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CONCEPTS, REVIEWS AND SYNTHESES

Climate controls over ecosystem metabolism: insights from a fifteen-year inductive artificial neural network synthesis for a subalpine forest

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Abstract Eddy covariance (EC) datasets have provided insight into climate determinants of net ecosystem productivity (NEP) and evapotranspiration (ET) in natural ecosystems for decades, but most EC studies were published in serial fashion such that one study's result became the following study's hypothesis. This approach reflects the hypothetico-deductive process by focusing on previously derived hypotheses. A synthesis of this type of sequential inference reiterates subjective biases and may amplify past assumptions about the role, and relative importance, of controls over ecosystem metabolism. Long-term EC datasets facilitate an alternative approach to synthesis: the use of *inductive* data-based analyses to re-examine past *deductive* studies of the same ecosystem. Here we examined the seasonal climate determinants of NEP and ET by analyzing a 15-year EC time-series from a subalpine forest using an ensemble of Artificial Neural Networks (ANNs) at the half-day (daytime/nighttime) time-step. We extracted relative rankings of climate drivers and driver–response relationships directly from the dataset with minimal a priori assumptions. The ANN analysis revealed temperature variables as primary climate drivers of NEP and daytime ET, when all seasons are considered, consistent with the assembly of past studies. New relations uncovered by the ANN approach include the role of soil moisture in driving daytime NEP during the snowmelt period, the nonlinear response of NEP to temperature across seasons, and the low relevance of summer rainfall for NEP or ET at the same daytime/nighttime time step. These new results offer a more complete perspective of climate–ecosystem interactions at this site than traditional deductive analyses alone.

Keywords Coniferous · Model-data assimilation · Photosynthesis · Fluxnet · Eddy covariance

Introduction

Over the past two decades, studies on ecosystem-to-global scale dynamics in the terrestrial carbon cycle have benefited from combined tower-based observations of CO_2, H_2O and energy fluxes, along with weather/climate variables (Wofsy et al. 1993; Flanagan et al. 2002; Monson et al. 2002; Baldocchi 2003). Early studies focused on the dynamics of specific sites, but as the number of sites grew, broader spatiotemporal analyses were conducted on climate determinants of regional-to-global scale patterns in the carbon cycle (Gilmanov et al. 2010; Beer et al. 2010; Xiao et al. 2011; Jung

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et al. 2011; Hilton et al. 2014). There remains a role and opportunity for single-site studies to uncover the mechanisms and processes that link climate to ecosystem metabolism, especially within the context of holding site constant while studying vegetation dynamics and climate variables across overlapping time spans, ranging from seasonal through interannual to decadal (Callahan 1984; Richardson et al. 2007; Scheffer et al. 2009; Dragoni et al. 2011; Pilegaard et al. 2011; Craine et al. 2012; Keenan et al. 2012).

Syntheses of multiple studies conducted at a single site tend to be conducted with serial hindsight. That is, researchers subjectively evaluate the conclusions of a past study by posing them as the hypotheses for a future study. This deductive approach carries forward the focus on states and processes that compose past hypotheses, and thus tends to canalize perspectives on the most important drivers of observed responses. This process of synthesis is often done in an informal manner, through statements of interpretation in the discussion sections of manuscripts, and with researchers providing subjective interpretations of current results within the context of past results. One approach that has been used to achieve a more formal synthesis is to use data to constrain process-based models through data assimilation (Luo et al. 2011; Keenan et al. 2011). This is a hypothetico-deductive approach, in which past knowledge and observational data are used to structure and parameterize models. The equations comprising such models represent hypotheses about how driving variables and observed effects interact with one another (Young et al. 1996; Braswell et al. 2005; Young 2006; Moffat et al. 2010; Zobitz et al. 2011; Keenan et al. 2011). The models are used to make predictions of outcomes (e.g. net ecosystem productivity, NEP) given a prescribed set of driving variables, and those model-simulated outcomes are compared to observations. To test the model (and the hypotheses implemented as equations), a statistical error can be estimated for the model-data match. If a model's predictions align with the observed data, the model's underlying hypotheses are deemed valid (Young 2006; Moffat et al. 2010).

An alternative to deductive approaches is to extract insight directly from the data using statistical models. This inductive approach can be designed to minimize the a priori hypotheses common in deductive analyses (Moffat et al. 2010). Although an inductive approach does not directly test mechanistic hypotheses for the processes of interest, it can reveal which drivers of the observed effects are the most important among a given set of drivers, whether information might be missing from deduced mechanistic models, and ultimately, the shape of the ecosystem response to drivers (Moffat et al. 2010). Artificial Neural Networks (ANNs) provide an advantageous tool for extracting patterns directly from large, highly variable datasets with few a priori assumptions (Moffat et al. 2010). ANNs are purely empirical models inspired by the biological neural networks of the nervous system (Olden et al. 2008). Because ANNs are non-parametric, and excellent at approximating nonlinear relationships in complex systems, ANNs are becoming more widely used in ecology. For a detailed description of ANNs and their applications, see Bishop (1995), Lek and Guégan (1999), Papale and Valentini (2003), Olden et al. (2008), and Moffat et al. (2010). In ecosystem ecology, ANNs have been used for multiple purposes, such as providing a benchmark for process-based model performance (Moffat et al. 2010; Keenan et al. 2012), correcting systematic error in the flux outputs of land–surface models (Abramowitz et al. 2007), and estimating carbon or water fluxes without relying on models of how plant physiology responds to environmental variables (Van Wijk and Bouten 1999; Moffat et al. 2010; Keenan et al. 2012).

In this study, we applied a data-based modeling strategy using ensembles of ANNs to a 15-year eddy flux dataset derived from the Niwot Ridge AmeriFlux site (US-NR1), located in a high-elevation, subalpine forest in western North America (Monson et al. 2002, 2010). Previous model-data fusion studies have been conducted at this site using Bayesian-type approaches (Sacks et al. 2006, 2007; Moore et al. 2008; Hu et al. 2010), and a set of over 50 past studies including observations and models have been published. It would be possible to conduct a traditional subjective, and deductive, synthesis of knowledge from these studies. However, our goal here is to conduct a new synthesis of available data and apply an inductive approach using ANNs to characterize seasonal drivers of NEP and ET. In conducting this synthesis we avoided a priori assumptions about controls and relationships. We then compared the more objective synthesis using the ANN with the lessons learned through the past hypothetico-deductive studies.

Methods

Site

Niwot Ridge is part of the Long-Term Ecological Research network, and the Niwot Ridge EC dataset is among the longest for forest sites (Monson et al. 2002; Williams et al. 2016). The Niwot Ridge AmeriFlux site is in a subalpine forest at high elevation (3050 m) in the Rocky Mountains, USA (40°1′58″N, 105°32′47″W). Mean annual temperature is 1.5 °C. Annual precipitation averages 800 mm, with 65% falling as snow (Scott-Denton et al. 2013). The secondary forest surrounding the site is approximately 120 years old and is dominated by Engelmann spruce (*Pinceae engelmanii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*). For a full site description see Greenland (1989), Monson et al. (2002, 2005) and Turnipseed et al. (2002, 2003).

Meteorological and eddy covariance measurements

The US-NR1 eddy-covariance flux tower was installed in November 1998. Net ecosystem CO_2 exchange (NEE) and latent and sensible heat fluxes were measured at a height of 21.5 m. We used 30-min averaged flux and climate data from January 1, 1999 to December 31, 2013 (AmeriFlux version 2015.11.10). Note that although NEE was used as an input to the ANN, we use the term net ecosystem productivity (NEP) throughout the text and figures to emphasize carbon uptake or loss with respect to the ecosystem, rather than to the atmosphere ($\mathrm{NEP} = -\mathrm{NEE}$). Evapotranspiration (ET) was calculated from latent heat flux. For further discussion of the eddy flux measurements at Niwot Ridge, see Monson et al. (2002), Turnipseed et al. (2002, 2003), Yi et al. (2008), and Burns et al. (2014, 2015, 2016). The data and further details on processing are available from the Niwot Ridge AmeriFlux web site (http://urquell.colorado.edu/data_ameriflux/). Historical daily snow water equivalent (SWE) was obtained from the Natural Resources Conservation Service (NRCS) SNOTEL site 663 (NIWOT) which is within 500 m of the flux tower.

Data treatment and grouping

Daytime and nighttime means were determined from 30-min averaged data for all meteorological and flux variables except snow water equivalent and precipitation. Snow water equivalent (SWE), a measure of snowpack water content, was available at a daily temporal resolution, and so the daytimes and nighttimes for each day of the year were assigned the same measurement. Precipitation was summed for each daytime and nighttime time step. Throughout this text, the terms ‘daytime’ and ‘nighttime’ refer to the daytime or nighttime means or sums of meteorological and flux observations. Daytime and nighttime bins for averaging or summation of 30-min data were determined based on sunrise and sunset times for each day of the year for the latitude and longitude of the Niwot Ridge site; if a given 30-min averaged period theoretically included any moment of photosynthetically active radiation (PAR) above zero, then that 30 min period was considered daytime.

For our target variables (NEP and ET), data was processed as follows: only non-gap-filled data (AmeriFlux flag 1, ‘okay’ for NEP data and AmeriFlux flag 1 and 5 for ET data) were used; we excluded 30-min periods from the daytime and nighttime NEP data that failed both the integral statistics and stationarity tests; we excluded NEP and ET data from 30-min periods during the nighttime with canopy-surface friction velocity (u_*) less than 0.2, which has been determined as the best threshold to distinguish atmospheric stability influences on fluxes (see Monson et al. 2002). These exclusions meant that some ‘daytime’ or ‘nighttime’ bins were incomplete, so we excluded ‘daytime’ and ‘nighttime’ data points if more than 50% of their constituent 30-min periods were missing. For non-bounded climate variables (air temperature, soil temperature, and net radiation) outliers more than three standard deviations from the mean were excluded. The number of available daytimes/nighttimes in each data grouping after quality control is shown in Online Resource material (Tables S1–S8).

We grouped the daytime and nighttime data based on annual or seasonal periods of interest (Table 1). To examine how the seasonal drivers of NEP and ET vary among years, we grouped climate and flux data for each year (1999–2013). To examine how the drivers of NEP vary across seasons, we grouped data into phenologically relevant ‘seasonal periods’ for training the ANN (Fig. 2b). The ‘snowmelt’ period included data from the first day of peak SWE to the first day with zero SWE. The ‘pre-monsoon’ period included data from zero SWE to the first day of the monsoon (defined as the first day after June 15 with 24-h summed precipitation greater than or equal to 10 mm). The ‘monsoon’ period included data from the first day of the monsoon to September 20 (arbitrarily chosen). The ‘post-monsoon’ period included data from September 21 to the date when SWE was greater than, or equal to, 25 mm for more than a week after September 20 (or after September 21st for ‘leap years’). The winter period was defined as the end of the post-monsoon period to the beginning of the ‘snowmelt’ period of the following calendar year.

Artificial neural network model framework

We used a modeling framework of multi-layered feed-forward artificial neural networks trained by backpropagation. The ANNs of this study consisted of two layers: the input (see ‘candidate seasonal drivers’ section below) fed into a hidden layer, and the outputs of the hidden layer fed into an output layer (Fig. 1). Only one hidden layer was used; feed-forward ANNs with a single hidden layer can approximate any continuous function with an arbitrary accuracy provided that no constraints are placed on the number of nodes or the magnitude of the nodal weights (Cybenko 1989). All ANNs were created and trained using Matlab’s neural network toolbox (Matlab version R 2014b; Beale et al. 2014).

For each ANN, workflow consisted of the following steps: data pre-processing, network creation, network configuration, initialization of weights and biases, network training, and network validation (Beale et al. 2014). For data pre-processing, all inputs (candidate seasonal drivers) and the target (−NEP and ET) were scaled so that all values were within the interval [−1 1] to correspond to the nearly linear range of the hyperbolic tangent sigmoid transfer function and to expedite training (Moffat 2012; Beale et al. 2014). Networks (Fig. 1) were created for daytime

Table 1 Summary of questions and the strategy to inform each question via data grouping and candidate drivers of net ecosystem productivity (NEP) and evapotranspiration (ET) fluxes for analysis with artificial neural networks

Questions	Data grouping	Candidate drivers
All data analysis		
What are the seasonal drivers of daytime and nighttime NEP and ET?	All daytime data and all nighttime data from 1999 to 2013	All candidate drivers: Air temperature (°C) Wind speed (m s^{-1}) Wind direction (deg. from north) Friction velocity, u_* (m s^{-1}) Precipitation (mm) Vapor pressure deficit (kPa) Soil temperature (°C) PAR (μmol m^{-2} s^{-1})[a] Net radiation (W m^{-2})[a] Humidity (percent) Soil moisture (m^3 m^{-3})[b] Snow water equivalent (mm)[c]
Interannual analysis		
What are the seasonal drivers of daytime and nighttime NEP and ET for individual years?	Each individual year from 1999 to 2013, daytime and nighttime data	Same as above
Seasonal analysis		
What are the drivers of daytime and nighttime NEP and ET within phenologically relevant seasonal periods?	Daytime and nighttime data from 1999 to 2013 grouped by seasonal period (Fig. 2b): Winter period Snowmelt period Pre-monsoon period Monsoon period Post-monsoon period All continuous data	Same as above
What is the response of NEP and ET to their relevant seasonal drivers?	All daytime data and all nighttime data from 1999 to 2013, and data grouped by periods (Fig. 2b)	Most relevant primary drivers: Air temperature (°C) Soil temperature (°C) (Additional responses in Online Resource Figs. S5–S14)

[a] Daytime only

[b] Soil moisture only available for 2002–2013

[c] Excluded for periods without snow cover (pre-monsoon and monsoon periods)

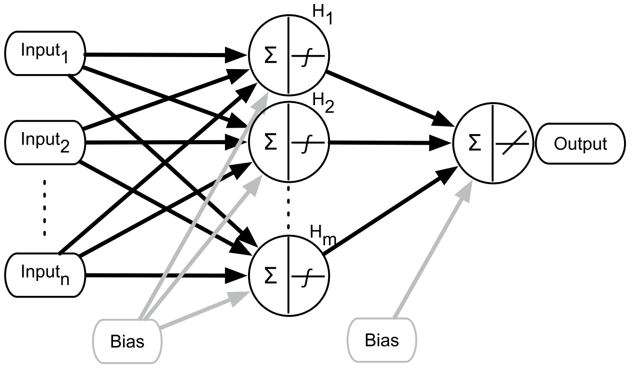

Fig. 1 Architecture of ANN models used in this study. For daytime data, benchmark ANNs had $n = 12$ or 11 inputs for periods with and without snowpack, respectively (see Table 1). For nighttime data, benchmark ANNs had $n = 10$ or 9 inputs for periods with and without snowpack. Primary driver ANNs had $n = 1$ input, and secondary driver ANNs had $n = 2$ inputs. All ANNs had $m = 8$ nodes in the hidden layer. *Black arrows* represent weights; *gray arrows* represent biases. *Dotted lines* represent inputs and hidden nodes not depicted (e.g. hidden nodes 3 through m). In a feedforward ANN, information flows in one direction: from the inputs, through the hidden layer to the output layer

and nighttime data of each seasonal period described above. Networks were configured with the input size equal to the number of candidate seasonal drivers (inputs) for each scenario and eight hidden layer nodes. Eight nodes were used for the hidden layer based on preliminary tests of the effect of node size on ANN performance (Online Resource Figs S3, S4). Before training, inputs and associated targets were randomly divided into three separate subsets for training (60% of data), validation (20% of data), and testing (20% of data). The 'training' and 'validation' subsets were both used during training. The 'training' subset was used for computing the performance gradient and updating weights (Beale et al. 2014). To avoid overfitting the data, network weights and biases were saved when the error of the 'validation' subset reached a minimum during the training process (Beale et al. 2014). Networks were trained in batch (epoch) mode using the Levenberg–Marquardt algorithm with mean-square error as the performance (merit) function. Each ANN scenario was repeated ten times, and the ANN with the lowest mean squared error from the 'testing' subset was selected for analysis of seasonal driver rankings. Stated uncertainty represents population standard deviations for ten ANNs trained with the same seasonal data grouping.

Candidate seasonal driver selection and relevance

To minimize a priori assumptions about which seasonal climate drivers are important, the starting set of candidates included all drivers that could potentially affect NEP and ET. We selected the following initial set of candidate drivers: air temperature (°C) measured at 21.5 m, wind speed (m s^{-1}) measured at 21.5 m, wind direction (degrees from true north) measured at 21.5 m, u_* (m s^{-1}), precipitation (mm) measured at 10.5 m, vapor pressure deficit (kPa) measured at 21.5 m, soil temperature (°C), incoming photosynthetically active photon flux density (PAR) (μmol m^{-2} s^{-1}) measured at 25.5 m, net radiation (W m^{-2}) measured at 25.5 m, relative humidity (percent) measured at 8 m, volumetric soil moisture (m^3 m^{-3}) measured at 0–15 cm depth, and snow water equivalent (mm). Because environmental variables may be cross-correlated with each other, a driver might appear to be more important than the actual driving variable (Moffat et al. 2010). Examination of the relationships between the driving variables shows the cross-dependencies and highlights the variables where those dependencies should be taken into account during interpretation of the results (Online Resource Fig.S1, S2).

To estimate the total explainable variability in the dataset, all candidate drivers were used as inputs for ANN training (Moffat et al. 2010). The r^2 between the target (observed NEP or ET) and ANN output served as a 'benchmark' of maximum mapping between the target and the candidate seasonal drivers (Moffat et al. 2010). This r^2 also showed how much variability remained unexplained due to measurement noise or unmeasured/omitted drivers of flux (Moffat et al. 2010). Because volumetric soil moisture was only available after the start of 2002, ANN benchmarks were calculated with and without volumetric soil moisture data. The results were similar (difference between including or excluding soil water content in benchmark r^2 values was usually less than 0.08, and only higher than 0.1 for year 2003 and 2004), and here we only report benchmarks without soil water content included for consistency across the 15-year dataset.

After an ANN performance benchmark was created, we performed a ranking of 'primary' drivers based on relevance, and then an identification of relevant 'secondary' drivers for each data grouping. To examine the relevance of each input as 'primary' seasonal drivers of flux, ANNs were trained with each candidate driver individually and ranked based on r^2. Next, the relevance of each input as a 'secondary' seasonal driver was examined by training ANNs with two inputs: the most relevant 'primary' seasonal driver plus each other input variable. For all ANNs (primary, secondary and benchmark) the coefficient of determination provided a measure of relevant information provided by the input(s) as described in Moffat et al. (2010; see also Van De Laar et al. 1999). We applied this approach to each 'seasonal period' independently. Because primary and secondary drivers could have similar relevance (r^2), the correlation coefficients (r) were compared after a Fisher r-to-z transformation (Fisher 1921). Each driver was compared

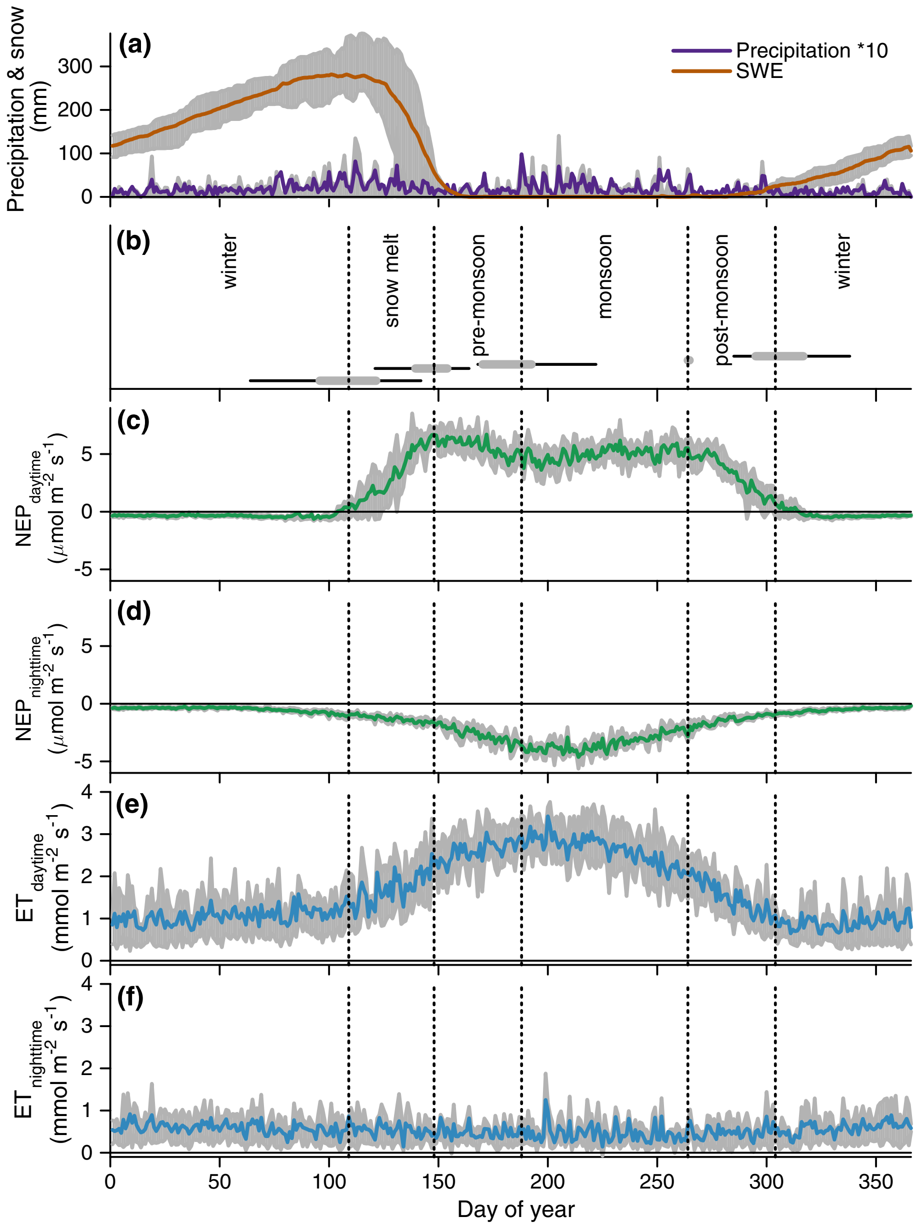

Fig. 2 Fifteen-year average seasonality of environment, net ecosystem productivity (NEP) and evapotranspiration (ET) at Niwot Ridge. **a** Mean daily (24 h) precipitation (*purple line*; multiplied by 10 for visualization) and snow water equivalent (SWE; *brown line*) with interquartile range (*grey*). **b** Boxplots showing median (*dotted line*), interquartile range (*grey*), and range (*black whiskers*; from $q3 + 1.5(q3 - q1)$ and $q1 - 1.5(q3 - q1)$, where $q1 = 25$th and $q3 = 75$th percentile) of transitions between seasonal periods. Seasonality of NEP (*green line*) for **c** daytime and **d** nighttime, and ET (*blue line*) for **e** daytime and **f** nighttime with interquartile range (*grey*). Color version of this figure is available online

to the next rank down for up to four drivers for each data grouping. The *z*-score from comparing the correlation coefficients indicates whether multiple drivers were 'tied' for 'significantly most relevant.' If more than three drivers for a given grouping were tied ($p > 0.05$ for two-tailed test), then no driver(s) were described as 'significantly most relevant.'

The response of a dependent variable to an individual driver can be captured by an ANN model with that individual driver as the sole input (Moffat et al. 2010). Examining the shape and form of the ecosystem response may provide insight into the mechanisms of ecosystem metabolism (Moffat et al. 2010). Ecosystem responses derived from an ANN trained with a single input driver do not exclude the influence of other drivers (i.e. they are not partial responses), and so the shape of the response may be influenced by other factors that co-vary with the driver in question over some or all of the observed range of variability. Thus, the ecosystem response to a single input is most informative for input drivers of high relevance (that account for much of variation in the response variable). We examined the NEP and ET responses to their most relevant primary drivers as determined from the ANNs trained on all the daytime or nighttime data (Table 1). Then, to investigate how the sensitivity of NEP to climate varies due to phenology or other seasonal changes in ecosystem dynamics, we plotted the single-driver ANNs for all daytime and nighttime data for each phenologically relevant seasonal period. Because ANN models vary due to the random assignment of weights during training, and the random division of the data into training, validation, and test datasets, an ensemble of 100 ANN models were trained for each primary driver, and mean and standard deviation of these 100 models were plotted for visualization.

Results

Climate drivers of net ecosystem productivity

For NEP, the benchmark r^2 values showed that the combined candidate drivers explained approximately 89 and 87% of the total variance in $\text{NEP}_{\text{daytime}}$ and $\text{NEP}_{\text{nighttime}}$ datasets, respectively (Fig. 3, Online Resource Tables S9, S10). Temperature variables emerged as the significantly most relevant seasonal drivers of $\text{NEP}_{\text{daytime}}$ and $\text{NEP}_{\text{nighttime}}$ for all data across all seasons (1999–2013); for $\text{NEP}_{\text{daytime}}$, the significantly most relevant drivers were air temperature above the canopy and soil temperature, and for $\text{NEP}_{\text{nighttime}}$, the most relevant driver was soil temperature (Fig. 3, Online Resource Tables S9 and S10). For individual years, the significantly most relevant primary drivers varied for $\text{NEP}_{\text{daytime}}$ (air temperature, soil temperature, or SWE), but always included soil temperature for $\text{NEP}_{\text{nighttime}}$ (Online Resource Tables S17 and S18). Training ANNs with two inputs—the most relevant and one other driver—revealed that the secondary drivers that produced the greatest improvement in performance for all data were relative humidity and VPD for $\text{NEP}_{\text{daytime}}$, improving the coefficient of determination by 0.14 and 0.12, respectively, above the 0.67 value for air temperature alone (Online Resource Table S13). For $\text{NEP}_{\text{nighttime}}$, air temperature and soil moisture produced the highest improvements when combined with soil temperature (Online Resource Table S14). Many candidate drivers were not relevant to dynamics in NEP. For all $\text{NEP}_{\text{daytime}}$ and $\text{NEP}_{\text{nighttime}}$ data, ANNs trained with wind speed, wind direction, u_*, or precipitation as the sole input yielded low performance ($r^2 < 0.2$; Fig. 3, Online Resource Tables S9 and S10), and as the secondary input (to air temperature) yielded little performance improvement ($r^2 < 0.1$; Online Resource Tables S13, S14).

Climate drivers of $\text{NEP}_{\text{daytime}}$ and $\text{NEP}_{\text{nighttime}}$ for phenologically relevant seasonal periods

Based on benchmarks, seasonal drivers explained more variation in NEP during some periods than others. All drivers explained 76% of variation in $\text{NEP}_{\text{daytime}}$ during snowmelt (Fig. 3a, Online Resource Table S9), but explained less variation as the seasons progressed (monsoon period benchmark $r^2 = 0.58$; Fig. 3a, Online Resource Table S9). By the post-monsoon period this trend reversed, and a high percentage of $\text{NEP}_{\text{daytime}}$ was again explained by all drivers (benchmark $r^2 = 0.80$; Fig. 3a, Online Resource Table S9). $\text{NEP}_{\text{nighttime}}$ followed a similar seasonal pattern of decreased total explainable variability during the monsoon (Fig. 3b, Online Resource Table S10).

ANNs trained on single climate variables for data grouped by seasonal period showed the best performance with temperature variables for most periods during both the daytime and nighttime. Yet there were two seasonal periods for which a temperature variable was not the significantly most relevant primary driver of NEP during the daytime: the snowmelt period and the monsoon period. During the snowmelt period, soil moisture was the significantly most relevant primary driver for $\text{NEP}_{\text{daytime}}$ (Fig. 3, Online Resource Table S9). During the monsoon period for $\text{NEP}_{\text{daytime}}$, no driver(s) emerged as significantly most relevant, but VPD explained more variation than air temperature (Fig. 3, Online Resource Table S9). The significantly most relevant secondary drivers of $\text{NEP}_{\text{daytime}}$ that emerged were PAR and net radiation (for monsoon), and soil moisture (for winter; Online Resource Table S13). For $\text{NEP}_{\text{nighttime}}$, soil temperature was the significantly most relevant driver for all periods except snowmelt, when air temperature was significantly most relevant, and pre-monsoon, when temperature variables were both most relevant (Online Resource Table S10). The relevance of secondary drivers of $\text{NEP}_{\text{nighttime}}$ was similar within most seasons, but during winter, air temperature, soil moisture, and SWE were most relevant (Online Resource Table S14). Also similar to the result for ANNs trained on all data, ANNs trained with wind speed, wind direction, u_*, or precipitation as the sole input (primary driver) for $\text{NEP}_{\text{daytime}}$ or $\text{NEP}_{\text{nighttime}}$ data grouped by seasonal period yielded low performance ($r^2 < 0.1$; Online Resource Table S9-10). As a secondary input to the most relevant primary driver for each period, these same variables produced little performance improvement (difference in $r^2 < 0.1$) for $\text{NEP}_{\text{nighttime}}$ and $\text{NEP}_{\text{daytime}}$ of all seasonal periods (Online Resource Table S13, S14).

We focused on temperature variables (soil or air temperature) for our examination of NEP responses because these were the most relevant drivers for all $\text{NEP}_{\text{daytime}}$ and $\text{NEP}_{\text{nighttime}}$ data (Fig. 3), many seasonal periods (Fig. 3), and most individual years (Online Resource Tables S17, S18). The response of $\text{NEP}_{\text{daytime}}$ to temperature resembled a physiological thermal performance curve, with a positive NEP response at low temperatures, and negative NEP response at higher temperatures (Figs. 5a, 6a). $\text{NEP}_{\text{nighttime}}$ responded negatively to air temperature and soil temperature (Figs. 5b, 6b).

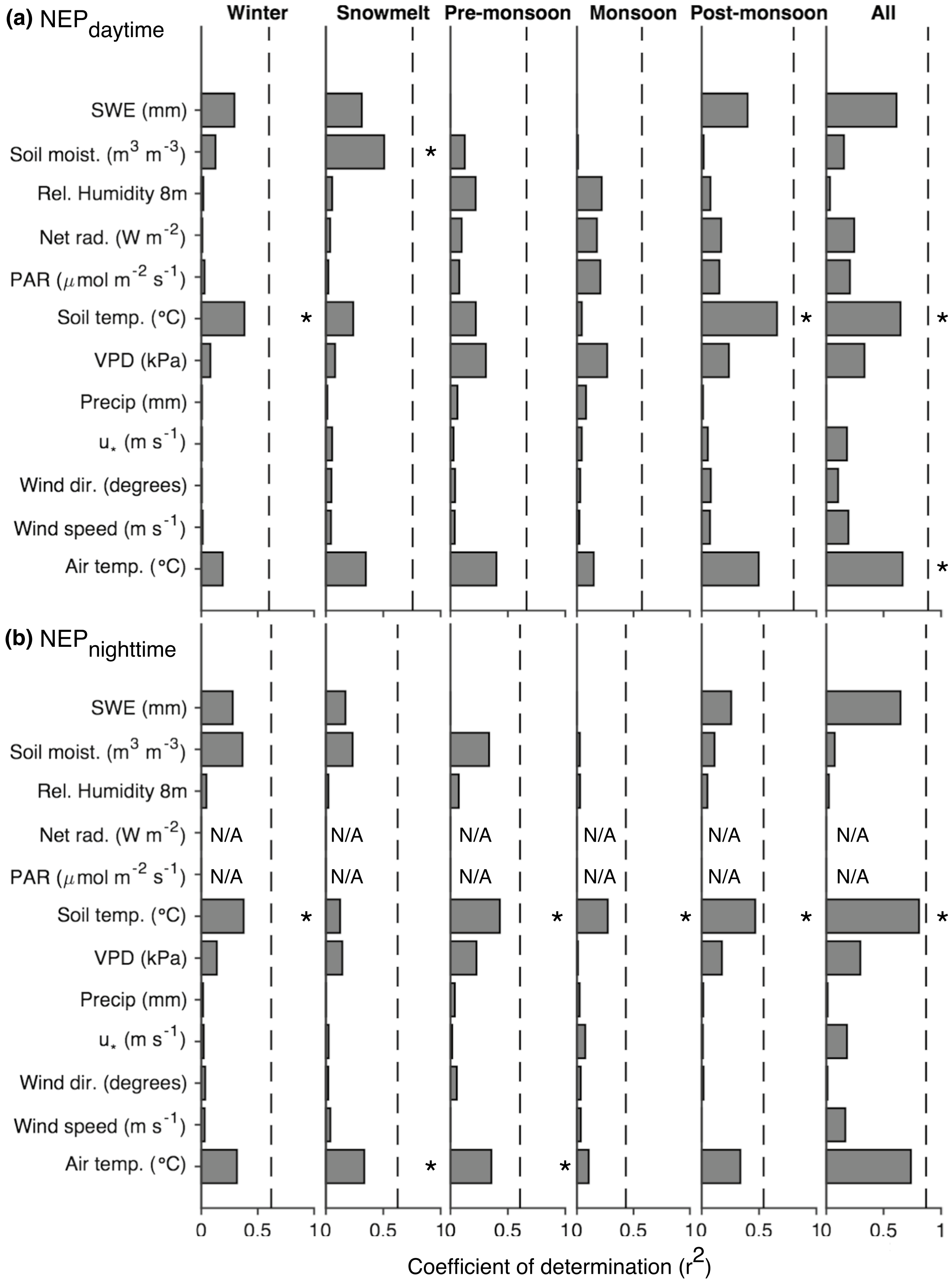

Fig. 3 Relevance of candidate drivers for seasonal data groupings (winter, snowmelt, pre-monsoon, monsoon, and post-monsoon) as well as all data for **a** daytime and **b** nighttime net ecosystem productivity (NEP). The bars indicate the performance (coefficient of determination) of an ANN with each candidate driver as a single input. For each data grouping, significantly highest relevance primary drivers are denoted with *asterisks*, and *vertical dotted line* indicates the benchmark ANN performance. The soil moisture time series started in 2002, so benchmark performances do not include soil moisture as an input, and the soil moisture row does not include 1999–2001. Abbreviations are used for snow water equivalent (SWE), moisture (moist.), relative (rel.), radiation (rad.), direction (dir.), temperature (temp.), incoming photosynthetically active radiation (PAR), vapor pressure deficit (VPD), and precipitation (precip)

Climate drivers of evapotranspiration

For ET, the benchmark r^2 values showed that, when combined, all daytime candidate drivers and nighttime candidate drivers explained 78 and 43% of the total variance in $ET_{daytime}$ and $ET_{nighttime}$, respectively (Fig. 4, Online Resource Tables S11 and S12). For $ET_{daytime}$, air temperature and soil temperature were significantly highest relevance drivers of all data (Fig. 4a, Online Resource Table S11), and air temperature, soil temperature, or both emerged as significantly most relevant primary driver(s) of $ET_{daytime}$ for many individual years, sometimes tied with SWE (Online Resource Table S19). For all $ET_{nighttime}$ data, no primary drivers emerged as significantly most relevant because performance was similar across more than four drivers, but u_* and wind speed were notably relevant (Online Resource Table S12), and for data grouped by each individual year, u_* and wind speed were the most relevant primary drivers of 2004 (Online Resource Table S20). The secondary drivers of $ET_{daytime}$ produced little improvement in performance across years (Online Resource Table S23).

Climate drivers of daytime and nighttime evapotranspiration for phenologically relevant seasonal periods

Like the NEP result, benchmarks varied by seasonal periods for ET with the lowest amount of variance explained in the post-monsoon for $ET_{daytime}$ and pre-monsoon for $ET_{nighttime}$ (Fig. 4, Online Resource Tables S11 and S12). For $ET_{nighttime}$ the candidate drivers explained a low amount of variation (pre-monsoon benchmark $r^2 = 0.36$), a decrease in 0.19 from the snowmelt period when ANNs performed best (Online Resource Table S12).

For all periods, the most relevant primary driver differed between $ET_{daytime}$ and $ET_{nighttime}$. For $ET_{daytime}$, the ANNs with humidity and VPD (winter period), and net radiation and PAR (monsoon period) variables as inputs showed the best performance (Fig. 4, Online Resource material S11). By contrast, for $ET_{nighttime}$, no significantly highest relevance drivers emerged, but wind speed and friction velocity (u_*) showed relatively high relevance as primary drivers for all periods, and VPD and relative humidity were high relevance during the monsoon (Fig. 4, Online Resource Table S12). Relatively high relevance $ET_{daytime}$ secondary drivers varied through time, from radiation variables (winter and snowmelt), to wind direction (pre-monsoon), to soil moisture (monsoon), and VPD (post-monsoon) but none were significantly highest secondary drivers for any seasonal period (Online Resource Table S15). For $ET_{nighttime}$ significantly highest relevance secondary drivers were relative humidity during the winter, and wind speed during the monsoon (Online Resource Table S16).

Examining the responses of $ET_{daytime}$ and $ET_{nighttime}$ to their most relevant primary drivers revealed differences between daytime and nighttime sensitivities across diurnal cycles and seasons. For all seasonal periods, ET in general showed little sensitivity to variation in air temperature when temperatures were subzero (Fig. 7a, b). $ET_{daytime}$, but not $ET_{nighttime}$ was more responsive to temperature during growing season (non-winter) seasonal periods (Fig. 7a, b).

Discussion and synthesis

Drivers of ecosystem metabolism considering all seasons together

Using an inductive approach focused on daily time-steps to evaluate seasonal patterns of ecosystem–climate relationships, we found that temperature was a predominant driver of NEP, inclusive of both daytime and nighttime periods of CO_2 exchange. Air temperature and soil temperature were the most relevant drivers of mean $NEP_{daytime}$, when data for all parts of the growing season were considered together (Fig. 3a, Online Resource Table S9), and soil temperature was the most relevant driver of mean $NEP_{nighttime}$ for all data (Fig. 3b, Online Resource Table S10). Mean $NEP_{daytime}$ responded positively to warming temperatures until daytime-average temperature surpassed about 12.5 °C, reached a peak, and responded negatively as average daily temperature approaches 20 °C (Fig. 5a). Extrapolations from nighttime respiration to daytime respiration are imperfect (Goulden et al. 1996; Speckman et al. 2014), and may exclude the effect of light-inhibition on leaf respiration (Wehr et al. 2016). That said, high respiration rates in warm temperatures likely contributed to the reversal in the response of $NEP_{daytime}$ to air temperature at high values (Fig. 5b), in addition to shifting photosynthetic temperature optima. $NEP_{nighttime}$ decreased with soil temperature (Fig. 6b), as expected given the exponentially positive responses of soil respiration, driven by high sensitivities of microbial respiration and microbial biomass to increasing temperature in this forest ecosystem (Monson et al. 2006a, b; Schmidt et al. 2009).

In a previous study of this same ecosystem, Huxman et al. (2003) used path analysis, a deductive statistical framework, to construct a model of correlations between seasonal climate and NEP and, like our study, showed that temperature is a dominant driver of seasonal dynamics in NEP. The observed effect of temperature was particularly relevant to our study because it also revealed a switch in ecosystem sensitivity to temperature during the growing season—from a positive effect (higher temperature caused higher NEP)

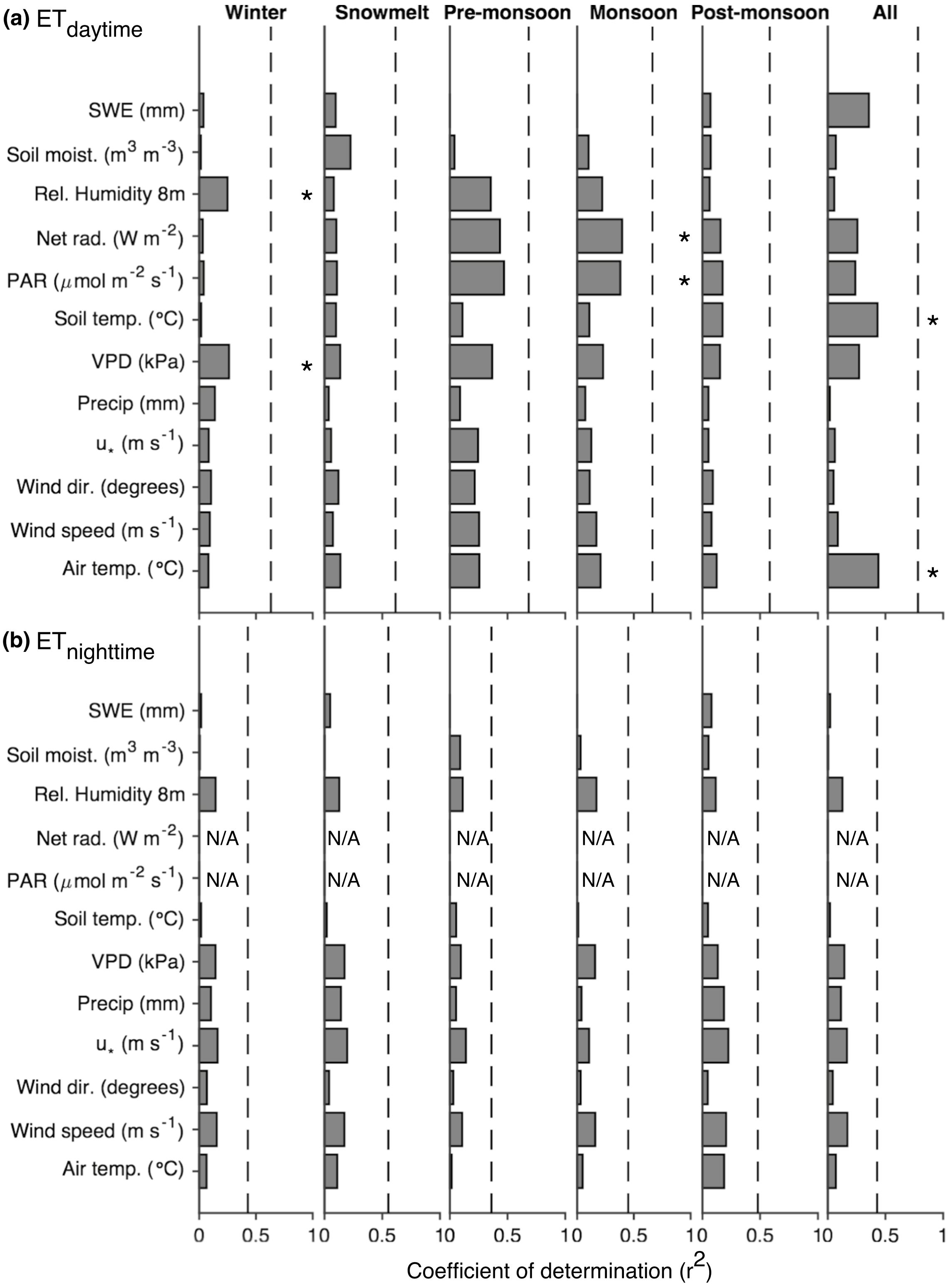

Fig. 4 Relevance of candidate drivers for seasonal data groupings (winter, snowmelt, pre-monsoon, monsoon, and post-monsoon) as well as all data for **a** daytime and **b** nighttime evapotranspiration (ET). The *bars* indicate the performance (coefficient of determination) of an ANN with each candidate driver as a single input. Significantly highest relevance primary drivers denoted with *asterisks*. The *vertical dotted line* indicates the benchmark performance from all drivers. Note that the soil moisture time series started in 2002, thus benchmark values shown here do not include soil moisture as an input, and the soil moisture row does not include 1999–2001. See Fig. 3 legend for abbreviations

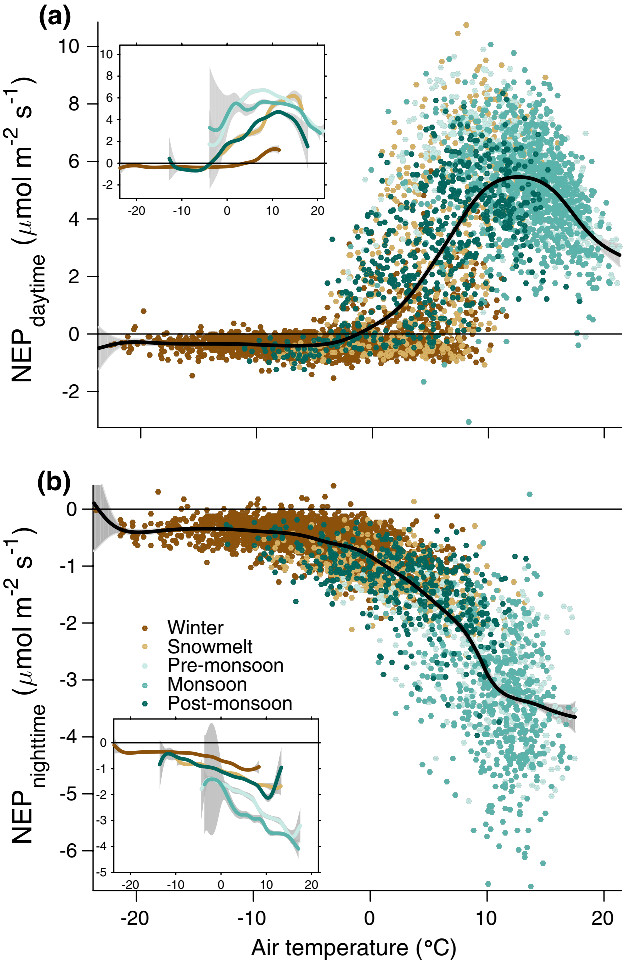

Fig. 5 Response of **a** daytime and **b** nighttime net ecosystem productivity (NEP) to air temperature. The points (*colored* by period) indicate observations (daytime or nighttime NEP means). The mean (*black line*) and standard deviation (*grey band*) from 100 ANNs show the modeled response and uncertainty. *Insets* show mean response (*colored lines*) and standard deviation (*grey bands*) of **a** daytime and **b** nighttime NEP to air temperature during specific seasonal periods. Color version of this figure is available online

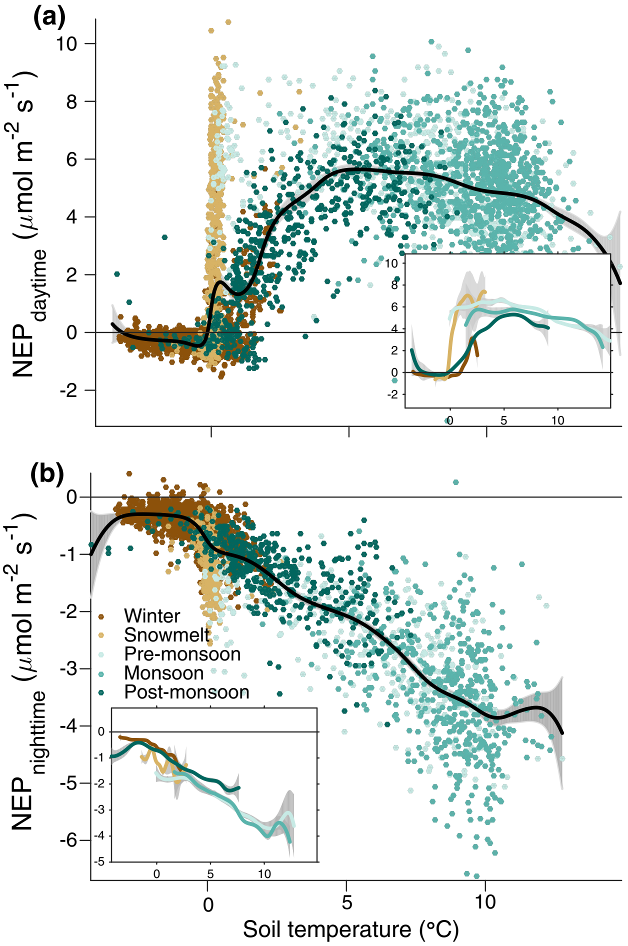

Fig. 6 Response of **a** daytime and **b** nighttime net ecosystem productivity (NEP) to soil temperature. The points (*colored* by period) indicate observations (daytime or nighttime NEP means). The mean (*black line*) and standard deviation (*grey band*) from 100 ANNs show the modeled response and uncertainty. Insets show mean response (*colored lines*) and standard deviation (*grey bands*) of **a** daytime and **b** nighttime NEP to soil temperature during specific seasonal periods. Color version of this figure is available online

during spring to a negative effect (higher temperature caused lower NEP) during mid-summer. The cause of the seasonal switch in temperature sensitivity, as reported in Huxman et al. (2003), was that ecosystem respiration rates were low during the spring because the presence of the snow pack kept soil temperatures and associated soil respiration rates relatively low, but increasing air temperatures stimulated gross ecosystem productivity, thus enhancing rates of NEP. During mid-summer, however, soil respiration rates for snow-free soil were assumed to increase due to direct thermal stimulation of the heterotrophic component (see Scott-Denton et al. 2003). These causes are also likely to be driving the seasonal switch in temperature sensitivity of NEP that we observed. It is informative that the simple path analysis deployed by Huxman et al. (2003) detected the seasonal reversal in ecosystem temperature response given that it was conditioned on only two years of data, compared to the fifteen years of data in this study. One conclusion that we have drawn from the comparison of these two studies is that it is possible to detect dominant seasonal drivers with a relatively short time-series span. The response of this subalpine system to temperature is sufficiently strong and consistent to emerge from only two years of study and within the scope of a deductive framework conditioned on prior knowledge of processes.

Our analysis, however, carried the power to situate the role of temperature within a broader context of other climate drivers. Our results showed that snow-water equivalent (SWE) as a primary driver yielded a coefficient of determination almost as high as that for temperature regarding NEP$_{daytime}$ and NEP$_{nighttime}$ (Fig. 3; Online Resource

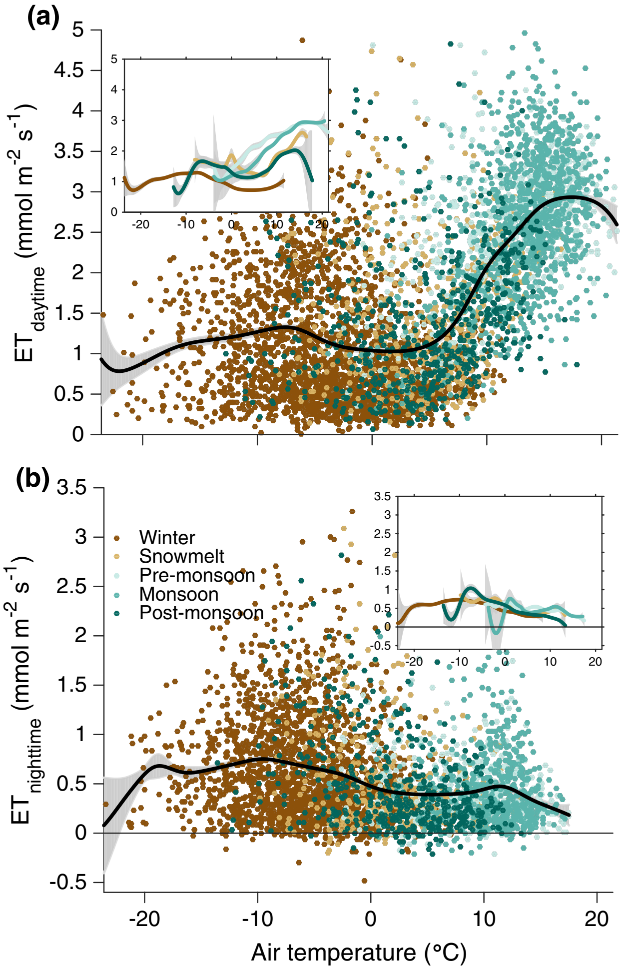

Fig. 7 Response of **a** daytime and **b** nighttime evapotranspiration (ET) to air temperature. The points (*colored* by period) indicate observations (daytime or nighttime ET means). The mean (*black line*) and standard deviation (*grey band*) from 100 ANNs show the modeled response and uncertainty. Insets show mean response (*colored lines*) and standard deviation (*grey bands*) of **a** daytime and **b** nighttime ET to air temperature during specific seasonal periods. Color version of this figure is available online

Tables S9 and S10). SWE and soil temperature are closely related with snow melting around 0 °C (Online Resource Fig. S1 and S2). We thus infer that temperature controls NEP not only through its interaction with photosynthetic optima and respiration rates during the non-winter periods, but also as an annual control over the physical state of water. The temperature and water effects are intertwined in their seasonal influences on ecosystem carbon metabolism, and whereas they were revealed in our analysis, they were not revealed in the simpler path analysis by Huxman et al. (2003).

One of the major contributions of our study was the power we had to reveal the nuanced controls of ET, which have generally been considered in less detail, compared to NEP, in past analyses of tower flux data. The ANN analysis revealed evidence that Niwot Ridge experiences an annual cycle in the predominance of demand (governed by atmospheric factors) versus supply (governed by water availability; Federer 1982) as limitations on daytime transpiration. The most relevant $\mathrm{ET}_{\mathrm{daytime}}$ driver, as identified in the ANN, shifted from soil moisture (suggesting supply limitation) for the snowmelt period, towards net radiation and PAR for the pre-monsoon through post-monsoon periods (Fig. 4a, Online Resource Table S11). Net radiation should increase evaporative demand (via increased energy to drive latent heat flux), but the photosynthetically active portion of the light spectrum can also affect supply to the atmosphere (via stomatal responses). Given that pre-monsoon $\mathrm{ET}_{\mathrm{daytime}}$, and to some extent monsoon $\mathrm{ET}_{\mathrm{daytime}}$, remained high at high VPD and low relative humidity, and that $\mathrm{ET}_{\mathrm{daytime}}$ was more sensitive to PAR during these same periods (Online Resource Figs. S10, S13 and S14), we hypothesize that during this part of the season, stomata act to maximize carbon gain, rather than minimize water loss. Thus, overall ET is likely limited by demand early in the growing season. During the post-monsoon period the ecosystem appeared to shift back to greater supply limitation, as $\mathrm{ET}_{\mathrm{daytime}}$ showed frequent declines at high VPD and showed little sensitivity to PAR (Online Resource Figs. S13 and S14). This seasonal shift from demand-limited to supply-limited ET is consistent with findings from a watershed model study for a northern Rocky Mountain site that experiences similar annual rainfall as that for Niwot Ridge (Emanuel et al. 2010).

$\mathrm{ET}_{\mathrm{nighttime}}$, which we expect to be driven by temperature, relative humidity, and wind speed (based on theory expressed in the Penman–Monteith and Clausius–Clayperon relations; Monson and Baldocchi 2014) was determined in large part by u_* or wind speed (Fig. 4b, Online Resource Table S12). Given that u_* is calculated from wind speed, and that these two variables are correlated (Online Resource Fig. S1 and S2), it is difficult to differentiate between them as independent candidate drivers. Nonetheless, this finding suggests several possibilities that warrant future investigation. Of the components of ET (evaporation and transpiration), evaporation is generally expected to dominate $\mathrm{ET}_{\mathrm{nighttime}}$, so our results suggest that wind speed or u_* may drive evaporation. Yet wind speed also decreases leaf surface resistance, providing a possible mechanism for impacting $\mathrm{ET}_{\mathrm{nighttime}}$ in the presence of positive nighttime transpiration (Dawson et al. 2007), which has been reported as relatively frequent in Engelmann spruce and subalpine fir, two of the dominant trees in the Niwot Ridge forest (Turnipseed et al. 2009). Any seasonality of a possible interaction between wind speed and transpiration could be difficult to detect because $\mathrm{ET}_{\mathrm{nighttime}}$ is slightly higher in the winter (Fig. 2f) when trees are dormant and sublimation dominates (Burns et al. 2015). The significance of u_* as a control over ET, independent of windspeed, might occur if canopy roughness differs depending on wind direction, thus affecting wind shear differentially. We did not partition u_* as a function of windspeed in the current analysis, and we have not pursued the potential for canopy roughness and shear interactions to control ET independent of windspeed. However, we note the potential for these interactions here as justification for not combining u_* and windspeed as a single driving variable in the analysis.

Another unexpected result was that wet precipitation (rain) did not show high relevance as a driver of $\mathrm{NEP}_{\mathrm{daytime}}$ or $\mathrm{NEP}_{\mathrm{nighttime}}$ flux for the continuous dataset (all data) or any seasonal period (Online Resource Tables S9-S10), and for ET, precipitation never explained more than 19% of the total ET variability for any seasonal period, daytime or nighttime (Online Resource Tables S11–S12). If the effects of precipitation on NEP or ET lag after the precipitation events by more than ~12 h, then our analysis would not have been expected to detect the relationship. Burns et al. (2015) found enhanced mid-day ET on dry days following a wet day during the warm season (May/June through September), so it is possible that we indeed missed this relation with respect to ET in our study due to a lag effect. Despite its lack of significance as a direct driver of NEP, we hypothesize the existence of indirect effects through other climate variables that did emerge as relevant drivers such as relative humidity and VPD. Relative humidity and VPD were relevant secondary drivers of all $\mathrm{NEP}_{\mathrm{daytime}}$ data when the primary driver was air temperature (Online Resource Table S13). Furthermore, soil moisture in the upper soil profile emerged as an important secondary driver of all $\mathrm{NEP}_{\mathrm{daytime}}$ data when the primary driver was soil temperature (Online Resource Table S13). These variables should be affected by rain or the increased cloud cover associated with rain events. It is also important to recognize that the low relevance of wet precipitation from this daytime/nighttime analysis does not signify that wet precipitation is unimportant at other time scales because the controls on NEP and ET vary with time (Barford et al. 2001; Siqueira et al. 2006; Richardson et al. 2007). Short-term (minutes to hours) responses to precipitation may not be captured in this analysis since eddy covariance data during precipitation are gap-filled, and precipitation could have a lagged effect on NEP or ET over several days which also may not be captured in the half-day-averaged time steps examined here. Since meteorology data time-step duration varies across process-based ecosystem models (Siqueira et al. 2006), future ecohydrology studies should examine how temporal resolution (e.g. daytime/nighttime versus half-hour) affects simulated interaction between precipitation, other climate variables, NEP, and ET.

Seasonal partitioning of drivers of ecosystem metabolism

NEP is much less sensitive to temperature during winter than during other periods; the ANN trained on winter daytime data only, showed net carbon loss during this season until mean daytime temperature rose several degrees above 0 °C. Similarly, winter $\mathrm{ET}_{\mathrm{daytime}}$ rates were relatively consistent at approximately 1 mmol $\mathrm{m}^2\ \mathrm{s}^{-1}$, regardless of temperature, but $\mathrm{ET}_{\mathrm{daytime}}$ increased with temperature as winter ended and the snow cover began to melt (Fig. 7a). Unlike daytime, the $\mathrm{NEP}_{\mathrm{nighttime}}$ and $\mathrm{ET}_{\mathrm{nighttime}}$ responses to temperature variables during winter were more aligned with those of other periods (Figs. 5b, 6b, 7b). The responses of $\mathrm{NEP}_{\mathrm{nighttime}}$ to soil temperature appeared similar across seasonal periods, and carbon release clearly increased with soil temperature during the winter (Fig. 6b). Together, the daytime and nighttime NEP and ET responses lead us to conclude that during the winter, trees cannot transpire and carry out leaf-level gas exchange, but soil respiration persists. This result aligns with previous studies on winter dynamics at Niwot Ridge that showed an active beneath-snow microbial community (Monson et al. 2006a, b; Lipson et al. 2009; Schmidt et al. 2009).

Previous climate–carbon relations studies at Niwot Ridge, all of which used a shorter span of data and tested explicit hypotheses in a deductive framework, focused on the role of the spring snowpack and the timing of its melt as the primary control over early season rates of CO_2 uptake (Monson et al. 2002, Huxman et al. 2003, Monson et al. 2005, Hu et al. 2010). Evidence was presented to support deep, late-winter snowpacks as a crucial resource allowing the forest to sequester atmospheric CO_2 at relatively high rates early in the growing season. Monson et al. (2005) discovered that trees in this forest can respond to spring snowmelt through rapid upregulation of photosynthetic capacity, and hypothesized that the primary advantage of the evergreen growth habit is to respond quickly to the availability of snowmelt water before the onset of mid-summer drought. Even later in the growing season, the importance of snowmelt water was shown to be important, as hydrogen and oxygen stable isotopes in water extracted from tree stems showed that most NEP in the forest was driven by snowmelt water, not mid-summer rain water (Hu et al. 2010).

Our analysis confirmed that the snowmelt period is indeed an important period controlling rates of atmospheric CO_2 uptake in this forest ecosystem. However, unlike previous studies, we identified soil moisture during the snowmelt period as more important in explaining variance in NEP, than temperature (Fig. 3a), and relative humidity and VPD were identified as the most important secondary drivers (based on the ANNs trained on single climate variables (Online Resource Table S13). From our analysis, we conclude that only after snow melt is completed does air temperature take on a direct role as the primary driver of seasonal dynamics in NEP. Thus, while temperature was identified as the primary determinant of NEP when assessed across all seasons together, it had a subordinate role to soil moisture during the earliest part of the season. There is a critical transition in controls, from soil moisture content to temperature, that occurs as the system emerges from snowmelt.

After the snowpack melt, NEP declines during the 'pre-monsoon' period relative to the late 'snowmelt' period (Fig. 2c). This decline occurs despite evidence that transpiration is less limited by water supply, and trees are actively taking up carbon. Previous studies have shown that increases in soil respiration are a major contributor to this NEP decrease, particularly rhizospheric respiration after trees prime soil with sugar exudates during the snowmelt (Scott-Denton et al. 2006; Weintraub et al. 2007). The ANN results suggest that after snowmelt, warming temperatures and snowpack-derived soil moisture provide favorable conditions for high soil respiration rates. The ANNs trained on pre-monsoon $NEP_{daytime}$ and $NEP_{nighttime}$ showed that temperature variables were the most relevant climatic variables for this period (Figs. 3, 4, Online Resource Tables S9, S10), and nighttimes during the pre-monsoon showed more carbon loss at above-zero soil temperatures than winter or snowmelt periods (Fig. 5b).

Although the monsoon rains in this region are relatively mild (Fig. 2a, b), monsoon rains are expected to play a role in supplying moisture to trees during the summer. However, as discussed above, in our analysis, rain remained of low relevance as a driver of NEP even during the monsoon period (Fig. 3). Also intriguing was our finding that much variation in NEP during the monsoon was unexplained by the climate drivers examined here (benchmark r^2, Figs. 3, 4). The most relevant drivers of $NEP_{daytime}$ and $NEP_{nighttime}$ (VPD and soil temperature, respectively) during the monsoon were still not very relevant (Fig. 3, Online Resource Tables S9, S10). Overall, $NEP_{daytime}$ and $NEP_{nighttime}$ became less explained by all of the climatic drivers as the growing season progressed from snowmelt to pre-monsoon to monsoon. These findings of (1) low precipitation relevance and (2) low total explainable variability suggest that day-to-day variation in NEP during the monsoon period was driven by factors not included in our candidate drivers, at least not at the time scale of this analysis. Deep soil moisture availability was not included as a candidate driver and is a promising explanation; water isotopic signatures suggest most xylem water derives from snowmelt late in the growing season for dominant tree species at this site (Hu et al. 2010). Thus, snowmelt water may buffer the forest from moisture variation during the monsoon.

The post-monsoon period, like that for snowmelt, was revealed as a transition period in which ecosystem metabolism switches, in this case from the upregulated phase of the growing season to the downregulated phase of winter. During this period the forest at Niwot Ridge experiences sub-zero air temperatures. Soil temperature is the most important temperature variable for both daytime and nighttime mean NEP (Fig. 3a, b), and NEP appears more sensitive to soil temperature above 0 °C during both the daytime and nighttime (Fig. 6a, b). $ET_{daytime}$ showed decreasing sensitivity to all primary candidate drivers during the post-monsoon (Fig. 4a, Online Resource Table S11). These results suggest that the freeze–thaw status of the soil controls day-to-day variations in NEP during this period. This contrasts with the snowmelt period, where the high significance of soil moisture during the daytime suggests photosynthesis is limited by water supply rather than controlled directly by soil temperature (Fig. 3a).

Conclusion

Studies that have examined long-term eddy-covariance datasets at individual sites have shown that doing so provides an independent means of corroborating, or challenging, our prior understanding of ecosystem processes. Insight into controls over ecosystem processes can be framed in general terms using the limited span of a flux time series coupled to a deductive analysis framework that tests hypotheses based on prior knowledge. However, an alternative inductive analytical framework of a longer time series offers confidence that such insight is unbiased by prior expectations or a priori assumptions. In this study, we showed that, overall, temperature plays an essential role in controlling $NEP_{daytime}$ and $NEP_{nighttime}$, as well as $ET_{daytime}$, which is consistent with a prior deductive analysis on a limited span of the same observational time series. With the longer time series of our study, and the inductive process we applied, however, we were able to discern much more detail about the interaction of drivers in determining seasonal responses to the climate, and in some cases, reveal the nuances of indirect effects of drivers on ecosystem metabolism. Our analysis has implications for deductive, process-based terrestrial biosphere models that use daytime and nighttime time-steps. Parsimonious process-based models should achieve reasonable model-data agreement when they include one of the most relevant 'primary' and according 'secondary' drivers of the complete daytime or nighttime time series because the ANNs with the two most relevant drivers performed almost as well as ANNs with all candidate drivers (reaching 69–97% of the benchmark performance for all data analyses). However, it is important to recognize that the total explainable variability (benchmark), the relative importance of climate drivers, and the NEP and ET responses to single drivers, all change seasonally, suggesting that phenology and climate variable interactions shift such that NEP and ET sensitivities to climate are dynamic throughout the year. Sophisticated process-based models intended for more complete ecophysiological representation should aim to reproduce these seasonal shifts. Discovering when process-based models fail to produce similar patterns to the ANN could diagnose model structures and parameterizations that need improvement for accurate representation of controls over ecosystem metabolism. Our study demonstrates that there is still much to be learned by applying inductive approaches to long-term data series as a means of understanding interactive mechanisms and synergies that emerge among the many co-varying climate drivers *over time,* thereby confirming or challenging our understanding of the nature of 'ecosystem metabolism'.

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Author contribution statement RKM conceived the study and obtained financial support for the work. LPA performed the artificial neural network analysis and wrote the initial manuscript draft. LPA, TFK, RKM and TEH collaborated to conduct and interpret the synthesis, as well as develop the text of the manuscript. SPB collected and synthesized the Niwot Ridge AmeriFlux data and participated in writing the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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