

## RESEARCH ARTICLE

# Nitrogen availability and summer drought, but not N:P imbalance, drive carbon use efficiency of a Mediterranean tree-grass ecosystem

Richard Nair<sup>1,2</sup>  | Yunpeng Luo<sup>3</sup> | Tarek El-Madany<sup>2</sup>  | Victor Rolo<sup>4</sup>  |  
 Javier Pacheco-Labrador<sup>5,6</sup> | Silvia Caldararu<sup>1</sup>  | Kendalynn A. Morris<sup>5</sup> |  
 Marion Schrumpp<sup>2,7</sup> | Arnaud Carrara<sup>8</sup> | Gerardo Moreno<sup>4</sup> | Markus Reichstein<sup>2</sup> |  
 Mirco Migliavacca<sup>2,9</sup>

<sup>1</sup>Discipline of Botany, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

<sup>2</sup>Department of Biogeochemical Integration, Max Planck Institute for Biogeochemistry, Jena, Germany

<sup>3</sup>Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

<sup>4</sup>Forest Research Group, INDEHESA, University of Extremadura, Plasencia, Cáceres, Spain

<sup>5</sup>Joint Global Change Research Institute, Pacific Northwest National Laboratory, College Park, Maryland, USA

<sup>6</sup>Environmental Remote Sensing and Spectroscopy Laboratory (SpecLab), Spanish National Research Council, Madrid, Spain

<sup>7</sup>Department of Biogeochemical Processes, Max Planck Institute for Biogeochemistry, Jena, Germany

<sup>8</sup>Fundación Centro de Estudios Ambientales del Mediterráneo (CEAM), Valencia, Spain

<sup>9</sup>European Commission Joint Research Centre, Ispra, VA, Italy

## Correspondence

Richard Nair, School of Botany, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland.  
 Email: [richard.nair@tcd.ie](mailto:richard.nair@tcd.ie)

## Abstract

All ecosystems contain both sources and sinks for atmospheric carbon (C). A change in their balance of net and gross ecosystem carbon uptake, ecosystem-scale carbon use efficiency ( $CUE_{ECO}$ ), is a change in their ability to buffer climate change. However, anthropogenic nitrogen (N) deposition is increasing N availability, potentially shifting terrestrial ecosystem stoichiometry towards phosphorus (P) limitation. Depending on how gross primary production (GPP, plants alone) and ecosystem respiration ( $R_{ECO}$ , plants and heterotrophs) are limited by N, P or associated changes in other biogeochemical cycles,  $CUE_{ECO}$  may change. Seasonally,  $CUE_{ECO}$  also varies as the multiple processes that control GPP and respiration and their limitations shift in time. We worked in a Mediterranean tree-grass ecosystem (locally called 'dehesa') characterized by mild, wet winters and summer droughts. We examined  $CUE_{ECO}$  from eddy covariance fluxes over 6 years under control, +N and +NP fertilized treatments on three timescales: annual, seasonal (determined by vegetation phenological phases) and 14-day aggregations. Finer aggregation allowed consideration of responses to specific patterns in vegetation activity and meteorological conditions. We predicted that  $CUE_{ECO}$  should be increased by wetter conditions, and successively by N and NP fertilization. Milder and wetter years with proportionally longer growing seasons increased  $CUE_{ECO}$ , as did N fertilization, regardless of whether P was added. Using a generalized additive model, whole ecosystem phenological status and water deficit indicators, which both varied with treatment, were the main determinants of 14-day differences in  $CUE_{ECO}$ . The direction of water effects depended on the timescale considered and occurred alongside treatment-dependent water depletion. Overall, future regional trends of longer dry summers may push these systems towards lower  $CUE_{ECO}$ .

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Global Change Biology* published by John Wiley & Sons Ltd.

## KEYWORDS

carbon cycle, carbon use efficiency, carbon-water interactions, eddy covariance, general additive model, N:P imbalance, phenology, semi-arid ecosystem

## 1 | INTRODUCTION

Rising atmospheric carbon dioxide ( $\text{CO}_2$ ) and associated climate change is buffered by carbon (C) sequestered and stored in terrestrial ecosystems, but ecosystem C exchange also responds to shifts in climate (Cao & Woodward, 1998). The balance between photosynthesis (i.e. Gross Primary Production, GPP) and ecosystem respiration ( $R_{\text{ECO}}$ ), Net Ecosystem Production (NEP), is the result of many processes responding to environmental conditions simultaneously. The ratio of NEP to GPP is the ecosystem scale carbon use efficiency ( $\text{CUE}_{\text{ECO}}$ ), incorporating both GPP and  $R_{\text{ECO}}$  (e.g. Fernández-Martínez et al., 2014; Sinsabaugh et al., 2017).  $\text{CUE}_{\text{ECO}}$  is a useful metric for understanding C uptake capacity of the terrestrial biosphere because CUE concepts—which can also be calculated using other productivity measures—normalize for productivity allowing for comparisons across dissimilar plant communities (Chen & Yu, 2019; DeLucia et al., 2007; Gang et al., 2019; Liu et al., 2019; von Buttlar et al., 2018; Zhang et al., 2009). Further, a positive  $\text{CUE}_{\text{ECO}}$  intuitively indicates net C assimilation, or an increase in ecosystem C storage, and a negative sign indicates net C loss.  $\text{CUE}_{\text{ECO}}$  derived from eddy covariance systems (EC) is especially useful, as they measure at high frequency (i.e. half hourly) and do not rely on biometric inventories. They also implicitly contain all ecosystem processes, including important belowground processes (e.g. Abramoff & Finzi, 2015) which may be ignored or badly proxied by inventory based CUEs. As  $\text{CUE}_{\text{ECO}}$  represents whole ecosystems, it is directly scalable to global concerns (Bradford & Crowther, 2013) and therefore useful for tracking changes in ecosystem C exchange over time (DeLucia et al., 2007; Zhang et al., 2009). Due to the coupling of biogeochemical cycles, changes in one can affect others (Gentine et al., 2019; Zaehle, 2013). These interactions are dynamic as phenology changes biological activity, and thus  $\text{CUE}_{\text{ECO}}$ , throughout the year (Manzoni et al., 2018; von Buttlar et al., 2018). In particular, progressive nitrogen (N) limitation due to  $\text{CO}_2$  fertilization (Coskun et al., 2016; Craine et al., 2018; Luo et al., 2004) and Nitrogen:Phosphorus (N:P) imbalance due to N deposition (Du et al., 2020; Peñuelas et al., 2012, 2013, 2020) affect GPP and  $R_{\text{ECO}}$  in different ways seasonally (El-Madany et al., 2021; Walker et al., 2021).

Arid- and semi-arid systems play an important role in the global C cycle, switching between net C sources and C sinks and driving overall interannual variability in global C sink strength (Ahlstrom et al., 2015). In other words, annual GPP and  $R_{\text{ECO}}$  are annually not proportional— $\text{CUE}_{\text{ECO}}$  varies in time. Both vegetation growth and microbial activity are also water limited for part of the year so this is driven by seasons and 'wet' and 'dry' years (El-Madany et al., 2020; Scott et al., 2015). Thus the timescale at which the ecosystem is observed may not only determine the strength of the net sink but if  $\text{CUE}_{\text{ECO}}$  observed is positive or negative at all. Although  $\text{CUE}_{\text{ECO}}$  is

less variable than its component fluxes (Manzoni et al., 2018), both climate and phenology, and soil nutrients such as N and P affect  $\text{CUE}_{\text{ECO}}$  (DeLucia et al., 2007; Gang et al., 2022; Zhang et al., 2014).

Phenology itself responds to climate change in complex ways (Piao et al., 2019; Richardson et al., 2013). While GPP is tightly linked to leaf activity which has a clear seasonal signal, respiration occurs from metabolism within living biomass and turnover of dead biomass whenever conditions are suitable for biological activity. Short-term endogenous (e.g. bud burst, Jeong et al., 2012) or exogenous (e.g. rain pulses, Xu et al., 2004) events also affect how photosynthesis and respiration are linked on sub-annual scales, sometimes directly linked to plant phenology (Migliavacca et al., 2015). As a result sub-annual patterns of resource distribution between plant physiological processes (Lapointe, 2001; Maseyk et al., 2008), organs (Luo et al., 2013), tissue stoichiometry (Meunier et al., 2017), allometry (Weiner, 2004) and community structure are not necessarily coordinated by fixed ratios and so can determine GPP and  $R_{\text{ECO}}$  independently (Butterfield & Malmström, 2009; Caldararu et al., 2014; Keenan et al., 2014; Luo et al., 2020). Generally, primary producers are limited by water and nutrient availability, but decomposers by C supply (Soong et al., 2020), and the availability of these resources changes throughout the year. On global scales, aridity might influence  $\text{CUE}_{\text{ECO}}$  (Migliavacca et al., 2021), because under unfavourable conditions there are greater costs (respiration) for equivalent function (growth and acquisition of resources such as nutrients and water). Even when nutrients such as N availability limit productivity, induced transpiration costs (Luo et al., 2020) could still limit overall  $\text{CUE}_{\text{ECO}}$  under higher fertility. Shifts between nutrient limitations may also cause abrupt changes in CUE; for example when P limitation was induced in N-rich *Zea mays* mesocosms, efficiency of biomass production increased (Verlinden et al., 2018). Furthermore, individual plants respond plastically to changes in nutrient availability via C allocation to organs and processes (Oldroyd & Leyser, 2020) independent of community-level observed co-limitation. This may explain why N addition may not alter local  $\text{CUE}_{\text{ECO}}$  (Ma et al., 2018), but N fertility does in global forests (Fernández-Martínez et al., 2014). Alternatively,  $\text{CUE}_{\text{ECO}}$  may be insensitive to changes in nutrient availability, depending on long and short term links between GPP and respiration (Bahn et al., 2009; Heinemeyer et al., 2012; Migliavacca et al., 2015).

In this study, we were interested in how  $\text{CUE}_{\text{ECO}}$  of an entire Mediterranean tree-grass ecosystem responded to ecosystem stoichiometry manipulated by long term +N (NT) and +N and +P (NPT) addition, compared to a control treatment (CT). Individual C and water flux responses are discussed for this site in El-Madany et al. (2021), but not the overall ecosystem C exchange. We examined  $\text{CUE}_{\text{ECO}}$  calculated from eddy covariance observations and how it was regulated by interannual variability in meteorological

conditions, nutrient treatments and their combined effects on vegetative phenology. Appropriate nutrient additions for this ecosystem were informed by a small-scale fully factorial experiment showing N limitation at plot level, with limited herbaceous response to P without N (Martini et al., 2019; Perez-Priego et al., 2015). For this reason, along with specific interest in N:P imbalance and limits to space, a P only treatment was omitted.

We examined  $CUE_{ECO}$  on three timescales: the annual scale, where coarse trends could be identified, the seasonal scale, with seasons defined by vegetation activity, where relationship to particular climate anomalies could be identified, and a 14-day scale, which allowed the fitting of interpretative models linking both to short term meteorology (e.g. rainy periods, heatwaves), incorporating vegetation change via spectral vegetation indexes from above-ground remote sensing.

*On the annual scale, we hypothesized:*

- $CUE_{ECO}$  would be driven by treatment. In general, additions of N and NP would increase ecosystem  $CUE_{ECO}$  via release from limitation, but known water deficits in NT due to vegetation phenology and ecophysiology would reduce  $CUE_{ECO}$  in this treatment relative to NPT, that is,  $CUE_{ECO}^{CT} < CUE_{ECO}^{NT} < CUE_{ECO}^{NPT}$ .
- Treatment effects on  $CUE_{ECO}$  would vary in individual years. Treatment effects would interact with both annual meteorological conditions and the length of vegetative seasons in determining annual  $CUE_{ECO}$ . Longer vegetative periods and wetter years would increase annual  $CUE_{ECO}$ .

*On the seasonal scale, we hypothesized:*

- Seasons dominated by green vegetation (autumn, winter and spring) would have positive  $CUE_{ECO}$  and fallow seasons (summer) negative  $CUE_{ECO}$ .
- Within the same seasons across years, wetter 'growing' seasons would have a higher  $CUE_{ECO}$  as water effects promote short term GPP more than C losses due to respiration and microbial activity. But in fallow seasons (dry-down and summer) water availability would lower  $CUE_{ECO}$  because microbial responses are faster and require less sustained water availability than vegetation recovery. These effects would not differ between nutrient treatments because productivity under N addition includes water deficits at this site, and also determine the vegetation activity used to define seasons.

*On the short term (14-day) scale, we hypothesized:*

- Interaction with water availability would be the main mechanism by which nutrient treatments affected short term  $CUE_{ECO}$ . Water stress should affect stomatal gas exchange and limit GPP, but some ecosystem respiration is always inevitable.
- Beyond environmental effects variables at this scale, we also expected a treatment effect of N availability in NT and NPT allowing more GPP, and so higher  $CUE_{ECO}$ .

## 2 | METHODS

### 2.1 | Study site

We worked at Majadas de Tiétar, in Extremadura, Spain (39°56'24.68"N, 5°46'28.70"W), a typical Mediterranean tree-grass 'dehesa', with 20–25 *Quercus ilex* (L.) trees ha<sup>-1</sup>, ca. 20% canopy cover. The MAT (mean annual temperature) is 16.7°C, and the MAP (mean annual precipitation) is 636 mm (El-Madany et al., 2021). Annual precipitation is very variable ( $\pm 50\%$ ), including seasonal timing and distribution. Typically, most rain falls between October and April with a long dry summer interspersed by occasional rains. The growing season begins following major autumn rains, typically in October, lasting until May–June when soil moisture depletion, high radiation, temperature or vapour pressure deficit (VPD) cause herbaceous layer senescence. A species-rich and seasonal herbaceous layer is used for grazing (<0.3 cows ha). During summer droughts cattle are usually moved to mountain areas. The soil is an Abruptic Luvisol, with a sandy loam upper layer (5/20/75 clay/silt/sand) above a thick clay layer (greater than 15% clay) which varies in depth across the site beginning between 30 and 100 cm.

At the site, three eddy covariance towers (FLUXNET: ES-LMa, ES-LM1, ES-LM2) and various ancillary instruments are in the same area, with homogeneous topography, meteorology and soil. Pre-treatment vegetation properties and carbon, energy and water fluxes did not differ (El-Madany et al., 2018; Nair et al., 2019). Meteorological variables were measured per tower, but we used a unified dataset as cross-footprint spatial variation should be smaller than sensor error. Fertilization treatments were in the 2014/2015 growing season on 20 ha, covering the 80% footprint climatology of respective EC towers (El-Madany et al., 2018, 2021). These added N to ES-LM1 (100 kg N ha<sup>-1</sup> as calcium-ammonium nitrate fertilizer, with calcium to balance the pH) and N and P (an additional 50 kg P, as triple superphosphate fertilizer and N as ammonium nitrate) to ES-LM2. This load was equivalent to 10 years atmospheric N deposition (Morris et al., 2019), with P sufficient to maintain average ecosystem-scale leaf N:P ratios. A supplementary N and P fertilization was made in 2016/2017 adding 20% of the initial fertilization and a small extra P addition (6 kg ha<sup>-1</sup>) was made in the 2019 autumn to start a re-fertilization which was ultimately delayed by the coronavirus pandemic. The towers/treatments are henceforth referred to as CT (control tower, ES-LMa), NT (ES-LM1) and NPT (ES-LM2).

Carbon, energy and water vapour fluxes were measured using the eddy covariance (EC) technique described in (El-Madany et al., 2018, 2021). Each tower had an EC system at 15 m consisting of a three-dimensional sonic anemometer (R3-50, Gill LTD) and infra-red gas analyser LI-7200 (LI-COR Bioscience) to measure CO<sub>2</sub> and H<sub>2</sub>O mixing ratios. Flux calculation (from 20 Hz data to half hourly flux estimates) was conducted using EddyPro 6.2, quality checked and storage fluxes added using a seven level CO<sub>2</sub> profile system to compute total net ecosystem exchange (NEE). Post-processing of flux data ( $u^*$  threshold detection, gap filling and partitioning) was conducted with REddyProc (Wutzler

et al., 2018). To allow assignment of data quality gaps from insufficient turbulence, violating standard EC assumptions, and to allow these to vary based on variable annual conditions, friction velocity ( $u^*$ ) thresholds were detected per tower per year and NEE data measured in half hour intervals with friction velocity below the thresholds removed (Papale et al., 2006). Alternate  $CUE_{ECO}$  based on fixed  $u^*$  are presented in S1 with smaller effects than the factors in this analysis. Time series were gap-filled using marginal distribution sampling and NEE was partitioned to GPP and  $R_{ECO}$  using night-time respiration temperature sensitivity (Reichstein et al., 2005). A single Star-Dot NetCam 5MP digital camera was mounted on each tower providing daily images used for phenology tracking using the 'PhenoCam' method (Richardson et al., 2018) described for our site in detail in Luo et al. (2018). Soil water content was measured per tower via four replicated sensors (ML3, Delta-T Devices Ltd) at 5 cm and an EnviroSCAN (Sentek) profile probe for measurements at 10 and 20 cm. Flux data are available starting in March 2014 for all sites. We used data until the end of the 2020 growing season.

## 2.2 | Definition of carbon use efficiency, scales of analysis and aggregation

We use ecosystem scale  $CUE_{ECO}$ , the ratio between NEP and GPP.  $CUE_{ECO}$  can be negative if NEP is negative (i.e. NEE is positive). At short time scales  $CUE_{ECO}$  becomes difficult to interpret because of short-term C storage (e.g. plant non-structural carbon) and autocorrelation in half-hourly data. We analysed three scales: annual, seasonal and 14-day. We first took the half-hourly GPP,  $R_{ECO}$  and NEE daily means, then aggregated them by computing the average across the period required. We only used daily averages if >75% of the total half hourly EC observations and >8 of the 'night time' (i.e. Potential Radiation <10  $Wm^{-2}$ ) observations were considered good quality by REdyProc (i.e.  $fqc$  0 and 1). If daily data from any tower was discarded, simultaneous data from the other two towers was also discarded to avoid biases between towers in the average values. We removed 50 days over the entire 6-year period. To aggregate at the short term scales, we block averaged at 14 days to reduce autocorrelation and preserve the independence of observations.

## 2.3 | Water availability

We used three different water availability metrics to account for different ways in which water could affect ecosystem function. Quality-controlled precipitation readings from rain gauges were our measure of immediate water inputs. We used the value from the unified cross-site meteorological dataset because error between sensors was expected to be bigger than spatial differences between towers. The other two metrics were calculated half-hourly per treatment and averaged across each aggregation step. Normalized soil moisture

(SWCn) was a linear transformation of the absolute range of the 5th to 95th percentile of measurements into a range (0–1) from the sensors in the top 20cm of soil (5, 10, 20cm), representing wetness of the surface layer of soil (El-Madany et al., 2020). We also used CSWI (Conservative Surface Wetness Index, Nelson et al., 2018) to account for general ecosystem 'wetness'. This is a shallow bucket model which can represent surface water storage relative to the last precipitation event, rapid evaporation from this surface storage especially after small rain events, and cloudy periods of low evaporation where surfaces stay wet. We used this metric because accounting for these dynamics of water storage was important due to the seasonal nature of our site and because this method avoided the impact of variation in soil texture around the soil moisture sensors. Lower values of CSWI indicate conditions with less water availability.

## 2.4 | Seasons, phenology and vegetation indexes

Because this ecosystem has strong seasonality reflected in vegetation activity we compared interannual  $CUE_{ECO}$  differences by assigning the seasons using PhenoCams imagery. PhenoCams provide daily digital photographs and can provide detailed phenological transition dates ('PTDs') and define phenological periods (e.g. Luo et al., 2018). We extracted PTDs for each treatment corresponding to changes between stationary and rising or falling greenness data (see Luo et al., 2018). These seasons (or *phenophases*) defined different phases of net vegetation activity (autumn, winter, spring, drydown, summer, see [supplementary material](#)) incorporating the ecosystem level plant life cycle because of bimodal, summer-dry Mediterranean phenology. We defined a *phenological year* as one cycle of five sequential phenophase seasons. A year was defined as one cycle of all five seasons with the start/end date of the year determined by date of summer–autumn transition. Because this date and hence the overall year length could vary, this contrasts with a hydrological year, with standard calendar date increment between years. Alternative calendar year definitions are insensitive to the rhythms of biological activity driven by changeable meteorology or nutrient availability effects (Luo et al., 2020). Our annual scale of six phenological years identified by the later year and majority of calendar dates in the period, for example, H2016 started in autumn 2015. The average difference and maximum difference between PTDs between years is shown in [Table 1](#) and definition of individual season PTDs is in [Figure S2](#). Because we allowed the phenological year and season to vary between treatments based on vegetation activity, there were minor differences in treatment level annual/seasonal means.

While we defined these seasonal transitions from PhenoCam imagery, the independent site-mounted PhenoCams are not intercalibrated so biases in absolute values may result from individual instrument variation (Richardson et al., 2018). For direct comparisons of vegetation activity in models, we used the normalized difference vegetation index (NDVI, Rouse et al., 1974) from the Sentinel-2 Mission (Copernicus Programme, European Space Agency), which provides comparable simultaneous observations of all sites and physical quantities (e.g.

surface reflection factors) simultaneously, at the expenses of lower frequency sampling and 10m spatial resolution. We used a combined dataset of Sentinel 2A imagery beginning on 20 July 2015, shortly after the fertilization and switched to more frequent Sentinel 2B imagery when it became available (28 March 2018). We averaged a 100m radius around each tower. The average gap between good quality days (cloudy overpasses filtered out) was 11 days although it could be as high as 30 days. We interpolated between points using a Kalman smoothing filter before averaging on the various scales used for analyses.

## 2.5 | Modelling approaches

The explanatory variables we used were: nutrient fertilization treatment (treatment), season and phenological year, plus the environmental variables air temperature at 2 m ( $T_a$ ), total precipitation (ppt), number of days with ppt > 0.5 mm ('rainy days'), photosynthetically active radiation (PAR), daytime vapor pressure deficit (VPD), SWCn, Conservative Surface Wetness Index (CSWI) and Sentinel-2 NDVI of the whole ecosystem (NDVI). The response variable was  $CUE_{ECO}$ . We performed all data analyses in R 4.0.3 (R Core Team, 2018).

Because the aggregation steps resulted in data sets of different sizes, we applied different analytical methods at different scales. We performed mixed linear models and analyses of covariance using lme4 (Bates, 2010) and generalized additive models (GAMs, Hastie

& Tibshirani, 1986) using the mgcv package in R (Wood, 2011). We show mixed model  $R^2$  using marginal ( $R^2_M$ ) and conditional ( $R^2_C$ , Nakagawa & Schielzeth, 2013) metrics, the former an estimate of goodness of fit with only fixed effects and the latter including random effects. We report deviance explained (the proportion of null deviance explained by the model) for GAMs, appropriate for non-normal errors. In all analyses unless otherwise mentioned, model selection was via  $AIC_C$ . Overall analysis structure is illustrated in Figure 1.

For the annual analysis (six phenological years), we first performed a linear mixed effect model with treatment (fixed effect) and phenological year (random effect). We fit two further independent models. Second, we fit a linear model including environmental controls instead of phenological year, beginning with treatment effect,  $T_a$ , ppt, rainy days, SWC, CSWI, plus treatment\*environment control interactions. Third, we again used linear models to explore how year length, growing season length, relative growing season length and annual productivity (mean GPP per day) and turnover (mean  $R_{ECO}$  per day), all interacting with treatments, controlled annual  $CUE_{ECO}$ . As we had few prior expectations about which variables were most important, we employed a data dredging approach using the MuMIn package (Bartoń, 2009) for both the second and third models comparing all possible variable combinations, with max. six terms per model, retaining all predictors in >50% of models within four  $AIC_C$  of the most parsimonious model for the overall best model.

TABLE 1 Mean transition dates (as 1st day of anterior season) for all five defined seasons as calendar day of year. Also shown are the mean difference between seasonal transition dates for the different treatments.

Season transition	Average DOY	Earliest DOY	Latest DOY	Average CT-NT (days)	Average CT-NPT (days)
SUMMER-AUTUMN	275	274	278	2	2
AUTUMN-WINTER	352	341	5	-2	1
WINTER-SPRING	66	29	88	-2	-9
SPRING-DRYDOWN	123	99	142	1	-8
DRYDOWN-SUMMER	186	175	199	2	1

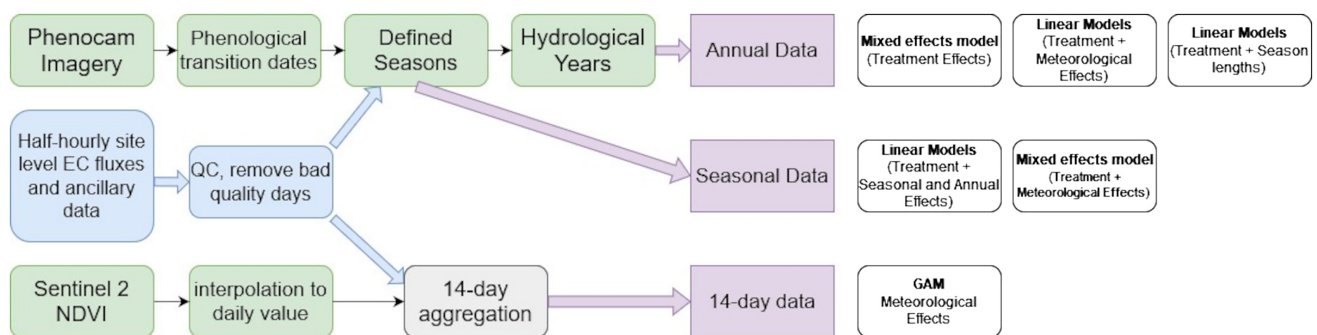


FIGURE 1 Summary of our data sources and analytical structure. PhenoCam imagery only informed season and year transitions, we used Sentinel2 NDVI for the 14-day analysis. We aggregated quality-controlled EC data by season and phenological years for the annual and seasonal scale while we used block average the 14-day scale. Blue boxes and arrows indicate data in the main flux and meteorology dataset, green boxes and arrows from elsewhere and purple arrows and boxes aggregated data. The analyses conducted are shown to the right of each level of data aggregation.

For seasonal analysis, across 30 season-phenological year combinations in the three treatments, we used linear mixed effects models. First, phenological year was a random effect and season and treatment were fixed effects to test the seasonal controls on  $CUE_{ECO}$ . Second, we fit a model where treatment and interaction with both environmental variables and the six sequential phenological years were fixed effects and season a random effect. Environmental variables were Ta, ppt, SWC and CSWI. Season was not nested within phenological year to avoid a singular fit. We did not include the rainy days, nor NDVI in this analysis because annual weather largely determined the PhenoCam-derived season. We performed a similar model dredging exercise as the annual analysis to arrive at the final models.

For the 14-day aggregation, we performed two analyses, (1) using mixed effects models and only considering year, season and treatment and (2) GAMs (Wood, 2006) to investigate climate, soil water variables and vegetation spectral status effects on  $CUE_{ECO}$ . GAMs were suitable as we were expecting non-linear trends. We fit models for these data where all predictors were available (i.e. autumn 2015 onwards). The potential predictors we used were Ta, PAR, VPD, ppt, SWCn, CSWI and NDVI. Because of the high covariation of half-hourly atmospheric environmental variables (Ta, PAR, VPD, ppt, SWCn, CSWI and NDVI), we performed a principal component analysis to reduce dimensionality. The first PCA axis (93% of the variance) represented all these variables together. High values of this meteorology axis, which we refer to as 'Dim.1', corresponded to high air Ta, PAR and VPD (S3). We did not use a similar reduction for Rain, SWCn and CSWI or the spectral indices as these represented processes on incomparable timescales. We used reduced maximum likelihood

(REML) estimation and manually penalized out non-informative smooths one by one, refitting the model each time. We applied a smoothness penalty on the whole model to prevent overfitting. We selected models via per-smooth penalties which allowed smooths to penalize to zero, removed non-significant and non-informative effects with  $F$ -value close to or equal zero, always removing *treatment\*factor* interactions before univariate smooths. We compared GCV (generalized cross validation) score at each step. We did not include interaction terms beyond a *treatment\*factor* term because of difficulty specifying these fairly across so many variables and the potential for overfitting a model on the aggregated data.

After selecting the most parsimonious GAM, we performed several additional checks. We examined variable concavity once the model was selected, which never exceeded 0.8. We checked the models performance using the `gam.check()` function of `mgcv`. We also evaluated performance of this GAM via model residuals against treatments, seasons and phenological years.

### 3 | RESULTS

#### 3.1 | Annual carbon flux response to fertilization

As observed from the eddy covariance fluxes without nutrient amendment, CT had a weak negative or neutral  $CUE_{ECO}$  over the 6 years. Annual  $CUE_{ECO}$  varied and there was no significant trend on this scale over time (Figure 2). Nutrient treatments increased annual  $CUE_{ECO}$ . Consequently, annual  $CUE_{ECO}$  was affected by treatments: both NT

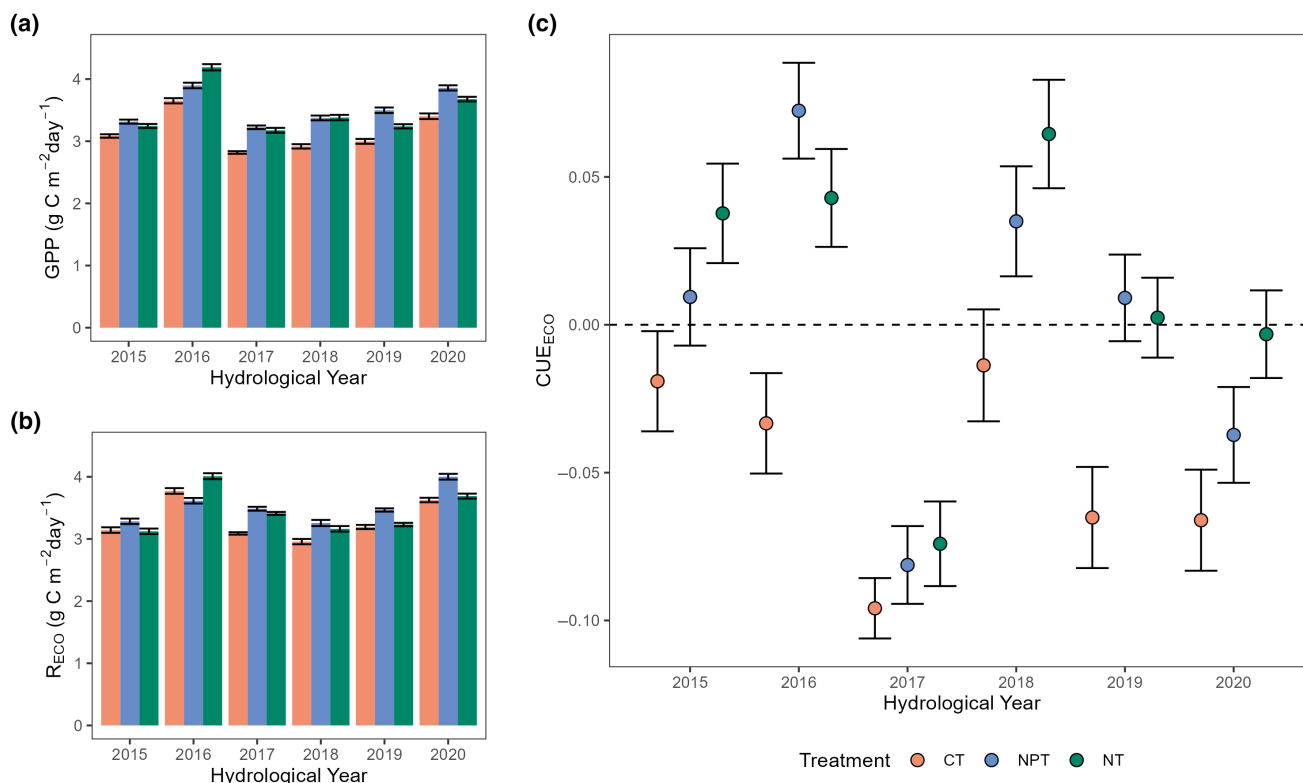
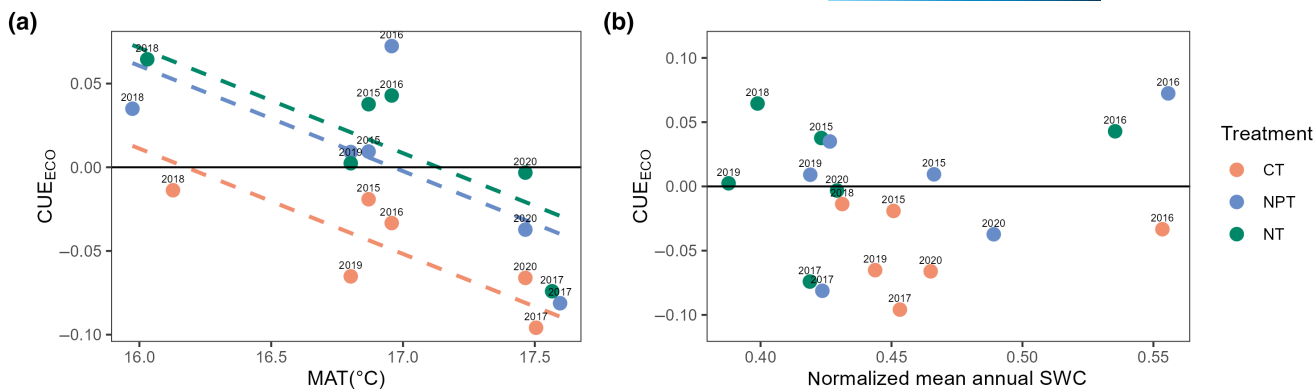


FIGURE 2 Mean annual (a) GPP (b)  $R_{ECO}$  and (c) annual  $CUE_{ECO}$  by phenological year. In all cases error bars show uncorrelated 95% CI.



**FIGURE 3** Relationship between environmental variables and annual CUE<sub>ECO</sub> showing (a) mean annual temperature and (b) normalized mean annual SWC. The grey dotted line indicates the best fit of an ANCOVA with treatment as covariate for CUE against the x axis variable (SWCn did not have a significant effect in the ANCOVA). Hotter and drier years tended to reduce CUE<sub>ECO</sub>, but it was clear from (b) that annual SWC obscured processes happening at finer scales—consistently low CUE in the N treatment happened at low SWC.

and NPT CUE<sub>ECO</sub> were significantly different ( $p < .01$ ) from CT but not from each other ( $p = .06$ ). Both GPP (Figure 2a) and R<sub>ECO</sub> (Figure 2b) were increased by fertilization for the entire treatment period, as previously reported (El-Madany et al., 2021). Most variation was explained by the annual year, when this was treated as a random effect in the model (i.e. no linear trend but intra-annual conditions affected the C cycle, Marginal  $R^2_M = .18$ , Conditional  $R^2_C = .91$ ). This marginal treatment effect was stronger for CUE<sub>ECO</sub> ( $R^2_M = .25$ ,  $R^2_C = .87$ ) than GPP ( $R^2_M = .21$ ,  $R^2_C = .91$ ) or R<sub>ECO</sub> ( $R^2_M = .06$ ,  $R^2_C = .81$ ).

Treating years as independent and using annual means of meteorological variables, we were also able to achieve good fit ( $R^2_{adj} = .79$ ), although not as good as the random annual effect. The most parsimonious model retained MAT ( $p < .001$ ) and SWC ( $p < .01$ ) alongside treatment ( $p < .01$ ) but no *treatment\*meteorology* interactions. Both treatments were significantly different than CT (both  $p < .005$ ) but not each other. Generally, hotter and drier years reduced CUE<sub>ECO</sub> (Figure 3).

We also tested the effect of total length of phenological year, total length of growing season, relative length of the growing season and average daily GPP on annual CUE<sub>ECO</sub> (Figure 4). The best predictors of CUE<sub>ECO</sub> were relative length of growing season and treatment (Figure 4c,  $R^2_{adj}$  of .85). Shorter absolute vegetative year length or absolute longer growing seasons also increased annual CUE<sub>ECO</sub> but were not as good predictors (Figure 4a,b). Similarly, daily mean GPP was less correlated despite the calculation of CUE<sub>ECO</sub> partially based on GPP (4d). We also checked for correlations between daily mean R<sub>ECO</sub> and absolute GPP with CUE<sub>ECO</sub>, neither of these had significant effects. In other words, CUE<sub>ECO</sub> was controlled by how long the summer drought lasted (Figure S4, although note the high leverage of nutrient treatments in 2017 and 2018 in Figure 4b).

### 3.2 | Seasonal trends

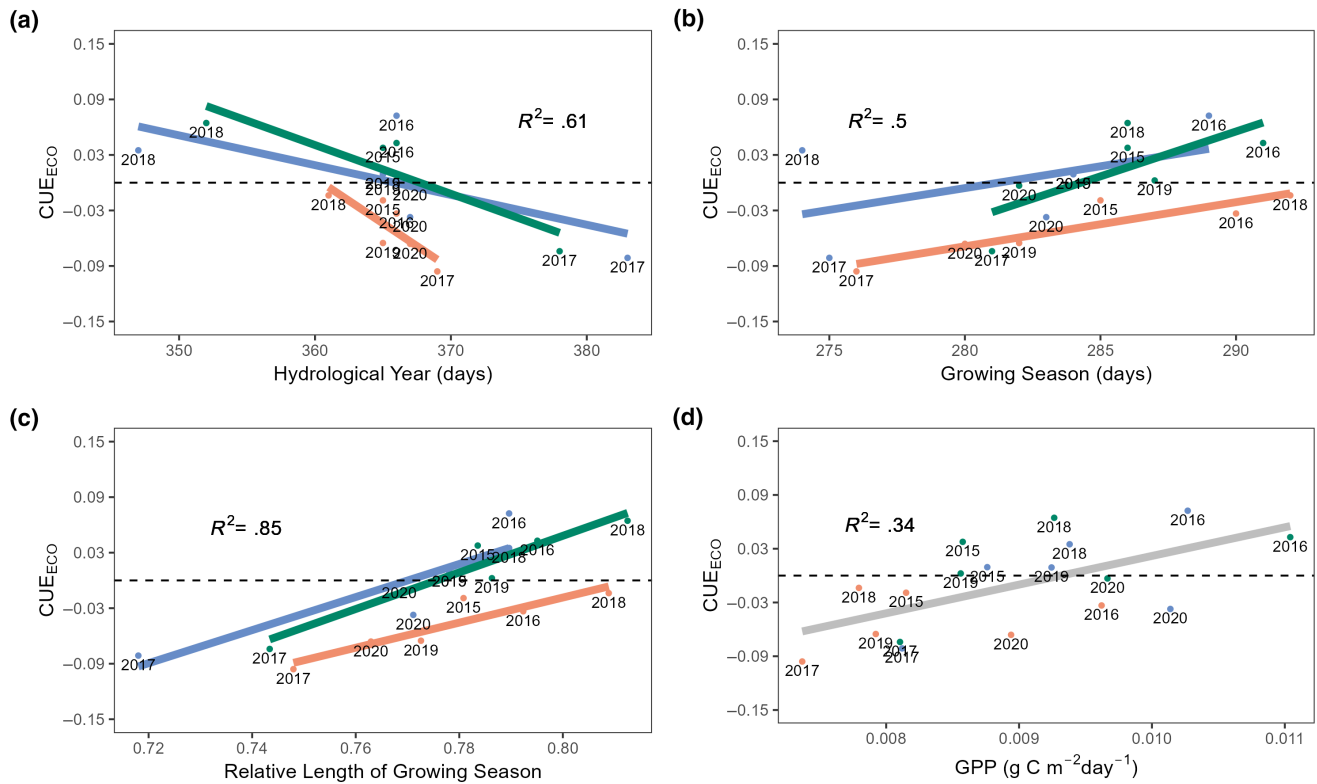
As expected, there were major differences in CUE<sub>ECO</sub> between seasons: 'growing period' had positive CUE<sub>ECO</sub>, and dry periods, where

most vegetation is dormant or dead, had strong negative CUE<sub>ECO</sub> (5a). CUE<sub>ECO</sub> was declining in summers and winters but had a positive trend in the drydown (5c).

When seasonal variation was controlled as a random effect ( $R^2_C = .91$ ), and we included meteorological variables and the numeric year in the model, the marginal component was small compared to season ( $R^2_M = .07$ ). This effect was due to treatment (n.s., but remaining in the most parsimonious overall model), CSWI ( $p = .001$ ) and the annual trend ( $p = .05$ ). Higher CSWI decreased CUE<sub>ECO</sub> in winter, drydown and summer (Figure 5b).

### 3.3 | Drivers of sub-seasonal variation

Environmental variables followed annual cycles (Figure S5) and explained around 75% (dev. explained) of 14-day variation. The most parsimonious model (Figure 6) had effects of 'Dim.1' (meteorology), SWCn, CSWI and NDVI. The largest effect was NDVI; positive CUE<sub>ECO</sub> required active vegetation. The NDVI effect started to saturate at around 0.5 (Figure 6e). The two wetness parameters had different effects: CUE<sub>ECO</sub> partial residuals were highest at low SWCn and at intermediate CSWI. Overall, variation in SWCn had a larger effect than CSWI. Although concavity assumptions were satisfied and including all three terms improved the model without reducing GCv, we note that environmental variables were not independent; CUE<sub>ECO</sub> cannot be  $>1$ . Conditions where summed partial residuals could achieve this (i.e. low SWC, intermediate CSWI where partial residuals together result in CUE<sub>ECO</sub>  $>1$ ) would not occur together; but both indicate more water. There was also a 'Meteorology' effect, higher values (i.e. warmer, drier) and lower values (cooler, wetter) raised CUE<sub>ECO</sub> compared to intermediate values but overall contribution was small. Treatment effects were evident in NDVI (a slight increase in CUE<sub>ECO</sub> partial residual) of fertilized treatments at high NDVI. There was also a treatment interaction with conditions: NT was slightly drier and CT treatment had an overall lower NDVI. Consequently, effects of the environmental conditions on the partial residual of CUE<sub>ECO</sub> must



**FIGURE 4** Relationship between year properties and annual  $CUE_{ECO}$  showing (a) absolute length of phenological year (b) absolute length of the growing season (autumn, winter and spring), (c) relative length of the growing season (length growing season/length annual year) and (d) mean daily GPP of the year. Both  $R_{ECO}$  per day and absolute GPP of the year did not have a significant relationship and are not shown. Lines show significant linear regressions, coloured indicate per-treatment, grey without a treatment effect.

be interpreted with reference to actual trends in these conditions between treatments.

## 4 | DISCUSSION

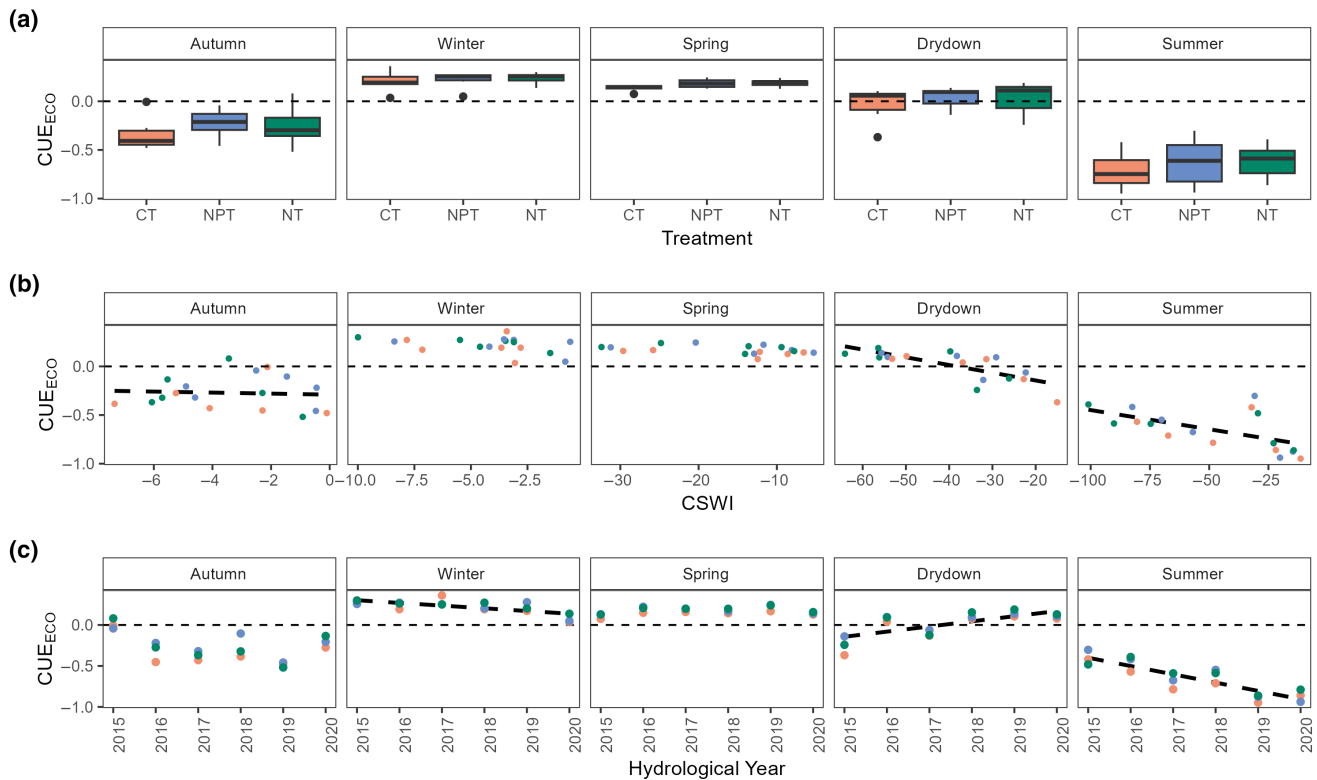
We expected nutrient addition of N and NP to increase annual  $CUE_{ECO}$  in sequence (control < N < NP) because of stronger water limitations with N alone (El-Madany et al., 2021; Luo et al., 2020). We expected to detect these effects at seasonal scale and even at shorter timescales, and to increase  $CUE_{ECO}$  in wetter 'growing' seasons. As expected, these effects were relatively small compared to variation in environmental conditions but they nonetheless remained determinants of  $CUE_{ECO}$  at all scales. Generally, nutrient treatments increased  $CUE_{ECO}$  but NT and NPT did not differ (Figure 2, Figure 3, Figure 6). Cool and wet years also increased  $CUE_{ECO}$  (Figure 3) as did both absolute and proportionally longer growing seasons, the latter usually corresponding to short phenological years (Figure 4). Short phenological years could also be caused by short summers if the next autumn's rain arrived early. However, at the seasonal scale, the treatment effect was not significant, and the wetness effect reversed—the more favourable conditions for a positive effect on  $CUE_{ECO}$  were drier drydowns and summers (Figure 5b). Over time, we also observed decreasing winter and summer  $CUE_{ECO}$  and increasing drydown  $CUE_{ECO}$  (Figure 5c). These trends illustrate the importance of timescale and context in examining  $CUE_{ECO}$ . At the

14-day timescale, positive  $CUE_{ECO}$  effects were found under lower soil moisture but not necessarily when ecosystem wetness was lowest (compare SWCn, CSWI, Figure 6c,d). NT and NPT had higher  $CUE_{ECO}$  partial residuals in periods with high NDVI and overall higher treatment level NDVI; that is, more active vegetation, independent of 'N:P imbalance'. This was offset by increased dryness in NT, evident through CSWI (Figure 6d). Overall these effects were stronger than PAR, represented by Dim.1 in the final GAM model. This modulating effect by water and interaction with N and NP additions was previously shown to impact growing season length and green up phenology (Luo et al., 2020), but here is shown to have different effects at different timescales.

### 4.1 | Effect of nutrient treatments on $CUE_{ECO}$

The biggest annual  $CUE_{ECO}$  in both NT and NPT treatments was in the wet (Figure 3) 2016 phenological year, which had a long growing season (Figure 4). Hence there was no annual effect of N:P imbalance, rather an effect of N fertilization when water was least limiting. Our N addition was 10x mean annual N deposition, applied irregularly and with a lower N load than most N fertilizations. Thus, chronic N deposition may increase C sinks in N-limited 'dehesas' and N fertilization, that is, pasture improvement, may be beneficial for overall C balance. This agrees with positive effects on soil organic carbon of over-seeding with legume-rich mixtures in 'dehesas' (Moreno





**FIGURE 5** Seasonal  $CUE_{ECO}$  between treatments and controls. (a) Treatment effects within seasons. NPT had a slightly higher CUE in some seasons. Dashed lines in (b) CSWI and (c) time trends indicate a significant trend ( $p < .05$ ) within seasons. Overall  $CUE_{ECO}$  is strongly driven by the phenological cycle but there were: (b) time trends within seasons— $CUE_{ECO}$  was declining in winter and summer; (c) the only meteorological variable in the most parsimonious seasonal meteorology model was CSWI;—wetter conditions tended to reduce  $CUE_{ECO}$ .

et al., 2021), and increases in similar grassland topsoil stocks in the long term from increases in N supply (Soussana et al., 2004).

At the 14-day scale, treatments enhanced  $CUE_{ECO}$  at higher NDVI for both NT and NPT (Figure 6e). Otherwise, the major differences between treatments were not on the effects of environmental variables but rather variable distribution. The most parsimonious model had effects of water variables CSWI and SWCn and vegetation index NDVI and a weak effect of the PAR-representing Dim.1; the amount of green vegetation was more important than light input for  $CUE_{ECO}$ . While we expected these to partially depend on each other they did not have high concurrency. Depletion in water was visible in CSWI in the N treatment while NDVI was also slightly higher (Figure 6i). Thus compensatory effects via faster depletion of finite water resources counterbalanced vegetative increases between NT and NPT (Bogdanovich et al., 2021; Nair et al., 2019), leading to no overall  $CUE_{ECO}$  differences when P is added alongside N.

## 4.2 | Underlying causes of treatment effects on $CUE_{ECO}$

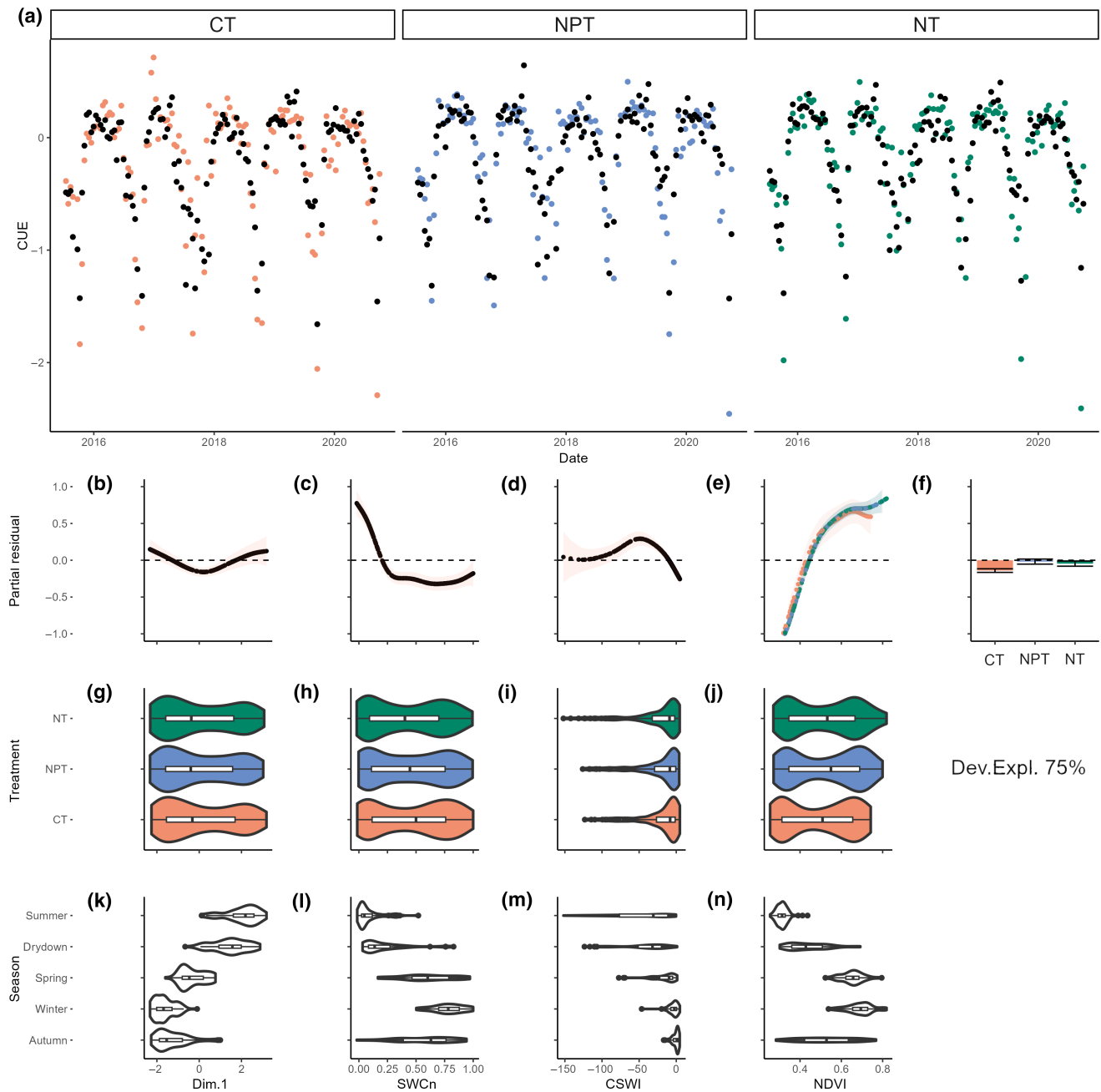
### 4.2.1 | GPP and respiration

At annual scales, GPP is a stronger predictor of  $CUE_{ECO}$  than  $R_{ECO}$  (Figure 2), but  $CUE_{ECO}$  is a result of both fluxes which are

semi-independently governed by different nutrient effects. Fertilization effects on GPP were higher under NPT than NT and at leaf level, N increased in NT but leaf P also increased in NPT (El-Madany et al., 2021). Leaf N and P affect photosynthesis in complement (Evans, 1989; Kergoat et al., 2008; Musavi et al., 2016), N-P co-limitation (Domingues et al., 2010) restricts global responses to ongoing C fertilization (Jiang et al., 2020), and at our site excess P affects photosynthetic parameters (Martini et al., 2019). However, this extra leaf P did not affect  $CUE_{ECO}$  as respiration also increased. Generally, alleviation of P limitation should reduce respiration by relieving co-limitation (Crous et al., 2017; Rowland et al., 2017), and the NPT treatment has been previously shown to have higher water use efficiency than NP at our site (El-Madany et al., 2021), although ecosystem-level effects may also be affected by shifts in allocation and community structure not reflected in these leaf level fluxes.

### 4.2.2 | Allocation and belowground and effects

Carbon allocation responses to the added nutrients could feedback to ecosystem  $CUE_{ECO}$ . We previously showed that deeper roots in NPT contrasts with increases in root: shoot ratio in NT (Nair et al., 2019). Both NT and NPT increase root: shoot ratio (Nair et al., 2019). Thus, belowground investment can have a positive or negative effect on ecosystem C status (Dijkstra et al., 2021) and



**FIGURE 6** Visual summary of the most parsimonious GAM model. In panel (a),  $CUE_{ECO}$  (colour) is compared against model predictions (black) with an overall dev. explained of 75% across the 5 years with all available data. Univariate smooths are shown for (b) 'Met. Variables' (higher values are hotter and dryer), (c) SWCn and (d) CSWI. Panel (e) shows the smooth with significant treatment-dependent smooth for NDVI. Error bars are  $2 \times$  standard errors. Box plots below each curve (Panels g to n) show the distribution of data between (g to j) treatments and (k to n) season; note that as well as a treatment dependent effect of the conditions, particularly NDVI and SWCn, the N treatment was slightly drier, and the control treatment had a lower NDVI. The model had no parametric treatment effect and the relative effect of treatments on the residual is shown in panel (f). In panel (e), the partial residuals for N and NP treatments overlap substantially.

other C use (e.g. changes in C to exudates or stability in SOC) could compensate and equalise overall  $CUE_{ECO}$ . In other systems, chronic N fertilization increases soil C concentrations (Cenini et al., 2015) but P addition effects are less consistent (Ding et al., 2021; Jiang et al., 2019). P addition also slows N-driven water losses at the ecosystem scale by improving the water use efficiency of the ecosystem (El-Madany et al., 2021; Luo et al., 2020). Overall, soil moisture has

complex effects on soil respiration (Moyano et al., 2013). Our fertilization may even have pushed the system gradually towards P excess over time as N was leached (Nair et al., 2020). In the NPT treatment, isotope tracers in root litter were recovered faster in living biomass, which may also indicate a faster turnover in this treatment (Nair et al., 2020). Hence productivity gains may be offset by net soil system changes affecting the soil component of  $R_{ECO}$  so overall

photosynthetic NPT benefits over N cancel out when the C cycle is considered alone.

An experiment using soil collected in February 2018 also showed fertilization legacy effects marginally increased microbial CUE and soil microbial communities in NPT had shifted metabolism to older substrates (Morris et al., 2022). These shifts may also contribute to  $CUE_{ECO}$  (Tahovská et al., 2020; Tao et al., 2023). Microbial CUE increases with temperature (Manzoni et al., 2012) and is seasonal (Simon et al., 2020; Ullah et al., 2021), with biomass peaking in autumn, capitalizing on release from moisture restrictions (Morris et al., 2019) and fresh carbon from root building (Nair et al., 2019). Aspects of GAM smooths in Figure 6 may be explained by microbial shifts not represented by the process-blind ecosystem level data for model fitting. Due to the integrative nature of EC data these distinctions may be invisible in our study. In the absence of data to fully parameterise this, an alternate approach would be to fit a model with process-based belowground assignment to such sites which can then be tested from frequency limited but targeted measurements of such difficult to observe properties (Caldararu et al., 2023).

#### 4.2.3 | Community dynamics

EC data also integrates whole ecosystem responses, but changes result from activity of individual organisms and communities (e.g. Craine et al., 2001) which respond on their own. We observed a higher whole system NDVI in fertilized treatments in summer (Figure S4) during the driest part of the year with least herbaceous biomass. This could be explained by structural differences in tree cover in NPT from CT or NT (El-Madany et al., 2018) but not differences between CT and NT, pointing towards differences in herbaceous communities. 'Dehesa' herbaceous communities are diverse and dynamic (Moreno et al., 2016) and herbaceous diversity (Fernández-Moya et al., 2011; Zeng et al., 2015) also responds to fertilization and N:P imbalance, while the structure of this layer controls ecosystem spectral dynamics (Pacheco-Labrador et al., 2017). Overall, herbaceous plants increased in net biomass (Nair et al., 2019) alongside aforementioned stoichiometric (El-Madany et al., 2021) and allocation shifts (Nair et al., 2019). A previous smaller scale experiment showed a shift towards grasses from forbs under N, P and NP fertilization, affecting whole canopy properties (Migliavacca et al., 2017). Changes in individual species included a higher abundance of the C4 species *Cyanodon dactylon* (L.) in NT which persisted into summers due to its drought adaptations (unpublished plant inventories). Combinations of these community structure effects alongside water cycling would feed into the higher NDVI in fertilized treatments (Figure 6), through different paths. Plant types also vary in water use efficiency (Tsialtas et al., 2001), root architecture (Tron et al., 2015) and leaf-level traits (Rumman et al., 2018), and can modify  $CUE_{ECO}$  both directly and indirectly via microbial associations (Schnitzer et al., 2011; Van Der Heijden et al., 2008). Indeed, in longer term experiments, plant species diversity can have higher benefit to soil C than N addition

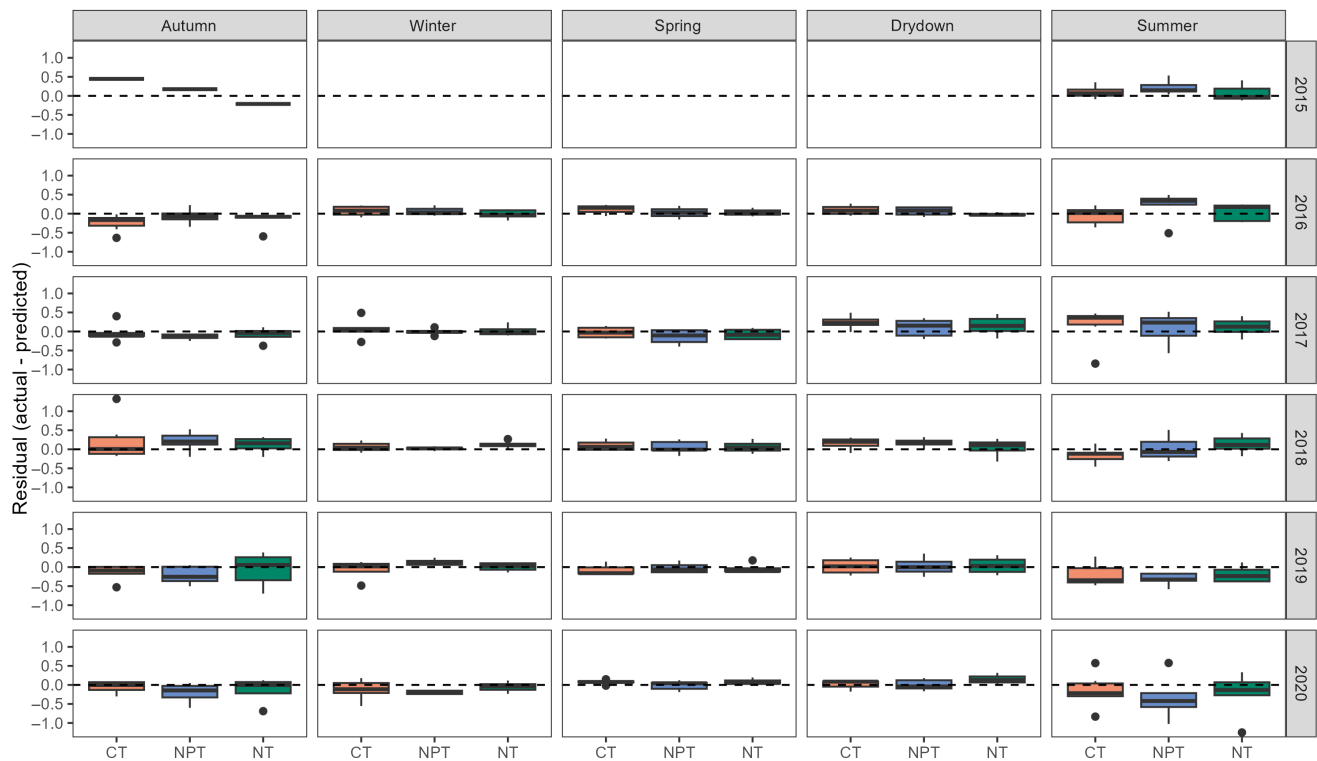
(Pastore et al., 2021) and diversity responses to nutrients drive microbial responses (Leff et al., 2015). As well as explaining the lack of a  $CUE_{ECO}$  response between treatments at this scale, diversity factors which are partially stochastic may also help explain residual differences between years. An important facet of holistic system understanding is potentially quantifying these changes and if, when and how they relate to overall ecosystem function.

#### 4.3 | Interannual variation and model performance between years and seasons

Different years had different overall and seasonal  $CUE_{ECO}$  between treatments (Figures 2–4). While our model on 14-day data performed well (overall dev. explained of 75%), there were times when it did not. The largest residuals (Figure 7) were in summer and autumn where rain pulses control short-term respiration (Casals et al., 2011). This was particularly strong in the 2017/2018 transition. 2017 had the shortest growing year (Figure 3), lowest  $CUE_{ECO}$  and followed the year with highest GPP (Figure 2a). Respiration, which is more uncertain than GPP, was the dominant flux during the dry summer. The model was notably bad at predicting the 2017 drydown and summer  $CUE_{ECO}$ , despite offsetting the influence of difficult to predict events via a PhenoCam-derived phenological year; autumn rains drive a pulse of  $CO_2$  efflux after the water-limited summer consuming C fixed in the previous growing seasons. This season-breaking input was usually considered as a summer due to starting the new phenological year based on rain-dependent vegetation PTD green up (Figure S6). However, rain in semi-arid systems is only a part of overall water inputs (Uclés et al., 2014) and dry season non-rainfall (dew, fog, soil water adsorption) inputs occur (Paulus et al., 2022). Intermittent summer rainfall may also mean dry season C dynamics differ due to diel shifts between photochemical-thermal and microbial degradation, as in dryer arid lands (Gliksman et al., 2017). Likewise intermittent summer storms during periods of high evaporation may not always surpass a threshold for long term responses despite rain input. Longer datasets lasting multiple years with well quantified rainfall and non-rainfall inputs may be the route to understanding such anomalies and/or fitting models which perform better in these conditions.

#### 4.4 | Different trends at different timescales

We observed no treatment effect at the seasonal scale, and a reversal of environmental effects; while less harsh years had higher  $CUE_{ECO}$ , dryer drydowns and summers had a positive effect on the metric. The most likely cause of a positive effect of drier drought period is accumulation of labile substrates and overall delay in turnover until sufficient moisture is available (Schaeffer et al., 2017); without water input, microbial respiration is limited but will occur eventually. Even with a flush of respiratory  $CO_2$  (Figure S6) at the end of summer, sustained dryness may have changed stability of C inputs. The



**FIGURE 7** Residuals from the GAM model (Figure 6) grouped by season and year. In some combinations the model fit better than others. Note the overall worse fit in autumn and summer, and high spread in drydown and summer 2017.

fate of this C could be a lagged response, simply delaying this into the autumn or longer-term stability. Long term (Deng et al., 2021) and extreme (Sippel, Reichstein, et al., 2018) droughts have received considerable research interest but shorter term effects may differ (van der Molen et al., 2011) and seasonal, but variable intensity drought stress requires thorough consideration of long term lag effects on C fluxes, beyond the scope of this study but likely critical for understanding these systems' control of interannual C cycle variability (Ahlstrom et al., 2015).

Trends observed may also indicate ongoing global change effects on  $CUE_{ECO}$  and carbon balance. Long term aridification trends (Cos et al., 2022; Paniagua et al., 2019) are particularly strong around the Mediterranean (Lionello & Scarascia, 2018) and cause progressively drier and warmer summers and warmer and drier winters potentially with a decrease in  $CUE_{ECO}$  (Figure 4). Drier summers are also usually long and so reduce the fraction of year suitable for growth (Figure 4c) and consequently annual GPP. Concurrently we observed decreasing  $CUE_{ECO}$  in winter and summer (Figure 5c). In a similar Spanish tree-grass ecosystem, experimental warming consistently increased total soil respiration (measured annually), but drought reduced it (Matías et al., 2021) so interactions between drought and heat no doubt affect  $CUE_{ECO}$ . At the 14-day scale drier summers have lower NDVI, and move CSWI towards a less positive effect. SWCn increased its partial residual at low values. This may be because local water dynamics were important in the driest conditions when both fluxes could be suppressed. PTD-based seasonal assignments mean that we cannot explain long summer decreases

in  $CUE_{ECO}$  wholly because of delays in autumn rains (Figure S6), although microbes may respond faster than vegetation, and are not reflected in the phenophase seasons.

The trend of increasing  $CUE_{ECO}$  in drydown while  $CUE_{ECO}$  decreased in summer may be due to progressively more acute drydowns with respiration and C losses delayed into summer (Figure 5b). On annual scales, increasing drydown  $CUE_{ECO}$  has a smaller effect because this season is shorter (Table 1). Overall warmer and drier summer conditions may also reduce  $CUE_{ECO}$  (Figure 3) because of decomposition of more non-labile SOC (Knorr et al., 2005) through more extreme shifts between warm dry and warm wet conditions. Indeed, summer warming and drought together accelerate soil carbon decomposition (San-Emeterio et al., 2023). This fraction is likely older carbon from previous years compared to the labile current year inputs (Knorr et al., 2005). Altogether these trends suggest future semi-arid Mediterranean systems may shift to being stronger ecosystem C sources through aridity or rain-pulse-driven losses of C from organic matter in longer summers, with a concurrent reduction in pasture productivity.

On the other hand, winter is not typically water limited in this relatively 'continental' site in central Iberia. Without such limitations, an extremely warm winter during our study period generated an exceptionally productive year but also led to increases in respiration limiting the net effect (Sippel, El-Madany, et al., 2018). Thus, decreasing winter  $CUE_{ECO}$  trends must be interpreted with care. Even though we tried to control for concurrency via model checks, warmer but wet periods could also reduce relative GPP through clouds

associated with rain. These conditions may have limited GPP due to light dependency but not limited respiration, which is indicated by dependence on CSWI (Figure 5). Cloudiness should also have affected radiation and air temperature in 'Meteorology' in the GAM, but the effect was weak, perhaps because a finer timescale was necessary. Warmer winters are particularly important in Mediterranean systems because the winter period is during the growing season but together this suggests that warmer winters may have limited the  $CUE_{ECO}$  effect.

Aside from direct carbon cycle effects, more dominant dry seasons may also interact with nutrient availability, particularly N. Nutrient availability can shift during growing seasons—turnover of dead biomass is not necessarily linked to immediate productivity (Klaus et al., 2016) and microbes are better competitors for immediate N availability than plants (Templer et al., 2012). More turnover delayed until autumn via drier and warmer summers and high N mobility in wet conditions mean N limits on productivity in Mediterranean systems may be stronger in the early season, in addition to potential progressive limitation (Luo et al., 2004) from  $CO_2$  fertilization effects. With simultaneous increases in demand and reductions in supply of N, such systems may move to stronger N limitation. From our study, this also suggests that  $CUE_{ECO}$  would decrease. On the other hand, delayed turnover may decrease leaching because as autumn begins plant N demand is low (Llorens et al., 2011) and so conversely delayed turnover might have long-term positive effects on N availability. N fertilization both increases GPP and water transpired, shortening growing seasons and intensifying drydowns (Luo et al., 2020); thus, N limitation may increase late season productivity and shorten phenological summers. However, because of climate-driven summer intensification and inevitable water losses at season's end, hypothetical longer growing seasons are unlikely to fully compensate N-limitation driven productivity limits. Thus, long term N feedbacks are complex and still unclear, interacting with growing season phenology and could be in either direction. Understanding nutrient cycling and whole system phenology responses under dynamic shifts in function in these dry summer systems is thus of great importance. Insight from winter-fallow systems without strong seasonal shifts may not be sufficient to understand such responses.

## 4.5 | Conclusion

N fertilization increased ecosystem CUE in our Mediterranean tree-grass site, and additional P fertilization had no distinct effects on whole system  $CUE_{ECO}$  despite several previously observed plant effects which could have been interpreted to lead to a more productive ecosystem. Hence N:P imbalance effects on allometry, stoichiometry, water-use and stress responses appeared to have been completely obscured at the ecosystem level by compensatory responses and intrinsic variability at three different levels of temporal aggregation. We also observed trends over the study period of decreasing  $CUE_{ECO}$  in winter and summers, and higher  $CUE_{ECO}$  in years with longer growing seasons and shorter summers, suggesting

a potential long-term trend towards more C losses as the climate warms and duration of summer dry period increases. Seasonal trends were governed by water availability and water effects both became more important and more complex the finer the timescale we considered. Consideration of phenology, weather and timescale on  $CUE_{ECO}$  is critically important for understanding this ecosystem parameter.

## AUTHOR CONTRIBUTIONS

**Richard Nair:** Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Yunpeng Luo:** Data curation; investigation; resources; writing – review and editing. **Tarek El-Madany:** Data curation; methodology; resources; writing – review and editing. **Victor Rolo:** Resources; writing – review and editing. **Javier Pacheco-Labrador:** Investigation; resources; software; writing – review and editing. **Silvia Caldararu:** Investigation; writing – review and editing. **Kendalynn A. Morris:** Investigation; writing – review and editing. **Marion Schrupf:** Methodology; writing – review and editing. **Arnaud Carrara:** Investigation; resources; writing – review and editing. **Gerardo Moreno:** Resources; writing – review and editing. **Markus Reichstein:** Conceptualization; writing – review and editing. **Mirco Migliavacca:** Conceptualization; methodology; writing – review and editing.

## ACKNOWLEDGEMENTS

This paper results from a large experimental study where many people who were not direct authors on this manuscript contributed to long term intellectual development. We are grateful for insight of MANIP experiment collaborators past and present, Oscar Perez-Priego, Jin-Hong Guan, Sinikka Paulus, Thomas Wutzler, Tiana Hammer, David Martini, Ladislav Sigut, Ekaterina Bogdanovitch, Ulisse Gomasasca, M. Pilar Martin, Rosario Gonzalez-Cascon. We also thank Daniel Pabon and Greg Duvallier for providing processed Sentinel data. Field experiments are also completely reliant on technical help and this one would not exist without Martin Hertel, Martin Strube, Olaf Kolle, Katrin Henkel and Ramon Lopez Jimenez. We also acknowledge Andrew Durso for proofreading the revised manuscript. Richard Nair acknowledges the Royal Society and Science Foundation Ireland through University Research Fellowship URF\R1\231376. Javier Pacheco-Labrador and Mirco Migliavacca acknowledge the German Aerospace Center (DLR) project oBEF-Accross2 'The Potential of Earth Observations to Capture Patterns of Biodiversity' (contract No. 50EE1912, DLR). G. Moreno and V. Rolo acknowledge the project PID2019-108313RB-C31/AEI/10.13039/501100011033 funded by the Spanish State Research Agency. V. Rolo was supported by the regional government of Extremadura (Spain) through a 'Talento' fellowship (TA18022). The overall MANIP experiment was funded by the Alexander von Humboldt Foundation Max Planck Research Prize to Markus Reichstein.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.13136805>. These data were derived from the following resources, available in the public domain: <https://doi.org/10.5281/zenodo.4450407>, <https://www.europe-fluxdata.eu/>, <https://phenocam.nau.edu/webcam/>, <https://dataspace.copernicus.eu/>.

## ORCID

Richard Nair  <https://orcid.org/0000-0002-6293-3610>

Tarek El-Madany  <https://orcid.org/0000-0002-0726-7141>

Victor Rolo  <https://orcid.org/0000-0001-5854-9512>

Silvia Caldararu  <https://orcid.org/0000-0001-5839-6480>

## REFERENCES

- Abramoff, R., & Finzi, A. C. (2015). Are above- and below-ground phenology in sync? *New Phytologist*, 205(3), 1054–1061. <https://doi.org/10.1111/nph.13111>
- Ahlstrom, A., Raupach, M. R., Schurgers, G., Smith, B., Arneeth, A., Jung, M., Reichstein, M., Canadell, J. G., Friedlingstein, P., Jain, A. K., Kato, E., Poulter, B., Sitch, S., Stocker, B. D., Viovy, N., Wang, Y. P., Wiltshire, A., Zaehle, S., & Zeng, N. (2015). The dominant role of semi-arid ecosystems in the trend and variability of the land CO<sub>2</sub> sink. *Science*, 348(6237), 895–899. <https://doi.org/10.1126/science.aaa1668>
- Bahn, M., Schmitt, M., Siegwolf, R., Richter, A., & Brüggemann, N. (2009). Does photosynthesis affect grassland soil-respired CO<sub>2</sub> and its carbon isotope composition on a diurnal timescale? *New Phytologist*, 182(2), 451–460. <https://doi.org/10.1111/j.1469-8137.2008.02755.x>
- Bartoń, K. (2009). *MuMIn: Multi-model inference* (1.47.1) [R]. <http://r-forge.r-project.org/projects/mumin/>, 2009
- Bates, D. M. (2010). *Lme4: Mixed-effects modeling with R*. <http://lme4.r-forge.r-project.org/Book>
- Bogdanovich, E., Perez-Priego, O., El-Madany, T. S., Guderle, M., Pacheco-Labrador, J., Levick, S. R., Moreno, G., Carrara, A., Pilar Martín, M., & Migliavacca, M. (2021). Using terrestrial laser scanning for characterizing tree structural parameters and their changes under different management in a Mediterranean open woodland. *Forest Ecology and Management*, 486, 118945. <https://doi.org/10.1016/j.foreco.2021.118945>
- Bradford, M. A., & Crowther, T. W. (2013). Carbon use efficiency and storage in terrestrial ecosystems. *New Phytologist*, 199(1), 7–9. <https://doi.org/10.1111/nph.12334>
- Butterfield, H. S., & Malmström, C. M. (2009). The effects of phenology on indirect measures of aboveground biomass in annual grasses. *International Journal of Remote Sensing*, 30(12), 3133–3146. <https://doi.org/10.1080/01431160802558774>
- Caldararu, S., Purves, D. W., & Palmer, P. I. (2014). Phenology as a strategy for carbon optimality: A global model. *Biogeosciences*, 11(3), 763–778. <https://doi.org/10.5194/bg-11-763-2014>
- Caldararu, S., Rolo, V., Stocker, B. D., Gimeno, T. E., & Nair, R. (2023). Beyond model evaluation—Combining experiments and models to advance terrestrial ecosystem science. *Biogeosciences*, 20(17), 3637–3649. <https://doi.org/10.5194/bg-20-3637-2023>
- Cao, M., & Woodward, F. I. (1998). Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature*, 393(6682), 6682. <https://doi.org/10.1038/30460>
- Casals, P., Lopez-Sangil, L., Carrara, A., Gimeno, C., & Nogués, S. (2011). Autotrophic and heterotrophic contributions to short-term soil CO<sub>2</sub> efflux following simulated summer precipitation pulses in a Mediterranean Dehesa. *Global Biogeochemical Cycles*, 25(3), GB3012. <https://doi.org/10.1029/2010GB003973>
- Cenini, V. L., Fornara, D. A., McMullan, G., Ternan, N., Lajtha, K., & Crawley, M. J. (2015). Chronic nitrogen fertilization and carbon sequestration in grassland soils: Evidence of a microbial enzyme link. *Biogeochemistry*, 126(3), 301–313. <https://doi.org/10.1007/s10533-015-0157-5>
- Chen, Z., & Yu, G. (2019). Spatial variations and controls of carbon use efficiency in China's terrestrial ecosystems. *Scientific Reports*, 9(1), 19516. <https://doi.org/10.1038/s41598-019-56115-5>
- Cos, J., Doblas-Reyes, F., Jury, M., Marcos, R., Bretonnière, P.-A., & Samsó, M. (2022). The Mediterranean climate change hotspot in the CMIP5 and CMIP6 projections. *Earth System Dynamics*, 13(1), 321–340. <https://doi.org/10.5194/esd-13-321-2022>
- Coskun, D., Britto, D. T., & Kronzucker, H. J. (2016). Nutrient constraints on terrestrial carbon fixation: The role of nitrogen. *Journal of Plant Physiology*, 203, 95–109. <https://doi.org/10.1016/j.jplph.2016.05.016>
- Craine, J. M., Elmore, A. J., Wang, L., Aranibar, J., Bauters, M., Boeckx, P., Crowley, B. E., Dawes, M. A., Delzon, S., Fajardo, A., Fang, Y., Fujiyoshi, L., Gray, A., Guerrieri, R., Gundale, M. J., Hawke, D. J., Hietz, P., Jonard, M., Kearsley, E., ... Zmudzzyńska-Skarbek, K. (2018). Isotopic evidence for oligotrophication of terrestrial ecosystems. *Nature Ecology & Evolution*, 2(11), 1735–1744. <https://doi.org/10.1038/s41559-018-0694-0>
- Craine, J. M., Wedin, D. A., & Reich, P. B. (2001). The response of soil CO<sub>2</sub> flux to changes in atmospheric CO<sub>2</sub>, nitrogen supply and plant diversity. *Global Change Biology*, 7(8), 947–953. <https://doi.org/10.1046/j.1354-1013.2001.00455.x>
- Crous, K. Y., O'Sullivan, O. S., Zaragoza-Castells, J., Bloomfield, K. J., Negrini, A. C. A., Meir, P., Turnbull, M. H., Griffin, K. L., & Atkin, O. K. (2017). Nitrogen and phosphorus availabilities interact to modulate leaf trait scaling relationships across six plant functional types in a controlled-environment study. *New Phytologist*, 215(3), 992–1008. <https://doi.org/10.1111/nph.14591>
- DeLucia, E. H., Drake, J. E., Thomas, R. B., & Gonzalez-Meler, M. (2007). Forest carbon use efficiency: Is respiration a constant fraction of gross primary production? *Global Change Biology*, 13(6), 1157–1167. <https://doi.org/10.1111/j.1365-2486.2007.01365.x>
- Deng, L., Peng, C., Kim, D.-G., Li, J., Liu, Y., Hai, X., Liu, Q., Huang, C., Shangguan, Z., & Kuzyakov, Y. (2021). Drought effects on soil carbon and nitrogen dynamics in global natural ecosystems. *Earth-Science Reviews*, 214, 103501. <https://doi.org/10.1016/j.earscirev.2020.103501>
- Dijkstra, F. A., Zhu, B., & Cheng, W. (2021). Root effects on soil organic carbon: A double-edged sword. *New Phytologist*, 230(1), 60–65. <https://doi.org/10.1111/nph.17082>
- Ding, W., Cong, W.-F., & Lambers, H. (2021). Plant phosphorus-acquisition and -use strategies affect soil carbon cycling. *Trends in Ecology & Evolution*, 36(10), 899–906. <https://doi.org/10.1016/j.tree.2021.06.005>
- Domingues, T. F., Meir, P., Feldpausch, T. R., Saiz, G., Veenendaal, E. M., Schrodt, F., Bird, M., Djagbletey, G., Hien, F., Compaore, H., Diallo, A., Grace, J., & Lloyd, J. (2010). Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands. *Plant, Cell & Environment*, 33(6), 959–980. <https://doi.org/10.1111/j.1365-3040.2010.02119.x>
- Du, E., Terrer, C., Pellegrini, A. F. A., Ahlström, A., van Lissa, C. J., Zhao, X., Xia, N., Wu, X., & Jackson, R. B. (2020). Global patterns of terrestrial nitrogen and phosphorus limitation. *Nature Geoscience*, 13(3), 221–226. <https://doi.org/10.1038/s41561-019-0530-4>
- El-Madany, T. S., Carrara, A., Martín, M. P., Moreno, G., Kolle, O., Pacheco-Labrador, J., Weber, U., Wutzler, T., Reichstein, M., & Migliavacca, M. (2020). Drought and heatwave impacts on semi-arid ecosystems' carbon fluxes along a precipitation gradient. *Philosophical Transactions of the Royal Society, B: Biological*

- Sciences*, 375(1810), 20190519. <https://doi.org/10.1098/rstb.2019.0519>
- El-Madany, T. S., Reichstein, M., Carrara, A., Martín, M. P., Moreno, G., Gonzalez-Cascon, R., Peñuelas, J., Ellsworth, D. S., Burchard-Levine, V., Hammer, T. W., Knauer, J., Kolle, O., Luo, Y., Pacheco-Labrador, J., Nelson, J. A., Perez-Priego, O., Rolo, V., Wutzler, T., & Migliavacca, M. (2021). How nitrogen and phosphorus availability change water use efficiency in a Mediterranean savanna ecosystem. *Journal of Geophysical Research: Biogeosciences*, 126(5), e2020JG006005. <https://doi.org/10.1029/2020JG006005>
- El-Madany, T. S., Reichstein, M., Perez-Priego, O., Carrara, A., Moreno, G., Pilar Martín, M., Pacheco-Labrador, J., Wohlfahrt, G., Nieto, H., Weber, U., Kolle, O., Luo, Y. P., Carvalhais, N., & Migliavacca, M. (2018). Drivers of Spatio-temporal variability of carbon dioxide and energy fluxes in a Mediterranean savanna ecosystem. *Agricultural and Forest Meteorology*, 262, 258–278. <https://doi.org/10.1016/j.agrformet.2018.07.010>
- Evans, J. R. (1989). Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia*, 78(1), 9–19. <https://doi.org/10.1007/BF00377192>
- Fernández-Martínez, M., Vicca, S., Janssens, I. A., Sardans, J., Luysaert, S., Campioli, M., Chapin, F. S., III, Ciais, P., Malhi, Y., Obersteiner, M., Papale, D., Piao, S. L., Reichstein, M., Rodà, F., & Peñuelas, J. (2014). Nutrient availability as the key regulator of global Forest carbon balance. *Nature Climate Change*, 4(6), 471–476. <https://doi.org/10.1038/nclimate2177>
- Fernández-Moya, J., Miguel-Ayanz, A. S., Cañellas, I., & Gea-Izquierdo, G. (2011). Variability in Mediterranean annual grassland diversity driven by small-scale changes in fertility and radiation. *Plant Ecology*, 212(5), 865–877. <https://doi.org/10.1007/s11258-010-9869-8>
- Gang, C., Wang, Z., You, Y., Liu, Y., Xu, R., Bian, Z., Pan, N., Gao, X., Chen, M., & Zhang, M. (2022). Divergent responses of terrestrial carbon use efficiency to climate variation from 2000 to 2018. *Global and Planetary Change*, 208, 103709. <https://doi.org/10.1016/j.gloplacha.2021.103709>
- Gang, C., Zhang, Y., Guo, L., Gao, X., Peng, S., Chen, M., & Wen, Z. (2019). Drought-induced carbon and water use efficiency responses in dryland vegetation of northern China. *Frontiers in Plant Science*, 10, 224. <https://doi.org/10.3389/fpls.2019.00224>
- Gentine, P., Green, J. K., Guérin, M., Humphrey, V., Seneviratne, S. I., Zhang, Y., & Zhou, S. (2019). Coupling between the terrestrial carbon and water cycles—A review. *Environmental Research Letters*, 14(8), 083003. <https://doi.org/10.1088/1748-9326/ab22d6>
- Gliksman, D., Rey, A., Seligmann, R., Dumbur, R., Sperling, O., Navon, Y., Haelen, S., De Angelis, P., Arnone, J. A., & Grünzweig, J. M. (2017). Biotic degradation at night, abiotic degradation at day: Positive feedbacks on litter decomposition in drylands. *Global Change Biology*, 23(4), 1564–1574. <https://doi.org/10.1111/gcb.13465>
- Hastie, T., & Tibshirani, R. (1986). Generalized additive models. *Statistical Science*, 1(3), 297–310. <https://doi.org/10.1214/ss/1177013604>
- Heinemeyer, A., Wilkinson, M., Vargas, R. A., Subke, J., Casella, E., Morison, J. I. L., & Ineson, P. (2012). Exploring the overflow tap theory: Linking forest soil CO<sub>2</sub> fluxes and individual Mycorrhizosphere components to photosynthesis. *Biogeosciences*, 9(1), 79–95. <https://doi.org/10.5194/bg-9-79-2012>
- Jeong, S.-J., Medvigy, D., Shevliakova, E., & Malyshev, S. (2012). Uncertainties in terrestrial carbon budgets related to spring phenology. *Journal of Geophysical Research: Biogeosciences*, 117(G1), G01030. <https://doi.org/10.1029/2011JG001868>
- Jiang, M., Caldararu, S., Zaehle, S., Ellsworth, D. S., & Medlyn, B. E. (2019). Towards a more physiological representation of vegetation phosphorus processes in land surface models. *The New Phytologist*, 222(3), 1223–1229. <https://doi.org/10.1111/nph.15688>
- Jiang, M., Caldararu, S., Zhang, H., Fleischer, K., Crous, K. Y., Yang, J., De Kauwe, M. G., Ellsworth, D. S., Reich, P. B., Tissue, D. T., Zaehle, S., & Medlyn, B. E. (2020). Low phosphorus supply constrains plant responses to elevated CO<sub>2</sub>: A meta-analysis. *Global Change Biology*, 26(10), 5856–5873. <https://doi.org/10.1111/gcb.15277>
- Keenan, T. F., Gray, J., Friedl, M. A., Toomey, M., Bohrer, G., Hollinger, D. Y., Munger, J. W., O'Keefe, J., Schmid, H. P., Wing, I. S., Yang, B., & Richardson, A. D. (2014). Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change*, 4(7), 598–604. <https://doi.org/10.1038/nclimate2253>
- Kergoat, L., Lafont, S., Arneith, A., Le Dantec, V., & Saugier, B. (2008). Nitrogen controls plant canopy light-use efficiency in temperate and boreal ecosystems. *Journal of Geophysical Research: Biogeosciences*, 113(G4), g04017. <https://doi.org/10.1029/2007JG000676>
- Klaus, V. H., Boch, S., Boeddinghaus, R. S., Hölzel, N., Kandelers, E., Marhan, S., Oelmann, Y., Prati, D., Regan, K. M., Schmitt, B., Sorkau, E., & Kleinebecker, T. (2016). Temporal and small-scale spatial variation in grassland productivity, biomass quality, and nutrient limitation. *Plant Ecology*, 217(7), 843–856. <https://doi.org/10.1007/s11258-016-0607-8>
- Knorr, W., Prentice, I. C., House, J. I., & Holland, E. A. (2005). Long-term sensitivity of soil carbon turnover to warming. *Nature*, 433(7023), 298–301. <https://doi.org/10.1038/nature03226>
- Lapointe, L. (2001). How phenology influences physiology in deciduous forest spring ephemerals. *Physiologia Plantarum*, 113(2), 151–157. <https://doi.org/10.1034/j.1399-3054.2001.1130201.x>
- Leff, J. W., Jones, S. E., Prober, S. M., Barberán, A., Borer, E. T., Firn, J. L., Harpole, W. S., Hobbie, S. E., Hofmockel, K. S., Knops, J. M. H., McCulley, R. L., La Pierre, K., Risch, A. C., Seabloom, E. W., Schütz, M., Steenbock, C., Stevens, C. J., & Fierer, N. (2015). Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe. *Proceedings of the National Academy of Sciences*, 112(35), 10967–10972. <https://doi.org/10.1073/pnas.1508382112>
- Lionello, P., & Scarascia, L. (2018). The relation between climate change in the Mediterranean region and global warming. *Regional Environmental Change*, 18(5), 1481–1493. <https://doi.org/10.1007/s10113-018-1290-1>
- Liu, Y., Yang, Y., Wang, Q., Du, X., Li, J., Gang, C., Zhou, W., & Wang, Z. (2019). Evaluating the responses of net primary productivity and carbon use efficiency of global grassland to climate variability along an aridity gradient. *Science of the Total Environment*, 652, 671–682. <https://doi.org/10.1016/j.scitotenv.2018.10.295>
- Llorens, P., Latron, J., Álvarez-Cobelas, M., Martínez-Vilalta, J., & Moreno, G. (2011). Hydrology and biogeochemistry of Mediterranean forests. In D. F. Levia, D. Carlyle-Moses, & T. Tanaka (Eds.), *Forest hydrology and biogeochemistry: Synthesis of past research and future directions* (pp. 301–319). Springer. [https://doi.org/10.1007/978-94-007-1363-5\\_14](https://doi.org/10.1007/978-94-007-1363-5_14)
- Luo, W., Jiang, Y., Lü, X., Wang, X., Li, M.-H., Bai, E., Han, X., & Xu, Z. (2013). Patterns of plant biomass allocation in temperate grasslands across a 2500-km transect in northern China. *PLoS One*, 8(8), e71749. <https://doi.org/10.1371/journal.pone.0071749>
- Luo, Y., El-Madany, T., Ma, X., Nair, R., Jung, M., Weber, U., Filippa, G., Bucher, S. F., Moreno, G., Cremonese, E., Carrara, A., Gonzalez-Cascon, R., Escudero, Y. C., Galvagno, M., Pacheco-Labrador, J., Martín, M. P., Perez-Priego, O., Reichstein, M., Richardson, A. D., ... Migliavacca, M. (2020). Nutrients and water availability constrain the seasonality of vegetation activity in a Mediterranean ecosystem. *Global Change Biology*, 26(8), 4379–4400. <https://doi.org/10.1111/gcb.15138>
- Luo, Y., El-Madany, T. S., Filippa, G., Ma, X., Ahrens, B., Carrara, A., Gonzalez-Cascon, R., Cremonese, E., Galvagno, M., Hammer, T. W., Pacheco-Labrador, J., Martín, M. P., Moreno, G., Perez-Priego, O., Reichstein, M., Richardson, A. D., Römermann, C., & Migliavacca, M. (2018). Using near-infrared-enabled digital repeat photography to track structural and physiological phenology in Mediterranean tree-grass ecosystems. *Remote Sensing*, 10(8), 1293. <https://doi.org/10.3390/rs10081293>

- Luo, Y., Su, B., Currie, W. S., Dukes, J. S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R. E., Oren, R., Parton, W. J., Pataki, D. E., Shaw, R. M., Zak, D. R., & Field, C. B. (2004). Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience*, 54(8), 731–739. [https://doi.org/10.1641/0006-3568\(2004\)054\[0731:PNLOER\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0731:PNLOER]2.0.CO;2)
- Ma, F., Song, B., Zhang, F., Quan, Q., Zhou, Q., & Niu, S. (2018). Ecosystem carbon use efficiency is insensitive to nitrogen addition in an alpine meadow. *Journal of Geophysical Research: Biogeosciences*, 123(8), 2388–2398. <https://doi.org/10.1029/2018JG004530>
- Manzoni, S., Čapek, P., Porada, P., Thurner, M., Winterdahl, M., Beer, C., Brüchert, V., Frouz, J., Herrmann, A. M., Lindahl, B. D., Lyon, S. W., Šantrůčková, H., Vico, G., & Way, D. (2018). Reviews and syntheses: Carbon use efficiency from organisms to ecosystems—Definitions, theories, and empirical evidence. *Biogeosciences*, 15(19), 5929–5949. <https://doi.org/10.5194/bg-15-5929-2018>
- Manzoni, S., Taylor, P., Richter, A., Porporato, A., & Ågren, G. I. (2012). Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytologist*, 196(1), 79–91. <https://doi.org/10.1111/j.1469-8137.2012.04225.x>
- Martini, D., Pacheco-Labrador, J., Perez-Priego, O., van der Tol, C., El-Madany, T. S., Julitta, T., Rossini, M., Reichstein, M., Christiansen, R., Rascher, U., Moreno, G., Martín, M. P., Yang, P., Carrara, A., Guan, J., González-Cascón, R., & Migliavacca, M. (2019). Nitrogen and phosphorus effect on sun-induced fluorescence and gross primary productivity in Mediterranean grassland. *Remote Sensing*, 11(21), 2562. <https://doi.org/10.3390/rs11212562>
- Maseyk, K. S., Lin, T., Rotenberg, E., Grünzweig, J. M., Schwartz, A., & Yakir, D. (2008). Physiology–phenology interactions in a productive semi-arid pine forest. *New Phytologist*, 178(3), 603–616. <https://doi.org/10.1111/j.1469-8137.2008.02391.x>
- Matías, L., Hidalgo-Galvez, M. D., Cambrollé, J., Domínguez, M. T., & Pérez-Ramos, I. M. (2021). How will forecasted warming and drought affect soil respiration in savannah ecosystems? The role of tree canopy and grazing legacy. *Agricultural and Forest Meteorology*, 304–305, 108425. <https://doi.org/10.1016/j.agrformet.2021.108425>
- Meunier, C. L., Boersma, M., El-Sabaawi, R., Halvorson, H. M., Herstoff, E. M., Van de Waal, D. B., Vogt, R. J., & Litchman, E. (2017). From elements to function: Toward unifying ecological stoichiometry and trait-based ecology. *Frontiers in Environmental Science*, 5, 18. <https://doi.org/10.3389/fenvs.2017.00018>
- Migliavacca, M., Musavi, T., Mahecha, M. D., Nelson, J. A., Knauer, J., Baldocchi, D. D., Perez-Priego, O., Christiansen, R., Peters, J., Anderson, K., Bahn, M., Black, T. A., Blanken, P. D., Bonal, D., Buchmann, N., Caldararu, S., Carrara, A., Carvalhais, N., Cescatti, A., ... Reichstein, M. (2021). The three major axes of terrestrial ecosystem function. *Nature*, 598(7881), 468–472. <https://doi.org/10.1038/s41586-021-03939-9>
- Migliavacca, M., Perez-Priego, O., Rossini, M., El-Madany, T. S., Moreno, G., van der Tol, C., Rascher, U., Berninger, A., Bessenbacher, V., Burkart, A., Carrara, A., Fava, F., Guan, J. H., Hammer, T. W., Henkel, K., Juarez-Alcalde, E., Julitta, T., Kolle, O., Martín, M. P., ... Reichstein, M. (2017). Plant functional traits and canopy structure control the relationship between photosynthetic CO<sub>2</sub> uptake and far-red sun-induced fluorescence in a Mediterranean grassland under different nutrient availability. *New Phytologist*, 214(3), 1078–1091. <https://doi.org/10.1111/nph.14437>
- Migliavacca, M., Reichstein, M., Richardson, A. D., Mahecha, M. D., Cremonese, E., Delpierre, N., Galvagno, M., Law, B. E., Wohlfahrt, G., Andrew Black, T., Carvalhais, N., Ceccherini, G., Chen, J., Gobron, N., Koffi, E., William Munger, J., Perez-Priego, O., Robustelli, M., Tomelleri, E., & Cescatti, A. (2015). Influence of physiological phenology on the seasonal pattern of ecosystem respiration in deciduous forests. *Global Change Biology*, 21(1), 363–376. <https://doi.org/10.1111/gcb.12671>
- Moreno, G., Gonzalez-Bornay, G., Pulido, F., Lopez-Diaz, M. L., Bertomeu, M., Juárez, E., & Diaz, M. (2016). Exploring the causes of high biodiversity of Iberian Dehesas: The importance of wood pastures and marginal habitats. *Agroforestry Systems*, 90(1), 87–105. <https://doi.org/10.1007/s10457-015-9817-7>
- Moreno, G., Hernández-Esteban, A., Rolo, V., & Igual, J. M. (2021). The enduring effects of sowing legume-rich mixtures on the soil microbial community and soil carbon in semi-arid wood pastures. *Plant and Soil*, 465(1), 563–582. <https://doi.org/10.1007/s11104-021-05023-7>
- Morris, K. A., Nair, R. K. F., Moreno, G., Schrupf, M., & Migliavacca, M. (2019). Fate of N additions in a multiple resource-limited Mediterranean oak savanna. *Ecosphere*, 10(11), e02921. <https://doi.org/10.1002/ecs2.2921>
- Morris, K. A., Richter, A., Migliavacca, M., & Schrupf, M. (2022). Growth of soil microbes is not limited by the availability of nitrogen and phosphorus in a Mediterranean oak-savanna. *Soil Biology and Biochemistry*, 169, 108680. <https://doi.org/10.1016/j.soilbio.2022.108680>
- Moyano, F. E., Manzoni, S., & Chenu, C. (2013). Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models. *Soil Biology and Biochemistry*, 59, 72–85. <https://doi.org/10.1016/j.soilbio.2013.01.002>
- Musavi, T., Migliavacca, M., van de Weg, M. J., Kattge, J., Wohlfahrt, G., van Bodegom, P. M., Reichstein, M., Bahn, M., Carrara, A., Domingues, T. F., Gavazzi, M., Gianelle, D., Gimeno, C., Granier, A., Gruening, C., Havránková, K., Herbst, M., Hrynkiv, C., Kalhori, A., ... Mahecha, M. D. (2016). Potential and limitations of inferring ecosystem photosynthetic capacity from leaf functional traits. *Ecology and Evolution*, 6(20), 7352–7366. <https://doi.org/10.1002/ece3.2479>
- Nair, R. K. F., Morris, K. A., Hertel, M., Luo, Y., Moreno, G., Reichstein, M., Schrupf, M., & Migliavacca, M. (2019). N:P stoichiometry and habitat effects on Mediterranean savanna seasonal root dynamics. *Biogeosciences*, 16(9), 1883–1901. <https://doi.org/10.5194/bg-16-1883-2019>
- Nair, R. K. F., Morris, K. A., Migliavacca, M., Moreno, G., & Schrupf, M. (2020). Plant-available N:P alters root litter N recycling in a Mediterranean tree–grass ecosystem. *Journal of Plant Nutrition and Soil Science*, 18(3), 517–529. <https://doi.org/10.1002/jpln.20200097>
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Nelson, J. A., Carvalhais, N., Cuntz, M., Delpierre, N., Knauer, J., Ogée, J., Migliavacca, M., Reichstein, M., & Jung, M. (2018). Coupling water and carbon fluxes to constrain estimates of transpiration: The TEA algorithm. *Journal of Geophysical Research: Biogeosciences*, 123(12), 3617–3632. <https://doi.org/10.1029/2018JG004727>
- Oldroyd, G. E. D., & Leyser, O. (2020). A plant's diet, surviving in a variable nutrient environment. *Science*, 368(6486), eba0196. <https://doi.org/10.1126/science.aba0196>
- Pacheco-Labrador, J., El-Madany, T. S., Martín, M. P., Migliavacca, M., Rossini, M., Carrara, A., & Zarco-Tejada, P. J. (2017). Spatio-temporal relationships between optical information and carbon fluxes in a Mediterranean tree-grass ecosystem. *Remote Sensing*, 9, 608. <https://doi.org/10.3390/rs9060608>
- Paniagua, L. L., García-Martín, A., Moral, F. J., & Rebollo, F. J. (2019). Aridity in the Iberian Peninsula (1960–2017): Distribution, tendencies, and changes. *Theoretical and Applied Climatology*, 138(1), 811–830. <https://doi.org/10.1007/s00704-019-02866-0>



- Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., Longdoz, B., Rambal, S., Valentini, R., Vesala, T., & Yakir, D. (2006). Towards a standardized processing of net ecosystem exchange measured with eddy covariance technique: Algorithms and uncertainty estimation. *Biogeosciences*, 3(4), 571–583. <https://doi.org/10.5194/bg-3-571-2006>
- Pastore, M. A., Hobbie, S. E., & Reich, P. B. (2021). Sensitivity of grassland carbon pools to plant diversity, elevated CO<sub>2</sub>, and soil nitrogen addition over 19 years. *Proceedings of the National Academy of Sciences*, 118(17), e2016965118. <https://doi.org/10.1073/pnas.2016965118>
- Paulus, S. J., El-Madany, T. S., Orth, R., Hildebrandt, A., Wutzler, T., Carrara, A., Moreno, G., Perez-Priego, O., Kolle, O., Reichstein, M., & Migliavacca, M. (2022). Resolving seasonal and diel dynamics of non-rainfall water inputs in a Mediterranean ecosystem using lysimeters. *Hydrology and Earth System Sciences*, 26(23), 6263–6287. <https://doi.org/10.5194/hess-26-6263-2022>
- Peñuelas, J., Janssens, I. A., Ciais, P., Obersteiner, M., & Sardans, J. (2020). Anthropogenic global shifts in biospheric N and P concentrations and ratios and their impacts on biodiversity, ecosystem productivity, food security, and human health. *Global Change Biology*, 26(4), 1962–1985. <https://doi.org/10.1111/gcb.14981>
- Peñuelas, J., Poulter, B., Sardans, J., Ciais, P., van der Velde, M., Bopp, L., Boucher, O., Godderis, Y., Hinsinger, P., Llusia, J., Nardin, E., Vicca, S., Obersteiner, M., & Janssens, I. A. (2013). Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. *Nature Communications*, 4, 2394. <https://doi.org/10.1038/ncomms3934>
- Peñuelas, J., Sardans, J., Rivas-Ubach, A., & Janssens, I. A. (2012). The human-induced imbalance between C, N and P in Earth's life system. *Global Change Biology*, 18(1), 3–6. <https://doi.org/10.1111/j.1365-2486.2011.02568.x>
- Perez-Priego, O., Guan, J., Rossini, M., Fava, F., Wutzler, T., Moreno, G., Carvalhais, N., Carrara, A., Kolle, O., Julitta, T., Schrupf, M., Reichstein, M., & Migliavacca, M. (2015). Sun-induced chlorophyll fluorescence and photochemical reflectance index improve remote-sensing gross primary production estimates under varying nutrient availability in a typical Mediterranean savanna ecosystem. *Biogeosciences*, 12(21), 6351–6367. <https://doi.org/10.5194/bg-12-6351-2015>
- Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25(6), 1922–1940. <https://doi.org/10.1111/gcb.14619>
- R Core Team. (2018). *R: A Language and Environment for Statistical Computing* [Computer software].
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., ... Valentini, R. (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm. *Global Change Biology*, 11(9), 1424–1439. <https://doi.org/10.1111/j.1365-2486.2005.001002.x>
- Richardson, A. D., Hufkens, K., Milliman, T., Aubrecht, D. M., Chen, M., Gray, J. M., Johnston, M. R., Keenan, T. F., Klosterman, S. T., Kosmala, M., Melaas, E. K., Friedl, M. A., & Frolking, S. (2018). Tracking vegetation phenology across diverse north American biomes using PhenoCam imagery. *Tracking vegetation phenology across diverse north American biomes using PhenoCam imagery. Scientific Data*, 5, 1–24. <https://doi.org/10.1038/sdata.2018.28>
- Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., & Toomey, M. (2013). Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, 169, 156–173. <https://doi.org/10.1016/j.agrformet.2012.09.012>
- Rouse, J. W., Haas, R. H., Deering, D. W., Schell, J. A., & Harlan, J. C. (1974). *Monitoring the Vernal Advancement and Retrogradation (Green Wave Effect) of Natural Vegetation* (E75-10354). <https://ntrs.nasa.gov/citations/19750020419>
- Rowland, L., Zaragoza-Castells, J., Bloomfield, K. J., Turnbull, M. H., Bonal, D., Burban, B., Salinas, N., Cosio, E., Metcalfe, D. J., Ford, A., Phillips, O. L., Atkin, O. K., & Meir, P. (2017). Scaling leaf respiration with nitrogen and phosphorus in tropical forests across two continents. *New Phytologist*, 214(3), 1064–1077. <https://doi.org/10.1111/nph.13992>
- Rumman, R., Atkin, O. K., Bloomfield, K. J., & Eamus, D. (2018). Variation in bulk-leaf <sup>13</sup>C discrimination, leaf traits and water-use efficiency–trait relationships along a continental-scale climate gradient in Australia. *Global Change Biology*, 24(3), 1186–1200. <https://doi.org/10.1111/gcb.13911>
- San-Emeterio, L. M., Jiménez-Morillo, N. T., Pérez-Ramos, I. M., Domínguez, M. T., & González-Pérez, J. A. (2023). Changes in soil organic matter molecular structure after five-years mimicking climate change scenarios in a Mediterranean savannah. *Science of the Total Environment*, 857, 159288. <https://doi.org/10.1016/j.scitotenv.2022.159288>
- Schaeffer, S. M., Homyak, P. M., Boot, C. M., Roux-Michollet, D., & Schimel, J. P. (2017). Soil carbon and nitrogen dynamics throughout the summer drought in a California annual grassland. *Soil Biology and Biochemistry*, 115, 54–62. <https://doi.org/10.1016/j.soilbio.2017.08.009>
- Schnitzer, S. A., Klironomos, J. N., HilleRisLambers, J., Kinkel, L. L., Reich, P. B., Xiao, K., Rillig, M. C., Sikes, B. A., Callaway, R. M., Mangan, S. A., van Nes, E. H., & Scheffer, M. (2011). Soil microbes drive the classic plant diversity–productivity pattern. *Ecology*, 92(2), 296–303. <https://doi.org/10.1890/10-0773.1>
- Scott, R. L., Biederman, J. A., Hamerlynck, E. P., & Barron-Gafford, G. A. (2015). The carbon balance pivot point of southwestern U.S. semi-arid ecosystems: Insights from the 21st century drought. *Journal of Geophysical Research: Biogeosciences*, 120(12), 2612–2624. <https://doi.org/10.1002/2015JG003181>
- Simon, E., Canarini, A., Martin, V., Séneca, J., Böckle, T., Reinthaler, D., Pötsch, E. M., Piepho, H.-P., Bahn, M., Wanek, W., & Richter, A. (2020). Microbial growth and carbon use efficiency show seasonal responses in a multifactorial climate change experiment. *Communications Biology*, 3(1), 584. <https://doi.org/10.1038/s42003-020-01317-1>
- Sinsabaugh, R. L., Moorhead, D. L., Xu, X., & Litvak, M. E. (2017). Plant, microbial and ecosystem carbon use efficiencies interact to stabilize microbial growth as a fraction of gross primary production. *New Phytologist*, 214(4), 1518–1526. <https://doi.org/10.1111/nph.14485>
- Sippel, S., El-Madany, T. S., Migliavacca, M., Mahecha, M. D., Carrara, A., Flach, M., Kaminski, T., Otto, F. E. L., Thonicke, K., Vossbeck, M., & Reichstein, M. (2018). Warm winter, wet spring, and an extreme response in ecosystem functioning on the Iberian Peninsula. *Bulletin of the American Meteorological Society*, 99(1), S80–S85. <https://doi.org/10.1175/BAMS-D-17-0135.1>
- Sippel, S., Reichstein, M., Ma, X., Mahecha, M. D., Lange, H., Flach, M., & Frank, D. (2018). Drought, heat, and the carbon cycle: A review. *Current Climate Change Reports*, 4(3), 266–286. <https://doi.org/10.1007/s40641-018-0103-4>
- Soong, J. L., Fuchslueger, L., Marañón-Jimenez, S., Torn, M. S., Janssens, I. A., Peñuelas, J., & Richter, A. (2020). Microbial carbon limitation: The need for integrating microorganisms into our understanding of ecosystem carbon cycling. *Global Change Biology*, 26(4), 1953–1961. <https://doi.org/10.1111/gcb.14962>
- Soussana, J.-F., Loiseau, P., Vuichard, N., Ceschia, E., Balesdent, J., Chevallier, T., & Arrouays, D. (2004). Carbon cycling and sequestration opportunities in temperate grasslands. *Soil Use and Management*, 20(2), 219–230. <https://doi.org/10.1111/j.1475-2743.2004.tb00362.x>

- Tahovská, K., Choma, M., Kaštovská, E., Oulehle, F., Bárta, J., Šantrůčková, H., & Moldan, F. (2020). Positive response of soil microbes to long-term nitrogen input in spruce forest: Results from Gårdsjön whole-catchment N-addition experiment. *Soil Biology and Biochemistry*, 143, 107732. <https://doi.org/10.1016/j.soilbio.2020.107732>
- Tao, F., Huang, Y., Hungate, B. A., Manzoni, S., Frey, S. D., Schmidt, M. W. I., Reichstein, M., Carvalhais, N., Ciais, P., Jiang, L., Lehmann, J., Wang, Y.-P., Houlton, B. Z., Ahrens, B., Mishra, U., Hugelius, G., Hocking, T. D., Lu, X., Shi, Z., ... Luo, Y. (2023). Microbial carbon use efficiency promotes global soil carbon storage. *Nature*, 1-5, 981-985. <https://doi.org/10.1038/s41586-023-06042-3>
- Templer, P. H., Mack, M. C., Chapin, F. S., Christenson, L. M., Compton, J. E., Crook, H. D., Currie, W. S., Curtis, C. J., Dail, D. B., D'Antonio, C. M. A., Emmett, B., Epstein, H. E., Goodale, C. L., Gundersen, P., Hobbie, S. E., Holland, K., Hooper, D. U., Hungate, B. A., Lamontagne, S., ... Zak, D. R. (2012). Sinks for nitrogen inputs in terrestrial ecosystems: A meta-analysis of 15N tracer Field studies. *Ecology*, 93(8), 1816-1829.
- Tron, S., Bodner, G., Laio, F., Ridolfi, L., & Leitner, D. (2015). Can diversity in root architecture explain plant water use efficiency? A modeling study. *Ecological Modelling*, 312, 200-210. <https://doi.org/10.1016/j.ecolmodel.2015.05.028>
- Tsialtas, J. T., Handley, L. L., Kassoumi, M. T., Veresoglou, D. S., & Gagianas, A. A. (2001). Interspecific variation in potential water-use efficiency and its relation to plant species abundance in a water-limited grassland. *Functional Ecology*, 15(5), 605-614.
- Uclés, O., Villagarcía, L., Moro, M. J., Canton, Y., & Domingo, F. (2014). Role of dewfall in the water balance of a semiarid coastal steppe ecosystem. *Hydrological Processes*, 28(4), 2271-2280. <https://doi.org/10.1002/hyp.9780>
- Ullah, M. R., Carrillo, Y., & Dijkstra, F. A. (2021). Drought-induced and seasonal variation in carbon use efficiency is associated with fungi:Bacteria ratio and enzyme production in a grassland ecosystem. *Soil Biology and Biochemistry*, 155, 108159. <https://doi.org/10.1016/j.soilbio.2021.108159>
- Van Der Heijden, M. G. A., Bardgett, R. D., & Van Straalen, N. M. (2008). The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*, 11(3), 296-310. <https://doi.org/10.1111/j.1461-0248.2007.01139.x>
- van der Molen, M. K., Dolman, A. J., Ciais, P., Eglin, T., Gobron, N., Law, B. E., Meir, P., Peters, W., Phillips, O. L., Reichstein, M., Chen, T., Dekker, S. C., Doubková, M., Friedl, M. A., Jung, M., van den Hurk, B. J. J. M., de Jeu, R. A. M., Kruijt, B., Ohta, T., ... Wang, G. (2011). Drought and ecosystem carbon cycling. *Agricultural and Forest Meteorology*, 151(7), 765-773. <https://doi.org/10.1016/j.agrformet.2011.01.018>
- Verlinden, M. S., Ven, A., Verbruggen, E., Janssens, I. A., Wallander, H., & Vicca, S. (2018). Favorable effect of mycorrhizae on biomass production efficiency exceeds their carbon cost in a fertilization experiment. *Ecology*, 99(11), 2525-2534. <https://doi.org/10.1002/ecy.2502>
- von Buttlar, J., Zscheischler, J., Rammig, A., Sippel, S., Reichstein, M., Knohl, A., Jung, M., Menzer, O., Arain, M. A., Buchmann, N., Cescatti, A., Gianelle, D., Kiely, G., Law, B. E., Magliulo, V., Margolis, H., McCaughey, H., Merbold, L., Migliavacca, M., ... Mahecha, M. D. (2018). Impacts of droughts and extreme-temperature events on gross primary production and ecosystem respiration: A systematic assessment across ecosystems and climate zones. *Biogeosciences*, 15(5), 1293-1318. <https://doi.org/10.5194/bg-15-1293-2018>
- Walker, A. P., De Kauwe, M. G., Bastos, A., Belmecheri, S., Georgiou, K., Keeling, R. F., McMahon, S. M., Medlyn, B. E., Moore, D. J. P., Norby, R. J., Zaehle, S., Anderson-Teixeira, K. J., Battipaglia, G., Brien, R. J. W., Cabugao, K. G., Cailleret, M., Campbell, E., Canadell, J. G., Ciais, P., ... Zuidema, P. A. (2021). Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO<sub>2</sub>. *New Phytologist*, 229(5), 2413-2445. <https://doi.org/10.1111/nph.16866>
- Weiner, J. (2004). Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, 6(4), 207-215. <https://doi.org/10.1078/1433-8319-00083>
- Wood, S. N. (2006). *Generalized additive models: An introduction with R*. New York: Chapman and Hall/CRC.
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models: Estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, 73(1), 3-36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>
- Wutzler, T., Lucas-Moffat, A., Migliavacca, M., Knauer, J., Sickel, K., Šigut, L., Menzer, O., & Reichstein, M. (2018). Basic and extensible post-processing of eddy covariance flux data with REdyProc. *Biogeosciences*, 15(16), 5015-5030. <https://doi.org/10.5194/bg-15-5015-2018>
- Xu, L., Baldocchi, D. D., & Tang, J. (2004). How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. *Global Biogeochemical Cycles*, 18(4), GB4002. <https://doi.org/10.1029/2004GB002281>
- Zaehle, S. (2013). Terrestrial nitrogen-carbon cycle interactions at the global scale. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 368(1621), 20130125. <https://doi.org/10.1098/rstb.2013.0125>
- Zeng, J., Liu, X., Song, L., Lin, X., Zhang, H., & Shen, C. (2015). Nitrogen fertilization directly affects soil bacterial diversity and indirectly affects bacterial community composition. *Soil Biology and Biochemistry*, 92, 41-49. <https://doi.org/10.1016/j.soilbio.2015.09.018>
- Zhang, Y., Xu, M., Chen, H., & Adams, J. (2009). Global pattern of NPP to GPP ratio derived from MODIS data: Effects of ecosystem type, geographical location and climate. *Global Ecology and Biogeography*, 18(3), 280-290. <https://doi.org/10.1111/j.1466-8238.2008.00442.x>
- Zhang, Y., Yu, G., Yang, J., Wimberly, M. C., Zhang, X., Tao, J., Jiang, Y., & Zhu, J. (2014). Climate-driven global changes in carbon use efficiency. *Global Ecology and Biogeography*, 23(2), 144-155. <https://doi.org/10.1111/geb.12086>

## SUPPORTING INFORMATION

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

**How to cite this article:** Nair, R., Luo, Y., El-Madany, T., Rolo, V., Pacheco-Labrador, J., Caldararu, S., Morris, K. A., Schrupf, M., Carrara, A., Moreno, G., Reichstein, M., & Migliavacca, M. (2024). Nitrogen availability and summer drought, but not N:P imbalance, drive carbon use efficiency of a Mediterranean tree-grass ecosystem. *Global Change Biology*, 30, e17486. <https://doi.org/10.1111/gcb.17486>