Quantifying ecological memory in plant and ecosystem processes

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Abstract

The role of time in ecology has a long history of investigation, but ecologists have largely restricted their attention to the influence of concurrent abiotic conditions on rates and magnitudes of important ecological processes. Recently, however, ecologists have improved their understanding of ecological processes by explicitly considering the effects of antecedent conditions. To broadly help in studying the role of time, we evaluate the length, temporal pattern, and strength of memory with respect to the influence of antecedent conditions on current ecological dynamics. We developed the stochastic antecedent modelling (SAM) framework as a flexible analytic approach for evaluating exogenous and endogenous process components of memory in a system of interest. We designed SAM to be useful in revealing novel insights promoting further study, illustrated in four examples with different degrees of complexity and varying time scales: stomatal conductance, soil respiration, ecosystem productivity, and tree growth. Models with antecedent effects explained an additional 18–28% of response variation compared to models without antecedent effects. Moreover, SAM also enabled identification of potential mechanisms that underlie components of memory, thus revealing temporal properties that are not apparent from traditional treatments of ecological time-series data and facilitating new hypothesis generation and additional research.

Keywords

Antecedent conditions, hierarchical Bayesian model, lag effects, legacy effects, net primary production, soil respiration, stomatal conductance, time-series, tree growth, tree rings.

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INTRODUCTION

Temporal phenomena are fundamental to ecology. The growth patterns encoded in tree rings, the timing of flowering and production within a season, and the scheduling of reproduction within an organism's lifespan are examples from early attempts to understand the role of time in ecology. Studies of ecological succession in the early 1900s provide a process-based interpretation of mechanisms underlying some ecological patterns over time and of the importance of antecedent events (Johnson & Miyanishi 2008). More recently, the timing of migration, flowering, and pollination has taken on critical importance given the potential for differences in activity between mutualistic partners within a rapidly changing climate (Visser & Both 2005; Elzinga *et al*. 2007). Assuming consistent relationships between space and time for evaluating ecological phenomena has been useful for tackling scientific challenges in ecology (Levin 1992), but ecological patterns and processes are rarely static (Chave 2013), thus challenging our approaches for addressing the importance of time in our science.

Despite the long history of studying the role of time in ecology, we still lack a solid understanding of the temporal linkages between abiotic events and biotic responses, their interactions, and feedbacks to the environment (e.g. Bardgett *et al*. 2005; Crooks 2005; Resco *et al*. 2009). For example, how do different abiotic events interact over time to drive ecological phenomena? How do ecological patterns and processes respond to perturbations at different time scales? Abiotic resources (e.g. water, nutrients) often are available to organisms in ephemeral pulses, and changes in their timing, duration, and magnitude can lead to significant changes in ecological structure and function (Schwinning & Sala 2004). For example, the effects of multiple precipitation events may

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be additive when the interval between pulses is short, but this effect decreases as the number of between-event dry days increases (Loik *et al.* 2004). In addition, after an extended dry period, the impact of a first pulse may or may not have consequences for the impact of subsequent events; however, we require better knowledge about the mechanisms relating ecological responses to rainfall timing to generate general principles.

Although precipitation, temperature, and other factors affect plant and ecosystem processes at multiple time scales, many analyses tend to assume, at least implicitly, that environmental conditions impact biological processes concurrently. Ecological disturbances, however, are frequently described in terms of time-since-disturbance (e.g. fire, flood, frost, or storm damage). Presumably, we could gain a greater understanding of the timing of many abiotic–biotic relationships with careful consideration of how past perturbations (resource pulses, disturbance, or environmental events) at different scales modify the response of biological processes to a recent event. For example, in semi-arid systems, antecedent temperature and water availability, averaged over several days or weeks, may be more important than current conditions for plant, soil, and ecosystem carbon exchange (Ogle & Reynolds 2002; Cable *et al.* 2008; Shim *et al.* 2009). Precipitation and temperature patterns of past months, seasons, or years can also impact soil respiration (Janssens *et al.* 2001; Fierer *et al.* 2006; Vargas *et al.* 2011), leaf-level gas exchange (Patrick *et al.* 2009), annual tree growth (i.e. ring widths, Fritts 1966; Graumlich 1991; Gagen *et al.* 2004), and ecosystem productivity (Leuning *et al.* 2005; Coops *et al.* 2007; Sala *et al.* 2012; Reichmann *et al.* 2013).

Despite their importance, we lack analytical frameworks for quantifying antecedent conditions and their effects on current processes, thus lending insight into ecological memory. Traditional schemes to evaluate ecological time-series data for drivers of current phenomena are often constrained by short-term experimentation, space-for-time substitutions, or arbitrary designations of the relative importance of past conditions that can introduce researcher bias. Here, we improve our capacity to evaluate the role of the past by developing an analytical framework for simultaneously quantifying the length, temporal patterns, and strength of ecological memory. Such a framework is expected to elicit new experiments to test underlying mechanisms and to improve forecasts of ecological responses to future environmental change by better contextualising the role of time.

ECOLOGICAL MEMORY

Ecological memory has been defined as 'the capacity of past states or experiences to influence present or future responses of the community' (Padisak 1992), and as 'the degree to which an ecological process is shaped by its past modifications of a landscape' (Peterson 2002). Our definition of memory aligns with these definitions, but we explicitly consider three primary components: (1) the *length* of the memory, which quantifies the time period(s) over which antecedent conditions or states affect current processes or states, (2) the *temporal pattern* of the memory, which is characterised by variation in the relative

importance of conditions occurring at different times into the past, including potentially important time lags and (3) the *strength* of the memory, which describes the degree to which antecedent conditions affect the process of interest.

Furthermore, we find it convenient to distinguish between *exogenous* and *endogenous* memory (Bengtsson *et al.* 2003; Lundberg & Moberg 2003; Golinski *et al.* 2008; Schaefer 2009; Barron-Gafford *et al.* 2014). Here, we use exogenous memory to refer to the effects of past external factors (typically environmental or abiotic) on the state of the system, as illustrated by impacts of winter freeze–thaw dynamics on subsequent ecosystem production (Kreyling *et al.* 2010). We use endogenous memory to refer to how past states of the system of interest influence current states of the same system, as in density dependent population growth where the current population growth rate and/or size depends are past population size (Golinski *et al.* 2008). For ecosystem-level processes (e.g. soil organic matter decomposition), the endogenous effects could reflect the influence of past decomposition patterns or other, often biologically mediated, ecosystem feedbacks (e.g. past litter fall rates, or past microbial biomass or activity). Endogenous effects, however, are infrequently explored in plant physiological and ecosystem ecology, which tend to emphasise exogenous factors, but quantification of endogenous memory may lend insight into potentially important biological feedbacks.

Our goal was to evaluate the length, temporal patterns, and strength of memory in plant and ecosystem processes, and to design a flexible quantitative framework that will enable us to do so with different conceptualisations of important biological dynamics. The framework should provide results that are easily interpretable to ecologists while retaining general appli-
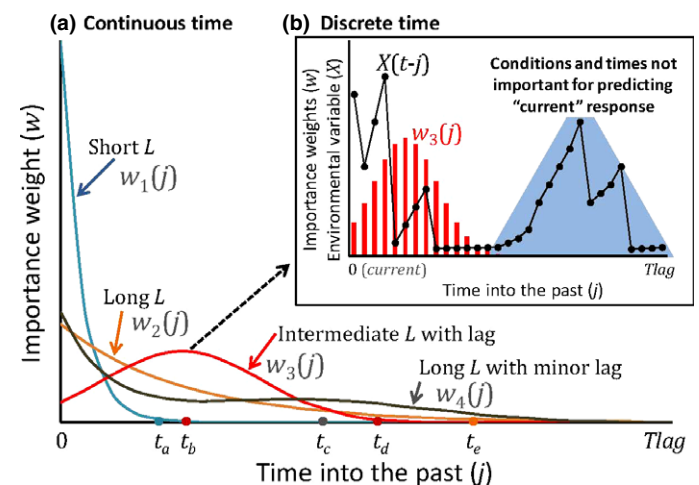
Figure 1 (a) Four hypothetical weight functions for continuous time. The weight function indicated by w_1 has a short memory length (L) such that conditions beyond $L = t_a$ units into the past do not affect the current process. Moreover, w_1 takes on its highest value at $j = 0$, thus, current conditions are most important. The weight function given by w_2 has a long memory ($L \leq t_e$), and current conditions are still most important. The weight function given by w_3 has a medium-length memory ($L \leq t_d$) and a lag (conditions experienced at $j = t_b$ are most important). And w_4 indicates that current conditions are most important, but a minor lag occurs around $j = t_c$. (b) Discretised weights associated with weight function w_3 (red bars); the discretised weights $w_3(j)$ multiply $X(t-j)$ to determine X_{ant} as illustrated in Box 1.

Box 1 Description of the general SAM approach
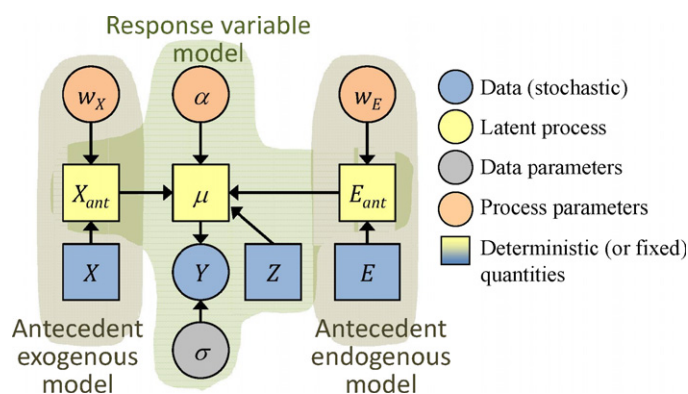
Each node indicates a quantity in the model, and the directed edges connecting nodes indicate conditional relationships (e.g. X_{ant} depends on X and w_X). The quantities can generally be classified as (1) stochastic data (e.g. the response of interest, Y), (2) fixed data (e.g. the observed covariates, X, Z and E), (3) latent or unknown processes such as the predicted response (μ) and the antecedent exogenous (X_{ant}) and endogenous (E_{ant}) covariates, (4) data parameters (e.g. σ) describing observation uncertainty and (5) process parameters (e.g. α) giving rise to the latent processes.

Example data model: For observation or time t, and for some potential transformation of Y, $g(Y)$, including $g(Y) = Y$, we might assume:

$$g(Y(t)) \sim Normal(\mu(t), \sigma)$$

Note that we are not restricted to the normal distribution.

Example process model for μ: The model for μ has the general form:

$$\mu(t) = f(X_{ant}(t), E_{ant}(t), Z(t), \alpha) + \varepsilon_t$$

Where f is a function to be determined on a case-by-case basis, and ε represents additional sources of uncertainty (e.g. random effects that may be indexed by t or some other indexing variable, such as location, individual, etc.); for simplicity, we did not include ε in the above graphical model. A vector of parameters (α) describes the effects of X_{ant}, E_{ant} and Z on the response of interest (Y or μ).

Example process model for X_{ant} and E_{ant}: For time period j into the past ($j = 0$ = current time):

$$X_{ant}(t) = \sum_{j=0}^{Tlag} X(t-j) \cdot w_X(j) \qquad E_{ant}(t) = \sum_{j=0}^{Tlag} E(t-j) \cdot w_E(j)$$

Example priors: For the weight vectors (w) and element k in the α vector:

$$w_X(1 : (Tlag + 1)), w_E(1 : (Tlag + 1)) \sim Dirichlet(1, 1, \ldots, 1),$$
$$\alpha_k \sim Normal(0, S), \sigma \sim Uniform(0, A)$$

Values of S and A are typically chosen to achieve relatively non-informative priors, and the normal and uniform priors could be exchanged for other distributions that may be more appropriate in particular cases.

cability. Here, we present a stochastic antecedent modelling (SAM) framework and apply it to four different case studies to illustrate how the framework can be used to reveal memory characteristics for processes spanning a range of time scales and system complexities: stomatal conductance, soil respiration, ecosystem annual net primary production, and annual tree growth. We use these examples to highlight issues surrounding five primary questions: (1) Does memory matter? (2) What are the temporal characteristics of memory? (3) What time scales are important for quantifying memory? (4) What

features underlie memory? (5) What mechanisms govern memory? We end with a discussion about potential considerations and extensions of the SAM framework beyond the illustrative examples provided in the current treatment.

THE STOCHASTIC ANTECEDENT MODELLING FRAMEWORK

Let $Y(t)$ represent an observed value of an ecological response of interest (e.g. population size, photosynthetic rate, plant bio-

mass) measured at time t. We characterise the variability of $Y(t)$ about its mean (or latent process), $\mu(t)$, with a probability distribution, which we refer to as the 'data model' (see Box 1). Next, we specify a model for $\mu(t)$ (Box 1) that incorporates the effects of antecedent exogenous (X_{ant}; e.g. antecedent soil water, temperature, precipitation), antecedent endogenous [E_{ant}; e.g. past values of Y or its latent value (μ)] and current conditions (Z). The effects of these variables on the current process are captured by the process parameters (e.g. α, a vector of effects parameters), and the magnitude and significance of the antecedent effects (components of α) characterise the overall *strength* of memory.

We define a stochastic model for each antecedent variable. A simple model for X_{ant} or E_{ant} sums over past conditions, weighted by their relative importance (w) (Fig. 1; Box 1). Unlike previous approaches (e.g. Ogle & Reynolds 2002; Leuning *et al.* 2005; Fierer *et al.* 2006; Cable *et al.* 2008), we do not arbitrarily compute X_{ant} or E_{ant} by assuming fixed values for w (e.g. such as computing the average of the past values over an arbitrarily chosen time period). For each time step j into the past, SAM allows data on Y to inform the *unknown* relative importance, $w(j)$'s, of past exogenous, $X(t-j)$, or endogenous, $E(t-j)$, variables for predicting the response at time t (Box 1). An important aspect of the model(s) for X_{ant} and E_{ant} is the specification of the time scales associated with computing the $w(j)$'s, including determining the number of past time periods to sum over (*Tlag*, Box 1), and the size of the time step j (e.g. every 6 h, daily, weekly, etc.). We describe potential strategies to addressing these issues in Appendix S1.

The *temporal pattern* of the memory is revealed by variation in the $w(j)$'s, and comparably high values for particular $w(j)$'s indicate potential lag times (e.g. for daily time steps, a high value of $w(4)$ would indicate a 4-day lag). The *length* of the memory describes the length of time over which past conditions significantly influence the current process. For example, the memory *length* (L) may be defined as the past time for which the cumulative weights achieve some specified threshold (c) that is 'close' to one, such that the solution for L satisfies $\sum_{j=0}^{L} w(j) = c$. For example, for daily time steps, if $L = 10$ (say, for $c = 0.90$), then this indicates a memory of length 10 days such that conditions occurring more than 10 days ago do not appreciably ($< 10\%$ chance) affect the current process of interest.

We implement SAM in a Bayesian framework because of its ability to accommodate the stochastic data model, the stochastic antecedent model, the non-linear model for μ that emerges by making X_{ant} and/or E_{ant} stochastic and required constraints on the w's; we refer readers to Gelman *et al.* (2004) and Ogle & Barber (2008) for a more thorough description of the Bayesian approach. Our interpretation of the w's as the relative importance of past conditions requires that each be between 0 and 1 and that all sum to 1. Thus, in the Bayesian context, we chose an appropriate prior (e.g. Dirichlet distribution, Gelman *et al.* 2004) that obeys these constraints (Box 1).

## EVALUATING ECOLOGICAL MEMORY WITH THE SAM FRAMEWORK

We present four case studies to illustrate our SAM framework. The first is based on annual aboveground net primary productivity (ANPP, g m^{-2} year^{-1}) of a shortgrass steppe ecosystem in northern Colorado; ANPP data summaries (sample means) were extracted from the literature (Lauenroth & Sala 1992). The second involves tree-ring widths (r, mm/year), an index of annual tree productivity, of *Pinus edulis* (pinyon pine) growing near Montrose, Colorado. The original r data were downloaded from the International Tree-Ring Data Bank (ITRDB 2007), and were contributed by Woodhouse *et al.* (2006). The third uses original data on soil respiration rates (R_s, µmol CO$_2$ m^{-2} s^{-1}) in two microhabitats (under shrubs vs. bunchgrasses) occurring in the Sonoran Desert near Tucson, Arizona (see Barron-Gafford *et al.* 2011, 2014). The fourth focuses on leaf-level stomatal conductance (g_s, mol H$_2$O m^{-2} s^{-1}) of a common desert shrub (*Larrea tridentata*, creosotebush) growing in the Chihuahuan Desert in southern New Mexico (see Ogle & Reynolds 2002).

These case studies were chosen because they represent processes operating at different biological, temporal, and/or spatial scales, as well as different complexities of endogenous and exogenous processes. The ANPP and r examples represent relatively long time scales (yearly) and the R_s and g_s examples represent short time scales (instantaneous, sub-daily rates). We use the ANPP case study to illustrate a simple application of the SAM framework, and the associated model code is provided in Appendix S2. The ANPP and r case studies are used to demonstrate nested memory time scales, and the r example also allows us to evaluate memory properties at different levels of organisation (e.g. individuals vs. populations). The g_s example illustrates how different memory components may operate at different, non-nested time scales (e.g. sub-daily to weekly). The R_s and r case studies both provide an evaluation of endogenous and exogenous memory, and the R_s example also explicitly evaluates the effects of current and antecedent factors, and their interactions.

Descriptions of the data and processes associated with each case study and the associated components comprising the Bayesian SAM framework are highlighted in Box 2. For the antecedent importance weights (w), it seems natural to us to choose monthly and annual time steps for the annual productivity variables (r and ANPP), and sub-hourly, hourly, and/or daily time steps for the fast (sub-daily) time-scale variables (g_s and R_s). The basic structure of the process model for μ in the g_s example is motivated by the model described in Ogle & Reynolds (2002), but we made significant modifications to include the antecedent variables and their effects. The model for R_s is described in detail in Barron-Gafford *et al.* (2014). The models developed for the ANPP and r case studies have not been previously described, but were motivated by empirical descriptions of the potential importance of past climate conditions (Fritts 1966; Graumlich 1991; Lauenroth & Sala 1992; Druckenbrod 2005; Sherry *et al.* 2008). In each case study, we opted for relatively simple models that are easy to interpret, motivated by the original publications, and that captured a significant amount of variation in the response variable (e.g. Table 1). Other, potentially better models could be applied, but a comprehensive examination of different models is beyond the scope of this study. Importantly, each case study and its associated SAM formulation offer unique attri-

Box 2 Summary of four different case studies spanning a diversity of processes and time scales. The models follow the framework outlined in Box 1, with modifications specific to each case study (see Box 1 for a description of the graphical model components).
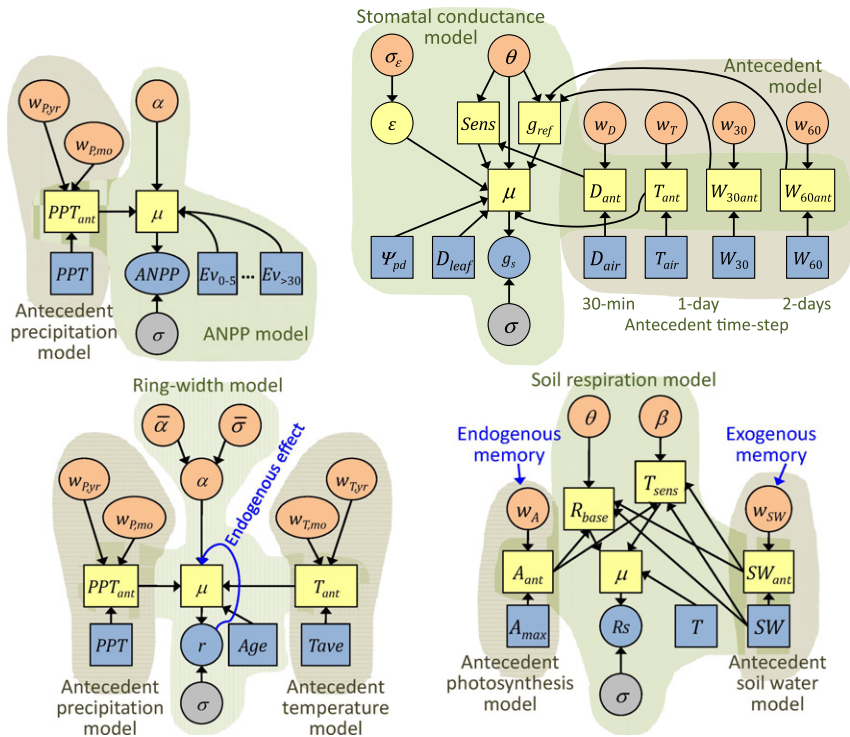
Data and data models: The response variables are $ANPP$ (annual net primary productivity), g_s (stomatal conductance), r (annual ring width) and R_s (soil respiration rate). The exogenous covariates are PPT (monthly precipitation), $Tave$ (mean monthly temperature), Ev_{0-5}, Ev_{5-15}, Ev_{15-30} and $Ev_{>30}$ (amount of annual precipitation received as 0–5, 5–15, 15–30 and > 30 mm events respectively), Ψ_{pd} (pre-dawn leaf water potential), D_{leaf} (leaf-to-air vapour pressure difference), D_{air} (atmospheric vapour pressure deficit), T_{air} (air temperature), T (soil temperature) and SW, W_{30}, and W_{60} (soil water content from 0–12, 0–30 and 30–60 cm respectively). The endogenous covariates are Age (tree age) and A_{max} (light-saturated photosynthesis). For $Y = ANPP$, $\log(r)$, g_s or $\log(R_s)$, year t ($ANPP$ and r) or observation time t (g_s and R_s) and tree core c (for r):

$$Y(t) \sim Normal\big(\mu(t), \sigma^2\big) \quad \text{or} \quad Y(t, c) \sim Normal\big(\mu(t, c), \sigma^2\big)$$

Process models for predicted response (μ): The antecedent exogenous variables corresponding to PPT, $Tave$, D_{air}, T_{air}, SW, W_{30} and W_{60} are represented by PPT_{ant}, T_{ant}, D_{ant}, T_{ant}, SW_{ant}, W_{30ant} and W_{60ant} respectively; A_{ant} is antecedent A_{max} (endogenous). The predicted response is denoted by μ, and quantities defining μ include the sensitivity of g_s to changes in D_{leaf} ($Sens$), reference g_s at $D_{leaf} = 1$ kPa (g_{ref}), base-line R_s at a specific reference T (R_{base}), and the temperature sensitivity of R_s (T_{sens}). The process models for μ are unique to each case study, but all incorporate the effects of antecedent variables:

ANPP model:

$$\mu(t) = \alpha_0 + \alpha_1 \cdot Ev_{0-5}(t) + \alpha_2 \cdot Ev_{5-15}(t) + \alpha_3 \cdot Ev_{15-30}(t) + \alpha_4 \cdot Ev_{>30}(t) + \alpha_5 \cdot PPT_{ant}(t)$$

Ring-width model:

$$\mu(t, c) = \alpha_0(c) + \alpha_1(c) \cdot Age(t, c) + \alpha_2(c) \cdot PPT_{ant}(t) + \alpha_3(c) \cdot T_{ant}(t) + \alpha_4(c) \cdot PPT_{ant}(t) \cdot T_{ant}(t) + \alpha_5(c) \cdot r(t-1, c)$$

Soil respiration model: For $Z = \log(R_{base})$ with $\alpha = \theta$ or $Z = T_{sens}$ with $\alpha = \beta$, and $f(T)$ is a non-linear function of T:

$$\mu(t) = \log(R_{base}(t)) + T_{sens}(t) \cdot f(T(t))$$
$$Z(t) = \alpha_0 + \alpha_1 \cdot A_{ant}(t) + \alpha_2 \cdot SW_{ant}(t) + \alpha_3 \cdot SW(t) + \alpha_4 \cdot SW_{ant}(t) \cdot SW(t)$$

Stomatal conductance model: Where f_S and f_g are non-linear functions of their corresponding variables (current and antecedent covariates) and parameters (θ):

Box 2 (Continued)

$$\mu(t) = g_{ref}(t) + Sens(t) \cdot D_{leaf}(t)$$

$$Sens(t) = f_S\big(\Psi_{pd}(t), D_{ant}(t), T_{ant}(t), \theta\big) \quad g_{ref}(t) = f_g\big(\Psi_{pd}(t), T_{ant}(t), W_{30ant}(t), W_{60ant}(t), \theta\big)$$

Process models for antecedent variables: The antecedent variables are defined similarly in all four examples, though, the time scale over which each is computed may differ:

Climate variables (for ANPP and r): For $X = PPT$ or $Tave$ (P or T subscript on w), $X_{ant} = PPT_{ant}$ or T_{ant}, year y into the past, and month m:

$$X_{ant}(t) = \sum_{y=0}^{4} \sum_{m=1}^{12} X(t-y, m) \cdot w_{X,mo}(m|y) \cdot w_{X,yr}(y)$$

$w_{X,mo}(m|y)$ is the relative importance of X occurring in month m conditional on year y.

Other variables (for g_s and R_s): For $X = A_{max}$, D_{air}, T_{air}, SW, W_{30} or W_{60} (with related subscripting for w), $X_{ant} = A_{ant}$, D_{ant}, T_{ant}, SW_{ant}, W_{30ant} or W_{60ant}, and time period j into the past:

$$X_{ant}(t) = \sum_{j=\tau}^{Tlag} X(t-j) \cdot w_X(j)$$

$\tau = 1$ for SW for R_s such that current SW is not included in SW_{ant} since it explicitly occurs in the μ model for R_s; $\tau = 0$ for all other variables. $Tlag$=5 days for A_{ant} and SW_{ant}, 7 days for T_{ant} and W_{30ant}, 7 two-day blocks for W_{60ant} and 6 half-hour blocks for D_{ant}.

Parameters and prior models: Variability in the observation errors is described by σ; α is a vector of coefficients describing the effects of the exogenous and endogenous covariates on μ, where the core-level α's in the r example vary around overall (mean) effects ($\bar{\alpha}$), and $\bar{\sigma}$ describes variability among cores. Similarly, θ and β are vectors describing the effects of the covariates on the latent components giving rise to μ. The w's are the weights describing the relative importance of the different antecedent covariates occurring at different times into the past. The prior models are similar across all four examples. Let k denote an element of each α, $\bar{\alpha}$, $\bar{\sigma}$, θ, and β vector, then:

$$w_{mo}(1:12|y), w_{yr}(1:5), w_X(1:(Tlag+1-\tau)) \sim Dirichlet(\mathbf{1}), \quad \alpha_k(c) \sim Normal(\bar{\alpha}_k, \bar{\sigma}_k)(\text{for } r \text{ model})$$

$$\text{or } \alpha_k \sim Normal(0, S), \bar{\alpha}_k, \theta_k, \beta_k \sim Normal(0, S), \text{and } \sigma, \bar{\sigma}_k \sim U(0, A)$$

Where $\mathbf{1}$ is a vector of ones whose length (12, 5 or $Tlag$+1- τ) is consistent with its corresponding w. 'Large' values of S and A were chosen for fairly non-informative priors; semi-informative priors were used for a subset of θ's and β's in the R_s model (see Barron-Gafford *et al.* 2014 for details).

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butes that allow us to address the five aforementioned questions about ecological memory (see Ecological Memory section).

Does memory matter?

If memory matters, then SAM's stochastic antecedent effects will improve our ability to predict the response variable of interest. We compared a model with antecedent effects (SAM approach) to a reduced model without antecedent effects; both models retain *current* exogenous or endogenous variables. In each case study, the SAM approach resulted in superior model fit (Table 1). The reduced model explained 46–47% (for g_s, ANPP, and r) to 70% (for R_s) of the variation in the observed data, whereas the SAM explained 70–75% (for g_s, ANPP, and r) to 88% (for R_s) of the variation. In addition, we computed the deviance information criterion (DIC, Spiegelhalter *et al.* 2002), a model comparison index that accounts for model fit while penalising model complexity. Although SAM led to greater model complexity (with the

exception of R_s), in all four case studies, it notably improved fit relative to the simple models as indicated by lower DIC values (Table 1). This aligns with others studies that have also shown improvement in model fits when including antecedent variables (e.g. Oesterheld *et al.* 2001; Leuning *et al.* 2005; Hawkins & Ellis 2010; Sala *et al.* 2012; Cable *et al.* 2013a; Barron-Gafford *et al.* 2014). The improved model performance yielded by SAM, however, is also accompanied by details on the characteristics of memory (i.e. length, temporal patterns and strength).

The *strength* of the memory response is quantified by the magnitude and significance of the X_{ant} and E_{ant} effects parameters (i.e. subcomponents of α in Box 1 and Box 2). In all four case studies, at least one or more of the antecedent drivers was statistically significant such that the 95% credible interval (CI) for its corresponding α term did not contain zero (Table S1). For example, PPT_{ant} had a significant positive effect on ANPP (Table S1 or Fig. 2). In the original study, Lauenroth & Sala (1992) did not directly evaluate the importance of antecedent precipitation, but they hypothesised that

Table 1 Summary of model comparison indices for the four case studies in Box 2: stomatal conductance (g_s), annual aboveground net primary productivity (*ANPP*), soil respiration (R_s) and tree-ring widths (*r*)

Example	Model	R^2	DIC	Dbar	pD
g_s	Reduced	0.46	−4735.0	−4764.0	28.7
	SAM	0.72	−5240.0	−5334.0	93.9
	Difference	0.26	−505.0	−570.0	65.2
ANPP	Reduced	0.47	454.1	446.6	7.6
	SAM	0.75	435.4	420.2	15.2
	Difference	0.28	−18.7	−26.4	7.6
R_s	Reduced	0.70	323.5	297.2	26.3
	SAM	0.88	187.5	164.5	22.9
	Difference	0.18	−136.0	−132.7	−3.4
r	Reduced	0.47	−2422.0	−2488.0	65.6
	SAM	0.70	−3413.0	−3518.0	105.1
	Difference	0.23	−991.0	−1030.0	39.5

Model fit is evaluated via the R^2 value obtained by regressing the predicted values (i.e. posterior means for μ, Boxes 2 and 3) on the observed data. The deviance information criterion (DIC) is the sum of two terms: a 'model fit' term (Dbar, lower values indicate better fit) and a 'penalty' term that represents the effective number of parameters in a model (pD, higher values reflect a more complex or parameter-rich model). A difference in DIC > 10 between two models provides strong support for the model with the lowest DIC (Spiegelhalter *et al.* 2002). For each example, we compared a model that incorporated antecedent effects (via SAM) to a reduced model that lacked antecedent effects. The difference between each model comparison statistic (R^2 or DIC) is provided as the SAM minus the reduced model value. Comparisons of DIC and Dbar are only relevant among models sharing the same data.

ANPP exhibited time lags of several years in response to past precipitation patterns, and reanalysis of this data found that the current and previous year's precipitation explained a significant amount of variation in ANPP (Oesterheld *et al.* 2001). In the tree-ring example, *r* was significantly correlated with PPT_{ant}, T_{ant}, and the previous year's ring width, $r(t-1, c)$ (Table S1). Higher precipitation in the past is expected to lead to greater growth in the current time period. The positive correlation between $r(t,c)$ and $r(t-1,c)$ is consistent with an autoregressive, AR(1), process, which is commonly used in dendrochronological analyses (Monserud & Marshall 2001; Griesbauer & Green 2010; Tingley *et al.* 2012), but which lacks the memory interpretations of the SAM approach.

What are the temporal characteristics of memory?

Having determined that antecedent effects are significant, we proceed to evaluate the length and temporal patterns of the memory response. If an antecedent effect is not significantly different from zero (i.e. it has weak memory or no memory), then its corresponding *w*'s are meaningless. In all four case studies, the posteriors for the *w*'s differed from the priors in meaningful ways. In the ANPP case study, the posterior for $w_{P,yr}$ (annual precipitation weights) was tighter than the prior, as reflected by comparatively narrow posterior 95% CIs (Fig. 2), and unlike the 'flat' prior, the posterior exhibited notable *temporal patterns*. For example, precipitation received 1–2 years ago was significantly more important than that received during the year of production or 4 years ago (i.e. the 95% CIs for $w_{P,yr}(1)$ and $w_{P,yr}(2)$ do not contain the posterior means for $w_{P,yr}(0)$ and $w_{P,yr}(4)$, and *vice versa*). The moderately low value for the current year's precipitation weight was not surprising since it sums over a subset of months that occurred after the ANPP harvests (i.e. $w_{P,mo} = 0$ for these months). Differences between the prior and posterior *w*'s were even more obvious for g_s (Fig. 3) and *r* (Fig. 4); the posterior CI widths were notably narrower than the prior CI widths, and a subset of *w*'s – e.g. the importance of deep soil water (W_{60}) experienced 7–8 weeks ago (w_{60}, *j* = 5; Fig. 3), and several $w_{P,mo}$'s associated with PPT_{ant} weights in the *r* model (Fig. 4) – are associated with posterior estimates that are significantly different from the prior.

Temporal patterns in the weights also revealed important *time lags*. For example, g_s exhibited a short lag with respect to shallow soil water (W_{30}), temperature (T_{air}) and vapour pressure deficit (D_{air}) such that conditions occurring the day prior to, the day of, or half-an-hour prior to the observed g_s, respectively, were most important for predicting g_s (Fig. 3b–d). Yesterday's soil water conditions were also most important
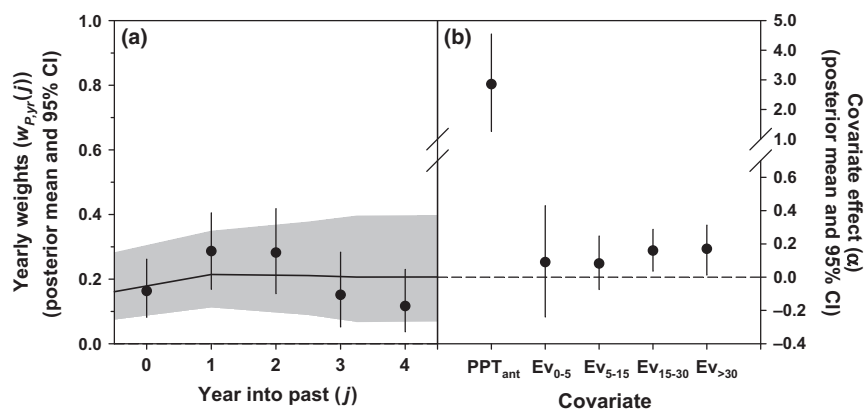
Figure 2 Example results from the shortgrass steppe aboveground net primary production (ANPP) model. The posterior means and 95% credible intervals (CIs) for (a) the yearly importance weights ($w_{P,yr}$) associated with antecedent precipitation (PPT_{ant}), and (b) the covariate effects (α's) in the ANPP mean model (Box 2). In (A), the grey region and the solid line denote the 95% CI prior region and prior mean for each $w_{P,yr}$. In (B), effects whose 95% CI does not contain zero are significantly different from zero (horizontal dashed line), as illustrated for the positive effects of PPT_{ant} and large precipitation events (i.e. $Ev_{15–30}$ and $Ev_{>30}$).
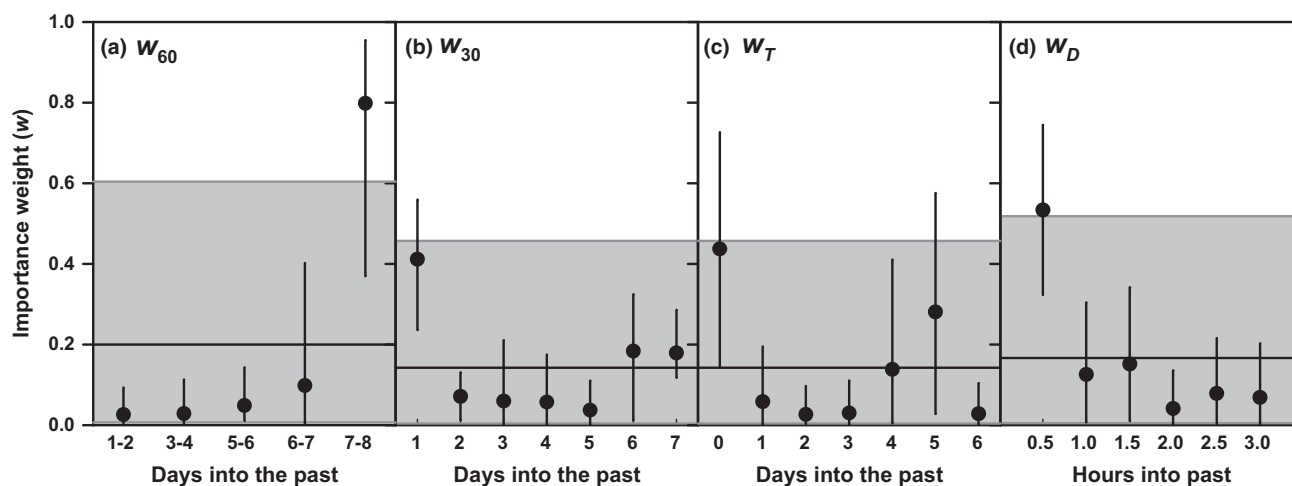
Figure 3 Importance weights (*w*) associated with stomatal conductance (g_s) (Box 2). Posterior means (filled symbols) and 95% credible intervals (CIs) for *w*'s associated with (a) antecedent deep (30–60 cm) soil water content (W_{60ant}), where the antecedent time scale associated with the weights (w_{60}) is defined as blocks of multiple (2) days, (b) the daily weights (w_{30}) associated with antecedent shallow (0–30 cm) soil water (W_{30ant}), (c) the daily weights (w_T) associated with antecedent air temperature (T_{ant}), and (d) the half-hourly weights (w_D) associated with antecedent vapour pressure deficit (D_{ant}). The prior means and 95% CI are indicated by the horizontal black lines and the shaded grey regions, respectively.

for R_s (Fig. 5b). In other situations, recent conditions conveyed relatively low importance compared to conditions occurring further in the past. For example, R_s exhibited an *c.* 3-day lag response to photosynthesis (A_{max}, an endogenous factor) in the shrub microsites (Fig. 5a and Barron-Gafford *et al.* 2014), and g_s exhibited a ≥ 7-week lag response to 'deep' soil water (W_{60}) (Fig. 3a). Longer lags were apparent for both annual productivity indices such that precipitation received 1–2 years (or 12–30 months) prior to production was most important for predicting *r* and *ANPP* (Figs 2 and 4).

Variation in the cumulative *w*'s provides insight into the *length* of the memory. For example, the length of the ANPP precipitation memory was *c.* 50 months, potentially spanning 42–57 months (Fig. 4). That is, precipitation occurring more than *c.* 50 months ago – or more than 38 months (*c.* 3.2 years) prior to the year of production – had little influence on the current year's ANPP. In the *r* example, the length of the memory varied depending on the driving variable (precipitation vs. temperature). The precipitation memory for *r* was *c.* 45 months, spanning 36–54 months (Fig. 4), and was slightly shorter than that of ANPP, but the temperature memory of *r* was comparatively long, *c.* 57 months, spanning a narrower range of possible values (50–57 months) (results not shown).

What time scales are important for quantifying memory?

Important to understanding the temporal features of memory is the time scales specified for modelling the weights. Note that we used nested weights in both the ANPP and *r* examples – yearly weights and monthly weights within each year – to account for memory patterns that reflect multiscale processes. In the ANPP example, the yearly *w*'s are well resolved (Fig. 2), while the monthly *w*'s are more uncertain (Fig. 4). Conversely, in the *r* example, each scale's patterns are well resolved (e.g. Fig. 4), and the monthly *w*'s suggest temporal memory variability linked to seasonal climate variability. For

example, precipitation received during the winter prior to ring formation appears to be most important for understanding variation in *r* for *Pinus edulis* at this site (Fig. 6). The monthly *w*'s for temperature ($w_{T,mo}$) are also fairly well resolved, but, unlike precipitation, they indicate that temperatures experienced during the previous summer are most important for predicting *r* (Fig. 6). Thus, the nested weight model allows us to identify coarse time-scale memory patterns (e.g. the importance of precipitation received during different years), and to partition these into memory effects that operate at finer time scales (e.g. the importance of precipitation received during different seasonal periods).

In the g_s example, we took a different approach to accommodate varying time scales, which depends on the exogenous driver of interest. For example, a 'slow' time scale was assumed in computing antecedent deep soil water (W_{60ant}) because the amount of deep soil water is expected to change relatively slowly, and the response of g_s to W_{60ant} is likely mediated through 'slow' physiological and hormonal feedbacks (Ju *et al.* 2006; Saha *et al.* 2008). Conversely, a 'fast' time scale is assumed for computing antecedent vapour pressure deficit (D_{ant}) because stomata are directly exposed to atmospheric conditions, which vary at minute to hourly scales, and they likely respond quickly to changes in vapour pressure deficit (Damour *et al.* 2010). Following Barron-Gafford *et al.* (2014), we only considered one time scale (daily) for R_s, and lags of similar time scales have been estimated for R_s in forest ecosystems (Vargas *et al.* 2011). We have found it useful, however, to employ varying, driver-dependent time scales, similar to the g_s example, in other analyses of temporally extensive soil and ecosystem respiration data (e.g. Cable *et al.* 2013a), and for R_s data spanning multiple years, longer (e.g. seasonal or yearly) memory effects may emerge from interactions with annual plant productivity dynamics (Janssens *et al.* 2001). In another study (Sonderegger *et al.* 2013), we allowed the time steps to vary such that we used relatively high resolution time steps for the recent
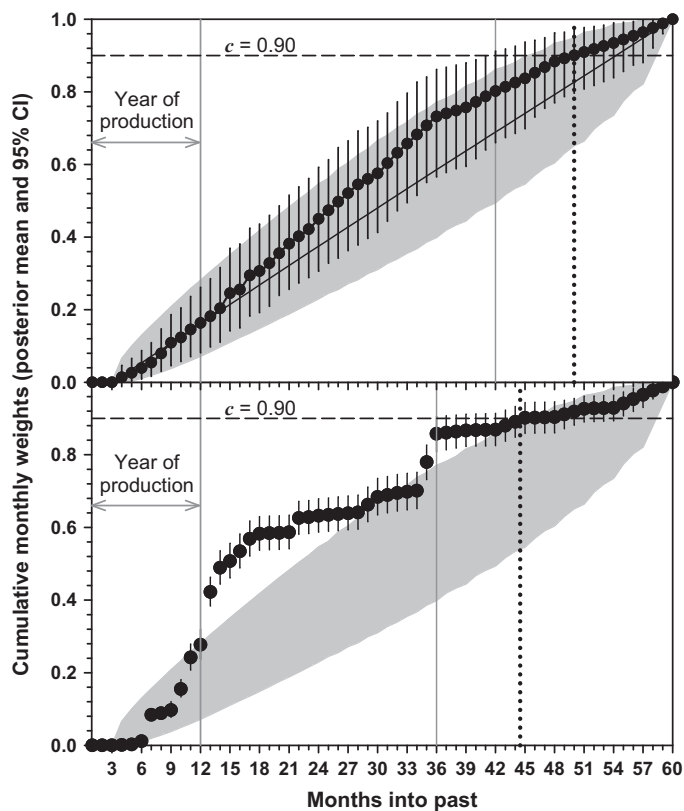
Figure 4 Cumulative monthly weights [posterior means and 95% credible intervals (CIs)] associated with antecedent precipitation (PPT_{ant}) in the models for (a) aboveground net primary production (ANPP) and (b) tree-ring widths (r) described in Box 2. Each cumulative monthly weight is analogous to a cumulative probability and is computed by summing the product $w_{P,mo}(m|y) \cdot w_{P,yr}(y)$ over past years (y) and months (m). The months and years are ordered from 'most recent' such that month $m = 12$ and year $y = 0$ correspond to December of the current year ('months into the past' = 1) and month $m = 1$ and year $y = 4$ corresponds to January 4 years prior to the current year ('months into the past' = 60). The horizontal dashed line represents the threshold ($c = 0.90$) used to determine the length (L) of the memory. The right-most vertical grey line indicates the minimum L (i.e. the earliest cumulative weight whose 95% CI contains c), and the vertical dotted line indicates the 'nominal' L (i.e. the cumulative weight that is nearly equal to c). The grey region indicates the 95% CI region associated with the priors specified for $w_{P,mo}$ and $w_{P,yr}$. The current year of production is associated with the first 12 months (i.e. for $m = 1, 2, \ldots, 12$ and $y = 0$).

past and coarser time steps for the more distant past (e.g. $j = 1, 2, 3$ and 4 corresponding to 0–2, 2–6, 6–14 and 14–22 weeks ago). We employed a similar approach in the r and ANPP examples (see Appendix S1). Varying time scales and time steps are straightforward to incorporate into the SAM framework, and we highlight additional approaches to achieving this in the Appendix S1.

What features underlie memory?

Here, we highlight potentially important features that may underlie memory patterns, including, but not limited to: interactions between different antecedent drivers and/or between antecedent and current drivers; endogenous vs. exogenous antecedent effects; differential memory responses of

sub-component processes; and memory responses that vary at different organisational levels.

In many cases, different antecedent drivers may interact to affect the response variable, as was the case for r and R_s (Table S1). For example, antecedent precipitation and temperature (PPT_{ant} and T_{ant}) interacted to influence r (Fig. 7) such that the positive effect of PPT_{ant} on tree growth was reduced under warmer conditions; i.e. when T_{ant} exceeded c. 13.1 °C (which occurred for c. 10% of the growth years), r was expected to be reduced by higher PPT_{ant}. In the R_s example, antecedent (SW_{ant}) and current (SW) soil water content interacted to affect both the base respiration rate (R_{base}) and the temperature sensitivity ($Sens$) in both microsites, and the direction of this interaction (negative) was consistent across microsites (Table S1). In particular, the response of R_s to a rain pulse – resulting in a change in SW – was amplified if the pulse broke a long dry spell (low SW_{ant}) and was muted or resulted in a reduction in R_s if the pulse occurred during a moist period (high SW_{ant}). In general, an antecedent variable's importance – the *strength* of ecological memory for it – likely depends on the current state of the system and other antecedent variables. Similarly, the quantification of effects of current conditions on processes of interest will likely require the evaluation of responses in the context of past conditions.

Exogenous or environmental factors are frequently acknowledged, but consideration of current and antecedent endogenous factors is rare, by comparison, especially in plant and ecosystem ecology. We explicitly included endogenous effects in the r and R_s case studies (Box 2). The SAM approach suggested that both endogenous – in the form of antecedent photosynthesis (A_{ant}), a biological component of the ecosystem potentially affecting another ecosystem process (i.e. R_s) – and exogenous – i.e. soil environmental conditions such as T, SW and SW_{ant} – factors govern R_s dynamics (Fig. 5, Table S1), the latter of which we have highlighted. The endogenous effect indicated that greater photosynthetic activity (higher A_{ant}) stimulated higher R_s (Fig. 5c, Table S1). The characteristics of the endogenous memory, however, differed between microsites; while the weights (w_A) associated with A_{ant} did not reveal clear temporal patterns in the grass microsites, shrub microsites exhibited a lag response such that A_{max} rates occurring 3 days prior to the day of measurement had the greatest influence on R_s (Fig. 5, Barron-Gafford *et al.* 2014). This is consistent with other studies that have found sub-daily measurements of R_s to lag behind photosynthesis by a few hours to a few days (Baldocchi *et al.* 2006; Vargas *et al.* 2011).

Likewise, the effect of past tree growth also revealed the importance of antecedent endogenous factors for predicting r. In particular, if a tree grew a lot last year, we expect it to grow a lot this year, which was supported by the positive effect of $r(t-1)$ (Fig. 7, Table S1). Although we did not directly include endogenous effects in the ANPP model, previous year's ANPP or tiller density have been shown to be important for predicting ANPP (Oesterheld *et al.* 2001; Sala *et al.* 2012; Reichmann *et al.* 2013). In our reanalysis of the aforementioned ANPP data, previous year's ANPP was positively (but not significantly) correlated with the ANPP residuals obtained from our SAM model, but it only explained an
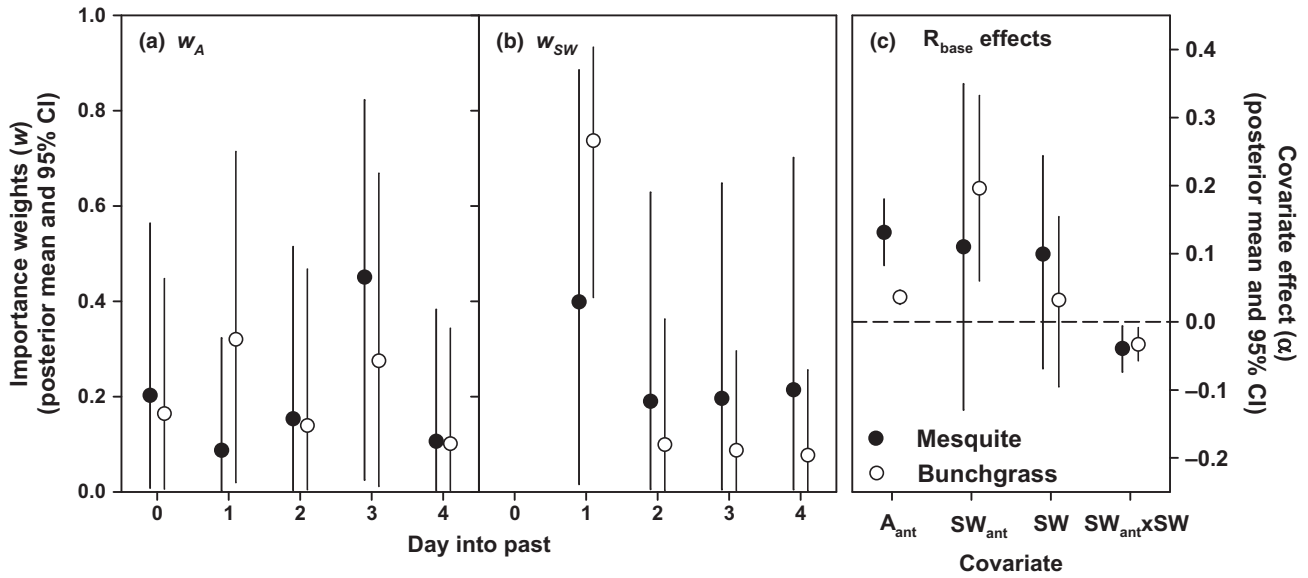
Figure 5 Example results for soil respiration (R_s) measured in two microsites, under shrub (mesquite, *Prosopis velutina*) and bunchgrass (*Eragrostis lehmanniana*) canopies (Box 2). Posterior means (filled symbols = mesquite; open symbols = bunchgrass) and 95% credible intervals (CIs) for (a) the daily endogenous weights (w_A) associated with antecedent photosynthesis (A_{ant}), which indicate a 3-day lag (highest weight) under mesquite, (b) the daily exogenous weights (w_{SW}) associated with antecedent soil water content (SW_{ant}), and (c) the covariate effects in the base rate (R_{base}) model for the mean R_s (μ, Box 2). Because current soil water (SW) is directly included in the sub-models for μ, it is thus not included in the calculation of SW_{ant}, hence $w_{SW}(0)$ in (b) is not estimated. In (c), R_{base} is significantly affected by A_{ant} and the interaction between SW and SW_{ant} in both microsites, but the main effect of SW_{ant} is only significant under bunchgrass.
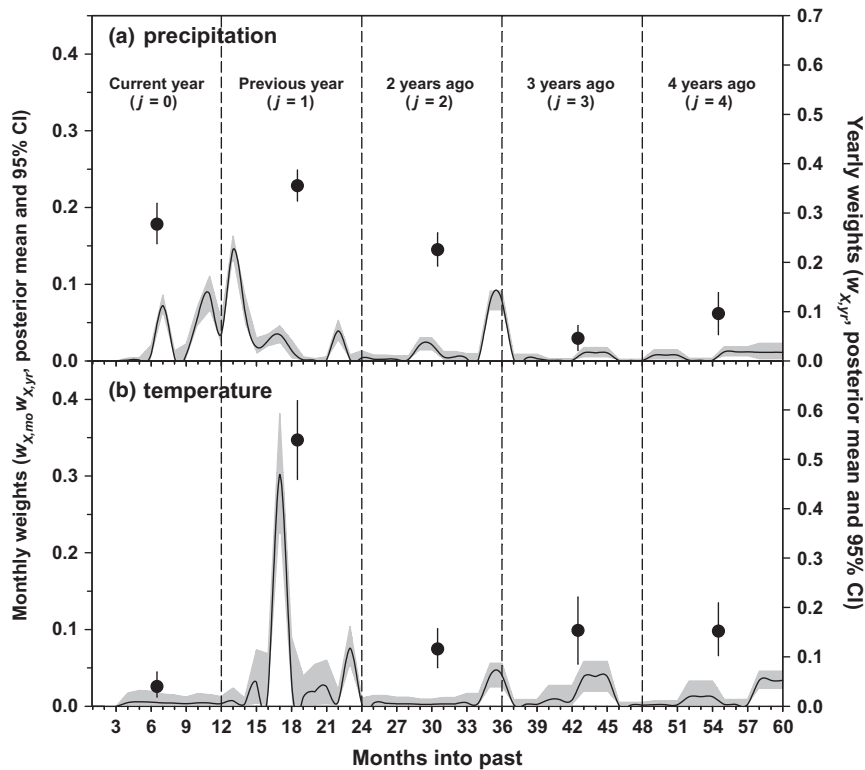
Figure 6 Posterior results [mean and 95% credible intervals (CIs)] for the annual ($w_{X,yr}$, filled symbols) and monthly ($w_{X,mo} \cdot w_{X,yr}$, solid lines and grey regions) weights associated with (a) antecedent precipitation (PPT_{ant}) and (b) antecedent temperature (T_{ant}) in the tree-ring-width (r) model. The vertical dashed lines separate each yearly block, where the first block (for year $j = 0$ and months 1–12) corresponds to the year of ring formation.
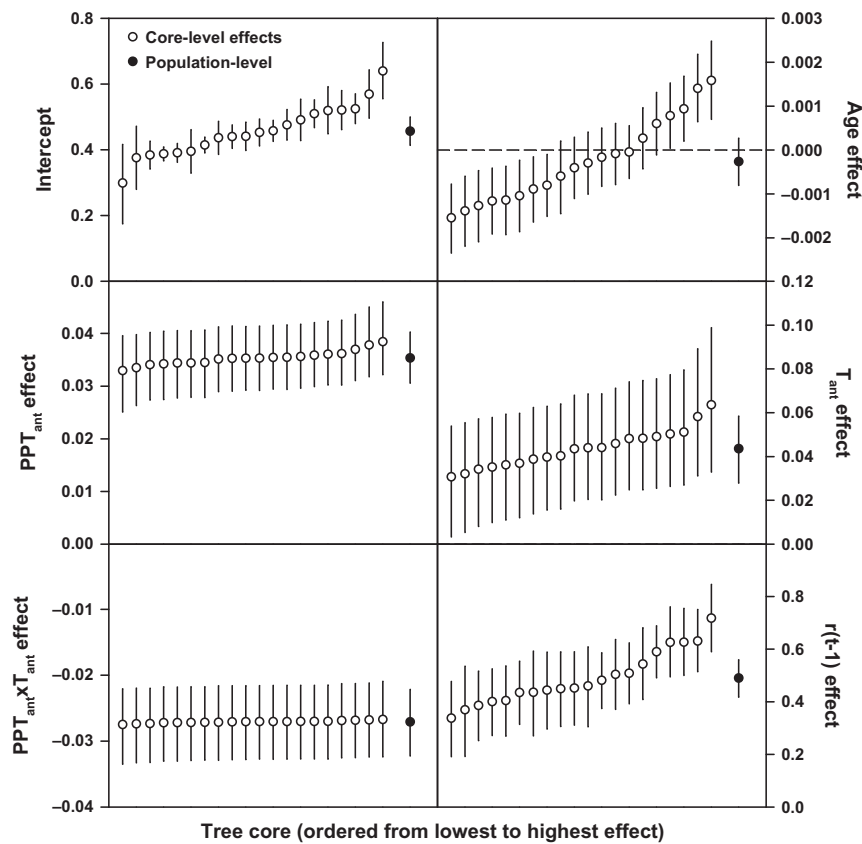
Figure 7 Posterior means and 95% credible intervals (CIs) for the core- or tree-level (open symbols) and population-level (filled symbols) covariate effects in the tree-ring width (r) model (Box 2). The horizontal dashed lines represent the zero line, and 95% CIs that overlap the zero line indicate non-significant effects. The endogenous effects of tree age (Age) and the previous year's ring width ($r(t-1)$) vary among trees (cores), whereas the exogenous effects of antecedent precipitation (PPT_{ant}), antecedent temperature (T_{ant}) and their interaction ($PPT_{ant} \times T_{ant}$) do not vary among trees.

additional 2% of the variation in ANPP. This is in contrast to previous studies that found a stronger effect of previous year's ANPP (Oesterheld *et al.* 2001; Sala *et al.* 2012; Reichmann *et al.* 2013), but unlike our flexible SAM approach, these studies assumed that only current and/or previous year's precipitation affected ANPP, and precipitation during each month was treated as being equally important. Regardless, as illustrated in the R_s and r case studies, the SAM approach highlighted the potentially critical role of endogenous factors for predicting the ecological processes of interest.

In most ecological situations, the response of interest reflects multiple, coupled sub-processes, each of which may possess their own memory characteristics. In the g_s and R_s case studies, we expressed these responses as functions of two sub-components: a base-line response (e.g. g_{ref} or R_{base}) and an environmental sensitivity term (e.g. *Sens* or T_{sens}) (Box 2). In both cases, each sub-component was significantly affected by antecedent exogenous (g_s and R_s) and endogenous (only applicable to R_s) factors (Table S1). However, the direction and magnitude of the antecedent response varied between sub-components. For example, antecedent temperature (T_{ant}) significantly affected stomatal behaviour by influencing both g_{ref} and *Sens*, but T_{ant} had opposing effects on *Sens* and g_{ref} (Table S1). In addition, we assumed that antecedent vapour pressure deficit (D_{ant}) only had the potential to influence *Sens*

(but not g_{ref}), reflecting a potential acclimation response of stomata to the prevailing vapour pressure conditions. In these examples, we specified the antecedent drivers to share the same temporal characteristics. For example, g_{ref} and *Sens* shared the same weights (w_T) for antecedent temperature (T_{ant}), and R_{base} and T_{sens} shared the same weights (w_A) for antecedent photosynthesis (A_{ant}). Of course, the explicit characterisation of memory patterns in the form of the weights (w's) makes the specification of different w's easy, in principle, within the SAM framework.

Different levels of organisation may also vary in their memory characteristics and responses to exogenous and endogenous drivers. The r case study nicely illustrates this because it included both individual-tree responses (via the α's, Box 2) and associated population-level responses (via the $\bar{\alpha}$'s, Box 2). Interestingly, the direction and magnitude of the exogenous effects of the antecedent climate variables (PPT_{ant}, T_{ant} and $PPT_{ant} \times T_{ant}$) were consistent across trees (Fig. 7), indicating that the response to these antecedent variables may be an intrinsic property of the population or, more generally, the species. Conversely, the effects of tree age and previous ring widths differed notably across trees (Fig. 7), implying that such endogenous effects may be an inherent property of individual trees, which likely reflects an ontogenetic or genotypic signal. This suggests that the model for r could be simplified

by assuming that the antecedent climate drivers operate at the population level (i.e. we could ignore the individual-level α_2, α_3 and α_4 terms), while retaining the individual-level endogenous effects (α_0, α_1 and α_5) (Box 2). Importantly, this hierarchical structure (e.g. α's nested in $\bar{\alpha}$'s) allowed us to evaluate the importance of current and antecedent factors at different levels of biological organisation.

What mechanisms govern memory?

The above-described memory characteristics (e.g. temporal patterns, length and strength) associated with processes operating at one or more time scales were not anticipated prior to analysing the data and are important in identifying new hypotheses to understand constraining processes. The SAM approach enables an improved, objective assessment of ecological processes and drivers by explicit consideration of memory characteristics that are relatively easy to interpret. We use our case studies to illustrate insight into potential mechanisms associated with our specific processes that deserve further exploration, but we do not provide a comprehensive evaluation of the mechanisms. Rather, we mean to demonstrate how SAM can be applied to facilitate hypothesis generation and future experimentation and model refinements.

In the tree growth example, the total (cumulative) importance weight of June to March precipitation prior to ring formation was c. 50% (Fig. 6). Precipitation, especially snow, received during this period likely is important for recharging 'deep' soil moisture, providing a water source for trees in the subsequent growing season (Loik et al. 2004, 2013). The next three most important precipitation periods correspond to spring snowmelt (April–June) during the year of growth, and to the winter/spring periods of the previous 2 years (Fig. 6). Likewise, precipitation during the most recent three winters is most important for ANPP (Fig. 2). The importance of these periods of precipitation, received over multiple years for both annual tree growth and ANPP, could be related to the exogenous effects of deep soil water recharge (Dodd & Lauenroth 1997) and/or to the concept of meristem limitation (Dalgleish & Hartnett 2006; Smith & Dukes 2013), where growth and establishment of perennial plants (endogenous factor) in previous years determine the growth potential in a particular year (e.g. Reichmann et al. 2013). However, given the sampling approaches used in the ANPP case study (all live and dead aboveground plant biomass was removed in each sample plot, Lauenroth & Sala 1992), meristem limitation effects were likely reduced (Sherry et al. 2008).

We discovered potential lags in the response of soil respiration (R_s) to past photosynthesis rates (A_{ant}, Fig. 5), with shrubs exhibiting longer lags than grasses (3–4 days vs. potentially 1 day). Such lags likely reflect time delays associated with the transport of carbohydrates from photosynthetic tissues to the rhizosphere (Baldocchi et al. 2006; Barron-Gafford et al. 2014) and/or the effects of past atmospheric conditions on photosynthesis (Baldocchi et al. 2006). For example, tall-statured woody plants are typically associated with relatively long carbohydrate transport times (on the order of 3–4 days, Bowling et al. 2002; Tang et al. 2005; Carbone & Trumbore 2007; Vargas et al. 2011), and shorter transport pathways in grasses may account for shorter lags. Plant species-specific priming effects associated with root exudation and consumption by microbes may also lead to microsite-dependent lag times in R_s (Cheng 2009). In addition, differences between microsites in the antecedent soil water weights (Fig. 5B) and the importance of current and antecedent soil water (Fig. 5c) may reflect differences in rooting distributions between grasses and shrubs (Jackson et al. 1996). For example, the rhizosphere of shallow-rooted grasses may be more strongly coupled to ephemeral surface soil water over relatively short time scales compared to more deeply rooted shrubs (e.g. Schwinning et al. 2002).

Stomatal behaviour of Larrea tridentata exhibited different lag responses to deep and shallow soil water (Fig. 3). These differences could be explained by Larrea's bimodal rooting distribution (Ogle et al. 2004) combined with the differential residence times of deep (long) vs. shallow (short) soil water (Sala et al. 1992). Thus, g_s may be partly constrained by how deep soil water conditions control endogenous processes (e.g. new leaf production and overall canopy display) that influence leaf gas exchange (Leffler et al. 2004). By contrast, shallow roots are likely to be inactive when surface soils are dry and quickly become active after rewetting (North & Nobel 1991), allowing for rapid uptake of water and nutrients. This would directly affect the water status of leaves and g_s, regardless of leaf age or canopy characteristics, resulting in short lag times between g_s and soil water availability. For physiologically or enzymatically mediated processes such as g_s and R_s, the importance of antecedent environmental conditions – e.g. past water, temperature, vapour pressure deficit, etc. – may also indicate an acclimatisation or acclimation response (Atkin & Tjoelker 2003; Smith & Dukes 2013).

In the tree growth example, why would the antecedent endogenous effects operate at the individual level, but the antecedent exogenous effects operate at the population or species level? The tree-specific age response (Fig. 7) likely reflects ontogenetic changes in tree growth patterns (Carrer & Urbinati 2004); for example, the age effect tended to differ by age class such that the correlation (ρ) between the core-level age effect, $\alpha_1(c)$, and the corresponding age of tree (core) c in 1910 was $\rho = -0.27$. Although $r(t)$ was positively correlated with last year's ring width, $r(t-1)$, for all trees, the magnitude of the $r(t-1)$ effect, $\alpha_5(c)$, differed among trees, which was also negatively correlated with the initial (1910) tree age ($\rho = -0.36$). Conversely, the antecedent climate effects appear to reflect the similar climatic conditions of the population. With direct measurements of individual trees' local soil water or canopy temperatures, we may have discovered tree-specific responses to antecedent microclimate conditions (Beckage & Clark 2003).

Potential considerations and extensions

In general, without additional model structure, the SAM framework may be limited to data sets with extensive temporal information (i.e. relatively long time-series). The length requirement of the time-series may depend on the inherent time scale of the process of interest. In the two 'slow' time-scale examples, ANPP measurements were reported for

50 years, and 91 growth rings were used for each tree. In the two 'fast' time-scale examples, g_s and R_s were measured over 16 and 27 non-consecutive days, respectively. While the g_s and R_s time-series were discontinuous in time and may seem relatively short, the sampling strategies resulted in data that spanned a wide range of exogenous and/or endogenous conditions. However, significant efforts in developing large data sets associated with ecological structure and function (e.g. FLUXNET, TERN and NEON) will yield more long-term data that will be available for rigorously quantifying ecological memory.

We chose case studies from arid and semi-arid ecosystems partly because these systems are likely to exhibit strong exogenous, and potentially endogenous, memory or legacy effects (e.g. Sala *et al.* 2012) given that they are often characterised by highly variable ecological responses and environmental drivers (e.g. water and temperature). Our SAM approach, however, could be extended to understand the length, temporal patterns, and strength of the memory in other extreme, more mesic, or potentially less variable systems. For example, SAM could be applied to boreal and arctic systems with storage-based hydrological dynamics, where the time scale for which soil moisture impacts plant and ecosystem carbon and water fluxes is drawn out over multiple years such that current flux dynamics are likely controlled by prior freeze-thaw cycles and permafrost degradation status (e.g. Iwata *et al.* 2012; Cable *et al.* 2013b). SAM could also be used to evaluate the antecedent exogenous and endogenous controls on the timing and magnitude of green-up and flowering in tropical forests, two globally important dynamic phenomena that are not well understood (e.g. Pau *et al.* 2013; Krishnaswamy *et al.* 2014; Morton *et al.* 2014). More generally, phenological processes are inherently temporal, and the rate and/or timing of leaf-out or flowering may depend on past phonological schedules. Long-term data sets – such as the 700 + year cherry blossom record from Japan (Aono & Kazui 2008) or from the National Phenology Network – could be used within the SAM framework to provide predictive ability of how ecological memory affects phenological processes, particularly in the face of changing climate. Moreover, we hypothesise that systems characterised by little temporal variation in climate drivers are likely to be more strongly controlled by endogenous memory (e.g. associated with effects of organismal size, past productivity, etc.) or exogenous disturbances (e.g. land-use or fire history), which could be tested with the SAM approach.

CONCLUSIONS

This study demonstrates that memory is important for understanding contemporary ecological processes, and the length, temporal patterns, and strength of the memory can vary greatly among processes spanning a range of temporal and spatial scales. Importantly, the stochastic antecedent modelling (SAM) framework provides an objective method for identifying these latent memory properties by explicitly quantifying antecedent exogenous and/or endogenous conditions and their effects on a diversity of ecological responses. We illustrated the utility of the SAM approach and the types of unique insights it provides by applying it to four distinctly

different data sets that represent processes operating at subdaily to interannual time scales. In all four examples, the SAM approach greatly improved our ability to predict the response of interest, revealing important lag periods and antecedent drivers. Although our examples were obtained from arid and semi-arid systems, the SAM approach is expected to be applicable to a diversity of systems characterised by temporal variation in the response(s) of interest and associated endogenous and/or exogenous drivers.

Our SAM framework may also be broadly applicable within and outside the field of ecology to understand the importance of time, and memory in particular. Different ecological subdisciplines use alternative descriptors to describe ecological memory, such as 'biological legacies' (e.g. landscape ecology) and 'antecedent effects' (e.g. ecosystem ecology). The ecological memory concept is captured in notions of lag effects, time delays, historical effects and buffering capacity (e.g. Bengtsson *et al.* 2003; Ogle & Reynolds 2004; Golinski *et al.* 2008; Schaefer 2009). The SAM approach provides a rigorous quantitative approach for exploring these different aspects of memory. Outside of ecology, memory has been used to describe the lag between atmospheric forcing and land surface hydrology (Koster & Suarez 2001; Lo & Famiglietti 2010), persistence of atmospheric chemical constituents (e.g. Varotsos & Kirk-Davidoff 2006) and changes in the physical structure of biological macromolecules (Yashima *et al.* 1999). Thus, the general SAM formulation is expected to be applicable for quantifying memory of a diversity of dynamic processes representing spatial and temporal scales spanning several orders of magnitude.

AUTHORSHIP STATEMENT

K.O. led all aspects of the study; K.O., J.J.B., G.A.B-G., L.P.B. and J.M.Y contributed to testing and applying the SAM framework with real data; G.A.B.-G., T.E.H and K.O. contributed data; all co-authors contributed to the development of the conceptual ideas and to writing the manuscript.

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