Thank you for your helpful comments. We have used these comments as a guide to improve the revised version of this manuscript. Notable changes include:

1) An updated title and notes throughout the text to clarify that this is primarily a sensitivity study and that we test representations of both minimum and nighttime conductance.
2) Inclusion of the soil moisture constraint in Eq. 1, and the addition of new Eq. 2 that shows how the soil moisture constraint is calculated in CLM.
3) Acknowledging that $g_{s,n}$ can possibly be simulated as a proportion of daytime $g_s$.

Please find the detailed response to each comment in italics below.

Comments from Reviewer Kevin Tu

Consistent with the first two reviewers, in particular reviewer Fisher, I believe the motivation behind this study is excellent, but that there are some issues that still need to be addressed which I describe below.

On reviewer Fisher’s suggestion for comparison to empirical observations, this study still lacks sufficient validation, for example the data presented in Figure 5 is poor at best for validating the model. Without any means to gauge if the model predictions are reasonable, this study is most effectively a sensitivity analysis that serves to highlight the need for additional studies, particularly field measurements, on nighttime conductance and how it is parameterized in land surface models.

**Author Response:** We agree that there is no satisfying way to evaluate the model results, and that this study is most effective as a sensitivity analysis. In response to this and below comments, we update the title and text to reflect that we are highlighting the sensitivity of simulated carbon and water cycles, as well as the need for additional studies. We have iterated over several new title possibilities, and selected the one we thought most suitable for this paper. However, we are open to other specific suggestions if the new title is not satisfactory.

I agree with the 2nd reviewer’s comments on the misleading title and attribution of the effects to nighttime conductance not being accurate - that the results indicate larger impacts on water and carbon fluxes occur when the minimum conductance during the day is altered rather than the nighttime conductance. Further, the authors agree and point out that the focus is really on stomatal conductance rather than nighttime or daytime minimum conductance per se, and as such, the title should not focus solely on minimum conductance. However, by the author’s own logic, the title should not focus solely on nighttime conductance either.

**Author Response:** The previous title was chosen based on the fact that we used observed nighttime conductance values to modify the CLM4.5, and was not an attempt to describe the methodology for how we used the observed values within the model. To
reduce the confusion, we now clarify that we modify both nighttime and minimum conductance representations using observations.

The authors also argue that it’s unclear whether the observations of nighttime conductance are equivalent to minimum conductance, thus their emphasis on nighttime conductance in the title. While the authors may have used observations of nighttime conductance, they clearly used them to alter both nighttime and minimum daytime conductance in the model (in the \( g_0 \) and \( g_{\text{min}} \) scenarios), with the result being larger effects of minimum daytime conductance. Both the methods and the results are not consistent with the bias towards nighttime conductance in the title.

**Author Response:** The use of "nighttime" in the title was to describe the observational data that we used. We have updated the title to reflect that we use these observational constraints to modify nighttime and minimum conductance representations in CLM4.5.

Further, not only were observations of nighttime conductance incorporated into the model, but a new parameterization of minimum daytime conductance was effectively incorporated as well (in the \( g_{\text{min}} \) scenario). Given that the title should reflect the content of the paper, the title should indicate to both nighttime and minimum conductance. This may not have been the original objective of the authors, but it does reflect what they actual did. In two of three approaches examined (the \( g_0 \) and \( g_{\text{min}} \) scenarios), the conductances were altered during both the nighttime and daytime.

**Author Response:** We agree that this title did not effectively convey the fact that our study was a sensitivity analysis comparing different possible methods representing nighttime and minimum conductance. We have updated the title to better indicate that this is a sensitivity study that tests different methodologies.

The authors indicate (L156) that the observations are most likely representative of maximum nighttime conductance, since most measurements were done during well-watered conditions without water stress, yet inconsistent with this, the observations were incorporated in the first approach (\( g_0 \)) as actual nighttime conductance (no soil moisture constraint was used). Substituting observations of maximum nighttime conductance directly for values of actual nighttime conductance seems illogical and physiologically unrealistic.

**Author Response:** We agree with the reviewer that this point was misrepresented in the text because the soil moisture stress function was, in fact, also applied to the \( g_0 \) simulation. For clarification, we now explicitly state that the \( g_0 \) simulation also uses the soil moisture constraint, and it is applied in the same way as in the unmodified simulation. The text now states: "Similar to the unmodified and \( g_0 \) simulations that adjust the \( g_0 \) parameter based on a soil wetness scalar \( (\beta_{\text{soil}}) \), the \( g_{\text{night}} \) and \( g_{\text{min}} \) modifications also adjusted the minimum \( g_s \) threshold..."
The real value and contribution of this study is as a sensitivity analysis of the BWB model, specifically the sensitivity of global water and carbon fluxes to the value of the BWB intercept in the CLM4.5. This would be consistent with the author’s statement in response to reviewer Fisher’s comment on the need for more empirical validation, that the "... primary aim is to highlight the high sensitivity of the hydrological and carbon cycles to these typically poorly constrained parameters".

The physical meaning of the BWB intercept and/or its physiological interpretation is debatable. Regardless, it’s important to characterize and understand the sensitivity of the CLM4.5, and water and carbon budgets in general, to this variable. As noted by reviewer Fisher, nighttime conductance and associated nighttime transpiration is an under-represented but potentially important process in models of land-atmosphere interaction. Clearly, this is what the authors set out to address. However, their efforts are confounded by the fact that the current parameterization of stomatal conductance using the BWB model in the CLM4.5 is not easily modified to include nighttime conductance. The issues raised by the reviewers highlight the empirical side of the BWB model, and the problems associated with attempting a mechanistic implementation (i.e. nighttime conductance) of a largely empirical model (i.e. the BWB intercept).

**Author Response:** We agree that it is important to characterize and understand the sensitivity of water and carbon budgets in CLM4.5, and acknowledge that the empirical nature of the BWB make it quite difficult to incorporate mechanistic processes like nighttime conductance. We include a more explicit acknowledgement of this point in the last paragraph of the discussion section by adding the text: "Indeed, the use of the BWB model at all is currently the subject of some debate (Bonan et al., 2014; De Kauwe et al., 2015), and this study additionally highlights how the empirical nature of the BWB model leads to difficulties when attempting to implement mechanistic processes."

Further, the observations are too far and few between to be representative of the actual BWB intercept (night or day) for a given PFT in a global model like CLM4.5. It would make more sense to use the observations merely as realistic constraints on the range of potential variation of the BWB intercept in a sensitivity analysis. Further still, if the objective is to determine the sensitivity of CLM4.5 to nighttime conductance it should be sufficient to examine only \( \text{?night} \). Once changes to daytime conductance are made (e.g. through changes in minimum conductance) the question then expands to daytime as well as nighttime conductance, which is really beyond the goal of this study. If the goal is truly focused on nighttime conductance then simply change nighttime conductance, and exclude both the \( \text{?gmin} \) experiment which involves changes to daytime conductance as well as the \( \text{?g0} \) experiment, which also includes changes to daytime conductance (and is unreasonable for other reasons as well, see above). If the goal is really to highlight the sensitivity of the model to nighttime conductance then the issue of daytime conductance being consistent with the nighttime conductance is beyond the scope of the study. More than anything, the \( \text{?gmin} \) experiment should be included only for discussion purposes, to address the issue of consistency between nighttime and daytime
conductance, rather than as an alternative method of modifying nighttime conductance. The authors could then focus the manuscript on their stated goal of "Sensitivity of global water and carbon budgets to nighttime conductance in CLM4.5".

**Author Response:** We agree that the data are sparse and would love to have a more comprehensive dataset to parameterize a global model like CLM to better constrain the actual range of conductances. We feel it is important to note, however, that often global models are parameterized using very few data (e.g., using a single $g_o$ and $g_1$ value for all C3 plants is also arguably not representative of the empirical BWB intercept), and this is a problem that we try to address by compiling a comprehensive dataset of nighttime conductance values. In this regard we believe it is better to allow values to vary by the type of plant rather than use one value for all plants, as is currently done. Both are based on observations, though the standard single value used is based on observations from a single study in the 1980’s that used three crops, five herbaceous plants, and a shrub; whereas the dataset compiled here includes data from multiple plant types and studies conducted through 2015. Therefore it is difficult to argue the current single-value approach used by most models does not need to be updated and improved by incorporating a larger, albeit still limited, dataset.

Given the paucity of available data, we agree that our simulations should serve as merely a realistic constraint on the range of potential variation, as recommended. We therefore emphasize throughout the text that we do not aim to determine a single, correct way of implementing nighttime or minimum conductance, but instead provide a range of possible scenarios based on different methodologies. Since $g_o$ is often thought to represent minimum stomatal conductance values, we first test adjusting this parameter in the BWB model. We test two additional methodologies that constrain minimum conductance in other ways. One of those methodologies assumes that daytime minimum conductance can be lower than nighttime conductance, and the other assumes that nighttime conductance is the lowest conductance a plant uses. Comparing these methodologies serves to highlight the possible structural uncertainty of the model. Additionally, we plot the possible range of canopy conductance and transpiration based on observational uncertainty in SI Figure 2, which clearly illustrates that the uncertainty in the observations swamps the model structural uncertainty.

We think that it is important to include the $\Delta g_{\text{min}}$ and $\Delta g_o$ experiments to illustrate both the functioning of the BWB model and also to highlight the uncertainty in knowledge about both daytime and nighttime minimum conductance values. Is nighttime conductance truly the minimum conductance value that a plant uses, or can daytime conductance be lower than nighttime conductance given the same water availability? This is an important question, particularly since the $\Delta g_{\text{night}}$ BWB implementation illustrates the possibility of lower daytime conductance using this representation. The inclusion of all these methodologies in the paper highlights the sensitivity of hydrology and carbon cycling to this model uncertainty. It also
demonstrates that different model representations can behave in ways that are not clearly physiological plausible, emphasizing the need for additional knowledge. By only including one model representation, we are unable to address the model structural sensitivity and cannot highlight the gaps in scientific knowledge.

On reviewer Fisher’s suggestion to incorporate the results synthesized in a Tree Physiology special issue in 2007, I do not feel the authors responded adequately. First, in contrast to the author’s claim that the papers in that special issue do not include environmental sensitivities of nighttime conductance, the paper by Dawson et al. provides a clear relationship between observations of nighttime conductance and days following rainfall, and changes in the ratio of nighttime to daytime conductance following rainfall, with greater fractions (~25%) during the wettest periods immediately following rainfall, with a decline of 5% per day after rain. As noted, "This relationship provides a strong and predictable index of water loss from plants at night based on daylight values...". This type of data should provide valuable information for parameterizing nighttime conductance as a function of daytime conductance and time since rainfall or soil moisture. Second, the authors note that some plant types are sensitive to environmental factors while others are not. This phenomena needs to be explained rather than used as evidence to discard the data. It could very well be that nighttime conductance is not a phenomenon parameterized as easily as the intercept of the BWB model constrained by soil moisture.

Author Response: The Dawson et al. 2007 paper nicely illustrates the concept that minimum conductance is connected to soil water availability and VPD, and we previously overlooked these data. In support of the Dawson et al. (2007) data, we adjust the nighttime conductance value based on soil water stress, which effectively functions to decrease nighttime conductance as days since rainfall increase.

We do not capture the change in ratio of nighttime to daytime conductance as a function of days since rainfall, and now note this within the discussion. We think that the development of a new, independent nighttime conductance model that predicts nighttime conductance based on the night/day ratio as soil water availability changes is a great next step to implementing nighttime conductance. In particular, the new text states: "A different implementation of $g_{s,n}$ might calculate $g_{s,n}$ as a proportion of daytime $g_s$ based on Dawson et al. (2007), who find that $g_{s,n}$ is a proportion of daytime $g_s$ that changes based on days since last rainfall. We do not test this potential method here, but acknowledge it as a viable alternative to be considered."

We are unsure what the reviewer is referring to when suggesting that we discard data based on plant sensitivity to environmental factors, but are happy to include an explanation of this phenomenon as requested if the lines are pointed out to us. We use nearly all the data in our parameterization, regardless of environmental sensitivity. The data that were not used in our parameterization (but are included in Table S1) were only plants that were parasitic or use the CAM photosynthetic pathway.
Justification for not using these was that parasitic plants often gain their water resources from host plants and therefore have little environmental pressure to minimize stomatal conductance; and CAM plants by definition open their stomatal at night to gain CO₂. These assumptions were explicitly stated in the text. We did not discard any data based on sensitivity to environmental factors.

Specific Comments

Equation 1: The full equation including the soil adjustment factor (βsoil) should be shown. Not showing the full equation can be confusing and potentially misleading. It would be informative to also show the βsoil parameterization and the parameter values by PFT, since poor parametrization of this function could lead to poor performance and unreasonable results, for example if βsoil did not adequately constrain g0 during drought conditions (e.g. in semi-arid regions).

Author Response: We have updated Eq. 1 to better illustrate how the soil moisture stress function is applied to stomatal conductance. This function is not a plant functional type parameter, but is applied at the column level. We now include the equation for the calculation of the soil moisture stress parameter as Eq. 2.

It's worth noting that in CLM4.5, soil drought also effectively impacts g1 by way of constraining Vcmax (I'm assuming this based on the fact that the authors state CLM is based on SiB2; Sellers et al. 1996).

Author Response: Yes, the soil moisture function is applied to Vc,max and therefore impacts A. It also is applied to leaf maintenance respiration. We now include text to note this: "It is also important to note that βsoil is also applied to the Vc,max (the maximum rate of carboxylation) parameter in the A equation, as well as to leaf maintenance respiration (Oleson et al. 2013)."

Are there differences between glasshouse and field gs,n values? Using glasshouse gs,n data needs to be validated since glasshouse conditions, including both plant and environmental, can be unrepresentative of actual field conditions and plant responses in the field. In the very least, glasshouse vs field data should be clearly indicated in Table 1.

Author Response: The data in Table 1 are averaged across field and glasshouse studies. This table is a summary of the raw data, which are presented in Table S1. The location of the study (field, glasshouse, etc.) is clearly indicated in the column titled "Location", so is readily available to readers. When separately averaged, the field data are similar to the overall averages for nearly all PFTs, and those PFTs with somewhat different average values fall well within the range of the standard deviation.

L115: It's not clear what the 'simulated PFT' is. Were the PFTs 'simulated' then replaced with observed values of g0? It probably just needs wordsmithing. If so, it
seems clearer to simply state that constant minimum gs values were assumed for each PFT for the method.

**Author Response:** *We removed the word "simulated" to reduce confusion.*

References are needed in Table 1 to know the source of the data.

**Author Response:** *The references for all the data presented in Table 1 are included in Table S1. Table 1 is a summary of all the data presented in Table S1.*

The data in Table 1 indicates that the entirety of boreal forests, both needleleaf evergreen and broadleaf deciduous, are each represented by a single measurement. This is poor parameter estimation at best and reinforces the notion that the observations would serve best as a guide for their potential range in a sensitivity analysis, rather than as direct estimates of nighttime conductance. Given the paucity of data, its unreasonable to expect that the observations will be robust representations of actual values of (maximum) nighttime conductance for all plants at every time-step throughout every growing season within each PFT.

**Author Response:** *Yes, it is true that boreal trees are poorly represented in our dataset. Similar to our response above, a single study providing a measurement for a boreal tree is arguably more globally representative of boreal tree gs,n than the current value (10 mmol m^{-2} s^{-1}) that is not based on data from any trees.*

Values in Table 1 should only be reported to significant digits. It's uninformative and potentially misleading to indicate conductance out to 8 decimal places.

**Author Response:** *Yes, we agree that reporting values to 8 decimal places is misleading. We have updated Table 1 accordingly.*
Incorporating observed nighttime conductance alters global hydrology and carbon budgets in CLM4.5.

5) The sensitivity of global hydrology and carbon budgets to observed nighttime and minimum stomatal conductance representations in CLM4.5. Representing nighttime and minimum conductance in CLM4.5: Global hydrology and carbon sensitivity analysis using observational constraints.


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Abstract

The terrestrial biosphere regulates climate through carbon, water, and energy exchanges with the atmosphere. Land surface models estimate plant transpiration, which is actively regulated by stomatal pores, and provide projections essential for understanding Earth’s carbon and water resources. Empirical evidence from 204 species suggests that significant amounts of water are lost through leaves at night, though land surface models typically reduce stomatal conductance to nearly zero at night. Here, we test the sensitivity of carbon and water budgets in a global land surface model, the Community Land Model (CLM) version 4.5, to three different methods of incorporating observed nighttime stomatal conductance values to a global land surface model, the Community Land Model (CLM) version 4.5, to better constrain carbon and water budgets. We find that our modifications increase transpiration up to 5% globally, reduce modeled available soil moisture by up to 50% in semi-arid regions, and increase the importance of the land surface in modulating energy fluxes. Carbon gain declines up to ~4% globally and >25% in semi-arid regions. We advocate for realistic constraints of minimum stomatal conductance in future climate simulations, and widespread field observations to improve parameterizations.

1. Introduction

Terrestrial plants must balance their need to obtain CO$_2$ with the risk of desiccation if transpiration continues unchecked. Higher plants evolved stomatal pores to control the exchange of water and carbon between the leaf interior and the atmosphere (Hetherington and Woodward, 2003). Stomatal function, thus, is the dominant control over terrestrial fluxes of water and carbon. Most large-
scale land-surface models use an empirical representation of stomatal conductance \( (g_s) \), similar to the Ball-Woodrow-Berry (BWB) model (Ball, 1988; Ball et al., 1987; Collatz et al., 1991; Leuning, 1995; Medlyn et al., 2011; Sellers et al., 1996), to calculate plant gas exchange. The BWB model is linear, with two constants, the intercept \( (g_o) \) and slope \( (g_1) \), and estimates \( g_s \) from the rate of CO\(_2\) assimilation \( (A) \), atmospheric humidity \( (h_r) \), and internal leaf CO\(_2\) concentration. The original BWB model parameters were fitted to observations of leaf gas exchange for ten plant species, with different \( g_o \) values for each species, ranging from -310 to 130 mmol m\(^{-2}\) s\(^{-1}\) (Ball, 1988). The Community Land Model (CLM), however, uses only two \( g_o \) values, (10 and 40 mmol m\(^{-2}\) s\(^{-1}\) for C\(_3\) plants and C\(_4\) plants, respectively; Collatz et al., 1991; Oleson et al., 2013; Sellers et al., 1996). Conductance during the night (and at other times when \( A \) is 0) is thus represented using \( g_o \). Recent advances in our ability to observe nighttime stomatal conductance (Caird et al., 2007; Phillips et al., 2010), \( g_{s,n} \), illustrate that values are often larger in the field than the BWB parameters used in the CLM. A comprehensive database (see Table S1) of 204 observed \( g_{s,n} \) values illustrates that the minimum BWB \( g_s \) values (equivalent to \( g_o \)) used in the CLM starkly differ with observed mean and median \( g_{s,n} \) values. The available data for \( g_{s,n} \) range from 0-450 mmol m\(^{-2}\) s\(^{-1}\) with an overall mean of 78 mmol m\(^{-2}\) s\(^{-1}\) (excluding hemi-parasites and CAM plants, which were omitted from model testing). Observations of \( g_{s,n} \) are, on average, ten times higher in broadleaf tropical deciduous species (Table 1; 129 mmol m\(^{-2}\) s\(^{-1}\)) and seven times higher in temperate broadleaf deciduous trees (73 mmol m\(^{-2}\) s\(^{-1}\)) compared to the 10 mmol m\(^{-2}\) s\(^{-1}\) used for C\(_3\) plants. Potential benefits of a high \( g_{s,n} \) might include the transport of nutrients (Dios et al., 2013; Scholz et al., 2007; Zeppel et al., 2014) or...
processes related to embolism repair, phloem transport, or xylem refilling that might improve carbon gain, but these ideas remain untested. Nonetheless, the discrepancy between parameterized $g_o$ and observed $g_{s,n}$ serves as motivation to investigate the sensitivity of simulated land surface processes to more realistic minimum $g_s$ values. Such field measurements of $g_{s,n}$ have not previously been incorporated into a global land surface model, despite the possible impacts on surface hydrology, ecosystem carbon gain, and land-atmosphere feedbacks.

We use a global land-surface model, the Community Land Model (CLM) version 4.5, forced with a data atmosphere and driven with observed ('satellite phenology') leaf area indices (CLM4.5SP), to test the sensitivity of the land surface to using realistic minimum $g_s$ from observed $g_{s,n}$, averaged by plant functional type (PFT; Table 1). Since the BWB approach is primarily intended to predict daytime stomatal behavior, the appropriate method for application of observed $g_{s,n}$ within the context of the BWB model is unclear. We therefore test three methodologies for implementing observed $g_{s,n}$: 1) modifying the BWB intercept ($g_o$); 2) setting a nighttime threshold value; and 3) setting a minimum threshold value. We anticipate that implementing observed $g_{s,n}$ values will increase plant transpiration, altering carbon and water budgets on regional and global scales.

2. Methods

2.1 Model Description and Simulation Designing

The CLM4.5SP model used here is an updated version of CLM4.0, originally described by Lawrence et al., (2011), with updated technical details for
v4.5 described by Oleson et al., (2013). The CLM4.5SP simulations were run with CRU-NCEP climate forcing data (combines Climate Research Unit (CRU) TS 3.2 monthly climatology with National Oceanic and Atmospheric Administration National Center for Environmental Prediction (NCEP) and NCAR 2.5° x 2.5° 6-hourly reanalysis; (downloaded at: http://dods.ipsl.jussieu.fr/igcmg/IGCM/BC/OOL/OL/CRU-NCEP/), a historical atmospheric dataset that includes observed precipitation, temperature, downward solar radiation, surface wind speed, specific humidity, and air pressure from 1901 through 2010, and did not include the influences of nitrogen deposition, land use change, or changing CO₂ concentrations. The CLM4.5SP uses the coupled Farquhar photosynthesis and BWB $g_s$ models to simulate plant physiology (Bonan et al., 2011; Oleson et al., 2013). The BWB $g_s$ is calculated based on the equation:

$$g_s = g_0 \beta_{soil} + g_1 (Ah_r/C_a) \quad (Eq. 1)$$

where $g_0$ and $g_1$ are empirical fitting parameters of the minimum $g_s$ and the slope of the conductance-photosynthesis relationship, respectively; $A$ is net carbon assimilation rate ($\mu$mol C m$^{-2}$ s$^{-1}$); $h_r$ is the fractional humidity at the leaf surface (dimensionless), and $C_a$ is the CO₂ concentration at the leaf surface ($\mu$mol mol$^{-1}$), and $\beta_{soil}$ is the soil wetness scalar, ranging from zero to one (see Oleson et al., 2013). $\beta_{soil}$ is calculated as:

$$\beta_{soil} = \sum_i w_i r_i \quad (Eq. 2)$$

where $w_i$ is a plant wilting factor for layer $i$ and $r_i$ is the fraction of roots in layer $i$. When implemented in the unmodified CLM4.5SP, $g_0$ is 10 mmol m$^{-2}$ s$^{-1}$ for all C$_3$ plants and 40 mmol m$^{-2}$ s$^{-1}$ for all C$_4$ plants, and is adjusted by $\beta_{soil}$ a soil wetness factor (varying from 0-1) every time-step. It is also important to note that $\beta_{soil}$ is
also applied to the \( V_{c,\text{max}} \) (the maximum rate of carboxylation) parameter in the \( A \) equation, as well as to leaf maintenance respiration (Oleson et al. 2013).

Values of \( g_{s,n} \) based on literature data (Table S1) are typically larger than the \( g_0 \) values used in current implementations of the BWB model. The \( g_{s,n} \) data, grouped and then averaged by PFT (Table 1), were used to modify simulated minimum \( g_s \) using three methodologies. First, the ‘\( \Delta g_0 \)’ method replaced the BWB minimum conductance, \( g_0 \), value for each simulated PFT with the observed \( g_{s,n} \) (Table 1), resulting in a uniform increase to \( g_s \) during both day and night (referred to as the \( \Delta g_0 \) simulation; tested previously by Barnard and Bauerle, 2013). Second, the \( \Delta g_{\text{night}} \) method implemented the BWB model in its standard form (Eq. 1; the \( g_o \) and \( g_1 \) values are the same as the control), but included a minimum threshold that was applied only at night, based on observed \( g_{s,n} \) for each PFT, below which \( g_s \) could not fall. In the \( \Delta g_{\text{night}} \) simulation, daytime \( \Delta g_s \) occasionally fell below the observed nighttime threshold on account of high vapor pressure deficit (VPD) or low assimilation rates. To avoid this potentially unrealistic behavior, we use a third method, ‘\( \Delta g_{\text{min}} \)’, which extended the observation-based threshold used in the \( \Delta g_{\text{night}} \) simulation to all times during the day or night, so that \( g_s \) never fell below the minimum threshold value found in Table 1. These three modified simulations were compared to a control simulation using the unmodified BWB formulation. Similar to the unmodified and \( \Delta g_0 \) simulations that adjust the \( g_o \) parameter based on a soil wetness scalar \( (\beta_{\text{soil}}) \), the \( \Delta g_{\text{night}} \) and \( \Delta g_{\text{min}} \) modifications also adjusted the minimum \( g_s \) threshold by a soil wetness scalar, \( \beta_{\text{soil}} \) that ranges from zero to one, at every time-step.

Each simulation was run for 25 years with monthly output to determine the
long-term impact of changing minimum conductance, and for one year with half-hourly output to determine the changes in diel patterns.

2.2 Data Collection

Values of $g_{s,n}$ were obtained from field and glasshouse studies, using Scopus (www.scopus.com), with data for 204 records across 150 species and cultivars (Table S1). Records available were predominately for temperate plants (93 records) and crops (34), with more data available for broad-leaf plant types (89) than needle-leaf plants (16; Zeppel et al., 2014). The data were collated by plant functional type (PFT), with means, medians, and standard deviations for each PFT presented in Table 1. Simulations presented here were run with mean values for each PFT, though median values were also tested and are presented in SI Figure 3 and SI Figure 4. Since there is large variability in the PFT responses, we present the range of variability in SI Figure 2.

The measurements of each $g_{s,n}$ value are generally obtained from steady state porometers, diffusion porometers, Licor 1600 and Licor 6400 gas exchange systems (Caird et al., 2007; Phillips et al., 2010), with a small number converted from sap flux (Benyon 1999) using an inverted Penman-Monteith equation. Different sampling methods may lead to different estimates of $g_{s,n}$ and measureable $g_{s,n}$ typically only occurs where VPD is above zero. For example, using a cuvette clamped over the leaf, which changes the leaf boundary layers, will be different compared to measurements from sap flow with an unaltered boundary layer. Data for $g_{s,n}$ were typically reported during well-watered conditions, which is ideal because the CLM4.5 calculates stomatal $g_s$ without
water stress and then adjusts $g_o$ values (and modifications additionally adjust $g_{night}$ and $g_{min}$ thresholds) using a soil wetness scalar.

### 2.3 Terrestrial Coupling Index

To investigate the impact of stomatal conductance changes on the degree to which land processes exert influence over the atmosphere, a terrestrial coupling index was calculated, allowing examination of the influence of a minimum $g_t$ threshold on land-atmosphere coupling. Following Dirmeyer (2011), the terrestrial segment of land-atmosphere coupling is defined as:

$$\text{Terrestrial Coupling Index (TCI)} = \sigma_w * \beta_{w,ET} \quad (\text{Eq. 23})$$

where $\sigma_w$ is the standard deviation of root-zone soil moisture relevant for transpiration across a given season (e.g., 25 years times 3 summer months), and $\beta_{w,ET}$ is the linear slope of monthly mean evapotranspiration and root-zone soil moisture. The TCI captures the variability ($\sigma_w$) and sensitivity of evapotranspiration to changes in soil moisture and returns units equivalent to those of evapotranspiration. Therefore, for a region to have high TCI, soil moisture must have high variability thus enabling any evapotranspiration-soil moisture sensitivity to manifest in the climate system. While this is strictly a metric for defining the terrestrial component of coupling, the terrestrial component has been used as a surrogate for the total soil moisture-precipitation coupling pattern because of the strong spatial pattern correlation (Wei and Dirmeyer, 2012).
3. Results and Discussion

3.1 Implementation of \( g_{s,n} \)

Incorporating observed minimum constraints on \( g_s \) in all modified simulations increased \( g_s \) and transpiration compared to the control simulation, illustrated in Fig. 1 for a highly impacted semi-arid location in Ethiopia (see Fig. S1 for other regions). The large variability in the observational dataset causes substantial uncertainty in the simulations, masking the differences among parameterizations and highlighting the impact of \( g_{s,n} \) on transpiration (Fig. S2).

The sensitivity of \( g_s \) and transpiration to the altered \( g_o \) parameter in the \( \Delta g_o \) simulation is large (Barnard and Bauerle, 2013; Bowden and Bauerle, 2008). Since the higher \( g_o \) is added to \( g_s \) in the BWB calculation at every model time step (see Eq. 1), altering \( g_o \) increases transpiration throughout the entire diel cycle, and produces changes in the daytime evaporative flux that are not supported by observations of \( g_{s,n} \). We consider that uniformly adjusting the \( g_o \) parameter does not represent the correct implementation of observed \( g_{s,n} \) values.

If \( g_o \) cannot be equated to plant minimum \( g_s \) in the BWB paradigm, this raises the possibility of whether \( g_o \) has a theoretical interpretation beyond an empirical fitting parameter. It is possible that \( g_o \) is equivalent to cuticular conductance (\( g_{cut} \)), or conductance that is not regulated by the stomatal guard cells (Caird et al., 2007), occurring during the day and night. Niyogi and Raman (1997) describe \( g_o \) as cuticular conductance, though there is no record of \( g_o \) being tested or described as \( g_{cut} \) previously. Studies that have quantified \( g_{cut} \) found that \( g_{cut} \) was a low proportion, < 10%, of total \( g_s \) and less than measured \( g_{s,n} \) (Caird et al., 2007; Zeppel et al., 2014). The values of \( g_o \) used in current implementations of the Ball-Berry model for C3 plants (10 mmol m\(^{-2}\) s\(^{-1}\)) fall
within the range of measured $g_{cut}$ values (4 to 20 mmol m$^{-2}$ s$^{-1}$; Caird et al., 2007).

Assuming $g_o$ does have a theoretical function of representing $g_{cut}$, rather than $g_{s,n}$, incorporating an observed threshold of minimum $g_s$ is necessary. Whether $g_o$ functions theoretically as $g_{cut}$ in the BWB model needs further evaluation, as adjusting simulated $g_o$ has large impacts on canopy conductance and transpiration (Fig 1; Barnard and Bauerle, 2013). Regardless, observed $g_{s,n}$ is larger than modeled $g_o$ and functions differently, and therefore should be considered independently in model parameterizations.

The $\Delta g_{min}$ and $\Delta g_{night}$ simulations represent the intended change in minimum $g_s$ with greater fidelity, by limiting the minimum value without increasing $g_s$ at every model time step. Interestingly, in restricting only nighttime conductance, the $\Delta g_{night}$ simulation allows daytime $g_s$ to decrease below the nighttime threshold during the dry season in semi-arid ecosystems (Fig. 1a). This occurs when $A_n$ nears zero in shade or low humidity, causing $g_s$ to fall to the default (lower) $g_o$. In contrast, the $\Delta g_{min}$ simulation restricts minimum $g_s$ at all times, and therefore daytime values are never less than the water-adjusted $g_{s,n}$. This increases canopy-averaged daytime $g_s$ and hence transpiration, compared to the unmodified simulation whenever daytime $g_s$ values fall below the minimum threshold (Fig. 1a, c).

The data in Table S1 is a compilation of all available published $g_{s,n}$ data to date, and reports $g_{s,n}$ values for 204 distinct plants. Of these, only four plants exhibit higher $g_{s,n}$ than daytime $g_s$ and two of those are Crassulacean acid metabolism (CAM) plants, which by definition open their stomata at night to gain carbon dioxide and close their stomata during the day, and were not used in our parameterization. These data suggest that, as expected, $g_{s,n}$ is typically less than
daytime \( g_s \). Most data presented in Table S1 are average values under non-drought stressed conditions, and are likely only reported for leaves in sunlit canopy layers. Thus, these data do not elucidate whether, at any given time, daytime values might drop below the nighttime threshold, but only suggest that, on average, they do not.

In the context of the model simulations, low daytime \( g_s \) occurs any time that \( \Delta h_r/C \) is low. These are conditions which are poorly illuminated (in shade or at dawn/dusk and night), or when humidity is low. The CLM4.5SP contains a representation of the shaded canopy, which has lower \( g_s \) and often reaches the minimum daytime threshold (\( g_o \) in the unmodified, \( \Delta g_o \) and \( \Delta g_{night} \) simulations; and \( g_{s,n} \) in the \( \Delta g_{min} \) simulation). The central issue in determining whether the \( \Delta g_{min} \) or \( \Delta g_{night} \) simulation is a better representation of minimum \( g_s \) is whether, under the same conditions in the real world, daytime \( g_s \) might be lower than \( g_{s,n} \).

For example, if observational data support that daytime \( g_s \) is less than \( g_{s,n} \) in shaded canopy layers given the same water availability, then the \( \Delta g_{night} \) simulation is a better parameterization. However, if observational data suggest that daytime \( g_s \) is consistently higher than \( g_{s,n} \) then the \( \Delta g_{min} \) simulation is a better parameterization. While observational data are not available to specifically answer this question, the available data (presented in Table S1) and data from Dawson et al. (2007), which suggest that \( g_{s,n} \) is a fraction of daytime \( g_s \), imply that daytime \( g_s \) is on average higher than \( g_{s,n} \), providing partial support for the \( \Delta g_{min} \) implementation. A different implementation of \( g_{s,n} \) might calculate \( g_{s,n} \) as a proportion of daytime \( g_s \) based on Dawson et al. (2007), who find that \( g_{s,n} \) is a proportion of daytime \( g_s \) that changes based on days since last rainfall. We do
not test this potential method here, but acknowledge it as a viable alternative to be considered.

The possible existence of a higher \( g_{s,n} \) compared to daytime \( g_s \) raises an interesting question about the potential selective advantage for leaves with a high \( g_{s,n} \). It is hypothesized that high \( g_{s,n} \) may provide a beneficial function to the plant, such as embolism repair or phloem transport (e.g., Dawson et al. 2007). Additionally, \( g_{s,n} \) may contribute to xylem refilling, potentially improving carbon gain by making water available when light conditions allow for photosynthesis (Dawson et al. 2007). Critically, it is not clear whether these potential functions are only relevant at night (and daytime \( g_s \) can be lower than \( g_{s,n} \)), or whether high \( g_{s,n} \) is representative of a general strategy of higher overall minimum \( g_o \). We are not aware of data that exist to support either possibility, and advocate for observations that will help determine the functional significance of \( g_{s,n} \).

From a model or theoretical perspective, it is important to note that the reason that simulated \( g_s \) values are reduced to as low as 10 mmol m\(^{-2}\) s\(^{-1}\) (or lower, if down-regulated for water stress) is a function of the universal parameterization of all C\(_3\) plants with that value of \( g_o \). Given that it is unlikely that this value is universal for all plants, we consider that the large difference between the \( \Delta g_{min} \) or \( \Delta g_{night} \) simulations is an artifact of the poorly constrained parameterization of the daytime BWB model.

It should be noted that all the minimum thresholds implemented in our simulations (\( \Delta g_o \), \( \Delta g_{night} \), and \( \Delta g_{min} \)) are adjusted by a soil water scalar (\( \beta_{soil} \)). Therefore, the nighttime (\( \Delta g_{night} \)) and the minimum (\( \Delta g_{min} \)) thresholds are...
altered according to the degree of soil moisture stress. When the daytime $g_s$ value is lower than the $g_{\text{night}}$ threshold in the $\Delta g_{\text{night}}$ simulation (Fig. 1c), the $g_{\text{night}}$ threshold is already down-regulated for water stress. In this scenario, the daytime minimum $g_s$ is less than the nighttime $g_s$ when water stress is equivalent.

Responses to dry soil conditions are mediated both through the minimum $g_s$ values, and through the impact of soil moisture on photosynthetic capacity and leaf maintenance respiration, which are also multiplied by $\beta_{\text{soil}}$. Many of the impacts of our simulations result from feedbacks between higher transpiration rates resulting in faster depletion of soil moisture store, and therefore greater constraint on photosynthesis. These results are all emergent features of the model and should not be interpreted as direct results of the altered parameterization.

3.2 Global Water and Carbon

When averaged over 25 years, incorporating observed rates of $g_{s,n}$ in the $\Delta g_{\text{min}}$ simulation increased transpiration losses up to 30% in the Amazon, and >30% in some arid regions, in part due to the small absolute magnitude of available soil water (Fig. 2a-c). Semi-arid regions are primarily broad-leaf shrub and C3 grass PFTs that have particularly high values (130 and 156 mmol m$^{-2}$ s$^{-1}$ respectively) of observed $g_{s,n}$ (Table 1), and have high nighttime vapor pressure deficits that interact with higher minimum $g_s$ values, causing large nighttime transpiration rates. Using median rather than mean values caused only small (<1.5%) differences in global transpiration (Fig. S3, Fig. S4). Though the magnitude of response is different depending on parameterization used, the
increases in transpiration imply that current model estimates of plant water loss are underestimated in many regions.

Simulated higher transpiration resulting from higher minimum $g_s$ also has ecosystem-scale ramifications for hydrology (McLaughlin et al., 2007). For example, the increased transpiration resulted in drier soils compared to the control simulation (Fig. 2g-i), with $\Delta g_{\text{min}}$ causing >40% soil moisture decreases in semi-arid ecosystems like the Southwestern United States and much of Australia (>10% in $\Delta g_{\text{night}}$). Additionally, the $\Delta g_{\text{min}}$ estimated changes to surface runoff are large in some regions, such as the 10-25% decreases in the tropics (5-10% in $\Delta g_{\text{night}}$; Fig. 2d-f), suggesting that current runoff estimates may be too large. It should be noted that the difference between the $\Delta g_{\text{min}}$ and $\Delta g_{\text{night}}$ simulations is largely due to changes in minimum $g_s$ that affect daytime $g_s$ (see Section 3.1).

Hydrologic changes in soil moisture and runoff in response to increased $g_s$ have previously been documented in catchments in southeastern United States (McLaughlin et al., 2007), and our results suggest that changes to stomatal conductance have similar consequences in CLM4.5SP simulations. Additionally, increasing minimum $g_s$ caused gross primary productivity (GPP) to decrease (Figure 3) by 10 to >25% in many semi-arid regions. These are regions where water availability already restricts GPP, and the decreases in soil moisture caused by higher transpiration likely impart even more drought-induced stomatal closure.

To more directly evaluate the potential influence of minimum $g_s$ on the climate system, we calculate the change in terrestrial coupling to the atmosphere. The terrestrial coupling index (Dirmeyer, 2011) estimates the degree to which changes in soil moisture control surface energy fluxes to the
This study uses root-zone soil moisture rather than soil moisture over spatially constant soil depth to highlight the direct impact of vegetation and minimum $g_s$ on surface fluxes. Here we calculate the terrestrial coupling index during boreal summer months when warmer temperatures allow for the highest $g_s$ rates. We find that the terrestrial coupling strength increases when using the $\Delta g_{\text{min}}$ implementation, but is generally unchanged for $\Delta g_{\text{night}}$ (Fig. 4), meaning root-zone soil moisture exerts a greater control on surface flux variability for $\Delta g_{\text{min}}$, largely due to the impact this simulation has on daytime $g_s$. This increased terrestrial coupling to the atmosphere largely mirrors the reductions in GPP and soil moisture in semi-arid ecosystems, and may reinforce climate extremes such as droughts or heat waves (Hirschi et al., 2011; Miralles et al., 2014).

### 3.3 Evaluating $g_{s,n}$

Evaluating the performance of the new $g_{s,n}$ parameterizations is challenging for numerous reasons. First, our model scales from leaf-level $g_s$ and $g_{s,n}$ estimates to canopy transpiration. The best way of evaluating the model is to compare simulated and observed canopy transpiration because the model captures the average of an entire canopy, which is comprised of multiple plant functional types, rather than individual plant functional types. Incorporating realistic minimum $g_s$ increases global evapotranspiration and decreases global runoff compared to globally-scaled observations, while estimates of GPP from all simulations fall within the range of global GPP estimates from observations (Table 2; Bonan et al., 2011, 2012; Li et al., 2011). However, these comparisons should be used with caution, since eddy covariance data used in estimating the GPP and evapotranspiration observations are susceptible to errors at night (Fisher et al., 2007; van Gorsel et al., 2008; Kirschbaum et al., 2007; Medlyn et al.,
2005) due to a lack of sufficient canopy turbulence that precludes detection of
nighttime transpiration using this measurement methodology, and are not useful
for evaluating the changes in water fluxes tested in this study. Other data for
evaluating model responses to minimum $g_s$ on large spatial scales are not yet
available.

A comparison of simulated canopy transpiration to transpiration
calculated from sap-flux data in Australia (Fig. 5) illustrates that a minimum $g_s$
threshold changes transpiration estimates during the early part of the night,
though simulated nighttime rates are still low compared to observations. All
model parameterizations fall within the observational range of uncertainty, but
under-predict nighttime and midday canopy transpiration during May and June,
and over-predict midday canopy transpiration in July. The lack of fidelity
between the various model parameterizations and the observations is likely
affected by the fact that observed meteorological data were unavailable to force
the model. Therefore, key parameters driving both daytime and nighttime
transpiration fluxes, such as VPD and soil water availability, were likely different
in the model simulations compared to the actual meteorological conditions at
Castlereagh during data collection. Additionally, because sap flow is measured at
the base of the tree, there is typically a lag between when sap flow is measured
and when the canopy transpires, and this lag is also notable in comparing
observed sap flow with simulated estimates of transpiration. Estimating
nighttime transpiration using sap flow methodology is also convoluted with the
refilling of aboveground water stores depleted during the day, and thus is not
directly comparable to our simulations. It should also be noted that the model
does not have a semi-arid plant functional type, so semi-arid plants are typically represented in the model as deciduous plant functional types.

Given that our study focused only on one aspect of the $g_s$ formulation within a land surface model, evaluating daytime $g_s$ and other aspects of the BWB model function (i.e., photosynthetic drivers of daytime $g_s$, feedbacks to water availability, etc.) are all subject to pre-existing deficiencies in the representation of a host of other model processes. For example, there are only two values of the $g_1$ (slope) parameter in the BWB model, one for C$_3$ and one for C$_4$ plants (Sellers et al., 1996), and this parameter has not been modified or comprehensively evaluated within the context of the CLM4.5SP. Indeed, the use of the BWB model at all is currently the subject of some debate (Bonan et al., 2014; De Kauwe et al., 2015), and this study additionally highlights how the empirical nature of the BWB model leads to difficulties when attempting to implement mechanistic processes. Further, daytime $g_s$ is also dependent on the photosynthetic capacity, and observations of $V_{\text{cmax}}$ and $J_{\text{max}}$ (Bonan et al., 2011; Kattge and Knorr, 2007) indicate very wide ranges of plant functional type variation in these properties, also limiting our confidence that the globally averaged parameters used in the default model will lead to accurate $g_s$ and transpiration at most locations. We choose not to focus on these and other parameters that effect daytime $g_s$ as it does not directly impact the representation of $g_{s,n}$ and is therefore beyond the scope of this paper.

4. Conclusion

The rate of minimum $g_s$ estimated from the BWB model used in many global land surface models is typically smaller than observed $g_{s,n}$ (Barnard and
Bauerle, 2013), as demonstrated in a review of 204 species (Zeppel et al., 2014). Including a nighttime or minimum \( g_s \) threshold based on observations results in simulated hydrologic changes, such as decreased soil moisture and runoff (Fig. 2), particularly in semi-arid regions where water availability already restricts growth. In addition to potentially increasing drought stress in sensitive regions, this has the impact of reducing plant growth (Fig. 3) and changing the modeled terrestrial coupling to the atmosphere (Fig. 4). The difference between the \( \Delta g_{\text{min}} \) and \( \Delta g_{\text{night}} \) simulations highlights one outstanding uncertainty: Does minimum daytime \( g_s \) decrease below nighttime \( g_s \)? While the balance of our arguments favors the \( \Delta g_{\text{min}} \) implementation of \( g_{\text{cn}} \), this study primarily illustrates the potential sensitivity of global simulations to minimum \( g_s \) considerations, and serves as motivation for additional field experiments, particularly in semi-arid areas, to discern better representations of low \( g_s \) conditions during daytime and nighttime. To better understand the future of these sensitive ecosystems, widespread field observations, quantification of minimum daytime \( g_s \) and a better understanding of the physiological causes and consequences of nighttime transpiration are necessary so that land surface models can robustly incorporate observations and theory.

5. Code and Data Availability

The code for CLM4.5 is publically available through Subversion code repository: https://svn-ccsm-models.cgd.ucar.edu/cesm1/release_tags/cesm1_2_2. To access the code, fill out a short, required registration to get a user name and password, necessary to gain access to the repository.

Guide can be found at: 

http://www.cesm.ucar.edu/models/cesm1.2/clm/models/lnd/clm/doc/UsersGuide/book1.html. All stomatal conductance data used in developing the implementations can be found in Table S1.

Author Contributions

DL, MZ, and RF conceived the project. MZ assembled the $g_{s,n}$ datasets; DL ran model simulations; and DL and AT analyzed model simulations, with guidance from RF. All authors contributed to writing the paper.

Acknowledgements

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## Tables

**Table 1.** Old and new minimum stomatal conductance values used in CLM4.5SP. Units are mmol m\(^{-2}\) s\(^{-1}\).

<table>
<thead>
<tr>
<th>Plant Functional Type</th>
<th>Old Value</th>
<th>Mean New Value</th>
<th>Median New Value</th>
<th>Standard Deviation</th>
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<td>10</td>
<td>16.896</td>
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<td>20.803</td>
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<td>35.367</td>
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*New Value, Standard Deviation and n are based on data pooled from the literature.*
<table>
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<tr>
<th>Simulation</th>
<th>$g_{an}$ data used</th>
<th>GPP (Pg C yr$^{-1}$)</th>
<th>ET ($10^3$ km$^3$ yr$^{-1}$)</th>
<th>Runoff ($10^3$ km$^3$ yr$^{-1}$)</th>
</tr>
</thead>
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<tr>
<td>Control</td>
<td>N/A</td>
<td>157.83</td>
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<td>Mean</td>
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</table>

$^a$Global gross primary productivity (GPP), evapotranspiration (ET) and runoff values. Observed values presented in Bonan et al. (2011), Welp et al. (2011), and Lawrence et al. (2011)
Figure Captions

Figure 1. Diurnal time-series of canopy conductance (a,c) and transpiration (b,d) for Ethiopia over five days in mid-January (a-b) and mid-July (c-d). The control simulation (solid black line) had lower conductance and transpiration than the Δg_o simulation (dotted red line) and the Δg_min simulation (dashed blue line). The Δg_night simulation (dot-dashed teal line) had higher nighttime conductance and transpiration than the control simulation, but similar daytime conductance and transpiration, allowing for daytime conductance to fall below the nighttime threshold. The Δg_o simulation added the observed gs,n values to the conductance calculation at every time, day or night, which is not theoretically aligned with the function of including observed gs,n. As a result, the Δg_o simulation was eliminated from further analyses. Note that all minimum thresholds (g_o, g_night, and g_min) were adjusted using a soil moisture scalar.

Figure 2. Simulated average transpiration (a), runoff (d), and soil moisture (g) for a control simulation; and percent change from control in transpiration (b-c), runoff (e-f), and soil moisture (h-i) after including a nighttime threshold (Δg_night; b,e,h) or a minimum gs threshold (Δg_min; c,f,i) based on observational data. Note that both nighttime and minimum thresholds were adjusted based on a soil moisture scalar.

Figure 3. Average gross primary productivity (GPP) for a control simulation (a), and percent change from control (b-c) after including a nighttime threshold (Δg_night; b) or a minimum gs threshold (Δg_min; c) based on observational data.
Note that both nighttime and minimum thresholds were adjusted based on a soil moisture scalar.

**Figure 4.** Terrestrial coupling for June-July-August for a control simulation (a), and the difference from control (b-c) after including a nighttime threshold ($\Delta g_{\text{night}}$; b) or a minimum $g_s$ threshold value ($\Delta g_{\text{min}}$; c) based on observational data. Note that both nighttime and minimum thresholds were adjusted based on a soil moisture scalar.

**Figure 5.** Average diel canopy transpiration for the months of May, June, and July in Castlereagh, Australia (observation, dotted black line), estimated from sap flux measurements of Red Gum and Iron Bark, the dominant tree species in the canopy. Average simulated canopy transpiration for the grid cell corresponding to Castlereagh, Australia for the control (unmodified; solid black line), $\Delta g_o$ (Ball-Berry $g_o$ parameter adjusted; red line), $\Delta g_{\text{night}}$ (minimum nighttime threshold added; teal line), and $\Delta g_{\text{min}}$ (minimum conductance threshold added; blue line) simulations. Error bars corresponding to the observations (dashed) and each simulation (solid) are colored accordingly, and are calculated as +/- one standard deviation from the mean. Note that the simulations use meteorological forcings from an atmospheric dataset (see Methods), not the local meteorology from when the measurements were collected (some meteorological data was collected at the site, but not all variables required by the model). The simulated grid cell covers a much larger area than the observational data collection site.
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