



The rhythm of ecosystems' breath: short-term forecasting of net ecosystem exchange improved via wavelet analysis.

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Abstract. Weather-driven disturbances, anthropogenic pressures, and biogenic stressors increasingly impact managed and natural ecosystems, with consequences for food security, carbon cycling, and ecosystem integrity. These disturbances of regular ecosystem functioning occur in many forms and alter ecosystem services such as net CO₂ uptake and physiological processes including photosynthesis and respiration. Local effects of climate change and global long-term warming motivates the need for enhanced monitoring of ecosystem stress and integrity in near-real-time. However, detecting early signs of ecosystem disturbance by tracking the response of flux magnitudes remains a major challenge due to the diversity of both disturbance and ecosystem types. To overcome this challenge and develop a more general approach for diagnosing ecosystem integrity, we focus on a feature common to all ecosystems: their response to light availability and temperature, reflected in the dominance of circadian (24 h) rhythms. To this end, we examine the response of the 24 h rhythm in net ecosystem CO₂ exchange (NEE). Using real-time continuous wavelet transform (CWT) analysis, we quantify the dominance of circadian rhythms in NEE across both cultivated and natural ecosystems. Specifically, we evaluate (i) whether NEE becomes 'more circadian' during the growing season; (ii) the directionality of the relationship between the 24 h rhythm and magnitude of NEE; and, finally, (iii) whether recent history of circadian rhythms of NEE can be leveraged to improve estimates of NEE in a short-term forecasting setting. We evaluate our method across 45 site-years of two distinct plant functional types whose functioning is well understood: European croplands and pulse-driven ecosystems from the dry tropics. Results consistently show that circadian rhythms are more sensitive than flux magnitudes, reacting earlier to disturbances. Therefore, we show how tracking the response of circadian rhythms provides an actionable lever to enhance short-term forecasts of NEE. This framework may provide a novel avenue for the early diagnosis of ecosystem stress and integrity. Because it relies solely on routinely collected 30 min flux measurements, it can be readily implemented within existing real-time carbon monitoring networks such as ICOS, NEON, AmeriFlux, MexFlux, ChinaFlux, JapanFlux, KOF, SAEON and TERN.



1 Introduction.

The frequency and magnitude of disruptions affecting terrestrial ecosystems have increased over the past three decades (Ummenhofer and Meehl, 2017; Bastos et al., 2020) and are expected to intensify due to anthropogenic climate change (Pörtner et al., 2022). Disruptions arise from weather extremes (Ummenhofer and Meehl, 2017), pest outbreaks (Running, 2008; Thakur et al., 2019), or direct human intervention (Altieri et al., 2015; Bowd et al., 2019; Kenko et al., 2023), with both existing observations and short-term projections evincing crop failure, biodiversity loss and compositional, structural, and functional changes in ecosystems at planetary scale (Zhu et al., 2016; Webber et al., 2016; Jennings and Harris, 2017; Nolan et al., 2018; Chen et al., 2019; Exbrayat et al., 2019; Beillouin et al., 2020; Trisos et al., 2020). Under global long-term warming, it is expected that natural ecosystems will experience a species pool shift to warm-affinity species (Zellweger et al., 2020), while in relation to agricultural land, significant negative impacts are expected on food security (Dawson et al., 2016).

Plants actively adapt their physiology in response to abiotic and biotic factors, with water availability, light harvesting and temperature acting as primary regulators (Chapin III et al., 2002; Blankenship, 2021). In turn, these regulators drive the magnitude of net ecosystem CO₂ exchange (NEE), i.e. the balance between carbon uptake through photosynthesis and release through respiration at the ecosystem scale. NEE time series represent the net ‘breathing’ signal of ecosystems, exhibiting pronounced circadian patterns (approximately around 24 h cycles) under stable conditions (Baldocchi, 2008b). In natural systems, climate drivers and ecosystem traits dominate NEE (Baldocchi, 2008a). Conversely, in cultivated systems, management practices are often the responsible driver for seasonal variability (Ciais et al., 2007; Ceschia et al., 2010; Kutsch et al., 2010; Kong et al., 2022), producing sharper flux transitions than the smoother, environmentally-driven patterns expected in natural ecosystems (Chu et al., 2021; Marconato et al., 2022).

Building on more than eight decades of methodological development in micrometeorology (Montgomery, 1948; Swinbank, 1951; Obukhov, 1951; Baldocchi, 2003; Foken et al., 2011), today, several regional networks exist using standardized methods to monitor gas exchange and terrestrial ecosystem functioning globally, using the eddy covariance (EC) technique—e.g. ICOS (Heiskanen et al., 2022), EUROFLUX (Aubinet et al., 2000), NEON (Keller et al., 2008; Elmendorf et al., 2016), AmeriFlux (Novick et al., 2018), MexFlux (Vargas et al., 2013, 2025), ChinaFlux (Yu et al., 2006), JapanFlux (Ueyama et al., 2025), KOF (Kang et al., 2018), SAEON (van Jaarsveld et al., 2007), and TERN (Cleverly et al., 2019). This development has made possible to resolve key ecophysiological variables in a standardized framework, e.g. how NEE responds to environmental drivers and management across natural and cultivated ecosystems (Baldocchi, 2008a; Ceschia et al., 2010; Herzfeld et al., 2021; Kong et al., 2022; Dudney et al., 2025) at 30-min time resolution. However, ecosystem responses to disruptions have traditionally been studied at coarser temporal scales, limiting insight into short-term CO₂ dynamics (Teng et al., 2024). The growing availability of continuous ecosystem flux observations enables detailed investigation of the temporal structure of NEE from sub-hourly to yearly timescales (Wang et al., 2025).

Environmental disturbances (such as droughts or frost) can alter the temporal structure of NEE, influencing the fate of a growing season, e.g. a net CO₂ sink may become a source (Running, 2008; Albrich et al., 2023) or resulting in crop failure (Bastos et al., 2020; Webber et al., 2020). The varying temporal structure of NEE, together with its sensitivity to disturbances



55 across timescales, motivates the use of frequency analysis to detect and predict such disturbances. The Fourier domain provides
a natural framework to investigate this, but standard time-frequency representations like the short-time Fourier Transform
(STFT) (Gabor, 1946) often offer poor low-frequency resolution. Multi-resolution approaches, such as continuous wavelet
transforms (CWT), although computationally heavier, can capture transients in low-frequency bands of non-harmonic signals,
as well as rapid changes at smaller timescales, as the ones displayed by e.g. ecosystem fluxes. For this reason, its use has been
60 explored in meteorology and climate science (Torrence and Compo, 1998). Hence, following this line of applied research, here
we propose the CWT as the feature space for analysis of disturbances of NEE.

Wavelet analysis has been applied to characterize ecosystem flux dynamics (Schaller et al., 2017), improve EC signal re-
construction (Aubert et al., 2025), and enhance flux partitioning through distinct frequency signatures (Schaller et al., 2017; Li
et al., 2023; Coimbra et al., 2025; Destouet et al., 2025). Moreover, its integration with forecasting methods has been shown to
65 improve predictive performance across geophysical time series (Bhardwaj et al., 2020). However, its application to ecosystem
disturbance detection and ecosystem disturbance evaluation, particularly at short time-scales, remains limited, representing a
clear research gap. Here, we match a CWT to half-hourly NEE data so that subtle flux disturbances become apparent in the
wavelet amplitude domain, and propose real-time CWT computation using only past information, enabling early diagnosis of
ecosystem disturbances. We hypothesize that harmonic amplitudes around the 24 h diurnal period are more sensitive distur-
70 bance indicators than NEE flux magnitudes, and therefore react earlier. Hence, lagged frequency-domain features may carry
predictive power for short-term (t+1) NEE forecasting. Specifically, here we test the following hypotheses:

- (H1) are ecosystems more circadian during the growing season?
- (H2) are circadian rhythms more sensitive to disturbances than NEE?
- (H3) is it possible to use the dynamics of circadian rhythms to improve short-term forecasts of NEE?

75 Tested on 45 site-years across natural and cultivated ecosystems, our results show that (H1) ecosystems are significantly more
circadian during the growing season, (H2) disturbances manifest earlier in the frequency domain than in the time domain, with
varying lead times evaluated up to 24 h, confirmed by directional Granger causality tests. Finally, including lagged frequency
features in one-step-ahead forecasting experiments resulted in measurable improvements in NEE prediction (H3). Together,
these three consistent observations show that the circadian rhythm of NEE is more sensitive to disturbances than NEE flux
80 magnitudes, and therefore this is reflected as a lead time of circadian rhythms in relation to the response of NEE. To our
knowledge, this study is the first to demonstrate a lead-follower relationship between circadian rhythms and NEE, and to
translate this insight into a practical forecasting framework through the application of wavelet analysis to short-term ecosystem
CO₂ exchange fluxes. In doing so, it opens new opportunities for enhanced early-warning capabilities, more robust detection
of ecosystem disturbances, and near-real-time assessment of ecosystem integrity.

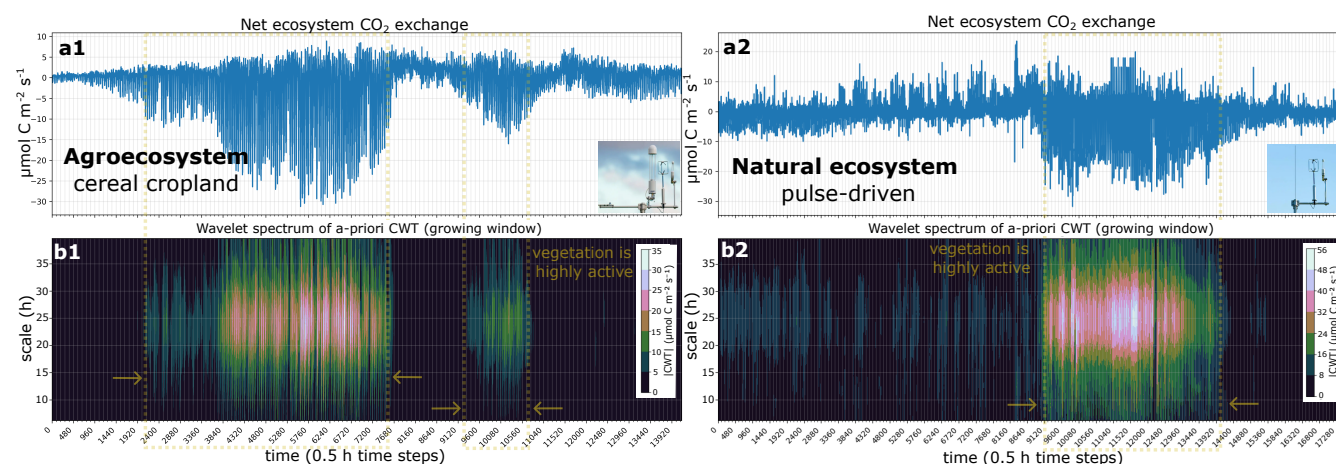


Figure 1. (a1, a2) Net ecosystem exchange (NEE) data series (the insets show two eddy-covariance instrumentation setups). (b1, b2) Wavelet amplitude spectrum of the *a priori* continuous wavelet transform (CWT), from 6.25 to 40, corresponding to (a). The two cases shown (columns) correspond to a representative agroecosystem cereal cropland series (left) and a natural, pulse-driven ecosystem series (right). The dashed orange spans indicate periods of high plant physiological activity, coinciding with a convergence of dominant wavelet amplitudes around the 24 scale.

85 2 Materials and Methods

2.1 Ecosystem CO₂ Flux Datasets

We consider NEE as the time series of interest, evaluated at 45 different ecosystem sites and years (referred to as 'site-years'). The 45 datasets analyzed originate from two contrasting ecological domains, (i) European agroecosystems (N=19) and (ii) natural pulse-driven ecosystems from dry tropical regions (N=26). These CO₂ flux time series are derived from direct measurements at eddy covariance stations in designated ecosystem monitoring sites and processed following standardized, state-of-the-art protocols (Gilberto et al., 2020). The resulting time series have a temporal resolution of 30 min, in compliance with Fluxnet requirements; European datasets are further compliant with the ICOS Ecosystem Thematic Centre (Rebmann et al., 2018). First, we considered European cropland sites from the ICOS network, monitoring representative arable food and bioenergy crops. These managed ecosystems are particularly well suited for our analysis because their NEE signals are relatively homogeneous, predictable, and strongly influenced by land-management practices (e.g. sowing, irrigation, fertilization, harvest). A subset of 19 site-years from European agroecosystems was analyzed (see Appendix), while the methodology is illustrated in detail for a representative site-year (i.e. FR-Aur-season-2, year: 2021). Due to the known management practices and homogeneity of agroecosystems, we consider them the 'easy cases' for our analysis. Second, we analyzed natural pulse-driven ecosystems from the AmeriFlux network, contributed by the Mexican Network, MexFlux. More specifically, we consider dry tropical forests and dry tropical shrublands, from ecosystems in north Mexico and southwestern US. The flux exchange dynamics of these systems are characteristically determined by few strong moisture-pulses—which can be acknowledged as 'climate-induced variation'



in ecosystem functioning—and were selected as representative natural ecosystems, yet partially constrained by climatology. In these environments, ecosystem functioning remains largely dormant during dry periods and is rapidly activated by the onset of rainfall, which triggers both ecosystem respiration and photosynthesis and produces a pronounced, but erratic, response in the NEE signal. A subset of 26 site-years was analyzed (see Appendix), while we illustrated the method for one selected representative site-year (i.e. US-Santa Rita Creosonte, 2014). Due to the characteristics of these time series, we consider them the ‘difficult cases’ for our analysis.

2.2 Method Overview

The methodological framework is designed to address the three hypotheses (H1-H3). To that end, we followed these steps: **1.** Obtain the NEE time series for different years at each ecosystem research site considered (Fig. 1 a). **2.** Compute the continuous wavelet transform for each site-year NEE in real-time, by only considering previous time samples for its computation at every time step. This makes the calculations of CWT strictly *a priori*, as for each point in time t only past history of the signal is used for computation. **3.** Compute the cumulative value of NEE and the amplitude of CWT around the diel scale (i.e. the period of 24 ± 2 h, hereafter referred to as ‘CWT_{24h}’) and evaluate these along the time axis. **4.** Analyse the relationship between CWT_{24h} and NEE. We did this by following these following steps:

- **4.1.** We evaluated the convergence of dominant periods toward the 24h cycle, either (i) outside or (ii) during the growing season (Appendix, Figure A1).
- **4.2.** We assessed the significance and effect size of the influence of previous values of CWT_{24h} over the cumulative NEE. For this, we used a Seasonal AutoRegressive Integrated Moving Average with eXogenous regressors analysis (SARIMAX).
- **4.3.** We assessed both the leader-follower relationship between CWT_{24h} and NEE and the extent to which variations in CWT_{24h} can predict subsequent changes in NEE through directional Granger causality analysis of CWT_{24h} and cumulative NEE.
- **4.4.** We assessed the predictive ability in short-horizon forecasts (t+1) with a XGBoost regressor and standard parameterization, by comparing a baseline implementation using only past NEE values with a CWT_{24h} enhanced version where previous frequency information becomes also available to the predictor.

Considered together, the methodology addresses the three hypotheses sequentially. We evaluated how circadian the rhythm of NEE becomes over the site-year (H1) by evaluating the convergence of the **power and amplitude** of the dominant periods per time frame (Appendix, Fig. A1). SARIMAX analysis quantifies the marginal influence of CWT_{24h} on NEE (H2). Granger causality analysis tests whether this influence is directional and potentially predictive in time (H2 towards H3). Finally, the rolling t+1 forecasting experiment evaluates whether this Granger-causal signal translates into actual, tangible, real-time predictive ability (H3). Note that here we employ Granger-causality as a tool to both verify that (i) disturbances do appear earlier in the frequency domain and that (ii) such effects on the circadian rhythm are predictive of effects on NEE magnitudes in the time domain; we do not infer physical causality between two signals that are naturally correlated. We provide the three analyses together, linking statistical influence, directional relationship of Granger causality of CWT_{24h} with respect to NEE, and a practical short-horizon forecasting value.



2.3 Theoretical Background

135 A note on the method for ecosystem flux monitoring and analysis is given in Appendix (A4).

2.3.1 Wavelet analysis.

Wavelet analysis (Torrence and Compo, 1998) can be used to identify the dominant variability modes of time series (here i.e. the NEE signal) and track how these modes change over time. In short, CWT is computed by performing 1-dimensional convolution of a "basis" wavelet, which is scaled and translated across a time series. This yields a multi-resolution time-frequency representation of the original signal, where a one dimensional time series is transformed into a two dimensional matrix of size $N \times M$, where the number of bands (or modes) N corresponds to the number of "basis" wavelet variations convoluted with the signal, and where M corresponds to the number of time frames resulting from the window size and total length of the original time series. Wavelet analysis is conventionally framed in terms of frequency (e.g. measured in Hz). However, given the extended time series examined here (up to one year at 0.5 h. resolution), we express wavelet scales as periods (τ) in time units (h), which results also more intuitive for interpreting ecosystem functioning dynamics. As basis wavelet we selected Morlet (Grossmann and Morlet, 1984), which is defined as a sinusoid modulated by a Gaussian:

$$\psi_0(\eta) = \pi^{-1/4} e^{(-i/\tau_0)\eta} e^{-\eta^2/2} \quad (1)$$

where η corresponds to a nondimensional time parameter, and τ_0 represents the nondimensional central period (Torrence and Compo, 1998).

150 2.4 Implementation details

We analyzed NEE data series using a continuous wavelet transform (CWT) based on a complex Morlet wavelet (implemented in PyWavelets) using the `cmor1.5-1.0` parameterization (Lee et al., 2019). This choice corresponds to a complex Morlet wavelet with bandwidth parameter $B = 1.5$ and center frequency $C = 1.0$. We selected the Morlet wavelet for three main reasons. First, it is non-orthogonal and well suited to represent smooth, continuous variations commonly observed in ecosystem flux time series. Second, its sinusoidal structure makes it particularly effective for capturing oscillatory behavior, such as diel cycles driven by photosynthesis and respiration. Third, its symmetric, localized shape closely reflects the temporal structure of the signals analyzed. Wavelet scales were defined starting from a scale $s_0 = 6.25$ h and extending to a maximum scale of 40 h, using $S = 80$ scales with a linear step size $\delta s = 0.34$ h. This scale spacing was selected heuristically, balancing temporal and frequency resolution with focus on the circadian period (24 h), while maintaining computational feasibility. The sampling interval of the input time series was set at $\delta t = 30$ min.

To ensure strict real-time modelling, we implemented this wavelet analysis in an *a priori* setting. At each time step t , the CWT was computed using only observations available up to t , and wavelet amplitude was extracted from the most recent coefficient. As a result, no future information contributes to the wavelet representation at any point in time. This design choice,



while computationally demanding—CWT computation scales as $O(N \times J)$ —, is essential for causal interpretation, predictive
165 modeling, and to simulate real-time online applications.

2.5 Assessment of Influence, Granger Causality and Prediction Power

2.5.1 Influence and Directional Granger causality.

To assess the influence of diel-scale wavelet activity on NEE, we employed a Seasonal AutoRegressive Integrated Moving-Average model with eXogenous regressors (SARIMAX), implemented using the SARIMAX class in `statsmodels` in Python
170 (Seabold and Perktold, 2010). SARIMAX models the target variable as a function of its own temporal dependence while explicitly testing the contribution of an external predictor, making it well suited for quantifying lead-lag relationships between time series. Specifically, deseasonalized NEE was modeled as a first-order autoregressive (AR) process, i.e. specifying (p: order for AR terms, d: differencing order, q: order for moving-average terms) = (1,0,0), with lagged values of the diel-scale wavelet amplitude (CWT_{24h}) included as exogenous variables. NEE at each time step is modeled as a linear function of its value at
175 the previous time step, plus the effect of lagged CWT_{24h} , and an error term. The autoregressive term accounts for the strong temporal persistence of NEE, which ensures that the estimated coefficients for CWT_{24h} represent predictive effects beyond NEE's intrinsic autocorrelation. We constructed a lagged exogenous variable matrix comprising CWT_{24h} values from 0.5 h to 24 h prior (i.e. from 1 to 48 half-hour lags), enabling assessment from sub-hourly to daily influence. Statistical significance of lagged coefficients was evaluated using standard z-tests and p-values. The SARIMAX analysis was used as a diagnostic to
180 demonstrate the temporal influence of wavelet-derived frequency information on NEE dynamics, rather than as a final predictive model. This lagged regression framework provides a complementary, model-based assessment of the directional influence suggested by lagged inflection points identified when jointly analyzing the time series of wavelet amplitude spectra at the diel scale (i.e. 24 h) and cumulative NEE fluxes (see Fig. 2 a).

To assess the directional predictive relationship between the 24 h component of the continuous wavelet transform (i.e.
185 CWT_{24h}) and net ecosystem CO_2 time series, we applied Granger causality analysis. Granger causality uses a nested linear model framework to test whether past values of one time series contain information that improves the prediction of another series, beyond what is explained by the latter's own history. This analysis complements the SARIMAX modeling framework (used to evaluate degree of influence) by formally testing lead-lag relationships between CWT_{24h} and NEE and by quantifying whether variability of the diurnal frequency band (CWT_{24h}) contributes to the predictability of net ecosystem CO_2 exchange
190 (NEE).

Because Granger causality assumes covariance stationarity, the analysis was performed on deseasonalized versions of both variables. The two time series were aligned at a half-hourly resolution and combined into a bivariate framework. The test was implemented using pairs of nested autoregressive linear models, comparing a restricted model including only past values of NEE with an unrestricted model that additionally included lagged values of CWT_{24h} . Granger causality was evaluated
195 over a range of lag lengths from 1 to 48 half-hourly steps (i.e. from 0.5 h up to 24 h), thereby providing a statistical test of directional predictive influence from sub-hourly to daily scales, distinct from simple cross-correlation. Statistical significance

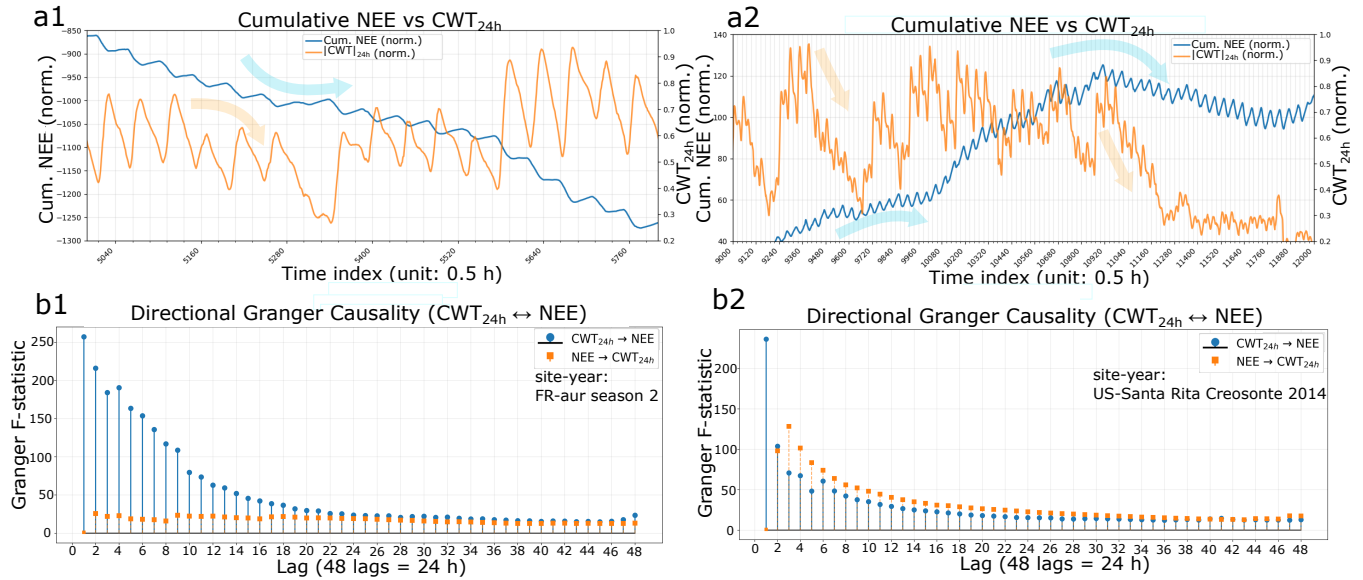


Figure 2. Influence of CWT_{24h} on NEE (left: European cropland; right: natural, pulse-driven ecosystem). (a1, a2) Exemplary cases of CWT_{24h} leading the response of NEE; the arrows indicate drops in CWT_{24h} leading to corresponding inflection points in NEE. (b1, b2) Directional Granger-causality between CWT_{24h} and NEE.

was assessed using: (i) F-tests comparing a restricted AR model of NEE vs. an unrestricted model that includes additionally lagged CWT_{24h}; (ii) likelihood-based statistics; and (iii) error distribution with Diebold-Mariano (DM) tests (Appendix, A2, Fig. A2, right column). Rejection of the null hypothesis indicated that CWT_{24h} provides additional Granger-causal information of NEE.

2.5.2 Short-horizon predictive power of CWT_{24h}.

We evaluated whether frequency amplitudes closest to the 24 h period (represented by CWT_{24h}) provide practical information for short-term forecast of NEE. Specifically, we tested whether diel-scale wavelet amplitude enhances short-term predictability of cumulative NEE. To that end, we set up a rolling one-step-ahead (t+1) forecasting experiment. Predictive performance was assessed using a rolling-window framework, in which models were trained on observations on the previous 10 days, i.e. from $t = t - 480$ to $t = t$, and used to generate one-step-ahead forecasts (t+1), with observed values used as lagged inputs at each step (i.e. no error propagation across forecasting steps). XGBoost was used as the regression method with a standard, non-optimized parameterization (Appendix, Table A3).

Two forecasting setups were compared: (i) a baseline model using only lagged values of the target variable (cumulative NEE) and cyclical time features, and (ii) an augmented model additionally including selected lagged values of the predictor variable (i.e. a number of $n_{lags} = 7$, CWT amplitude in the 24 ± 2 h band, CWT_{24h}), as identified by Granger causality analysis (section 2.5.1). For simplicity, n_{lags} was set to 7 (i.e. 3.5 h) as a fixed, parsimony-motivated choice, informed in



aggregate by the Granger analysis, not selected per site. We made this design choice to keep the model reasonably simple and avoid unnecessary complexity. Feature vectors consisted of short autoregressive histories of the target, selected predictor lags, and sinusoidal representations of diurnal time. Models were re-estimated at each forecast origin, and predictive performance was evaluated using RMSE over all rolling forecasts. This framework allowed to test whether the inclusion of CWT_{24h}-based predictors improved short-horizon forecast accuracy, beyond the intrinsic persistence and diurnal structure of NEE. Finally, we examined the temporal structure of forecast performance improvements by analyzing $\Delta RMSE$, defined as the time-resolved difference between the baseline and exogenous model errors ($\Delta RMSE_t = RMSE_{base,t} - RMSE_{exog,t}$). Positive values indicate points in time where CWT_{24h}-based predictors improve one-step-ahead forecasts, enabling identification of periods when frequency-domain information contributes most strongly to predictive performance.

3 Results and Discussion

Our main results are prediction improvements of NEE (Section 3.2), validated across 45 site-years; in Section 3.1 we show and discuss consistent observations which served as diagnostic and motivation.

3.1 Diagnostic of Influence and Directional Granger Causality.

First, we relied on a SARIMAX framework, which allowed us to explicitly separate the intrinsic autocorrelation of NEE from the delayed effects of CWT_{24h}. We observed systematic declines in CWT_{24h} preceding inflection points in NEE in both cultivated and natural ecosystems. These precursory signatures are apparent for short-lived disturbances (e.g. flash droughts) as well as for longer-term transitions, such as the seasonal fade-out of NEE associated with end-of-season senescence (Fig. 2, a2). We observed that, in both cultivated and natural ecosystems, lagged values of CWT_{24h} exert a significant influence on NEE (see Appendix), that we evaluated up to 48 time steps before (i.e. 24 h). The specific lags exhibiting the strongest effects varied across site-years, with no clear or systematic pattern (Appendix, Fig. A2).

The Granger causality tests consistently indicated a strong predictive influence of CWT_{24h} on NEE (Fig. 2, b1-b2, extended results in Appendix). Although both series exhibit pronounced diurnal structure, the tests revealed a clear directionality in predictive power, with forward causality (CWT_{24h} → NEE) in croplands usually being about one order of magnitude higher than reverse causality (NEE → CWT_{24h}), for short lag times (i.e. 1-6 h of difference between the two signals). The largest contrasts between forward and reverse causality occurred at short lag times, within ≤ 10 h for cropland sites and ≤ 4 h for natural pulse-driven ecosystems, indicating that diel-scale wavelet amplitude contains particularly strong short-term predictive information for NEE dynamics. Together, these diagnostics motivated the use of CWT_{24h} as a predictor, which we evaluate formally in Section 3.2.

3.2 Short-Horizon Predictive Power of CWT_{24h}.

For all 45 site-years, short-term forecasts of NEE improved as a result of adding the recent history of CWT_{24h} as predictor (Table 1). Improvements were assessed using $\Delta RMSE$: the difference between the baseline model and the CWT_{24h}-augmented

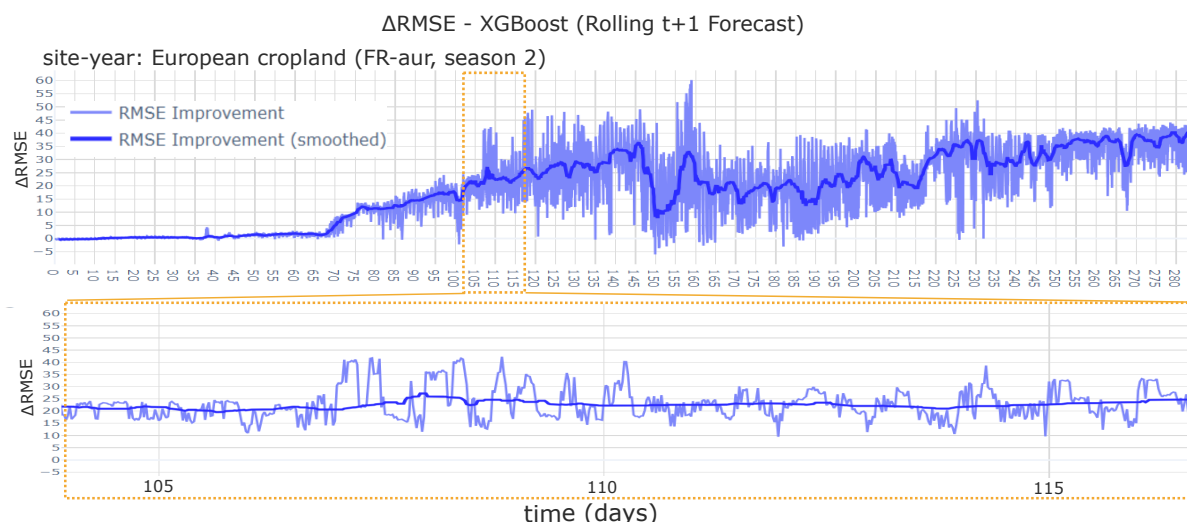


Figure 3. Improved one-step-ahead ($t+1$) forecasts of net ecosystem CO_2 exchange (NEE) obtained by including lagged CWT_{24h} features. Dataset: European cropland site FR-Aur-season-2. Positive values of ΔRMSE indicate improved predictive performance relative to the baseline model. The dashed square highlights a temporal zoom-in window, revealing pronounced diel patterns in ΔRMSE . Additional results are shown in Appendix (Table A1, Table A2, Fig. A3).

Table 1. Main results across 45 site-years. $\Delta\text{RMSE}_{\{\text{prior}, \text{in}, \text{after}\}}$ indicates, respectively, the improvement before, during, or after the physiologically active period (i.e. the growing season), in each site-year. P.D.: pulse driven ecosystem (from north Mexican or south US dry regions); Agro.: agroecosystem (European cropland). Extended results are given in Appendix (Table A1, Table A2, Fig. A3). Positive is better.

Type		$\Delta\text{RMSE}_{\text{prior}}$	$\Delta\text{RMSE}_{\text{in}}$	$\Delta\text{RMSE}_{\text{after}}$
P.D.	mean	1.43	2.98	2.76
	median	0.90	2.34	2.00
Agro.	mean	0.82	3.93	4.96
	median	0.33	1.01	1.41

model (where positive means improvement; Fig. 3). The forecasting experiments showed improved predictive performance when frequency-domain information (i.e. CWT_{24h}) was included, a pattern observed across all 45 site-years (site-specific results are provided in Appendix). The augmented setup, incorporating selected lagged CWT_{24h} features as predictors of NEE in $t+1$ forecasts, outperformed the baseline model relying solely on autoregressive NEE features in all experiments, (with one only exception out of 129 experiments, i.e. BE-Lon seas-3, $\Delta\text{RMSE}_{\text{prior}}$, see Appendix). This indicates that CWT_{24h} provides predictive information beyond the intrinsic persistence of NEE, enhancing real-time short-term forecasting. Two general trends emerged: (i) improvements in croplands (ΔRMSE) were larger than in natural pulse-driven ecosystems; and (ii)



improvements increased during the growing season ($\Delta RMSE_{in}$), in some cases persisting or gradually decaying afterward ($\Delta RMSE_{after}$). A summary of results is presented in Table 1, while results detailed at site-year level are given in Appendix (Table A1 and Table A2). The a-priori wavelet coefficient $CWT_{j,t}$, representing the instantaneous amplitude of NEE oscillations at period s_j (that we selected at 24 ± 2 h, to evaluate circadian cycles), was computed using only information available up to time t , with no future information being used at each forecast origin. Consequently, CWT_{24h} is suitable for real-time deployment, and interpretable as a measure of directional coupling between circadian rhythms and NEE flux magnitudes in the physiological functioning of ecosystems. These properties make it well suited for short-horizon forecasting and near-real-time monitoring applications, highlighting the potential of CWT-derived metrics for integration into an operational ecosystem monitoring framework. The temporal structure of $\Delta RMSE$, characterized by larger forecast improvements during nighttime (Fig. 3), was consistently observed across ecosystems. This may indicate that the exogenous model (i.e. the one including lagged features of CWT_{24h}) most effectively leverages information from the circadian cycle during periods without daylight. The interpretation of this observation stays out of the scope of the present study and is left for future work. However, we intuitively interpret it as possibly caused by the combination of these two factors: (i) at night, respiratory processes dominate NEE since photosynthetic uptake is absent, so that NEE may be less of a composite signal, hence less difficult to predict when including CWT_{24h} ; or (ii) the improvements may be explained due to higher atmospheric stability at night.

3.3 Outlook and Future Work.

Our observations of the relationship between circadian rhythms (CWT_{24h}) and NEE suggest opportunities to develop metrics for ecosystem diagnosis that may be broadly applicable across ecosystem types. Circadian rhythms showed consistent Granger-causal relationships with NEE and strong predictive performance, with high dominance during ‘stable periods’ and rapid changes during ‘disturbed periods’. These dynamics could potentially be used to derive metrics characterizing the robustness and elasticity of circadian rhythms, providing a basis for ecosystem diagnosis and the development of early-warning signals of ecosystem disturbance. Ecosystem fluxes can vary substantially, both across years at the same site and among ecosystems experiencing similar climatic conditions. In contrast, the physiological responses underlying net ecosystem CO_2 exchange are driven, at least in part, by recurring diel environmental cycles, particularly light availability and temperature. The consistency of these drivers and their relationship with ecosystem functioning may therefore provide a basis for developing diagnostic metrics that are less dependent on ecosystem-specific flux magnitudes.

4 Conclusion.

In this study, we evaluated the relationship between the rhythm and the magnitude of NEE for different site-years of two contrasting ecosystem types: (i) European agroecosystems ($N = 19$), and (ii) pulse-driven ecosystems from dry tropical shrublands and dry tropical forests ($N = 26$).

First, for all 45 cases evaluated, we observed that the rhythm of NEE becomes more circadian during the growing season, demonstrated by the consistent observations made on its continuous wavelet transform (i.e. CWT): the convergence of



dominant amplitudes around the 24 h cycle during the growing period (i.e. CWT_{24h}). We attribute this effect to the biological activity occurring during this period, driven by enhanced photosynthesis and respiration (H1). Second, we observed that circadian rhythms are more sensitive to disturbances than the magnitude of NEE, confirmed by directional Granger causality tests (H2). This is, circadian rhythms lead the response of NEE fluxes, with varying lead times for agroecosystems and natural pulse-driven ecosystems. Third, circadian rhythms carry predictive information of NEE which can be leveraged in a real-time short-term forecasting framework (H3). We showcased improved predictive performance as a practical implementation using a standard XGBoost regressor. This methodological approach was evaluated for 45 sites across two contrasting ecosystem settings that enable clear ecophysiological interpretation of the NEE signal: (i) managed European croplands and (ii) natural ecosystems primarily regulated by moisture pulses, such as dry tropical forests and dry tropical shrublands. Notably, in both croplands and pulse-driven natural systems, frequency-domain information consistently provided the strongest improvements in short-term ($t+1$) forecasts during nighttime periods, when ecosystem respiration dominates net CO_2 exchange. This consistent pattern suggests that diel-scale wavelet amplitude captures aspects of ecosystem functioning that are not fully disclosed by magnitude-based flux metrics alone. Overall, these findings outline a promising pathway, real-time deployable, for integrating time–frequency information into short-term forecast and rapid diagnostic systems of ecosystem functioning and productivity. This may be of particular interest for established networks that operate continuous, high-frequency carbon-flux measurements, such as ICOS, NEON, AmeriFlux, MexFlux, ChinaFlux, JapanFlux, KOF, SAEON and TERN.

Code and data availability. Code and data will be made public upon acceptance of this manuscript, by hosting them in a DOI-compliant Github public repository. Documentation to ensure reproducibility will be provided.

Appendix A: Appendix

A1 Summary of Additional Results

We report below, in Tables A1 and A2, the results summarized in Table 1, expanded per site-year, to allow the reader have a closer look at differences between site-years and ecosystem types. Table A1 contains the results of pulse-driven ecosystems, while Table A2 contains results for agroecosystems.



Table A1. Extended results across the 26 natural pulse-driven (P.D.) site-years. $\overline{\Delta\text{RMSE}}_{\text{in}}$ indicates the average improvement as a result of including lagged features of CWT_{24} in prediction experiments of t+1 forecast of NEE. The underscripts indicate prior, inside, or after the physiologically active period in each site-year (in $\mu\text{molC}^{-1}\text{m}^{-2}\text{s}^{-1}$). SD: standard deviation. For simplicity, all experiments have been run with $n_{\text{lags}} = 7$ (i.e. 3.5 h). Positive means better.

Type	Site	Year	$\overline{\Delta\text{RMSE}}_{\text{prior}} \pm \text{SD}$	$\overline{\Delta\text{RMSE}}_{\text{in}} \pm \text{SD}$	$\overline{\Delta\text{RMSE}}_{\text{after}} \pm \text{SD}$
P.D.	MX-Tes (AmeriFlux, 2026a)	2004	5.07 ± 0.81	4.67 ± 0.79	2.22 ± 1.58
		2005	0.61 ± 1.17	3.95 ± 1.72	1.44 ± 0.73
		2006	0.36 ± 0.66	1.92 ± 3.45	0.48 ± 1.86
		2008	2.09 ± 1.41	0.65 ± 2.33	2.54 ± 2.87
P.D.	MX-Ray (Watts and Rodriguez, 2021)	2008	0.06 ± 0.29	0.52 ± 0.52	1.46 ± 0.37
		2009	0.11 ± 0.16	0.14 ± 0.42	0.62 ± 0.32
		2010	0.31 ± 0.43	0.36 ± 0.40	0.85 ± 0.36
		2011	0.01 ± 0.13	0.53 ± 0.46	0.97 ± 0.42
P.D.	MX-Ala (AmeriFlux, 2026b)	2012	0.18 ± 0.15	0.53 ± 0.17	0.78 ± 0.30
		2017	2.13 ± 0.94	4.67 ± 1.85	3.96 ± 2.43
		2018	0.99 ± 1.65	4.24 ± 9.67	5.78 ± 2.20
		2019	0.35 ± 0.40	1.50 ± 1.53	0.43 ± 2.53
P.D.	MX-Vaq (Delgado-Balbuena et al., 2019)	2020	1.41 ± 0.80	4.21 ± 0.74	1.85 ± 0.68
		2011	0.39 ± 0.70	5.14 ± 2.13	4.34 ± 2.03
		2012	0.17 ± 0.64	0.96 ± 1.11	0.06 ± 0.54
		2013	2.76 ± 0.99	5.97 ± 1.28	4.17 ± 0.99
P.D.	US-SRC (Sanchez-Mejia et al., 2014)	2014	0.45 ± 0.68	2.80 ± 2.24	4.73 ± 1.56
		2015	1.68 ± 1.27	1.19 ± 2.00	2.15 ± 2.79
		2016	1.18 ± 2.44	2.34 ± 4.78	0.96 ± 3.18
		2008	0.13 ± 9.64	1.10 ± 0.9	2.28 ± 0.92
P.D.	US-SRC (Sanchez-Mejia et al., 2014)	2009	1.93 ± 0.96	2.63 ± 0.27	2.36 ± 0.54
		2010	4.00 ± 2.61	8.25 ± 0.92	8.63 ± 2.70
		2011	0.80 ± 0.96	1.75 ± 1.57	0.65 ± 1.42
		2012	5.25 ± 2.47	4.97 ± 1.51	6.32 ± 0.94
		2013	1.00 ± 0.57	2.33 ± 0.93	1.81 ± 0.72
		2014	3.63 ± 1.87	10.27 ± 4.85	9.94 ± 4.02



Table A2. Extended results across the 19 agroecosystem (Agro.) site-years. $\overline{\Delta RMSE}_{in}$ indicates the average improvement as a result of including lagged features of CWT_{24} in prediction experiments of t+1 forecast of NEE. The underscripts indicate prior, inside, or after the physiologically active period in each site-year (in $\mu mol C^{-1} m^{-2} s^{-1}$). SD: standard deviation. Seas.: season. Only one case (in bold) shows $\Delta RMSE < 0$. Positive means better.

Type	Site	Season # (Year)	$\overline{\Delta RMSE}_{prior} \pm SD$	$\overline{\Delta RMSE}_{in} \pm SD$	$\overline{\Delta RMSE}_{after} \pm SD$
Agro.	FR-Aur (ICOS, 2026a)	seas. 1 (2019)	6.20 ± 3.17	20.80 ± 8.15	31.86 ± 5.47
		seas. 2 (2021)	1.75 ± 2.98	21.73 ± 10.18	27.15 ± 10.38
Agro.	FR-Em2 (ICOS, 2021d)	seas. 1 (2017)	2.62 ± 2.15	6.73 ± 2.67	8.57 ± 3.94
		seas. 2 (2018)	0.27 ± 0.20	4.37 ± 2.01	4.44 ± 1.83
		seas. 3 (2019)	0.33 ± 0.69	0.89 ± 0.91	0.97 ± 0.76
Agro.	FR-Lam (ICOS, 2026b)	seas. 1 (2021)	0.48 ± 0.15	1.52 ± 1.10	0.56 ± 1.28
		seas. 2 (2022)	0.33 ± 0.69	0.89 ± 0.91	0.97 ± 0.76
		seas. 3 (2023)	0.08 ± 0.35	0.36 ± 0.34	1.25 ± 0.43
Agro.	DE-Kli (ICOS, 2021c)	seas. 1 (2018)	0.60 ± 0.85	0.88 ± 1.68	1.57 ± 1.67
		seas. 2 (2020)	0.89 ± 0.97	9.10 ± 3.26	5.42 ± 2.59
		seas. 3 (2021)	0.72 ± 0.3	3.18 ± 2.88	4.39 ± 3.75
Agro.	DE-Geb (ICOS, 2021b)	seas. 1 (2021)	0.23 ± 0.17	0.76 ± 0.37	1.09 ± 1.40
		seas. 2 (2022)	0.24 ± 0.17	0.89 ± 0.32	1.15 ± 0.38
		seas. 3 (2023)	0.15 ± 0.47	0.11 ± 0.31	0.11 ± 0.56
Agro.	BE-Lon (ICOS, 2021a)	seas. 1 (2019)	0.1 ± 0.35	1.17 ± 0.70	0.62 ± 0.52
		seas. 2 (2022)	0.23 ± 0.17	0.76 ± 0.37	1.09 ± 0.40
Agro.	DK-Vng (Revenga et al., 2024; ICOS, accessed 2026)	seas. 1 (2021)	0.78 ± 0.45	1.12 ± 1.27	1.64 ± 1.79
		seas. 2 (2022)	0.19 ± 0.28	0.80 ± 1.05	2.18 ± 1.57
		seas. 3 (2023)	0.41 ± 0.48	2.00 ± 1.79	3.42 ± 2.28

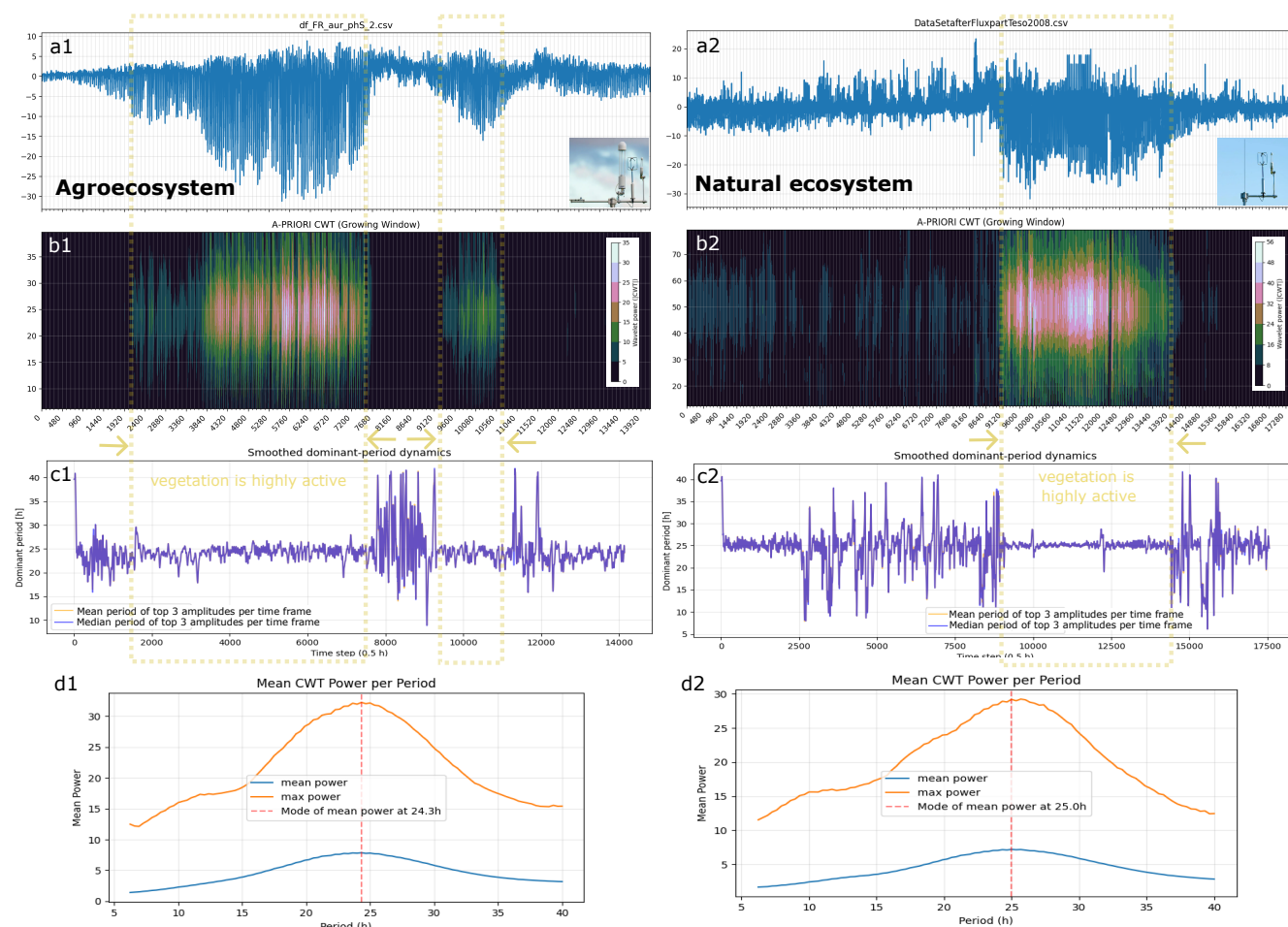


Figure A1. Extended graphical diagnostics illustrating two representative cases: agroecosystems and natural pulse-driven ecosystems (see Fig. 1). Panels c1–c2 show that convergence toward the diel cycle coincides temporally with the period of highest physiological activity in vegetation. Panels d1–d2 indicate that, when considering the full time series, the distributions of both mean and maximum power (across scales) exhibit an attraction toward the circadian period, i.e. 24 h.

A2 Extended Graphic Results

We provide 3 sets of additional graphic diagnostics, i.e. Fig. A1, Fig. A2 and Fig. A3, which extend the results shown in Figs. 1, 2 and 3, respectively.

A3 Description of XGBoost Predictor used

310 In the forecasting experiment, we employed the regressor class reported in Table A3, with fixed hyperparameters that were not optimized. The model class and hyperparameter configuration were deliberately kept constant to ensure clarity and facilitate

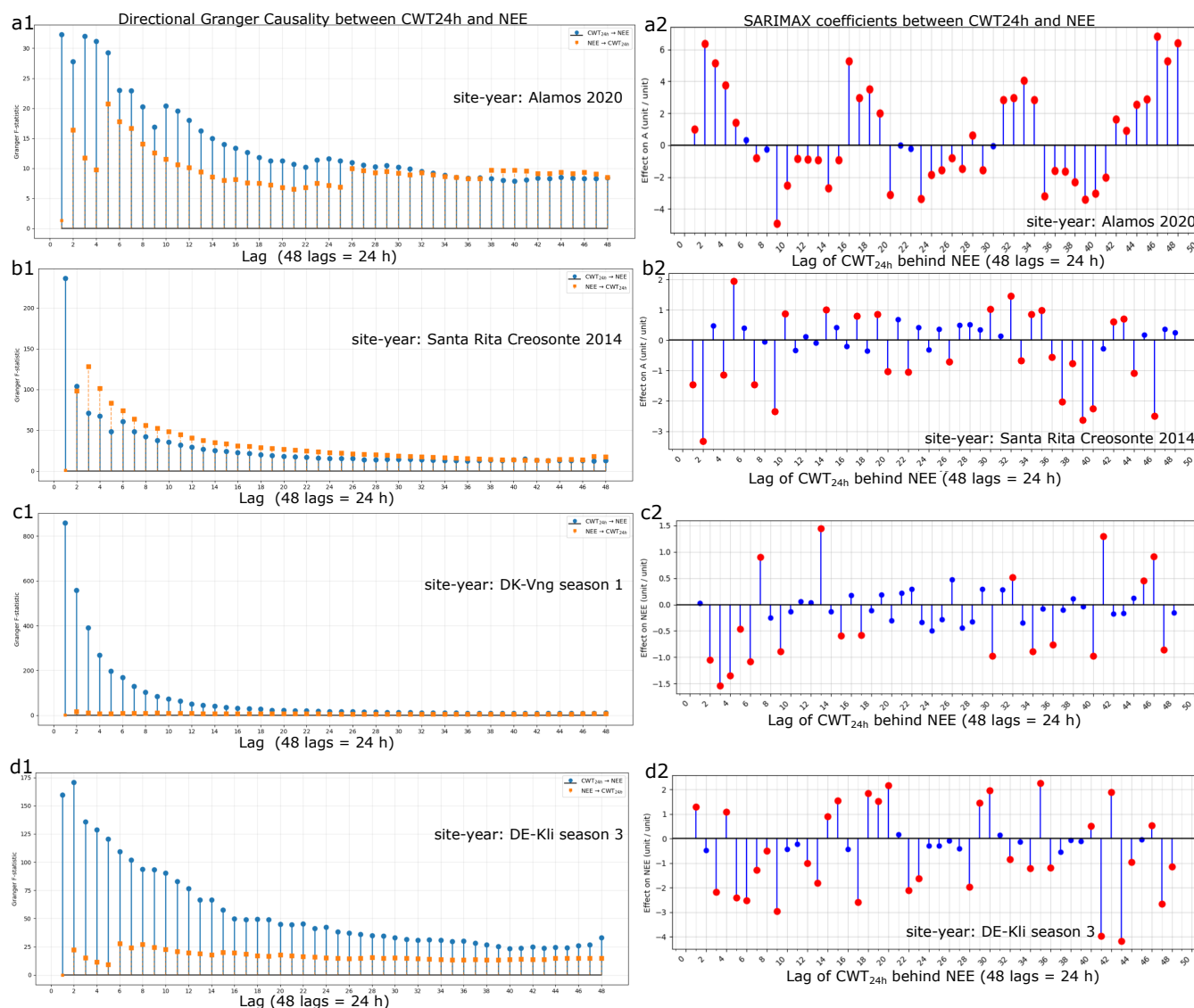


Figure A2. Extended graphical diagnostics illustrating four representative cases: natural pulse-driven ecosystems (a, b) and agroecosystems (c, d; see Fig. 2). We observed how for natural pulse-driven ecosystems (a1, b1) the directionality of the Granger causality test resulted much weaker than for agroecosystems (c1, d1), quantified as larger differences between (CWT_{24h} → NEE), and (NEE → CWT_{24h}). In the SARIMAX analysis, no systematic pattern was observed for the presence of significant lags (red dots in panels of right column) between CWT_{24h} and NEE.

interpretation of the experimental outcomes. Both the baseline and augmented models used the same specification, differing only in the inclusion of exogenous wavelet-based features (i.e. lags of CWT_{24h}).

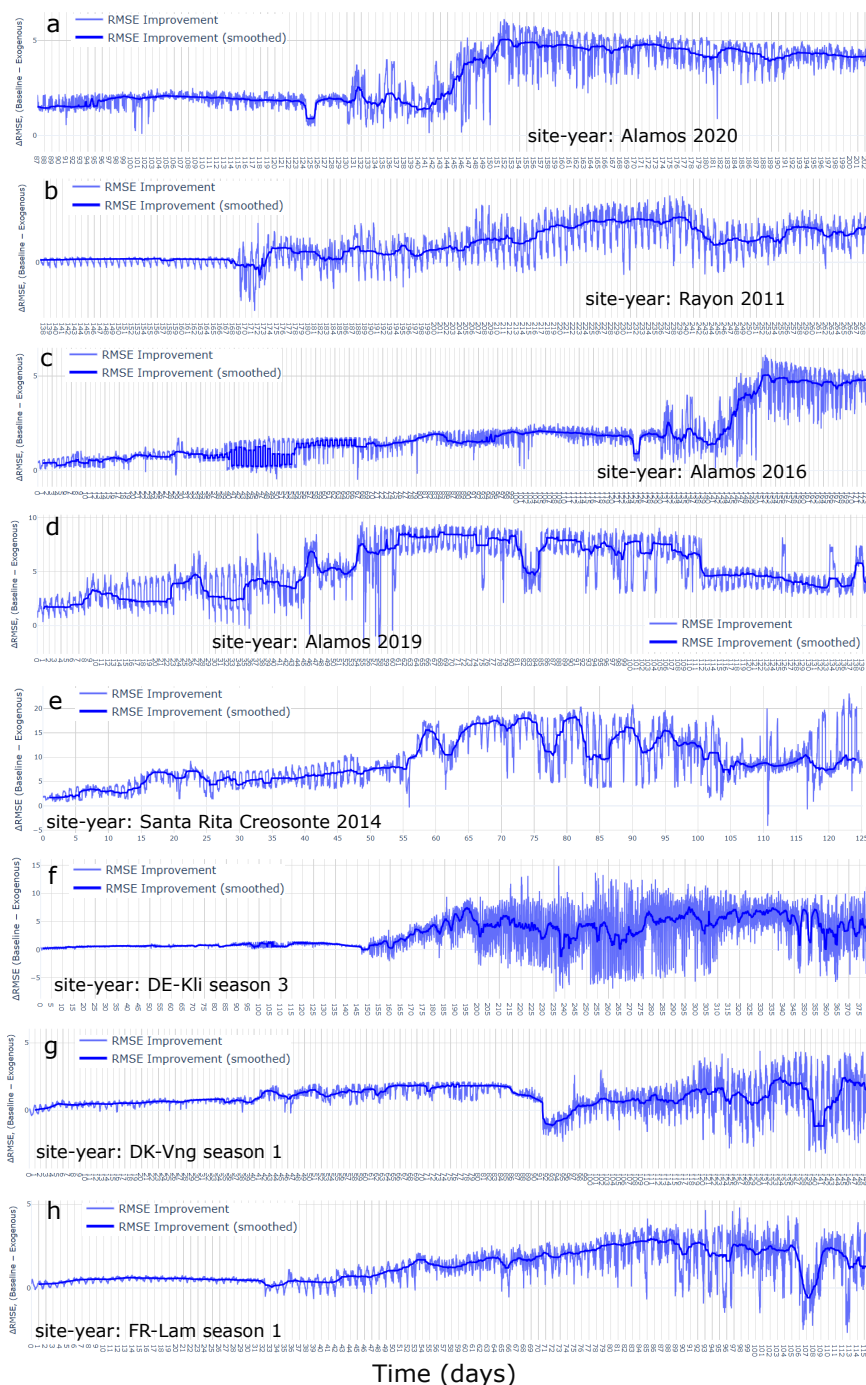


Figure A3. Extended graphical results (ΔRMSE , extending main results of Tables 1, A1, A2, and Fig. 3), showcased for a set of eight site-years, from either pulse-driven natural ecosystems (a, b, c, d, e), or agroecosystems (f, g, h). Positive means better.



Table A3. XGBoost regressor configuration used in the rolling one-step-ahead (t+1) forecasting experiments. All hyperparameters correspond to a standard, non-optimized setup and were kept fixed across sites and experiments.

Parameter	Value
Regressor class	Extreme gradient-boosted decision trees (XGBoost)
Objective function	reg:squarederror
Number of estimators	50
Maximum tree depth	3
Learning rate	0.05
Subsample ratio	0.8
Column subsample ratio	0.8
Early stopping	Not used
Feature scaling	Standardization (zero mean, unit variance)
Forecast horizon	One step ahead (t+1)
Training strategy	Rolling window trained on previous 480 datapoints (i.e. 10 days) with observed inputs used at each step

A4 Note on the eddy covariance method for ecosystem flux analysis.

315 The eddy covariance theory rests on the assumption that the variance of scalar values measured at a single point (e.g. temperature, gas concentration), broken down into a mean value and a fluctuating component, are positively correlated with the variance in the vertical wind component, so that they present a positive covariance that is proportional to the flux to be estimated (e.g. CO₂ flux). The eddy covariance method (Foken and Foken, 2021) therefore estimates fluxes from the covariance between the fluctuations of vertical wind velocity, w' , and scalar concentration, c' . For CO₂ fluxes in molar form (sign may vary based on convention), an ecosystem flux is defined as

$$F \approx -\rho \overline{w'c'} \quad (\text{A1})$$

with ρ representing air density.

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