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Complex terrain influences ecosystem carbon responses to temperature and precipitation

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Key Points:

- AmeriFlux data reveal that terrain complexity influences the response of ecosystem CO_2 fluxes to temperature and precipitation
- In complex terrain, CO_2 responses to climate variables are organized by topographic variables associated with water and energy availability
- Complex terrain gives rise to emergent ecosystem behaviors that may not be captured by current land surface modeling approaches

Supporting Information:

- Supporting Information S1

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Abstract Terrestrial ecosystem responses to temperature and precipitation have major implications for the global carbon cycle. Case studies demonstrate that complex terrain, which accounts for more than 50% of Earth's land surface, can affect ecological processes associated with land-atmosphere carbon fluxes. However, no studies have addressed the role of complex terrain in mediating ecophysiological responses of land-atmosphere carbon fluxes to climate variables. We synthesized data from AmeriFlux towers and found that for sites in complex terrain, responses of ecosystem CO_2 fluxes to temperature and precipitation are organized according to terrain slope and drainage area, variables associated with water and energy availability. Specifically, we found that for tower sites in complex terrain, mean topographic slope and drainage area surrounding the tower explained between 51% and 78% of site-to-site variation in the response of CO_2 fluxes to temperature and precipitation depending on the time scale. We found no such organization among sites in flat terrain, even though their flux responses exhibited similar ranges. These results challenge prevailing conceptual framework in terrestrial ecosystem modeling that assumes that CO_2 fluxes derive from vertical soil-plant-climate interactions. We conclude that the terrain in which ecosystems are situated can also have important influences on CO_2 responses to temperature and precipitation. This work has implications for about 14% of the total land area of the conterminous U.S. This area is considered topographically complex and contributes to approximately 15% of gross ecosystem carbon production in the conterminous U.S.

Plain Language Summary Land-based ecosystems remove carbon dioxide from Earth's atmosphere, filling a critical role in the global carbon balance. Approximately half of Earth's land area occupies hilly or mountainous terrain (i.e., complex terrain), but relatively little research has examined how complex terrain influences the ability of ecosystems to remove carbon dioxide from the atmosphere. We analyzed data from 30 research towers around the United States used to measure carbon dioxide movement between ecosystems and the atmosphere. Some towers were located in complex terrain, and others were located in relatively simple, flat terrain. For each site, we examined patterns of carbon dioxide exchange (photosynthesis, respiration, and the net exchange) in response to changes in temperature and precipitation. For towers located in complex terrain, we found that the average slope angle surrounding a site predicted daily responses of carbon dioxide exchange to temperature and the average drainage area surrounding a site predicted annual responses of carbon dioxide exchange to precipitation. Towers in simple terrain showed no such relationships. The results show that in complex terrain, slope and drainage area affect ecosystem carbon cycles in predictable ways. The patterns and behavior that we observed apply to approximately 14% of the conterminous United States.

1. Introduction

Uncertainty in the response of terrestrial carbon fluxes to climate dynamics remains a major challenge to predicting the future behavior of the global carbon cycle [*Piao et al.*, 2013; *Friedlingstein et al.*, 2014]. Discrepancies between carbon model predictions and ground-based observations have been attributed to landscape heterogeneities [*Sitch et al.*, 2008; *Schaefer et al.*, 2012; *Pappas et al.*, 2015], which are driven partly by terrain complexity [*Novick et al.*, 2016]. Terrain complexity produces strong heterogeneities and gradients in environmental variable (e.g., radiation, temperature, precipitation, and soil water content), which influence interactions among topography, soil, microbial communities, vegetation, and climate [*Running et al*., 1987; *Grayson et al*., 1997; *Du et al*., 2015]. These heterogeneities and gradients often produce emergent behaviors, meaning that landscape carbon dynamics behave in more complex and unpredictable ways than dynamics at finer scales [*Schimel et al*., 2002; *Emanuel et al*., 2011].

More than 50% of the world's terrestrial landscapes are situated in complex terrain [*Rotach et al*., 2014]. Here we define complex terrain to include planar slopes steep enough to induce lateral water flow, convergent hillslopes, rolling or rough topography, and other topographic features commonly associated with hilly and mountainous areas. These regions play a significant role in regional and global climatological, hydrological, and biogeochemical processes [*Whiteman*, 2000; *Viviroli and Weingartner*, 2004] and include some of the world's most climatically sensitive ecosystems [*Seddon et al*., 2016]. Moreover, many of these landscapes have been identified as significant terrestrial sinks for atmospheric CO_2 and play important roles in the regulation of Earth's climate system [*Pacala et al*., 2001; *Schimel et al*., 2002; *Piao et al*., 2006]. Yet knowledge of carbon dynamics in these environments, including processes and factors influencing responses to climate, is limited [*Schimel et al*., 2002; *Schimel and Braswell*, 2005; *Wohl et al*., 2012].

Ecosystem carbon fluxes such as gross ecosystem production (GEP) of carbon, ecosystem respiration (RE), and the net ecosystem production (NEP) of carbon are sensitive to changes in local water, temperature, and energy conditions [*Nemani et al*., 2003; *Running et al*., 2004]. Site-specific studies highlight the influences of complex terrain on the redistribution of light, water, microbial activity, and other resources [*Lyons and Halldin*, 2004; *Chen et al*., 2013; *Du et al*., 2015], revealing the potential for terrain to mediate responses of carbon fluxes to climate variability. However, conceptual frameworks and ecological models of land-atmosphere interactions often assume that ecosystem carbon fluxes arise primarily from soil and plant interactions with climate, typically ignoring effects of terrain on heterogeneity within these ecosystems [*Running and Coughlan*, 1988; *Collins et al*., 2006]. This assumption may suffice for relatively flat landscapes [*Rotach et al*., 2014], but case studies demonstrate that topographic variability, as an internal characteristic of terrestrial ecosystems, influences both spatial and temporal dynamics of ecosystem-scale carbon fluxes [*Hwang et al*., 2012; *Riveros-Iregui et al*., 2012].

Complex terrain exerts influence on boundary layer processes [*Finnigan and Belcher*, 2004; *Poggi et al*., 2008; *Rotach et al*., 2017], and a growing body of research focuses on the implications for CO_2 exchange [e.g., *Katul et al*., 2006; *Rotach et al*., 2014]. However, no general framework exists for evaluating the impacts of terrain on the underlying ecophysiological processes contributing to GEP, RE, and NEP, despite increasing evidence that ecological behavior is influenced by terrain complexity [*Levin*, 1992; *Hwang et al*., 2012; *Riveros-Iregui et al*., 2012]. Apart from a few site-specific studies, no work has studied the effects of terrain complexity on ecosystem carbon fluxes, in general. With this in mind, we evaluated relationships between terrain complexity and the response of ecosystem carbon fluxes to climate variables within the AmeriFlux tower network, evaluating responses of GEP, RE, and NEP to temperature (hereafter γ_{GT}, γ_{RT}, and γ_{NT}, respectively) and precipitation (hereafter $\gamma_{GP,}$ $\gamma_{RP,}$ and γ_{NP}, respectively) for sites located in both complex and simple terrains. We considered daily, monthly, seasonal, and annual responses for 30 tower sites covering a range of terrain conditions determined by geospatial analysis of topography surrounding each tower. We hypothesized that intersite correlations between terrain and responses of GEP, RE, and NEP to temperature and precipitation would emerge in only in complex terrain, where topographic heterogeneity drives the distribution of water and energy in ways not present in flat (noncomplex) terrain. In the absence of controlled, landscape-scale experiments, such results would help to identify both landscapes and positions within the landscape that may be experiencing similar ecological behavior.

2. Methods

2.1. Carbon, Climate, and Terrain Data

Ecosystem fluxes (i.e., NEP, RE, and GEP) and supporting meteorological data were obtained from the AmeriFlux network database (http://public.ornl.gov/ameriflux). We selected 30 eddy covariance tower sites with at least 4 years of quality-controlled daily data (i.e., Level 4) and covering a broad range of biomes, climates, and terrain conditions (Figures 1 and S1 and Tables S1 and S2 in the supporting information). Data were further screened to remove outliers [*Papale et al*., 2006], and negative values of GEP were set to zero

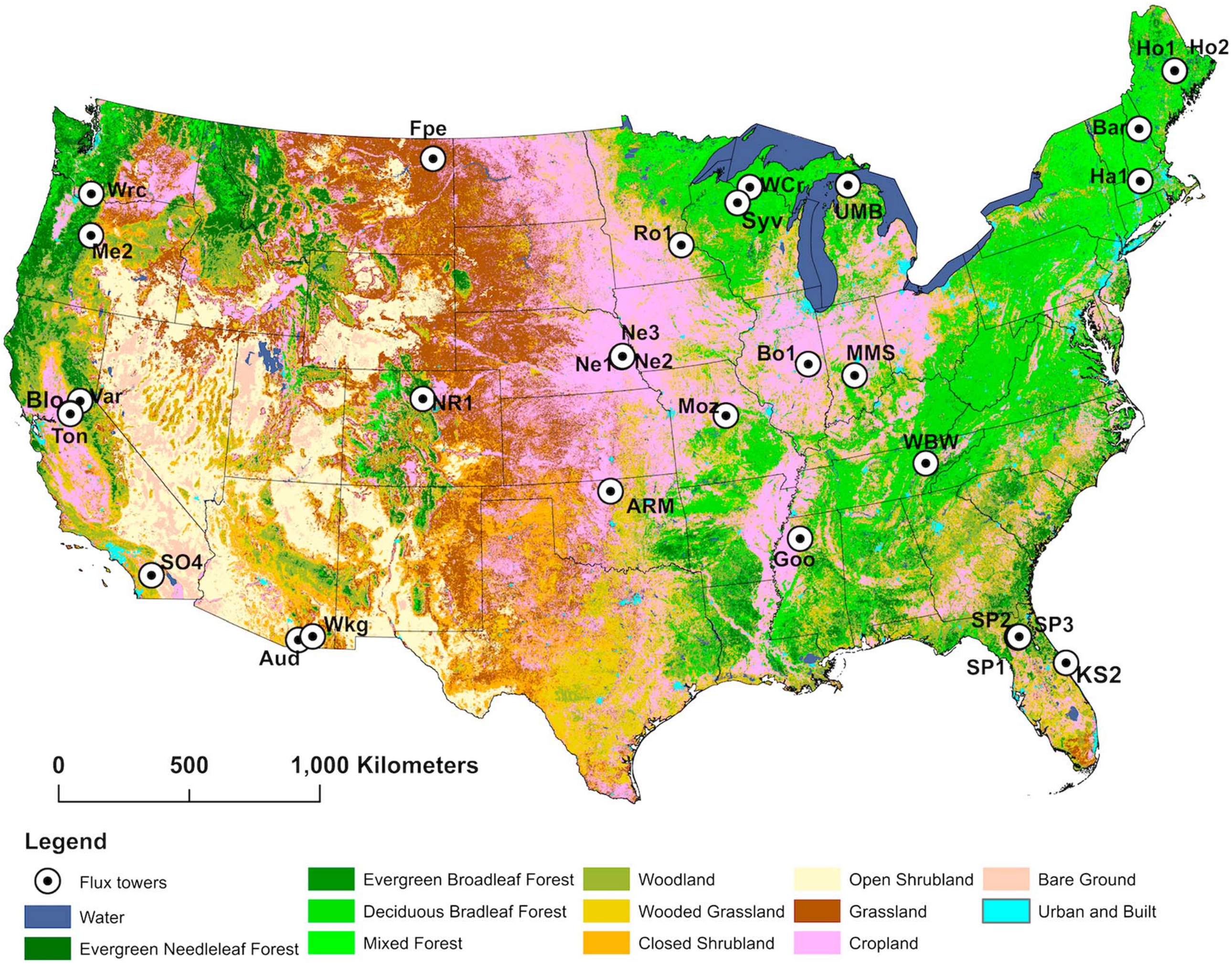

Figure 1. Location of AmeriFlux tower sites used in this study with land cover shown in the background. These sites cover a wide range of biomes as defined by the International Geosphere and Biosphere Programme, including closed shrublands (two sites), cropland (five sites), deciduous broadleaf forests (seven sites), evergreen needleleaf forests (nine sites), grasslands (five sites), mixed forests (one site), and woody savannas (one site).

and transferred the flux to RE to maintain the observed NEP [*Schaefer et al*., 2012]. If there were remaining gaps in the data set, we used the following criteria: (1) gaps >5 days in NEP and temperature data were filled by using mean values of the site series for the same period and (2) gaps <5 days were filled using the mean value in 15 points moving window. The NEP was computed from AmeriFlux NEE observations integrated temporally (i.e., daily, monthly, seasonally, and annually) and inverted in sign so that positive NEP indicates a net carbon accumulation by the ecosystem and negative NEP indicates net carbon release. The GEP and RE data that we obtained were derived following *Reichstein et al*. [2005]. Missing meteorological data from tower sites were supplemented with data from the DAYMET database [*Thornton et al*., 2014], which is publicly available at (http://daymet.ornl.gov/). Daily data were then aggregated into monthly, seasonal, and annual scales for further analysis.

We used a 10 m U.S. Geological Survey digital elevation model (https://viewer.nationalmap.gov/basic/) to derive terrain variables representative of conditions within the flux tower footprint. These variable included local terrain slope, upslope drainage area, and topographic ruggedness index. Upslope drainage area is defined as the area of land contributing to surface or subsurface flow at any point on a landscape, which we computed following *Seibert and McGlynn* [2007]. This terrain variable is linked to the spatial redistribution of soil water and associated biogeochemical processes in soils [*Sponseller and Fisher*, 2008; *Riveros-Iregui and McGlynn*, 2009; *Chatterjee and Jenerette*, 2011; *Creed and Sass*, 2011]. The topographic ruggedness index measures the sum of elevation differences among a neighborhood of DEM cells, computed following *Riley et al.* [1999].

Initially, all terrain variables were derived for each site for a circle with 5 km radius (about 78.5 km^2), with the flux tower situated at the center. This large radius ensured accurate calculation of nonlocal variables (i.e., drainage area) in the vicinity of the tower. The gridded terrain data were then clipped to a standardized footprint comprising a 1 km radius surrounding each tower to estimate terrain characteristics within the circular area. We did not aim to represent the exact flux footprint as it might be estimated from footprint modeling [e.g., *Kljun et al.*, 2015]. Given the additional data requirements and site-specific assumptions (e.g., vegetation roughness) needed for footprint modeling, we instead chose a consistent area around each tower to represent the general topography associated with the site. We computed both the mean and variance of each terrain variable for each site.

2.2. Data Analysis

Stepwise multiple and simple least squares linear regressions were used to assess relationships between climate variables and carbon fluxes across sites and temporal scales (daily, monthly, seasonal, and annual). These analyses enabled us to determine when and at which temporal scale GEP, RE, and NEP were monotonic functions of either temperature or precipitation and when and at which temporal scale both climate variables contributed significantly to the response of carbon fluxes among sites. We tested correlations between climate variables (temperature and precipitation) and carbon fluxes for daily, monthly, seasonal, and annual scales and computed the responses for all time scales. The flux response to either temperature or precipitation (γ) is defined as the slope of the linear least squares regression between an ecosystem flux and a climate variable at a particular time scale (e.g., the response of annual GEP to annual precipitation, annual γ_{GP}).

We determined the degree of terrain complexity for each site using the topographic ruggedness index (TRI) and the variance of upslope drainage area. The TRI and the variance of upslope drainage area were used as grouping criteria for an unsupervised K-means cluster analysis [*Hartigan and Wong*, 1979]. The analysis objectively placed each AmeriFlux site into one of two clusters. The centroids of the two clusters confirmed that they represented less complex terrain and more complex terrain.

We tested global correlations (i.e., correlations among all sites) between γ and terrain variables and also between γ and potential confounding factors including mean site elevation, mean annual temperature, and mean annual precipitation. For each cluster we performed stepwise multiple linear regression to determine significant terrain variables influencing carbon flux responses at each time scale. Once significant terrain variables were identified at all time scales, we computed the correlation between terrain variables and carbon flux responses by linear regression. We used multiple regression analysis to identify the codependence of carbon flux responses to annual precipitation on both terrain slope and upslope drainage area.

The eddy covariance method used to measure ecosystem carbon fluxes at AmeriFlux sites has known biases related to interactions between complex terrain and atmospheric boundary layer processes [*Katul et al.*, 2006]. These interactions can lead to situations in which the vertical eddy flux does not equal NEE. For example, stable atmospheric conditions, which often occur at night, can lead to the accumulation of respired CO_2 in air beneath tower sensors. In some complex terrain, including steep slopes and highly convergent topography, these conditions lead to katabatic flows that transport CO_2 downhill and away from the site [*Leuning et al.*, 2008; *Blanken et al.*, 2009]. These advective fluxes are not captured in the vertical eddy flux and can lead to overestimates of NEE.

Because our study focuses on the ecophysiological processes associated with CO_2 fluxes, we conducted an extra analysis to ensure that our results were not an artifact of terrain influences on boundary layer flows. For each tower site, we recomputed daily mean values of NEP, RE, and GEP during daytime hours (10:00 AM through 4:00 PM). By scrutinizing fluxes measured during daylight hours, we isolate a subset of half-hourly data sets in which unstable atmospheric conditions are most likely to exist [*Kaimal and Finnigan*, 1994], maximizing convection and minimizing terrain influences on atmospheric flows. Temperature and precipitation responses based on daytime means are likely to represent ecophysiological processes and exclude artifacts of terrain-related advection during stable atmospheric conditions.

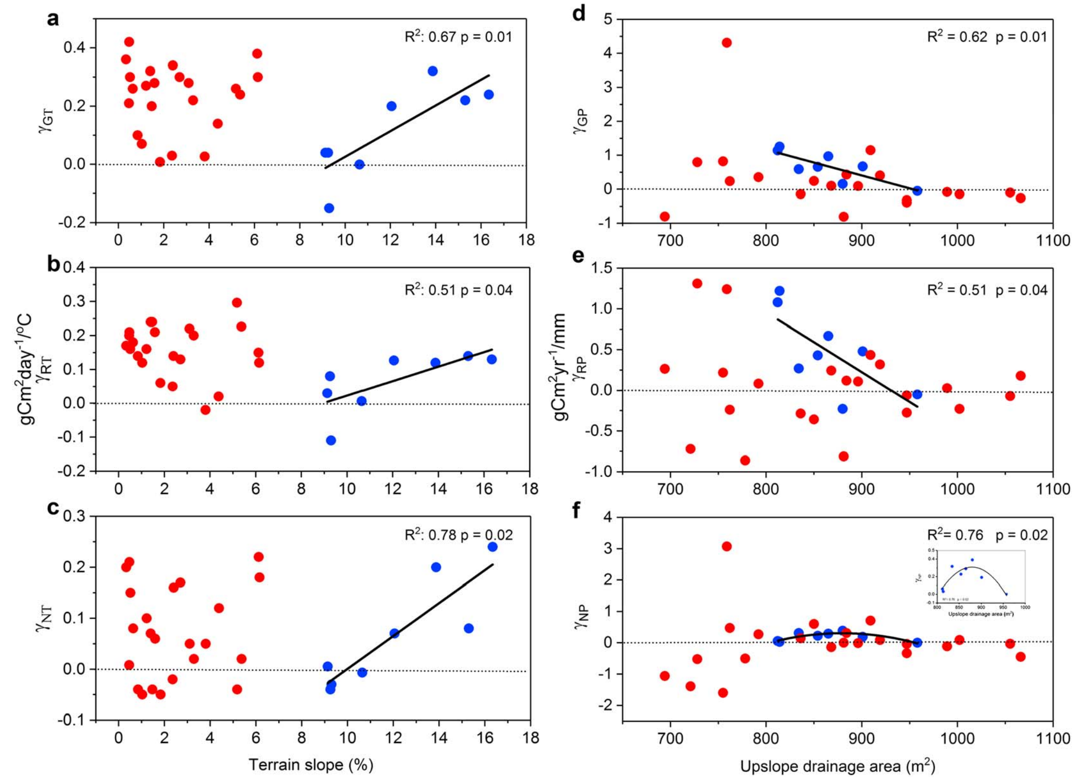

Figure 2. Relationships between responses of CO_2 fluxes to climate variables and terrain metrics; the red symbols show sites in the flat terrain cluster, and the blue symbols show sites in the complex terrain cluster. Individual panels show (a–c) daily temperature responses and (d–f) annual precipitation responses. The dotted lines on panels indicate $\gamma = 0$, and the solid lines show significant linear regressions between terrain variables and responses for sites in complex terrain.

To emphasize the important role of complex terrain in carbon cycling at the continental scale, we used data from the Moderate Resolution Imaging Spectroradiometer (MODIS) gross primary product (GPP)/net primary product (MOD17) data set [*Zhao et al.*, 2005] to provide an estimate annual carbon sequestration by complex terrain for the conterminous U.S. Although such carbon flux estimates do not incorporate the emergent behaviors investigated in this research, MODIS provides a spatially contiguous data set that allowed us to approximate the magnitude of carbon sequestration in complex terrain across the conterminous U.S. We used bivariate frequency distributions to identify areas of the conterminous U.S. having similar terrain slope and upslope drainage area to the AmeriFlux sites evaluated in this study. All statistical and geospatial analyses were performed using MATLAB R2015b and ArcGIS 10.3.

3. Results

We analyzed a total of 178 site years of data (Table S3), and we found that responses of carbon fluxes to temperature and precipitation varied considerably across temporal scales and among sites. The unsupervised K-means cluster analysis of terrain variables identified eight sites as occupying complex terrain and placed the remaining 22 sites in the cluster of noncomplex terrain (Figure 2 and Table S2). For the eight sites situated in complex terrain, we found that topographic slope and upslope drainage area explained between 51% and 78% of site-to-site variation in the response of fluxes to temperature and precipitation depending on the time scale (Figure 2). Specifically, mean topographic slope of the surrounding landscape was correlated with temperature responses γ_{GT}, γ_{RT}, and γ_{NT} at each of the time scales that we tested (Table S4), but daily correlations were strongest between temperature responses and terrain slope (Figures 3a–3c). In other words, as terrain became steeper, GEP, RE, and NEP became more responsive to diel temperature fluctuations.

Among towers in complex terrain, we found that mean upslope drainage area was correlated with annual precipitation responses, γ_{GP}, γ_{RP}, and γ_{NP} (Figures 3d–3f). The two constituent fluxes, GEP and RE, both

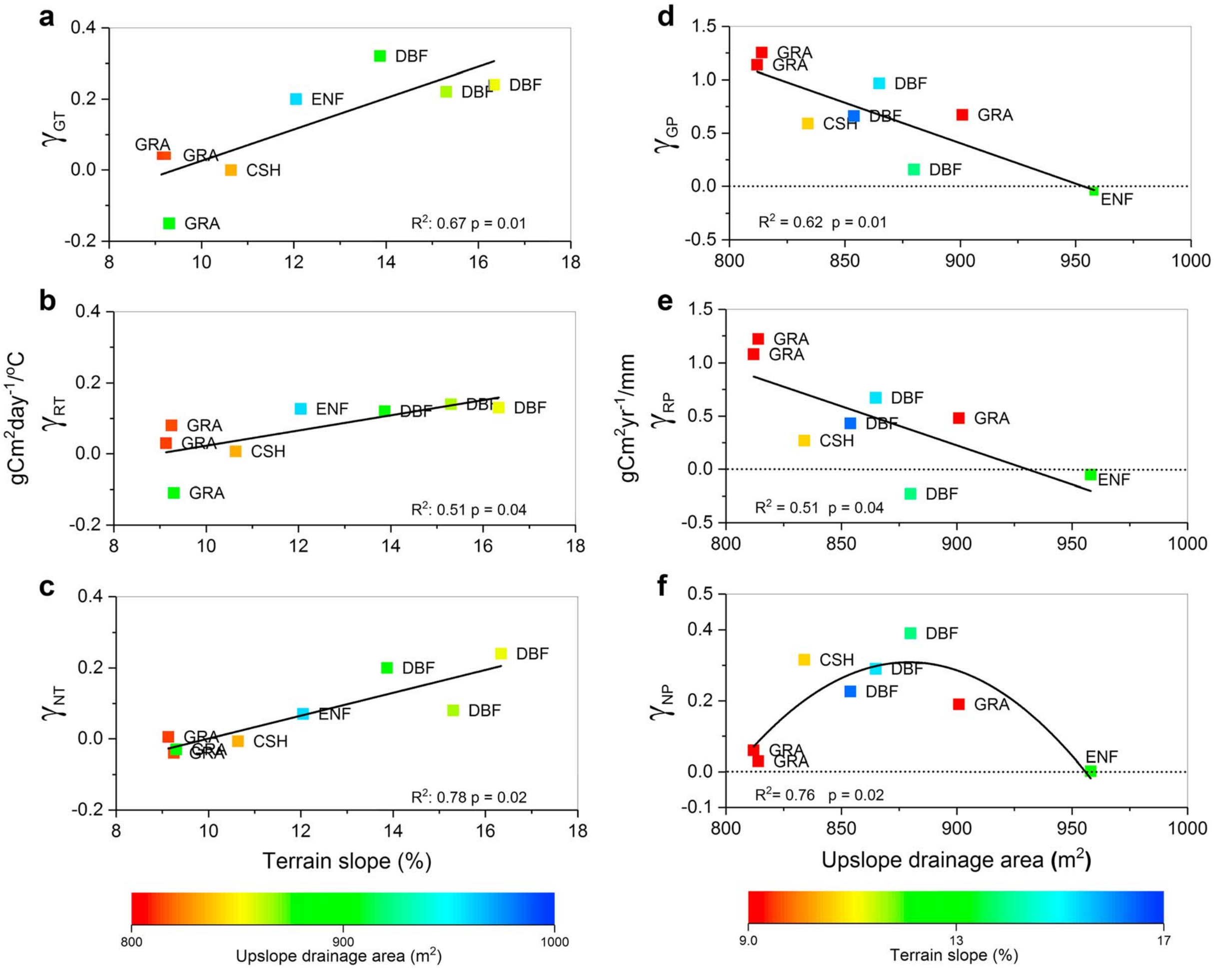

Figure 3. Relationships between responses of CO_2 fluxes to climate variables and terrain metrics for sites in complex terrain (i.e., blue points shown in Figure 2). Individual panels are (a–c) daily temperature responses and (d–f) annual precipitation responses. The dotted lines on panels indicate $\gamma = 0$, and the solid lines show significant linear regressions (Table S4). The labels indicate ecosystem type as defined by The International Geosphere–Biosphere Programme: GRA (grassland), DBF (deciduous broadleaf forests), ENF (evergreen beedleleaf forests), and CSH (closed shrublands).

responded linearly, becoming less responsive to annual precipitation as mean drainage area of the landscape increased (Figures 3d and 3e). However, the relationship between annual γ_{NP} and upslope drainage area was nonmonotonic, with peak response occurring at a mean upslope drainage area of approximately 900 m^2. For complex sites with mean upslope drainage areas below this threshold, γ_{NP} increased with drainage area, but above this threshold the flux response decreased with upslope drainage area (Figure 3f). The 22 tower sites located in flat (i.e., noncomplex) terrain exhibited very weak or nonexistent relationships between terrain variables and the responses of carbon fluxes to temperature and precipitation (Figure 2 and Table S4). Our analysis of daytime (10:00 A.M.–4:00 P.M.) fluxes shows similar coefficients of determination for each regression, confirming that these results do not stem from measurement biases associated with atmospheric boundary layer flows in certain types of complex terrain (Figure S4).

Multiple regression analysis between terrain variables and CO_2 flux responses to annual precipitation in complex terrain sites showed that γ_{GP} was predominantly dependent upon upslope drainage area (Figure 4a). On the other hand, the combined effects of terrain slope and drainage area on γ_{RP} elicited a bidirectional response (Figure 4b), in which greatest positive responses were associated with small upslope drainage areas and greatest negative responses associated with large drainage areas. Relationships between γ_{GP} and γ_{RP} and the two terrain variables revealed a nonlinear response of γ_{NP} to terrain (Figure 4c). Annual γ_{NP} was greatest for low to intermediate slopes with intermediate to high upslope drainage areas.

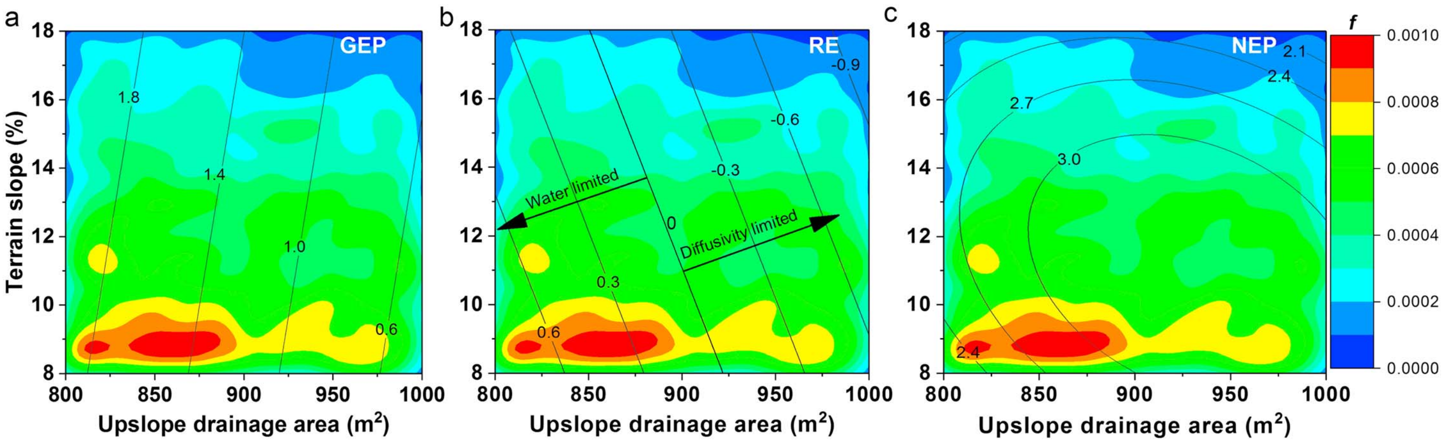

Figure 4. Codependence of annual CO_2 responses to precipitation on both terrain slope and drainage area. The black contour lines are annual responses to precipitation (g C m^{-2} yr^{-1}/mm) derived from multiple regression analysis. The colored contours in the background are bivariate frequency distributions of complex terrain in the conterminous U.S. (i.e., Figure 5a). The arrows show potential limitation of ecosystem respiration by water availability or gas diffusivity in soils.

4. Discussion

4.1. Influences of Terrain on CO_2 Responses to Temperature and Precipitation

The results presented here show that ecosystem carbon assimilation and respiration responses to diel temperature fluctuations are sensitive to terrain slope, but only in complex terrain (Figures 2a–2c). Sites in complex terrain had mean terrain slopes in excess of approximately 9%, and above this threshold daily flux responses to temperature increased linearly with increasing terrain slope (Figures 3a–3c). This phenomenon is likely related to the influence of topographic slope on local energy and water balances, because direct solar radiation and soil dryness generally increase with terrain inclination [*Hanna et al.*, 1982; *Zhang et al.*, 2010]. Thus, ecosystems in steep terrain experience greater diel variations in photosynthetically active radiation, air temperature, and soil temperature compared to similar ecosystems in flat terrain. Such increased variability may be associated with greater variability in short-term carbon assimilation and belowground respiration rates [*Kang et al.*, 2003]. Above the 9% threshold, increases in terrain slope may further accentuate diel temperature variability and associated fluctuations in energy and water availability related to plant and soil CO_2 processes. These findings span multiple ecosystem types and climate regimes, and we identified no clear effects of mean elevation, mean temperature, or mean precipitation on the results (Table S1 and Figures S2 and S3).

The decline in GEP response to precipitation with increasing drainage area (Figure 3d) likely reflects increased availability of soil water in landscape positions with greater drainage areas. As drainage areas increase, lateral redistribution of soil water allows soil water storage to increase in volume and persist for longer periods [*Tenhunen et al.*, 2001], leading to less vegetation water stress [*Emanuel et al.*, 2010] and decreased response of GEP to precipitation variability at wetter sites [*Hwang et al.*, 2012]. Soil water availability may similarly explain the decline in γ_{RP} with upslope drainage area (Figure 3e). In a given climate, landscapes with smaller upslope drainage areas tend to be drier than landscapes with larger upslope drainage areas [*Beven and Kirkby*, 1979], and small precipitation inputs have greater potential to enhance both below and aboveground respiration in these drier landscapes [*Riveros-Iregui et al.*, 2012]. As upslope drainage area increases, water availability increases due to greater and longer duration of water supplied by lateral soil water redistribution [*Grayson et al.*, 1997]. Eventually, these landscapes may experience reduced RE due to limitations in oxygen availability and gas diffusivity [*Riveros-Iregui et al.*, 2012]. These factors likely contribute to the changing sign of annual γ_{RP} observed among sites in complex terrain (Figure 3e).

The observed nonmonotonic relationship between the annual γ_{NP} and upslope drainage area (Figure 3f) reflects the combined response of both GEP and RE to increasing water availability. For landscapes with small upslope drainage areas, GEP and RE are highly responsive to precipitation, whereas for landscapes with large upslope drainage areas, GEP and REP are less responsive to precipitation. Similar response magnitudes but opposite directions of fluxes result in minimally responsive γ_{NP} at sites where the mean upslope drainage area is either very high or very low. At intermediate upslope drainage areas, the response of GPP is greater than RE, resulting in a higher positive γ_{NP}.

Multiple regression analysis revealed that γ_{GP} was largely a function of upslope drainage area (Figure 4a), confirming the strong dependence of γ_{GP} on soil water availability [*Huxman et al*., 2004]. The observed bidirectional response of γ_{RP} to the combined effect of terrain slope and drainage area (Figure 4b) is consistent with known landscape-scale limitations of RE by water availability at drier landscape positions (i.e., small drainage area) and by gas diffusivity limitations at wetter landscape positions (i.e., large drainage areas) [*Riveros-Iregui et al*., 2012]. Likewise, greatest annual γ_{NP} (Figure 4c) corresponds to areas of the landscape where soil water is expected to accumulate and persist following storms or snowmelt [*Beven and Kirkby*, 1979] but not to the extent that excess soil water limits the responsiveness of carbon fluxes to changes in annual precipitation. These results help to clarify interactions among terrain characteristics that give rise to ecological behavior not apparent when investigating effects of slope and drainage area separately.

Relationships between terrain variables and the responses of carbon fluxes to temperature and precipitation were weak or nonexistent in flat terrain (Table S4). Results from flat landscapes are consistent with the prevailing conceptual framework, which asserts that energy and water balances arise primarily from soil and vegetation characteristics and that vertical interactions among soils, plants, and the atmosphere dominate landscape-scale behavior [*Running and Coughlan*, 1988; *Collins et al*., 2006]. Our results suggest that carbon fluxes in flat terrain are less likely to be influenced by relatively minor fluctuations in energy balance components caused by terrain heterogeneity or by the lateral redistribution of water and other resources across the landscape. These topographically simple sites lack combinations of slope and drainage area found in more complex terrain and therefore lack the spatial heterogeneity in water and energy that likely produce the behavior that we observed in complex environments. Although both flat and complex sites share similar ranges of variability in responses of carbon fluxes to climate variables, only complex sites exhibit clear organization of this variability with respect to slope or drainage area.

Altogether, these results suggest that above certain thresholds of terrain complexity, responses of CO_2 fluxes to temperature and precipitation vary predictably with terrain characteristics. These patterns are independent of other landscape features such as mean climate conditions or ecosystem type. We found that much of the complex terrain in the conterminous U.S. corresponds with high response of annual carbon fluxes to precipitation (Figure 4c). Therefore, overlooking the terrain dependence of these variations in ecosystem responses to certain climate variables may lead to either underestimation or overestimation of carbon fluxes, with profound impacts on larger-scale carbon budgets.

4.2. Implications

Land surface components of Earth system models are central in representing the interactions between terrestrial biosphere and the atmosphere [*Fisher et al*., 2014b; *Davison et al*., 2016]. Realistic representation of land surface heterogeneity is fundamental for predicting key land processes such as GPP and RE [*Ke et al*., 2013]. Particularly, subgrid heterogeneity in vegetation and topography can significantly influence the estimates of energy and mass fluxes. These subgrid heterogeneities are often represented in land surface models [*Fisher et al*., 2014a; *Melton and Arora*, 2014; *Prentice et al*., 2015], but they tend to be parameterized separately, with few exceptions [*Leung and Ghan*, 1998]. Although this parameterization approach helps to provide more realistic representations of biogeochemical processes within a land surface model pixel, it may not capture emergent behavior arising from interactions between landscape components such as topography and vegetation or between terrain characteristics such as slope and drainage area.

The results presented here support the assertion that interactions between vegetation and terrain may lead to emergent behavior in carbon fluxes. As discussed in section 4.1, variability in CO_2 responses to temperature and precipitation was clearly organized according to terrain slope and drainage area, but only for sites located in complex terrain (Figure 3 and Table S2). This result suggests that in complex terrain, topographic variables interact with each other and with vegetation in different ways to influence carbon cycling. These interactions can produce linear (Figures 3a–3e), bidirectional (Figure 4b), or nonlinear responses (Figure 4c) of carbon fluxes to temperature and precipitation. Current approaches to parameterizing landscape components in land surface models may not capture these types of behaviors. Representing these types of interactions and emergent behaviors in models of the carbon cycle will take careful thought to balance process

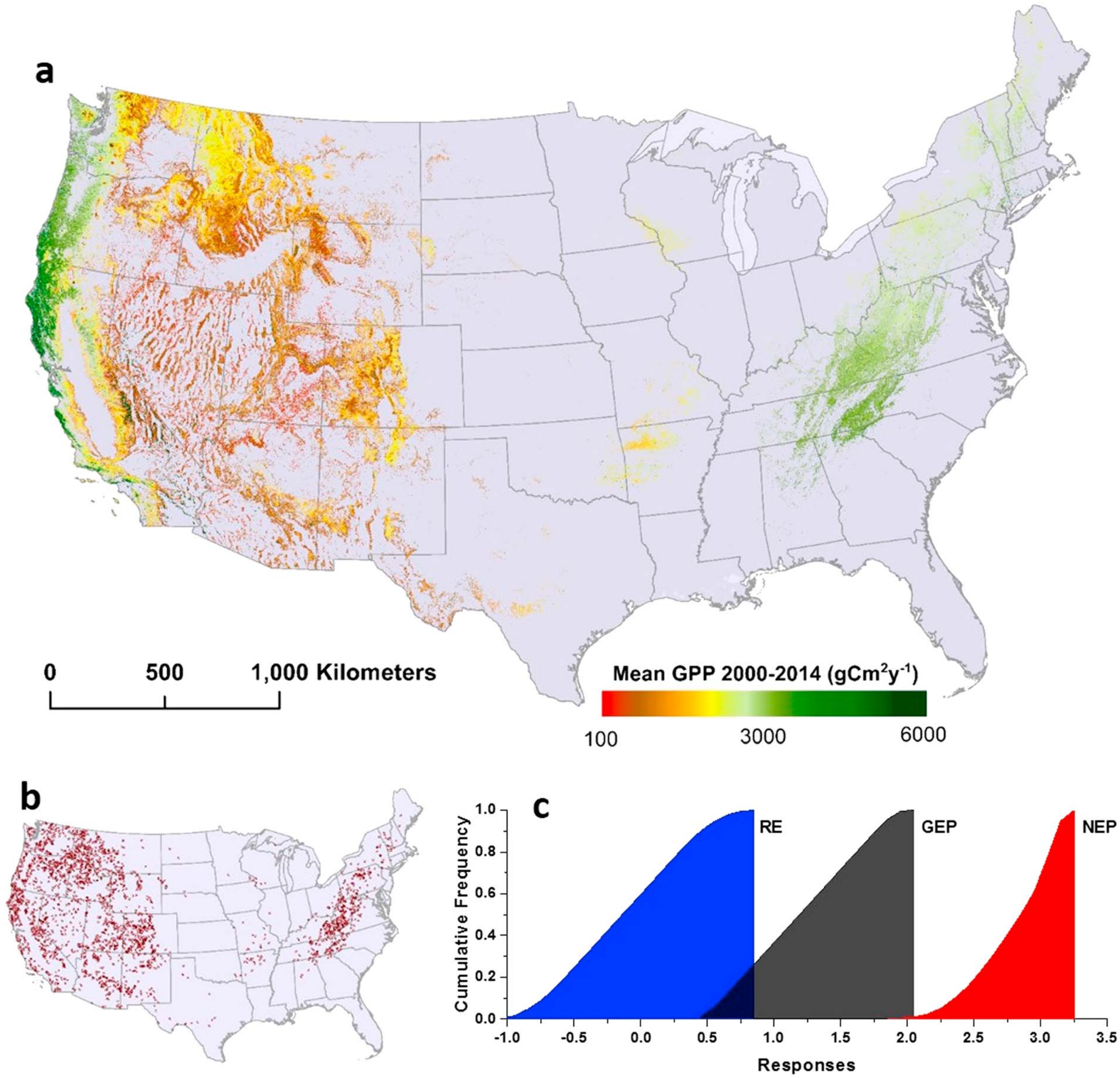

Figure 5. Complex terrain in the conterminous U.S. accounts for (a) 14% of the territory and (b) approximately 1.13 Gt of gross primary production per year, estimated from MODIS satellite observations [*Zhao et al.*, 2005]. The red highlighting Figure 5b shows land area with the same range of terrain values identified in our study, 8 to 18% terrain slope and 800–1000 m^2 drainage area, which constitutes about 2800 km^2 of the conterminous U.S. (c) Cumulative frequency distributions of CO_2 responses to annual precipitation (g C m^{-2} yr^{-1}/mm) for complex terrain in the conterminous U.S. show the variability of these responses across the areas highlighted in Figure 5b. Sign of the RE response indicates potential limitations by diffusivity (negative values) and by water availability (positive values).

representation with computational demands, but doing so may help to address uncertainties that remain in models of the terrestrial carbon cycle [*Piao et al.*, 2013; *Friedlingstein et al.*, 2014].

Our results underscore the importance of accounting for the effects of complex terrain on the redistribution of resources that are directly linked to ecosystem carbon cycling (e.g., water and light). Likewise, our findings emphasize the need for models to recognize the heretofore unparameterized role of terrain in driving ecological responses at spatial scales that are typically considered “subgrid resolution” by regional and global carbon models [*Collins et al.*, 2006].

This work has implications for about 14% of the total conterminous U.S. that is considered topographically complex, as defined by our previously identified threshold of 9% terrain slope. Estimates of GEP from MODIS remote sensing products [*Zhao et al.*, 2005] suggest that these areas of complex terrain sequester approximately 1.13 Gt of carbon sequestration per year (Figure 5a). This number corresponds to approximately 15% of total annual carbon sequestration for the conterminous U.S., excluding the impacts of natural disasters such as drought, fire, and tropical storms [*Xiao et al.*, 2010]. These satellite-derived estimates of carbon sequestration do not account for the emergent behavior identified in this study, but they are still useful for understanding the approximate magnitude of the U.S. terrestrial carbon sink that could be influenced by the processes underlying such behavior.

A much smaller subarea of about 2800 km^2 within the conterminous U.S. falls within the exact ranges of slopes and drainage areas represented by AmeriFlux towers that we identified as occupying complex terrain (Figure 5b). Although small in total area, these landscapes are widely dispersed across the conterminous U.S. (Figure 5b). About 30% of this area experiences very high NEP response to annual precipitation (Figure 5c). These large NEP responses derive, at least in part, from interactions between terrain and ecological processes that directly influence the response of GEP and RE to precipitation. Our results provide the first evidence that complex terrain mediates the response of carbon fluxes to temperature and precipitation across a range of ecosystems. Given the prevalence of complex terrain worldwide and its potential to influence the terrestrial carbon cycle in such landscapes, this work adds to our understanding and provide insights of how the biotic and abiotic components of terrestrial ecosystems function within the global carbon cycle.

5. Conclusions

The results presented here demonstrate that in terrestrial ecosystems, the responses of carbon fluxes to temperature and precipitation can be influenced by topography in complex terrain. These results are fundamentally different from prior studies, which have focused on the ability of complex terrain to modify the atmospheric boundary layer and drive advective flows. Our work does not discount the importance of these prior studies; rather, it suggests that complex terrain also influences key ecophysiological processes associated with CO_2 exchange. We found that terrain slope and drainage area, which are often associated with water and energy availability, impact daily responses of carbon fluxes to temperature (in the case of slope) and annual responses of carbon fluxes to precipitation (in the case of drainage area). These topographic variables interact with vegetation and soils in complex ways to give rise to a broad spectrum of responses to climate variables. We found no such influences in flat terrain, suggesting that the traditional conceptualization of vertical soil-vegetation-atmosphere dynamics holds for these systems. The terrain impacts identified in this work have implications for approximately 14% of the total land area of the conterminous U.S., an area that is responsible for approximately 15% of conterminous U.S. carbon sequestration. Prevailing conceptual frameworks and models may not be able to capture these terrain-derived responses, and our results highlight new opportunities to improve conceptual understanding and models of ecosystem carbon dynamics.

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