College of Arts and Sciences

Department of Biological Sciences

THE UNIVERSITY OF
ALABAMA
ARTS & SCIENCES

Dr. Gregory Starr, Professor
Department of Biological Sciences
3097A Shelby Hall
Tuscaloosa, AL. 35487
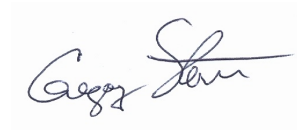
gstarr@ua.edu
205-348-0556

December 15, 2018

Dear Dr. Still

Please find enclosed our revised manuscript, mss# bg-2018-322, title, "Quantifying energy use efficiency via entropy production: A case study from longleaf pine ecosystems." We have completed all revisions per the Reviewer's' comments and suggestion. We would like to thank them for their constructive reviews which have help to improve the manuscript. Below are the Reviewer's' comments in normal black font and our responses to the comments in blue. We have include in our online submission both a marked and clean copy of the revised manuscript. Please contact me if you have any questions regarding the manuscript.

Sincerely,

Gregory Starr, Ph.D.
Professor of Global Change Biology
University of Alabama

1

Reviewer 1: Alex Kleidon

Reviewer's comment: *First, the entropy balance is used in Eq. 9, stating that the "overall change in entropy production (S) over time (t) in kJ m-2 K-1 of the ecosystem [is estimated] by adding entropy flux and entropy production". This is incorrect. What Eq. 9 formulates is the entropy balance. It balances the change in entropy on the left hand side of the equation (dS/dt) with the sum of all entropy exchange fluxes (J) and all entropy production terms (σ). This balance is typically assumed to be zero in a steady state, i.e., dS/dt = 0, which then allows one to diagnose entropy production from the difference in entropy exchange fluxes. This is in fact what the authors do to diagnose entropy production in Eqs. 3.6 and 3.7 to diagnose entropy production by absorption of radiation. Yet, the authors later use dS/dt in Eq. 4.8 to derive an efficiency. This efficiency should be zero, otherwise they did not do the balancing correctly. So there is a major inconsistency in the methodology that needs to be resolved.*

Authors' response: We have changed the calculation for dS/dt and now focused on the entropy outputs and inputs and internal entropy production, to quantify the change in entropy (dS/dt). Please see section 2.5 (Eq. 4.9) and the results section 3.6 in the revisions.

Reviewer's comment: *Second, entropy production by absorption of longwave radiation is estimated using net longwave radiation at the surface (Eq. 3.7). What is the justification for using net long- wave radiation, rather than gross fluxes? After all, the downwelling longwave radiation of the surface adds an entropy flux of Rldown/Tsky, while the emission of radiation from the surface exports entropy at the rate of Rlup/Tsrf. Using the difference of these two fluxes (assuming that dS/dt=0) yields an entropy production of σ = Rlup/Tsrf - Rl- down/Tsky, which is not the same as (Rlup - Rldown) * (1/Tsrf - 1/Tsky). The authors should correct this, or explain why their expression is justified. The same reasoning applies to the application of net ecosystem exchange, where I think that also gross fluxes should be used, not net fluxes.*

Authors' response: Thank you for pointing out the mistake. We have adjusted our calculations following the Brunsell et al. (2011) approach using incoming longwave radiation to calculate entropy production as follows: $R_{l,in}$ x $(1/T_{srf}-1/T_{sky})$. We acknowledge that calculating the $R_{l,up}/T_{srf}$ and $R_{l,down}/T_{sky}$ will estimate the incoming and outgoing entropy transfer associated with longwave radiation, but not the entropy produced due to absorption of longwave radiation and conversion to heat during this process (as shown in Brunsell et al. 2011). Please see section 2.5 (Eq. 4.7) in the manuscript.

We have also eliminated the efficiency ratio calculations of metabolic activity and now quantify the overall change in metabolic energy using solely NEE. We believe that using direct fluxes is superior, as it avoids any influence of model bias, as R_{eco} is estimated using temperature data. However, we have changed the analysis to comparing metabolic energy and entropy changes in the systems (see section 2.5 and the results section 3.5), rather than using a ratio to quantify metabolic efficiency. We have also changed our analysis to using daily average half-hourly fluxes for all variables in the manuscript following your comment.

Reviewer's comment: *Additional insights gained from entropy fluxes and entropy production The authors link their entropy-based analysis to rather general concepts such as resilience and energy use efficiency. Yet, I do not see the additional insights gained by using entropy production, rather than an analysis based on the entropy, water, and carbon balance. Why does the entropy-based analysis provide more or novel insights that cannot be obtained by just an interpretation based on fluxes? The authors do not really answer this question within the manuscript and do not use the results to show this, as they only focus on an entropy-based analysis.*

In terms of interpreting the observations, I think that there is a critical step missing that relates the observed differences to an interpretation of processes, and this cannot be gained by just looking at entropy. For instance, temperature changes result from changes in the energy balance, as temperature is a measure for heat content. Yet, the energy balance is not even shown or discussed. Likewise, to understand changes in evaporation, I would expect a water balance being discussed. Instead, this study directly diagnoses entropy fluxes and thereby skips this process-based level of interpretation. It does not show and interpret the fluxes of the energy, water, and carbon balances separately, and does not demonstrate that something else can be learned by looking at entropy.

By lumping all aspects of the land surface into entropy production, I think that this neglects those aspects that are relevant for ecosystems from those that are irrelevant. The relevant flux for ecosystems is primarily the uptake of carbon, as this provides the chemical energy for terrestrial ecosystems. Plants live from the energy they fix during carbon assimilation, and, quite frankly, care little about the entropy production of other processes.

For this manuscript to provide more solid insights, I think it needs a more process based interpretation using the available data, it needs to be more specific regarding those terms that are really relevant to ecosystems, and it needs to at least discuss why there is more to be gained by looking at entropy-based diagnostics.

Authors' response: We have added an analysis and discussion of energy fluxes and the sites' energy balances to show the novelty of the entropy approach and to highlight specifically that the inclusion of entropy production gives more insights about the energy efficiencies and ecosystem function. Please see sections 3.3 and 3.4 for the results. To estimate the entropy budget of ecosystems, it is of particular importance to quantify entropy production based on the absorption of radiation, as this term is of similar magnitude as the entropy fluxes of LE and H together at our sites. We have also added a more thorough introduction and discussion of the topic.

We have also included soil moisture content and rainfall in our analysis to quantify changes in entropy fluxes and entropy production, but an analysis of the whole water budget was beyond the scope of this research project.

We kindly disagree with the reviewer's comment that the relevant flux for ecosystems is solely the carbon flux. For ecosystems (encompassing not only plant organisms), the partitioning of heat fluxes plays a significant role in their function, because the physical and biological processes are interconnected. LE in particular plays a large role in the maintenance of the surface temperature in ecosystems and is one of the largest contributors to entropy export in our ecosystem.

Minor comments:

Abstract: "Our study provides foundational evidence of how MEP can be used to determine resiliency across ecosystems globally" - I am not at all convinced and doubt this conclusion. The authors provide no discussion why a diagnosis based on entropy fluxes yields more or better insights than the diagnosis of energy, water, and carbon balances. I see this as a critical missing bit in this manuscript.

Authors' response: We have adjusted the discussion and methodology to show that entropy metrics can give further insights about differences in ecosystem function at the three longleaf pine sites, in addition to using energy fluxes. Our revisions focus on the entropy import and export, as well as the internal entropy production, to quantify how close these ecosystems are to a thermodynamic steady state.

Introduction, page 2, line 16: MEP is referred to as a principle in the text. At best, it is a "proposed" principle, or better hypothesis, as it is not generally being accepted.

Authors' response: We have adjusted the sentence accordingly.

page 2, line 24: How can agricultural systems exceed MEP if MEP already describes the maximum? This does not make sense. What I can imagine is that agricultural systems maintain a different state because of nutrient inputs, but then, the boundary conditions are changed because there are additional exchange fluxes across the system boundary. Also, why would this excessive entropy production be unsustainable? As long as the nutrient input can be maintained, I see no reason why it should be unsustainable.

Authors' response: We have altered our introduction to focus more on the importance of entropy exchanges and entropy production in ecosystems. The section of MEP and MEP in agricultural systems has therefore been eliminated.

page 3, line 9: What are entropy efficiency ratios? In thermodynamics, efficiency is used to describe the conversion efficiency of one form of energy into another, and this involves entropy (like the well-known Carnot limit). But to speak of efficiency for entropy does not make sense to me.

Authors' response: We have adjusted our revisions to avoid the use of "entropy efficiency".

page 6, line 4: How can two unknowns (GEE and Reco) be estimated from one equation? I think there is some information missing here.

Authors' response: We have added a more detailed description of how these fluxes were obtained (see section 2.4).

page 6, line 8: The authors convert the units from W m-2 K-1 to kJ m-2 K-1. The unit should be kJ m-2 K-1 month-1 (i.e., the time is missing, throughout the whole manuscript), since entropy production refers to a rate, and not to an amount. But I do not understand the motivation for not keeping the units

Authors' response: We have adjusted the units accordingly and are now using daily averages of half-hourly energy and entropy fluxes in W m^{-2} and W m^{-2} K^{-1}, respectively.

page 6, line 14: Radiative entropy production actually includes a factor of 4/3, as it does not deal with heat, but with radiation (the additional contribution of 1/3 is due to radiation pressure). I think it needs a brief explanation why this factor was omitted.

Authors' response: We avoided this factor assuming that the incoming and outgoing radiation does not assert radiation pressure (see Ozawa et al. 2003; Kleidon and Lorenz, 2005; Fraedrich and Lunkeit, 2008; Kleidon, 2009; Pascale et al., 2012). Please see section 2.5.

page 7, line 2: What do you mean by "to calculate the change in entropy of the metabolic system". Do you refer to entropy production? If you want to estimate entropy production, this would relate to dissipation of carbohydrates, which in turn relates to respiration. So I do not understand why NEE is being used.

Authors' response: As noted above, we have changed the calculation of metabolic energy and entropy solely using NEE data without quantifying an efficiency ratio. Instead we are now comparing results for NEE energy and entropy.

*page 7, line 14: Why is net longwave radiation being used to calculate entropy production? The entropy fluxes of longwave radiation are Rl,down/Tsky and Rl,up/Tsrf as the authors write earlier in the manuscript. But this is not the same as Rl,net * (1/Tsrf - 1/Tsky). (See major comment above)*

Authors' response: We have altered this calculation method in section 2.5. Please see our response above.

page 7, line 20: dS/dt refers to the change in entropy with time, not change in entropy production. It should be zero in steady state, otherwise one cannot calculate entropy production from entropy fluxes. (See major comment above)

Authors' response: You are correct. As noted above, we have fixed this error.

page 7, line 29/30: Why are these expressions referred to as MEP? I see no connection to MEP. They just formulate radiative entropy production. Also, what's the difference to Eq. 3.6 and 3.7?

Authors' response: We have revised this section to make it clearer that we are talking about an assumption. If this assumption does not necessarily reflect reality, it still gives us a means to compare different ecosystems or sites with respect to how they reflect, absorb and emit radiation.

page 8, line 3: "an ecosystem maximizes its entropy production when it converts all incoming Rs and Rl into work". This is not correct. First, work is something different than entropy production. Second, it is impossible to convert all incoming radiation into work, as it would imply that there is no energy left to maintain a temperature that is greater than T = 0K.

Authors' response: As noted above, we have changed the dS/dt section, and have excluded this ratio analysis.

page 8, line 3: ". . . MEP.. is often negative or 0". No! Entropy production must always be greater or equal to zero, otherwise there is something wrong in the formulations! Spontaneous reductions in entropy are only possible at the microscopic scale during extremely short time periods but are practically irrelevant at the scale of ecosystems.

Authors' response: We have adjusted the sentence accordingly in section 2.6.

page 8, line 7: "maximum entropy of metabolism". What do you mean by this?

Authors' response: We apologize for the confusion with this statement. We have changed our analysis to using net fluxes and are now looking at metabolic activity, rather than efficiency at the site by comparing energy and entropy fluxes of NEE at the sites.

page 8, line 13: You express the efficiency as the ratio of the entropy flux associated with net ecosystem exchange to the energy flux of GEE. Should this not compare gross energy fluxes, rather than net exchange to gross exchange

Authors' response: We have excluded the analysis of metabolic efficiency in the revised paper.

page 8, line 16: This expression merely describes a radiative entropy flux, but not entropy production, or a maximum in entropy production.

Authors' response: We have altered the section including the whole ecosystem entropy budget; this section was omitted.

page 8, line 18: This expression does not give an efficiency, because in steady state (a condition needed to estimate entropy production from fluxes), dS/dt = 0 so this expression is zero as well.

Authors' response: As noted above, we have altered the calculation.

I stop here with commenting, because I think that the methodology has a number of flaws that I wonder how much these impact the results. In addition, as expressed earlier, I think that the overall motivation for this entropy-based analysis needs to be improved.

Authors' response: We have substantially altered the introduction and discussion in the revised manuscript to improve clarity about the methodology and as to why entropy metrics are useful in quantifying differences in ecosystem function.

Response to reviewer 2

Major Comments

Reviewer's comment: *The authors need to provide a more detailed overview of the concept of entropy. Are these concepts definable for biological systems? What are the caveats? How do they fit in with the second law of thermodynamics (and concepts of disorder and free energy)?*

Author's response: We have added more background information on the concept of entropy, specifically tailored towards biological systems.

Reviewer's comment: *The framework presented in this study is built on Stoy et al., 2014, which in turn used a formulation by Holdway et al., 2010. These essentially simplify the concept of entropy to temperature normalization of fluxes of energy, carbon and water exchange. While a temperature normalized index for these quantities is likely to be highly useful in itself, does it warrant invoking entropy? Moreover, there are several inconsistencies, and not adequate explanation for how entropy for different fluxes is estimated. For instance, eq 4.6. which the authors define as the entropy efficiency of metabolism, is essentially a ratio of NEE:GPP. This has been previously identified as carbon use efficiency and extensively studied (for. e.g. see DeLucia et al., 2007 and references therein). In many instances, it is unclear how energy and entropy are related. It would be useful to present side-by-side comparisons.*

Author's response: You are correct; the concept of thermodynamic entropy applied in our study is essentially a normalization of energy fluxes to temperature, as the magnitude of entropy fluxes and entropy production is a function of the temperature from which flux originated. This can be helpful in determining differences in energy use efficiency in ecosystems, specifically for the sites as these differed in sky, air, surface and soil temperatures. We are now using half-hourly fluxes for all energy and entropy in our calculations. Furthermore, we have omitted the section on metabolic efficiency ratios and are now focusing on metabolic activity in terms of energy and entropy (see section 2.5 and 3.5).

Three examples

Reviewer's comment: *1. Page 3, line 3: how does the entropy dissipation through sensible heat relate to energy dissipation? These concepts need to be clarified. 2. Fig. 4. Why look at JLE instead of LE fluxes? What is additionally learned from this? 3. Page 10, line 31. JNEE not being related to soil moisture. This claim (I say claim since data is not shown) would be highly interesting if it is contrasted with the NEE response to soil moisture. There are more rigorous formulations (e.g. Wu et al., 2017) as well as critical discussions (e.g. Volk and Paulus, 2010).*

Author's response: An analysis of entropy fluxes is preferable in ecosystems which are exposed to different environmental variables, such as differences in surface and air temperatures, which affect the magnitude of entropy fluxes and entropy production. For example, two systems could have similar magnitudes of LE, but differ in J_{LE} due to differences in air or surface temperatures. For the ecosystem which maintains a higher surface/air temperature, the entropy flux would be lower, suggesting that it is less efficient in exporting entropy across its boundaries. By calculating the difference between entropy outputs and inputs, as well as internal entropy production, one can estimate how close an ecosystem is to a thermodynamic "steady state" and

therefore how organized it is. This cannot be accomplished by studying the energy balance alone. We have added a more thorough introduction and discussion of why entropy metrics can be more useful in describing energy use efficiency.

Reviewer's comment: *Another cause for concern is that that inferences are not quantitatively supposed. There are several instanes where analysis is restricted to 'eyeballing' relationships between different curves, and correlation coefficients are not presented. In some occasions this leads to the authors making inferences that are not backed up by the data that is presented.*

Author's response: We have added tables of Type III effect summaries for all models in the supplementary materials.

Reviewer's comment: *The writing is overly descriptive, and often disconnected with the conclusions. Is this study describing entropy fluxes and efficiency ratios and how these vary with different environmental conditions, or is it trying to use these variables to understand site differences? The result is an unclear combination of the two. I would recommend the Authors' to stick to a storyline that is supported by the data.*

Author's response: Thank you for this valuable comment. We used environmental variables to understand changes and differences in entropy production and fluxes and thus changes in energy efficiency at our three sites. We have added an explanation of the objective of this study.

Reviewer's comment: *Finally, there are several instances where the authors discuss the effect of soil moisture and rainfall on various fluxes/processes in the text (e.g. lines 13,19, 31 on page 10, line 25 on page 11) but do not choose to show these data. In my opinion these data are critical and need to be discussed (since it is a drought recovery study).*

Author's response: We have added figures showing all significant effects included in our models.

Reviewer's comment: *In light of these observations, I would not recommend this manuscript in its current form for publication in Biogeosciences. I think the authors provide very valuable observations, but should consider either re-framing the study or provide a more critical discussion on the concept of MEP, as well as consider extensive revisions on the writing as well as presentation of data.*

Author's response: We have altered the introduction and discussion to reflect your comment.

Figures

Reviewer's comment: *There are several instances where curves are classified as significantly different, but do not appear significantly different from each other at all (Fig. 1d, for instance). The authors need to expand figure captions, since in the current form it is hard to infer what is being shown. E.g. Figure 4 has three time series (one for each site in most panels) but only one for sub panels b and e. It is unclear what data are presented. There are similar issues with Figs. 5-7.*

Author's response: We have added supplementary tables with all type 3 effects for all models included in this manuscript to show where there are significant differences among the independent variables. However, we note in figure captions when interactive effects were not significant, thus only showing a single black line (for example see fig. 6 for panels (g), (h) and (o)).

Reviewer's comment: *I also feel that the authors rely on too much on summarizing data and do not explain how or why this is done (again, eg. Fig 4b and d). What are the data that are presented in these analyses?*

Author's response: We have changed our analysis to estimating entropy from mean half hourly energy fluxes to daily time-steps (W m^{-2} K^{-1}).

Reviewer's comment: *The authors need to include sub panels in the text (Fig. 4a, b etc.).*

Author's response: Thank you for this suggestion; we have added sub-panel information to the text.

Reviewer's comment: *Figure 1 has inconsistent units for temperature. For instance, subpanels c and e are plotted in units of Kelvin but d and f are in deg. C. Also, VPD is plotted in Figure 1 but not discussed at all amongst other discussions of Fig. 1 (Sec. 3.1).*

Author's response: We have added Figure 2 for sky, air, surface and soil temperatures with consistent units. We have also added more text describing differences in VPD (see section 3.1).

Reviewer's comment: *Fig 2. Why are monthly means shown here, while the rest of the paper annual means are presented?*

Author's response: We are now using daily average half hourly estimates in our models. All figures will show these values on the same timestep, with the exception of SI Figure S1, as it seemed more appropriate to show monthly sums of rainfall, as differences among the sites and years became more apparent this way.

Reviewer's comment: *Table 1: Please provide LAI estimates (if available) and also disturbance history, since this is a key component of your overall conclusions.*

Author's response: We have added LAI data for the mesic and xeric site. Unfortunately that information was not available for the intermediate site. We have also added fire disturbance history for all sites to Table 1.

Minor comments

Reviewer's comment: *Page 2 Line 1-2: Turbulent exchange of... specify (for e.g. momentum, heat, gases). Line 3: Maybe just use examples related to terrestrial ecosystems? Are these examples of the butterfly effect in terrestrial ecosystems?*

Author's response: We have adjusted the sentence accordingly.

Reviewer's comment: *Page 5 Lines 5-9: This assumes energy balance closure. Please describe why you closed the energy balance.*

Author's response: To accurately describe the entropy balance for ecosystems, we are required to have a closed energy balance. Following your and reviewer 1's comments, we have added a more detailed description of the energy balance and energy partitioning at the three sites (see section 2.2)

Reviewer's comment: *Page 6 Eq. 2: Describe briefly how NEE was partitioned into source and sink terms.*

Author's response: We have added a more detailed description on how we partitioned NEE into GEE and R_{eco} following Whelan et al. (2013) and Starr et al. (2016).

Reviewer's comment: *Page 7 eq. 3.6. and 3.7: Unclear why net fluxes are used. Line 23: Are periods of rainfall excluded from the analyses? Where is this described? eq 4.1 and 4.2: Why is 4.1. formulated using incoming radiation whereas as 4.2 using net fluxes?*

Author's response: We have revised this section and are estimating entropy production as follows:

$$\sigma Rs = Rs, in - Rs, out \left(\frac{1}{Tsrf} - \frac{1}{Tsun} \right)$$

$$\sigma Rl = Rs, in \left(\frac{1}{Tsrf} - \frac{1}{Tsun} \right)$$

For the actual entropy production calculation only shortwave radiation that was absorbed by the ecosystem would be converted into heat, whereas for the MEP calculation we quantified the maximum entropy production, assuming that an efficient ecosystem would absorb all $R_{s,in}$. In contrast, for $R_{l,in}$ energy is absorbed and then reemitted by the ecosystem rather than reflected.

Reviewer's comment: *Page 8 eq. 4.8 is essentially carbon use efficiency (see major comment above).*

Author's response: We have omitted the section on metabolic ratios and focus on energy and entropy of the metabolic system using NEE.

Reviewer's comment: *Page 9 Line 11. Subpanels missing. Lines 21-24: temperatures differences do not appear to be significantly different across sites in Fig. 1.*

Author's response: We kindly note that even though these figures appear to not show significant differences in temperature across the sites, our statistical results indicate that there were in fact significant differences in temperature. We have added supplementary type-3 results for all models to show this.

Reviewer's comment: *Page 10. Sec. 3.2. Methods for this analysis are not presented. I think this section should be merged with Sec. 2.1. (site description), as it doesn't appear to be a result of this study (unless methods are presented). Line 14: Soil moisture data seems important here (and in other places). Line 15: VPD effects are discussed first but EVI figure shown first in Fig. 4. Line 23: This is not correct according to Fig. 4. Line 23: See major comment above.*

Author's response: We have added a description of the methods that were used to estimate understory biomass for the three sites. In addition we have added graphs for all significant effects in the models. The description of all variables has been ordered to be consistent with the text.

Reviewer's comment: *Page. 13 Line 1: What does 'preservation' on LE mean? Again, these are hard to interpret in the absence of absolute fluxes (see major comment above). Line 8: Ecosystems do not 'experience' LE (or JLE), but rather the interactions between the ecosystem and the overlying atmosphere determines the LE flux. Line 13: Clarify what this means.*

Author's response: As noted above, we have added an analysis of the energy balance to show absolute fluxes. We also have changed the wording and made sure to not "personalize" ecosystems throughout this manuscript.

Reviewer's comment: *Page 14 Line 8: should read "at the more biodiverse site (i.e. mesic)" Line 11: What was the contribution of the C4 understory photosynthesis to overall ecosystem photosynthesis? Did you measure this? Lines 25-30: This is incorrect. Annual (and monthly) changes in EVI do not reflect changes in biomass. Biomass includes the carbon stored in the trunks, branches and stems of trees (among other pools), which do not fluctuate in forests at these timescales. Instead, at these timescales EVI is a measure of canopy greenness that is related to net photosynthesis (see Sims et al., 2008).*

Author's response: We have changed the sentence accordingly. Unfortunately, we have no estimates of variation in ecosystem fluxes from differences in understory composition at our sites. However, in another study we showed that the understory contributes about 50% to R_{eco}, using soil respiration data. We have also corrected the definition of EVI in the text.

Quantifying energy use efficiency via entropy production: A case study from longleaf pine ecosystems

Susanne Wiesner[1], Christina L. Staudhammer[1], Paul C. Stoy[2], Lindsay R. Boring[3,4], Gregory Starr[1]

[1]Department of Biological Sciences, University of Alabama, Tuscaloosa, AL. 35487. USA.

5 [2]Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717, USA

[3]Jones Ecological Research Center, Newton, GA 39870, USA.

[4]Odum School of Ecology, University of Georgia, Athens, GA, 30602, USA

Correspondence to: Gregory Starr (gstarr@ua.edu)

Abstract. Ecosystems are open systems that exchange matter and energy with their environment. They differ in their efficiency
10 in doing so as a result of their location on Earth, structure, and disturbance, including anthropogenic legacy. Entropy has been
proposed to be an effective metric to describe these differences as it relates energy use efficiencies of ecosystems to their
thermodynamic environment (i.e. temperature) but has rarely been studied to understand how ecosystems with different
disturbance legacies respond when confronted with environmental variability. We studied three sites in a longleaf pine
ecosystem with varying levels of anthropogenic legacy and plant functional diversity, all of which were exposed to extreme
15 drought. We quantified radiative (eff_{rad}), metabolic and overall entropy changes – as well as changes in exported to imported
entropy (eff_{flux}) in response to drought disturbance and environmental variability using 24 total years of eddy covariance data
(8 years per site). We show that structural and functional characteristics contribute to differences in energy use efficiencies at
the three study sites. Our results demonstrate that ecosystem function during drought is modulated by decreased absorbed solar
energy and variation in the partitioning of energy and entropy exports owing to differences in site enhanced vegetation index
20 and/or soil water content. Low eff_{rad} and slow adjustment of eff_{flux} at the anthropogenically altered site prolonged its recovery
from drought by approximately one year. In contrast, stands with greater plant functional diversity (i.e., the ones that included
both C3 and C4 species) adjusted their entropy exports when faced with drought, which accelerated their recovery. Our study
provides a path forward for using entropy to determine ecosystem function across different global ecosystems.

1 Introduction

25 Ecosystems utilize resources, such as solar radiation, nutrients and water, to maintain a state far from thermodynamic
equilibrium (Amthor, 2010; Beer et al., 2009; Finzi et al., 2007; Thomas et al., 2016). Understanding ecosystem resource use
efficiency is crucial, as anthropogenic and climate induced changes around the globe continue to alter ecosystem structure and
function (Haddeland et al., 2014; Porter et al., 2012; Reinmann and Hutyra, 2016; Thom et al., 2017).

Ecosystems are open and dynamic systems that exchange matter and energy with their surroundings as described by the
30 ecosystem energy balance:

$$R_n = R_{s,in} - R_{s,out} + R_{l,in} - R_{l,out} = LE + H + G + M \quad\quad (1)$$

1

where R_n is net radiation, $R_{s,in}$ and $R_{s,out}$ are incident and upwelling shortwave radiation, and $R_{L,in}$ and $R_{L,out}$ are incoming and upwelling longwave radiation, respectively. The terms LE, H and G represent energy exports through latent heat, sensible heat and ground heat fluxes, respectively and M is an energy storage term comprised of changes in biomass accumulation through metabolic processes (Holdaway et al. 2010). M is often neglected due to the assumption of a steady state over longer periods

5 and because M is much smaller in magnitude compared to other fluxes, but it imposes a control on energy fluxes, like R_n, LE and H, through changes in leaf area and reflective properties, as well as through active biotic control in response to changes in environmental variables (i.e., stomata opening and closing due to water availability (Hammerle et al., 2013).

From equation 1, ecosystem energy exchange is a function of its thermodynamic environment - the heat transfer of a system with its surroundings - which differs based on the different mechanisms by which heat is transported: conduction, convection,

10 radiation. Complicating our understanding of ecosystem energy dynamics is the fact that more frequent fluctuations in environmental variables are expected as a result of global climate change, including extreme events like droughts, which will alter the resource efficiency of ecosystems across the globe and with it their resilience (Franklin et al., 2016; Woodward et al., 2010).

It is hypothesized that ecosystems aim to optimize their energy use and thus maximize their balance of entropy production and

15 entropy exports to avoid thermodynamic equilibrium (Schneider and Kay, 1994; Schymanski et al., 2010). The magnitude of entropy production and entropy fluxes in ecosystems depends on thermodynamic gradients (i.e., thermal gradients, chemical gradients, etc.) between organisms and their surroundings (Kleidon, 2010). Ecosystems invest energy to build more complex structures (i.e., self-sustainability; Müller and Kroll, 2011; Virgo and Harvey, 2007), which can enhance their entropy export and therefore keep the ecosystem far from thermodynamic equilibrium (Odum, 1988; Schneider and Kay, 1994; Holdaway et

20 al., 2010; Skene, 2015). For example, forest stands with more vertical structure were found to be more efficient in harvesting available light, which consequently increased their productivity (Bohn and Huth, 2017; Hardiman et al., 2011). Productive sites with greater leaf area can maintain higher latent energy (LE) fluxes, which increases their entropy export (Meysman and Bruers, 2010, Brunsell et al., 2011); LE fluxes also maintain lower ecosystem surface temperatures and thereby greater entropy production. On the contrary, large values of H caused by surface temperatures that are greater than air temperatures, result in

25 lower entropy production (LeMone et al., 2007). This has been shown in deforested landscapes (Bonan, 2008; Khanna et al. 2017), as well as comparative studies of different vegetation types and in ecosystems with heterogeneity in their vegetation distribution (Holdaway et al., 2010; Brunsell et al., 2011; Kuricheva et al., 2017).

Here, we evaluate how efficiently ecosystems use energy by assessing ecosystem entropy production as well as by quantifying the ratios in entropy imports and exports (eff_{flux} and dS/dt) in three study ecosystems that represent an edaphic and management

30 gradient. We do so by measuring their structural complexity over an eight-year period via the enhanced vegetation index (EVI) and variation in annual understory biomass, and in relation to the energy and entropy partitioning of incoming energy from solar radiation. We build upon the techniques proposed by Holdaway et al. (2010), Brunsell et al. (2011), and Stoy et al. (2014), by calculating entropy production and entropy fluxes within longleaf pine (*Pinus palustris* Mill.) ecosystems. The sites differed in ecosystem structure (i.e., basal area, Table 1) and plant functional diversity due in part to differences in soil water holding

35 capacity, as well as different levels of anthropogenic legacy. The sites were exposed to a severe drought in the beginning of

2

this study, which we used to quantify entropy exchanges in response to the disturbance. First, we compare and contrast differences in ecosystem energy fluxes (i.e., R_n, LE, H, G and the net ecosystem exchange of carbon dioxide, NEE) and entropy fluxes (J_{LE}, J_H, J_G, J_{NEE} and radiative entropy production) in response to changes in structural and environmental variables (EVI, SWC, VPD, and precipitation). Next, we quantify how entropy exports and entropy production at the different sites adjust to changes in incoming entropy when exposed to drought. We do so by estimating radiative efficiency (eff_{rad}), the ratio of entropy production to an empirical maximum entropy production (MEP), and ratios of daily imported and exported entropy fluxes (eff_{flux}), as well as through the overall change in entropy (dS/dt) at the sites. We hypothesize that: (1) the xeric site will have a higher entropy flux from J_H and J_G, but lower J_{NEE} due to its lower EVI and lower basal area, which will result in more variable dS/dt compared to the other sites; (2) the mesic site will maintain higher eff_{rad} due to its greater structural complexity (i.e., plant functional diversity and basal area) and thus greater absorptive capacity for solar radiation compared to the other sites; (3) the intermediate site will have lower eff_{rad} and eff_{flux} compared to the mesic and xeric sites, as a result of its lower plant functional diversity (i.e. low abundance of C4 species) and structural complexity, causing lower absorption of solar radiation and export of entropy through LE.

2 Materials and Methods

2.1 Site description

This study was conducted at the Joseph W. Jones Ecological Research Center in southwestern Georgia, USA (31.2201° N, 84.4792° W) from January 2009 to December 2016. The three sites are maintained by frequent low intensity fire on a two-year return interval and were last burned in 2015 (Starr et al., 2016). The climate is humid subtropical with a mean annual precipitation of 1310 mm (Kirkman et al., 2001). Mean temperature extremes range from 3 °C to 16 °C in winter and 22 °C to 33 °C in summer (NCDC, 2011).

The three sites differ based on soil moisture availability, as a result of differences in soil drainage. The mesic site lies on somewhat poorly drained sandy loam over sandy clay loam and clay textured soils (Goebel et al., 1997; 2001). Soils at the intermediate site are well drained and have a depth to the argillic horizon of ~165 cm (Goebel et al., 1997). The xeric site lies on well-drained deep sandy soils with no argillic horizon (Goebel et al., 1997). All sites are situated within 10 km of each other and have average elevations of 165, 155, and 160 m for the mesic, intermediate, and xeric sites, respectively.

95-year-old longleaf pine trees (*Pinus palustris* Mill.) dominate the overstory of all sites, and overall basal area (B_A) and diameter at breast height (DBH) varied by site (Table 1). The overstories of each site also contain a small proportion of oak trees; The xeric site has the highest proportion with 22 %, versus 8 % and 7.7 % at the mesic and intermediate sites, respectively. The understory at the mesic and xeric sites is largely covered with perennial C4 grass species, such as wiregrass (*Aristida beyrichiana* [Trin.]), whereas woody species dominate the intermediate site. composition and abundance of other plant species varies by site (Kirkman et al., 2001; 2016). Soil perturbation at the intermediate site affected species richness, so that wiregrass is almost absent.

We acquired EVI for 2009 through 2016 for all three sites from the online data pool at lpdaac.usgs.gov via the NASA Land Processes Distributed Active Archive Center (LP DAAC) and the USGS Earth Resources Observation and Science Center

3

Deleted: ecosystem resilience through the calculation of entropy efficiency ratios. We focused on entropy production from the absorption of radiation (eff_{rad}) and metabolic activity (eff_M), as well as overall ecosystem function (i.e., entropy production from LE, H, metabolism and radiation; eff_s).

Deleted: We hypothesize that (1) the xeric site will have a higher entropy flux from sensible heat (J_H) due to its lower vegetation coverage and lower basal area, and therefore higher partitioning into H rather than LE, which will lower its overall entropy efficiency compared to the mesic site, (2) the mesic site will be able to maintain higher entropy efficiencies (eff_{rad}, eff_M and eff_s) due to its structural complexity (i.e., species diversity and basal area), and (3) the intermediate site will have lower eff_{rad}, eff_s and eff_M compared to the mesic and xeric sites, as a result of its lower biodiversity and structural complexity, a consequence of its anthropogenic legacy.¶
We show that a combination of different entropy efficiency ratios revealed how structural and functional characteristics in this ecosystem contribute to energy use efficiencies at the three sites. Our results demonstrate that resilience to disturbance is a function of entropy efficiency, as low efficiencies at anthropogenically altered sites prolonged the recovery from drought by approximately a year. In contrast, more biodiverse stands (in overstory and understory) were able to maintain high entropy/energy use efficiencies, which increased their resilience to and recovery from drought.¶

Deleted: ,

Deleted: with

Deleted: of oak trees in the overstory

Deleted: at

Deleted: The

Deleted: overstory and understory

Deleted: , resulting in an understory dominated by woody species

Deleted: monthly

(EROS), using MODIS Aqua and Terra data products (MYD13Q1 and MOD13Q1; DAAC, 2008) to quantify changes in ecosystem structure from disturbance. EVI products for the sites were available on an eight day basis and linearly interpolated to obtain daily estimates. We also acquired Palmer Drought Severity Indices (PDSI) for Southwest Georgia from the National Oceanic and Atmospheric Administration data archive for 2009 to 2016 to identify the months of drought disturbance (Dai et al., 2004).

5

Understory composition and biomass was estimated annually from 2009 through 2013. Thereafter, the collection frequency became biannual, so that 2014 and 2016 were missing in the data collection. Understory biomass was estimated using 0.75 m² clip plots, which were randomly located by tossing a plot frame from pre-installed litter trap positions (n = 20 per site; Wiesner et al. 2018). All live and dead vegetation, smaller than 1 m in height was clipped and analyzed in our laboratory. Vegetation

10 was classified by plant family (here, forbs, ferns, legumes, wiregrass, other grasses, and woody plants), and each sample was dried to constant weight.

Net ecosystem exchange of CO₂ measurements. Net ecosystem exchange (NEE) was measured continuously at 10 Hz at all three sites from January 2009 to December 2016 using open-path eddy covariance (EC) techniques (Whelan et al., 2013). Data were stored on CR-5000 dataloggers (Campbell Scientific, Logan, UT). CO_2 and water vapor concentration were measured

15 with an open path infrared gas analyzer (IRGA, LI-7500, LI-COR Inc., Lincoln, NE) and wind velocity and sonic temperature were measured with a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Logan, UT). These sensors were installed ~4 m above mean canopy height at each site (34.5, 37.5, and 34.9 m for the mesic, intermediate and xeric sites, respectively), ~0.2 m apart to minimize flow distortion between the two instruments and vertically aligned to match the sampling volume of both instruments.

20 **2.2 Sensible and latent heat flux measurements**

Net energy fluxes of LE and H were estimated in W m⁻² using temperature and wind velocity measurements from the sonic anemometer, as well as water vapor density measurements from the IRGA:

$$LE = \lambda \rho_a \overline{w'q'} \qquad (2.1)$$

$$H = \rho_a c_p (\overline{w'T_s'} - 0.000321 T_s \overline{w'q'}) \qquad (2.2)$$

25 where λ is the latent heat of vaporization (J kg⁻¹), ρ_a is the density of air (kg m⁻³), c_p is the specific heat of air (kJ kg⁻¹ K⁻¹), w' is the instantaneous deviation of vertical wind speed (w, m s⁻¹) from the mean, and q' and T_s' are the instantaneous deviations of water vapor concentration (kg kg⁻¹) and sonic temperature (Kaimal and Gaynor, 1991) from their respective means. The overbars in Eqs. 1.1 and 1.2 signify the time-averaged covariance. Missing H and LE were gap-filled on a monthly basis using simple linear models as a function of R_n.

30 In cases where energy balance closure was not achieved, energy fluxes of H and LE were corrected using the Bowen method following Twine *et al.* (2000), where fluxes are adjusted using residual energy and the estimated Bowen ratio ($\beta = H/LE$), which assumes that β was correctly measured by the EC system:

$$LE = \frac{1}{1+\beta} (R_n - G) \qquad (2.3)$$

4

$$H = \beta \times LE \tag{2.4}$$

Closing the energy balance is important to quantify differences in energy and entropy fluxes by site, as according to the First law of Thermodynamics energy is always conserved. To quantify differences in environmental drivers and site variation between energy and entropy fluxes, we established models of average daily energy fluxes (described in section 2.7)

5 **2.3 Meteorological instrumentation**

Meteorological data above the canopy were also collected and stored on the CR-5000 dataloggers (Campbell Scientific, Logan, UT). Meteorological data measured on the towers included: photosynthetically active radiation (PAR; LI-190, LI-COR Inc., Lincoln, NE), global radiation (LI-200SZ, LI-COR Inc., Lincoln, NE), incident and outgoing shortwave and longwave radiation to calculate R_n (NR01, Hukseflux, thermal sensors, Delft, The Netherlands), precipitation (TE525 Tipping Bucket

10 Rain Gauge, Texas Electronics, Dallas, TX), wind direction and velocity (Model 05103-5, R.M. Young, Traverse City, MI), air temperature (T_{air}) and relative humidity (RH; HMP45C, Campbell Scientific, Logan, UT), and barometric pressure (PTB110, Vaisala, Helsinki, Finland).

Soil temperature (T_{soil}), volumetric water content of the soil (SWC) and soil heat flux (G) were measured in one location near the base of each tower at each site every 15 seconds and averaged every 30 minutes on an independently powered CR10X

15 datalogger. T_{soil} was measured at depths of 4 and 8 cm with insulated thermocouples (Type-T, Omega Engineering, INC., Stamford, CT), and G was measured at a depth of 10 cm with soil heat flux plates (HFP01, Hukesflux, Delft, The Netherlands). SWC was measured within the top 20 cm of the soil surface using a water content reflectometer probe (CS616, Campbell Scientific, Logan, UT).

2.4 Data processing

20 Raw EC data were processed using EdiRe (v.1.4.3.1184; Clement, 1999), which carried out a two-dimensional coordinate rotation of the horizontal wind velocities to obtain turbulence statistics perpendicular to the local streamline. Fluxes were calculated for half-hour intervals and then corrected for mass transfer resulting from changes in density not accounted for by the IRGA. Barometric pressure data were used to correct fluxes to standard atmospheric pressure. Flux data screening was applied to eliminate 30-min fluxes of NEE, H and LE, resulting from systematic errors as described in Whelan et al. (2013)

25 and Starr et al. (2016). Such errors encompassed (amongst other things): rain, poor coupling of the canopy and the atmosphere (defined by the friction velocity, ustar), and excessive variation from half-hourly means.

Gross ecosystem exchange (GEE) and ecosystem respiration (R_{eco}) were estimated from eddy covariance measurements of net ecosystem exchange of CO_2 (NEE; $\mu mol\ m^{-2}\ s^{-1}$) at a time resolution of half an hour, from which GEE and R_{eco} can be estimated as follows:

30 $$GEE = -NEE + R_{eco} \tag{3}$$

Missing half hourly data were gap-filled as described in Whelan et al. (2013) and Starr et al. (2016). Daytime and nighttime data were estimated utilizing a Michaelis-Menten approach for (PAR > 10 $\mu mol\ m^{-2}\ s^{-1}$) and a modification of the Lloyd and Taylor (1994) model (PAR $\leq$ 10 $\mu mol\ m^{-2}\ s^{-1}$), respectively. Monthly equations were used to gap-fill data; however, where too

few observations were available to produce stable and biologically reasonable parameter estimates, annual equations were used. NEE partitioning to estimate daytime R_{eco} was performed by using the nighttime gap-filling equation, and then utilizing equation (3) to estimate GEE. Nighttime GEE was assumed to be zero.

2.5 Entropy production calculations

5 Half-hourly Net ecosystem exchange of CO_2 was converted to W m^{-2} (NEE_e) using the assumption that one micromole of CO_2 stores approximately 0.506 J, where 1 J m^{-2} s^{-1} equals 1 W m^{-2} (Nikolov et al., 1995).

For entropy production and fluxes of shortwave (R_s) and longwave radiation (R_l) we followed established approaches of Brunsell *et al.* (2011), Holdaway *et al.* (2010), and Stoy *et al.* (2014). The half-hourly entropy flux produced through absorption of R_s emitted by the surface of the sun (J_{Rs}, W m^{-2} K^{-1}) was calculated as:

10
$$J_{Rs} = \frac{R_{s,net}}{T_{sun}} \qquad (4.1)$$

where sun surface temperature (T_{sun}) was assumed to be 5780 K, with $R_{s,net}$ defined as the difference of incident and upwelling R_s. The entropy flux of R_l (J_{Rl}, W m^{-2} K^{-1}) was calculated as:

$$J_{Rl} = \left(\frac{R_{l,in}}{T_{sky}} - \frac{R_{l,out}}{T_{srf}}\right) \qquad (4.2)$$

where $R_{l,in}/T_{sky}$ is the entropy flux of $R_{l,in}$ as incoming R_l ($J_{Rl,in}$), and $R_{l,out}/T_{srf}$ is the entropy flux of $R_{l,out}$ as outgoing R_l ($J_{Rl,out}$).

15 surface temperature (T_{srf}; K) was calculated from upwelling R_l ($R_{l,out}$):

$$T_{srf} = \left(R_{l,out} \middle/ (A \times e_{srf} \times k_B)\right)^{1/4} \qquad (4.2.1)$$

with emissivity of the surface calculated as $e_{srf} = 0.99-0.16\alpha$ (Juang et al., 2007), the view factor A was assumed to be unity, and the Stefan-Boltzmann constant $k_B = 5.67 \times 10^{-8}$ W m^{-2} K^{-4}. The shortwave albedo (α) was calculated as the daily average of noontime outgoing R_s ($R_{s,out}$) divided by $R_{s,in}$. The sky temperature, T_{sky} (K), was calculated from $R_{L,in}$ using the Stefan-

20 Boltzmann equation:

$$T_{sky} = \left(R_{l,in} \middle/ (A \times e_{srf} \times k_B)\right)^{1/4} \qquad (4.2.2)$$

where the emissivity of the atmosphere (e_{atm}) was assumed to be 0.85, following Campbell and Norman (1998).

All other ecosystem entropy fluxes J_{LE}, J_H, J_G, and J_{NEE} (W m^{-2} K^{-1}) were calculated by dividing the energy fluxes by temperature as:

25
$$J_x = \frac{x}{T_y} \qquad (4.3)$$

where $x = LE$, H, G and NEE_e, and T_y = was assumed to be T_{air} (for J_{LE}, J_H and J_{NEE}; K) or T_{soil} (for J_G, in K). We used the energy of NEE (NEE_e) directly measured with the EC towers, to calculate the change in entropy of the metabolic system.

We also calculated entropy produced from evaporation associated with mixing of saturated air from the canopy with the fraction of air in the atmosphere that has RH below 100 % (JLE_{mix}), following Holdaway *et al.* (2010):

30
$$JLE_{mix} = ET \times R_v \times \ln(RH) \qquad (4.4)$$

6

where the evapotranspiration rate, $ET = LE/\rho_a\lambda$, λ is the latent heat of vaporization of water, and R_v is the gas constant of water vapor (0.461 kJ kg^{-1} K^{-1} for moist air).

The sum of entropy of ecosystem fluxes (J, W m^{-2} K^{-1}) for each half-hour was then calculated by adding all entropy fluxes between the surface and atmosphere:

$$J = J_{Rl} + J_{Rs} + J_{LE} + J_H + J_G + J_{NEE} + JLE_{mix} \hspace{2cm} (4.5)$$

The conversion of low entropy R_s and R_l to high entropy heat at the surface through absorption of R_s and R_l, respectively, was calculated as:

$$\sigma_{Rs} = R_{s,net}\left(\frac{1}{T_{srf}} - \frac{1}{T_{sun}}\right) \hspace{2cm} (4.6)$$

$$\sigma_{Rl} = R_{l,in}\left(\frac{1}{T_{srf}} - \frac{1}{T_{sky}}\right) \hspace{2cm} (4.7)$$

where T_{srf} is the radiometric surface temperature (Eq. 3.2.1) and σ_{RS} and σ_{Rl} are in W m^{-2} K^{-1}.

The overall half-hourly entropy production (σ, W m^{-2} K^{-1}) was then calculated as the sum of the entropy productions of R_s and R_l:

$$\sigma = \sigma_{Rl} + \sigma_{Rs} \hspace{2cm} (4.8)$$

We excluded the factor 4/3, which is associated with the transfer of momentum exerted by electromagnetic radiation on a surface (Wu et al., 2008), in our calculations of σ and J for entropy production and entropy fluxes because we assumed that radiation pressure at the sites would be negligible (see Ozawa et al. 2003; Kleidon and Lorenz, 2005; Fraedrich and Lunkeit, 2008; Kleidon, 2009; Pascale et al., 2012). Finally, we estimated half-hourly change in entropy production (S) over time (t) in W m^{-2} K^{-1} of the ecosystem by adding entropy flux of imports ($J_{Rs,net}$, $R_{Rl,in}$) and exports (i.e., J_{LE}, J_H, J_G, J_{NEE}, $J_{Rl,up}$, JLE_{mix}) and entropy production:

$$dS/dt = J + \sigma \hspace{2cm} (4.9)$$

Note that this approach does not account for entropy production due to frictional dissipation of entropy from rainfall or subsurface water flow, as these would be of even smaller magnitude than entropy production from metabolic activity of the ecosystem (Brunsell et al., 2011). Here negative dS/dt represents the export of entropy of the ecosystem to its surroundings.

2.6 Ecosystem entropy models for radiation and ecosystem fluxes

We estimated half-hourly MEP of the radiation budget (MEP_{rad}) in W m^{-2} K^{-1}, to compare site differences in radiation energy use and entropy dissipation.

Empirical MEP (MEP_{rad}) was determined following Stoy et al. (2014), by estimating the MEP of half-hourly R_s (MEP_{Rs}) and R_l (MEP_{Rl}):

$$MEP_{Rs} = R_{s,in}\left(\frac{1}{T_{air}} - \frac{1}{T_{sun}}\right) \hspace{2cm} (5.1)$$

$$MEP_{Rl} = R_{l,net}\left(\frac{1}{T_{srf}} - \frac{1}{T_{air}}\right) \hspace{2cm} (5.2)$$

$$MEP_{rad} = MEP_{Rs} + MEP_{Rl} \hspace{2cm} (5.3)$$

Deleted: $JLE_{mix} = ET \times R_v \times ln(RH)$ (3.4)

Deleted: λ, λ

Deleted: R_v

Deleted: kJ

Deleted: $J = J_{Rl} + J_{Rs} + J_{LE} + J_H + J_G + J_{NEE} + JLE_{mix}$ (3.5)

Deleted: $\sigma_{Rs} = R_{s,net}\left(\frac{1}{T_{srf}} - \frac{1}{T_{sun}}\right)$ (3.6)
$\sigma_{Rl} = R_{l,net}\left(\frac{1}{T_{srf}} - \frac{1}{T_{sky}}\right)$ (3.7)

Deleted: kJ

Deleted: kJ

Deleted: $\sigma = \sigma_{Rl} + \sigma_{Rs}$ (3.8)

Deleted: overall

Deleted: kJ

Deleted: $dS/dt = J + \sigma$ (3.9)

Deleted: MEP calculations
We estimated MEP of the radiation budget (MEP_{rad}), metabolic

Deleted: budget (MEP_M),

Deleted: overall entropy (MEP_s) in kJ m^{-2} K^{-1}, to compare their effectiveness in quantifying

Deleted: function.

We assume that under ideal conditions, an ecosystem maximizes its entropy production when it converts all incoming R_s and R_l into work (Stoy et al., 2014). While this assumption does not necessarily reflect reality in natural ecosystems, this method gives us a means to compare different sites with respect to their reflective and absorptive capacities *versus* a reference ecosystem that absorbs and dissipates all incident solar energy. Note that MEP_{Rl} is often of lower magnitude than MEP_{Rs}

5 because here we assume that an efficient ecosystem would dissipate less energy through sensible heat, such that T_{srf} would approach T_{air}.

The half-hourly entropy ratio of radiation is then calculated using σ from Eq. 4.8 as follows:

$$eff_{rad} = \frac{\sigma}{MEP_{rad}} \qquad (5.4).$$

We then estimated the variable eff_{flux} as the ratio of incoming radiation entropy (J_{Rs} and $J_{Rl,in}$) and the sum of exported entropy

10 fluxes (J_{LE}, J_H, J_G, J_{NEE}, and $J_{Rl,up}$) to assess how entropy was partitioned into entropy production and entropy fluxes over the different study years.

2.7 Statistical analyses

We estimated average daily values for all response variables to decrease autocorrelation for statistical analysis. We first tested for significant differences in environmental and structural variables among the three sites prior to the entropy analysis. We

15 estimated simple general linear mixed models (GLMM) using the R package *nmle* to look at differences among sites for: rain, SWC, vapor pressure deficit (VPD), EVI, T_{srf}, T_{air}, T_{sky} and T_{soil}, as well as $R_{s,in}$, $R_{s,out}$, $R_{l,in}$ and $R_{l,out}$. All response variables were daily means, for rainfall we calculated monthly sums to estimate differences among the sites. We included a random effect for day of measurement, to account for repeated measurements, as well as an AR(1) structure to account for temporal autocorrelation among measurements. The model of rainfall only included year and site as independent variables and no

20 random effects. Independent variables for the other models were month, year and site, as well as their interactions. Subsequently, we estimated GLMMs of daily energy (R_n, LE, H, G and NEE_e) and entropy fluxes (J_{LE}, J_H, J_G, and J_{NEE}), entropy production (σ), entropy ratios (eff_{rad} and eff_{flux}) and overall entropy (dS/dt) to quantify their differences by environmental and structural variables by site. For all models we included random effects and an AR(1) autoregressive correlation structure to account for repeated daily measurements. All models initially included independent variables for site,

25 year and month, mean EVI, SWC, VPD and daily rainfall sums. We also included interactions of environmental variables with site, site with year and site with month, to determine changes in the energy efficiency over the study period among sites. Independent variables and their interactions were deemed significant when p<0.05. We used a Tukey adjustment to test for significant differences among sites. GLMM Analyses were performed via the R packages *nlme*, *lsmeans*, and *car* (Fox and Weisberg, 2011; Lenth, 2016; Pinheiro et al., 2014).

8

3 Results

3.1 Differences in environmental, radiative and temperature variables among sites

All three sites experienced severe drought from mid-2010 through mid-2012 (Fig. S1, Supplementary Information). There was no significant difference between the mesic and xeric sites in rainfall sums, but the intermediate site had lower rainfall sums (~20 mm per month) compared to the other sites (Table S1). SWC was significantly lower at the xeric (<19 %) compared to mesic and intermediate sites (~20 %) for all years of this study (Fig. 1a and b, Table S2). SWC and EVI decreased during the drought at all sites, but only significantly so at the mesic site. VPD significantly increased at all sites during the drought. For all years, EVI was significantly lower (0.02-0.04) at the xeric site compared to the other two sites (Fig. 1e and f), while the intermediate site had significantly higher EVI compared to the mesic site, except in 2010.

Daily T_{srf} at the mesic site was significantly higher than the xeric site for all years except 2012, 2014 and 2016 (Fig. 2a). From 2012 to 2016 the intermediate site had higher T_{srf} compared to the other two sites. T_{air} was significantly lower at the mesic site compared to the intermediate and xeric sites for all years, except in 2014, and in 2012, when the xeric site had higher T_{air} compared to the intermediate (Fig. 2a). T_{soil} was significantly lower at the mesic site compared to the other sites, except in 2013, when there was no significant difference between the mesic and xeric sites. For all years, daily T_{soil} was significantly higher at the xeric site compared to the intermediate site except for 2011 and 2012, when the intermediate site was significantly higher.

$R_{s,out}$ was significantly higher at the xeric site compared to the other sites, except for 2014, where we found no significant difference between the intermediate and xeric sites. Daily $R_{s,out}$ was also significantly lower at the mesic site, compared to the intermediate site, except in 2009. Average daily $R_{l,out}$ was significantly lower at the mesic site compared to the intermediate site during all years, except for 2011 and 2012, and compared to the xeric site for all years, except for 2011, the intermediate site had significantly higher $R_{l,out}$ compared to the xeric site during 2013, 2014 and 2016. As a consequence of these component fluxes, R_n was significantly higher at the xeric site compared to the intermediate site for all years except 2009 and 2014 (SI Fig. S2a, Table S3). Average R_n was significantly lower at the mesic site compared to the xeric site in 2013 and 2016, and was significantly higher compared to the xeric site from 2009 to 2011. Average daily R_n significantly increased at the intermediate and xeric sites but showed no change at the mesic site with an increase in EVI (SI Fig. S3a).

Environmental, radiative and temperature variables also tended to be significantly different among months within site, and in many instances among sites by month. Differences followed seasonal patterns, as noted in SI Fig. S2 and SI Table S2.

3.2 Understory wiregrass and woody abundance at the sites

Wiregrass was virtually absent at the intermediate site for all years of this study (Fig. 4a), whereas woody species were more abundant compared to the others. The mesic and xeric sites both had higher proportions of wiregrass in the understory (~25 % versus 5 % at the intermediate site), which slightly decreased during 2011 (Fig. 4a). In addition, woody biomass increased to ~75 g m^{-2} at the xeric site during 2011, but not at the mesic site. In 2012, woody biomass decreased to ~40 g m^{-2} at the xeric

and intermediate sites and remained low during the following years at the xeric site, but increased at the intermediate site (>100 g m^{-2}, Fig. 4b).

3.3 Energy fluxes of H, LE, and G

LE was significantly lower at the intermediate site compared to the mesic site for all years, except 2011, and compared to the xeric site for all years, except for 2015. We found no significant difference between the mesic and xeric sites in 2009, 2010, 2014 and 2016, but for the other years of this study the xeric site had significantly higher LE. LE significantly increased at all sites with higher EVI, with a greater increase at the intermediate and a smaller increase at the xeric site, compared to the mesic site (SI Fig. S3g). LE significantly increased at all sites with an increase in SWC and VPD (SI Fig. S3e and f). LE at the intermediate site was significantly lower compared to the other sites for all levels of VPD (SI Fig. S3g). LE was significantly lower with higher rainfall, with no significant differences among sites (SI Fig. S3h).

There was no significant difference in H between the mesic and intermediate sites, except in 2011 and 2013, when the mesic site was higher than the intermediate, and in 2015 and 2016, when the reverse occurred. H was significantly lower at the xeric site compared to the mesic site for all years except for 2014 and 2016, and compared to the intermediate site for all years except 2011 and 2013. Average H was significantly higher at the mesic site compared to the xeric site during the months of May through October (SI Fig. S2b). The intermediate site had significantly lower H compared to the other two sites for the months of January through March and the xeric site had significantly lower H for June through October. Compared to the other two sites, average H was significantly lower at the intermediate site when EVI was greater than 0.4, and significantly higher at the xeric site for EVI > 0.5 (SI Fig. S3i). Average H significantly decreased at all sites with an increase in SWC (SI Fig. S3j). Average daily H significantly increased at all sites with an increase in VPD, with a lower decrease at the intermediate site (SI Fig. S3k).

G was significantly lower at the intermediate site during 2016 (negative), compared to 2009 through 2011 and 2014. Average daily G was positive during summer months, and negative during winter months (October through March) at all sites (SI Fig. S2b). Average daily G significantly decreased with an increase in EVI at the mesic and intermediate site, but had no significant change at the xeric site (SI Fig. S3m). G was significantly less positive at the xeric site compared to the other sites for EVI < 0.3, but was significantly more negative at the intermediate site compared to the mesic and xeric sites when EVI was above 0.4. Average G significantly decreased (to negative) with an increase in SWC (SI Fig. S3n), and significantly increased (to positive) with an increase in VPD, but only at the intermediate and xeric sites (SI Fig. S3o). Daily rainfall did not significantly alter G at the sites, but the intermediate had significantly more negative G compared to the other two sites (2-10 W m^{-2}) when daily rainfall was positive (SI Fig. S3p).

3.4 entropy fluxes of J_H, J_{LE}, and J_{NEE} and J_G and entropy production

For all years, average daily σ was significantly higher at the mesic site compared to the intermediate site (by > 0.01 – 0.036 W m^{-2} K^{-1}; Fig. 5a, Table S4), while σ was not significantly different between the mesic and xeric sites for almost all years (Fig 5a). Average daily σ significantly increased with EVI, independent of site (Fig. 6a), and also significantly increased with

10

SWC and VPD, with a greater slope at the xeric site (Fig. 6b and c). Average daily σ significantly decreased at all sites with an increase in rainfall (noting that entropy production from rainfall itself is not considered here and assumed to be approximately equal amongst ecosystems), and σ was significantly lower at the intermediate site during rainy periods compared to the other two sites (Fig. 6d). There was no significant difference in σ at the mesic and xeric sites for all levels of rain.

5 The xeric site had significantly higher average daily J_{LE}, ranging from ~0.22 to 0.28 W m^{-2} K^{-1}, versus the intermediate site with ~0.18 – 0.25 W m^{-2} K^{-1} (Fig. 5a, Table S4) for all years, except 2015. J_{LE} at the xeric site was also higher than the mesic site in 2011 through 2013 and in 2015, ranging from 0.2 to 0.26 W m^{-2} K^{-1}. The mesic site had ~0.01-0.06 W m^{-2} K^{-1} higher J_{LE} compared to the intermediate site, except in 2011. J_{LE} significantly increased with greater EVI and SWC (Fig. 6e and f). J_{LE} was significantly higher at the xeric site compared to the other sites for EVI < 0.4. J_{LE} was significantly higher at the xeric 10 site compared to the other sites when SWC was above 19%, similar to the model of LE. J_{LE} significantly increased with VPD, and significantly decreased with rainfall (Fig. 6g and h). Unlike the model results for LE, the effects of VPD were not significantly different by site.

Models of H and J_H were similar, except that J_H in the mesic and xeric sites were not significantly different in 2015 (Fig. 5a, Table S4). Average daily J_H was significantly higher at the mesic site in 2011 and 2012 (~0.2-0.24 W m^{-2} K^{-1}) compared to 15 the intermediate (~0.19 W m^{-2} K^{-1}; Fig. 5a) and xeric sites (~0.16-0.20 W m^{-2} K^{-1}). In 2009, 2010 and 2012, the xeric site had significantly lower J_H compared to the other sites (by ~ 0.02 W m^{-2} K^{-1}). J_H decreased only at the mesic and intermediate sites with increasing EVI (Fig. 6i) such that the intermediate site had significantly lower J_H compared to the other sites when EVI was above 0.4. J_H decreased with increased SWC at all sites, and the xeric site had significantly lower J_H compared to the other sites when SWC was above 19 % (Fig. 6j). VPD significantly increased J_H at all three sites, with a greater increase at the xeric 20 site (Fig. 6k). J_H significantly decreased at all sites with increased rainfall, where the intermediate site had significantly lower J_H compared to the mesic and xeric sites when rainfall was greater than 40 mm per day (Fig. 6l).

Average daily J_G was not significantly different among the years 2009-2014 and 2016 at the mesic site, but significantly increased during 2015 (Fig. 5a, Table S4), similar to the model results for G. Similarly, J_G was significantly lower at the intermediate site during 2016 (negative). J_G at the xeric site was not significantly different by year. Average daily J_G was 25 positive during summer months, and negative during winter months at all sites (Fig. 5b). Average daily J_G significantly decreased from positive to negative at the mesic and intermediate sites with an increase in EVI, with no significant change at the xeric site (Fig. 6m), similar to the model of G. J_G was significantly more negative at the intermediate site compared to the other sites for EVI > 0.4. Average J_G only significantly decreased at the intermediate and xeric sites (to negative), such that J_G was significantly more negative at the two sites when SWC was above 18% (Fig. 6n). J_G significantly increased with greater 30 VPD, independent of site (Fig. 6o). Similar to the model of G, daily rainfall did not significantly alter the magnitude of J_G at the sites. However, the intermediate had significantly more negative J_G compared to the other two sites when daily rainfall increased (Fig. 6p).

11

3.5 Metabolic energy and entropy

Metabolic energy was consistently more negative at the mesic site, compared to the other sites for all years in this study (Fig 7a, Table S5). The intermediate and xeric sites exported metabolic energy from 2009 through 2011, which was greater at the intermediate site for 2010. NEE_e significantly increased to more negative at all sites during May and significantly decreased during August through October, which resulted in positive NEE_e at the intermediate site (Fig. 7b). NEE_e significantly decreased at all sites with an increase in EVI, which was greater at the xeric site (Fig. 7c). An increase in SWC resulted in decreasing NEE_e, independent of site (Fig. 7d). An increase in VPD significantly decreased NEE_e to more negative at all sites, with a greater decrease at the intermediate site (Fig. 7e). Increases in rainfall significantly increased NEE_e to positive at all sites, where the intermediate site had a greater increase compared to the other sites (Fig. 7f).

In contrast to the model of NEE_e, results of the model of J_{NEE} indicated that the mesic site had significantly more negative J_{NEE} compared to the other sites during most years; but during 2011 J_{NEE} was significantly less negative at the site compared to the intermediate and xeric sites (Fig. 7g). The intermediate site had consistently more negative J_{NEE} compared to the xeric site, except for 2014 where J_{NEE} significantly decreased at the site. J_{NEE} was more negative during summer months at all sites with no significant differences between the mesic and xeric sites (Fig. 7h, Table S5). Values of J_{NEE} significantly decreased with an increase in EVI, independent of site (Fig. 7i), different from the model of NEE_e. SWC significantly decreased J_{NEE} at all sites, with a greater slope at the mesic site (Fig. 7j). Higher VPD significantly increased J_{NEE} similar to the model of NEE_e; however slopes were more similar among the sites (Fig. 7k). Rainfall significantly decreased J_{NEE} to less negative with a greater slope at the intermediate site, similar to the model of NEE_e (Fig. 7l).

3.6 Entropy models

From 2011 through 2016, eff_{rad} was significantly higher at the mesic site (0.89-0.93), compared to the intermediate (0.88-0.91) and xeric (0.88-0.92) sites, which were not significantly different (Fig. 8a). Average eff_{rad} did not significantly change with EVI, but significantly increased with higher SWC (Fig. 8c), independent of site. Higher VPD significantly decreased values of eff_{rad} at all sites (Fig. 8d). The mesic site had significantly higher values of eff_{rad} compared to the other two sites for all levels of VPD (Fig. 8d). Rainfall significantly increased values of eff_{rad} at all sites, with a greater increase at the intermediate site (Fig. 8e, Table S6).

Daily average eff_{flux} was significantly greater at the mesic site for most of the measurement period (Fig. 9a, Table S6). eff_{flux} was significantly higher at the xeric site compared to the intermediate site for the years 2009, 2011, and 2013 through 2015. For 2012 and 2016 the intermediate site had significantly greater eff_{flux} compared to the xeric site. Greater EVI only significantly increased eff_{flux} at the mesic site, which had higher eff_{flux} compared to the other sites for all levels of EVI (Fig. 9c). The intermediate site had significantly lower eff_{flux} compared to the xeric site when EVI was above 0.3. An increase in SWC significantly decreased values of eff_{flux} only at the intermediate and xeric sites, with a greater decrease at the xeric site (Fig. 9d). Higher VPD significantly decreased eff_{flux} at all sites, with a greater decrease at the intermediate site (Fig. 9e). Rainfall significantly increased eff_{flux} at all sites, where the intermediate site showed the highest increase (Fig. 9f).

There was no significant difference in dS/dt among sites for all years and months, except in 2014, where the intermediate site had significantly higher dS/dt compared to the other sites (Fig. 10a, Table S6). In addition, the xeric site accumulated dS/dt during 2012 such that it was significantly different from the other sites. An increase in EVI and VPD resulted in a significant increase in dS/dt, independent of site (Fig. 10c and d). SWC and rainfall were not significant in the model of dS/dt. The diurnal variation in dS/dt was greater at the mesic and xeric sites during the drought years 2010, 2011 and 2012, compared to the intermediate site, specifically during nighttime (SI Fig. S4). At the intermediate site dS/dt varied more during the years 2014 and 2016, as seen by greater entropy accumulation during nighttime hours and greater export during daytime hours for the year 2014.

4 Discussion

Here we describe differences in energy use efficiencies of sites with varying structural complexities (i.e., understory composition, basal area, DBH) using metrics of energy and entropy. Different from our expectations, environmental and structural effects on energy and entropy fluxes were not different with the exception of NEE_e and J_{NEE}. These results suggest that differences in the thermodynamic environment among sites (i.e., air and surface temperatures) did not contribute to changes in entropy export in response to environmental variables. Nevertheless, metabolic entropy (J_{NEE}) decreased during the drought at all sites (Fig. 7), whereas NEE_e showed no significant change at the intermediate and xeric sites. The different results were a function of T_{air}, which increased during the summer of 2011, especially at the intermediate and xeric sites, thus lowering the flux of J_{NEE} (Fig. 7). The decrease in J_{NEE} suggests that metabolic activity at all sites was similarly affected by low rainfall, increasing VPD, and changes in temperature, demonstrating a decrease in physiological activity of plant species during drought (Barron-Gafford et al., 2013). This decrease in metabolic efficiency supports a previous study at the mesic and xeric sites, which found lower electron transport and carboxylation capacity during drought (Wright et al., 2012). Differences in the underlying reflective capacities at the sites significantly altered their entropy production and resulted in variations in entropy exchanges (Stoy et al., 2014). The more structurally complex mesic site had more negative metabolic entropy (J_{NEE}), which translates to greater energy accumulation, in addition to greater radiation entropy and export efficiencies (eff_{rad}, eff_{flux}) compared to the intermediate site, which had greater land use legacy and was structurally less complex. Although the radiation entropy ratio (eff_{rad}) indicated that both the intermediate and xeric sites were equally energy efficient, eff_{flux} showed prolonged recovery of energy efficiency from drought by one year. Entropy change over time (dS/dt) did not significantly vary at the mesic site, but was more variable at the xeric and intermediate sites following the drought. We hypothesized that the xeric site would have higher H and J_H, due to its open canopy and sandy soils and therefore lower volumetric heat capacity. In contrast to our first hypothesis, the mesic and intermediate sites and not the xeric site had a more pronounced increase in H and J_H when EVI decreased during drought (Fig. 1). Lower H and J_H at the xeric site was a consequence of greater energy partitioning into LE, enabled by greater transpiration rates of plant functional types present at the site (deciduous and evergreen oaks in the understory, mid- and overstory; Klein et al., 2013; Renninger et al., 2015; Stoy et al., 2006). This result was confirmed, as J_H fluxes did not significantly change with an increase in EVI, whereas J_{LE} increased,

13

suggesting that evapotranspiration and the cooling of leaf and soil surfaces had greater influence on the partitioning of available energy. In contrast, J_H increased more at the mesic and xeric sites with increasing VPD, suggesting that drier air increased the sensible heat flux from the surface to the atmosphere (Massmann et al., 2018). Similarly, as VPD increased so did σ at all sites. This response was also observed in Kuricheva et al. (2017), where drier summers resulted in greater entropy production, likely

5 because an increase in VPD correlated with greater absorption of solar radiation and partitioning to H (Fig. 3a). Even though plant abundance was lower at the xeric site, its species composition was better adapted to drought conditions, which allowed for higher J_{LE} compared to the other sites (Roman et al., 2015). Furthermore, an increase in EVI during summer months at the xeric site increased J_{LE}, demonstrating that greater leaf area enhanced ecosystem function (Peng et al., 2017; Zhu et al., 2016). Interestingly, J_{LE} did not vary significantly by site with changes in VPD, which supported the findings of Whelan et al. (2013)

10 that all sites had similar stomatal regulation to increases in VPD. Overall, the xeric site had higher J_{LE} compared to the other sites for EVI < 0.5, even though the site basal area was almost half that of the mesic and intermediate sites (Table 1). An overstory composed of more oak species at the xeric site (~20 %) along with the C_4 understory resulted in higher transpiration during spring and summer, compared to stands containing just pine trees (Klein et al., 2013; Renninger et al., 2015; Stoy et al., 2006). Additionally, C_4 grasses and oak species at the xeric site were better adapted to drought (i.e., anisohydric response;

15 Osborne and Sack, 2012; Roman et al., 2015), which may enable higher entropy production and lower variability in the structural integrity (i.e., lower decreases in EVI; Fig. 1e). This suggests that the understory plays a crucial role in the structure and function of more open canopy ecosystems (Aoki, 2012; Lin, 2015), in addition to more productive overstory trees during summer. This led to similar entropy export efficiencies at all sites as evidenced by all sites having comparable dS/dt. Nevertheless, as σ increased with greater absorption of radiation due to an increase in EVI, J_H decreased as a result of higher

20 SWC, resulting in temporary entropy accumulation at the xeric site during the end of 2012, (SI Fig. 4), which may have contributed to higher T_{air} compared to the other sites (Fig. 2).

In contrast, the mesic site was affected by the interaction of biological and radiative forces, as J_{LE}, J_{NEE} and eff_{rad} decreased more severely with decreasing plant leaf area compared to the xeric site (lower EVI; Fig. 1e). As a consequence of lower LE and J_{LE} during the drought, more energy was partitioned into H in 2011 (Fig. 6), as air, soil and surface temperatures increased

25 due to lower leaf area (Figs. 1 and 2), indicating a shift of ecosystem function (Ban-Weiss et al., 2011) towards lower quality energy degradation (Kuricheva et al., 2017). This initially depleted soil moisture storage at the mesic site (Fig. 1) and further decreased LE and J_{LE} (Kim and Wang, 2012; Lauri et al., 2014). Nevertheless, the shift in energy partitioning at the mesic site allowed for the maintenance of dS/dt during drought, by export of entropy which had accumulated during nighttime hours (SI Fig. S4), demonstrating an adaptation of the site to changes in resource availability (Basu et al., 2016; Brodribb et al., 2014).

30 In contrast, the xeric and intermediate sites showed greater variability in annual dS/dt following the drought when rainfall returned to pre-drought levels and SWC increased (Fig. 10a). Nevertheless, the rapid increase in J_{LE} in 2012 at the mesic and xeric sites indicated an increase in ecosystem function through greater evapotranspiration. This provides evidence of recovery following the drought, because J_{LE} is of higher quality entropy dissipation (Kuricheva et al., 2017), coupling both mass and heat dynamics (Brunsell et al., 2011), whereas J_H is a function of the thermal gradient (Kleidon, 2010; LeMone et al., 2007).

14

Moved (insertion) [1]

Deleted: In contrast, plant species at the mesic were adapted to higher soil water conditions, such that eff_r decreased, as the quality of entropy dissipation through other fluxes leads to lower J_{LE} (Kuricheva et al., 2017). This is because J_{LE} couples both mass and heat dynamics (Brunsell et al., 2011), whereas J_H is only a function of the thermal gradient (Kleidon, 2010; LeMone et al., 2007). Nevertheless, J_H increased at all sites during the first year of drought and then remained higher compared to pre-drought conditions, indicating a shift of ecological

Deleted: at all sites

Deleted: . However, the rapid increase in J_{LE} and decrease in albedo in 2012 at the mesic and xeric sites indicated ecosystem recovery. This provides evidence of rapid adaptation of the plant canopy to drought, which allowed for greater eff_{rad}. Nevertheless, the xeric site was less efficient in using available radiation energy, indicated by high

Moved (insertion) [2]

In generally, plant species at the mesic site were better adapted to higher soil water conditions, as entropy and energy fluxes did not change as drastically with increasing SWC compared to the other sites.

This recovery of EVI following drought also allowed for greater eff_{rad} at the sites. But eff_{rad} was higher at the mesic site despite lower EVI compared to the intermediate site. This finding supports our second hypothesis, that sites with greater plant functional diversity maintain greater radiative entropy efficiency. the mesic site efficiently used available energy from incoming solar radiation (Fig. 2) through lower reflection of R_s and by emitting less longwave radiation (Lin, 2015). Eff_{rad} decreased during the initial drought year because all sites reflected more R_s, likely a consequence of a change in EVI, as well as leaf angle from a decrease in SWC and altered plant hydraulics. Higher eff_{rad} and eff_{flux} at the mesic site are consistent with enhanced function due to greater plant diversity in the understory (Fig. 4a). For example, wiregrass, a C_4 species, can maintain photosynthetic rates under high temperatures (Osborne and Sack, 2012; Ward et al., 1999), which allows for greater energy storage during unfavorable environmental conditions (Brunsell et al., 2011). Despite higher wiregrass biomass in the understory, the xeric site was less efficient in using available radiation energy, indicated by high $R_{s,out}$ and $R_{l,out}$ (Brunsell et al., 2011). Structural limitations of the canopy (i.e., lower basal area) impeded the efficient absorption of available radiation, therefore lowering eff_{rad} (Norris et al., 2011). Furthermore, larger proportions of deciduous oak trees at the xeric site (Table 1), which typically shed their leaves during the winter, lowered the capacity of the system to acquire radiation (Baldocchi et al., 2004; Fig. 8b). This inefficiency was also confirmed by model results for J_{NEE}, which, in contrast to NEE_e revealed lower metabolic efficiency relative to the intermediate site, reflecting differences in basal area and site EVI. These results demonstrate that the mesic site was better adapted to changes in resource availability by way of altering its reflective properties, where energy partitioning adjusted to maintain steady entropy exports relative to incoming entropy (Gunawardena et al., 2017; Otto et al., 2014; Taha et al., 1988).

Nevertheless, metabolic activity at all sites was a source for entropy ($J_{NEE} > 1$) during rainy periods, demonstrating an inefficiency in maintaining optimal function when environmental pressure was imposed on the system. greater metabolic efficiency at the mesic site resulted in more rapid increases in the structural complexity as indicated by a decrease in $R_{s,out}$ following the drought when compared to the intermediate site (Brunsell et al., 2011; Holdaway et al., 2010). Metabolic activity (in energy terms) at the intermediate site was largely dependent on EVI (i.e., leaf area), demonstrating lower biological control of individual plant species (i.e., stomatal control; Urban et al. 2016), but a strong influence of total leaf area on metabolic function and the export of entropy (Brunsell et al., 2011; Fig. 4 and 6). This was further illustrated at the intermediate site through less negative metabolic energy (NEE_e) when EVI was ~ 0.25 (Fig. 7c). Even though EVI in 2012 was greater at the intermediate site this did not correspond to higher J_{LE} (Fig. 5a), which was also shown by a lack of significant change in entropy exports with changes in EVI (eff_{flux}, Fig. 9c). The result of lower metabolic function at the intermediate site is intriguing as the mesic and intermediate sites were structurally similar, based on similar B_A, mean DBH and overstory tree composition (Table 1). The inefficiency appears to be a consequence of anthropogenic modification, which homogenized the ecosystem, leading to a decrease in plant functional types (Table. 1; Fig. 3), thereby reducing values of eff_{rad} and eff_{flux}. This result provides evidence that the intermediate site was less efficient in absorbing energy and dissipating entropy compared to the mesic site, resulting in slower adaptation to drought. Similar results were shown in Lin et al. (2015), where disturbed sites had

15

predominantly lower entropy production rates, as well as in Lin et al. (2018) where greater surface temperature led to decreased σ, which we also observed at the intermediate site. Our third hypothesis was therefore supported, as the intermediate site had lower eff_{flux} relative to the mesic and xeric sites. Lower plant functional diversity, specifically the lack of wiregrass, due to soil perturbations that took place prior to stand establishment (>95 years ago), likely lowered metabolic function, which in turn

5 affected entropy exports at the intermediate site and its recovery from drought. For example, a negative J_G at the intermediate site was observed with increasing SWC suggesting poor soil water drainage, which is also likely a consequence of agricultural legacy (Kozlowski, 1999). A prolonged increase in eff_{flux} compared to the other sites showed that the intermediate site did not adapt its entropy exports, in addition to greater reflection of R_s during drought recovery. This result indicates that differences in soil conditions and lower plant functional diversity at the intermediate site reduced entropy exports compared to the other

10 sites (Meysman and Bruers, 2010), such that plant functional types present at the site could not rescue the ecosystem's function during disturbance (Elmqvist et al., 2003)1. Furthermore, while the intermediate site showed no change in dS/dt during the drought, following the drought the export of entropy significantly increased, resulting in more unstable conditions (Fig. 10a). The increase in entropy export corresponded to high annual rainfall and soil moisture conditions (Figs. 1 and S1), once more suggesting that soil characteristics were altered due to its agricultural legacy. The lower ability to adapt to changes in resource

15 availability at the intermediate site could induce its degradation if environmental fluctuations, become more frequent and severe with climate change (Mori, 2011; Siteur et al., 2016). This could further exacerbate instabilities for nearby sites, as changes in the reflective properties of degraded sites can alter microclimate and weather patterns across whole ecosystems (Norris et al., 2011).

We conclude that the analysis of entropy dynamics, in relation to structural and environmental variables gives valuable insights

20 into the functional complexity of ecosystems and their ability to adapt to drought. a combination of entropy fluxes and entropy ratios revealed how differences in structural and/or functional characteristics affect energy efficiencies in longleaf pine ecosystems. Our results show that all sites demonstrated adaptive capacity to extreme drought, as indicated by a lack of significant change in dS/dt, except for greater variations at the xeric and intermediate sites following the drought. We show that overall low entropy exports at the site with greater land use legacy had the potential to decrease ecosystem function

25 (Meysman and Bruers, 2010), especially during high rainfall events. Changes in climate and natural and human induced disturbances are becoming more frequent and severe (IPCC, 2014), demanding more predictive power about how changes in ecosystem structure and function will alter resilience to disturbances. Future policy, conservation or restoration applications depend on reliable measures such as the metrics presented here, to monitor ecosystem function following disturbances (Haddeland et al., 2014; Porter et al., 2012; Reinmann and Hutyra, 2016; Thom et al., 2017). This is especially critical for

30 anthropogenically modified systems, as their land use history can affect changes in energy use efficiency and thus alter their ability to recover from disturbances (Bürgi et al., 2016; Foster et al., 2003). The application of entropy metrics could improve our understanding of the interaction of structure, function and legacy on energy use efficiency across a variety of global ecosystems.

Author contribution

Moved up [4]:), demonstrating lower biological control of individual plant species (i.e., stomatal control; Urban et al.

Deleted: In contrast to the mesic and xeric sites, metabolic activity at the intermediate site was largely dependent on EVI (i.e., leaf area and biomass…

Moved up [5]: (Brunsell et al., 2011; Fig. 4 and 6).

Deleted: 2016), but a strong influence of the amount of biomass, and therefore higher photosynthetic capacity, present at the site

Deleted: For example, even though the increase in EVI in 2012 was greater at the intermediate site (Fig. 1) this did not correspond to higher J_{LE} or a decrease in albedo. To illustrate, the intermediate site was unable to maintain negative metabolic entropy production, when biomass was below a certain threshold (EVI <0.35). This resulted in lower ecological function and lower quality entropy production, as energy was dissipated more through J_H, rather than J_{LE} (Brunsell et al., 2011). This reduced entropy efficiencies (eff_{rad}, eff_M and eff_s) at the site when contrasted to the mesic and xeric sites (Fig. 6 and 7), which affected its recovery from drought. In contrast, the mesic site was able to maintain a negative value when EVI was ≥ 0.2, indicating greater adaptive capacity of individual plant species, which "rescued" ecosystem function (Elmqvist et al., 2003). Our third hypothesis was therefore partially supported, as the intermediate site had lower eff_M and eff_s. Although eff_{rad}, as an indicator for ecosystem radiation efficiency, showed that the intermediate site was more efficient in using available energy and producing entropy compared to the xeric site; it did not acclimate eff_{rad} to changes in SWC (Fig. 7), which resulted in slower adaptation to drought. The result of lower eff_M and eff_s at the intermediate site is intriguing as the mesic and intermediate sites were structurally similar, based on similar B_A, mean DBH and overstory tree compositions (Table 1). The inefficiency was a consequence of anthropogenic modification, which homogenized the ecosystem, leading to a decrease in biodiversity (Table. 1; Fig. 3). This was a results of soil perturbations from anthropogenic … [22]

Deleted: quality

Deleted: fluxes

Deleted: Furthermore,

Deleted: different

Deleted: efficiency

Deleted: demonstrate

Deleted: ecosystem resilience was mediated

Deleted: ecosystem entropy efficiency, which was a function

Deleted: plant biodiversity and ecosystem structure, as well as anthropogenic legacy.

Deleted: ecological function at anthropogenically altered sites has

Deleted: , and therefore inhibit optimal energy use efficiency

Deleted: with disturbances

Deleted: theories

Deleted: theory of MEP

Deleted: maintain

Deleted: services and ecological

Deleted: MEP theory

References

Amthor, J. S.: From sunlight to phytomass: On the potential efficiency of converting solar radiation to phyto-energy, New Phyt., 188(4), 939–959, doi:10.1111/j.1469-8137.2010.03505.x, 2010.

Aoki, I.: Entropy Principle in Living Systems (Min–Max Principle), Entropy Principle for the Development of Complex Biotic Systems, (Chapter 2), 87–88, doi:10.1016/B978-0-12-391493-4.00008-1, 2012.

Baldocchi, D. D., Xu, L. and Kiang, N.: How plant functional-type, weather, seasonal drought, and soil physical properties alter water and energy fluxes of an oak–grass savanna and an annual grassland, Agric. For. Meteorol., 123(1-2), 13–39, doi:10.1016/j.agrformet.2003.11.006, 2004.

Ban-Weiss, G. A., Bala, G., Cao, L., Pongratz, J. and Caldeira, K.: Climate forcing and response to idealized changes in surface latent and sensible heat, Environ. Res. Lett., 6(3), 034032, doi:10.1088/1748-9326/6/3/034032, 2011.

Basu, S., Ramegowda, V., Kumar, A. and Pereira, A.: Plant adaptation to drought stress, F1000Research, 5(0), 1554, doi:10.12688/f1000research.7678.1, 2016.

Beer, C., Ciais, P., Reichstein, M., Baldocchi, D., Law, B. E., Papale, D., Soussana, J. F., Ammann, C., Buchmann, N., Frank, D., Gianelle, D., Janssens, I. A., Knohl, A., Köstner, B., Moors, E., Roupsard, O., Verbeeck, H., Vesala, T., Williams, C. A. and Wohlfahrt, G.: Temporal and among-site variability of inherent water use efficiency at the ecosystem level, Global Biogeochem. Cycles, 23(2), n/a–n/a, doi:10.1029/2008GB003233, 2009.

Bohn, F. J. and Huth, A.: The importance of forest structure to biodiversity–productivity relationships, R. Soc. open sci., 4(1), 160521, doi:10.1098/rsos.160521, 2017.

Bonan, G. B.: Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science, 320(5882), 1444-1449, doi: 10.1126/science.1155121, 2008.

Brodribb, T. J., McAdam, S. A. M., Jordan, G. J. and Martins, S. C. V.: Conifer species adapt to low-rainfall climates by following one of two divergent pathways, Proc Natl Acad Sci USA, 111(40), 14489–14493, doi:10.1073/pnas.1407930111, 2014.

17

Deleted: MEP

Deleted: Abu-Hamdeh, N. H.: Thermal properties of soils as affected by density and water content, Biosystems Engineering, 86(1), 97–102, doi:10.1016/s1537-5110(03)00112-0, 2003.

Brunsell, N. A., Schymanski, S. J. and Kleidon, A.: Quantifying the thermodynamic entropy budget of the land surface: Is this useful? Earth Sys. Dyn., 2(1), 87–103, 2011.

Bürgi, M., Östlund, L. and Mladenoff, D. J.: Legacy effects of human land use: Ecosystems as time-lagged systems, Ecosystems, 20(1), 94–103, doi:10.1007/s10021-016-0051-6, 2016.

5 Campbell, G. S. and Norman, C. G.: An introduction to environmental biophysics, Springer Science & Business Media. 1998.

Clement, R.: EdiRe data software, School of Geosciences, The University of Edinburgh, Edinburgh, Scotland. 1999.

DAAC, O.: MODIS collection 5 land products global subsetting and visualization tool: MOD13Q1 MODIS/Terra and MYD13Q1 MODIS/Aqua Vegetation Indices, NASA EOSDIS Land Processes DAAC, USGS Earth Resources Observation and Science EROS Center, 2008.

10 Dai, A., Qian, T., Dai, A., Trenberth, K. E. and Qian, T.: A Global Dataset of Palmer Drought Severity Index for 1870–2002: Relationship with Soil Moisture and Effects of Surface Warming, http://dx.doi.org/10.1175/JHM-386.1, 5(6), 1117–1130, doi:10.1175/JHM-386.1, 2004.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. and Norberg, J.: Response diversity, ecosystem change, and resilience, Front. Ecol. Environ., 1(9), 488–494, doi:10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2, 15 2003.

Finzi, A. C., Norby, R. J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W. E., Hoosbeek, M. R., Iversen, C. M., Jackson, R. B., Kubiske, M. E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D. R., Schlesinger, W. H. and Ceulemans, R.: Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2, Proc Natl Acad Sci USA, 104(35), 14014–14019, doi:10.1073/pnas.0706518104, 2007.

20 Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D. and Knapp, A.: The importance of land-use legacies to ecology and conservation, BioScience, 53(1), 77–88, doi:10.1641/0006-3568(2003)053[0077:TIOLUL]2.0.CO;2, 2003.

Fox, J. and Weisberg, S.: car: Companion to Applied Regression, Second Edition. Thousand Oaks CA, 2011.

Franklin, J., Serra-Diaz, J. M., Syphard, A. D. and Regan, H. M.: Global change and terrestrial plant community dynamics, Proc Natl Acad Sci USA, 113(14), 3725–3734, doi:10.1073/pnas.1519911113, 2016.

25 Fraedrich, K. and Lunkeit, F.: Diagnosing the entropy budget of a climate model, Tellus A: Dynamic Meteorology and Oceanography, 60, 921–931, doi: 10.3402/tellusa.v60i5.15498, 2008.

Goebel, P. C., Palik, B. J., Kirkman, L. K. and West, L.: Field guide: landscape ecosystem types of Ichauway. Joseph W. Jones Ecological Research Center at Ichauway, Newton, Report number 97–1. 1997.

Goebel, P. C., Palik, B. J., Kirkman, L. K., Drew, M. B., West, L. and Pederson, D. C.: Forest ecosystems of a Lower Gulf 30 Coastal Plain landscape: Multifactor classification and analysis, J. Torrey Bot. Soc., 128(1), 47, doi:10.2307/3088659, 2001.

Gunawardena, K. R., Wells, M. J. and Kershaw, T.: Utilising green and bluespace to mitigate urban heat island intensity, Science of the Total Environment, The, 584-585, 1040–1055, doi:10.1016/j.scitotenv.2017.01.158, 2017.

Haddeland, I., Heinke, J., Biemans, H., Eisner, S., Flörke, M., Hanasaki, N., Konzmann, M., Ludwig, F., Masaki, Y., Schewe, J., Stacke, T., Tessler, Z. D., Wada, Y. and Wisser, D.: Global water resources affected by human interventions and climate 35 change, Proc Natl Acad Sci USA, 111(9), 3251–3256, doi:10.1073/pnas.1222475110, 2014.

18

Deleted: Brookes, J. D., Aldridge, K., Wallace, T., Linden, L. and Ganf, G. G.: Multiple interception pathways for resource utilisation and increased ecosystem resilience, Hydrobiologia, 552(1), 135–146, doi:10.1007/s10750-005-1511-8, 2005.¶

Deleted: Cochran, F. V., Brunsell, N. A. and Suyker, A. E.: A thermodynamic approach for assessing agroecosystem sustainability, Ecol. Indic., 67, 204–214, doi:10.1016/j.ecolind.2016.01.045, 2016.¶

Deleted: Dantas-Torres, F.: Climate change, biodiversity, ticks and tick-borne diseases: The butterfly effect, International Journal for Parasitology: Parasites and Wildlife, 4(3), 452–461, doi:10.1016/j.ijppaw.2015.07.001, 2015.¶
Dewar, R. C.: Maximum entropy production and the fluctuation theorem, J. Phys. A: Math. Gen., 38(21), L371–L381, doi:10.1088/0305-4470/38/21/L01, 2005.¶
Dyke, J. and Kleidon, A.: The maximum entropy production principle: Its theoretical foundations and applications to the Earth system, Entropy, 12(3), 613–630, doi:10.3390/e12030613, 2010.¶

Deleted: Endres, R. G.: Entropy production selects nonequilibrium states in multistable systems, Sci. Rep., 7(1), 1–13, doi:10.1038/s41598-017-14485-8, 2017.¶
England, J. L.: Dissipative adaptation in driven self-assembly, Nature nanotechnology, 10(11), 919–923, doi:10.1038/nnano.2015.250, 2015.¶

Hammerle, A., Haslwanter, A., Tappeiner, U., Cernusca, A., & Wohlfahrt, G.: Leaf area controls on energy partitioning of a temperate mountain grassland. Biogeosciences, 5(2), doi: 10.5194/bg-5-421-2008, 2008.

Hardiman, B. S., Bohrer, G., Gough, C. M., Vogel, C. S. and Curtis, P. S.: The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest, Ecology, 92(9), 1818–1827, doi:10.1890/10-2192.1, 2011.

5 Holdaway, R. J., Sparrow, A. D. and Coomes, D. A.: Trends in entropy production during ecosystem development in the Amazon Basin, Philos T Roy Soc B, 1437–1447, doi:10.1098/rstb.2009.0298, 2010.

IPCC: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, edited by Core Writing Team, R. K. Pachauri, and L. A. Meyer, IPCC, Geneva. 2014.

10 Juang, J.-Y., Katul, G., Siqueira, M., Stoy, P. and Novick, K.: Separating the effects of albedo from eco-physiological changes on surface temperature along a successional chronosequence in the southeastern United States, Geophys Res Lett, 34, 1–5, doi:10.1029/2007GL031296, 2007.

Kaimal, J. C. and Gaynor, J. E.: Another look at sonic thermometry, Boundary-Layer Meteorol, 56(4), 401–410, doi:10.1007/BF00119215, 1991.

15 Khanna, J., Medvigy, D., Fueglistaler, S., & Walko, R.: Regional dry-season climate changes due to three decades of Amazonian deforestation. Nature Climate Change, 7(3), 200, doi: 10.1038/nclimate3226, 2017.

Kim, Y. and Wang, G.: Soil moisture-vegetation-precipitation feedback over North America: Its sensitivity to soil moisture climatology, Journal of Geophysical Research Atmospheres, 117(17), 1–18, doi:10.1029/2012JD017584, 2012.

Kirkman, L. K., Giencke, L. M., Taylor, R. S., Boring, L. R., Staudhammer, C. L. and Mitchel, R. J.: Productivity and species
20 richness in longleaf pine woodlands: Resource-disturbance influences across an edaphic gradient, Ecology, 97(9), 2259–2271, doi:10.1002/ecy.1456, 2016.

Kirkman, L. K., Mitchell, R. J., Helton, R. C. and Drew, M. B.: Productivity and species richness across an environmental gradient in a fire-dependent ecosystem, Am. J. Bot., 88(11), 2119–2128, 2001.

Kleidon, A., & Lorenz, R. D. (Eds.). Non-equilibrium thermodynamics and the production of entropy: life, earth, and beyond.
25 Springer Science & Business Media, 2004.

Kleidon, A.: Nonequilibrium thermodynamics and maximum entropy production in the Earth system. Naturwissenschaften, 96(6), 1-25, https://doi.org/10.1007/s00114-009-0509-x, 2009.

Kleidon, A.: A basic introduction to the thermodynamics of the Earth system far from equilibrium and maximum entropy production, Philos T Roy Soc B, 365(1545), 1303–1315, doi:10.1098/rstb.2009.0310, 2010.

30 Kleidon, A., Malhi, Y. and Cox, P. M.: Maximum entropy production in environmental and ecological systems, Philos T Roy Soc B, 365(1545), 1297–1302, doi:10.1098/rstb.2010.0018, 2010.

Klein, T., Shpringer, I., Ben Fikler, Elbaz, G., Cohen, S. and Yakir, D.: Relationships between stomatal regulation, water-use, and water-use efficiency of two coexisting key Mediterranean tree species, For. Ecol. Manage., 302, 34–42, doi:10.1016/j.foreco.2013.03.044, 2013.

Kozlowski, T. T.: Soil compaction and growth of woody plants. Scandinavian Journal of Forest Research, 14(6), 596-619, doi.org/10.1080/02827589908540825, 1999.

Kuricheva, O., Mamkin, V., Sandlersky, R., Puzachenko, J., Varlagin, A. and Kurbatova, J.: Radiative entropy production along the paludification gradient in the southern taiga, Entropy, 19(1), 43, doi:10.3390/e19010043, 2017.

5 Lauri, P.-É., Marceron, A., Normand, F., Dambreville, A., Hortsys, U. P. R. and Island, R.: Soil water deficit decreases xylem conductance efficiency relative to leaf area and mass in the apple, The Journal of Plant Hydraulics, 1(Wery 2005), e0003, 2014.

LeMone, M. A., Chen, F., Alfieri, J. G., Tewari, M., Geerts, B., Miao, Q., Grossman, R. L. and Coulter, R. L.: Influence of land cover and soil moisture on the horizontal distribution of sensible and latent heat fluxes in southeast Kansas during
10 IHOP_2002 and CASES-97, Journal of Hydrometeorology, 8(1), 68–87, doi:10.1175/JHM554.1, 2007.

Lenth, R. V.: Least-Squares Means: The R Package lsmeans, J. Stat. Soft., 69(1), doi:10.18637/jss.v069.i01, 2016.

Lin, H.: Thermodynamic entropy fluxes reflect ecosystem characteristics and succession, Ecol. Model., 298, 75–86, doi:10.1016/j.ecolmodel.2014.10.024, 2015.

Lin, H., Zhang, H., & Song, Q.: Transition from abstract thermodynamic concepts to perceivable ecological indicators.
15 Ecological Indicators, 88, 37-42, doi: 10.1016/j.ecolind.2018.01.00, 2018.

Massmann, A., Gentine, P., & Lin, C.: When does vapor pressure deficit drive or reduce evapotranspiration?, arXiv preprint arXiv:1805.05444, doi: 10.5194/hess-2018-553, 2018.

Meysman, F. J. R. and Bruers, S.: Ecosystem functioning and maximum entropy production: a quantitative test of hypotheses, Philos T Roy Soc B, 365(1545), 1405–1416, doi:10.1098/rstb.2009.0300, 2010.

20 Mori, A. S.: Ecosystem management based on natural disturbances: Hierarchical context and non-equilibrium paradigm, Journal of Applied Ecology, 48(2), 280–292, doi:10.1111/j.1365-2664.2010.01956.x, 2011.

Müller, F. and Kroll, F.: Integrating ecosystem theories - Gradients and orientors as outcomes of self-organized processes, International Journal of Design and Nature and Ecodynamics, 6(4), 318–341, doi:10.2495/DNE-V6-N4-318-341, 2011.

NCDC: Monthly Station Normals of Temperature, Precipitation, and Heating and Cooling Degree Days 1981–2010, National
25 Climatic Data center, Asheville, NC. 2011.

Nikolov, N. T., Massman, W. J. and Schoettle, A. W.: Coupling biochemical and biophysical processes at the leaf level: an equilibrium photosynthesis model for leaves of C_3 plants, Ecol. Model., 80(2-3), 205–235, doi:10.1016/0304-3800(94)00072-P, 1995.

Norris, C., Hobson, P. and Ibisch, P. L.: Microclimate and vegetation function as indicators of forest thermodynamic efficiency,
30 Journal of Applied Ecology, 49(3), 562–570, doi:10.1111/j.1365-2664.2011.02084.x, 2011.

Odum, H. T.: Self-Organization, transformity, and information, Monthley Weather Review, 242(4882), 1132–1139, doi:10.1126/science.242.4882.1132, 1988.

Osborne, C. P. and Sack, L.: Evolution of C_4 plants: A new hypothesis for an interaction of CO_2 and water relations mediated by plant hydraulics, Philos T Roy Soc B, 367(1588), 583–600, doi:10.1098/rstb.2011.0261, 2012.

Deleted: Marín, D., Martín, M., Serrot, P. H. and Sabater, B.: Thermodynamic balance of photosynthesis and transpiration at increasing CO2 concentrations and rapid light fluctuations, BioSystems, 116, 21–26, doi:10.1016/j.biosystems.2013.12.003, 2014.

20

Otto, J., Berveiller, D., Bréon, F. M., Delpierre, N., Geppert, G., Granier, A., Jans, W., Knohl, A., Kuusk, A., Longdoz, B., Moors, E., Mund, M., Pinty, B., Schelhaas, M. J. and Luyssaert, S.: Forest summer albedo is sensitive to species and thinning: How should we account for this in Earth system models? Biogeosciences, 11(8), 2411–2427, doi:10.5194/bg-11-2411-2014, 2014.

5   Ozawa, H., Ohmura, A., Lorenz, R. D., & Pujol, T.: The second law of thermodynamics and the global climate system: A review of the maximum entropy production principle. Reviews of Geophysics, 41(4), doi:10.1029/ 2002RG000113, 2003.

Pascale, S., Gregory, J. M., Ambaum, M. H., Tailleux, R., & Lucarini, V.: Vertical and horizontal processes in the global atmosphere and the maximum entropy production conjecture. Earth System Dynamics, 3(1), 19-32, https://doi.org/10.5194/esd-3-19-2012, 2012.

10 Peng, S., Schmid, B., Haase, J. and Niklaus, P. A.: Leaf area increases with species richness in young experimental stands of subtropical trees, Journal of Plant Ecology, 10(1), 128–135, doi:10.1093/jpe/rtw016, 2017.

Pinheiro, J., Bates, D., DebRoy, S. and Sarkar, D.: "nlme" Linear and Nonlinear Mixed Effects Models, 3rd ed., 2014.

Porter, E. M., Bowman, W. D., Clark, C. M., Compton, J. E., Pardo, L. H. and Soong, J. L.: Interactive effects of anthropogenic nitrogen enrichment and climate change on terrestrial and aquatic biodiversity, Biogeochemistry, 114(1-3), 93–120,
15 doi:10.1007/s10533-012-9803-3, 2012.

Reinmann, A. B. and Hutyra, L. R.: Edge effects enhance carbon uptake and its vulnerability to climate change in temperate broadleaf forests, Proc Natl Acad Sci USA, 114(1), 201612369–112, doi:10.1073/pnas.1612369114, 2016.

Renninger, H. J., Carlo, N. J., Clark, K. L. and Schäfer, K. V. R.: Resource use and efficiency, and stomatal responses to environmental drivers of oak and pine species in an Atlantic Coastal Plain forest, Front. Plant Sci., 6(103), 317,
20 doi:10.3389/fpls.2015.00297, 2015.

Roman, D. T., Novick, K. A., Brzostek, E. R., Dragoni, D., Rahman, F. and Phillips, R. P.: The role of isohydric and anisohydric species in determining ecosystem-scale response to severe drought, Oecologia, 179(3), 641–654, doi:10.1007/s00442-015-3380-9, 2015.

Schymanski, S. J., Kleidon, A., Stieglitz, M., & Narula, J.: Maximum entropy production allows a simple representation of
25 heterogeneity in semiarid ecosystems. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365(1545), 1449-1455, doi:10.1098/rstb.2009.0309, 2010.

Schneider, E. D. and Kay, J. J.: Complexity and thermodynamics. Towards a new ecology, Futures, 26(6), 626–647, doi:10.1016/0016-3287(94)90034-5, 1994.

Siteur, K., Eppinga, M. B., Doelman, A., Siero, E. and Rietkerk, M.: Ecosystems off track: rate-induced critical transitions in
30 ecological models, Oikos, 125(12), 1689–1699, doi:10.1111/oik.03112, 2016.

Starr, G., Staudhammer, C. L., Wiesner, S., Kunwor, S., Loescher, H. W., Baron, A. F., Whelan, A., Mitchell, R. J. and Boring, L.: Carbon Dynamics of Pinus palustris Ecosystems Following Drought, Forests, 7(5), 98, doi:10.3390/f7050098, 2016.

Skene, K. R.: Life's a gas: A thermodynamic theory of biological evolution. Entropy, 17(8), 5522-5548, doi:10.3390/e17085522, 2015.

Deleted: Patzek

Deleted: . W.: Thermodynamics of agricultural sustainability:

Deleted: case

Deleted: US maize agriculture, Critical

Deleted: in Plant Sciences, 27

Deleted: 272–293,

Deleted: 1080/07352680802247971, 2008

Deleted: Perry, G. L. W.: Landscapes, space and equilibrium: shifting viewpoints, Progress in Physical Geography, 26(3), 339–359, doi:10.1191/0309133302pp341ra, 2002.

Deleted: Ripl, W.: Management of water cycle and energy flow for ecosystem control: the energy-transport-reaction (ETR) model, Ecol. Model., 78(1-2), 61–76, doi:10.1016/0304-3800(94)00118-2, 1995.

Stoy, P. C., Katul, G. G., Siqueira, M. B. S., Juang, J.-Y., Novick, K. A., McCarthy, H. R., C. Oishi, A., Uebelherr, J. M., Kim, H.-S. and Oren, R.: Separating the effects of climate and vegetation on evapotranspiration along a successional chronosequence in the southeastern US, Glob. Chang. Biol., 12(11), 2115–2135, doi:10.1111/j.1365-2486.2006.01244.x, 2006.

Stoy, P. C., Lin, H., Novick, K. A., Siqueira, M. B. S. and Juang, J.-Y.: The role of vegetation on the ecosystem radiative entropy budget and trends along ecological succession, Entropy, 16(7), 3710–3731, doi:10.3390/e16073710, 2014.

Taha, H., Akbari, H., Rosenfeld, A. and Huang, J.: Residential cooling loads and the urban heat island—the effects of albedo, Building and Environment, 23(4), 271–283, doi:10.1016/0360-1323(88)90033-9, 1988.

Thom, D., Rammer, W. and Seidl, R.: The impact of future forest dynamics on climate: interactive effects of changing vegetation and disturbance regimes, Ecol. Monogr., 87(4), 665–684, doi:10.1002/ecm.1272, 2017.

Thomas, R. T., Prentice, I. C., Graven, H., Ciais, P., Fisher, J. B., Hayes, D. J., Huang, M., Huntzinger, D. N., Ito, A., Jain, A., Mao, J., Michalak, A. M., Peng, S., Poulter, B., Ricciuto, D. M., Shi, X., Schwalm, C., Tian, H. and Zeng, N.: Increased light-use efficiency in northern terrestrial ecosystems indicated by CO_2 and greening observations, Geophysical Research Letters, 43(21), 11,339–11,349, doi:10.1002/2016GL070710, 2016.

Twine, T. E., Kustas, W. P., Norman, J. M., Cook, D. R., Houser, P. R., Meyers, T. P., Prueger, J. H. and Wesley, M. L.: Correcting eddy covariance flux underestimates over grassland, Agric. For. Meteorol., 103, 279–300, doi:10.1016/S0168-1923(00)00123-4, 2000.

Virgo, N. and Harvey, I.: Entropy Production in Ecosystems, in Advances in Artificial Life, vol. 4648, pp. 123–132, Springer, Berlin, Heidelberg. 2007.

Ward, J. K., Tissue, D. T., Thomas, R. B., and Strain, B. R.: Comparative responses of model C_3 and C_4 plants to drought in low and elevated CO_2, Glob. Chang. Biol., 5(8), 857–867, doi:10.1046/j.1365-2486.1999.00270.x, 1999.

Whelan, A., Mitchell, R., Staudhammer, C. and Starr, G.: Cyclic occurrence of fire and its role in carbon dynamics along an edaphic moisture gradient in longleaf pine ecosystems, edited by B. Bond-Lamberty, PLoS ONE, 8(1), e54045, doi:10.1371/journal.pone.0054045, 2013.

Woodward, G., Perkins, D. M. and Brown, L. E.: Climate change and freshwater ecosystems: impacts across multiple levels of organization, Philos T Roy Soc B, 365(1549), 2093–2106, doi:10.1098/rstb.2010.0055, 2010.

Wright, J. K., Williams, M., Starr, G., McGee, J., & Mitchell, R. J.: Measured and modelled leaf and stand-scale productivity across a soil moisture gradient and a severe drought. Plant, cell & environment, 36(2), 467-483, DOI: 10.1111/j.1365-3040.2012.02590.x, 2012.

Wu, W., & Liu, Y.: Radiation entropy flux and entropy production of the Earth system. Reviews of Geophysics, 48(2), doi: 10.1029/2008RG000275, 2010.

Zhu, J., Jiang, L. and Zhang, Y.: Relationships between functional diversity and aboveground biomass production in the Northern Tibetan alpine grasslands, Sci. Rep., 6(March), 1–8, doi:10.1038/srep34105, 2016.

Table 1: Stand characteristics at the mesic, intermediate and xeric sites at the Joseph W. Jones Ecological Research Center, Newton, GA, USA.

Characteristic	Mesic	Intermediate	Xeric
Mean DBH (cm)	25.9	42.5	22.5
B$_A$ *P. palustris* (m^2 ha^{-1})	17.7	14.6	8.9
B$_A$ all tree spp. (m^2 ha^{-1})	19.0	15.7	11.0
Proportion of oak overstory trees (%)	6.8	7.0	19.1
LAI (m^{-2} m^{-2})	1.0[a]	unknown	0.69[a]
Wiregrass in the understory (%)	28	5	24
Woody species in the understory (%)	12	15	10
Prescribed fire	Early spring of 2009, 2011, 2013, 2015	Early spring of 2009, 2011, 2013, 2015	Early spring of 2009, 2011, 2013, 2015

a Wright et al. 2012
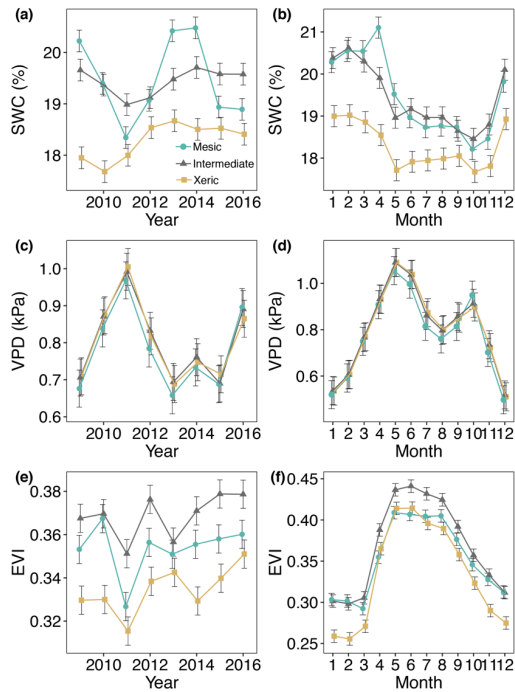
Figure 1: Least square mean predicted values from the mixed model results for Environmental and structural variables for the years 2009-2016 at the mesic, intermediate and xeric sites, with average annual (a, c, and e) and monthly (b, d, and f) means of (a and b) soil water content (SWC), (c and d) vapor pressure deficit (VPD), and (e and f) enhanced vegetation index (EVI). Error bars respresent standard errors (SE).

5
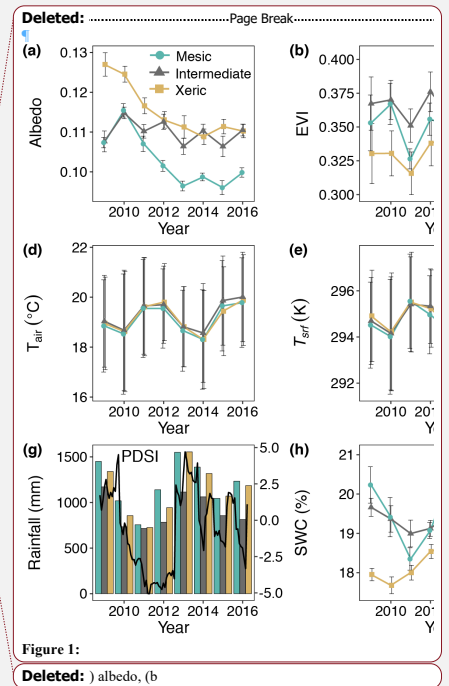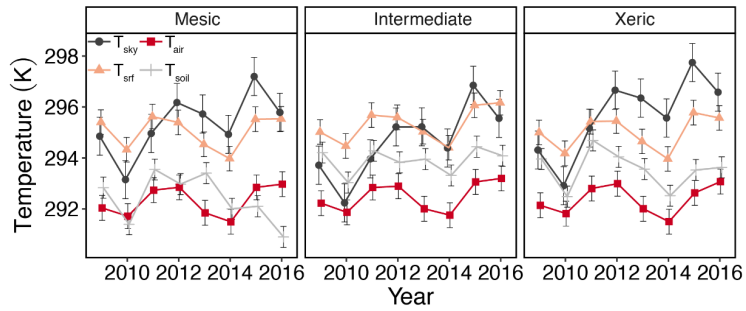
Figure 2: Least square mean predicted values from the mixed model results for annual sky temperature (T_{sky}), air temperature (T_{air}), surface temperature (T_{srf}), and soil temperature (T_{soil}) at the mesic, intermediate and xeric sites. Error bars represent SE.
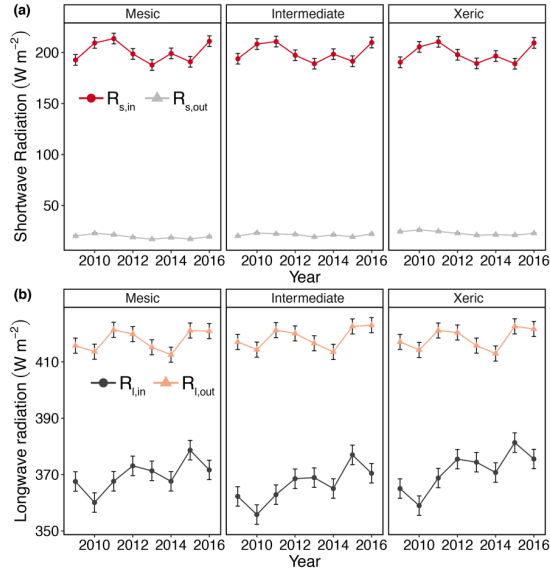
Figure 3: Least square mean predicted values from the mixed model results of annual average radiation at the mesic, intermediate and xeric sites for the years 2009-2016. (a) annual incoming and outgoing shortwave radiation ($R_{s,in}$ and $R_{s,out}$), and (b) annual incoming and outgoing longwave radiation ($R_{l,in}$ and $R_{l,out}$). Error bars represent SE.

5

Figure 4: (a) Wiregrass and (b) woody understory biomass from 2009 through 2015 at the mesic, intermediate and xeric sites. Note that the sampling protocol changed to a 2-year measurements cycle in 2013, such that measurements were not made in 2014 and 2016.

Deleted: 3
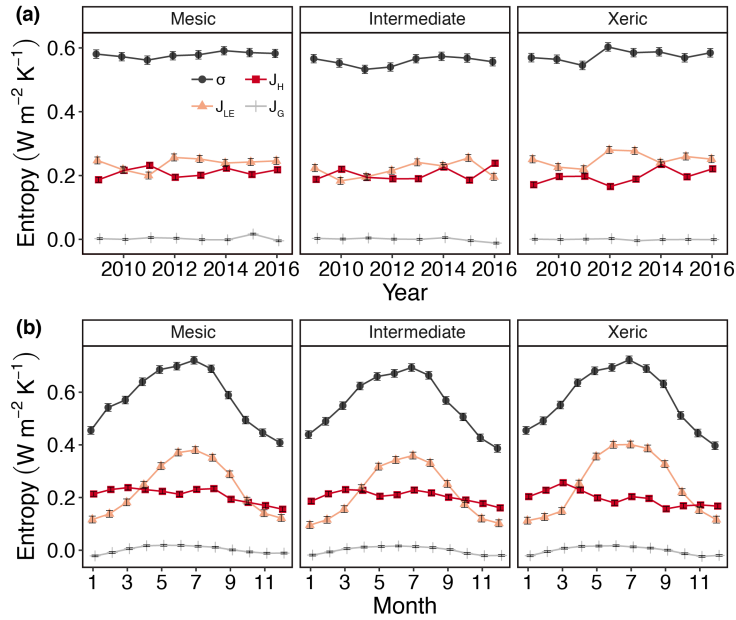
Figure 5: Least square mean predicted values from the mixed model results of annual (a) and monthly (b) average entropy production (σ) and entropy fluxes of latent energy (J_{LE}), sensible heat (J_H), and ground heat (J_G) at the mesic, intermediate and xeric sites. Error bars represent SE.
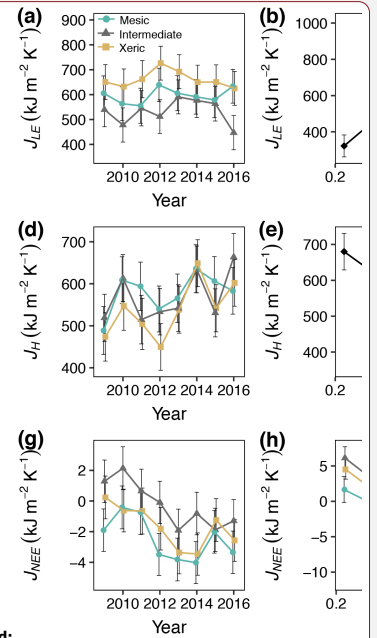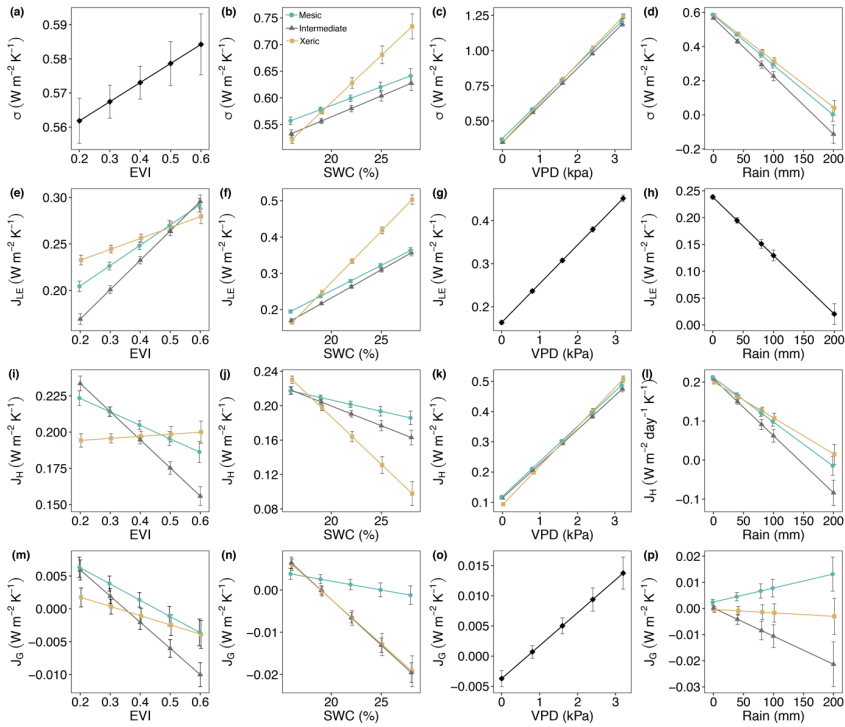
Figure 6: Least square mean predicted values from the mixed model results for interactive effects of (a, e, i, m) Enhanced Vegetation Index (EVI), (b, f, j, n) soil water content (SWC), (c, g, k, o) vapor pressure deficit (VPD), and (d, h, l, p) rain on (a-d) entropy production (σ) and entropy fluxes of (e-h) latent energy (J_{LE}), (i-l) sensible heat (J_H), and (m-p) ground heat (J_G). For (g), (h) and (o) the interaction with site was not significant, as signified by a single black line. Error bars represent SE.

Figure 7: Least square mean predictive values from the mixed model results for interactive effects of site with (a and g) year, (b, c, h, and i) enhanced vegetation index (EVI), (d and j) soil water content (SWC), (e and k) vapor pressure deficit (VPD), and (f and l) rain on (a-f) the metabolic energy flux (NEE_e) and (g and l) metabolic entropy fluxes of (J_{NEE}). For (d) and (e) the interaction with site was not significant, as indicated by a single solid black line. Error bars represent SE.
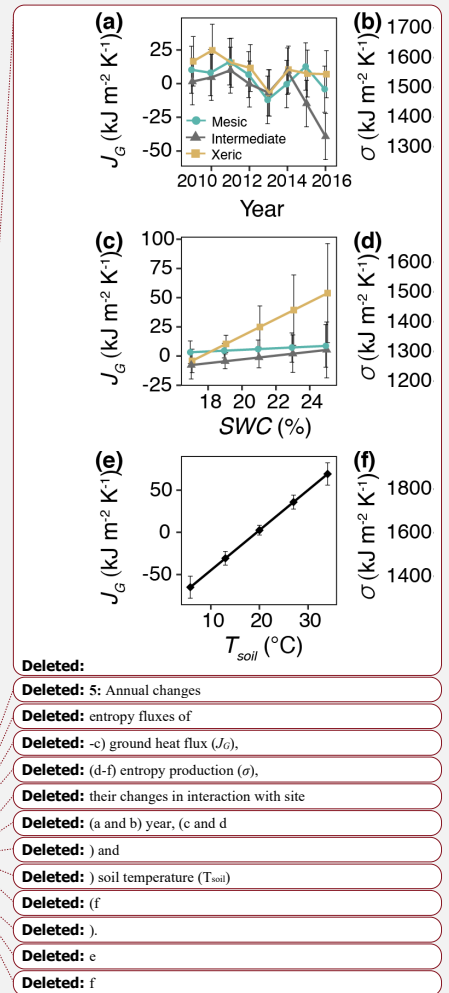
Deleted:

Deleted: 5: Annual changes

Deleted: entropy fluxes of

Deleted: -c) ground heat flux (J_G),

Deleted: (d-f) entropy production (σ),

Deleted: their changes in interaction with site

Deleted: (a and b) year, (c and d

Deleted:) and

Deleted:) soil temperature (T_{soil})

Deleted: (f

Deleted:).

Deleted: e

Deleted: f
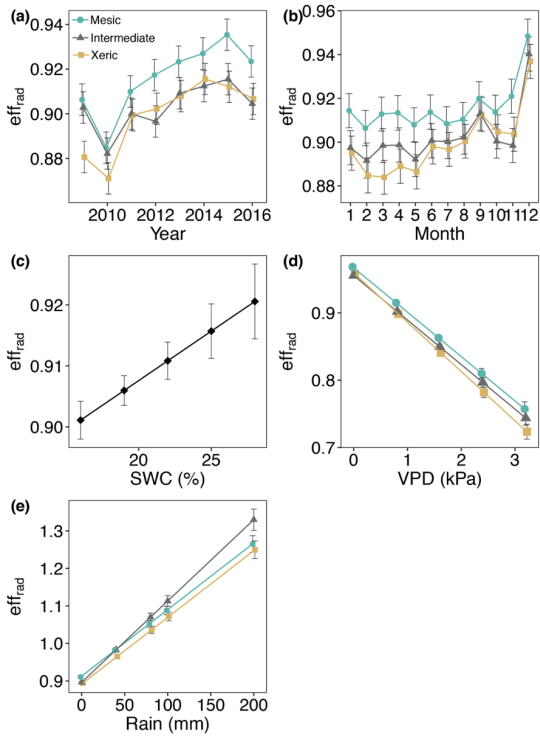
Figure 8: Least square mean predicted values from the mixed model results for average daily half-hourly radiative entropy efficiencies (eff_rad) at the mesic, intermediate and xeric sites for the interactions of site with (a) year, (b) month, (c) soil water content (SWC), for which the interaction with site was not significant, (d) vapor pressure deficit (VPD), and (e) rain. The enhanced vegetation index was not significant in the model. Error bars represent SE.
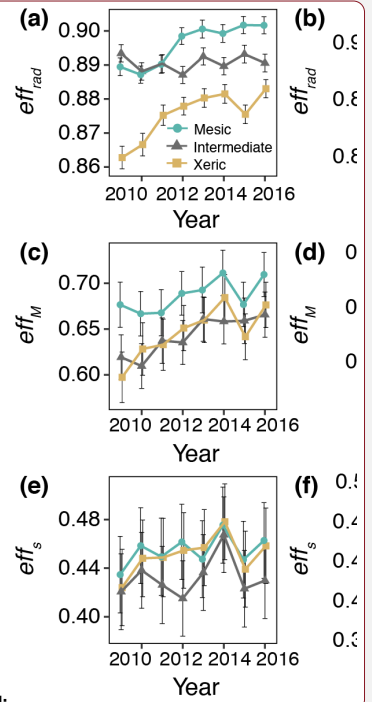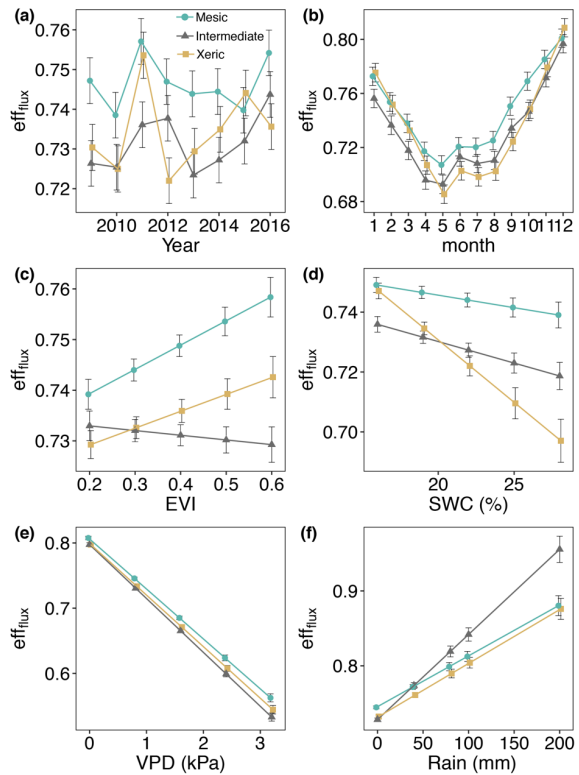
Figure 9: Least square mean predicted values from the mixed model results for average daily half-hourly flux entropy efficiencies (eff$_{flux}$) at the mesic, intermediate and xeric sites for the interactions of site with (a) year, (b) month, (c) enhanced vegetation index (EVI), (d) soil water content (SWC), (e) vapor pressure deficit (VPD, and (f) rain. Error bars represent SE.
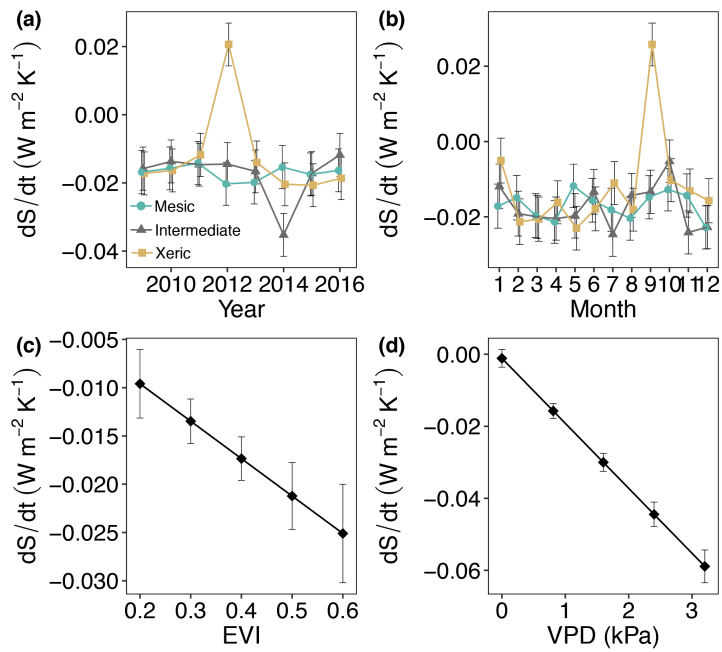
Figure 10: Least square mean predicted values from the mixed model results for average daily entropy for the mesic, intermediate and xeric sites by (a) year (a) month, (c) enhanced vegetation index (EVI), and (d) vapor pressure deficit (VPD). Soil water content and rain, as well as the interactions with site were not significant in the model. Error bars represent SE.

"Quantifying energy use efficiency via entropy production: A case study from longleaf pine ecosystems"

Table S1: Type 3 effects for model of rain

Effect	Sum Sq.	Df	F value	Pr(>F)
Site	30607	2	4.2059	0.0159
Year	95938	7	3.7667	< 0.001

5

Deleted: is the

Table S2: Type 3 effects for the models of environmental variables and radiation

Model	Effect	Chisq	Df	p-value
SWC	Site	6561.692	2	< 0.001
	Year	23.764	7	0.0013
	Month	94.089	11	< 0.001
	Site:Year	2629.617	14	< 0.001
	Site:Month	1398.986	22	< 0.001
VPD	Site	245.268	2	< 0.001
	Year	33.981	7	< 0.001
	Month	100.044	11	< 0.001
	Site:Year	214.101	14	< 0.001
	Site:Month	232.327	22	< 0.001
EVI	Site	2510.727	2	< 0.001
	Year	15.868	7	0.0264
	Month	597.701	11	< 0.001
	Site:Year	294.805	14	< 0.001
	Site:Month	791.727	22	< 0.001
T_{sky}	Site	2202.369	2	< 0.001
	Year	23.089	7	0.0017
	Month	912.141	11	< 0.001
	Site:Year	440.318	14	< 0.001
	Site:Month	63.082	22	< 0.001
T_{srf}	Site	438.625	2	< 0.001
	Year	12.844	7	0.076
	Month	1423.846	11	< 0.001
	Site:Year	435.639	14	< 0.001
	Site:Month	778.064	22	< 0.001
T_{air}	Site	1419.775	2	< 0.001
	Year	9.954	7	0.1912
	Month	1231.11	11	< 0.001
	Site:Year	1311.82	14	< 0.001
	Site:Month	336.866	22	< 0.001
T_{soil}	Site	5110.24	2	< 0.001
	Year	16.817	7	0.0186
	Month	1901.818	11	< 0.001
	Site:Year	1922.717	14	< 0.001
	Site:Month	5270.008	22	< 0.001
$R_{s,in}$	Site	0.9664	2	0.6168
	Year	16.3199	7	0.0224
	Month	763.0665	11	< 0.001
	Site:Year	121.9389	14	< 0.001
	Site:Month	170.75	22	< 0.001
$R_{s,out}$	Site	4161.151	2	< 0.001
	Year	48.782	7	< 0.001
	Month	682.874	11	< 0.001
	Site:Year	816.733	14	< 0.001
	Site:Month	1780.397	22	< 0.001
$R_{l,in}$	Site	2479.339	2	< 0.001
	Year	22.578	7	0.0020
	Month	1005.462	11	< 0.001
	Site:Year	482.99	14	< 0.001
	Site:Month	72.965	22	< 0.001
$R_{l,out}$	Site	226.43	2	< 0.001
	Year	13.07	7	0.0704
	Month	1433.87	11	< 0.001
	Site:Year	137.39	14	< 0.001
	Site:Month	980.18	22	< 0.001

Table S3: Type 3 effects for the models of energy

Model	Effect	Chisq.	Df	Pr(>Chisq)
R_n	Year	20.6658	7	0.0042975
	Month	1927.222	11	< 0.001
	SWC	58.6889	1	< 0.001
	Site	650.5143	2	< 0.001
	EVI	12.2151	1	0.0005
	Rain	140.9816	1	< 0.001
	VPD	1756.8922	1	< 0.001
	Month:Site	120.9114	22	< 0.001
	SWC:Site	24.2945	2	< 0.001
	Site:EVI	7.3321	2	0.0256
	Site:VPD	16.6743	2	0.0002
	Year:Site	263.8642	14	< 0.001
LE	Year	20.7768	7	0.0041
	Month	754.2793	11	< 0.001
	SWC	455.4372	1	< 0.001
	Site	476.4295	2	< 0.001
	EVI	149.9341	1	< 0.001
	Rain	116.5615	1	< 0.001
	VPD	1043.0314	1	< 0.001
	Month:Site	369.8495	22	< 0.001
	SWC:Site	130.9093	2	< 0.001
	Site:EVI	43.0759	2	< 0.001
	Site:VPD	5.3897	2	0.0676
	Year:Site	564.6937	14	< 0.001
H	Year	39.525	7	< 0.001
	Month	108.742	11	< 0.001
	SWC	29.086	1	< 0.001
	Site	90.131	2	< 0.001
	EVI	25.974	1	< 0.001
	Rain	95.918	1	< 0.001
	VPD	1320.893	1	< 0.001
	Month:Site	301.757	22	< 0.001
	SWC:Site	35.234	2	< 0.001
	Site:EVI	41.862	2	< 0.001
	Site:VPD	29.24	2	< 0.001
	Site:Rain	16.416	2	0.0003
	Year:Site	351.685	14	< 0.001
G	Year	9.1742	7	0.2404
	Month	180.4785	11	< 0.001
	SWC	37.8658	1	< 0.001
	Site	200.7208	2	< 0.001
	EVI	33.4003	1	< 0.001
	Rain	0.1512	1	0.6974
	VPD	36.7781	1	< 0.001
	Month:Site	375.8069	22	< 0.001
	SWC:Site	38.7949	2	< 0.001
	Site:EVI	8.2576	2	0.0161
	Site:Rain	14.6424	2	0.0007
	Site:VPD	6.4624	2	0.0395
	Year:Site	990.9702	14	< 0.001

Table S4: Type 3 effects for models of entropy

Model	Effect	Chisq	Df	Pr(>Chisq)
σ	Year	4.9661	7	0.664
	Month	606.5841	11	< 0.001
	SWC	39.387	1	< 0.001
	Site	152.0689	2	< 0.001
	EVI	3.2469	1	0.0716
	Rain	250.7508	1	< 0.001
	VPD	2189.9512	1	< 0.001
	Month:Site	156.1348	22	< 0.001
	SWC:Site	23.5738	2	< 0.001
	Site:VPD	10.0017	2	0.0067
	Site:Rain	8.8673	2	0.0119
	Year:Site	122.0744	14	< 0.001
J_{LE}	Year	21.216	7	0.0035
	Month	726.81	11	< 0.001
	SWC	456.76	1	< 0.001
	Site	493.661	2	< 0.001
	EVI	148.839	1	< 0.001
	Rain	127.775	1	< 0.001
	VPD	1011.278	1	< 0.001
	Month:Site	367.42	22	< 0.001
	SWC:Site	162.581	2	< 0.001
	Site:EVI	42.076	2	< 0.001
	Year:Site	560.321	14	< 0.001
J_H	Year	38.625	7	< 0.001
	Month	101.071	11	< 0.001
	SWC	25.483	1	< 0.001
	Site	93.504	2	< 0.001
	EVI	25.804	1	< 0.001
	Rain	94.524	1	< 0.001
	VPD	1208.397	1	< 0.001
	Month:Site	315.446	22	< 0.001
	SWC:Site	39.127	2	< 0.001
	Site:EVI	44.953	2	< 0.001
	Site:VPD	30.372	2	< 0.001
	Site:rRain	14.251	2	0.0008
	Year:Site	370.91	14	< 0.001
J_G	Year	7.6197	7	0.3673
	Month	180.1628	11	< 0.001
	SWC	35.1066	1	< 0.001
	Site	234.691	2	< 0.001
	EVI	31.1994	1	< 0.001
	Rain	0.8563	1	0.3548
	VPD	29.1953	1	< 0.001
	Month:Site	299.2461	22	< 0.001
	SWC:Site	56.2234	2	< 0.001
	Site:EVI	11.0306	2	0.004
	Site:Rain	22.1752	2	< 0.001
	Year:Site	1082.405	14	< 0.001

Table S5: Type 3 effects for models of metabolic energy (NEE_ε) and entropy (J_{NEE})

Effect	Chisq		Df	Pr(>Chisq)	Effect
	Year	29.646	7	0.0001102	
	Month	74.127	11	< 0.001	
	SWC	19.826	1	< 0.001	
	Site	779.838	2	< 0.001	
	EVI	75.114	1	< 0.001	
NEE_ε	Rain	300.884	1	< 0.001	
	VPD	327.07	1	< 0.001	
	Month:Site	742.229	22	< 0.001	
	Site:EVI	14.519	2	0.0007	
	Site:VPD	11.067	2	0.0034	
	Site:Rain	42.48	2	< 0.001	
	Year:Site	520.107	14	< 0.001	
	Year	100.0912	7	< 0.001	
	Month	734.3098	11	< 0.001	
	SWC	102.5001	1	< 0.001	
	Site	472.4768	2	< 0.001	
	EVI	123.4161	1	< 0.001	
J_{NEE}	Rain	85.0485	1	< 0.001	
	VPD	839.139	1	< 0.001	
	Month:Site	675.38	22	< 0.001	
	SWC:Site	24.5701	2	< 0.001	
	Site:VPD	9.1967	2	0.0101	
	Site:Rain	22.9547	2	< 0.001	
	Year:Site	3070.236	14	< 0.001	

Deleted: budget (eff_{rad}), (c and d) the

Table S6: Type 3 effects for models of entropy efficiency

Model	Effect	Chisq	Df	Pr(>Chisq)
eff$_{rad}$	Site	321.3179	2	< 0.001
	Year	28.9597	7	0.0002
	Month	31.1969	11	0.001
	VPD	269.8436	1	< 0.001
	Rain	295.7158	1	< 0.001
	SWC	6.6371	1	0.001
	Site:Month	78.91	22	< 0.001
	Site:VPD	10.683	2	0.0048
	Site:Rain	17.7766	2	0.0001
	Site:Year	165.2804	14	< 0.001
eff$_{flux}$	Mite	938.8639	2	< 0.001
	Year	9.2791	7	0.2332
	Month	251.1215	11	< 0.001
	VPD	1204.1726	1	< 0.001
	EVI	5.4535	1	0.0195
	Rain	122.5276	1	< 0.001
	SWC	8.9111	1	0.0028
	Site:Month	307.582	22	< 0.001
	Site:SWC	25.8864	2	< 0.001
	Site:VPD	17.4305	2	0.0002
	Site:Rain	51.4031	2	< 0.001
	Site:EVI	15.1919	2	0.0005
	Site:Year	517.3889	14	< 0.001
dS/dt	Site	12.945	2	0.0016
	Year	5.9043	7	0.551
	Month	16.8799	11	0.1115
	VPD	114.1762	1	< 0.001
	EVI	4.207	1	0.0403
	Site:Month	103.0141	22	< 0.001
	Site:Year	135.7525	14	< 0.001
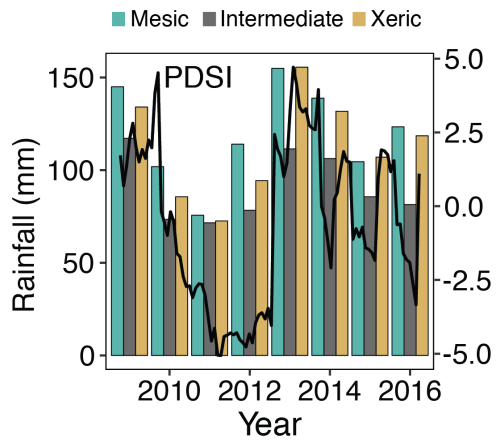
Figure S1: Monthly rainfall sums and Palmer Drought Severity Index (PDSI) for the mesic, intermediate and xeric sites from 2009 through 2016.
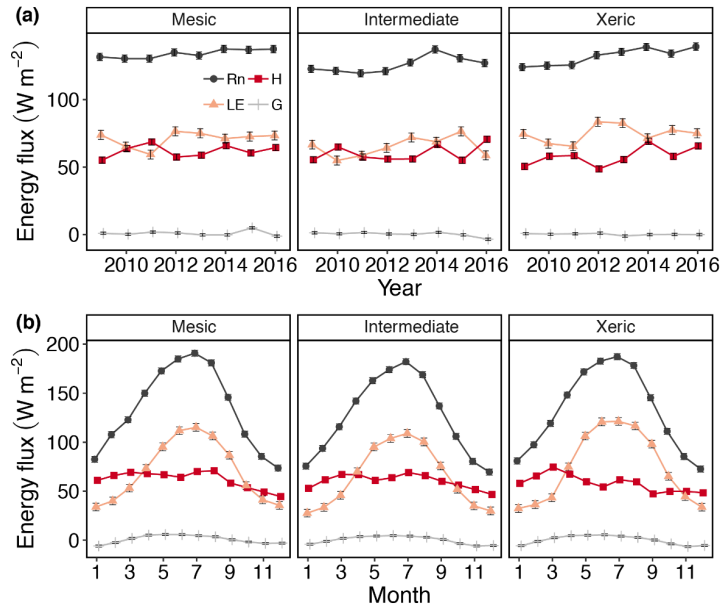
Figure S2: Least square mean predicted values from the mixed model results for annual (a) and monthly (b) changes of the energy fluxes of net radiation (R_n), latent energy (LE), sensible heat (H), and ground heat (G) at the mesic, intermediate and xeric sites. Error bars represent standard errors (SE).
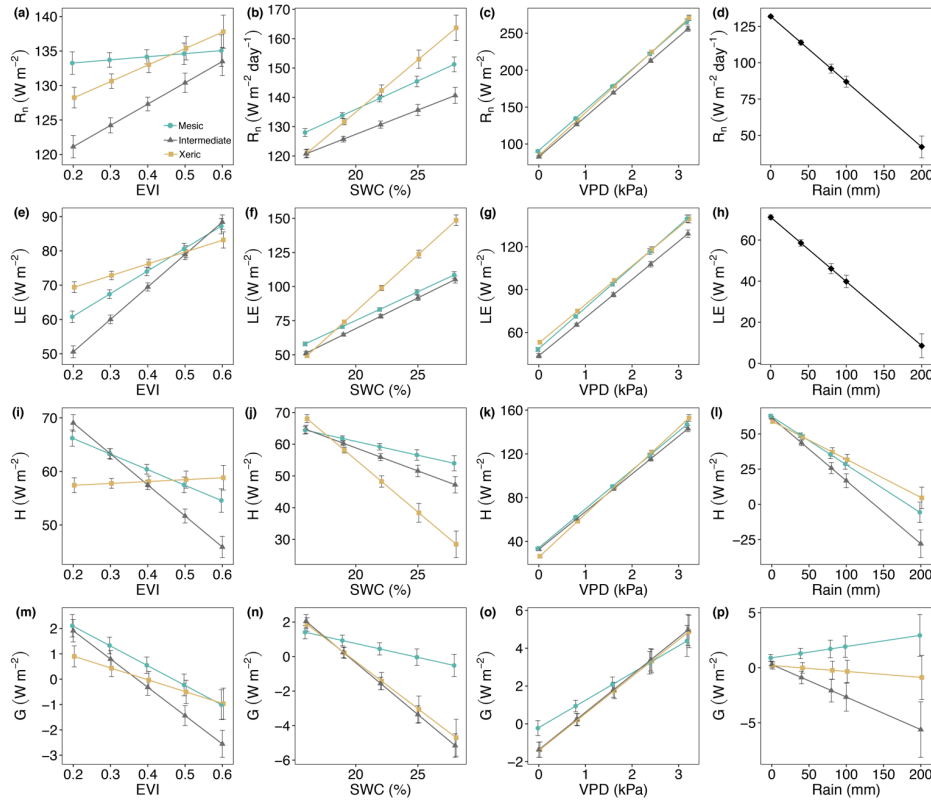
Figure S3: Least square mean predicted values from the mixed model results for interactive effects of (a, e, i, m) enhanced vegetation index (EVI), (b, f, j, n) soil water content (SWC), (c, g, k, o) vapor pressure deficit (VPD) and (d, h, l, p) rain on the energy fluxes of (a-d) net radiation (R_n), (e-h) latent energy (LE), (i-l) sensible heat (H), and (m-p) ground heat (G). For (d) and (h) the interaction with site was not significant, as indicated by a single solid black line. Error bars represent SE.

Deleted: (*eff_M*), and (e and f) the overall entropy efficiency (*eff_s*), as …

Deleted: site and

Deleted: c,

Deleted:) year,

Deleted: , d

Deleted:) enhanced vegetation index (EVI). The interaction of site and EVI was not significant in (b).
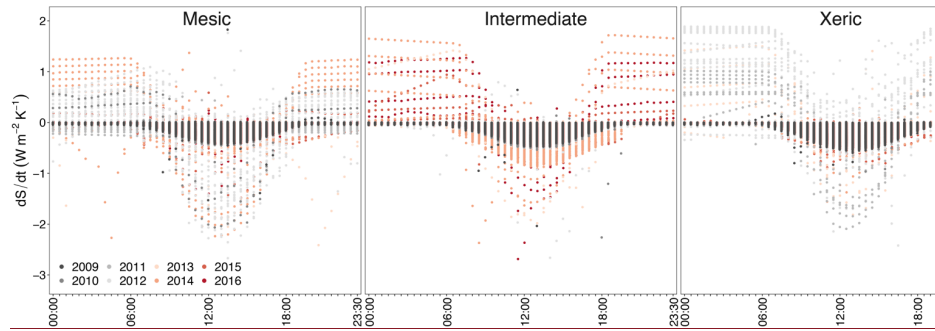
Deleted: --------------------------------Page Break--------------

Figure 7: Differences in the entropy efficiencies by for radiation entropy efficiency (eff_{rad}) in interaction with site and (a) soil water content (SWC), (b) vapor pressure deficit (VPD), and (c) air temperature (T_{air}), as well as (d) metabolic entropy efficiency (eff_M) in interaction with site and SWC.
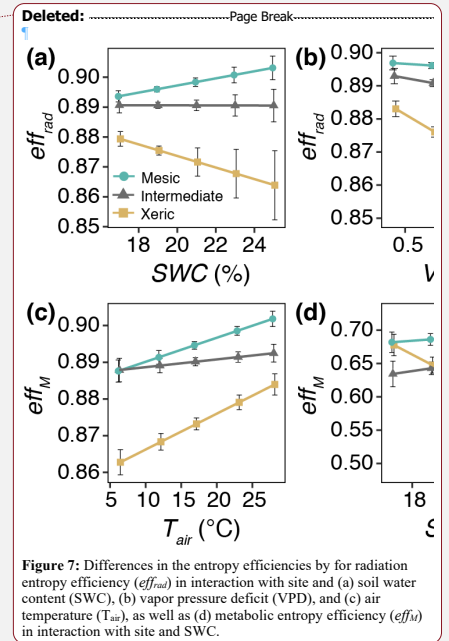
Page 2: [1] Deleted	revised	12/15/18 1:09:00 PM

Page 2: [2] Deleted	revised	12/15/18 1:09:00 PM

Page 2: [3] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [4] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [4] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [4] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [5] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [5] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [5] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [6] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [6] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [6] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [6] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [7] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [7] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [7] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [7] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [7] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [7] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [7] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [7] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [7] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [7] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [7] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [8] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [8] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [8] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [8] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [8] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [8] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [8] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [8] Deleted	revised	12/15/18 1:09:00 PM

Page 8: [8] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 8: [8] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 8: [8] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 8: [8] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 8: [8] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 9: [9] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 9: [10] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 9: [11] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 9: [12] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 9: [13] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 9: [14] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 9: [15] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 9: [16] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 9: [17] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 13: [18] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 13: [19] Deleted	**revised**	**12/15/18 1:09:00 PM**

Page 13: [21] Deleted	revised	12/15/18 1:09:00 PM

Page 16: [22] Deleted	revised	12/15/18 1:09:00 PM