying ways C stored within these vegetation types respond to burning. Furthermore, while a general increase in the relative abundance of Gram-positive to Gram-negative bacteria has been found, some studies have found that certain phyla within both Gram-positive and Gram-negative taxa dominate during droughts (Acosta-Martínez et al., 2014; Naylor & Coleman-Derr, 2017). Acosta-Martínez et al. (2014) found that the abundance of *Rubrobacter* within the Gram-positive group increased during drought and these bacteria have been correlated with higher C contents within aggregates (Davinic et al., 2012). Abundance of *Proteobacteria* within Gram-negative groups also increased under drought and have shown to be important in N and C cycling including N fixation (Acosta-Martínez et al., 2008, 2014; Kersters et al., 2006). Understanding shifts within specific microbial assemblages and their associated functions within each vegetation type could help predict how ecosystem services of rangelands might respond to changes in the future hydrologic regimes (Ma et al., 2015). Further studies are needed to identify the functional bacterial groups of each vegetation type and how microbial assemblage interacts to affect the biogeochemical cycling of these systems.

4.4 | Multiple soil-based ecosystem services of a Working Ranch

While Scrub diverged from the rest of the vegetation types in the multiple ecosystem services provision ratings, they could not be grazed, reducing the productivity potential of a ranch. Thus, strategically placing Scrub or maintaining it in erosive and unproductive areas could increase multiple ecosystem services on the ranch while not foregoing productivity. Perennial grasses were established by changing the intensity and timing of grazing on grassland areas where perennial species exist and represent a vegetation type with higher ecosystem provisioning potential than annual grasslands while still providing forage productivity. This grazing management intervention could increase the multiple ecosystem services provisioning on this rangeland while maintaining productivity by converting annual grasses to perennial grassland. However, as Eastburn et al. (2018) find, the cost and long-term outcome uncertainty of establishing perennial grassland is an impediment to adopting these practices and potentially low resistance to reinvasion by exotics makes these vegetation types vulnerable to conversion back to lower states of ecosystem service provisioning. However, as interest and support for building soil health and providing multiple ecosystem services on rangelands increase and climate uncertainty creates increased exposure to risk, the cost-to-benefit analysis of managing for more heterogenous landscapes may shift to where adaptive management practices, such as maintaining or implementing a mosaic of vegetation types, are considered less risky (Hodbod et al., 2016).

4.5 | Limitations of this study and future studies

This study aimed to understand how varying vegetation type across a ranch influences soil health indicators related to ecosystem service categories (C sequestration, water regulation, nutrient cycling, and belowground biodiversity) while controlling for soil type. This study was preliminary in nature and focused on extensive collection of varying soil health indices, rather than intensive sampling to capture the vast heterogeneity that rangelands contain. Where possible, sampling was done on the same aspect, hillslope position, and soil type to control for these confounding factors. However, future studies should sample from multiple cross-sections of these factors (vegetation type × hillslope position × soil type) to better understand how heterogeneity may interact to influence soil health indicator variability and, thus, ecosystem provisioning of the ranch as a whole. Furthermore, this research was conducted on one ranch in one microclimate at one-time point. Future studies should ideally include multiple climatic regions and multiple time points within the season to understand how climate and seasonality might interact with vegetation type to influence soil health and ecosystem provisioning potential. Studies encompassing state and transition models, as described in Eastburn et al. (2017) along with the framework provided here, could lend themselves neatly to uncovering the potential co-benefits and trade-offs of managing varying vegetation types in rangeland systems. Ultimately, process-based linkages described here may provide a working example of how to manage ranches as functional mosaics of strategically maintained vegetation types.

5 | CONCLUSIONS

Rangelands have the potential to provide a diversity of ecosystem services. Our results suggest that managing multiple soil-based ecosystem service outcomes is possible by maintaining or managing for a mosaic of vegetation types within a ranch operation. Soils in the assessed vegetation types display differences in many soil health parameters. These parameters are connected to critical soil ecosystem functions like C, nutrient, and water cycling. Understanding how strategically managed vegetation types contribute to a ranch's ecosystem functioning and services is paramount, given the increasing loss of rangelands to urbanization and agricultural intensification (Biggs & Huntsinger, 2021; Fairbairn et al., 2021). In California, where land values are high, and water is limited, ranchers are continually under pressure to either sell their land to commercial developers or to convert to more high-value agricultural uses, such as vineyards, with devastating consequences for GHG emissions and water extraction in a severely water-limited state (Biggs & Huntsinger, 2021; Cameron et al., 2017; Fairbairn et al., 2021).

California is increasingly looking to leverage working lands to sequester C as part of its Climate Change Scoping Plans (CARB, 2017). Much of the focus has been on managing grazing to increase C storage on rangeland; however, the scientific evidence for achieving C sequestration goals via grazing in semi-arid climates is limited (Biggs & Huntsinger, 2021). This is due, in part, to a lack of California-based studies, especially in more perennialized coastal rangelands, the vast heterogeneity in climate, geology, and soil types on rangelands throughout the state that makes quantifying C sequestration especially challenging, and abiotic factors such as limited moisture (Biggs & Huntsinger, 2021; Stanley et al., 2023). Outside of grazing management, past research in semi-arid areas suggests that increasing riparian habitat and silvopasture, and reducing erosion can increase C sequestration on rangelands (Biggs & Huntsinger, 2021). As the results from this study support, increasing perennial grassland could increase C storage while maintaining grazing areas, and maintaining or establishing scrubland on erosive or unproductive areas could increase C storage and improve water provisioning. However, multicriteria decision-making frameworks should be employed to assess trade-offs, such as foregone livestock production, in the multitude of services rangelands provide (Eastburn et al., 2017). In states, like California, where rangeland loss to development or agricultural intensification is occurring at increasing rates, preventing rangeland conversion should be prioritized to maximize socioecological benefits to the broader community. State incentives that go beyond the narrow focus of C sequestration and instead recognize the importance of managing the mosaic of rangeland vegetation and their interactions to maximize ecosystem services and minimize trade-offs are of paramount importance.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, Hannah Waterhouse, upon reasonable request.

ORCID

Hannah Waterhouse https://orcid.org/0000-0002-8387-4453
Felipe Aburto https://orcid.org/0000-0001-9472-930X
Gordon Rees https://orcid.org/0000-0002-7162-1889
Deirdre E. Griffin-LaHue https://orcid.org/0000-0001-5711-797X
Devin A. Rippner https://orcid.org/0000-0002-0206-8477
Zhiyuan Tian https://orcid.org/0000-0003-1740-117X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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