Land use change and El Niño-Southern Oscillation drive decadal carbon balance shifts in Southeast Asia

Masayuki Kondo, Kazuhito Ichii, Prabir K. Patra, Joseph G. Canadell, Benjamin Poulter, Stephen Sitch, Leonardo Calle, Yi Y. Liu, Albert I.J.M. van Dijk, Tazu Saeki, Nobuko Saigusa, Pierre Friedlingstein, Almut Arneth, Anna Harper, Atul K. Jain, Etsushi Kato, Charles Koven, Fang Li, Thomas A.M. Pugh, Sönke Zaehle, Andy Wiltshire, Frederic Chevallier, Takashi Maki, Takashi Nakamura, Yosuke Niwa & Christian Rödenbeck

An integrated understanding of the biogeochemical consequences of climate extremes and land use changes is needed to constrain land-surface feedbacks to atmospheric CO₂ from associated climate change. Past assessments of the global carbon balance have shown particularly high uncertainty in Southeast Asia. Here, we use a combination of model ensembles to show that intensified land use change made Southeast Asia a strong source of CO₂ from the 1980s to 1990s, whereas the region was close to carbon neutral in the 2000s due to an enhanced CO₂ fertilization effect and absence of moderate-to-strong El Niño events. Our findings suggest that despite ongoing deforestation, CO₂ emissions were substantially decreased during the 2000s, largely owing to milder climate that restores photosynthetic capacity and suppresses peat and deforestation fire emissions. The occurrence of strong El Niño events after 2009 suggests that the region has returned to conditions of increased vulnerability of carbon stocks.

DOI: 10.1038/s41467-018-03374-x
Southeast Asia is unique among tropical regions because the region is highly susceptible to the influence of El Niño-Southern Oscillation (ENSO) and is subject to highest deforestation rates in the tropical regions. In the recent past, Southeast Asia experienced large CO₂ emissions, ranging from 0.81 to 1.2 Pg C yr⁻¹ due to the drought-induced fires during the 1997/1998 El Niño, and a substantial loss of forest area (2.5 Mha in the 1990s) due to forest conversion to oil palm and rubber tree plantations. However, contrary to the intensively studied Amazon Basin and Congo Basin with permanent plot sample data, the recent states of net CO₂ flux (balance between CO₂ uptake and release by the land biosphere) across Southeast Asia remain highly uncertain.

The Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC) provided a synthesis of the global net CO₂ flux. However, disregard of land use change (LUC) in the biosphere models (the bottom-up approach) resulted in an underestimation of CO₂ release for the tropical regions when compared with the atmospheric CO₂ inversions (the top-down approach). Both climate and LUC need to be integrated into analyses to adequately estimate the net CO₂ flux and to reconcile results from different approaches. Such an integrated effort has not been undertaken for Southeast Asia.

Here we investigate the decadal variability of the net CO₂ flux (termed Net Biome Production: NBP, the negative sign (−) for a net sink and the positive sign (+) for a net source) in Southeast Asia over the period 1980–2009 using an ensemble of seven terrestrial biosphere model simulations from the TRENDY model intercomparison project (Supplementary Table 1), an ensemble of five atmospheric CO₂ inversions that cover longer than two decades (Supplementary Tables 2, 3) and a remote-sensing-based annual biomass change estimated by Global Aboveground Biomass Carbon version 1.0 (Supplementary Fig. 1). We demonstrate that consideration of LUC processes to biosphere models brings consistency in interannual and decadal variability of the net CO₂ flux between the bottom-up, top-down and remote-sensing-based approaches, indicating carbon balance shifts towards a net source from the 1980s to 1990s, and towards a net sink from the 1990s to 2000s. Subsequently, we quantify the contributions to the decadal NBP variability from CO₂ fertilization, climatic conditions and LUC using three sets of TRENDY simulations (Supplementary Fig. 2) where biosphere models were forced with varying CO₂, climate and historical LUC (TRENDY S3), along with simulations forced with varying CO₂ and climate (TRENDY S2), and varying CO₂ only (TRENDY S1). Our results show that increased LUC emissions during the 1990s was the major factor responsible for the shift towards a net source between the 1980s and 1990s, and the enhanced CO₂ fertilization and absence of strong El Niño events during the 2000s for the shift towards a net sink between the 1990s and 2000s. The milder climate sustained during the 2000s is of particular importance to a high carbon assimilation by plant ecosystems in Southeast Asia, inducing a strong net uptake that cancels a large proportion of CO₂ release from ongoing LUC in the region.

Results

The effect of LUC on net CO₂ flux. We find agreement in interannual variability of NBP between the TRENDY S3 and atmospheric CO₂ inversions for the period 1980–2009, and the annual biomass change (hereafter, Δbiomass) for the period 1994–2009, as indicated by high correlations between the three estimates (r = 0.67–0.70, p < 0.01, Fig. 1a; detailed inter-model comparisons in Supplementary Figs. 3, 4). However, this agreement is not found in a comparison with the TRENDY S2, which indicates continuously strong CO₂ uptake throughout the 30-year period. The inclusion of LUC (adding LUC to the model forcing as in TRENDY S3; Supplementary Fig. 5) changed both the patterns of the spatial variability of NBP (Fig. 1b; individual model results in Supplementary Fig. 6) as well as the sign of mean annual NBP from a large sink to a weak source for the period 1980–2009; flux changed from −0.18 ± 0.09 Pg C yr⁻¹ in the TRENDY S2 (average ± 1σ as model-by-model variability) to 0.09 ± 0.12 Pg C yr⁻¹ in the TRENDY S3. This result confirms that the LUC emissions are a key factor in NBP estimation for Southeast Asia, as its contribution to NBP is large, so much as to cancel the CO₂ uptake due to the effect of CO₂ fertilization.

The decadal shifts of net CO₂ flux and attributions. The inter-decadal mean NBP estimates from the TRENDY S3, atmospheric CO₂ inversions and Δbiomass yield a consistent pattern of decadal variability, indicating that an increased net source from the 1980s to the 1990s is largely decreased in the 2000s (Fig. 1c; individual model results in Supplementary Fig. 7). By isolating the contributions of the effects from CO₂ fertilization, climate and LUC to NBP using the TRENDY model simulations (Methods), we found that the shift towards a stronger net source from the 1980s to the 1990s is primarily attributable to the intensifying LUC (Fig. 1d; individual model results in Supplementary Fig. 8a), which increased the net source from 0.21 ± 0.11 Pg C yr⁻¹ (the 1980s) to 0.31 ± 0.13 Pg C yr⁻¹ (the 1990s). In contrast, a reduced net source (i.e. stronger sink) from the 1990s to the 2000s is attributed to the effects of CO₂ fertilization and climate (Fig. 1d; Supplementary Fig. 8b, c), with the former inducing a change from −0.23 ± 0.08 Pg C yr⁻¹ (the 1990s) to −0.28 ± 0.09 Pg C yr⁻¹ (the 2000s), and the latter from 0.09 ± 0.11 Pg C yr⁻¹ (the 1990s) to 0.001 ± 0.11 Pg C yr⁻¹ (the 2000s).

We examine the robustness of these decadal shifts by applying non-parametric trend tests to the periods 1980–1999 and 1990–2009 (Mann–Kendall and Theil slope tests; Methods). Using the NBP estimates including individual TRENDY models, we found that trends of increasing CO₂ uptake for the period 1990–2009 tend to be more statistically significant (p < 0.05) than those of increasing CO₂ release for the period 1980–1999 (Fig. 2a). Further analysis of the individual TRENDY models shows statistically significant trends of increasing CO₂ release due to the LUC effect for the period 1980–1999 and of increasing CO₂ uptake in response to the CO₂ fertilization and climate effects for the period 1990–2009 (Fig. 2b, c). This multi-model trend analysis suggests that the decadal NBP shift from the 1990s to 2000s is more robust than that from the 1980s to 1999s, which means that the CO₂ fertilization and climate conditions in the 2000s are more influential to NBP than the enhanced LUC activities in the 1990s, distinguishing the 2000s from previous decades. It is reasonable to expect that the CO₂ fertilization is partly responsible for the decadal NBP shift from the 1990s to 2000s because atmospheric CO₂ is the main factor driving NBP towards a net sink via promoting the photosynthetic carbon fixation. The increased CO₂ fertilization effect in the 2000s coincides with higher CO₂ concentrations in the 2000s (379 ppm) than those in the 1980s (346 ppm) and the 1990s (361 ppm), decadal averages based on flask sampling data at the Mauna Loa Observatory: Data—NOAA Earth System Research Laboratory, https://www.esrl.noaa.gov/gmd/ccgg/trends/data.html). As for the climate effect, a net source in the 1980s and 1990s makes a transition to carbon neutral in the 2000s (Fig. 1d), implying a climate favourable for CO₂ uptake in the 2000s.

Weak phase of ENSO in the 2000s. In order to elucidate the climate effect on NBP in the 2000s, we have analysed mean annual NBP (i.e. the TRENDY S3, atmospheric CO₂ inversion
Fig. 1 Interannual and decadal variability of net CO₂ flux in Southeast Asia for 1980–2009. a Interannual variability of ensemble averaged NBP from the TRENDY (grey: TRENDY S2; orange: TRENDY S3) and atmospheric CO₂ inversions (cyan) for the period 1980–2009, and annual biomass change (dashed green line: Δbiomass) for the period 1994–2009. Shading for the TRENDY and atmospheric CO₂ inversions represents 1σ variation among models. A top-right panel shows correlation coefficients (r) between interannual variability of the three NBP estimates for the overlapping periods (1980–2009 for the TRENDY and atmospheric CO₂ inversions; 1994–2009 for the TRENDY and Δbiomass, and for the atmospheric CO₂ inversions and Δbiomass) and statistical significance is indicated by **p < 0.01. Negative values in NBP represent a net sink, and positive values a net source. b Spatial variability of mean annual NBP from the TRENDY (seven model ensemble average) for the period 1980–2009. Results are shown for the three simulations: forced with varying CO₂ only (left: TRENDY S1); varying CO₂ and climate (middle: TRENDY S2); and varying CO₂, climate and LUC (right: TRENDY S3). Bar graphs represent mean annual NBP by the TRENDY simulations (grey: TRENDY S1 and S2; orange: TRENDY S3) for the period 1980–2009 with error bars representing 1σ variation among models. c Decadal NBP budgets from the TRENDY (grey: TRENDY S2; orange: TRENDY S3) and atmospheric CO₂ inversions (cyan) for the 1980s, 1990s and 2000s, with error bars representing 1σ variation among models. Decadal budgets from annual biomass changes are shown with dashed horizontal lines for the 1990s (1994–1999) and 2000s (2000–2009). d Decadal variability of the attributing factors to NBP from the TRENDY (crimson: the CO₂ fertilization effect, green: the climate effect and white: the LUC effect) with error bars representing 1σ variation among models.
and Δbiomass) and components of NBP from the TRENDY model simulations: LUC emissions, fire emissions and plant CO₂ exchange (difference between CO₂ uptake by photosynthesis and release by plant respiration and decomposition), in relation to variability in the Multivariate ENSO Index (MEI: NOAA ESRL, http://www.esrl.noaa.gov/psd/data/correlation/mei.data). CO₂ fluxes between the years that seasonal MEI indicates a moderate-to-strong tendency towards El Niño (hereafter, intense El Niño years; Methods) and the rest of years are compared for the three decades. In the 1980s and 1990s, which are characterized by the occurrence of strong and persistent El Niño events (e.g. 1982/1983, 1987/1988, and 1997/1998; Fig. 3), all the three estimates of NBP show a clear tendency towards a net loss of CO₂ from the land in the intense El Niño years compared with the rest of years, with differences amounting to 0.13–0.14 and 0.14–0.26 Pg C yr⁻¹, respectively (Fig. 4a, b). In the 2000s, however, no intense El Niño is indicated by MEI (Fig. 3), resulting in a near-neutral carbon balance (Fig. 4c). This result suggests that, in addition to enhanced growth from the CO₂ fertilization, the absence of intense El Niño events is one of the primary causes for the reduced net emission of Southeast Asia in the 2000s.

The investigation of the intense El Niño years revealed that the strength of ENSO largely affects plant CO₂ exchange and fire emissions, taking into account peat and deforestation fires (results from Community Land Model (CLM); Methods). In the 1980s and 1990s, CO₂ uptake by plants notably shifted towards a net emission by 0.07–0.09 Pg C yr⁻¹ in the intense El Niño years when compared with the remaining years (Fig. 4a, b). Likewise, fire emissions by CLM show larger emissions by 0.11 Pg C yr⁻¹ in the intense El Niño years than the rest of years in the 1980s and by 0.14 Pg C yr⁻¹ in the 1990s. A caveat is that the strength of ENSO had negligible influence on the magnitude of fire emissions simulated without considering the contribution from peat and deforestation fires (an ensemble average excluding CLM). In contrast with plant CO₂ exchange and fire emissions, the magnitude of LUC emissions was nearly unchanged regardless of El Niño conditions. This may be expected, because carbon removal by deforestation, and wood and crop harvesting is

**Fig. 2** Trends in net CO₂ flux and its components for the past 30 years. Results of two trend tests (Mann-Kendall and Theil slope tests) on a, net CO₂ flux (NBP) from the TRENDY S3 (seven models: blue circles for 1980–1999 and red circles for 1990–2009, and ensemble average: a cyan upper triangle for 1980–1999 and an orange upper triangle for 1990–2009) are shown along with those on the atmospheric CO₂ inversions (ensemble average: a cyan lower triangle for 1980–1999 and an orange lower triangle for 1990–2009) and Δbiomass (a green square for 1994–2009). The trend tests on attributing factors to NBP are illustrated for b, the LUC effect and c, CO₂ fertilization-climate effects. Size of markers indicates statistical significance of trends: larger (p < 0.05) and smaller (p ≥ 0.05)
triggered by human activities, which do not directly respond to climate conditions (with the possible exception of fire following deforestation).

**Climate sensitivity of CO2 fluxes in Southeast Asia.** Temperature and water availability to plants (indicated by Standardized Precipitation Index: SPI) explained most variability in plant CO2 exchange in Southeast Asia. Among the main meteorological inputs for the TRENDY models (i.e. temperature, precipitation and short-wave radiation) and three types of SPI (based on 3-, 6-, and 9-month moving windows of rainfall accumulation, see Methods), temperature and SPIs are the variables that show a significant association with seasonal variability in plant CO2 exchange; a positive relationship in the former and a negative relationship in the later (Fig. 5a; interannual variability of individual variables in Supplementary Fig. 9). The strong relationships found with SPIs suggest that cumulative precipitation over preceding months is more effective to plant CO2 exchange than simple monthly precipitation, and the empirically upscaled eddy flux data (the FLUXCOM global carbon flux dataset; Methods) confirm these relationships (Fig. 5a). Furthermore, both TRENDY and FLUXCOM data indicate that CO2 uptake by plants decreased due to reduced photosynthesis (Gross Primary生产力) during periods with large increases in temperature and decreases in water availability associated with El Niño (Fig. 5b, c, and Supplementary Fig. 10). The smaller spread in temperature and SPI anomalies during 2000–2009, compared to the 1980–1999 period, implies that weak ENSO variability during the 2000s sustained the high carbon assimilation capacity of plants in Southeast Asia.

In addition to CO2 fluxes from plant ecosystems, our results emphasize fire emissions as an apparent contributor to net CO2 flux resulting from severe droughts. Particularly, contrasting fire emissions between the intense El Niño years and other years highlights the importance of peat and deforestation fire emissions in the carbon balance of Southeast Asia. The occurrence of strong fire emissions indicated by CLM is found in the years of negative precipitation anomalies corresponding to the intense El Niño years (Supplementary Fig. 11), which is consistent with fire emissions estimated by the Global Fire Emissions Database version 4.1s (GFED4.1s) and reports from remote-sensing-based and model-based studies. However, even with the emissions from peat and deforestation fires, CO2 emissions in the intense El Niño years are still considered as an underestimate of the reality because the TRENDY models, including CLM, do not consider emissions from peat oxidative decompositions following peat fire events, which could promote even larger CO2 emissions during El Niño events.

**Discussion**

Our results indicate that a synthesis of multiple approaches (i.e. top-down, bottom-up and remote-sensing-based approaches) is an effective method to constrain regional carbon balance and to elucidate causes for major changes in a projection of CO2 fluxes.

The implementation of LUC processes to biosphere models is required to estimate net CO2 flux in Southeast Asia, as indicated by agreement in the interannual and decadal variability of net CO2 flux between the biosphere models, atmospheric CO2 inversions and ΔBiomass, which has not addressed in the tropical regions before this study. Our analysis provides new insights for reconciling the top-down and bottom-up regional fluxes over the tropical regions, where wide gaps were reported in the previous IPCC assessment, and also serves as a useful precedent for future regional carbon balance assessments by REgional Carbon Cycle Assessment and Processes (RECCAP).

The strength of ENSO exerts a strong control on the carbon balance of Southeast Asia, causing the unique variability in the decade of 2000s. Along with the recent enhancement of CO2 fertilization effect, we showed that a milder, less variable, climate due to the absence of intense El Niño events contributed to the reduction of CO2 emissions between the 1990s and 2000s. A recent synthesis of regional emissions of the greenhouse gases (GHG) indicates that Southeast Asia is characterized by the largest emissions not only of CO2 from ecosystems but also of agricultural methane and nitrous oxide among the world regions. Our results suggest that the land response to weak natural climate variability could serve as a strong mitigation to CO2 emissions, even for the world largest ecosystem GHG emitter.

One aspect not addressed here is the role of La Niña (the opposite phase to El Niño) in the decadal NBP shift. La Niña can also induce a milder climate condition, which in turn occasionally enhances regional CO2 uptake. We emphasize the significance of El Niño events in the Southeast Asian carbon balance because of a difference in the impact on tropical CO2 fluxes between the two climate phenomena. As illustrated in Fig. 6a, b, linear relationships between seasonal MEI and NBP anomaly (based on the ensembles of the TRENDY models and atmospheric CO2 inversions; individual model results in Supplementary Figs. 12, 13 and Supplementary Table 4) demonstrate that moderate and strong El Niño events (i.e. MEI >-1) in the 1980s and 1990s are directly related to a large net source by the land
one of the strongest events during the past 30 years (Fig. 3). However, its contribution to the decadal carbon balance shift in the 2000s is incomparable to that from the absence of moderate and strong El Niño events (Fig. 6e). Given the response of the land biosphere to El Niño events, we suggest that the dominant driver of the NBP shift in the 2000s is the absence of moderate and strong El Niño events, with La Niña events playing a lesser role.

The absence of moderate-to-strong El Niño events in the 2000s was a unique case where a natural climate cycle acted to mitigate CO₂ emissions in Southeast Asia, albeit only for a limited period. Our estimates of NBP for the period 2010–2016 (see Methods) indicate net CO₂ emissions comparable to those in the 1980s and 1990s during El Niño events after 2009 such as the 2015/2016 El Niño (Fig. 8d). An assessment of climate model simulations suggest that surface ocean warming over the eastern equatorial Pacific may lead to an increase in the frequency of intense El Niño events in the future⁵⁰, reducing the likelihood that natural climate cycles offer mitigation of CO₂ emissions, and therefore leading to stronger positive carbon-climate feedback. In the long term, national-level efforts for forest conservation and ecosystem management, such as the Reduce Emissions from Deforestation and forest Degradation (REDD+) project, are critical to protecting the current CO₂ sink capacity of the Southeast Asia⁴¹, ⁴².

**Methods**

**Sign convention for net CO₂ flux.** In this study, we chose the sign convention for net CO₂ flux that is commonly used in top-down analyses: the negative sign (−) for a net sink and the positive sign (+) for a net source. This sign convention is consistently used throughout the analysis regardless of the TRENDY models, atmospheric CO₂ inversions and annual biomass change, and it is also applied not only to NBP but also to plant CO₂ exchange. It should be noted that a common sign convention for these variables in bottom-up analyses are opposite to this study⁴³.

**Bottom-up net CO₂ flux.** Outputs from the TRENDY model intercomparison project version 2 (TRENDY)⁴⁴, ⁴⁵ were used to calculate the bottom-up net CO₂ flux. Simulations of the biosphere models that participated in the TRENDY were prepared with a consistent forcing dataset: (1) atmospheric CO₂ concentration for 1860–2012 based on ice-core measurements and stationary observations from NOAA, (2) driving dataset for 1901–2012 based on a merging between Climate Research Unit (CRU) TS3.2 0.5° × 0.5° monthly climate data⁴⁶ and National Centers for Environmental Prediction (NCEP) and National Center for Atmospheric Research Reanalysis2 2.5° × 2.5° 6-hourly climate data⁴⁷, and (3) 0.5° × 0.5° gridded annual LUC dataset for 1860–2012⁴⁸.

The TRENDY models were simulated under three protocols: a protocol that considers variability in atmospheric CO₂ (TRENDY S1); a protocol that considers variability in CO₂ and climate (TRENDY S2); and a protocol that considers variability in CO₂, climate and historical LUC (TRENDY S3). For each protocol, the models first established an equilibrium state of carbon balance by a spin-up run, which is forced with the 1860 CO₂ concentration (287.14 ppm), recycling climate mean and variability from the early decades of the twentieth century (i.e. 1901–1920) and constant 1860 crops and pasture distribution. Then, simulations for two transient periods were conducted. For the period 1861–1990, the models were forced with varying CO₂ concentration and recycling climate (as in spin-up) in the TRENDY S1 and S2, and in addition varying LUC in the TRENDY S3. After the 1861–1900 period, the models were consecutively run for the 1901–2012 period with varying CO₂ concentration and recycling spin-up climate in the S1, varying CO₂ concentration and climate in the TRENDY S2 and S3, and varying LUC in the TRENDY S3. A summary of the forcing data configuration for these simulations is shown in Supplementary Fig. 2.

Among the participating models, we selected seven models that satisfy necessary criteria for the analyses such that models provide monthly NBP outputs for all three simulations and an explicit output of annual LUC emissions. Specifically, they are the CLM version 4.5⁴⁹, Integrated Science Assessment Model (ISAM), Joint UK Land Environment Simulator (JULES) version 3.2⁵⁰, Lund-Potsdam-Jena DGVM wsl (LPJ)⁵¹, LPJ-GUESS⁵², Orchidee-CN (O-CN)⁵³ and Vegetation Integrative Simulator for Trace gases (VISIT)⁵⁴. Spatial resolutions of the TRENDY model outputs are not consistent among these seven models; fine resolutions were used in some models and coarse resolution in others (Supplementary Table 1). For models whose outputs were submitted with coarse spatial resolution, we rescaled grids so that all seven model outputs have the consistent spatial resolution of 0.5° × 0.5°.
**LUC emissions.** The LUC forcing for the TRENDY models provides gridded historical transitions of land use, based on annual changes of cropland and pastureland area, and wood harvest from the UN Food and Agricultural Organization (FAO) national statistics. Historical changes in annual area of cropland and pastureland were determined by the HistorY Database of the global Environment (HYDE) model version 3.146, which takes the FAO national statistics for cropland and pastureland as the main input source, and spatializes the statistics at the spatial resolution of $5' \times 5'$ using allocation algorithms and time-dependent weighting.

---

**Fig. 5** Climate sensitivity of seasonal plant CO2 exchange by the biosphere models and empirical upscaling. **a** Correlation coefficients ($r$) in relationship between seasonal anomalies of plant CO2 exchange induced by the climate effect (TRENDY S2–S1) and climate variables (temperature, precipitation, short-wave radiation and three types of SPIs) for the period 1980–2009. Results are shown for seven individual TRENDY models and the ensemble of the TRENDY and FLUXCOM data. Statistical significances are indicated by ** $p < 0.01$ and * $p < 0.05$. Relationships between seasonal anomalies of plant CO2 exchange and temperature, and SPI–6 months for the periods 1980–1999 and 2000–2009, for **b** the TRENDY and **c** FLUXCOM. All relationships are shown along with the 95% confident ellipses and linear regressions. Square markers indicate data corresponding to the intense El Niño years and circle markers to the rest of years. All relationships with SPI are calculated as SPI leads plant CO2 exchange by 3 months.
maps based on global historical population density, soil suitability, distance to rivers, lakes, slopes and biome distributions. The HYDE cropland and pastureland status were then combined with the wood harvest status based on the FAO national wood harvest statistics in order to extend global land use patterns, including transitions of cropland, pastureland, primary and secondary lands (an extended version of HYDE). First, the gridded cropland and pastureland area from the HYDE model was rescaled from $5 \times 5'$ to $0.5 \times 0.5'$ resolution, and at the same time, fractions occupied by cropland and pastureland was calculated for each rescaled grid cell. By subtracting fractions of cropland and pastureland (and water/ice if any) from each grid cell, fractions of natural vegetation (primary or secondary lands) was also determined for each grid cell. Distinction between primary and secondary lands (previously disturbed by human activities or not) and fractions of these land types occupied in each grid cell were determined based on the spatialized FAO wood harvest data with empirically estimated biomass density maps produced.
Satellite-based annual biomass change. We used the satellite-based gridded (0.25° × 0.25°) global aboveground biomass covering the period 1993–2012 (Global Aboveground Biomass Carbon version 1.0) to estimate the annual biomass changes (Abiomass)52. The global aboveground biomass is estimated based on harmonized vegetation optical depth (VOD) data derived from multiple passive microwave satellite sensors, including Special Sensor Microwave Imager, Advanced Microwave Scanning Radiometer for Earth Observation System, FengYun-3B Microwave Radiometer Imager and Windsat. The obtained VOD data are converted to aboveground biomasses via an empirical relationship between the VOD data and satellite-based spatial map of aboveground biomass for tropical regions53. The global distribution of total biologically active carbon is estimated by applying empirical equations, obtained from literatures for different forests and non-forest vegetation, to the aboveground biomass data. We calculated Abiomass by simply taking differences between the total biomass data of current and preceding years for each grid cell for the period 1994–2009, and aggregated the grid data for the Southeast Asia region.

Empirical upscaling of eddy flux data. We used the empirical upscaling of eddy flux observations to compare the climate sensitivity of CO2 fluxes by the TRENDY model simulations. The FLUXCOM global carbon flux dataset66, 67 is an ensemble of daily carbon fluxes estimated from machine learning algorithms (Random Forest66, Artificial Neural Network67 and Multivariate Adaptive Regression Splines68) trained with 224 eddy flux tower observations and climate data. The training of the three machine learning algorithms were conducted separately for GPP and RE with explanatory variables with spatial (e.g. plant functional type), spatial and seasonal (e.g. mean seasonal variations of land surface temperature, vegetation index) and spatial, seasonal and interannual (e.g. climate variables) variations were used. Using the trained machine learning algorithms and spatial input data, MOGIS product (with no interannual variations) and climate variables (with interannual variations) from CRUNCEPv6 (http://esgf.extra.cea.fr/thredds/catalog/store/p529view/cruncep/V6_1901_2014/catalog.html), spatio-temporal GPP and RE were forced with grids of 0.5° × 0.5° spatial resolution and daily time step for the period 1980–2013. Subsequently, spatiotemporal variability of GPP and RE exchange was calculated by mass balance from the upcaled GPP and RE products (i.e. GPP-RE).

In the analysis, we compared CO2 fluxes induced by the climate effect (TRENDY S2-S1) against the FLUXCOM because CO2 fluxes from the FLUXCOM are results of upsampling natural vegetation fluxes, which make ideal products to evaluate regional climate sensitivity of CO2 fluxes from plants. It should be noted that the FLUXCOM data do not account for CO2 losses from LUC because no predictor variables about LUC were used in its estimation.

Tests for significance of decadal trend of net CO2 flux. We applied the two commonly used non-parametric tests for the slope in linear regression, Mann–Kendall and Theil slope tests53, 54, for the detection of robust trends in NBP and its attributing factors (i.e. the CO2 fertilization, climate and LUC effects). Mann–Kendall test takes a list of data ordered in time and calculates test statistics (i.e. Mann–Kendall Z), in which takes the number of positive and negative differences between paired data and normalizes it by a square root of its variance. Theil slope calculates the slope of linear regression as the median of all slopes between paired values of data in a given sequence.

Tests were conducted for the periods 1980–1999 and 1990–2009 to multiple estimates of annual NBP: (1) an ensemble average of the atmospheric CO2 (WDCGG), Comprehensive Observation Network for TRace gases by AirLiner (CONTRAIL) and GLOBALVIEW with prior fluxes (land and ocean fluxes, fire emissions and CO2 emissions of the land use change), (2) for the past-1960 period (prior to availability of the FAO statistics) is mainly induced by historical population density. Decadal changes in fractions occupied by cropland, pastureland, primary and secondary lands for Southeast Asia by the extended HYDE data are shown in Supplementary Fig. 3.

LUC dependence on the TRENDY models account for the net effect of LUC on terrestrial carbon cycle including instantaneous and legacy emissions. In each model, forest area changes (deforestation or afforestation) in response to annual changes in cropland and pastureland area predefined by the forcing data, resulting in a relative forest area changes due to LUC among the models (minor differences occur due to dynamic vegetation). However, specific schemes for LUC modelling are left to the discretion of each modelling group, which means that fundamental assumptions and levels of complexity in LUC modelling vary among the models: for instance, distinction of primary and secondary forests, implementation of wood and crop harvests, consideration of residue carbon after deforestation and turnover rates of a product pool (Supplementary Table 1). These different schemes of LUC modelling induce non-negligible variations in estimates of LUC emissions upon close examination. Thus, application of LUC emissions by the TRENDY is limited to long-term and regional-scale analyses, which aim to capture strong signals or trend shifts of CO2 uptake or release. Further details of the LUC modelling in the TRENDY are provided in ref. 35, and a comprehensive comparison of LUC emissions by the TRENDY and other independent assessments in Asia is conducted in ref. 49.
inversions, (2) an ensemble average and (3) individual outputs of the seven models from the TRENDY, and (4) Abiomass for the period 1994–2009 (Fig. 2a). For trends of the attributing factors to NBP, we take the combined effect of CO2 fertilization and climate (NBP from the TRENDY S2) and the LUC effect (difference in NBP between the TRENDY S3 and S2) from the TRENDY model simulations, and applied the tests to an ensemble average and seven individual model outputs (Figs. 2b, c).

Condition for intense El Niño years. We categorized the conditions for El Niño and La Niña years based on seasonal variability in the MEI obtained from US National Oceanic and Atmospheric Administration (NOAA: http://www.esrl.noaa.gov/psd/data/). First, a simple categorization is conducted under a rule that seasonal MEI (i.e. 3-month averages, JFM, AMJ, JAS andOND) falls within the predefined range at least one season of year, such that MEI < –1 (strong/moderate La Niña), –1 ≤ MEI ≤ –1 (weak ENSO), 1 < MEI ≤ 2 (moderate El Niño) and MEI > 2 (strong El Niño). To characterize the intensity of El Niño events, however, not only the magnitude but also the duration of seasonal MEI needs to be considered. Therefore, we then defined Intense El Niño years, which refer to years that seasonal MEI values falls with MEI >1 (moderate or strong seasonal MEI and seasonal NBP anomaly (i.e. 3-month averages, JFM, AMJ, JAS shorter periods (e.g. 1 to 3 months) indicates changes in land surface water and higher probability of wet events and negative values indicating the opposite.

Then, the data are extracted from the TRENDY S3 and atmospheric CO2 inversion data from 2010 to 2012 simulations, and applied the tests to an ensemble average and seven individual models. Global Aboveground Biomass Carbon version 4.12. Carlson, K. M. et al. Committed carbon emissions, deforestation, and community land conversion from oil palm plantation expansion in West Kalimantan, Indonesia. Proc. Natl. Acad. Sci. USA 109, 7559–7564 (2012). Lewis, S. L. et al. Increasing carbon storage in intact African tropical forests. Nature 457, 1003–1006 (2009). Bruijnzeel, R. J. W. et al. Long-term decline of the Amazon carbon sink. Nature 519, 344–348 (2015). Ciais, P. et al. in Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds Stocker, T. F. et al.) Ch. 6 (Cambridge University Press, Cambridge and New York, 2013). Schimel, D., Stephens, B. B. & Fisher, J. B. Effect of increasing CO2 on the terrestrial carbon cycle. Proc. Natl. Acad. Sci. USA 112, 436–441 (2014). Siegert, F. et al. Increased damage from fires in logged forests during droughts caused by El Niño. Nature 414, 437–440 (2001). van der Werf, G. R. et al. Climate regulation of fire emissions and deforestation in equatorial Asia. Proc. Natl. Acad. Sci. USA 105, 20350–20355 (2008). Giglio, L. et al. Analysis of daily, monthly, and annual burned area using the fourth-generation global fire emissions database (GFED4). J. Geophys. Res. Biogeosci. 118, 317–328 (2013). Field, R. D. & Shen, S. S. P. Predictability of carbon emissions from biomass burning in Indonesia from 1997 to 2006. J. Geophys. Res. Biogeosci. 113, G04024 (2008). van der Werf, G. R. et al. Carbon emissions from fires in tropical and subtropical ecosystems. Glob. Change Biol. 9, 547–562 (2003). Hirano, T. et al. Carbon dioxide emissions through oxidative peat decomposition on a burnt tropical peatland. Glob. Change Biol. 20, 555–565 (2014). Ezing, I. G., Rayner, P. J. & Ciais, P. Carbon cycle uncertainty in Regional Carbon Cycle Assessment and Processes (RECCAP). Biogeosciences 10, 2889–2904 (2012). Keenan, T. F. et al. Recent pause in the growth rate of atmospheric CO2 due to enhanced terrestrial carbon uptake. Nat. Commun. 7, 13428 (2016). Tian, H. et al. The terrestrial biosphere as a net source of greenhouse gases to the atmosphere. Nature 531, 225–228 (2016). Poulter, B. et al. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. Nature 509, 600–603 (2014). Ahlström, A. et al. Carbon cycle. The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink. Science 348, 895–899 (2015). Bastos, A., Running, S. W., Gouveia, C. & Trigo, R. M. The global NPP dependence on ENSO: La Niña and the extraordinary year of 2011. J. Geophys. Res. Biogeosci. 118, 1247–1255 (2013). Chang, J. et al. Benchmarking carbon fluxes of the ISIMIP2a biome models. Environ. Res. Lett. 12, 045002 (2017). Cai, W. et al. Increasing frequency of extreme El Niño events due to greenhouse warming. Nature 484, 111–116 (2014). Ziegler, A. D. et al. Carbon outcomes of major land-cover transitions in SE Asia: great uncertainties and REDD+ policy implications. Glob. Change Biol. 18, 3087–3099 (2012). Zarin, D. J. et al. Can carbon emissions from tropical deforestation drop by 50% in 5 years? Glob. Change Biol. 22, 1336–1347 (2016). Chapin, F. S. et al. Reconciling carbon cycle concepts, terminology, and methods. Ecosystems 9, 1041 (2006).
34. Sitch, S. et al. Recent trends and drivers of regional sources and sinks of carbon dioxide. *Biogeosciences* **12**, 653–679 (2015).

35. Le Quéré, C. et al. Global carbon budget 2015. *Earth Syst. Sci. Data* **7**, 349–396 (2015).

36. Harris, I. et al. Updated high-resolution grids of monthly climatic observations—the CRU TS3.10 Dataset. *Int. J. Climatol.* **34**, 623–642 (2014).

37. Kistler, R. et al. The NCEP–NCAR 50-year reanalysis: monthly means CD-ROM and documentation. *Bull. Amer. Meteor. Soc.* **82**, 247–267 (2001).

38. Hurtt, G. C. et al. Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Clim. Change* **109**, 117–161 (2011).

39. Lawrence, D. M. et al. Parameterization improvements and functional and structural advances in version 4 of the community land model. *J. Adv. Model. Earth Syst.* **3**, M03001 (2011).

40. Jain, A. K. et al. CO₂ emissions from land-use change affected more by nitrogen cycle, than by the choice of land-cover data. *Glob. Change Biol.* **19**, 2893–2906 (2013).

41. Clark, D. B. et al. The Joint UK Land Environment Simulator (JULES), model description—Part 2: carbon fluxes and vegetation dynamics. *Geosci. Model Dev.* **4**, 701–722 (2011).

42. Sitch, S. et al. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic vegetation model. *Glob. Change Biol.* **9**, 161–185 (2003).

43. Smith, B., Prentice, I. C. & Sykes, M. T. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Glob. Ecol. Biogeogr.* **10**, 621–637 (2001).

44. Zaehle, S. & Friend, A. D. Carbon and nitrogen cycle dynamics in the O-CN land surface model, I: Model description, site-scale evaluation and sensitivity to parameter estimates. *Glob. Biogeochem. Cycle* **24**, GB1005 (2010).

45. Ito, A. Evaluation of the impacts of deforestation by tropical cyclones on a Japanese forest's carbon budget using flux data and a process-based model. *J. Geophys. Res.* **115**, F04013 (2010).

46. Klein Goldewijk, K. et al. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Glob. Ecol. Biogeogr.* **20**, 73–86 (2011).

47. Hurtt, G. C. et al. Projecting the future of the US carbon sink. *Proc. Natl. Acad. Sci. USA* **99**, 1389–1394 (2002).

48. Jain, A. K., Meiyappan, P., & Richardson, T. in *Earth System Modeling* (eds Brown, D. G. et al.) (Cambridge University Press, Cambridge and New York, 2013).

49. Calle, L. et al. Regional carbon and nitrogen cycle, than by the choice of land-cover data. *Glob. Change Biol.* **9**, 161–185 (2003).

50. Smith, B., Prentice, I. C. & Sykes, M. T. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Glob. Ecol. Biogeogr.* **10**, 621–637 (2001).

51. Ito, A. Modelling of carbon cycle and fire regime in an east Siberian larch forest. *Ecol. Model.* **187**, 121–139 (2005).

52. Krinner, G. et al. A dynamic global vegetation model for studies of the coupled atmosphere–biosphere system. *Glob. Biogeochem. Cycle* **19**, GB1015 (2005).

53. Li, F. et al. Quantifying the role of fire in the Earth system—Part 1: improved global fire modeling in the Community Earth System Model (CESM1). *Biogeosciences* **10**, 2293–2314 (2013).

54. Olson, D. M. et al. Terrestrial ecoregions of the world a new map of life on earth. * Bioscience* **51**, 933–938 (2001).

55. Hurtt, G. C. et al. The upscaling of land-use history: three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands. *Glob. Change Biol.* **12**, 1208–1229 (2006).

56. van der Werf, G. R. et al. Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009). *Atmos. Chem. Phys.* **10**, 11707–11735 (2010).

57. Friedlingstein, P. et al. Climate-carbon cycle feedback analysis: results from the C4MIP model intercomparison. *J. Clim.* **19**, 3337–3353 (2006).

58. Fisher, J. B. et al. African tropical rainforest net carbon dioxide fluxes in the twentieth century. *Philos. Trans. R. Soc. Ser. B* **368**, 20120376 (2013).

59. Patra, P. K. et al. Carbon balance of South Asia constrained by passenger aircraft CO₂ measurements. *Atmos. Chem. Phys.* **11**, 4163–4175 (2011).

60. Rödenbeck, C. et al. CO₂ flux history 1982–2001 inferred from atmospheric data using a global inversion of atmospheric transport. *Atmos. Chem. Phys.* **3**, 1919–1964 (2003).

61. Maki, T. et al. New technique to analyse global distributions of CO₂ concentrations and fluxes from non-processed observational data. *Tellus B* **62**, 797–809 (2010).

62. Chevalier, F. et al. CO₂ surface fluxes at grid point scale estimated from a global 21 year reanalysis of atmospheric measurements. *J. Geophys. Res.* **115**, D21307 (2010).

63. Niwa, Y. et al. Imposing strong constraints on tropical terrestrial CO₂ fluxes using passenger aircraft based measurements. *J. Geophys. Res.* **117**, D11303 (2012).

64. Liu, Y. Y. et al. Recent reversal in loss of global terrestrial biomass. *Nat. Clim. Change* **5**, 470–474 (2015).

65. Saatchi, S. S. et al. Benchmark map of forest carbon stocks in tropical regions across three continents. *Proc. Natl. Acad. Sci. USA* **108**, 9899–9904 (2011).

66. Jung, M. et al. Compensatory water effects link yearly global land CO₂ sink changes to temperature. *Nature* **541**, 516–520 (2017).

67. Tramontana, G. et al. Predicting carbon and energy fluxes across global FLUXNET sites with regression algorithms. *Biogeosciences* **13**, 4291–4313 (2016).

68. Breiman, L. Random forests. *Mach. Learn.* **45**, 5–32 (2001).

69. Haykin, S. *Neural Networks: A Comprehensive Foundation* (Prentice Hall, Englewood Cliff, 1998).

70. Friedman, J. H. Multivariate adaptive regression splines. *Ann. Stat.* **19**, 1–67 (1991).

71. Kendall, M. G. *Rank Correlation Methods* 4th edn (Charles Griffin, London, 1975).

72. Theil, H. A rank-invariant method of linear and polynomial regression analysis I. *Ned. Akad. Wensch Proc.* **53**, 386–392 (1956).

73. Cormick, M. F., Thomason, L. W. & Trepte, C. R. Atmospheric effects of the Mt Pinatubo eruption. *Nature* **373**, 399–404 (1995).

74. Mercado, L. M. et al. Impact of changes in diffuse radiation on the global land carbon sink. *Nature* **458**, 1014 (2009).

75. Orlowsky, B. & Seneviratne, S. Elusive drought: uncertainty in observed trends and short- and long-term CMIP5 projections. *Hydrol. Earth Syst. Sci.* **17**, 1765–1781 (2013).

Acknowledgements

This research was supported by Environment Research and Technology Development Funds from the Ministry of the Environment of Japan (2-1401) and the Environmental Restoration and Conservation Agency (2-1701) and Asia-Pacific Network for Global Change Research (APN: grant#ARCP2011-11NMY-Patra/Canadell). We acknowledge Dr. Tomo’omi Kumagai for providing information about the current status of land use change in Southeast Asia and Mr. Yuji Yanagi for pre-processing the TRENDY model outputs for the analyses. This work is dedicated in memory of Dr. Rikié Suzuki who was the devoted leader of Department of Environmental Geochemical Cycle Research at the Japan Agency for Marine-Earth Science and Technology.

Author contributions

M.K. designed the analyses with support from K.I., P.K.P., J.G.C., B.P. and L.C. M.K. conducted the analyses, prepared figures and tables, and organized the manuscript. P.K.P., B.P., S.S., Y.Y.L., A.I.M.v.D., T.S., P.F., A.A., A.H., A.K.I., E.K., K.C., F.L., T.A.M.P., S.Z., A.W., F.C., T.M., T.N., Y.N. and C.R. contributed data to the analyses. K.I., P.K.P., J.G.C., B.P., S.S., L.C., Y.Y.L., A.I.M.v.D., T.S., F.L., F.C. and N.S. contributed to the writing of the manuscript.

Additional information

Supplementary Information accompanies this paper at https://doi.org/10.1038/s41467-018-03374-x.

Competing interests: The authors declare no competing interests.

Reprints and permission information is available online at http://npg.nature.com/reprintsandpermissions/

Publisher’s note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.