RESEARCH REVIEWS

WILEY **Global Ecology and Biogeography** A Journal of Macroecology

Interannual variability of ecosystem carbon exchange: From observation to prediction

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Abstract

Aim: Terrestrial ecosystems have sequestered, on average, the equivalent of 30% of anthropogenic carbon (C) emissions during the past decades, but annual sequestration varies from year to year. For effective C management, it is imperative to develop a predictive understanding of the interannual variability (IAV) of terrestrial net ecosystem C exchange (NEE).

Location: Global terrestrial ecosystems.

Methods: We conducted a comprehensive review to examine the IAV of NEE at global, regional and ecosystem scales. Then we outlined a conceptual framework for understanding how anomalies in climate factors impact ecological processes of C cycling and thus influence the IAV of NEE through biogeochemical regulation.

Results: The phenomenon of IAV in land NEE has been ubiquitously observed at global, regional and ecosystem scales. Global IAV is often attributable to either tropical or semi-arid regions, or to some combination thereof, which is still under debate. Previous studies focus on identifying climate factors as driving forces of IAV, whereas biological mechanisms underlying the IAV of ecosystem NEE are less clear. We found that climate anomalies affect the IAV of NEE primarily through their differential impacts on ecosystem C uptake and respiration. Moreover, recent studies suggest that the carbon uptake period makes less contribution than the carbon uptake amplitude to IAV in NEE. Although land models incorporate most processes underlying IAV, their efficacy to predict the IAV in NEE remains low.

Main conclusions: To improve our ability to predict future IAV of the terrestrial C cycle, we have to understand biological mechanisms through which anomalies in climate factors cause the IAV of NEE. Future research needs to pay more attention not only to the differential effects of climate

anomalies on photosynthesis and respiration but also to the relative importance of the C uptake period and amplitude in causing the IAV of NEE. Ultimately, we need multiple independent approaches, such as benchmark analysis, data assimilation and time-series statistics, to integrate data, modelling frameworks and theory to improve our ability to predict future IAV in the terrestrial C cycle.

1 | INTRODUCTION

Terrestrial ecosystems have sequestered an average of nearly 30% of anthropogenic CO_2 emissions since the 1960s (Ballantyne, Alden, Miller, Tans, & White, 2012; Le Quéré et al., 2014). However, the magnitude of this terrestrial carbon (C) sequestration varies from year to year (Le Quéré et al., 2013), changing from a *c.* 0.5 Gt C/year C source in 1987 to a 4.0 Gt C/year C sink in 2011. The large interannual variability (IAV) of land C uptake, rather than oceanic C uptake, primarily contributes to the yearly variation in atmospheric CO_2 concentration (Figure 1; Bousquet et al., 2000; Houghton, 2000; Knorr et al., 2007). Thus, understanding the causes of the interannual variability (IAV) in land C sequestration is essential for future projections of the coupled C cycle and climate system. At ecosystem scales, many studies have also found that the IAV of net ecosystem CO_2 exchange (NEE) with the atmosphere is a ubiquitous phenomenon across almost all sites of eddy-flux measurements (Baldocchi, Chu, & Reichstein, 2017; Baldocchi, Falge, Gu, et al., 2001; Baldocchi, Ryu, & Keenan, 2016; Yuan et al., 2009). However, the mechanisms underlying the IAV in NEE across scales from the ecosystem to the globe have not been fully understood to an extent that can help improve our predictive capability of the C cycle. If the IAV of NEE is caused purely by climatic variability, we can extrapolate measurements from one year to another year as long as we have realistic climatic data and scenarios. If climate variability induces indirect effects on ecosystem processes via biogeochemical regulation, we need long-term observations to develop sound understanding of relationships between NEE and climatic variables before we can reasonably predict C fluxes. In these circumstances, ecological models that do not include appropriate mechanisms often successfully simulate NEE in one year but fail in others (Griffis & Rouse, 2001; Keenan, Baker, et al., 2012).

This paper comprehensively assesses the current status of our understanding of the IAV of the land C sink. We first review literature on the phenomena of the IAV of the land C sink at global, regional and ecosystem scales, and then identify regional contributions to the global IAV of NEE and the driving climate factors and biological mechanisms underlying the IAV of NEE at the ecosystem scale. We then evaluate model efficacy in predicting IAV and explore causes for the mismatches between models and data. Finally, we offer recommendations for future studies to measure and model IAV better in order to improve

our predictive understanding of the global C cycle. This review suggests that the IAV in NEE results from anomalies in climatic variables, such as temperature, precipitation and radiation, which differentially influence photosynthetic C uptake and respiratory C release processes through biological regulation.
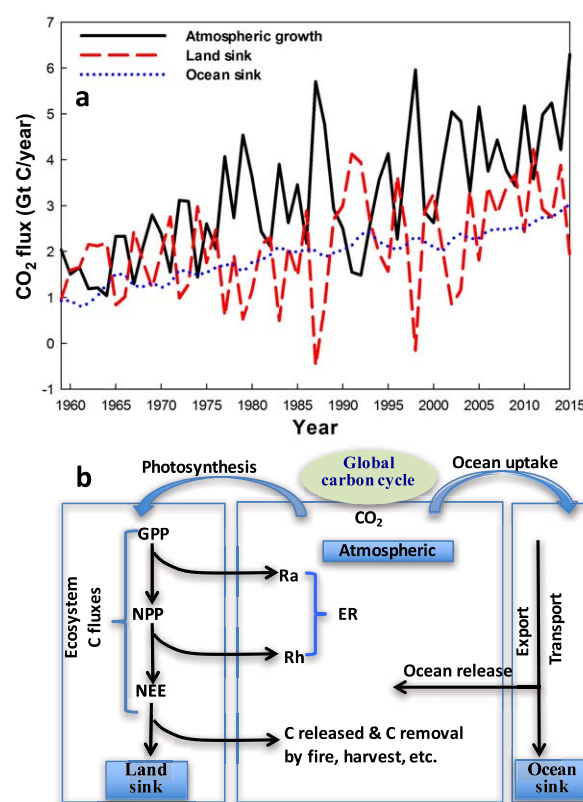

FIGURE 1 (a) The interannual variability of atmospheric CO_2 growth rate, land and ocean carbon sinks from 1958 to 2015. (b) Conceptual diagram linking the terms and processes used in this review. Atmospheric CO_2 is taken up by the land and the ocean. In terrestrial ecosystems, plants take up CO_2 to form gross primary productivity (GPP). Some of the photosynthetic carbohydrate is released into the atmosphere via autotrophic respiration (Ra). The remaining carbohydrate forms net primary productivity (NPP). Soil organic matter is decomposed by microbes via heterotrophic respiration (Rh) to release CO_2 into the atmosphere. The balance of carbon uptake and release at the ecosystem level forms net ecosystem exchange (NEE). At the regional or global scale, the land carbon (c) sink is formed by excluding non-biotic C release or removal caused by fire, harvest or other disturbances

2 | OBSERVED PHENOMENA OF INTERANNUAL VARIATION IN LAND CARBON SINK AT GLOBAL AND ECOSYSTEM SCALES

The phenomenon of the IAV of the C cycle was first reported from long-term measurements of the atmospheric CO_2 mixing ratio at the South Pole (Keeling, Adams, et al., 1976) and Mauna Loa observatories (Keeling, Bacastow, et al., 1976). At those observatories, the long-term change in the atmospheric CO_2 growth rate was found to be highly variable; it could double or halve from one year to the next. This fluctuation was first considered to be associated with the Southern Oscillation and primarily oceanic events (Bacastow, 1976). The phenomenon of IAV of atmospheric CO_2 concentration was then detected again from the measurement of 2,419 samples of air collected in the North Pacific Ocean during 1959–1981 (Keeling, Whorf, Wong, & Bellagay, 1985). The data record of atmospheric CO_2 observations is now more than five decades long, and the annual growth rate continues to exhibit high variability, with rates spanning an order of magnitude from as low as 0.29 ppmv in 1964 to as high as 3.15 ppmv in 2015 (esrl.noaa.gov).

The anomaly in the annual growth rate of atmospheric CO_2 concentration is now primarily attributed to the IAV in the land C sink (Figure 1; Houghton, 2000; Le Quéré et al., 2013). Houghton (2000) reviewed the four components that determine the atmospheric CO_2 growth rate: C emissions from fossil fuel burning, net C emissions from land use changes, ocean uptake, and the residual land sink. His review concluded that the most important contributor to the IAV of atmospheric CO_2 growth rate is the changes in land sink as induced by anomalies in climate variables. The IAV in ocean CO_2 uptake is thought to be too small to explain the anomaly in atmospheric CO_2 growth rate (Le Quéré, Orr, Monfray, Aumont, & Madec, 2000). In comparison, the land C sink can strongly regulate the atmospheric CO_2 growth rate to the extent of no increase between 2002 and 2012 despite increasing anthropogenic emissions (Keenan et al., 2016).

Both atmospheric inversions and ground-based observations show that the land C sink varies greatly from year to year. Estimates of NEE at the global scale from atmospheric inversion approaches showed that the detrended global NEE ranged from an anomaly of 1.78 Pg C/year in 1983 to −1.66 Pg C/year in 1992 in comparison with the mean value of NEE of −1.52 Pg C/year over the 35 years (Figure 2a). At regional scales, some tropical regions had the largest IAV, with SD in annual gross primary production (GPP) of the order of 200–250 g C/m^2 (Xiao et al., 2016). Relative to the long-term mean, GPP over Europe decreased by 30% in 2002 because of drought when comparing the period between 1998 and 2002, resulting in a strong anomalous net source of NEE (0.5 Pg C/year) to the atmosphere, which is a net C sink during normal years (Ciais et al., 2005).

The IAVs of the land C sink at global and regional scales are in agreement with observations at ecosystem scales. For example, the observed NEE by the eddy covariance towers changed from 74 to 930 g C/m^2/year at the site US-Blo (Blodgett Forest in the Sierra
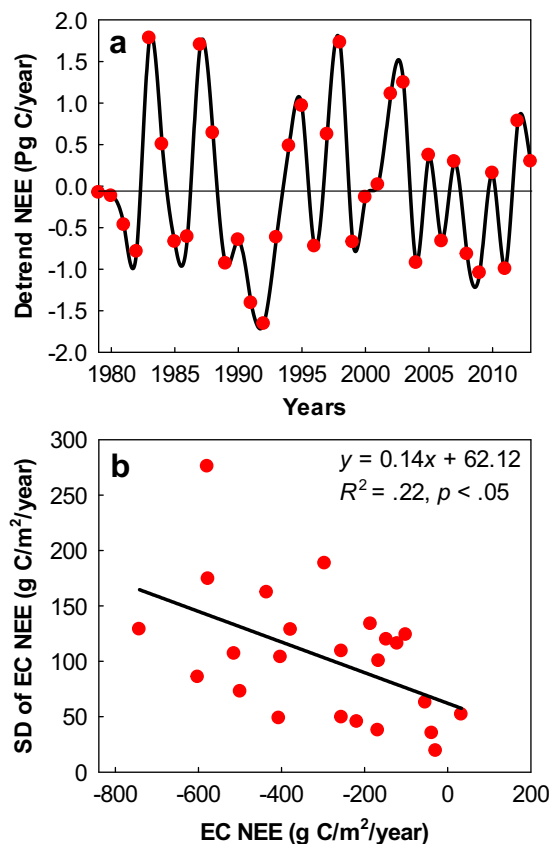

FIGURE 2 Interannual variability of terrestrial ecosystem carbon fluxes at (a) global and (b) ecosystem scales. (a) The detrended yearly anomaly of atmospheric inversed net ecosystem exchange (NEE) at the global scale from 1978 to 2013. (b) The SD of eddy covariance (EC) measured NEE versus its average annual values at 24 sites with measurements > 8 years. See the Supporting Information for detailed methods

Mountains of California) and from −158 to 240 g C/m^2/year at the site Be-Bra (De Inslag Forest in Brasschaat, Belgium) during the period from 1997 to 2007 (Fu, Stoy, et al., 2017). Across the 24 sites that have > 8 years of continuous measurement, the SD of NEE on average accounts for 50% of annual NEE (Figure 2b). Besides eddy covariance-measured NEE at the ecosystem scale, other observations, such as tree-ring chronologies, showed large IAV in wood production in response to climate variability (Carrer & Urbinati, 2006). Results from long-term ecological research (LTER) programmes have also demonstrated strong IAV in aboveground net primary productivity (NPP), which is associated with precipitation changes, at 11 LTER sites across North America (Knapp & Smith, 2001).

Overall, scientists have used different approaches to quantify the IAV of land NEE at different spatial scales. The top-down atmospheric method using CO_2 inversions is effective to illustrate the global scale IAV, whereas the flux-tower observations have the advantage of providing process understanding of the IAV of NEE at the ecosystem scale. Nonetheless, inferences from both atmospheric inversions and observations at the ecosystem scale indicate that the IAV of ecosystem C exchange is a ubiquitous phenomenon.

3 | REGIONAL CONTRIBUTIONS TO THE INTERANNUAL VARIATION OF GLOBAL LAND CARBON SINK

The IAV of the global land C sink is attributable to different regions; for example, tropical areas are reported to play an important role in influencing the IAV of terrestrial NEE (W. Wang et al., 2013; X. Wang et al., 2014). Specifically, the IAV of the tropical land C sink is significantly correlated with tropical land-surface air temperature during 1959–2011, with an interannual temperature sensitivity of 3.5 ± 0.6 Pg C/year/K. The relationship between interannual changes in NEE and temperature in tropical areas appears to be stronger than corresponding relationships with precipitation and radiation (W. Wang et al., 2013). Moreover, X. Wang et al. (2014) found that the sensitivity of land C sink variability to tropical temperature IAV varies with time and has increased by a factor of 1.9 ± 0.3 over the past five decades. Across coupled climate–carbon cycle models, the sensitivity of tropical land C sink to climate anomaly over the 21st century is constrained to be 53 ± 17 Pg C/K (Cox et al., 2013).

Recent studies have also shown that semi-arid areas lead to a larger contribution to the IAV of the land C sink than other regions (Ahlström et al., 2015; Poulter et al., 2014). Specifically, semi-arid systems contributed *c.* 39% of the IAV in global net biome production, compared with tropical ecosystems (19%), extratropical forests (30%) and grasslands and croplands (17%) (Ahlström et al., 2015). Semi-arid regions contributed 57% of the global IAV of global GPP, which was controlled by the IAV of precipitation in these regions (Y. Zhang et al., 2016). In semi-arid regions, vegetation is sparse and productivity is typically low compared with tropical and boreal systems given strong water deficits in semi-arid regions (Avitabile et al., 2016; Beer et al., 2010). However, ecosystem C fluxes can respond quickly to precipitation events (e.g. Huxman et al., 2004), leading to a unique land C sink signature. It is important also to note that transient CO_2 release attributable to the 'Birch' effect in response to precipitation pulses is a notable property of arid and semi-arid ecosystems (Birch, 1958; Unger, Máguas, Pereira, David, & Werner, 2010). Whereas the Birch effect operates at shorter temporal scales (hours to weeks), associated respiratory pulses can add up to impact the IAV of NEE (Jarvis et al., 2007). The sensitivity of semi-arid systems to an increasing frequency of precipitation extremes is noticeable in global land C uptake dynamics (Ahlström et al., 2015; Frank et al., 2015), further demonstrating the central role of semi-arid ecosystems in the IAV of terrestrial CO_2 fluxes.

The debate regarding the role of temperature in tropical regions and precipitation in semi-arid regions on the IAV of global land C uptake is proposed to be resolved by a recent study, which simultaneously evaluated the IAV of land C uptake to the fluctuations in both temperature and water availability at local to global scales (Jung et al., 2017). Jung et al. (2017) revealed that water availability and temperature are the dominant drivers of IAV of NEE at local areas, whereas temperature is the main driver for the global IAV of NEE because of the compensation amongst the responses of different regions to water availability (Figure 3). In other words, the controlling factors and
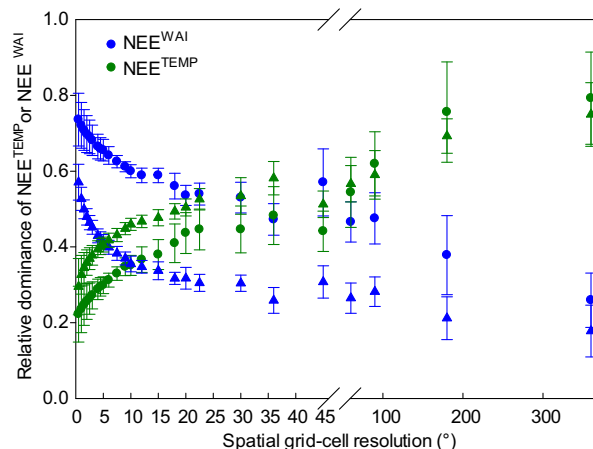

FIGURE 3 The relative importance of temperature versus water availability in causing the interannual variability of land net ecosystem exchange (NEE) at different spatial scales. The relative dominance of temperature on NEE (NEE^{TEMP}) increases, whereas the relative dominance of water availability on NEE (NEE^{WAI}) decreases, with increasing spatial scales (adopted from Jung et al., 2017)

mechanisms underlying the IAV of NEE varied at different spatial scales (Table 1), and the importance of IAV at the ecosystem or local scales would be cancelled out when aggregating to a regional or global scale. Therefore, to gain a better understanding of the IAV of land C uptake, it is necessary to understand ecosystem-level NEE variability and the mechanisms that control it.

4 | THE IMPORTANCE OF CLIMATE AND OTHER FORCING FACTORS TO THE INTERANNUAL VARIATION OF ECOSYSTEM NET ECOSYSTEM CO_2 EXCHANGE

Studies on the causes of the IAV of ecosystem NEE usually examine the relationship between the yearly anomalies of NEE and the anomalies of climate factors. Variations in temperature, precipitation and solar radiation have been reported as the most important climate factors controlling IAV in NEE in different ecosystems. Below, we discuss how those climate and other forcing factors impact IAV of NEE, with a focus on the mechanisms and process understanding.

4.1 | Drought and precipitation regimes

The timing and magnitude of precipitation regimes influences GPP and ecosystem respiration (ER), thus causing variability of NEE (see the concepts in Figure 1b). Water availability is the overall dominant driver of the IAV in NEE at local scales (Jung et al., 2017). Drought causes IAV of NEE in most ecosystems, even those not commonly associated with drought, such as tropical forests (Keppel-Aleks et al., 2014; Ma et al., 2012; Xiao et al., 2014; L. Zhang et al., 2014). Amazon basin-wide net ecosystem productivity (NEP, the inverse of NEE) was reduced in drought years (Gatti et al., 2014). In wet tropical forests, drought considerably reduces respiration, but tends to impact GPP

TABLE 1 Scales of phenomena, driving factors, biological mechanisms and future research recommendations for understanding the interannual variability of net ecosystem carbon dioxide exchange

	Global	Regional	Ecosystem
Phenomena	Variation in yearly growth rate of atmospheric CO_2 concentration	Yearly anomalies of regional NEE under heat waves, large-scale drought and fires	Yearly variation in NEE observed by eddy-flux towers, NPP from long-term ecological research sites, tree rings
Driving factors	Primarily anomalies of temperature	Anomalies of both temperature and precipitation, with varying roles in different regions	Temperature, precipitation, radiation and disturbances play different roles in different ecosystems
Biological mechanism or attributes	Attributable to different regions, among which tropical and semi-arid areas contribute most	Not yet well examined	Differential climate sensitivity of photosynthesis versus respiration. Carbon uptake amplitude plays more important role than carbon uptake period
Model predictive skill	No mechanistic models yet tested except some statistical models	Land models used to examine IAV in different regions	Models perform poorly, mainly because of a lack of model calibration of phenological and physiological responses, and lag mechanisms
Recommendation for future research	Explore which regions contribute most to the global IAV and how these contributions are changing in a changing climate	Reveal the drivers and causes of IAV of NEE in different regions	Promote long-term observations, especially in less-studied areas. Better understand biological mechanisms. Use data–model fusion approaches to improve model prediction

Abbreviations: IAV = interannual variability; NEE = net ecosystem carbon dioxide exchange; NPP = net primary productivity.

less, as a consequence of increased light availability (Bonal et al., 2008; Saleska et al., 2003). In temperate ecosystems, however, eddy covariance observations indicate that drought-induced reductions in GPP often exceed those of ER, leading to a reduction in ecosystem carbon uptake (Schwalm et al., 2010; Shi et al., 2014). Drought-induced IAV of GPP (Cai et al., 2014; Zscheischler et al., 2014) is primarily attributable to the associated decrease in stomatal conductance (Novick et al., 2016; Zeng, Mariotti, & Wetzel, 2005) and increases in vegetation mortality, dry woody material and wildfire occurrence (X. Zhang et al., 2013). The magnitude of changes in those biogeochemical processes are related to drought intensity and duration, the plant functional type (Welp, Randerson, & Liu, 2007), soil characteristics (Pinter, Balogh, & Nagy, 2010) and topography (Kljun et al., 2006).

Besides the amount of precipitation, other attributes of precipitation regimes (e.g., the magnitude, frequency, interval and seasonal distribution of precipitation events) are also responsible for the IAV of NEE (Guo et al., 2012). For some ecosystems, significant differences in the timing and magnitude of precipitation events are more important than annual precipitation itself for determining the IAV of NEE. For example, C sequestration often occurs after heavy precipitation in arid and semi-arid regions, including temperate regions with high evaporative demand (Novick et al., 2004), whereas smaller precipitation events often only stimulate respiratory responses of microorganisms (Huxman et al., 2004; Reynolds, Kemp, Ogle, & Fernández, 2004).

Precipitation can affect C cycling through its effects on soil water content (SWC) (Knapp et al., 2008), temperature (Guo et al., 2015) and incident radiation (Nijp et al., 2015) and also through its regulation of soil nutrient availability and species composition (Sala & Lauenroth, 1982). The effects of precipitation regimes on the IAV of the C cycle

are often ecosystem specific. Studies have found that precipitation regimes with larger but fewer precipitation events may have opposite effects on productivity in semi-arid ecosystems (Heisler-White, Knapp, & Kelly, 2008; Thomey et al., 2011) versus meadows or relatively humid ecosystems (Fay, Carlisle, Knapp, Blair, & Collins, 2003; Harper, Blair, Fay, Knapp, & Carlisle, 2005; Heisler-White, Blair, Kelly, Harmoney, & Knapp, 2009; Knapp et al., 2008). Therefore, biological mechanisms modify C cycling in response to precipitation regimes (Figure 4). Lengthening of growing seasons can partly offset the effects of drought (Wolf et al., 2016) on annual NEE, further emphasizing the importance of multiple factors in controlling the IAV of NEE.
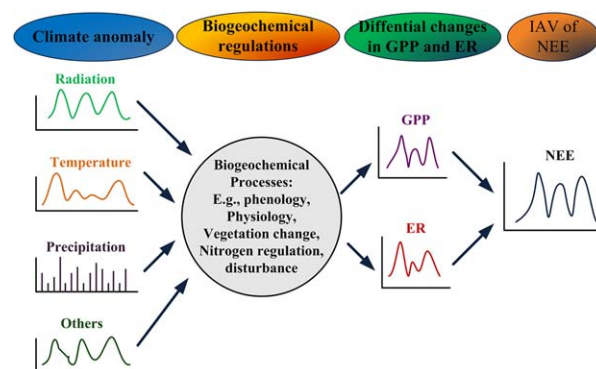

FIGURE 4 Schematic diagram for the conceptual relationships between climate anomalies, biogeochemical regulation and the interannual variability of carbon fluxes. Interannual variability (IAV) in net ecosystem exchange (NEE) is ultimately caused by anomaly in climate variables, which influence a variety of biogeochemical processes, resulting in differential changes in photosynthesis (gross primary productivity, GPP) and respiration (ecosystem respiration, ER)

4.2 | Temperature

Temperature affects all aspects of ecosystem C processes, including photosynthesis and respiration. Increasing temperature can directly stimulate enzyme activity and accelerate both photosynthesis and respiration rates, or reduce them through enzyme denaturation if temperature becomes too high. If the photosynthesis and respiration of plants and ecosystems are significantly different in response to temperature changes, the IAV of NEE will have a statistical correlation with annual average temperature (Rocha & Goulden, 2008; Wen, Wang, Wang, Yu, & Sun, 2010). Field experiments suggest that climate warming also tends to extend growing seasons, enhance nutrient availability, shift species composition and alter ecosystem water dynamics (Luo, 2007), which further affects the IAV of NEE.

Even if the IAV of NEE may not have a significant relationship with the anomalies of mean annual temperature for a given ecosystem, it is often correlated with the anomalies of growing season temperature. For example, spring temperature helps to determine forest leaf onset and affects the length of the growing season, thus leading to the IAV of NEE (Richardson et al., 2013; Wu et al., 2012). Many studies have found that annual ecosystem C fluxes are closely correlated with spring temperature across years (Keenan et al., 2014; Krishnan et al., 2008). In addition, autumn temperature changes are significantly correlated with changes in GPP and NEE (J. Zhang et al., 2011). Autumn and winter temperature anomalies may affect respiration more than photosynthesis given the negligible or minor contribution of photosynthesis to NEE during those seasons (Piao et al., 2008; Yuan et al., 2009) and can result in lagged effects to subsequent growing seasons (Barford et al., 2001). Thus, besides the direct effects of temperature on the physiological activities of photosynthesis and respiration, temperature change may also cause the IAV of C fluxes by changing plant phenology and growing season, as illustrated in the conceptual Figure 4.

4.3 | Radiation

Radiation has a more important role than climate factors at local scales, although it is a smaller driver of IAV of fluxes at the global scale, which experiences little year-to-year variability in solar radiation (Jung et al., 2017). Light-sensitive ecosystems respond to interannual changes in light availability, and in fact, minor drought can increase the photosynthesis of tropical forests if it results in more light (Oliphant et al., 2011). Radiation causes the IAV of terrestrial GPP not only via its magnitude but also via light quality (Ichii, Hashimoto, Nemani, & White, 2005; Nemani et al., 2003). Diffuse radiation has a large influence on the IAV of NEE (Cox et al., 2013; Reichenau & Esser, 2003). For instance, Gu et al. (2003) described the effects of the Pinatubo volcano eruption in 1991, which produced a large number of volcanic aerosols, resulting in the worldwide increase of diffuse radiation in the following 2 years on temperate forest NEE. The increase in diffuse radiation enhanced noontime photosynthesis at Harvard Forest in cloudless conditions by 23% in 1992 and 8% in 1993, respectively. Another study by Mercado et al. (2009) suggested that the increasing fraction of diffuse radition

resulted in a 23.7% increase in global terrestrial C sink between 1960 and 1999.

In general, diffuse radiation influences the IAV of NEE at least in four ways. First, the increasing clouds and aerosols change the composition of the radiation spectrum (Gatebe, Kuznetsov, & Melnikova, 2014; Navrátil, Špunda, Marková, & Janouš, 2007) and increase the proportion of blue light (van Gorsel et al., 2013). Second, increasing clouds and aerosols decrease direct radiation, reducing the frequency of light saturation of canopy photosynthesis and making the canopy more responsive to changes in radiation (Farquhar & Roderick, 2003; Knohl & Baldocchi, 2008). Third, the increasing clouds and aerosols, to a certain extent, simultaneously reduce temperature, which decreases ecosystem respiration (M. Zhang et al., 2010, 2011). Fourth, diffuse radiation penetrates the plant canopy more effectively, which can increase total canopy photosynthesis (Cheng et al., 2015; Roderick, Farquhar, Berry, & Noble, 2001). Combined, these factors influence both photosynthesis and radiation and demonstrate the need to include diffuse radiation measurements at tower measurements worldwide to understand the relationship between solar radiation and the IAV of ecosystem NEE.

4.4 | Other driving factors

Fires and other disturbances, such as pests and disease, can induce C release from ecosystems to the atmosphere. Approximately 70% of global fire CO_2 emissions are from savanna and grassland systems, where regrowth occurs rapidly after a fire and absorbs a significant fraction of CO_2, which is often of similar magnitude to the original emissions. The C loss triggered by the fire event in one area can be compensated by C gain during recovery in other areas. Thus, on average, fire plays a minor role in the IAV of land C uptake at global scales (Van der Werf et al., 2010), but is often an important contributing factor to regional C fluxes, especially in relationship to drought (Poulter et al., 2014). A synthesis of multiple data sources of atmospheric CO_2 growth rate, land use change, fire emission and land carbon fluxes showed a significant correlation between atmospheric CO_2 growth rate and fire emission, but the magnitude in variation attributable to fire emission was too small to explain the IAV of CO_2 growth rate (S. L. Piao, unpublished result). Global emission of C from human disturbance (i.e. deforestation, shifting cultivation, wood harvest and regrowth) or pests or diseases also has a small contribution to the IAV of global land C uptake (Houghton, 2010).

5 | BIOLOGICAL MECHANISMS UNDERLYING INTERANNUAL VARIATION IN ECOSYSTEM NET ECOSYSTEM CO_2 EXCHANGE

The apparent relationships between climate anomalies and the IAV of ecosystem NEE suggest underlying ecological mechanisms, which are essential for explaining the impacts of climate anomalies on ecosystem C cycling. Here, we synthesize studies on biological mechanisms into three categories: statistical inference, differential changes in GPP and

ER, and relative contributions of ecosystem C uptake phenology and physiology to the IAV of ecosystem NEE.

5.1 | Statistical inference of biotic controls on interannual variation of ecosystem net ecosystem CO_2 exchange

Variability in climate drivers may directly affect fluxes, but may also indirectly affect fluxes by altering the response of biota to climate (Figure 4). To isolate direct effects of climatic anomalies on ecosystem metabolic processes (e.g., photosynthesis and respiration) from their indirect effects, Hui, Luo, and Katul (2003) proposed a homogeneity-of-slopes model to identify the functional change contributing to IAV in NEE. The model uses multiple regression analysis to partition the observed variation in NEE to four components, namely, the functional change, the direct effect of interannual climatic variability, the direct effect of seasonal climatic variation, and random error. The results showed that functional change provided slightly larger explanation than interannual climatic variability for the observed variation in NEE and ecosystem respiration (RE) at the Duke Forest AmeriFlux site from 1997 to 2001 (Hui et al., 2003). Using the same statistical method, Shao et al. (2015) evaluated the relative contributions of climate effect and biotic effect to the IAV in C fluxes for the 65 sites in the Northern Hemisphere. They found that overall, the relative contribution of biotic effect and climate effect to the IAV in NEE was 57 ± 14 and 43 ± 14%, respectively. Similar results were documented by Richardson, Hollinger, Aber, Ollinger, and Braswell (2007), who suggested that 40% of the variance in modelled ecosystem NEE can be attributed to variation in environmental drivers, and 55% to variation in the biotic response to this forcing at the annual time step. Polley, Frank, Sanabria, and Phillips (2008) also used the regression analysis proposed by Hui et al. (2003) to distinguish direct effects of IAV in climate on fluxes from biotic effect (functional change) and found that functional change accounted for more than twice the variance in fluxes of direct effects of climatic variability. These studies highlight how the IAV of NEE is strongly regulated by the response of ecological processes, such as plant photosynthesis and respiration, as well as phenology and physiology, to climate variability (Figure 4).

5.2 | Differential changes in photosynthesis and respiration

Observed NEE reflects a fine balance between canopy photosynthetic C influx into and respiratory efflux out of an ecosystem (Figure 1b). Differential changes in the relative magnitude of these two opposite fluxes determine the IAV of NEE (Figure 4). Carbon fluxes attributable to photosynthesis and respiration are large relative to the difference between them (i.e. NEE), which means that small differences in the relative changes in photosynthesis or respiration can lead to large IAV of NEE. For the climate sensitivity of photosynthesis and respiration, some studies reported that ecosystem respiration is more variable than photosynthesis between years (Valentini et al., 2000), whereas other studies have indicated that IAV of NEE is most often associated with

variations in GPP and NPP rather than C release (i.e., ecosystem respiration (Re) and heterotrophic respiration (Rh)) (Ahlström et al., 2015; Ciais et al., 2005; Novick et al., 2015; Stoy et al., 2008).

For the relative sensitivity of photosynthesis versus respiration in response to variability in controlling factors, it was found that GPP was more sensitive to drought stress than ER in most ecosystems, especially in semi-arid and mediterranean climates, which experience large variability in the amount of rainfall in the growing season (Allard, Ourcival, Rambal, Joffre, & Rocheteau, 2008; Pereira et al., 2007). Nevertheless, temperature anomalies tend to change ER more than GPP (Yvon-Durocher, Jones, Trimmer, Woodward, & Montoya, 2010). For example, based on a 9-year eddy covariance measurement record, years with autumnal warming reduced the annual CO_2 sink because of the stimulation of ER in a black spruce forest (Ueyama, Iwata, & Harazono, 2014). Moreover, nitrogen deposition tends to favour GPP more than ER at the ecosystem scale (Fernández-Martínez et al., 2014). Disturbance events (e.g., clear-cuts and fires), likewise change GPP as well as ER (Beringer, Hutley, Tapper, & Cernusak, 2007). Despite decades of research on the GPP and ER, our ability to produce an estimate of global photosynthesis and respiration with a high accuracy confidence still remains elusive, needless to mention the mechanisms underlying their IAV. Future research on mechanisms underlying the IAV of ecosystem NEE has to provide fundamental explanations for the IAV of GPP and ER.

5.3 | Relative contributions of carbon uptake phenology and physiology

Climate change influences the terrestrial C cycle by modifying the C uptake rate and C uptake period, which primarily correspond to plant physiology and phenology, respectively. It has been demonstrated that spatial and temporal variations in GPP are jointly controlled by changes in plant phenology and physiology (Xia et al., 2015). NEE is also strongly correlated with growing season length and regulated by plant phenology (Baldocchi, Falge, & Wilson, 2001). Using NEE estimated through atmospheric inversion, the IAV of land C uptake was determined by the IAV of the C uptake period and the C uptake amplitude (the maximal C uptake rate), of which C uptake amplitude played much stronger role than C uptake period (Fu, Dong, et al., 2017). Likewise, analysis of regional GPP data products generated by a vegetation photosynthesis model also showed a dominant role of plant physiology in IAV of GPP in North America (Zhou et al., 2017).

As illustrated in the conceptual Figure 5, C uptake period or amplitude may change differently in various ecosystem types in response to climate change, resulting in different impacts on IAV of NEE (Fu, Stoy, et al., 2017). For example, in boreal or temperate ecosystems, warmer spring or autumn periods may lengthen the C uptake period by advancing C uptake activity in spring or by delaying C uptake activity in autumn (Figure 5a,b). In subtropical forests or arid and semi-arid grasslands, summer drought may depress C uptake amplitude during the mid-growing season (Figure 5c,d).

The attribution of IAV of NEE to C uptake period and amplitude provides mechanistic explanations on how climate factors control the
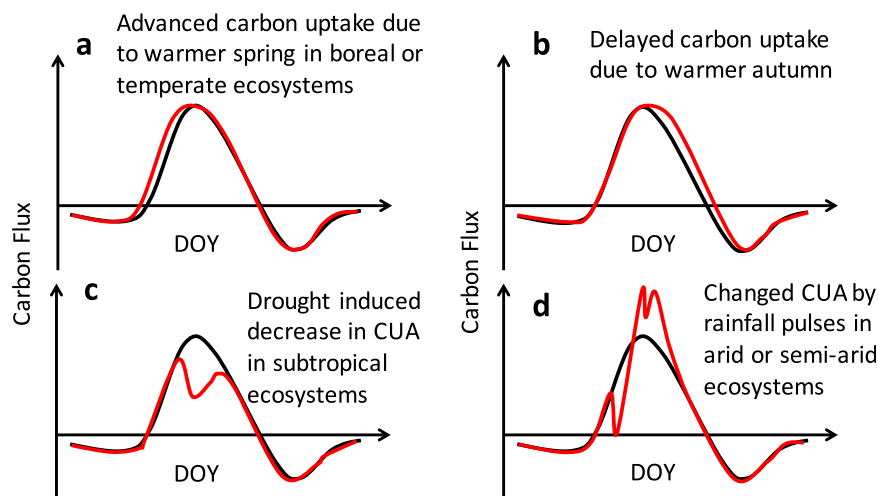
FIGURE 5 Conceptual figures for the attributions of carbon uptake period (carbon sink days) and carbon uptake amplitude (the maximal carbon uptake rate, CUA) to the interannual variability of ecosystem net carbon uptake. The black curve means the average year and the red curve indicates any specific year that changes in carbon uptake period and/or amplitude following Fu, Stoy, et al. (2017). DOY means day of the year

IAV of the terrestrial C cycle. Given that C uptake period and amplitude are two processes that occur in different seasons, they may have different controlling climatic factors (Fu, Stoy, et al., 2017). Climate factors may have compensatory effects on C uptake period and amplitude, leading to negligible impacts on annual NEP. For example, a longer growing season caused by spring warming may result in higher GPP or NEE, whereas warmer and drier summers may suppress summer production, potentially offsetting the increase in ecosystem C uptake (Angert et al., 2005; Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007). The C uptake period/amplitude framework provides a simple mechanism for understanding how ecosystem physiology and phenology interact with climate variables to influence the IAV of NEE and GPP.

6 | CHALLENGES IN PREDICTING THE INTERANNUAL VARIATION OF THE LAND CARBON CYCLE

The efficacy of land surface models for reproducing the observed IAV of the terrestrial carbon cycle depends on the scale of interest. At the global scale, the IAV of NEE is primarily determined by changes in tropical temperatures and precipitation (W. Wang et al., 2013), with large contributions in some years from semi-arid regions (Poulter et al., 2014) and high-latitude ecosystems (Ahlström et al., 2015). Such large-scale global signals are driven by large-scale events, such as the El Nino Southern Oscillation, which itself remains difficult to predict (Kleeman & Moore, 1997), as are the impacts of climate variability on IAV at the ecosystem scale.

Observations of IAV at the ecosystem scale provide an excellent opportunity to test land surface models, given that many anomalous climate events (such as summer heat waves and extreme droughts) often occur at specific sites. When tested against such site-scale observations, however, land surface models typically perform very poorly.

For example, Keenan, Baker, et al. (2012) tested 16 land surface models and three remote sensing products against observed IAV at 11 long-term observation sites and found that none of the models reproduced the observations. A lack of lagged responses to anomalous climatic events (Keenan, Baker, et al., 2012), a poor representation of phenological signals (Richardson et al., 2013) and model formulation (Dietze et al., 2011; Schwalm et al., 2010) have been highlighted as potential causes of model–data mismatch for IAV at the site scale. Integrating models with observations through data assimilation has proved useful in diagnosing the exogenous and endogenous causes of such model–data mismatch (Keenan, Davidson, et al., 2012). For example, Desai (2010) found that the ability of a land surface model to replicate IAV was significantly improved when observations were used to minimize parameter error through model–data fusion. Such approaches of better integrating models, data and theory (Luo, Keenan, & Smith, 2015; Williams et al., 2009) should guide future efforts for improving our ability to model the IAV of NEE.

The mismatch between models and observations is often an issue of scale and initialization. Models tend to be parameterized using observations at the finest possible time-scale, either the half-hourly or hourly resolution that aligns with the native resolution of eddy covariance observations, or the sub-daily, daily or monthly time step of the model itself. This approach of conditioning models that are tuned to fine-scale data then aggregated to coarser scales in time often successfully matches NEE observations at diurnal to seasonal time-scales (Braswell, Sacks, Linder, & Schimel, 2005; Stoy et al., 2013), but simulating annual NEE and its IAV remains stubbornly elusive (Figure 6). Despite extensive research using a number of advanced analytical techniques, including wavelet decomposition (Stoy et al., 2005), and techniques from model–data fusion, including scale-dependent parameter estimation (Mahecha et al., 2010), it is difficult to identify causal features in climate time series that correspond to ecosystem-scale fluxes at interannual time-scales (Stoy et al., 2009). A promising approach
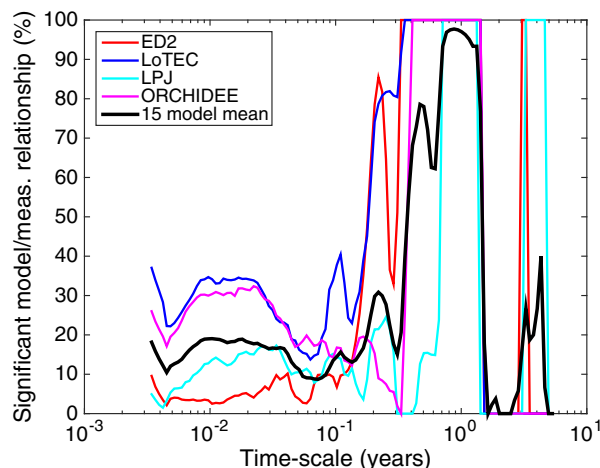
FIGURE 6 The percentage of time, at time-scales from days to multiple years, in which there is a significant relationship between eddy covariance measurements of net ecosystem exchange (NEE) at Harvard Forest and four different ecosystem models (including a multi-model mean) using the wavelet coherence approach of Grinsted, Moore, and Jevrejeva (2004) following Stoy et al. (2013)

that has been applied at the ecosystem level to understand connections between climate variables and ecosystem responses, including relationships among the coupled processes of GPP and ER, is spectral Granger causality (Detto et al., 2012). Spectral Grainger causality quantifies relationships amongst signals at different frequencies and thereby also IAV, but has not been used to help disentangle ecosystem responses to climatic variability at interannual time-scales to date. In brief, expanding our analytical toolbox may improve our ability to quantify nonlinear, lagged and multiscale relationships amongst climate and carbon cycling for the purpose of improving model representation of these dynamics.

7 | CONCLUDING REMARKS AND FUTURE RESEARCH

Interannual variability in terrestrial C fluxes is a ubiquitous phenomenon at global, regional and ecosystem scales. The IAV in global land C fluxes is primarily responsible for the anomaly in atmospheric CO_2 growth rate. However, linking the IAV of C fluxes across scales is still challenging. In particular, the regions that contribute most to the global IAV are still under debate, as are the contributions of these regions to global IAV in a changing climate. Tropical regions have been considered responsible for global IAV mainly because of their large climate variability related to El Niño/Southern Oscillation, and the arid and semi-arid regions also exhibit strong IAV signals.

Regardless of spatial scales, the IAVs in land C fluxes are ultimately attributable to climate variables, either directly or indirectly through biological responses to climate or via extreme events. It has been identified that anomalies in temperature, precipitation and radiation are key causes for IAV in ecosystem C fluxes. Radiation plays a key role locally but contributes less at the global scale. Precipitation anomalies are important to the IAV of NEE at local and regional scales but tend to be

compensated globally, whereas the control of temperature over the IAV of NEE occurs at scales from the ecosystem to the globe. The anomalies in climate variables differentially influence photosynthetic C uptake and respiratory C release to generate IAV in NEE. As photosynthesis and respiration are two opposite fluxes determining NEE, slightly differential effects of anomalous temperature, precipitation and radiation on photosynthesis and respiration could generate strong IAV in NEE. Although a few studies have explored this issue, how anomalies in temperature, precipitation and radiation cause differential impacts on photosynthesis and respiration is largely unclear. Moreover, recent methodological advances improve our ability to understand relative contributions of the C uptake period and amplitude.

The present generation of ecosystem models has low predictive skills for IAV in NEE, although most of the key C processes have been integrated into models. Our understanding of the differential changes in photosynthesis and respiration in anomalous climate conditions has not yet been converted into improving model predictive skills. To develop our ability to predict IAV of NEE in the future, we have to understand the biological mechanisms underlying IAV of C fluxes and evaluate their relative importance so that various mechanisms can be incorporated appropriately into models. Research efforts are also needed to benchmark land model performance against observations of IAV of ecosystem C fluxes (Luo et al., 2012). Data assimilation is an effective approach to minimizing model–observation mismatches and diagnosing model uncertainty, and new techniques from time-series analysis and statistics can further improve our ability to understand how climate and carbon interact. Better integration of models, data and theory should guide future efforts for improving our ability to predict the IAV of surface–atmosphere C exchange at scales from the ecosystem to the globe.

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