Web links to the author's journal account have been redacted from the decision letters as indicated to maintain confidentiality.

28th Apr 20

Dear Mr Ritter,

Your manuscript entitled "Maximum constraint on the response of terrestrial productivity to rainfall variability" has now been seen by three reviewers, and I include their comments at the end of this message. They find your work of interest, but some potentially important points are raised. We are interested in the possibility of publishing your study in Communications Earth & Environment, but we would like to consider your responses to these concerns and assess a revised manuscript before we make a final decision on publication.

We therefore invite you to revise and resubmit your manuscript, along with a point-by-point response that takes into account the points raised. Please highlight all changes in the manuscript text file.

We are committed to providing a fair and constructive peer-review process. Please don't hesitate to contact us if you wish to discuss the revision in more detail.

Please use the following link to submit your revised manuscript, point-by-point response to the reviewers' comments (which should be in a separate document to any cover letter) and the completed checklist:
[link redacted]
** This url links to your confidential home page and associated information about manuscripts you may have submitted or be reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage first **

We hope to receive your revised paper within four weeks; please let us know if you are not able to submit within this time.

We understand that due to the current global situation, the time required for revision may be longer than usual. We would appreciate it if you could keep us informed about an estimated timescale for resubmission, to facilitate our planning. Of course, if you are unable to estimate, we are happy to accommodate necessary extensions nevertheless.

Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further. We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

Best regards,

Heike Langenberg, PhD

Chief Editor
Communications Earth and Environment

On Twitter: @CommsEarth

EDITORIAL POLICIES AND FORMATTING

We ask that you ensure your manuscript complies with our editorial policies. Please ensure that the following formatting requirements are met, and any checklist relevant to your research is completed and uploaded as a Related Manuscript file type with the revised article.

Editorial Policy: Policy requirements

Furthermore, please align your manuscript with our format requirements, which are summarized on the following checklist:
Communications Earth & Environment formatting checklist

In the event that the manuscript is accepted we will be providing further guidance on formatting but please ensure that the manuscript generally complies with our house style at this stage. The main points are as follows:

* ABSTRACT: less than 150 words and accessible. It should include the background and context of the work, the phrase 'Here we' (present/show/suggest) to indicate where the description of your own work starts, and then the methods/data, main results and conclusions of the paper.

*The text must be split into:
- INTRODUCTION (<1000 words): includes the background and rationale for the work. The final paragraph should be a brief summary of the main results and conclusions. The results of the current study should only be discussed in this final paragraph.
- RESULTS: split into subheaded sections; ensure that the subheadings are no longer than 60 characters including spaces.
- DISCUSSION: without subheadings.
- METHODS: split into subheaded sections; ensure that the subheadings are no longer than 60 characters including spaces

* SUPPLEMENTARY INFORMATION should be organised logically, with all items labelled as one of the following item types, and cited in the main article:
- Supplementary Figures, labelled and referred to as i.e. Supplementary Figure 1 throughout both the Supplementary Information and the main text
- Supplementary Tables, labelled as above
- Supplementary Notes, labelled as above
- Supplementary Discussion
- Supplementary Methods
- Supplementary References

Data: All Communications Earth & Environment manuscripts must include a section titled "Data Availability" at the end of the Methods section or main text (if no Methods). More information on this policy, and a list of examples, is available at <a

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In addition, Communications Earth & Environment endorses the principles of the Enabling FAIR data project (http://www.copdess.org/enabling-fair-data-project/). We ask authors to make the data that support their conclusions available in permanent, publically accessible data repositories. (Please contact the editor if you are unable to make your data available).
In particular, the Data availability statement should include:
- Unique identifiers (such as DOIs and hyperlinks for datasets in public repositories)
- Accession codes where appropriate
- If applicable, a statement regarding data available with restrictions
- If a dataset has a Digital Object Identifier (DOI) as its unique identifier, we strongly encourage including this in the Reference list and citing the dataset in the Data Availability Statement.

DATA SOURCES: All new data associated with the paper should be placed in a persistent repository where they can be freely and enduringly accessed. We recommend submitting the data to discipline-specific, community-recognized repositories, where possible and a list of recommended repositories is provided at http://www.nature.com/sdata/policies/repositories.

If a community resource is unavailable, data can be submitted to generalist repositories such as figshare or Dryad Digital Repository. Please provide a unique identifier for the data (for example a DOI or a permanent URL) in the data availability statement, if possible. If the repository does not provide identifiers, we encourage authors to supply the search terms that will return the data. For data that have been obtained from publically available sources, please provide a URL and the specific data product name in the data availability statement. Data with a DOI should be further cited in the methods reference section.

Please refer to our data policies at http://www.nature.com/authors/policies/availability.html.

REVIEWER COMMENTS:

Reviewer #1 (Remarks to the Author):

The authors seek to to isolate the impact of rainfall variability on the GPP of five dominant terrestrial biomes. They compared the productivity of between ecosystems with similar climates but differences in rainfall variability. The authors found that while the mesic grasslands and forests showed a slight sensitivity to interannual rainfall variability, their GPP increased in response to higher rainfall frequency. The authors also found that xeric grasslands responded to high interannual variance and intra annual frequency. They suggest that this points to a hydrological resilience that ecoystems to maintain GPP under either higher or lower rainfall variability. Finally, the authors suggest that their research quantifies bias in rainfall variability simulation.The authors address major research and data gaps and propose a new statistical method and rainfall frequency index-unranked

Gini index to isolate the influence of rainfall variability.
Line 124: "cold forest" is not a common ecosystem are you referring to Taiga
Line 129: : "cold grassland" is not a common ecosystem are you referring to portions of arctic tundra and montane grasslands
Line 137: "warm-dry grasslands" are not a common ecosystem term
line 149: shade from the clouds

Reviewer #2 (Remarks to the Author):

Comments to Ritter et al. of Communications Earth & Environment

The authors presented an interesting study to attribute the contribution of rainfall variability control on terrestrial productivity. They tested 4 different metrics for measuring rainfall variability and used GPP as proxy of vegetation productivity. A statistical paring method was used to obtain the attribution results. Generally, this manuscript is well written and easy to understand. I have the following comments for the authors to consider:

Firstly, if you search global GPP products, there are way more than one products. Wu usually see significant differences in these GPP products. Will using different GPP products give you different results? This needs to be tested such that we know the reported results are robust enough. Here are the references for some other GPP products:
Jung, M., Schwalm, C., Migliavacca, M., Walther, S., Camps-Valls, G., Koirala, S., Anthoni, P., Besnard, S., Bodesheim, P., Carvalhais, N., Chevallier, F., Gans, F., Goll, D.S., Haverd, V., Köhler, P., Ichii, K., Jain, A.K., Liu, J., Lombardozzi, D., Nabel, J.E.M.S., Nelson, J.A., O'Sullivan, M., Pallandt, M., Papale, D., Peters, W., Pongratz, J., Rödenbeck, C., Sitch, S., Tramontana, G., Walker, A., Weber, U., & Reichstein, M. (2020). Scaling carbon fluxes from eddy covariance sites to globe: synthesis and evaluation of the FLUXCOM approach. Biogeosciences, 17, 1343-1365
Luo, X., Keenan, T.F., Fisher, J.B., Jiménez-Muñoz, J.-C., Chen, J.M., Jiang, C., Ju, W., Perakalapudi, N.-V., Ryu, Y., & Tadić, J.M. (2018). The impact of the 2015/2016 El Niño on global photosynthesis using satellite remote sensing. Philosophical Transactions of the Royal Society B: Biological Sciences, 373

Secondly, besides mean temperature, precipitation, and biome, there are other factors that could potentially contribute to the responses of plant productivity, such as soil. How could you separate the contribution from soil with those from rainfall variability?

Thirdly, the impact of rainfall variability on biogeochemical processes are rarely discussed in the main text and Fig. 4. There should be a potential pathway that soil biogeochemistry can have an impact on plant productivity under different rainfall variability scenarios.

Other comments:

L55: Focusing on “five biomes distributed over four continent” was not well justified. Is this due to data availability (precipitation data from rain gauges) or any other reasons? A Lot of land areas are not included in this study, including those in China, Africa, South America, and the broader tropic region.

L65: I would say they are “confounding variables”

L90: reflectance->surface reflectance; fluorescence->solar-induced chlorophyll fluorescence

L90-L91: it would be much better to cite the [40] here.

Reviewer #3 (Remarks to the Author):

Ritter et al. present a unique and novel approach to quantifying how rainfall, or really, precipitation (P), variability impacts terrestrial productivity. Their main findings address how intra-annual (P frequency, # of dry days, P intensity) and interannual precipitation (coef. Of variability) variability differentially impacts productivity in cold and warm grasslands and forests. The main contributions of this paper are its robust sampling/statistical approach and global scope that is far more expansive and more generalizable than many studies related to this topic. One of the biggest results of the paper is that intraannual P variability has more influence of terrestrial production than interannual variability does in many of the major biomes studied.

While I believe that the results will have a substantial impact on the field, I confess that I had difficulty digesting the results. I believe this stems from the use of three intra-annual variability metrics (one of them being a new rainfall frequency metric, UGI) that are correlated to some degree and one interannual variability metric. Also, the sign convention used in Fig. 3 leads to negative values which are interpreted always in the positive, e.g.,, positive impacts of GPP due to an increased rain frequency and rainy days. In any event, the presentation could be improved. Also, I found the arguments for the mechanisms of ETR and FWA to explain the enhanced productivity in xeric systems in years with more evenly distributed rainfall as dubious and unnecessary (since there is no consensus in the prior literature as to if this is a surprising result even if this is the common conceptual model). These concerns are elaborated further below.

Comments specific to the text:

L1. Isn't this about precipitation (rain and snow) rather than just rainfall?
L16. Conversely? Wouldn't conversely be positive to IAV and negative to intra-annual frequency? Suggest rewriting sentence.
L19. "...or lower rainfall variability …" where is lower rainfall variability mentioned above?
L20. What do you mean by "Climate models have difficulties in simulating rainfall variability"? These statements need to be better unpacked.
L24. Isn't this saying the opposite of L20?
L33. Can this last method be reframed? This doesn't seem to describe another method to investigate "the relationship between rain variability and plant productivity" like the other two do.
L94 "...within a selected pair of grid cells …"
L101. It seems like Fig. 3 is always being interpreted the opposite way (contrapositive, I believe this is called) from the way that it intuitively conveys. I finally got it (I think) as lower values of the variability metrics denote decreases in GPP (so the contrapositive is true). Surely there is another way that you can make this figure to make it more intuitive. Furthermore, the UGI takes getting used to and the term rainfall frequency is often used in place of it even though increases in UGI mean less

evenly distributed in time and decreased frequency.
L106. Perfect example of what I just said above. Fdry increases with LESS rainy days.
L138. Here and elsewhere, “preference” is frequently used which seems a little anthropomorphic.
L143-145. The rest of this paragraph and Fig. 4 folllowing this sentence seems to be an attempt to explain this result and evokes two mechanisms: ETR and FWU. However, I find this explanation weakly supported and dubious. In xeric systems, more regular rainfall is likely to have little impact on reducing evaporative demand because even in a more regular rainfall year the system is still dominated by a xeric climate with, by definition, infrequent and scant rainfall and energy is rarely limited. In order to achieve significant ETR you would have to have a much wetter climate. Also, FWU hasn’t been widely documented in xeric systems, (maybe I’m wrong) or at least its impact on productivity haven’t been. In any event, since the system is xeric, the amount of time the plant water stress could be alleviated by it would still be very limited even in a year with more regular rainfall.
L171-175. As stated above, I would be hesitant to include this mechanistic explanation as a major conclusion of your study.

On behalf of my co-authors, I would like to warmly thank the three anonymous reviewers, whose contribution greatly improved the manuscript, “Maximum constraint on the response of terrestrial productivity to precipitation variability”.

Please find in the following my detailed point-by-point response to the three reviewers.

Reviewer #1

Line 124: "cold forest" is not a common ecosystem are you referring to Taiga

Line 129: "cold grassland" is not a common ecosystem are you referring to portions of arctic tundra and montane grasslands

Line 137: "warm-dry grasslands" are not a common ecosystem term

The five biomes created in our study (cold, warm-dry, warm-wet grasslands and cold, warm forests) are based on a cluster analysis performed with long-term P-T data on a subset of two landcover types: grasslands (that include savannahs and shrublands), and forests (that include deciduous, evergreen, mixed and woody savannahs). The pooling of standard biomes listed by the International Geosphere-Biosphere Program has been performed to increase the sample size. The five *generic* names are therefore not standardized, but they overlap with existing biomes, for example boreal forests and cold forests. The specific fraction of each standardized biomes present in our generic biomes is available in Supplementary Table 1. This has been clarified in the manuscript, line 91-94.

Line 149: shade from the clouds

Corrected line 196.

Reviewer #2

Firstly, if you search global GPP products, there are way more than one products. Wu usually see significant differences in these GPP products. Will using different GPP products give you different results? This needs to be tested such that we know the reported results are robust enough.

This comment lead to the most significant change in our manuscript. In addition to SATFLUX, we included two others global GPP products in the main body of the text, FLUXCOM RS+METEO, and VPM. Only consistent patterns between at least two products have been discussed in the updated version of the manuscript. We prove here that our results are robust for all biomes, at the exception of the cold grasslands. A novel result was the importance of heavy events in xeric grasslands that was not correctly captured by SATFLUX alone. This result supports the conceptual model of Knapp et al. (2008) based on soil moisture fluctuations. However, our former discussion based on the importance of rainfall frequency in xeric grasslands is also supported by VPM, which leads to a stimulating discussion on the diversity of pathways used by this biome to mitigate water-stress.

Secondly, besides mean temperature, precipitation, and biome, there are other factors that could potentially contribute to the responses of plant productivity, such as soil. How could you separate the contribution from soil with those from rainfall variability?

The pairing method has precisely been developed to answer this question. Soil differences within each pair of grid cells will increase the variability in the results, but the median value of the control population regarding difference in productivity within each pair remains close to 0. In other words: even if soil characteristics drastically vary between sites with same mean long-term precipitation and temperature, the fact that pairs with similar rainfall variability characteristics have a similar productivity proves that the effect of all other confounding variables (including soil) is statistically minimized by the use of a median value on a large population. You can notice that the tail of the control histogram presented in Fig. 2 can exceptionally reach 100% of difference in productivity between two sites part of a same pair. While these cases possibly come from differences in soil characteristics, they are extremely rare.

Thirdly, the impact of rainfall variability on biogeochemical processes are rarely discussed in the main text and Fig. 4. There should be a potential pathway that soil biogeochemistry can have an impact on plant productivity under different rainfall variability scenarios.

This comment leads to the second most important change in the manuscript. Fig. 4 has been modified to include the relationship between nutrient availability and precipitation patterns. Discussion on the importance of soil nutrients is presented line 201-211, and line 245-248.

L55: Focusing on “five biomes distributed over four continent” was not well justified. Is this due to data availability (precipitation data from rain gauges) or any other reasons? A Lot of land areas are not included in this study, including those in China, Africa, South America, and the broader tropic region.

The method has been updated line 430-435 to clarify the absence of data in the Southern hemisphere and most of Asia. It comes from a combination of the absence of long-term daily precipitation measurements, extensive agriculture or urbanization (such as India), and the necessity to have at least 50% of forests or 50% of grasslands (for example, a grid cell with 33% forests, 33% grasslands and 34% water would be discarded).

L65: I would say they are “confounding variables”

Corrected.

L90: reflectance->surface reflectance; fluorescence->solar-induced chlorophyll fluorescence

Corrected.

L90-L91: it would be much better to cite the [40] here.

This part has been removed from the manuscript.

Reviewer #3

I confess that I had difficulty digesting the results.

We hope that the updates brought to the present manuscript will make our study more appetizing.

I believe this stems from the use of three intra-annual variability metrics (one of them being a new rainfall frequency metric, UGI) that are correlated to some degree and one interannual variability metric.

This comment is unclear, because all existing rain metrics are correlated to some extent. We chose 3 of them because they represent different mechanisms (drought, rainwater infiltration, year-to-year variability, and rain irregularity), and we proved that the Unranked Gini-index is more holistic compared to other indices in studying the response of ecosystems to rain frequency (Supplementary Fig. 6).

Also, the sign convention used in Fig. 3 leads to negative values which are interpreted always in the positive, e.g.,, positive impacts of GPP due to an increased rain frequency and rainy days. In any event, the presentation could be improved.

L101. It seems like Fig. 3 is always being interpreted the opposite way (contrapositive, I believe this is called) from the way that it intuitively conveys. I finally got it (I think) as lower values of the variability metrics denote decreases in GPP (so the contrapositive is true). Surely there is another way that you can make this figure to make it more intuitive. Furthermore, the UGI takes getting used to and the term rainfall frequency is often used in place of it even though increases in UGI mean less evenly distributed in time and decreased frequency.

L106. Perfect example of what I just said above. Fdry increases with LESS rainy days.

We improved the presentation of the discussion and the method. We only kept one convention in the figure and manuscript: positive values mean higher productivity with higher variability (drier days, heavier events, more irregular rain), and negative values mean lower productivity with higher variability. We minimized the use of “rain frequency” (which is confusing, because high frequency is opposed to high variability), and preferred “irregular rain”.

Also, I found the arguments for the mechanisms of ETR and FWA to explain the enhanced productivity in xeric systems in years with more evenly distributed rainfall as dubious and unnecessary (since there is no consensus in the prior literature as to if this is a surprising result even if this is the common conceptual model). These concerns are elaborated further below.

L143-145. The rest of this paragraph and Fig. 4 folllowing this sentence seems to be an attempt to explain this result and evokes two mechanisms: ETR and FWU. However, I find this explanation weakly supported and dubious. In xeric systems, more regular rainfall is likely to have little impact on reducing evaporative demand because even in a more regular rainfall year the system is still dominated by a xeric climate with, by definition, infrequent and scant rainfall and energy is rarely limited. In order to achieve significant ETR you would have to have a much wetter climate. Also, FWU hasn’t been widely documented in xeric systems, (maybe I’m wrong) or at least its impact on productivity haven’t been. In any event, since the system is xeric, the amount of time the plant water stress could be alleviated by it would still be very limited even in a year with more regular rainfall.

Two updates brought to the manuscript have nuanced our discussion based on ETR and FWU, with a higher focus on the root water uptake pathway: (i) the VPM and FLUXCOM GPP products show that heavier events increase the productivity of xeric grasslands and (ii) The discussion now includes the possible influence of nutrient availability.

Xeric grasslands benefit from higher year-to-year variability and heavier events, which illustrates that root water-uptake is a major pathway. We do not contest this point, and it is now clearly indicated in the conclusive paragraph. *However*, the productivity of xeric grasslands also declines with more irregular rain. This result is robust for two global GPP products and requires a mechanistic explanation. Ross et al. (2012), who found similar results, focused on the soil moisture – plant relationship, but we disagree with this interpretation. Due to the xeric climate you mentioned, light and regular events are not likely to increase the soil moisture compared to heavy and irregular events that can penetrate deeper in the soil (conceptual model of Knapp et al., 2008). So we need to *at least* question the importance of pathways other than root water-uptake. We presented two of them, (i) Evapotranspiration reduction, which simply is a generic term that merges all different strategies to mitigate water stress from vapor pressure deficit and temperature regulation; and (ii) Foliar Water Uptake, which recently received a lot of attention from the community with 233 listed species (Berry et al., 2019)!

So far, manipulative experiments only focused on the relationship between soil moisture and productivity, while ignoring, *by design*, ETR and FWU mechanisms. We simply suggest that these two processes might be more important than previously thought. This is a hypothesis that will need to be verified on the field by observational studies.

L1. Isn't this about precipitation (rain and snow) rather than just rainfall?

The title has been changed.

L16. Conversely? Wouldn't conversely be positive to IAV and negative to intra-annual frequency? Suggest rewriting sentence.

L19. "...or lower rainfall variability …" where is lower rainfall variability mentioned above?

L20. What do you mean by "Climate models have difficulties in simulating rainfall variability"? These statements need to be better unpacked.

The abstract has completely been rewritten.

L24. Isn't this saying the opposite of L20?

"Long term mean precipitation" is more accurate. Precipitations averaged over 30 years can be considered as stationary, while mean annual precipitations show a larger year-to-year variability with climate change.

L33. Can this last method be reframed? This doesn't seem to describe another method to investigate "the relationship between rain variability and plant productivity" like the other two do.

This method has been clarified, line 33.

L94 “...within a selected pair of grid cells …”

Corrected, line 104.

L138. Here and elsewhere, “preference” is frequently used which seems a little anthropomorphic.

We restricted the word preference to two sentences only, line 212 and 231.

L171-175. As stated above, I would be hesitant to include this mechanistic explanation as a major conclusion of your study.

The major conclusion of the study is based on 4 biomes (warm-wet, warm-dry grasslands, warm and cold forests), 1 major pathway (root-water uptake) and 3 secondary pathways (influence of precipitation patterns on nutrient availability, ETR and FWU). We notably changed the abstract and added the results about boreal forests that are important.

REFERENCES

Ross, I. *et al.* How do variations in the temporal distribution of rainfall events affect ecosystem fluxes in seasonally water-limited Northern Hemisphere shrublands and forests? *Biogeosciences* **9**, 1007–1024 (2012).

Knapp, A. K. *et al.* Consequences of More Extreme Precipitation Regimes for Terrestrial Ecosystems. *Bioscience* **58**, 811–821 (2008).

1st Sep 20

Dear Dr Ritter,

Your manuscript titled "Maximum constraint on the response of terrestrial productivity to precipitation variability" has now been seen by our reviewers 2 and 3, whose comments appear below. In light of their advice I am delighted to say that we are happy, in principle, to publish a suitably revised version in Communications Earth & Environment under the open access CC BY license (Creative Commons Attribution v4.0 International License).

We therefore invite you to revise your paper one last time to address the remaining concerns of our reviewers. At the same time we ask that you edit your manuscript to comply with our format requirements and to maximise the accessibility and therefore the impact of your work.

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Please review our specific editorial comments and requests regarding your manuscript in the attached "CommsEarth Final revisions information checklist". Please outline your response to each request in the right hand column.

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We hope to hear from you within two weeks; please let us know if you need more time.

Best regards,

Heike Langenberg, PhD

Chief Editor
Communications Earth and Environment

On Twitter: @CommsEarth

REVIEWERS' COMMENTS:

Reviewer #2 (Remarks to the Author):

This is my second review of this manuscript. I found the authors addressed all of my comments nicely and I am now happy to suggest to accept it for publication.

Reviewer #3 (Remarks to the Author):

The authors have done good job addressing the mainly minor concerns of the reviewers. I have only a few small minor edits to consider (attached in teh annotated manuscript), and I recommend the paper's publication.

Maximum constraint on the response of terrestrial productivity to precipitation variability

François Ritter[1,*], Max Berkelhammer[1,*] and Cynthia Garcia-Eidell[1]

[1]Department of Earth and Environmental Sciences, University of Illinois at Chicago, Chicago, IL 60607, USA

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Rainfall variability has been impacted by climate change on inter and intra-annual timescales, and controlled experiments have documented the potential influence this may have on future ecosystem productivity. However, the response of ecosystems to rainfall variability is difficult to constrain due to myriad physiological and abiotic variables that limit terrestrial productivity. Here we present a novel statistical framework to isolate the impact of rainfall variability on the gross primary productivity of five biomes that collectively account for 50% of global land area. The productivity of mesic grasslands and forests decreases by ~28% and ~7% (respectively) in response to more irregular rain within the year, while the sensitivity is halved in response to higher year-to-year variability. Xeric grasslands share similar results on the intra-annual scale, but their productivity increases with higher inter-annual rainfall variability. Conversely, the productivity of boreal forests increases under higher variability on both temporal scales. Climate models have difficulty capturing rainfall variability and this study quantifies the potential consequence of this bias on projections of the terrestrial carbon sink.

1. Introduction

Long-term mean precipitation has shown a remarkable stationarity over the historical record despite warming[1]. However, climate models predict that precipitation variability is expected to be more impacted by climate change[2-4], with evidence of these changes now emerging from observations[5-8]. Given that water availability is a major limiting factor for most biomes[9], changes in rainfall patterns (such as less frequent but more intense storms) can have dramatic consequences on ecosystem composition and productivity[10]. Earlier studies have investigated the relationship between rain variability and plant productivity through three main approaches: (i) The first method uses Rainfall Manipulation Plots (or RaMPs), where rainwater is collected before it reaches the canopy and then redistributed with fewer but larger events[11]; (ii) A second approach is to run land-atmosphere models fed with different precipitation patterns to simulate the vegetation growth response[12]; and, (iii) The last method is to select several sites of the same biome but with different precipitation patterns and analyze how rain variability influences their productivity, without altering the surrounding environment[13,14]. The first two approaches mainly focus on how rain frequency affects soil moisture and, consequently, productivity while ignoring other ecological mechanisms related to rain frequency, such as leaf wetting[15] or vapor pressure deficit[16] that are, by design, discarded in RaMPs due to the absence of control on air moisture and are poorly captured in models due to their coarse grid size. To generate a more holistic estimate of the effects of rain frequency on productivity, we have developed a variant of the third approach that establishes a global constraint on how productivity is affected by rainfall variance by comparing the productivity between ecosystems with similar mean climate states but different rain variability.

One of the challenges in generalizing the response of a biome to rainfall variance emerges from the diversity of ecophysiological characteristics (canopy height, rooting depth, stomatal response to soil moisture), soil types (nutrient pool, porosity, conductivity) and mean climate state that modulate the sensitivity of ecosystems to precipitation patterns. Consequently, former studies have produced diverging results[17,18] on responses to both *intra-annual* (precipitation frequency & intensity within the year) and *inter-annual* variability (alternation of pluvial and drought years). For example, larger but less frequent events can have a negative[13,19] or positive[20] impact depending on the ecosystem type. Similarly, more extreme wet and dry years reduce the productivity of grasslands[21] or, conversely, enhance the resilience of tropical ecosystems by forcing the development of more complex hydraulic systems[22]. Studies agree that higher rain variability is more likely to benefit xeric over mesic habitats[12,17,21,23], but the overall direction and magnitude of change in terrestrial productivity due to rain variability have never been estimated empirically at a scale larger than isolated plots.

This study quantifies the long-term (2001-2018) contribution of intra-annual and inter-annual rainfall variability to the productivity of five biomes distributed over four continents (Fig. 1). To achieve this, we address the following issues that have limited previous studies:

(i) Rainfall is a stochastic process with high spatial and temporal variability and its variance has been quantified with numerous metrics[6-8,12]. Thus far, existing literature has not established a set of agreed-upon Rainfall Variability Parameters (RVP) that are globally relevant for ecosystem productivity and can be aggregated and scaled spatially and temporally.

(ii) As described earlier, plant growth is affected by many variables: mean precipitation & mean temperature (first order drivers), plant & soil type, but also fire frequency or grazing patterns. A new statistical method is required to isolate the influence of rainfall variability on productivity from these confounding variables.

The first issue is associated with the well-known "coarse-graining problem", where information is lost through spatial & temporal averaging[24]. Weather stations with daily precipitation are therefore more appropriate than gridded (i.e. mechanistic, geospatial modeled or remotely-sensed) precipitation data products of rain that do not retain the full spectrum of information on rain variability[25]. Using daily rainfall with continuous records back to 2001, we calculated four RVPs per station: one on the inter-annual scale and three on the intra-annual scale (Fig. 2a,b). While the RVPs are correlated with one another (Supplementary Fig. 7), they each emphasize the effects of specific ecological mechanisms. The coefficient of variation (CV) is connected to ecosystem resilience to drought years[21], the fraction of dry days (f_{dry}) is correlated to droughts and absence of cloud cover[2] and the rain intensity (α) affects the mean infiltration depth[12]. We also introduce a new rain frequency metric, the Unranked-Gini index (UGi), which is unitless and describes how irregularly distributed the annual precipitation amount is, spanning 0 (rainfall is equally distributed every day) to 1 (rainfall is concentrated the first or last day of the year). This new metric is more holistic compared to existing rain frequency indices because it accounts for the temporality of rain events which we hypothesized to have a critical influence on the productivity of different biomes (Supplementary Fig. 6).

The second issue has driven experimental designs that focus on individual plots where confounding factors, such as different soil types, can be disregarded. However, when aggregated, these isolated studies on the plot scale have given rise to a broad range of inconsistent results that justify the need for a global estimate of the impact of rainfall variability. We first created five biomes based on their land cover type (grasslands or forests, croplands excluded) and their long-term mean temperature (T) and precipitation (P) aggregated from the daily weather stations present within 0.5° × 0.5° grid cells (Fig. 1a,b). These biomes are associated with *generic* names (e.g., warm forests or cold grasslands) because they represent different ecological communities sharing similar canopy height that have been pooled to increase the sample size (Supplementary Table 1). While Net Primary Production has been the more traditional metric to study the influence on rainfall variance on ecosystems, we chose to base our analysis on the response of Gross Primary Production (GPP) because advanced estimates through combined satellite data and in-situ measurements are readily available, and changes in photosynthesis can be linked directly to the response of stomatal conductance to soil moisture and vapor pressure deficit without also needing to consider the response of respiration. Three state-of-the-art global GPP products were utilized in this study: SATFLUX[26], FLUXCOM RS+METEO[27] (simply FLUXCOM in the following) and the Vegetation Photosynthesis Model or VPM[28]. To isolate the impact of each RVP (UGi, α, f_{dry} or CV) on the GPP of a biome, a new statistical approach was developed which we refer to as *the pairing method* (example in Fig. 2c). The mean precipitation, temperature and biome type are set as fixed variables within a selected pair of grid cells, and we compare two populations of pairs, *control* (RVP is fixed) and *experiment* (RVP is varying), to detect how each RVP influences GPP across the population of all paired grid cells. The combined effects from all confounding variables (e.g., soil type or fires) and sub-grid scale heterogeneity in precipitation are presumed to increase the variance of the productivity within the populations, but the median on the large sample size retains the *direction* and *magnitude* of change in GPP due to RVP (see Supplementary Methods).

Our results provide a clear and consistent constraint on the directional response of the productivity of terrestrial ecosystems to rainfall variance that did not emerge from previous work based on site-level studies. The development of the Unranked Gini-Index provides unequivocal evidence that intra-annual rain frequency is a more critical determinant of productivity than inter-annual variability for all biomes, and we observe biome-specific responses to precipitation variability. In agreement with our expectations, warm-wet grasslands and warm forests have decreased in productivity in response to higher rainfall variability, though the former is four times more sensitive (i.e. a 28% decrease in grasslands and 7% decline for forests). Conversely, cold forests show higher productivity with higher rainfall variability and especially in response to longer droughts, which likely arises from the importance of incident radiation as a primary limiting factor, but also of snow as a water source in these ecosystems. One surprising pattern that emerges is a temporal decoupling between the way warm-dry grasslands respond to rain irregularity on an inter-annual scale (increase in productivity) or intra-annual scale (decline in productivity). The positive response of GPP to higher inter-annual variance was expected but the negative response to irregular rain within the growing season is a novel result. Particularly, short gaps between rain events emerge as more beneficial for warm-dry grasslands relative to large events that infiltrate deep into the soil. We hypothesize that more frequent rain events improve the nutrient availability and mitigate water stress through mechanisms such as foliar water uptake or reduced evapotranspiration, which could explain the temporal decoupling observed in this biome.

2. Results

2.1 Consistency between GPP products

We recognize that a significant source of uncertainty in this analysis can be associated with the derivation of GPP from various ecosystem models and/or satellite retrievals. We therefore chose to conduct the analysis on three products that were derived independently. These products share results with consistent direction and magnitude of change for all biomes except in cold grasslands (Fig. 3). The absolute maximum percentage of change in GPP for grasslands due to intra-annual variability (UGi, α or f_{dry}) ranges from 17% to 28%, while forests are 3 to 4 times less sensitive (~7% of change). Inter-annual variability (CV) has a lesser impact than intra-annual RVPs, with a maximum of 8-12% of change for grasslands and 3% change for forests.

FLUXCOM shows a sensitivity in the response of productivity to UGi that is 4 to 5 times lower compared to the other two products. On average for the three grasslands, the absolute change in GPP to UGi for FLUXCOM is 4 ± 2 % (1 standard deviation), compared to 23 ± 11 % for SATFLUX and 17 ± 5 % for VPM. FLUXCOM is the only product that directly assimilates precipitation to improve GPP estimates, and we hypothesize that it leads to a reduced sensitivity to UGi because this metric is correlated to mean annual precipitations that were fixed in the pairing method (Supplementary Fig. 5a and 8b). While the results from all the GPP products are presented in Fig. 3, the discussion about rainfall frequency will only focus on the results from SATFLUX and VPM. More generally, only the common patterns that emerge from at least two GPP products will be discussed.

2.2 Cold biomes

Cold forests yield higher productivity with higher rainfall variability on both intra-annual (drier days, more irregular rain, heavier events) and inter-annual scale (more extreme drought and wet years). The fraction of dry days has the largest impact on productivity, with an increase of 7% in GPP, compared to an increase of only 2% from higher inter-annual variability. The maximum difference of temperature between two pairs has been set to 1.5 °C (see Method), and cold forests are the only biome where the sensitivity to temperature is high enough that variations in temperature within this threshold had an impact on productivity similar to the RVPs (Supplementary Fig. 5b). For the cold grasslands, no consistent patterns emerged between the GPP products and we therefore draw no conclusions on how rainfall variance influences this biome.

2.3 Warm biomes

In contrast to the cold forests, the productivity of warm forests and warm-wet grasslands decreases with higher rainfall variability on both intra-annual and inter-annual scales. UGi has the largest impact on both biomes, with more irregular rain leading to a 7% and 28% decrease in the GPP of warm forests and warm-wet grasslands, respectively. In comparison, higher inter-annual variability only leads to a 3% and 8% decrease, respectively. While precipitation intensity has no effect on warm-wet grasslands, heavier events have a slightly negative, but statistically significant, impact on warm forests (2% of decrease in GPP).

Interestingly, productivity of warm-dry grasslands decreases with more irregular rain (by 17%) but increases with heavier events (by 13%) and higher year-to-year variability (by 12%). SATFLUX is the only product that shows a low sensitivity to long-term mean annual precipitation within the pairing procedure for this biome, while the two other products are sensitive to slight increases in long-term P (Supplementary Fig. 5), certainly due to the correlation between P and UGi (Supplementary Fig. 8).

3. Discussion

Based on the results from previous studies, we presumed that irregularly distributed precipitation through the year (defined as UGi ~ 1) would be detrimental to ecosystems. In our study, temperate biomes, that are neither water nor energy-limited like the warm-wet grasslands and warm forests, showed a particularly significant and negative response to unevenly distributed rainfall. Indeed, it has been shown that rain frequency plays an important role in the spatial distribution of these biomes[29]. The primary benefit of evenly distributed rainfall is that it mitigates two stressful situations: floods[30] (waterlogged/hypoxic soils and loss of available precipitation through runoff) and droughts[31] (water-stress eventually leading to down regulation of photosynthesis and plant senescence). While the first order pathway that links precipitation distribution to productivity is through soil moisture and root water uptake, we also note that there are other pathways that can enhance the positive response to frequent rainfall (Fig. 4). This includes, for example, Evapotranspiration Reduction[32] (ETR) where if precipitation regularly falls, then a decrease in vapor pressure deficit[16], and cooling of the surface due to the latent heat released during evaporation or shade from the clouds[10] increases the available water. In addition, frequent rainfall may increase the potential for Foliar Water Uptake[33] (FWU) where persistent water availability on the leaf surfaces rehydrates the plant through the droplet absorption, which has a particularly critical role in the ecohydrology of arid environments[34-36] where dew formation typically occurs once a week[37]. Furthermore, precipitation distribution influences nutrient cycling. A positive feedback exists between accumulation of organic matter (primarily driven by precipitation and temperature) and concentration of nutrients in the soil[38]. The balance between nutrient availability and plant nutrient uptake is however complex, and depends on microbial community composition, decomposition rates or turnover times that covary with precipitation and temperature. Inconsistent results have been found in the past between manipulative experiments that study the short-term response of an ecosystem that was put under stress, and observational studies interested in nutrient levels that represent the long-term adaptation of ecosystems to a specific climate[39]. The direction and magnitude of the impact of precipitation patterns on nutrient availability therefore remain uncertain. Future studies could benefit from adopting a similar approach as used here to isolate how nutrient availability is influenced by precipitation variance.

On the contrary, we see a clear preference for higher rain variability in cold forests which arises because the accumulation of snow and its incremental melting during the spring is a more critical determinant of water availability than the evenness to which precipitation is delivered through the year[40]. Because these ecosystems are energy-limited, cold forests primarily benefit from more insolation (higher f_{dry}) and warmer temperatures to improve their productivity (Supplementary Fig. 5). This result is not reproduced for the cold grasslands that have a lower mean annual precipitation and are therefore more water-limited (Supplementary Table 1). The large discrepancies between GPP products for this biome might originate from the pooling of different land cover types, such as Shrublands or Savannahs, that have disparate plant functional responses (Supplementary Table 1). Another possible explanation is the inability of satellite data-driven models to capture productivity anomalies from these low canopy ecosystems, which often have snow cover that influences reflectance estimates of productivity.

In general, inter and intra-annual rainfall variability are correlated[41] (Supplementary Fig. 7a) as drought years are typically associated with poorly distributed rainfall (Supplementary

Fig. 8), and biomes typically respond in the same direction to changes on either timescale. It can be presumed that climate change would, in fact, increase the variance of rainfall on both timescales. However, warm-dry grasslands displayed opposing responses to an increase in UGi (loss of productivity with irregular rain) and increase in CV (gain in productivity). The preference of xeric ecosystems for higher inter-annual variability has previously been observed[17,21] and explained through the mechanism that during years with high rainfall, water will infiltrate the soil deeper, mitigating evaporation losses and therefore increasing the soil water availability over months or even years[23]. The asymmetric gain in GPP during pluvial years relative to the reduction during dry years has been well documented and explains the high level of resilience of xeric environments to water stress[42].

While the positive impact of heavier events (high α) on warm-dry grasslands supports the conceptual model based on soil moisture fluctuations, the negative impact of irregularly spaced precipitation events points to additional mechanisms not directly associated with deep rainfall infiltration, such as ETR or FWU. In other words, large gaps between rainfall events lead to a decrease of moisture available on the canopy or soil surfaces, which, in turn, increases VPD and drives evaporative water loss. Because these processes occurring at the leaf surface or within the canopy are known to be poorly represented in models and neglected in rainfall manipulation experiments, they have not previously been considered as critical pathways by which rainfall variability influences productivity. Additionally, nutrient availability has been observed to decrease with increasing aridity in drylands based on a long-term observational study[43], and less frequent events might negatively affect the nutrient cycling. We hypothesize that the combined effects of all these secondary processes match the benefit of a higher deep soil moisture content from larger irregular rainfalls (Fig. 4c). This hypothesis is supported by the results of a previous study that found a negative impact of less frequent events on dry shrublands[13]. However, their discussion was based on the difference in plant functional traits between grasslands and shrublands (rooting depths), and the existence of an intermediate rain frequency to reach optimum soil moisture levels, depending on the plant and soil type. The decoupled response of xeric grasslands to intra- and inter-annual rain frequency illustrates how the resilience of these ecosystems may emerge from their capacity to optimize the limited water pools either during periods of high inter-annual variance, when the soil moisture mechanism is dominant, or during periods of evenly distributed precipitation events. This contrasts with the other biomes, where dry years are associated with higher water stress because decrease in rainfall frequency leads to an overall weaker resilience to drought.

It is expected that there will be a shift towards larger and more infrequent rainfall events with warming. Our results suggest with high confidence that boreal forests will respond positively to this change, and mesic ecosystems will be put under higher stress. Xeric grasslands will have to rely more on the root water-uptake pathway and be deprived of the previously mentioned secondary pathways that are possibly crucial to mitigate water stress. The response of energy-limited grasslands, savannahs and shrublands remains uncertain. At the exception of the boreal forests, these responses would act in opposition, and with a similar absolute magnitude, to the increase in productivity from CO_2 fertilization effect. Current projections of how much the strength of the terrestrial carbon feedback will increase in response to warming and higher CO_2 may be significantly affected by the processes captured in this study.

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Figures

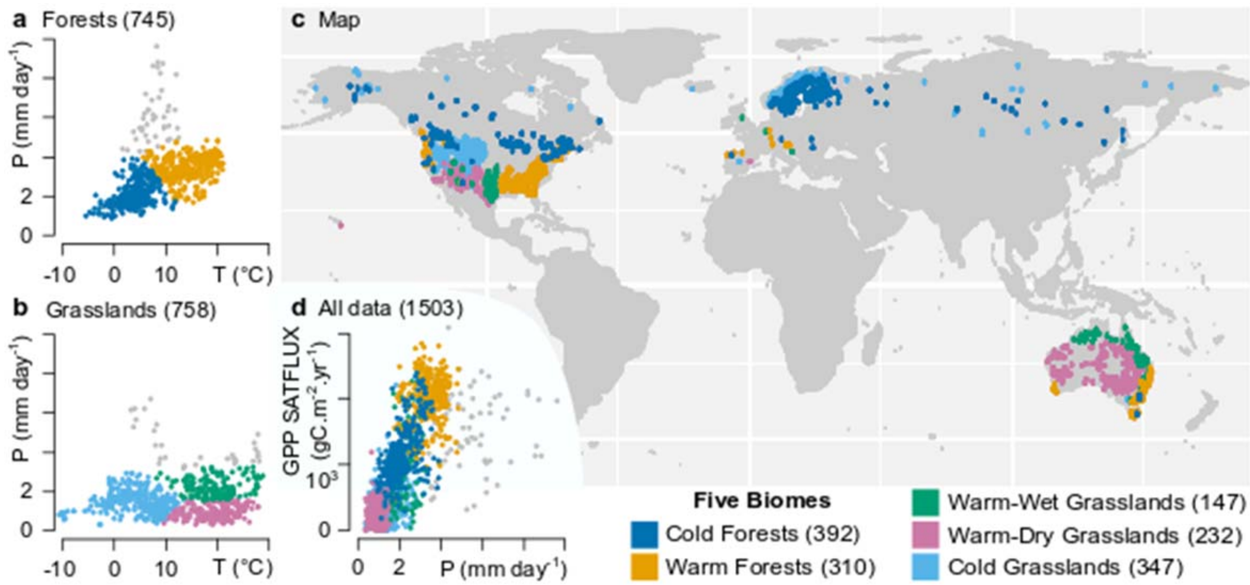

Fig. 1 | Characteristics of the five biomes. a,**b**, Relationship between long-term mean precipitation and temperature for all forested and grassland grid cells (0.5° × 0.5°), respectively. A cluster analysis was used to objectively separate forested and grassland sites into cold, warm, wet and dry subsets. **c**, Map of the grid cells. **d**, Relationship between GPP from SATFLUX and mean precipitation for all grid cells. For panels **a**, **b** and **d** the number of grid cells is indicated in parenthesis and tropical grid cells are shown in grey but discarded from subsequent analysis due to the small sample size. See Supplementary Table 1 for more information.

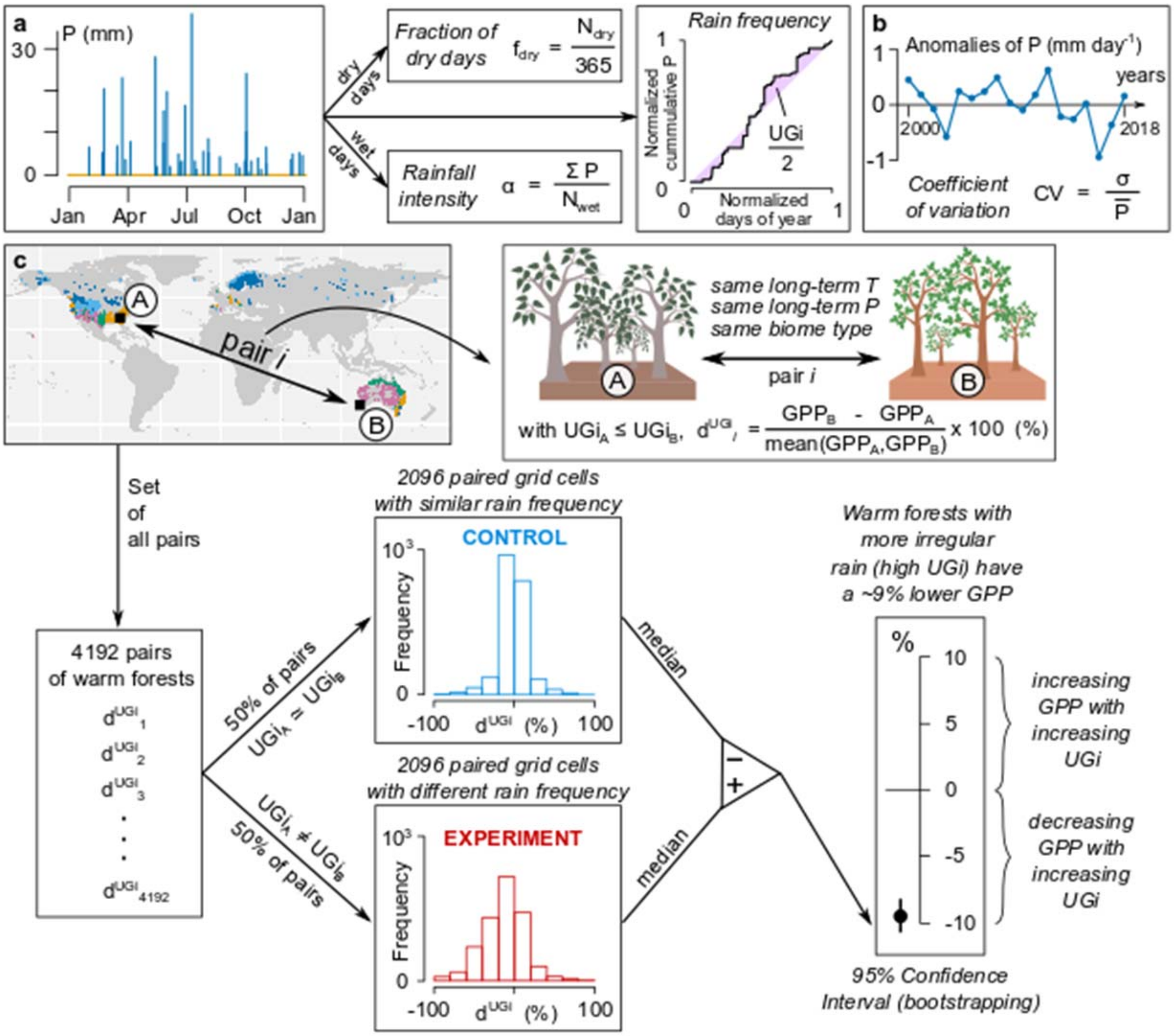

Fig. 2 | Rainfall variability parameters and pairing method. a, Three intra-annual rainfall variability parameters (α, f_{dry} and UGi). **b**, One inter-annual rainfall variability parameter (CV). **c**, Pairing method illustrated with an example of the long-term impact of UGi (related to rain irregularity) on the GPP of warm forests (SATFLUX). Two grid cells A and B are paired if they share same biome and climatological P and T values, and their percentage of difference in GPP is calculated (d^{UGi}). The set of all possible pairs of warm forests (n=4192) is divided into a *control* (similar UGi within each pair) and *experiment* (different UGi within each pair) population to compare their median value of d^{UGi} (bottom right). This procedure was repeated for all rainfall parameters, all biomes and all GPP products to generate Fig. 3.

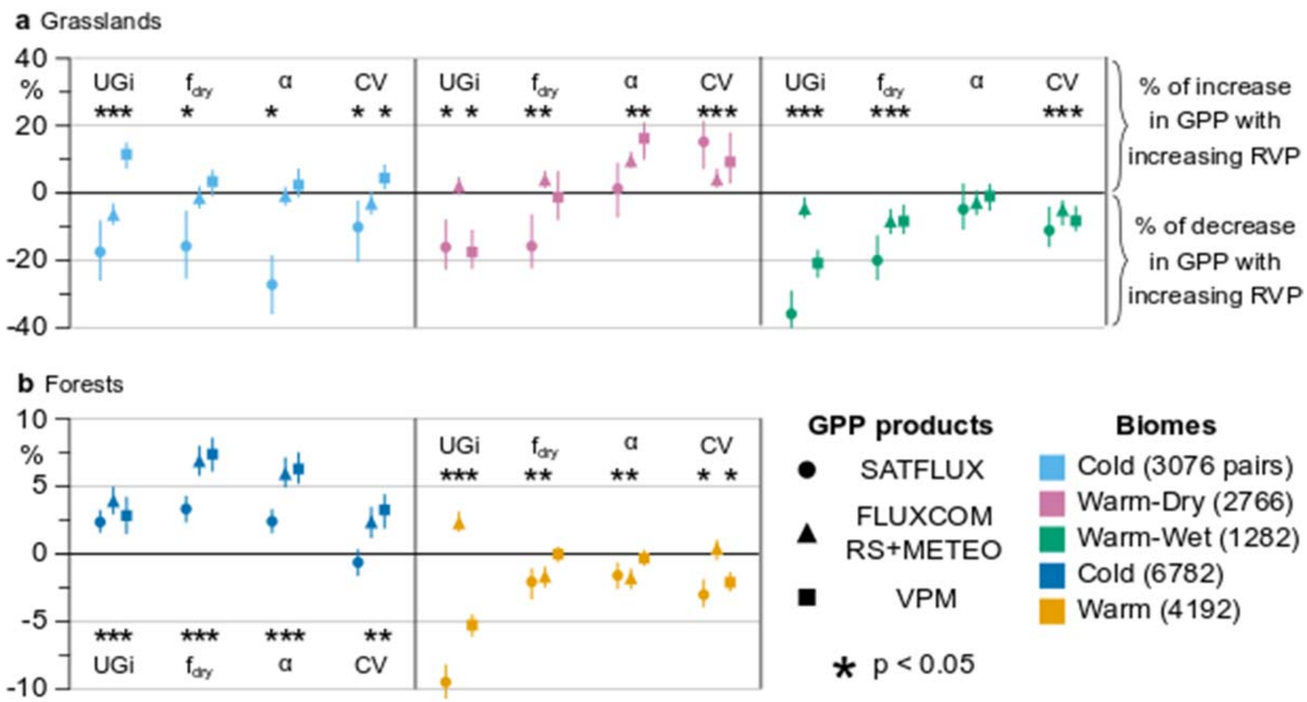

Fig. 3 | Long-term impact of rainfall variability on the productivity of grassland and forested biomes. a,**b**, Percentage of increase in GPP (positive values) or decrease in GPP (negative values) of the grasslands (**a**) and forests (**b**) due to higher rainfall variability, quantified by the rain irregularity (UGi), fraction of dry days (f_{dry}), rain intensity (α) and coefficient of variation (CV). Uncertainties (95% confidence interval) are calculated using a bootstrapping technic (Supplementary Method). Circles are associated with SATFLUX data, triangles with FLUXCOM RS+METEO and squares with VPM. See Fig. 2c as an example.

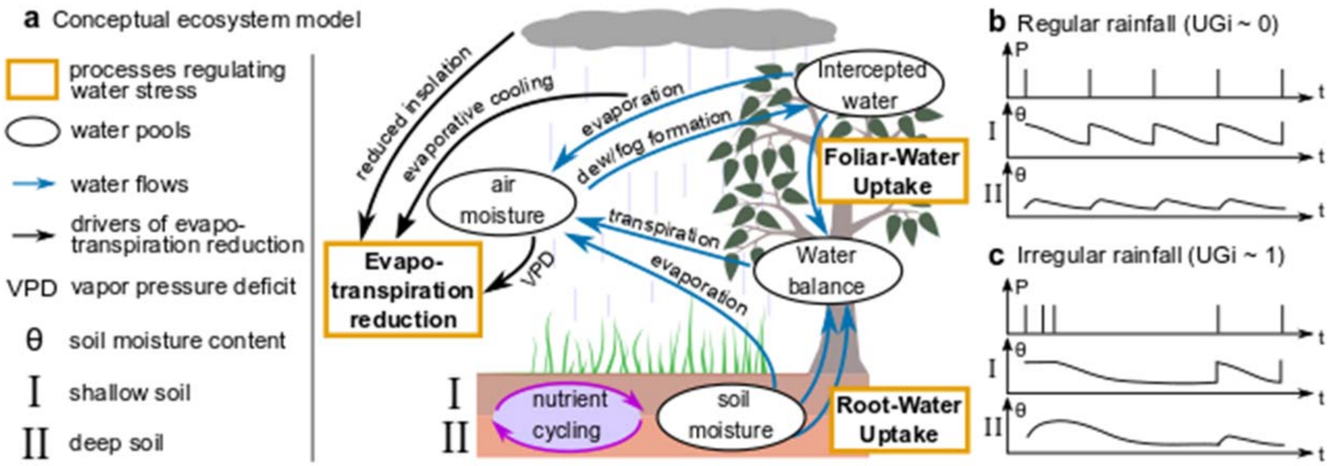

Fig. 4 | Key processes relating rainfall variance to ecosystem productivity. a, Water-stress mitigated by three mechanisms: root water uptake, foliar water uptake and evapotranspiration reduction that includes energy (decrease in temperature) and water (increase in air moisture) components. Direction and magnitude of the nutrient response to rainfall variability remains poorly constrained. **b,c** Idealized response of soil moisture content (divided into two layers) to regular rainfall (**b**) and irregular rainfall (**c**).

4. Method

4.1 Land cover type

We classify biomes using the Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Type Product (MCD12Q1, 500 m resolution, 2001-2018). The total of 17 classes from the International Geosphere-Biosphere Program (IGBP) are merged into four generic classes: forests (includes deciduous, evergreen, mixed and woody savannahs), grasslands (includes shrublands and savannahs), croplands (includes urban & mosaic) and “other” (remaining classes). Area-averaged land cover type for each 0.5° × 0.5° grid is estimated from this data. Cells with more than 5% croplands are discarded. Only cells with more than 50% forests or 50% grasslands are considered, and they must contain at least 1 weather station with long-term daily precipitation. This strict condition explains why the Southern hemisphere is absent from the analysis (at the exception of Australia), as well as most of Asia.

4.2 Gross Primary Production

We use three global monthly gridded GPP datasets at a 0.5° spatial resolution. For each product, only long-term (15-18 years) GPP average for each grid cell are analyzed. The first product is SAFLUX[26], with data available from 2001 to 2018. It is a light-use efficiency model trained using in-situ eddy covariance measurements (FLUXNET) and based on MCD43 surface reflectance from MODIS and Solar induced chlorophyll Fluorescence from GOME-2. The second product is FLUXCOM RS+METEO[27] that upscales FLUXNET observations using a machine learning method and uses a combination of MODIS and gridded meteorological products to estimate fluxes from 2001 to 2015. The last product is the Vegetation Photosynthesis

Model (VPM GPP V20). It is a light-use efficiency model similar to SATFLUX and can separate productivity from C3 and C4 plants[28]. Data are available from 2000 to 2016.

For each grid cell, a *year** is first defined as 365 days centered around maximum GPP from SATFLUX of the seasonal component given by the STL package in R using a LOESS fit. This is done so southern and northern hemisphere sites can be treated the same in terms of precipitation timing.

4.3 Precipitation

We use 2597 weather stations from the Global Historical Climatology Network-daily (GHCN-daily[44]). Stations with more than 3 invalid *years** (> 5% missing daily P values per *year**) between 2001-2018 are discarded. For each valid *year**, mean P, f_{dry}, UGi and α are calculated. They are then temporally averaged for each station, and CV is calculated. All parameters are finally spatially averaged using all the RVP values calculated from each weather station within the grid cell. There are, on average, 1.7 stations per grid cell (see Supplementary Fig. 1).

4.4 Temperature.

Due to a lack of data in the GHCN-daily temperature, monthly CPC global temperatures[45] from 2001 to 2018 (0.5° × 0.5°) are used for clustering of biomes and pairing of grid cells (Supplementary Fig. 2). It has no effect on our estimation of the GPP response to changing RVP (Supplementary Fig. 5b).

4.5 Biomes selection.

A cluster analysis is performed for the grasslands and forests to select a subset of five biomes sharing similar long-term P & T (Fig. 1a,b). The KMEANS package in R is used, and the number of clusters (3 for the forests, 4 for the grasslands) is decided based on the P & T range and the sample size required for the pairing method. Tropical biomes are discarded due to a too small sample size, and the characteristic of each biome (P, T, GPP, RVPs, IGBP fraction) is presented in the Supplementary Table 1.

4.6 Pairing method.

Details are provided in Supplementary Methods 1. A pair is defined as two grid cells sharing same biome, same long-term P (t-test, $p > 0.05$) and their difference in long-term T is smaller than 1.5 C. Through this procedure, the effect of T & P on the GPP of two paired grid cells is considerably reduced and becomes much lower than the influence of UGi (Supplementary Fig. 5). The difference of productivity within each pair (d^{RVP}, in %) is denoted with a positive (resp. negative) sign if GPP is increasing (resp. decreasing) with higher RVP (UGi, α, fdry or CV). For each biome and each RVP, the entire population of pairs is equally divided into a *control* (similar RVP for both members of a pair) and *experiment* (different RVP for both members of a pair) population and the median values of each population's d^{RVP} are compared. Confidence intervals are calculated on the 2.5-97.5 % quantile of a population created by bootstrapping of the pairing procedure (N=10000). Figure 2c provides a schematic depiction of the pairing method applied to UGi for the warm forest biome.

4.7 Unranked-Gini Index.

This rainfall frequency parameter is defined as twice the absolute area delimited by the 1:1 curve and the normalized cumulative precipitation curve (versus normalized time window, see Fig. 2a). This novel index is inspired by two former studies[46,47], however by normalizing the precipitation we are able to compare across xeric and mesic sites, and the calculation of an absolute area (instead of a standard deviation) is similar to the Gini-Index[7] (Supplementary Fig. 3a,b). Unlike the Gini-index, UGi does not require the precipitation to be ranked. The ecological information contained in the chronology of the rain events is therefore conserved, which is not the case for other common indices like the mean interval between rainfall events[12], the Gini index or the wet-Gini index[7]. The high sensitivity of GPP to UGi relative to other indices highlights its skill as an ecohydrological rainfall parameter (Supplementary Fig. 6).

Methods references

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Author contributions

F.R and M.B. conceived the study and prepared the manuscript. C.G.E. provided the GPP product. All the authors discussed the results and contributed to editing the manuscript.

Competing interest declaration

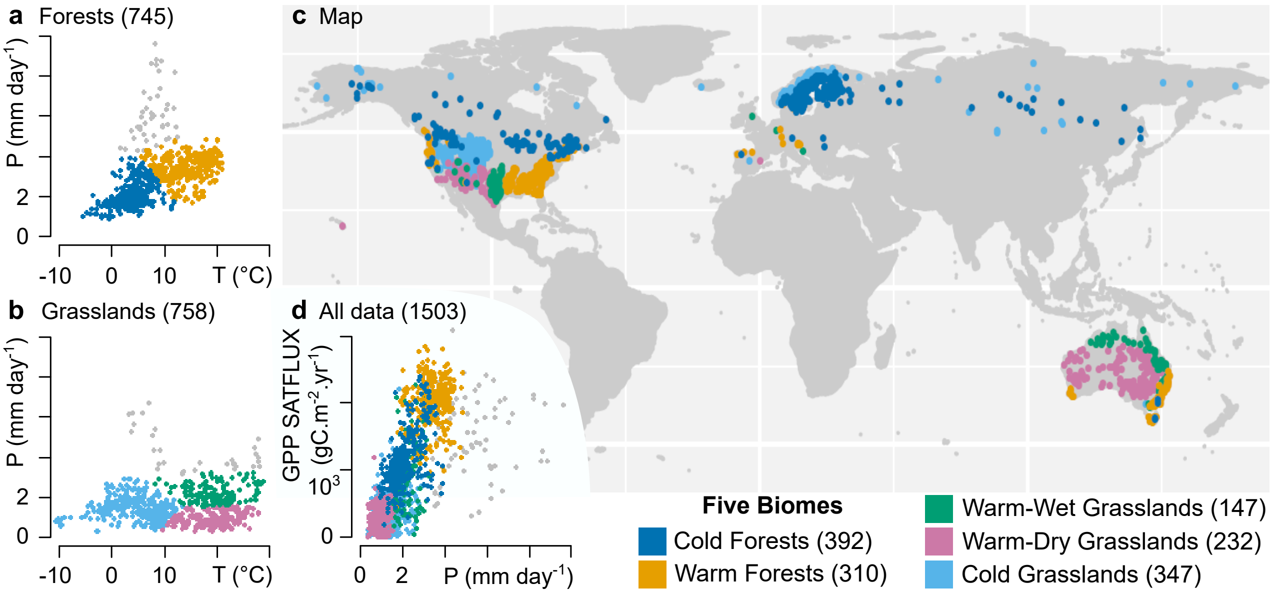
The authors declare no competing interests.

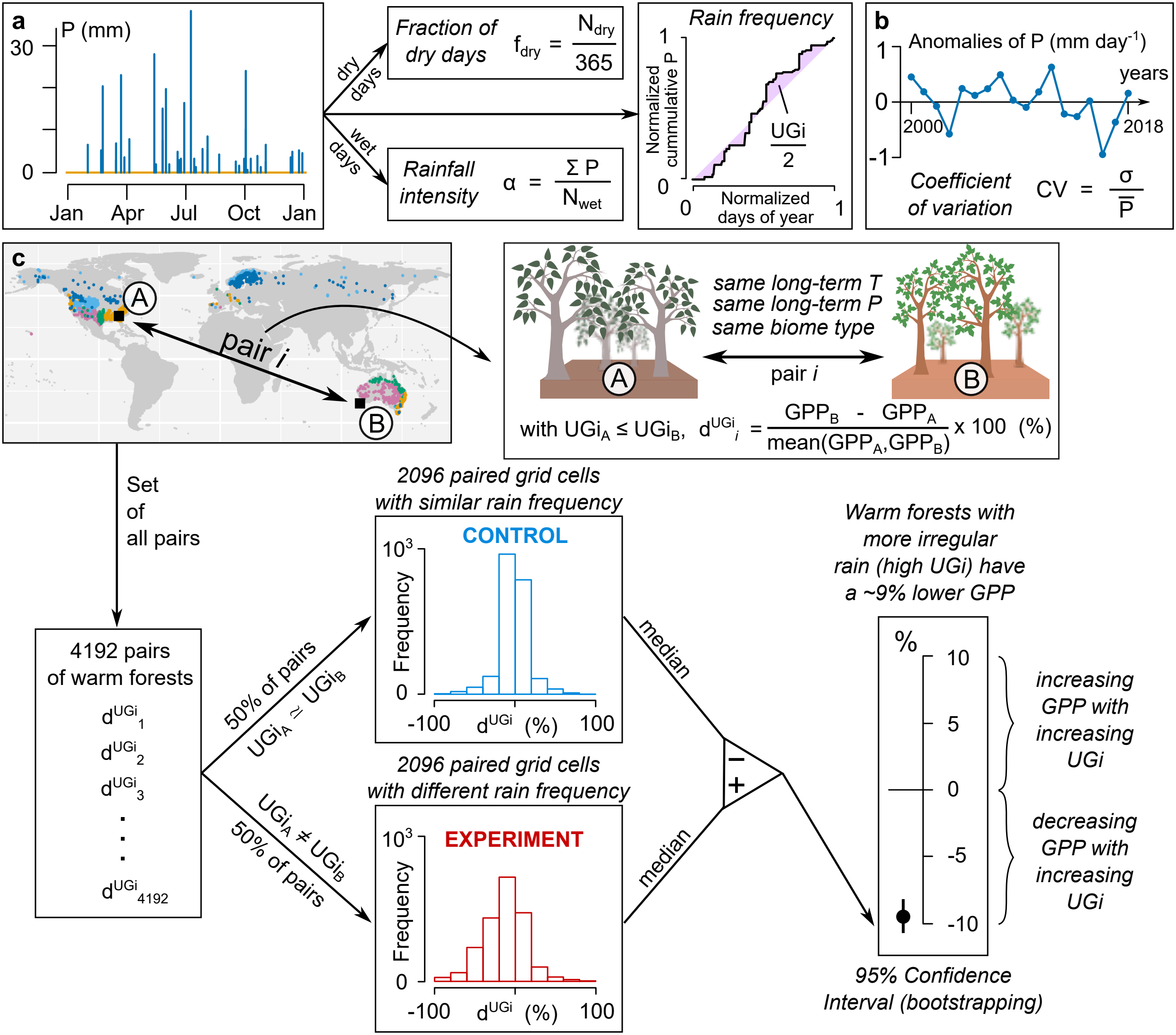
Data Availability

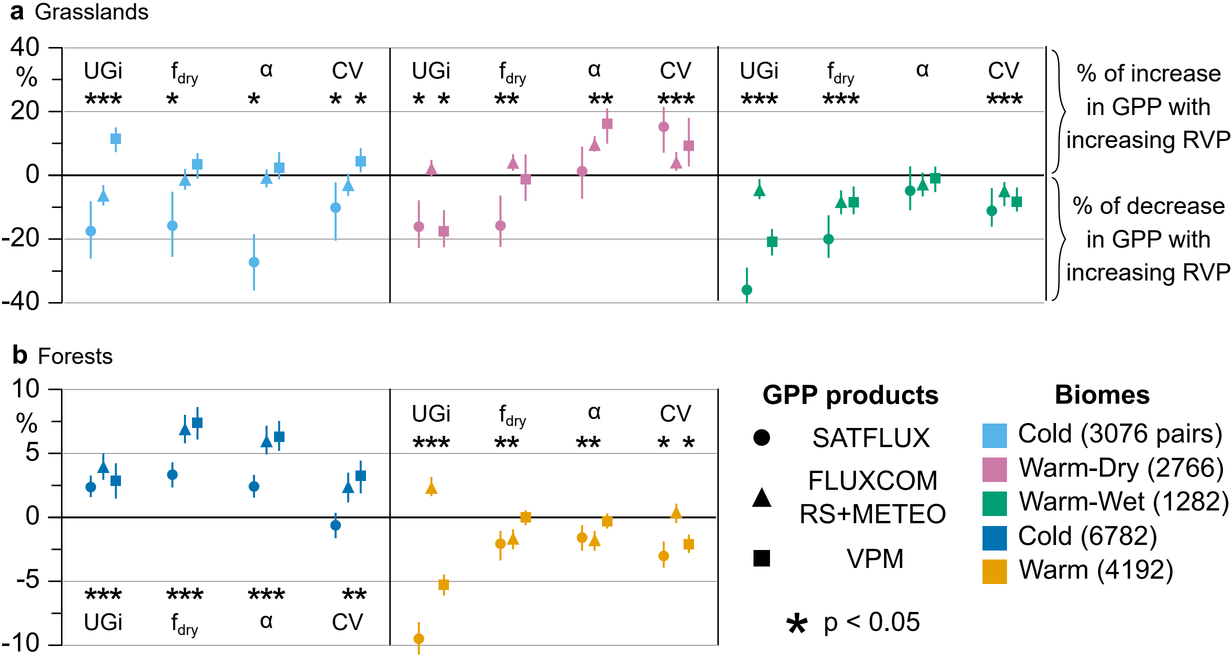
Raw data: MODIS MCD12Q1 https://doi.org/10.5067/MODIS/MCD12C1.006; GHCN https://www.ncdc.noaa.gov/ghcnd-data-access; FLUXCOM http://www.fluxcom.org/; SATFLUX https://avdc.gsfc.nasa.gov/index.php?site=228529134&id=54&go=list&path=%2Fmonthly/0.5x0.5; VPM https://figshare.com/articles/Annual_GPP_at_0_5_degree/5048005; CPC ftp://ftp.cpc.ncep.noaa.gov/precip/PEOPLE/wd52ws/global_temp/. Processed data: https://figshare.com/articles/dataset/Maximum_constraint_on_the_response_of_terrestrial_productivity_to_precipitation_variability/12687908.

Code Availability

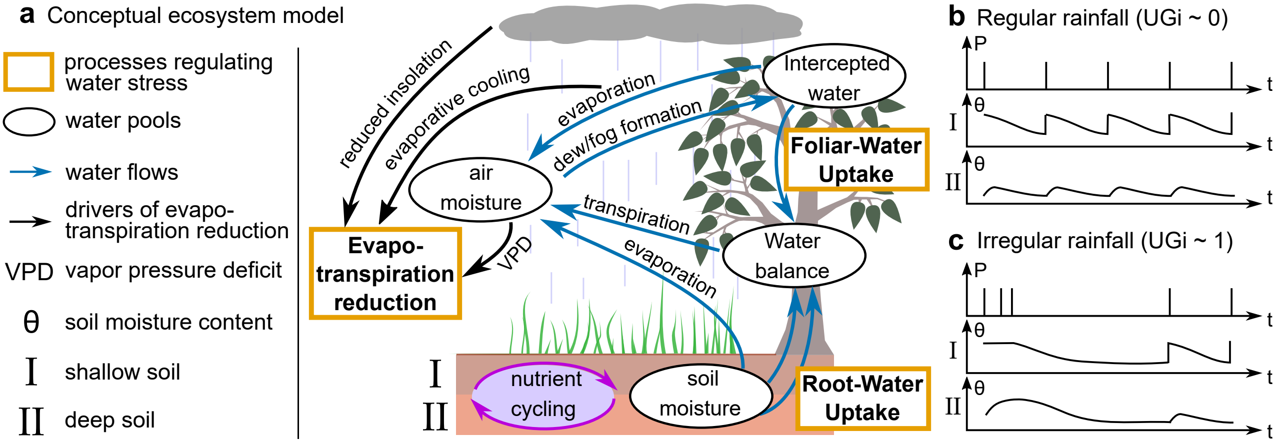
The algorithm used to perform the analysis presented in this article can be downloaded at https://figshare.com/articles/dataset/Maximum_constraint_on_the_response_of_terrestrial_productivity_to_precipitation_variability/12687908.


a Forests (745)
P (mm day-1)
2
0
-10
0
10
T (°C)
b Grasslands (758)
P (mm day-1)
2
0
-10
0
10
T (°C)
c Map
d All data (1503)
GPP SATFLUX (gC.m-2.yr-1)
10^3
0
0
2
P (mm day-1)
Five Biomes
Cold Forests (392)
Warm Forests (310)
Warm-Wet Grasslands (147)
Warm-Dry Grasslands (232)
Cold Grasslands (347)


a
P (mm)
30
0
Jan
Apr
Jul
Oct
Jan
dry days
wet days
Fraction of dry days
f_dry = N_dry / 365
Rainfall intensity
α = Σ P / N_wet
Rain frequency
Normalized cummulative P
Normalized days of year
UGi / 2
b
Anomalies of P (mm day-1)
years
2000
2018
Coefficient of variation
CV = σ / P̄
c
A
B
pair i
same long-term T
same long-term P
same biome type
with UGi_A ≤ UGi_B, d^UGi_i = (GPP_B - GPP_A) / mean(GPP_A,GPP_B) x 100 (%)
Set of all pairs
4192 pairs of warm forests
d^UGi_1
d^UGi_2
d^UGi_3
d^UGi_4192
50% of pairs
UGi_A ≃ UGi_B
UGi_A ≠ UGi_B
2096 paired grid cells with similar rain frequency
CONTROL
2096 paired grid cells with different rain frequency
EXPERIMENT
Frequency
d^UGi (%)
-100
100
median
Warm forests with more irregular rain (high UGi) have a ~9% lower GPP
increasing GPP with increasing UGi
decreasing GPP with increasing UGi
95% Confidence Interval (bootstrapping)



a Grasslands
40
%
20
0
-20
-40
UGi
f dry
α
CV
***
*
*
* *
UGi
f dry
α
CV
* *
**
**
***
UGi
f dry
α
CV
***
***
***
% of increase in GPP with increasing RVP
% of decrease in GPP with increasing RVP
b Forests
10
%
5
0
-5
-10
UGi
f dry
α
CV
***
**
**
* *
***
***
***
**
UGi
f dry
α
CV
GPP products
SATFLUX
FLUXCOM RS+METEO
VPM
Biomes
Cold (3076 pairs)
Warm-Dry (2766)
Warm-Wet (1282)
Cold (6782)
Warm (4192)
* p < 0.05


a Conceptual ecosystem model
processes regulating water stress
water pools
water flows
drivers of evapo-transpiration reduction
VPD vapor pressure deficit
θ soil moisture content
I shallow soil
II deep soil
reduced insolation
evaporative cooling
evaporation
dew/fog formation
Intercepted water
Foliar-Water Uptake
air moisture
transpiration
evaporation
Water balance
VPD
Evapo-transpiration reduction
nutrient cycling
soil moisture
Root-Water Uptake
I
II
b Regular rainfall (UGi ~ 0)
P
t
θ
I
t
θ
II
t
c Irregular rainfall (UGi ~ 1)
P
t
θ
I
t
θ
II
t

All the suggestions from Reviewer #3 have been corrected and updated, except two:

1) *This paragraph needs to be moved to the Results. Also, why is this (a summary of the major results) put here before showing the results?*

The conclusive paragraph at the end of the introduction comes from the format required by the journal *Communications Earth and Environment*. In particular, there is no conclusion section.

2) *Suggest just using "FLUXCOM" in Fig. 3 legend as well.*

I kept FLUXCOM RS+METEO in the Fig. 3 because some people only read the abstract and the figures. I preferred to keep the legend as detailed as possible to avoid confusion with other FLUXCOM products.