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Stefanos Mystakidis^{1,4}, Sonia I Seneviratne^{1,2}, Nicolas Gruber^{2,3} and Edouard L Davin¹

¹ Institute for Atmospheric and Climate Science, ETH Zurich, Zurich, Switzerland

² Center for Climate Systems Modeling, ETH Zurich, Zurich, Switzerland

³ Environmental Physics, Institute of Biogeochemistry and Pollutant Dynamics, ETH Zurich, Zurich, Switzerland

⁴ Author to whom any correspondence should be addressed.

E-mail: stefanos.mystakidis@env.ethz.ch and edouard.davin@env.ethz.ch

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Supplementary material for this article is available [online](#)

Abstract

The feedbacks between climate, atmospheric CO₂ concentration and the terrestrial carbon cycle are a major source of uncertainty in future climate projections with Earth systems models. Here, we use observation-based estimates of the interannual variations in evapotranspiration (ET), net biome productivity (NBP), as well as the present-day sensitivity of NBP to climate variations, to constrain globally the terrestrial carbon cycle feedbacks as simulated by models that participated in the fifth phase of the coupled model intercomparison project (CMIP5). The constraints result in a ca. 40% lower response of NBP to climate change and a ca. 30% reduction in the strength of the CO₂ fertilization effect relative to the unconstrained multi-model mean. While the unconstrained CMIP5 models suggest an increase in the cumulative terrestrial carbon storage (477 PgC) in response to an idealized scenario of 1%/year atmospheric CO₂ increase, the constraints imply a ca. 19% smaller change. Overall, the applied emerging constraint approach offers a possibility to reduce uncertainties in the projections of the terrestrial carbon cycle, which is a key determinant of the future trajectory of atmospheric CO₂ concentration and resulting climate change.

1. Introduction

The anthropogenic CO₂ emissions from the burning of fossil fuels and land use changes combined with emissions of other non-CO₂ greenhouse gases and aerosols are not only the primary driver for climate change, but have set in motion global-scale perturbations of the biogeochemical cycles on land and in the ocean (Ciais *et al* 2013). Terrestrial ecosystems currently mitigate the anthropogenic perturbation of the carbon cycle by absorbing about a third of the anthropogenic CO₂ emissions (Pan *et al* 2011, Sitch *et al* 2015, Le Quéré *et al* 2016), but it is unclear whether this enormous ecosystem service will continue unabated into the future, since both changes in atmospheric composition and climate impact substantially the land carbon uptake and storage (Lashof 1989, Friedlingstein *et al* 2006, Ciais *et al* 2013).

The response of the terrestrial carbon cycle to changes in atmospheric CO₂ concentration and

temperature, known as the concentration-carbon (β) and climate-carbon (γ) feedbacks, respectively, is a major determinant of the future climate change (Cox *et al* 2000, Jones *et al* 2003, Friedlingstein *et al* 2006, Friedlingstein and Prentice 2010, Booth *et al* 2012). However, the estimates of these feedbacks based on recent Earth system models (ESMs), i.e., models that include comprehensive representations of the biogeochemical processes on land and in the ocean, show a large range in their strength (Friedlingstein *et al* 2006, Boer and Arora 2012, Arora *et al* 2013). Moreover, uncertainties in these feedbacks have the potential to trigger uncertainties in many other features of the simulated earth system in ESMs (Friedlingstein *et al* 2014).

Statistical relationships between observable short-term (interannual) and long-term (decadal) variations of different aspects of the Earth system might provide emergent constraints on ESM projections under the condition that there is a theoretical understanding of

Table 1. CMIP5 models used in this study.

Model name	Land surface model	Resolution	Reference
CanESM2	CLASS2.7+CTEM1	2.8125° × 2.8125°	Arora <i>et al</i> (2011)
CESM1-BGC	CLM4.0	0.9° × 1.25°	Long <i>et al</i> (2013)
GFDL-ESM2M	LM3	2.5° × 2°	Dunne <i>et al</i> (2012, 2013)
HadGEM2-ES	JULES+TRIFFID	1.875° × 1.25°	Collins <i>et al</i> (2011) Jones <i>et al</i> (2011)
IPSL-CM5A-LR	ORCIDE	3.75° × 1.875°	Dufresne <i>et al</i> (2013)
MIROC-ESM	MATSIRO+SEIB-DGVM	2.8125° × 2.8125°	Watanabe <i>et al</i> (2011)
MPI-ESM-LR	JSBACH+BETHY	1.875° × 1.875°	Raddatz <i>et al</i> (2007) Brovkin <i>et al</i> (2009) Maier-Reimer and Wetzel (2005)
NorESM1-ME	CLM4.0	2.5° × 1.9°	Iversen <i>et al</i> (2013)

the identified relationship (Knutti 2010). These may include constraints on precipitation (Allen and Ingram 2002) and temperature (Gillett *et al* 2013, Stegehuis *et al* 2013, Schmidt *et al* 2014), as well as constraints on the snow-albedo feedback, (Hall and Qu 2006, Hall *et al* 2008, Qu and Hall 2014), cloud feedbacks (Klein and Hall 2015), climate sensitivity (Knutti *et al* 2006, Sherwood *et al* 2014) and sea ice (Massonnet *et al* 2012).

This study attempts to provide constraints on both γ and β for land based on recent ESMs. For γ , we use a multiple constraint approach making use of a range of data products which adds confidence to the constrained feedbacks since a good agreement only with respect to one metric does not necessarily guarantee good performance with respect to other metrics and/or other aspects and variables of the Earth system (Knutti 2010, Mahowald *et al* 2016). In contrast to recent studies, which have constrained more specific aspects of the land carbon cycle such as γ in the tropics (Cox *et al* 2013, Wenzel *et al* 2014), atmospheric CO₂ mole fraction (Hoffman *et al* 2014), cumulative carbon sequestration (Zachle *et al* 2014, Wieder *et al* 2015), gross primary productivity (GPP) (Mystakidis *et al* 2016, Wenzel *et al* 2016), Leaf Area Index (Mahowald *et al* 2016), we present constraints both on γ and β at the global scale. Constraining the two feedbacks simultaneously is important since their balance ultimately determines the long-term behavior of the terrestrial carbon sink. Thus, our approach enables to ultimately quantify the consequences of these constraints on future changes in the land carbon storage.

2. Data and methodology

2.1. Datasets

2.1.1. CMIP5 models

The basis of our analyzes are gridded estimates of GPP, net biome productivity (NBP), temperature (tas), precipitation (pr) and evapotranspiration (ET) (hfls) from 8 ESMs (table 1) that submitted results in the framework of the CMIP5 project (Taylor *et al* 2012). These ESMs differ widely in terms of resolution,

complexity and variations of the component models and many other aspects. Most relevant in the context of this study is their differences in the handling of the terrestrial nitrogen cycle, as this has been shown to have large implications for their sensitivity to changing atmospheric CO₂ concentration and climate (Thornnton *et al* 2009, Goll *et al* 2012, Wania *et al* 2012, Smith *et al* 2014). Namely, only two of the studied models, i.e., CESM1-BGC and NorESM1-ME (which share the same terrestrial carbon cycle component; CLM4.0), include an interactive nitrogen cycle, i.e., they consider the nitrogen content of the soils as a factor limiting growth.

We used output from the historical concentration-driven experiments, in which atmospheric CO₂ concentrations were prescribed as an input to the different ESMs. We also used output from idealized 140 year long simulations where the atmospheric CO₂ concentration was prescribed as an input to the models, increasing at a rate of 1%/yr, starting from its pre-industrial value (ca. 285 ppm) until quadrupling by the end year of the simulations (year 140). The 1%/yr increase in atmospheric CO₂ simulations we employed in this study include: (a) ‘biogeochemically’ coupled experiments (esmFixClim1) that neglect the radiative forcing effect of CO₂ and are therefore considered to be uncoupled with respect to climate change (radiative forcing remained preindustrial) and (b) fully coupled experiments (1pctCO₂) that include both the effect of increasing CO₂ and climate change on the terrestrial biosphere and the associated feedbacks. Thus, in the first (esmFixClim1) experiment just the concentration-carbon feedback is considered, while in the second (1pctCO₂) experiment, both feedbacks are active, i.e., concentration- and climate-carbon feedbacks.

2.1.2. Reference products for ET, NBP, precipitation and temperature

As reference dataset for ET we use the newly compiled LandFlux-Eval synthesis product that include in a merged manner 14 different individual gridded ET datasets (observation-based, satellite products and

model estimates of ET) over the period 1989–2005 with a spatial resolution of 1.0° (Mueller *et al* 2013). The interquartile range (IQR) of the different ET datasets contained in the LandFlux-Eval synthesis product was taken as a measure of the likely range in ET.

For NBP, we use the estimates from the global carbon project (GCP; Le Quéré *et al* (2016)) where the net land carbon uptake was estimated as the residual of the different components of the anthropogenic carbon budget. By definition, this residual-based estimate of annual NBP is only available at the global scale (<http://cdiac.ornl.gov/GCP/>). Further, it is subject to large uncertainties since it accumulates the uncertainties in the different components of the carbon budget that are propagated to the estimate of the land sink (Li *et al* 2016). To take this into consideration, we employed additional reference datasets for NBP, based on results from atmospheric CO_2 inversions performed within the framework of the Transcom3 intercomparison effort (Gurney *et al* 2002, 2003, 2004, Baker *et al* 2006). Specifically, we used output from the JENA (Rödenbeck 2005), JMA (Maki *et al* 2010), LSCEa (Piao *et al* 2009), NICAM (Niwa *et al* 2012) and RIGC (Patra *et al* 2005) products. Atmospheric CO_2 inversions offer a method to estimate sources and sinks of carbon (Ciais *et al* 2010) since atmospheric CO_2 concentrations reflect the CO_2 sources and sinks in natural ecosystems. Albeit they differ in spatial coverage and base periods, these model products (Gurney *et al* 2004, Gurney and Eckels 2011) agree well regarding the sign and the magnitude of NBP with observational products based on forest inventories (Pan *et al* 2011) or estimates of the land sink based on carbon isotopes (e.g. $^{13}\text{C}/^{12}\text{C}$ ratio; Ciais *et al* (1995)). Moreover, these observation-based inversion products are totally independent of the ESMs used in the CMIP5 models and they provide robust interannual variations for NBP at large scales (Peylin *et al* 2013).

We employed a total of 6 precipitation datasets to constrain the models, using datasets that are either based exclusively on rain gauge observations or based on combinations between rain gauge observations and satellite-derived estimates. These precipitation products include the CPC (Xie and Arkin 1997), CRU (Harris *et al* 2014), GPCC (Rudolf and Schneider 2005), GPCP (Adler *et al* 2003), PREC/L (Chen *et al* 2002) and University of Delaware (Legates and Willmott 1990) datasets. As reference datasets for temperature we use the products from CRU (Harris *et al* 2014), ERA-Interim (Dee *et al* 2011) and the University of Delaware (Willmott and Robeson 1995).

All datasets (CMIP5 models and observation-based products except for the GCP estimate) were interpolated bi-linearly to a common grid with a resolution of $0.5^\circ \times 0.5^\circ$. When integrating NBP and GPP over different regions, we also accounted for the land fraction in each grid cell.

2.2. Methods

2.2.1. Carbon cycle feedbacks

We calculated the carbon cycle feedbacks in the CMIP5 models following the methodology introduced by Wenzel *et al* (2014), which differs little from that used in the Coupled Climate Carbon Cycle Model Intercomparison project (C^4MIP ; Friedlingstein *et al* (2006)). Based on this approach, the ‘biogeochemically’ coupled (‘uncoupled’) simulations were used to compute the concentration-carbon feedback, which can be translated into a model’s CO_2 fertilization effect. In these simulations, the change in the land carbon storage ($\Delta \text{C}^{\text{bgc-coupled}}$) is proportional to the change in atmospheric CO_2 concentration in these experiments ($\Delta \text{CO}_2^{\text{bgc-coupled}}$) multiplied by the concentration-carbon feedback (β):

$$\Delta \text{C}^{\text{bgc-coupled}} = \beta \cdot \Delta \text{CO}_2^{\text{bgc-coupled}}. \quad (1)$$

The climate-carbon feedback was estimated from the fully coupled (1pct CO_2) experiments. Since the change in atmospheric CO_2 concentration is indistinguishable in the biogeochemically coupled and fully coupled experiments, the change in the land carbon storage in the fully coupled simulations ($\Delta \text{C}^{\text{fullyc}}$) equals the change in atmospheric CO_2 concentration in these simulations ($\Delta \text{CO}_2^{\text{fullyc}}$) multiplied by the concentration-carbon feedback (β) plus the temperature change (ΔT^{fullyc}) in the coupled experiment multiplied by the climate-carbon feedback (γ):

$$\Delta \text{C}^{\text{fullyc}} = \beta \cdot \Delta \text{CO}_2^{\text{fullyc}} + \gamma \cdot \Delta T^{\text{fullyc}}. \quad (2)$$

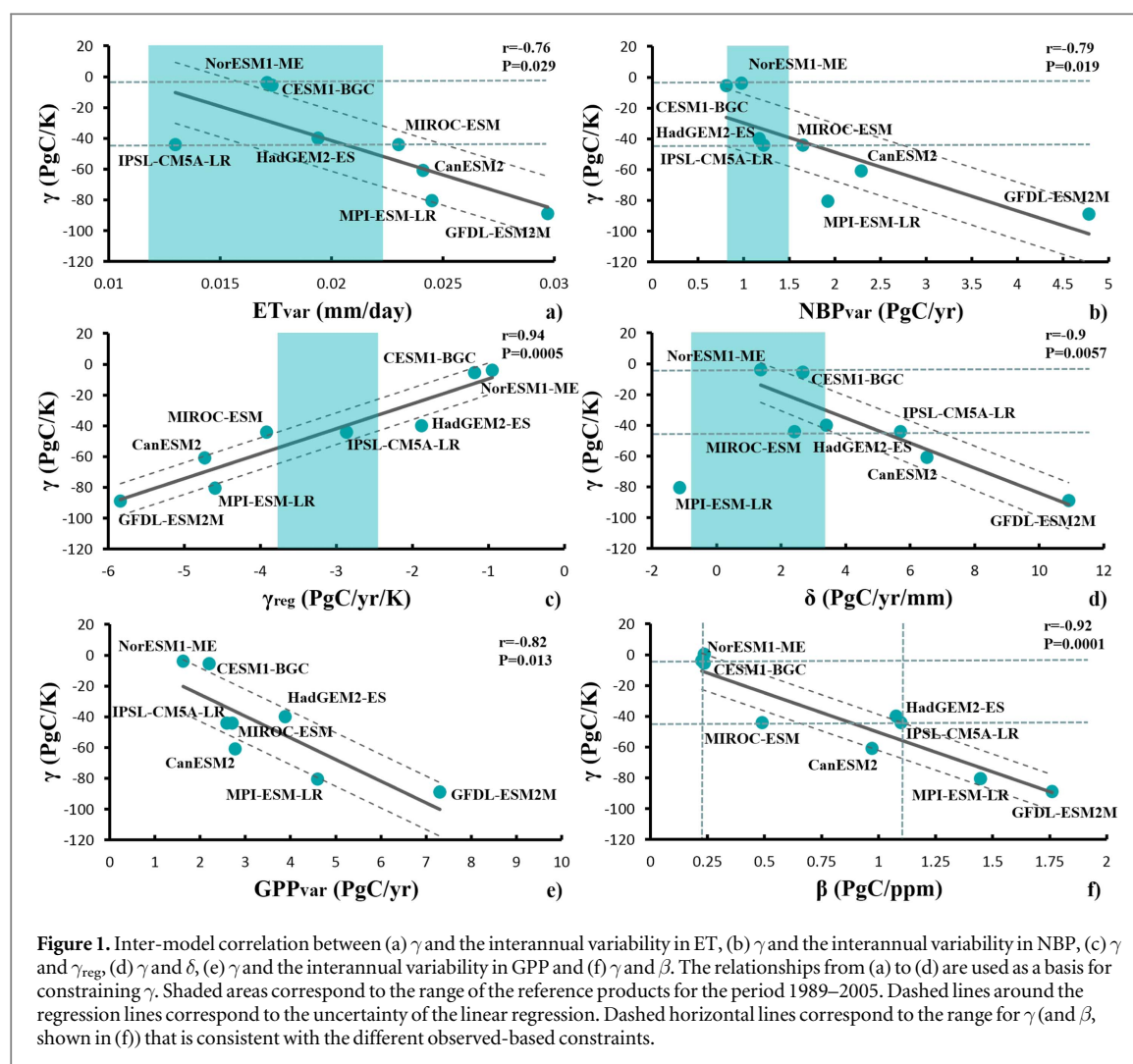
In all models except one, the two feedbacks were calculated during the period between the year 1 and year 140 of the idealized simulations. In the case of GFDL-ESM2M the feedbacks were calculated for a different time window, since the model hold the atmospheric CO_2 concentration after the year of doubling (year 70) constant. Therefore, we calculated the feedbacks for this model for the period between the year 28 (atmospheric CO_2 concentration corresponds to 2000 levels in the historical experiments) and the year 70 (atmospheric CO_2 concentration corresponds to 2045 levels based on the representative concentration pathway (RCP) 8.5 experiment; van Vuuren *et al* (2011)).

2.2.2. Response of NBP to climate variations

The response of NBP to interannual variations in temperature and precipitation was derived empirically based on a multiple regression approach as in Piao *et al* (2013). Based on this approach, NBP can be derived as a linear combination of anomalies in temperature and precipitation:

$$\text{NBP} = \gamma_{\text{reg}} \cdot x_T + \delta \cdot x_{\text{PR}} + \epsilon, \quad (3)$$

where γ_{reg} and δ are the partial regression coefficients that represent the responses of NBP to temperature ($\text{PgC yr}^{-1} \text{K}^{-1}$) and precipitation ($\text{PgC yr}^{-1} \text{mm}^{-1}$), respectively. The symbols x_T and x_{PR} are the detrended anomalies in annual temperature and precipitation,



respectively, and ϵ is the error term. We calculated the observation-based responses of NBP to temperature and precipitation (γ_{reg} and δ) based on a total of 108 different combinations of the reference products (6 for NBP \times 6 for precipitation \times 3 for temperature) for the 1989–2005 period and using the ‘*regmultlin*’ function in NCL (https://ncl.ucar.edu/Document/Functions/Built-in/reg_multlin.shtml).

2.2.3. Observational constraints approach

We constrain the full ensemble of CMIP5 models (prior ensemble) based on the emergent relationships we establish in the result section (figure 1) and using several observation-based products as constraints. The constraints are applied globally based on the annual means for the period 1989–2005, which is determined by the availability of the observation-based products. The ‘constrained’ ensemble is constructed by removing models not lying within the uncertainty range of the observation-based constraints. Since we applied several constraints, we decided to exclude only models that are outside the range of all constraints (i.e., a model can be retained even if it complies with only one constraint).

The climate-carbon feedback is constrained based on global contemporary variations in ET (ETvarcon) and NBP (NBPvarcon), as well as the response of NBP to variations in temperature (γ_{reg} con) and precipitation (δ con). A summary of the various constraints employed for γ is shown in table 2. A common characteristic in all these approaches is that the observed interannual variability of the terrestrial carbon fluxes can be used to constrain the long-term response of these fluxes, implying that the same processes operate at these different time scales. In the case of ET, the uncertainty range is defined based on the IQR of the different ET datasets contained in the LandFlux-Eval ET product. In the case of NBP and its responses to interannual variations in temperature (γ) and precipitation (δ), the uncertainty range is defined based on the full range of the various observation-based estimates.

In the absence of direct observational constraints, the concentration-carbon feedback is constrained based on the strong inter-model relationship we identify between the two feedbacks in the CMIP5 models (figure 1(f)).

Table 2. Summary of the various constraint approaches used for the climate-carbon feedback (γ).

Ensemble	Rationale	Reference products	Definition of the uncertainty range
ETvarcon	ET is a proxy for GPP. Interannual variations in GPP are a response to climate variations (figures S5, S6) and drive the variations in the carbon sink (figure 2(b), S3)	LandFlux-Eval synthesis dataset (Mueller <i>et al</i> 2013)	IQR of the different ET datasets contained in the LandFlux-Eval synthesis product
NBPvarcon	Interannual variations in NBP (correlated with GPP variations; figures 2(b), S3) are a response to climate variations	NBP from the Global Carbon Project and 5 atmospheric CO ₂ inversion products	Full range of the different reference products for NBP (5 inversions and GCP estimate)
δ con and γ_{reg} con	The interannual variations in NBP are related to variations in climate (e.g. temperature and precipitation; figures S7, S8). The sensitivity of NBP to temperature and precipitation variations is related to γ	NBP from the Global Carbon Project and 5 atmospheric CO ₂ inversion products, 6 precipitation datasets and 3 temperature datasets	Full range of the 108 combinations between the various observation-based products

3. Results

3.1. Emergent relationships

We find in the CMIP5 models a statistically significant inter-model correlation between the global climate-land carbon feedback strength (γ) and the magnitude of the interannual variations in global ET ($r = -0.76$, $P = 0.029$; figure 1(a)), NBP ($r = -0.79$, $P = 0.019$; figure 1(b)), GPP ($r = -0.82$, $P = 0.013$; figure 1(e)) and the response of NBP to variations in temperature ($r = 0.94$, $P = 0.0005$; figure 1(c)) and precipitation ($r = -0.9$, $P = 0.0057$; figure 1(d)) over the period 1989–2005. These different relationships can be used as a basis for constraining γ . While these correlations do not automatically imply a causal mechanism, we argue, in line with previous studies (Cox *et al* 2013, Wenzel *et al* 2014), that they emerge because the short-term (interannual) and the long-term (decadal to centennial) sensitivities of the terrestrial carbon fluxes to climate are highly linked.

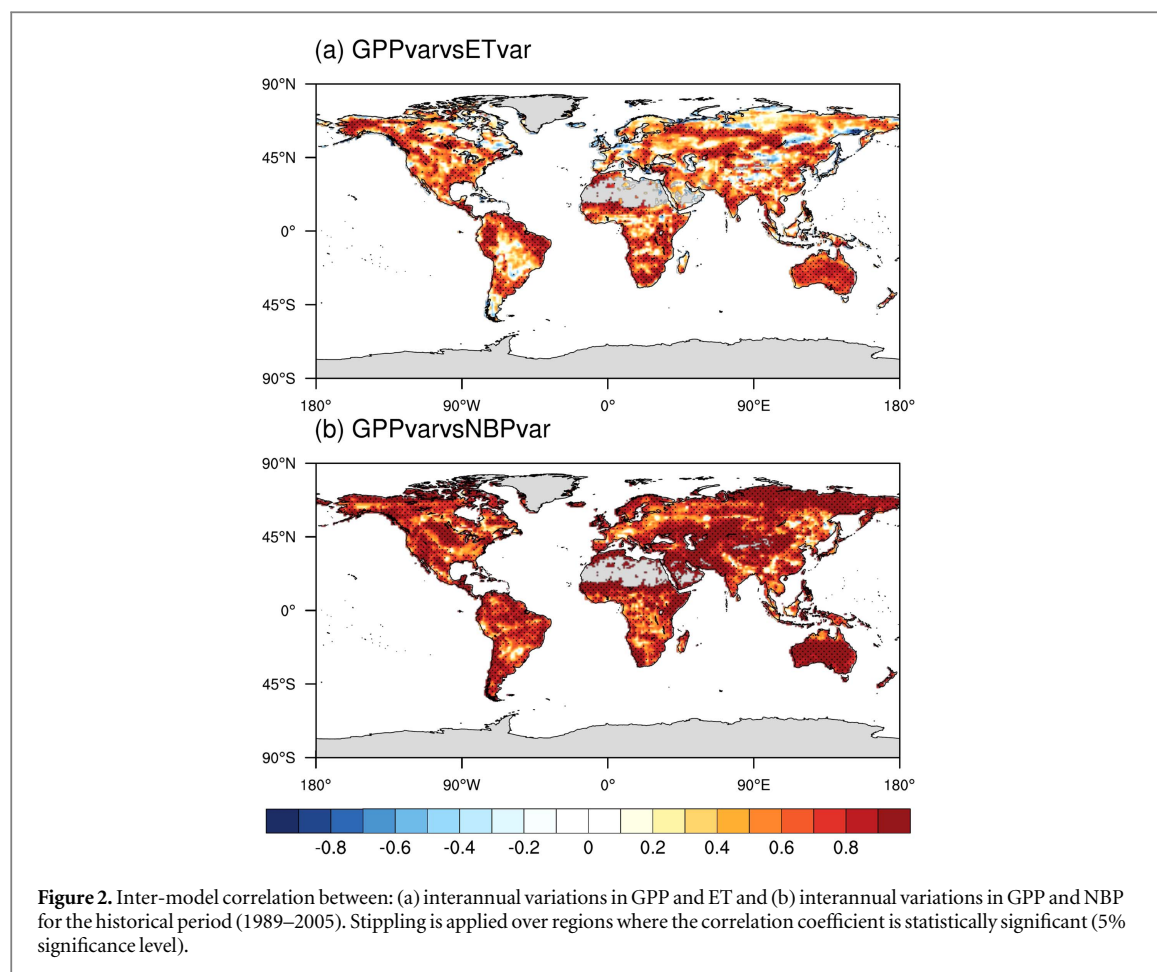
More specifically, interannual variations in GPP, ET and NBP are essentially driven by variations in climate (figure S5, S6), as also shown in previous observational and modeling studies (Tian *et al* 1998, Luyssaert *et al* 2007, Reichstein *et al* 2007, Ciais *et al* 2009, Weber *et al* 2009, Friedlingstein *et al* 2010, Le Maire *et al* 2010, Jung *et al* 2011, Poulter *et al* 2014, Ahlström *et al* 2015, Anav *et al* 2015). The short-term (e.g. ET, NBP, GPP interannual variations) and the long-term (γ) sensitivities are correlated in the models (figures 1(a)–(e)) presumably because simulated GPP, ET and NBP respond to climate variations in a similar way whether these variations occur from year to year or over longer time scales. In other words, models that are particularly sensitive to interannual climate variations (i.e., larger anomalies in ET, GPP and NBP—also highly correlated each other, figures S1–S4) will also tend to have a higher sensitivity to future warming (higher γ).

GPP variations are strongly correlated with ET variations, in the CMIP5 models, both at the regional

(figures 2(a), S2) and the global scale ($r = 0.77$, $P = 0.025$; figure S1(a)), reflecting the well-established coupling between plant photosynthesis and transpiration. As a consequence, the year-to-year variations in ET during the historical period are also highly correlated with γ . However, current observation-based products for global GPP do not offer robust estimates for the interannual variability (Anav *et al* 2015), preventing the emergent relationship between γ and the interannual variations in GPP to be used as a constraint at this time. But, the high relationship between GPP and ET variations offers the opportunity to use observation-based estimates of interannual ET variations as a proxy for interannual GPP variations and thus as a constraint on γ .

In order to better understand the strong inter-model relationships between γ and the response of NBP to interannual variations in temperature (γ_{reg}) and precipitation (δ) (figures 1(c), (d)), we further investigate the link between ecosystems and climate variations, which are related to the climate-carbon feedback, by analyzing in both models and observations the relationship between contemporary interannual anomalies in NBP and in the potential drivers temperature (γ_{reg}) and precipitation (δ), respectively. The analysis focuses on temperature and precipitation since these two climate variables are known to be key determinants of the productivity of ecosystems (Nemani *et al* 2003, Poulter *et al* 2014, Ahlström *et al* 2015, Anav *et al* 2015, Murray-Tortarolo *et al* 2016, Seddon *et al* 2016).

During the period 1989–2005, the different combinations between the observation-based products for NBP, temperature and precipitation agree on a negative response of NBP to variations in temperature (γ_{reg}) ranging from about -3.8 to -2.5 PgC yr⁻¹ K⁻¹. In the case of precipitation (δ), the results range between -0.8 and 3.4 PgC yr⁻¹ mm⁻¹ with most of the combinations showing a positive response of NBP to interannual variations in precipitation. The negative



relationship between NBP and temperature translates into a lower terrestrial carbon sink during warm years, caused either by increased respiration in response to warmer temperatures (Kätterer *et al* 1998, Davidson and Janssens 2006, Bond-Lamberty and Thomson 2010, Conant *et al* 2011, Lu *et al* 2013) and/or by lower photosynthesis in regions where plants operate close to their optimal temperature. The positive relationship between NBP and precipitation suggests that wet years are favorable for plant productivity, resulting in enhanced terrestrial carbon uptake. This mechanism is valid in several ecosystems in the mid-latitudes and in the tropics. In particular, in tropical ecosystems the relationship between NBP and precipitation (as well as temperature) anomalies is more pronounced during ENSO events (Jones and Cox 2001, Gurney *et al* 2003). Warm and dry conditions during these events cause substantial reductions in plant production and enhance respiration resulting in lower storage on land in tropical land ecosystems (Gatti *et al* 2014) and in a stronger climate-carbon feedback that relates to interannual variations in climate. Eventually, these anomalies in the carbon sink are mirrored in the atmospheric CO₂ growth rate.

Consistent with the observation-based products, the CMIP5 models show negative and positive responses of NBP to interannual variations in temperature and precipitation, respectively, both globally

(figures 1(c), (d), S9, S10) and regionally (figure S7,S8). However, they simulate a large spread in the strength of these relationships, with most of the models tending to be oversensitive to interannual variations in precipitation (figure 1(d)) compared to the reference products (as already shown in Piao *et al* (2013) for the global averages in the offline TRENDY simulations). The relationship between γ and the responses of NBP to variations in temperature and precipitation are strong and statistically significant also for a longer time period in the observation record where fewer reference data products are available (e.g., 1985–2009, see figures S1(c), (d)). We note here that the high soil moisture-dependence of soil respiration in MPI-ESM-LR (Wenzel *et al* 2014) decouples the relationship between NBP and precipitation (negative) in this model mainly owing to enhanced decomposition in wet years, which overwhelms the possible enhancement of plant productivity in response to higher soil water availability. For this reason, we have excluded MPI-ESM-LR when calculating the best fit linear regression between γ and δ (figure 1(d)).

These ‘responses’ of NBP to climate variations need to be interpreted carefully since the multi-linear regression approach does not take into account the effect of synergistic/antagonistic effects between the two drivers and also neglects other confounding mechanisms and drivers of plant productivity. Thus,

Table 3. Global γ and β over land based on the idealized 1% CO₂ per year experiments, change in the cumulative land carbon storage based on the RCP8.5 ($\Delta \text{NBP}_{\text{RCP8.5}}$; PgC; calculated between the year 2005 and 2100) and 1pctCO₂ ($\Delta \text{NBP}_{1\text{pctCO}_2}$; PgC) experiments and changes in the turnover time (yr) of vegetation ($\Delta \tau_{\text{veg}}$), soil ($\Delta \tau_{\text{soil}}$) and total ($\Delta \tau$) carbon content in the 1pctCO₂ experiment. The changes in the turnover times are defined as the difference between the last and the first 20 years of the 1pctCO₂ experiment.

Model name	γ	β	$\Delta \text{NBP}_{\text{RCP8.5}}$	$\Delta \text{NBP}_{1\text{pctCO}_2}$	$\Delta \tau_{\text{veg}}$	$\Delta \tau_{\text{soil}}$	$\Delta \tau$
CanESM2	−61	0.97	102	492	0.5	−7.3	−2.6
CESM1-BGC	−5.4	0.24	−100	177	−0.4	−2.2	−1.5
GFDL-ESM2M	−89	1.76	195	570	−0.3	−4.7	−2.6
HadGEM2-ES	−40	1.08	332	711	−0.9	−5.2	−3.3
IPSL-CM5A-LR	−44	1.1	311	718	0.4	−5.1	−2.1
MIROC-ESM	−44	0.49	−82	152	−0.7	−8.0	−4.8
MPI-ESM-LR	−80	1.44	257	818	−0.2	−13.7	−6.7
NorESM1-ME	−3.7	0.23	−195	177	−0.4	−4.6	−1.5

this method for calculating γ_{reg} and δ might describe reasonably well the response of NBP to temperature and precipitation in the models, since most of them lack many other processes that influence the carbon cycle, while it might not always work for the observation-based products. Indeed, this seems to be the case in the models since there is a strong and significant correlation between γ and the response of NBP to interannual variations in temperature (γ_{reg} ; figure 1(c)). Thus, the assumption that the same processes control γ in the short-term and long-term scales is valid at least in the model world.

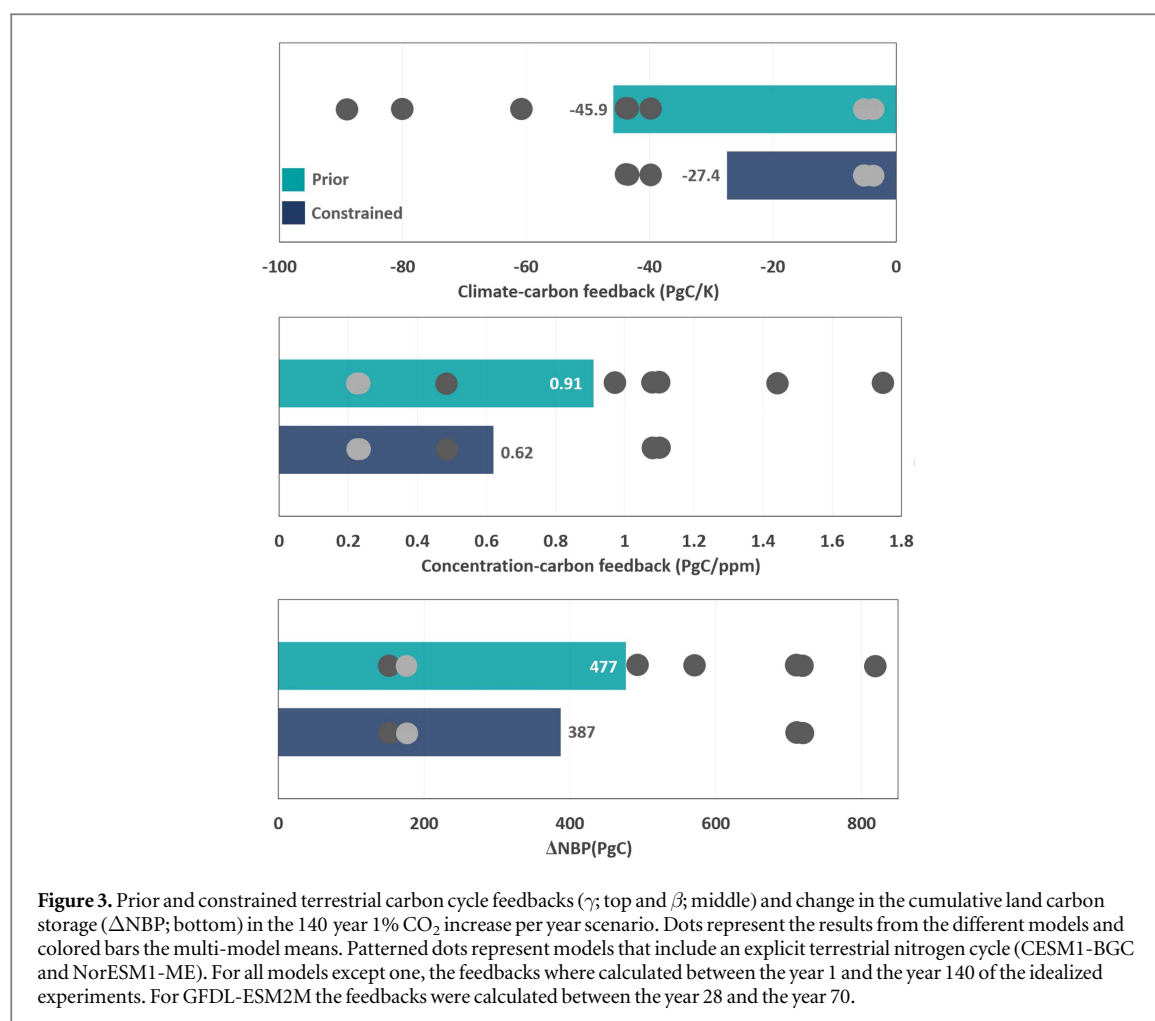
3.2. Constrained climate-carbon feedback

The magnitude of the climate-carbon feedback varies markedly across the CMIP5 models (table 3), as already shown earlier (Arora *et al* 2013, Ciais *et al* 2013). Several reasons might explain this large range including, for instance, biases in the underlying simulated climate or the diverse and sometimes inadequate representation of land biogeochemical and biophysical processes in the different ESMs (Plattner *et al* 2008, Hawkins and Sutton 2009, Anav *et al* 2013, Piao *et al* 2013, Hoffman *et al* 2014, Friedlingstein 2015). All models simulate a negative γ ranging from about −3.7 (NorESM1-ME) to −89 PgC/K (GFDL-ESM2M) with a multi-model mean of −45.9 and a model range of 85 PgC K^{−1}, respectively. The low sensitivity in CESM1-BGC (also seen in NorESM1-ME) was attributed earlier to increased nitrogen mineralization, caused by increased respiration that provides additional nitrogen inputs to vegetation and compensates as a result, the carbon losses through the process of respiration (Arora *et al* 2013)—an effect not considered in the other carbon-only ESMs. The simulated magnitude of the climate-carbon feedback in the CMIP5 models lies within the range of the C⁴MIP models (Friedlingstein *et al* 2006). The different observation-based constraints suggest a substantially lower response of the terrestrial carbon cycle to climate change (γ) and a significant decrease in the inter-model range. Specifically, the magnitude of the climate-carbon feedback for the constrained multi-model mean is lowered by 40% (figure 3), from −45.9

to −27.4 PgC K^{−1}, while the observational constraints half the inter-model spread from 85 to 40 PgC K^{−1}. Another indication that γ might be overestimated in the CMIP5 models relates to the tendency of some models to simulate high total carbon in vegetation and soils (Todd-Brown *et al* 2012, Anav *et al* 2013, Carvalhais *et al* 2014) and thus high amounts of carbon, contained in these pools, are exposed to the warming.

3.3. Constrained concentration-carbon feedback

We find a statistically highly significant negative correlation between γ and β in the ESMs ($r = -0.92$, $P = 0.0001$; figure 1(f)) with models having a more negative γ having a more positive β . This strong relationship is likely the consequence of a pool effect. In other words, models with a higher β , i.e., stronger fertilization effect, tend to accumulate more carbon in vegetation and soils, thereby increasing the risk of carbon losses due to climate change. Keeping in mind that this relationship is a model-derived feature not directly verifiable based on observations, we examined the consequences of the constrained γ on β . All CMIP5 models simulate a positive β , but with substantial inter-model variation, ranging from about 0.24 PgC ppm^{−1} for CESM1-BGC and NorESM1-ME to about 1.76 PgC ppm^{−1} for GFDL-ESM2M, resulting in a multi-model mean of 0.91 PgC ppm^{−1}. The much lowest response to CO₂ in CESM1-BGC and NorESM1-ME originates likely from the strong limitation that nitrogen imposes on the strength of CO₂ fertilization compared to carbon-only models (Thornton *et al* 2009, Zaehle *et al* 2010). In the case of the MIROC-ESM model, the relatively low response to CO₂ (0.49 PgC ppm^{−1}) can be attributed to the empirical treatment of photosynthesis in its land surface module, implicitly including the role of nutrient limitations on CO₂ fertilization (Ito and Oikawa 2002, Arora *et al* 2013). Selecting only the models complying with the observation-based constraints described in the previous section, results in a substantially lower estimate of γ . Specifically, the constraint reduces the concentration-carbon feedback by 30% from 0.9 PgC ppm^{−1} to 0.6 PgC ppm^{−1}



(figure 3) and also reduces the range by 40% (0.2–1.1 PgC ppm^{-1}).

3.4. Resulting future land carbon uptake

By the end of the fully coupled experiments corresponding to a quadrupling of the preindustrial atmospheric CO_2 concentration, all models simulate a high cumulative carbon sink in the terrestrial biosphere (table 3, figure S11(b)), ranging from 152 PgC (MIROC-ESM) to 818 PgC (MPI-ESM-LR). The change in the annual net land-atmosphere flux, calculated as the difference in NBP between the last and the first 20 years of the simulation, also shows a large range, with all but two models (GFDL-ESM2M and MIROC-ESM) simulating an increased sink by the end of the simulation (figure S11(d)). In those models that simulate an increase in NBP, this change is driven by the increase in GPP, that more than compensates the increased losses stemming from the faster turnover time of total carbon in soils and vegetations (table 3). The latter is mainly driven by faster soil decomposition and to a lesser extent by faster autotrophic respiration rates in response to the warming (table 3). The decrease in NBP in GFDL-ESM2M and MIROC-ESM is due to the faster turnover time of soil carbon, that more than compensates the increase in GPP. For

GFDL-ESM2M, this is a consequence of the model's setup since, as mentioned earlier, the forcing in this model stabilized at the year of CO_2 doubling. Hence, GPP in GFDL-ESM2M stays constant in these experiments after this moment, allowing respiration to regulate NBP and reduce the sink strength in this model.

Obviously, the constrained feedbacks have an impact on the future change in the land carbon storage, since their balance determines NBP (see equation (2)). The observation-based constraints suggest a multi-model mean NBP that is about 19% lower (figure 3) and they reduce the inter-model range of the change in the land carbon storage by about 15% to a range of 151–718 PgC . In the constrained models, the lower CO_2 fertilization effect still more than compensates the lower response to climate change, resulting in a lower terrestrial carbon uptake. These results concerning the magnitude of the future changes in NBP are not easy to extrapolate to other scenarios, since the numbers are likely quite sensitive to the specific emission/concentration scenario applied. However, the lower sink in the constrained ensembles can be related to results from other scenarios (e.g., RCP8.5 experiment) since models simulating large changes in NBP in the idealized 1%/yr increase in CO_2 experiments

simulate also large changes in future NBP in the RCP8.5 simulations (table 3, $r = 0.96$, $P = 0.0012$). By the end of the RCP8.5 experiment, the models simulate, on average, a cumulative change in NBP of 102 PgC (table 3) while for the same experiment the constrained models have a storage on land that is about 50% lower (53 PgC).

4. Conclusions

This study provides revised estimates of the global feedbacks involving the terrestrial carbon cycle, the atmospheric CO₂ concentration and climate change as simulated by comprehensive ESMs used in the framework of CMIP5. Compared to the prior ensemble, the models constrained by several observation-based products have a ca. 40% lower sensitivity to climate change (climate-carbon feedback) and a ca. 30% lower sensitivity to CO₂ (concentration-carbon feedback). Combining the two constrained feedbacks reduces the cumulative terrestrial NBP by about 19% in the mean, and reduces the model range by 17% in the 1% CO₂ increase per year scenario.

The results for γ are consistent with findings from recent studies showing that the suite of models used in recent model intercomparison projects (e.g. C⁴MIP and CMIP5) tends to be overly sensitive to climate (see Cox *et al* (2013), Wenzel *et al* (2014) for the tropics). The identified lower response to CO₂ in the constrained models is in line with the tendency of current models to likely overestimate CO₂ fertilization (Hungate *et al* 2003, Piao *et al* 2013, Kolby Smith *et al* 2015). Moreover, the identified lower capacity of ecosystems to store carbon is consistent with results from recent studies providing nutrient availability constraints on CMIP5 model projections (Zaehle *et al* 2014, Wieder *et al* 2015), as well as with spatially and temporally explicit ET and GPP constraints on the historical and RCP8.5 CMIP5 terrestrial carbon cycle simulations (Mystakidis *et al* 2016).

The added value of this study can be summarized in three points. First, the findings give insights on the magnitude of the constrained feedbacks at the global scale, which leads to a better understanding of the future changes in the Earth system. Second, this study presents constraints on both β and γ using the high correlation between the two feedbacks in the CMIP5 models. The latter finding suggests that models with high atmospheric CO₂ fertilization effect on NBP also have higher sensitivity of NBP to climate change, suggesting that the competition between the two feedbacks ultimately determines the land carbon storage. Third, the use of several data products as observation-based constraints adds more confidence to the constrained quantities. Encouragingly, all the different emergent constraints used in this study show

consistent results and suggest that the constrained feedbacks involving the terrestrial carbon cycle and the climate system are at the low end of the ESMs range.

It is important to consider a few caveats. The most critical one relates to the identified emergent relationships and specifically to the fact that these relationships cannot be evaluated based on observations. This caveat is valid for all emergent constraints proposed in the literature. Moreover, the observational constraint approach cannot be expected to compensate for uncertainties due to processes that are either missing or underrepresented in current ESMs (Friedlingstein 2015). Some of them may include nutrient limitations on ecosystems (Norby *et al* 2010, Zaehle *et al* 2010, Fernández-Martínez *et al* 2014), permafrost-carbon feedbacks (Koven *et al* 2011, 2015, Schuur *et al* 2015), several disturbance processes especially, land use change (Brovkin *et al* 1999, 2004, 2013, Houghton *et al* 2012), and soil moisture stress and associated mortality (Allen *et al* 2015) that is not well represented in current terrestrial biogeochemistry models, at least not for tropical ecosystems (Wang *et al* 2014). In general, the emergent constraints work since in current ESMs the same processes appear to drive the short-term variability and the long-term sensitivity to climate change. Whether this holds true in reality is presently unknown.

Another limitation relates to uncertainties in the simulated fluxes at the regional scale. For instance, a model might show the right performance in simulating a global quantity in the historical period, but this might be a result of compensating regional biases (Jiang *et al* 2015, Mystakidis *et al* 2016). Thus, a model that matches the contemporary variations in the water and carbon fluxes at the global scale well does not automatically imply that the model correctly simulates the interannual variations in these fluxes at the regional scale. Similarly, a model might capture the correct response of NBP to interannual variations in temperature (γ_{reg}) and precipitation (δ) due to a compensation between the response of photosynthesis and respiration to climate. The lack of robust observation-based global estimates of the interannual variations in photosynthesis and respiration make it difficult to address the latter caveat at this time. The development of more spatially explicit observation-based products for the terrestrial water and carbon fluxes would certainly help to address these two caveats and most importantly to better understand the mechanisms controlling the terrestrial carbon cycle.

Finally, after recognizing the above-mentioned caveats we conclude that the results of this study can provide guidance to model development and help in producing more reliable future projections of several other aspects of the Earth system.

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The University of Delaware dataset is available at: <http://esrl.noaa.gov/psd/data/gridded/data/UDelAirTPrecip.html>. The ERA-Interim dataset can be found at: <http://esrl.noaa.gov/psd/data/gridded/data.erainterim.html>

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