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Climate control of terrestrial carbon exchange across biomes and continents

Chuixiang Yi[1], Daniel Ricciuto[2], Runze Li[3], John Wolbeck[1], Xiyan Xu[1], Mats Nilsson[4], Luis Aires[5,117], John D Albertson[6,117], Christof Ammann[7,117], M Altaf Arain[8,117], Alessandro C de Araujo[9,117], Marc Aubinet[10,117], Mika Aurela[11,117], Zoltán Barcza[12,117], Alan Barr[13,117], Paul Berbigier[14,117], Jason Beringer[15,117], Christian Bernhofer[16,117], Andrew T Black[17,117], Paul V Bolstad[18,117], Fred C Bosveld[19,117], Mark S J Broadmeadow[20,117], Nina Buchmann[21,117], Sean P Burns[22,117], Pierre Cellier[23,117], Jingming Chen[24,117], Jiquan Chen[25,117], Philippe Ciais[26,117], Robert Clement[27,117], Bruce D Cook[28,117], Peter S Curtis[29,117], D Bryan Dail[30,117], Ebba Dellwik[31,117], Nicolas Delpierre[32,117], Ankur R Desai[33,117], Sabina Dore[34,117], Danilo Dragoni[35,117], Bert G Drake[36,117], Eric Dufrêne[32,117], Allison Dunn[37,117], Jan Elbers[38,117], Werner Eugster[21,117], Matthias Falk[39,117], Christian Feigenwinter[40,117], Lawrence B Flanagan[41,117], Thomas Foken[42,117], John Frank[43,117], Juerg Fuhrer[7,117], Damiano Gianelle[44,117], Allen Goldstein[45,117], Mike Goulden[46,117], Andre Granier[47,117], Thomas Grünwald[48,117], Lianhong Gu[2,117], Haiqiang Guo[49,117], Albin Hammerle[50,117], Shijie Han[51,117], Niall P Hanan[52,117], László Haszpra[53,117], Bernard Heinesch[10,117], Carole Helfter[54,117], Dimmie Hendriks[55,117], Lindsay B Hutley[56,117], Andreas Ibrom[57,117], Cor Jacobs[38,117], Torbjörn Johansson[58,117], Marjan Jongen[59,117], Gabriel Katul[60,117], Gerard Kiely[61,117], Katja Klumpp[62,117], Alexander Knohl[21,117], Thomas Kolb[34,117], Werner L Kutsch[63,117], Peter Lafleur[64,117], Tuomas Laurila[11,117], Ray Leuning[65,117], Anders Lindroth[58,117], Heping Liu[66,117], Benjamin Loubet[23,117], Giovanni Manca[67,117], Michal Marek[68,117], Hank A Margolis[69,117], Timothy A Martin[70,117], William J Massman[43,117], Roser Matamala[71,117], Giorgio Matteucci[72,117], Harry McCaughey[73,117], Lutz Merbold[74,117], Tilden Meyers[75,117], Mirco Migliavacca[76,117], Franco Miglietta[77,117], Laurent Misson,[78,117,118], Meelis Mölder[58,117], John Moncrieff[27,117], Russell K Monson[79,117], Leonardo Montagnani[80,81,117], Mario Montes-Helu[34,117], Eddy Moors[82,117], Christine Moureaux[10,83,117], Mukufute M Mukelabai[84,117], J William Munger[85,117], May Myklebust[65,117], Zoltán Nagy[86,117], Asko Noormets[87,117], Walter Oechel[88,117], Ram Oren[89,117], Stephen G Pallardy[90,117], Kyaw Tha Paw U[39,117], João S Pereira[59,117], Kim Pilegaard[57,117], Krisztina Pintér[86,117], Casimiro Pio[91,117], Gabriel Pita[92,117], Thomas L Powell[93,117], Serge Rambal[94,117], James T Randerson[46,117], Celso von Randow[95,117], Corinna Rebmann[64,117], Janne Rinne[96,117], Federica Rossi[77,117], Nigel Roulet[97,117], Ronald J Ryel[98,117], Jorgen Sagerfors[4,117], Nobuko Saigusa[99,117], María José Sanz[100,117], Giuseppe-Scarascia Mugnozza[101,117], Hans Peter Schmid[102,117], Guenther Seufert[103,117], Mario Siqueira[89,117], Jean-François Soussana[62,117], Gregory Starr[104,117], Mark A Sutton[105,117], John Tenhunen[106,117], Zoltán Tuba,[86,117,118], Juha-Pekka Tuovinen[11,117], Riccardo Valentini[107,117], Christoph S Vogel[108,117], Jingxin Wang[109,117], Shaoqiang Wang[110,117], Weiguo Wang[111,117], Lisa R Welp[112,117], Xuefa Wen[110,117], Sonia Wharton[113,117], Matthew Wilkinson[20,117], Christopher A Williams[114,117],

Georg Wohlfahrt[50,117], Susumu Yamamoto[115,117], Guirui Yu[110,117], Roberto Zampedri[44,117], Bin Zhao[49,117] and Xinquan Zhao[116,117]

[1] School of Earth and Environmental Sciences, Queens College, City University of New York, NY 11367, USA
[2] Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA
[3] Department of Statistics, Pennsylvania State University, University Park, PA 16802, USA
[4] Department of Forest Ecology, The Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden
[5] CESAM and Department of Environmental Engineering, School of Technology and Management, Polytechnic Institute of Leiria, Portugal
[6] Department of Civil and Environmental Engineering, Duke University, Durham, NC 22708-0287, USA
[7] Federal Research Station Agroscope Reckenholz-Tänikon, Reckenholzstrasse 191, 8046 Zürich, Switzerland
[8] School of Geography and Earth Sciences, McMaster University, Hamilton, ON, L8S 4K1, Canada
[9] Instituto Nacional de Pesquisas da Amazonia, Programa LBA, Campus-II, Manaus—Amazonas 69060, Brazil
[10] University of Liege, Gembloux Agro-Bio Tech, Unit of Biosystem Physics, 2 Passage des Déportés, 5030 Gembloux, Belgium
[11] Finnish Meteorological Institute, Climate Change Research, FI-00101 Helsinki, Finland
[12] Department of Meteorology, Eötvös Loránd University, H-1117 Budapest, Pázmány sétány 1/A, Hungary
[13] Climate Research Division, Environment Canada, Saskatoon, SK, S7N 3H5, Canada
[14] INRA, UR1263 EPHYSE, Villenave d'Ornon F-33883, France
[15] School of Geography and Environmental Science, Monash University, Clayton, Victoria 3800, Australia
[16] Institute of Hydrology and Meteorology, Dresden University of Technology, Pienner Straße 23, D-01737, Tharandt, Germany
[17] Land and Food Systems, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada
[18] University of Minnesota, 115 Green Hall 1530 Cleveland Avenue N. St Paul, MN 55108, USA
[19] Royal Netherlands Meteorological Institute, 3730 AE De Bilt, The Netherlands
[20] Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH, UK
[21] ETH, Zurich, Institute of Plant Science, Universitaetsstrasse 2, Zuerich 8092, Switzerland
[22] National Center for Atmospheric Research, Boulder, CO 80307-3000, USA
[23] UMR INRA-INA PG—Environment and Arable Crops Unit 78850 Thiverval-Grignon, France
[24] Department of Geography, University of Toronto, Toronto, ON, M5S 3G3, Canada
[25] Department of Environmental Sciences, University of Toledo, Toledo, OH 43606-3390, USA
[26] LSCE, UMR CEA-CNRS, Batiment 709, CE, L'Orme des Merisiers, F-91191 Gif-sur-Yvette, France
[27] School of GeoSciences, The University of Edinburgh, Mayfield Road, Edinburgh, EH9 3JU, UK
[28] Biospheric Sciences Branch, NASA's Goddard Space Flight Center, Greenbelt, MD 20771, USA
[29] Department of Evolution, Ecology, and Organismal Biology, Ohio State University, Columbus, OH 43210, USA
[30] Department of Plant, Soil, and Environmental Science, University of Maine, Orono, ME 04469, USA
[31] Wind Energy Division, Risø National Laboratory for Sustainable Energy, Technical University of Denmark, PO 49, DK-4000 Roskilde, Denmark
[32] Université Paris-Sud, Bâtiment 362, Ecologie, Systematique et Evolution, Orsay Cedex F-91405, France
[33] Department of Atmospheric and Oceanic Sciences, University of Wisconsin, Madison, WI 53706, USA
[34] Northern Arizona University, School of Forestry Northern Arizona University, Flagstaff, AZ 86001, USA
[35] Atmospheric Science Program, Department of Geography, Indiana University, Bloomington, IN 47405, USA
[36] Smithsonian Environmental Research Center, Edgewater, MD 21037, USA
[37] Department of Physical and Earth Science, Worcester State College, 486 Chandler Street Worcester, MA 01602, USA
[38] ESS-CC, Alterra Wageningen UR, 6700 AA Wageningen, The Netherlands
[39] Atmospheric Science Group, LAWR, UC Davis, Davis, CA 95616, USA

[40] Institute for Meteorology, Climatology and Remote Sensing, University of Basel, Klingelbergstrasse 27, CH-4056 Basel, Switzerland
[41] Department of Biological Sciences, University of Lethbridge, 4401 University Drive, Lethbridge, AB, T1K 3M4, Canada
[42] Department of Micrometeorology, University of Bayreuth, 95440 Bayreuth, Germany
[43] USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect, Fort Collins, CO 80526, USA
[44] IASMA Research and Innovation Centre, Fondazione E Mach, Environment and Natural Resources Area, San Michele all'Adige, I38010 Trento, Italy
[45] Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720, USA
[46] Department of Earth System Science, University of California, Irvine, CA 92697, USA
[47] INRA, UMR 1137 Ecologie et Écophysiologie Forestierès, F54280, Champenoux, France
[48] Technische Universität Dresden, Institute of Hydrology and Meteorology, Department of Meteorology, Piennerstrasse 9, 01737 Tharandtt, Germany
[49] Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, Fudan University, Shanghai 200433, People's Republic of China
[50] University of Innsbruck, Institute of Ecology Sternwartestrasse 15, Innsbruck 6020, Austria
[51] Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, People's Republic of China
[52] Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA
[53] Hungarian Meteorological Service, H-1675 Budapest, PO Box 39, Hungary
[54] Centre for Ecology and Hydrology (Edinburgh) Bush Estate Penicuik, Midlothian, EH26 0QB, UK
[55] Department of Hydrology and Geo-Environmental Sciences, Boelelaan 1085, 1081 HV, VU University Amsterdam, The Netherlands
[56] School of Environmental and Life Sciences, Charles Darwin University, Darwin, NT 0909, Australia
[57] Biosystems Division, Risø National Laboratory for Sustainable Energy, Technical University of Denmark, PO 49, DK-4000 Roskilde, Denmark
[58] Geobiosphere Science Centre, Physical Geography and Ecosystems Analysis, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden
[59] Instituto Superior de Agronomia, Universidade Técnica de Lisboa, Tapada da Ajuda 1349-017 Lisboa, Portugal
[60] School of the Environment, Duke University, Durham, NC 27708-0328, USA
[61] Civil and Environmental Engineering Department, University College Cork, Cork, Republic of Ireland
[62] INRA, Unité d'Agronomie, 234, Avenue du Brézet, F-63000 Clermont-Ferrand, France
[63] Johann Heinrich von Thünen-Institut (vTI), Institut für Agrarrelevante Klimaforschung, Bundesallee 50, 38116 Braunschweig, Germany
[64] Department of Geography, Trent University, Peterborough, ON, K9J 7B8, Canada
[65] CSIRO Marine and Atmospheric Research, PO Box 3023, Canberra, ACT, 2601, Australia
[66] Department of Physics, Atmospheric Sciences and Geoscience, Jackson State University, Jackson, MS 39217, USA
[67] Rende Division, Institute for Atmospheric Pollution, Consiglio Nazionale delle Ricerche, 87036 Rende, Italy
[68] Institute of Systems Biology and Ecology, Division of Ecosystems Processes Lab. of Plants Ecological Physiology, Na Sadkach 7 370 050, Ceske Budejovice, Czech Republic
[69] Centre d'études de la forêt Faculté de Foresterie et de Géomatique, Université Laval, QC G1V 0A6, Canada
[70] University of Florida, Gainesville, FL 32611, USA
[71] Argonne National Laboratory, Biosciences Division, Argonne, IL 60439, USA
[72] National Research Council, Institute of Agroenvironmental and Forest Biology, 00015 Monterotondo Scalo (RM), Italy
[73] Department of Geography, Queen's University, Kingston, ON, K7L 3N6, Canada
[74] Max-Planck Institute for Biogeochemie, Jena, D-07745, Germany
[75] NOAA/ATDD, Oak Ridge, TN 37831-2456, USA
[76] Remote Sensing of Environmental Dynamics Laboratory, DISAT, Università degli Studi di Milano-Bicocca, Italy
[77] CNR-IBIMET, Istituto di Biometeorologia, via Giovanni Caproni 8, 50145 Firenze, Italy
[78] CNRS-CEFE, 1919 route de Mende, 34293 Montpellier Cedex 5, France
[79] Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA
[80] Servizi Forestali, Agenzia per l'Ambiente, Provincia Autonoma di Bolzano, 39100 Bolzano, Italy

[81] Faculty of Sciences and Technologies, Free University of Bozen-Bolzano, Piazza Università 1, 39100, Bolzano, Italy
[82] Alterra Green World Research, Wageningen, NL 6700 AA, The Netherlands
[83] University of Liege, Gembloux Agro-Bio Tech, Unit of Crops Management, 2 Passage des Déportés, 5030 Gembloux, Belgium
[84] Zambian Meteorological Department, Western Province, Mongu, Zambia
[85] Division of Engineering and Applied Science, Department of Earth and Planetary Science, Harvard University, Cambridge, MA 02138, USA
[86] Institute of Botany and Ecophysiology, Agricultural University of Gödöllô, H-2103 Gödöllô, Páter Károly u. 1, Hungary
[87] Department of Forestry and Environmental Resources, North Carolina State University, NC 29695, USA
[88] Department of Biology, San Diego State University, San Diego, CA 92182-4614, USA
[89] Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC 27708-0328, USA
[90] Department of Forestry, University of Missouri, Columbia, MO 65211, USA
[91] CESAM and Department of Environment, University of Aveiro, Aveiro 3810-193, Portugal
[92] Instituto Superior Tecnico, Mechanical Engineering Department, 1049-001 Lisboa, Portugal
[93] The Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA
[94] DREAM, CEFE, CNRS, UMR5175, 1919 route de Mende, F-34293 Montpellier Cedex 5, France
[95] Earth System Science Center, National Institute of Space Research, Cachoeira Paulista, SP 12630, Brazil
[96] Department of Physics, FI-00014, University of Helsinki, Finland
[97] Department of Geography, McGill University 805, Sherbrooke Street West Montréal, QC, H3A 2K6, Canada
[98] Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA
[99] Center for Global Environmental Research, National Institute for Environmental Studies, 16-2 Onogawa, Tsukuba 305-8506, Japan
[100] Centro de Estudios Ambientales del Mediterraneo, Parque Tecnologico, Charles H Darwin 14, E-46980 Paterna, Spain
[101] Agricultural Research Council, Department of Agronomy, Forestry and Land Use, 00184 Rome, Italy
[102] Atmospheric Environmental Research Institute of Meteorology and Climate Research, Forschungszentrum Karlsruhe, Garmisch-Partenkirchen, Germany
[103] Institute for Environment and Sustainability, Joint Research Center European Commission, TP 280, I-21020 Ispra, Italy
[104] Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487-0206, USA
[105] Atmospheric Sciences Centre for Ecology and Hydrology (CEH), Bush Estate, Penicuik, Midlothian, EH26 0QB, UK
[106] Department of Plant Ecology, University of Bayreuth, 95440 Bayreuth, Germany
[107] Department of Forest Environment and Resources, University of Tuscia, I-01100 Viterbo, Italy
[108] The University of Michigan Biological Station, Pellston, MI 49769, USA
[109] School of Mathematics, Liaoning Normal University, Dalian 116039, People's Republic of China
[110] Institute of Geographic Sciences and Natural Resource Research, Chinese Academy of Science, Beijing 100101, People's Republic of China
[111] IMSG@National Center for Environmental Predictions, NOAA, Camp Springs, MD 20746, USA
[112] Geosciences Research Division, Scripps Institution of Oceanography, University of California, La Jolla, CA 92093, USA
[113] Atmospheric, Earth and Energy Division, Lawrence Livermore National Laboratory, Livermore, CA 94551, USA
[114] Graduate Degree Program in Geography, Clark University, Worcester, MA 01610-1477, USA
[115] Okayama University, Okayama 700-8530, Japan
[116] Northwest Plateau Institute of Biology, Chinese Academy of Sciences, Xining 810001 Qinghai, People's Republic of China

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Abstract

Understanding the relationships between climate and carbon exchange by terrestrial ecosystems is critical to predict future levels of atmospheric carbon dioxide because of the potential accelerating effects of positive climate–carbon cycle feedbacks. However, directly observed relationships between climate and terrestrial CO_2 exchange with the atmosphere across biomes and continents are lacking. Here we present data describing the relationships between net ecosystem exchange of carbon (NEE) and climate factors as measured using the eddy covariance method at 125 unique sites in various ecosystems over six continents with a total of 559 site-years. We find that NEE observed at eddy covariance sites is (1) a strong function of mean annual temperature at mid- and high-latitudes, (2) a strong function of dryness at mid- and low-latitudes, and (3) a function of both temperature and dryness around the mid-latitudinal belt (45°N). The sensitivity of NEE to mean annual temperature breaks down at ∼16 °C (a threshold value of mean annual temperature), above which no further increase of CO_2 uptake with temperature was observed and dryness influence overrules temperature influence.

Keywords: NEE, climate control, terrestrial carbon sequestration, temperature, dryness, eddy flux, biomes, photosynthesis, respiration, global carbon cycle

S Online supplementary data available from stacks.iop.org/ERL/5/034007/mmedia

1. Introduction

Determining the relationships between terrestrial carbon exchange and climate is fundamentally important because climate–carbon cycle feedback could significantly accelerate (or decelerate) future climate warming (Zeng *et al* 2004, 2005). Globally, the observed growth rate anomaly of atmospheric CO_2 concentration is correlated with the multivariate El Niño-Southern Oscillation index (Heimann and Reichstein 2008). Inversion modeling (Bousquet *et al* 2000) and biome-based analyses of climate anomalies (Zhou *et al* 2008) suggest that the oceanic carbon reservoir is a minor player in this variability. Instead, variations in the atmospheric CO_2 growth rate result largely from the impact of climate on terrestrial carbon sequestration (Nemani *et al* 2003, Xiao and Moody 2004), including regional impacts of extreme climate conditions such as heat waves and droughts (Ciais *et al* 2005, Xiao *et al* 2009).

On much smaller spatial scales, large amounts of data have been collected continuously over the last two decades using the eddy covariance technique to measure directly the net ecosystem exchange of CO_2 (NEE) between the biosphere and the atmosphere (Baldocchi *et al* 2001, Law *et al* 2002). Although a typical eddy covariance footprint is relatively small (ca. 1 km^2), NEE variability at these sites is often representative of variability over much larger spatial scales as a result of the spatial coherence of climate anomalies (Ciais *et al* 2005, Nemani *et al* 2003, Xiao and Moody 2004). These temporal variations in NEE, the imbalance between photosynthesis (fixation of atmospheric carbon dioxide into organic carbon) and ecosystem respiration (plant and microbial respiration converting organic carbon into atmospheric carbon dioxide), are caused predominately by climatic drivers on daily and seasonal timescales (Law *et al* 2002). Although several synthesis efforts have been conducted across eddy-flux tower sites, the role of climatic drivers in causing NEE variability across multiple sites on annual or longer timescales is still not clear (Law *et al* 2002, Valentini *et al* 2000, Reichstein *et al* 2007).

Determining the environmental controls on NEE is complicated because NEE is the difference between photosynthesis and ecosystem respiration, and climate variations may affect these two components in different ways. Spatial variability in respiration is strongly correlated with temperature, precipitation and substrate supply (Raich *et al* 2002, Ryan and Law 2005), and gross primary productivity has been shown to be subject to climate-based limiting factors—temperature, precipitation and/or radiation, depending on the region (Law *et al* 2002). This paper seeks to identify the climate controls on spatial NEE variability globally as represented within FLUXNET, a global network of eddy covariance tower sites (Baldocchi *et al* 2001). Other studies have shown that non-climate factors, especially disturbance, are a major factor causing NEE variability (Oren *et al* 2006, Thornton *et al* 2002, Foley *et al* 2005). The role of disturbance history may be underplayed in FLUXNET synthesis studies because the number of recently disturbed sites is limited. However, we expect that other recent estimates that emphasize the effects of other non-climate factors such as nitrogen (Magnani *et al* 2007, Sutton *et al* 2008) have downplayed the role of climatic interactions.

2. Data and sites

The present analysis is based on 559 site-years of eddy covariance data measured from 125 sites throughout the world from 1992 to 2008 (supplementary table S1 available at stacks.iop.org/ERL/5/034007/mmedia). The latitudes

[117] These authors are listed alphabetically and contributed equally to this work.
[118] Deceased.

vary from 37°S to 71°N, longitudes are broadly covered, and elevation ranges from −2 to 3288 m (supplementary figure S1 available at stacks.iop.org/ERL/5/034007/mmedia). The climatic zones of the sites include polar tundra, maritime temperate, continental temperate, humid subtropical, Mediterranean, arid, semi-arid, tropical monsoon, and tropical wet-and-dry climates. The vegetation types include grassland, evergreen needle-leaf forest, deciduous broad-leaf forest, mixed forest, permanent wetland, open shrubland, closed shrubland, savanna, evergreen broad-leaf forest, and tundra. Stand age ranges from young seedlings to 500 years old (Paw U *et al* 2004). Sites from all ecosystem types with at least one year of complete NEE and meteorological data are included. NEE and meteorological data used in this analysis are taken from standardized files archived in the FLUXNET-LaThuile database which includes data from the AmeriFlux, Fluxnet-Canada, CARBOEUROPE, USCCC, ChinaFlux, OzFlux, CarboAfrica, and AsiaFlux networks. These data have been quality controlled and gap-filled by consistent methods (Papale *et al* 2006, Moffat *et al* 2007, Reichstein *et al* 2005). Meteorological variables used include air temperature, net radiation and precipitation. We have developed a new method to gap-fill the half-hourly meteorological data to produce reliable annual averages (see Methods in the supplementary data available at stacks.iop.org/ERL/5/034007/mmedia). In many cases, the site principal investigators have submitted revised annual NEE estimates based on more detailed, site-specific reanalyses. The data were used in this analysis only in those years when temperature, precipitation, net radiation, and NEE all met the gap-filling criteria (see Methods in the supplementary data available at stacks.iop.org/ERL/5/034007/mmedia).

Eddy-flux measurements are inherently uncertain due to: (1) advection errors caused by complex terrain (Aubinet *et al* 2005, Feigenwinter *et al* 2008) and complicated canopy structure (Yi 2008); (2) imbalance errors in the energy budget (Massman and Lee 2002, Foken 2008), and (3) the stochastic nature of turbulence (Hollinger and Richardson 2005, Moncrieff *et al* 1996). These errors have been studied intensively and remain to be quantified exactly for all sites (Reichstein *et al* 2007). The largest sources of uncertainty that have been quantified in a standardized way in annual NEE result from u^* filtering, gap-filling of missing data, and turbulent sampling errors (supplementary materials available at stacks.iop.org/ERL/5/034007/mmedia).

3. Grouping analysis

We hypothesize that two direct climatic controls on NEE, temperature and dryness (Budyko 1974), interact in complex ways with non-climatic or indirect climatic factors such as disturbance history, species, soil type and nutrient availability. Although it is not possible to develop a predictive global relationship of NEE with these variables, we ask does the dominant climate factor at individual sites follow distinct geographic patterns? While it is overly simplistic to argue that NEE is a function of two climate variables, it is possible to gain insight into global scale processes through the use of an objective statistical method to group sites by their dominant climate control.

We used a mixture regression model (see supplementary materials available at stacks.iop.org/ERL/5/034007/mmedia) to segregate sites into three groups (supplementary table S1 available at stacks.iop.org/ERL/5/034007/mmedia): (1) T-group: variations in NEE are best explained by mean annual temperature alone; (2) D-group: variations in NEE are best explained by a dryness index alone; and (3) B-group: NEE is co-limited by both mean annual temperature and dryness. An independent approach—a nonparametric kernel regression (Wand and Jones 1995) analysis of NEE against mean annual temperature and dryness for all three groups—provides a strong foundation for grouping the sites in this way. The pattern of contour lines in the contour plot for all 125 sites indicates a complex and mixed relationship for temperature and dryness (figure 1(a)), in which NEE at colder sites is generally a function of temperature and at warmer sites is generally a function of dryness. The kernel regression also confirms that the sites are successfully segregated according to their functional dependence. The contour plot for the T-group (figure 1(b)) shows that the contour lines are almost parallel to the dryness index axis. This implies that NEE is a monotonic function of temperature, and that the dryness index does not significantly influence the NEE of the sites in the T-group. The contour plot for the D-group (figure 1(c)) shows that the contour lines are almost parallel to the temperature axis. This implies that NEE is a monotonic function of the dryness index, and that the temperature does not significantly influence the NEE of the sites in the D-group. The contour plot for the B-group shows that the contour lines are neither parallel to the temperature axis nor parallel to the dryness index axis. This implies that both the temperature and the dryness index are contributors to the amount of NEE in the sites in the B-group. Moreover, NEE seems to linearly decrease as temperature increases or the dryness index decreases (figure 1(d)).

In the T-group, 84% of spatial variations in NEE can be explained by mean annual temperature (figure 2(a)), while in the D-group, 81% of spatial variation in NEE can be accounted for by a dryness index (figure 2(b)). However, in the smaller B-group, NEE is co-limited by mean annual temperature and dryness, and the correlations between the NEE and individual climate factors are relatively weak (figures 3(a) and (b)). We speculate that the variance in NEE unexplained by the climate factors in these three groups is primarily driven by non-climate factors such as stand age, disturbance history, species composition, or canopy leaf area index, reflecting local variation in nutrient and water availability (Raich *et al* 2002). These non-climate factors are also likely to play a role in the grouping algorithm and account for sites with similar temperature and dryness being grouped differently.

4. Discussion and concluding remarks

The empirical subdivision of groups also corresponds to latitudinal zonation (supplementary figure S1 available at stacks.iop.org/ERL/5/034007/mmedia): most sites of the temperature-limited group were located in the zones of

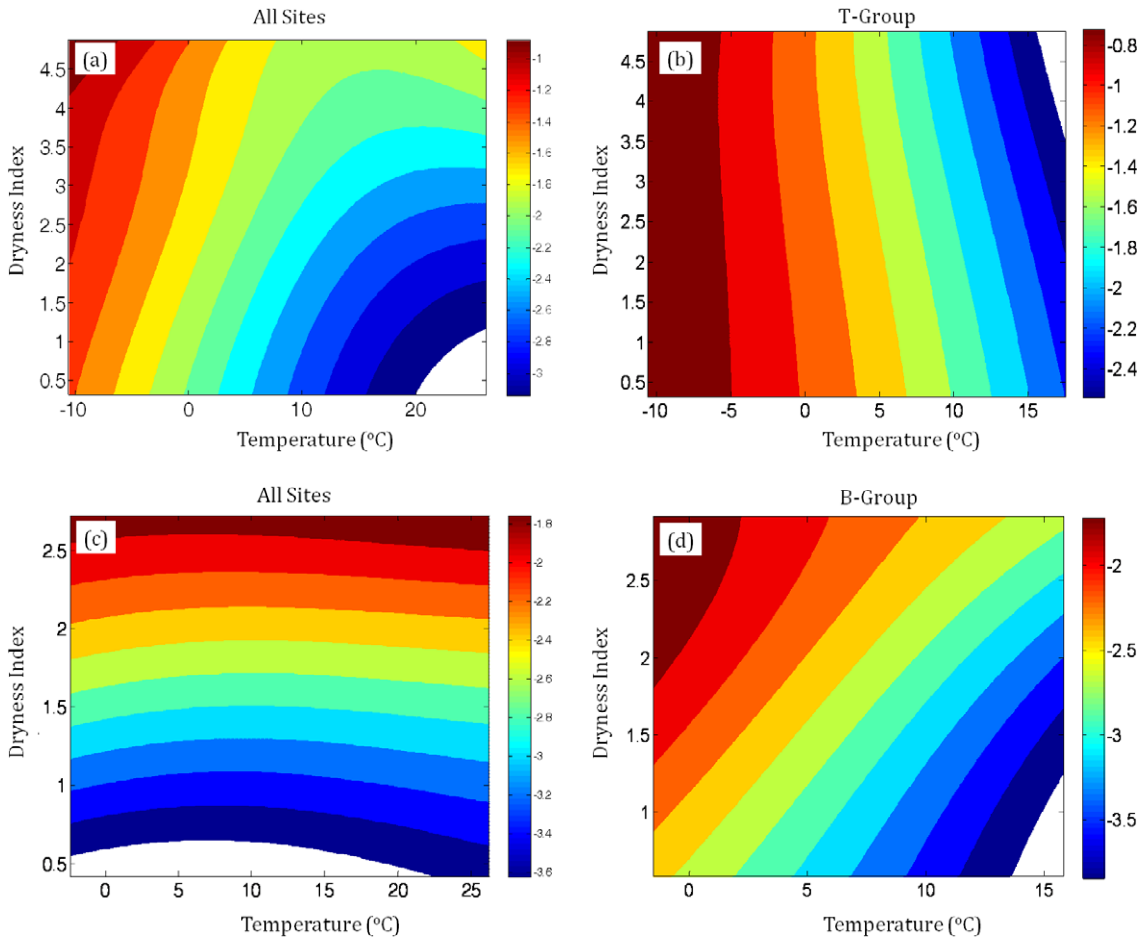

Figure 1. Contour plots of site-average NEE (tC ha^{-1} yr^{-1}) of: (a) all the 125 sites; (b) the T-group (47 sites); (c) the D-group (47 sites); and (d) the B-group (32 sites). These contour plots of the regression surface were produced by two-dimensional kernel regression (Wand and Jones 1995) based on the grouping data of the T-group, the D-group, the B-group, and the entire 125 sites (see Methods section and supplementary table S1 available at stacks.iop.org/ERL/5/034007/mmedia). The kernel regression is a commonly used nonparametric regression technique, which assumes the regression function is a smooth function of predictor variables rather than imposing a pre-specific functional form (parametric model) on the regression function.

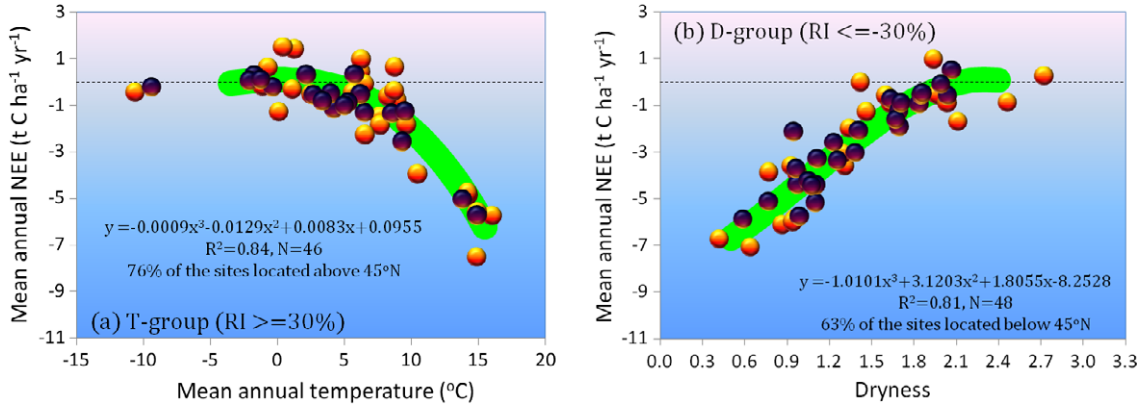

Figure 2. Climatic controls of the site-average net ecosystem exchange (NEE) across the FLUXNET sites (see supplementary table S1 available at stacks.iop.org/ERL/5/034007/mmedia): (a) temperature-limited group; and (b) dryness-limited group. The negative NEE values indicate that atmospheric carbon is assimilated by terrestrial ecosystems, while the positive NEE values indicate that terrestrial organic carbon is converted into atmospheric carbon. The filled circles with mango color in (a) are the site-average NEE of the sites in the prototype T-group with very high posterior probability (>99%) belonging to the temperature group, while the filled circles with mango color in (b) are the site-average NEE of the sites in the prototype D-group with very high posterior probability (>99%) belonging to the dryness group (see the Methods section and supplementary table S1 available at stacks.iop.org/ERL/5/034007/mmedia). The thick green lines represent model predictions.

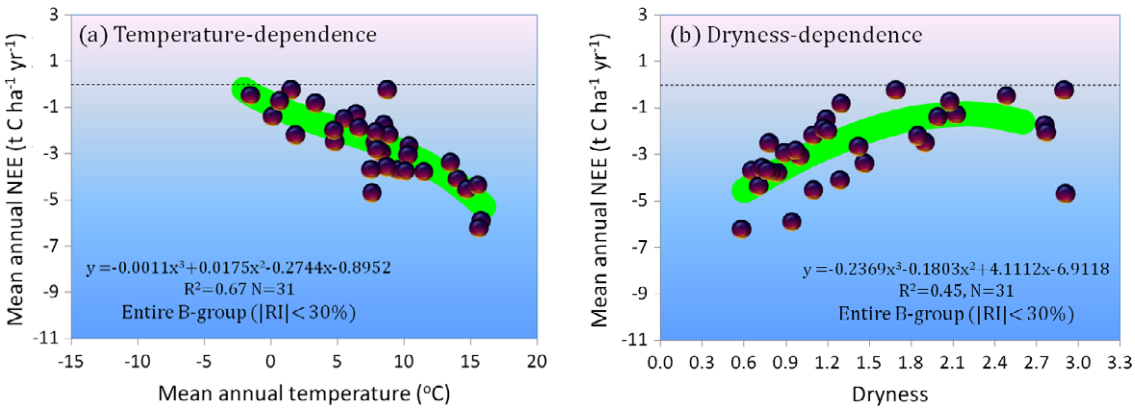

Figure 3. The site-averaged NEE of B-group sites that are sensitive to both: (a) temperature and (b) dryness.

temperate and boreal climate (76% are located above 45°N, supplementary figure S2(a) available at stacks.iop.org/ERL/5/034007/mmedia), while most sites of the dryness-limited group were located in the zones of subtropical climate (63% are located below 45°N, supplementary figure S2(b) available at stacks.iop.org/ERL/5/034007/mmedia). The B-group sites were almost symmetrically distributed around 45°N (supplementary figure S2(c) available at stacks.iop.org/ERL/5/034007/mmedia). The controlling function of temperature for terrestrial carbon exchanges breaks down as mean annual temperature approaches 16 °C. All sites with mean annual temperature above 16 °C are in the dryness group (figures 2(a) and 3(a)). Our findings suggest that NEE at mid-to-high latitudes is controlled largely by the mean annual temperature, while at mid-to-low latitudes, it is controlled largely by dryness. The geographic region around 45°N is a transition zone where many sites are co-limited by both temperature and dryness.

The global empirical patterns of NEE driven by climate gradients found in this paper are partially supported by another global data analysis conducted by Nemani *et al* (2003) based on correlation between 18 years climate data and net primary production (NPP) derived from spatially continuous satellite data. This modeling study found that NPP is largely controlled by temperature at mid-to-high latitudes, while at subtropical and tropical it is controlled by radiation and water, i.e. by dryness (ratio of net radiation to precipitation) as was used in our analysis. Even though the predicted ecological variables used here (NEE) and in Nemani *et al* (2003)'s analysis (NPP = NEE − soil respiration) were not the same, the consistent climate-driven spatial patterns derived from the two independently global datasets at least indicates that climate control plays an important role in the terrestrial carbon cycle. On the other hand, it is noted that our findings are different from the individual site analyses on climate control of NEE (e.g. Dunn *et al* 2007). These analyses study the temporal variability of NEE based on the measurements from a single site, i.e. how climate factors drive NEE changes from year to year. Our analysis studies the spatial variability of NEE based on measurements from many sites, i.e. how spatial gradients of climate drive NEE changes from location to location. Our data analysis demonstrated that spatial variability of NEE is 2.5 times greater than temporal variability of NEE (see discussion in section 3 of supplementary materials available at stacks.iop.org/ERL/5/034007/mmedia). Therefore, the existing differences between temporal variability and spatial variability are expected.

Why is the average annual temperature the main climate driver of NEE at mid- and high-latitudes? The most likely reason is that higher average annual temperature also reflects prolonged growing seasons in cold climate regions and hence increases carbon uptake in biomass (White *et al* 1999, Malhi 2002, Kato and Tang 2008) relative to heterotrophic decomposition. At many sites, respiration rates lag NPP rates proportionally after disturbance, and a larger NPP resulting from a longer growing season contributes to higher uptake (Goulden *et al* 1996, Leuning *et al* 2005). In the absence of other factors, we therefore expect higher carbon uptake at warmer sites within the temperature group. This speculation is partially supported by previous studies with limited data (Goulden *et al* 1996, Leuning *et al* 2005). In warm climate regions (low-latitudes), growing season length is less likely to be affected by temperature variations because these regions either experience a year-round growing season or a growing season that is limited by factors other than temperature, mainly water stress. The global-biome-climate data analysis (Zhou *et al* 2008) indicates that the mean annual temperature of C4 grassland biome is about 23 °C, in other words it is much larger than the threshold value of 16 °C, and hence C4 sites are much more likely to be in a dryness group according to our findings above. It is well known in physiology that the assimilation of C4 ecosystems, which resides mainly in the subtropical regions (Ehleringer *et al* 2005), is independent of temperature but is limited by water stress (Lambers *et al* 1998). This fact partially supports our findings that the NEE-driver of a site with mean annual temperature larger than 16 °C is likely to be dryness and such sites are likely located in tropical or subtropical regions.

The majority of the 125 sites are recovering from past disturbance rather than being actively disturbed, and thus are in the 'slow in' instead of the 'rapid out' phase of carbon flow in the terrestrial biosphere as conceptualized by Korner (2003). Disturbance history and stand age play a large role in NEE variability (Amiro *et al* 2010), which is seen at chronosequence sites with similar climates (Ryan and Law 2005). Though

the temperature and dryness groups are correlated well with their respective indices, the overlap of the two groups in temperature–dryness space suggests that NEE is controlled by a complex interaction of climate and non-climate factors. Our results do not support the recent suggestion that a single abiotic factor such as nitrogen supply dominates NEE (Magnani *et al* 2007, Sutton *et al* 2008).

Links between terrestrial CO_2 exchanges and climate controls are clearly demonstrated by many site-years of data from the eddy-flux tower networks. Our findings are essential to understand how future climate change may affect terrestrial CO_2 exchanges with the atmosphere in the 21st century (Qian *et al* 2010). In the IPCC 2007 report, projected warming in the 21st century is expected to be greatest over land and at high northern latitudes, while projected decreases in precipitation are likely in most subtropical land regions (IPCC 2007). Although climate controls on long-term changes in NEE may be different from controls on spatial variability of NEE, our results imply that the most likely future climate change scenarios could strongly intensify terrestrial CO_2 uptake in high-latitudes and weaken CO_2 uptake in low-latitudes.

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References

Amiro B D *et al* 2010 Ecosystem carbon dioxide fluxes after disturbance in forests of North America *J. Geophys. Res.* at press (doi:10.1029/2010JG001390)

Aubinet M *et al* 2005 Comparing CO_2 storage and advection conditions at night at different CARBOEUROFLUX sites *Bound.-Layer Meteorol.* **116** 63–93

Baldocchi D *et al* 2001 FLUXNET: a new tool to study the temporal and spatial variability of eco-system-scale carbon dioxide, water vapor, and energy flux densities *Bull. Am. Meteorol. Soc.* **82** 2415–34

Bousquet P *et al* 2000 Regional changes in carbon dioxide fluxes of land and oceans since 1980 *Science* **290** 1342–6

Budyko M I 1974 *Climate and Life* (New York: Academic) p 508

Ciais Ph *et al* 2005 Europe-wide reduction in primary productivity caused by the heat and drought in 2003 *Nature* **437** 529–33

Dunn A L, Barford C C, Wofsy S C, Goulden M L and Daube B C 2007 A long-term record of carbon exchange in a boreal black spruce forest: means, responses to interannual variability, and decadal trends *Glob. Change Biol.* **13** 577–90

Ehleringer J R, Cerling T E and Dearing M D (ed) 2005 *A History of Atmospheric* CO_2 *and its Effect on Plants, Animals, and Ecosystems* (New York: Springer)

Feigenwinter C *et al* 2008 Comparison of horizontal and vertical advective CO_2 fluxes at three forest sites *Agric. Forest Meteorol.* **148** 12–24

Foken T 2008 The energy balance closure problem: an overview *Ecol. Appl.* **18** 1351–67

Foley J A *et al* 2005 Global consequences of land use *Science* **309** 570–4

Goulden M L *et al* 1996 CO_2 exchange by a deciduous forest: response to interannual climate variability *Science* **271** 1576–8

Heimann M and Reichstein M 2008 Terrestrial ecosystem carbon dynamics and climate feedbacks *Nature* **451** 289–92

Hollinger D Y and Richardson A D 2005 Uncertainty in eddy covariance measurements and its application to physiological models *Tree Physiol.* **25** 873–85

IPCC 2007 Summary for policymakers *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* ed M L Parry, O F Canziani, J P Palutikof, P J van der Linden and C E Hanson (Cambridge: Cambridge University Press) pp 7–22

Kato T and Tang Y 2008 Spatial variability and major controlling factors of CO_2 sink strength in Asian terrestrial ecosystems: evidence from eddy covariance data *Glob. Change Biol.* **14** 2333–48

Korner C 2003 Slow in, rapid out—carbon flux studies and Kyoto targets *Science* **300** 1242–3

Lambers H, Chapin F S and Pons T L 1998 *Plant Physiological Ecology* (New York: Springer)

Law B E *et al* 2002 Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation *Agric. Forest Meteorol.* **113** 97–120

Leuning R *et al* 2005 Carbon and water fluxes over a temperate Eucalyptus forest and a tropical wet/dry savanna in Australia: measurements and comparison with MODIS remote sensing estimates *Agric. Forest Meteorol.* **129** 151–73

Magnani F *et al* 2007 The human footprint in the carbon cycle of temperate and boreal forests *Nature* **447** 848–51

Malhi Y 2002 Carbon in the atmosphere and terrestrial biosphere in the 21st century *Phil. Trans. R. Soc.* A **360** 2925–45

Massman W J and Lee X 2002 Eddy covariance flux corrections and uncertainties in long-term studies of carbon and energy exchanges *Agric. Forest Meteorol.* **113** 121–44

Moffat A M *et al* 2007 Comprehensive comparison of gap filling techniques for eddy covariance net carbon fluxes *Agric. Forest Meteorol.* **147** 209–32

Moncrieff J B, Malhi Y and Leuning R 1996 The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water *Glob. Change Biol.* **2** 231–40

Nemani R R, Keeling C D, Hashimoto H, Jolly W M, Piper S C, Tucker C J, Myneni R B and Running S W 2003 Climate-driven increases in global terrestrial net primary production from 1982 to 1999 *Science* **300** 1560–3

Oren R *et al* 2006 Estimating the uncertainty in annual net ecosystem carbon exchange: spatial variation in turbulent fluxes and sampling errors in eddy-covariance measurements *Glob. Change Biol.* **12** 883–96

Papale D *et al* 2006 Towards a standardized processing of net ecosystem exchange measured with eddy covariance technique: algorithms and uncertainty estimation *Biogeosciences* **3** 571–83

Paw U K T *et al* 2004 Carbon dioxide exchange between an old-growth forest and the atmosphere *Ecosystems* **7** 513–24

Qian H F, Joseph R and Zeng N 2010 Enhanced terrestrial carbon uptake in the northern high latitudes in the 21st century from the Coupled Carbon Cycle Climate Model Intercomparison Project model projections *Glob. Change Biol.* **16** 641–56

Raich J W, Potter C S and Bhagawati D 2002 Interannual variability in global soil respiration, 1980–94 *Glob. Change Biol.* **8** 800–12

Reichstein M *et al* 2005 On the separation of net ecosystem exchange into assimilation and ecosystem respiration review and improved algorithm *Glob. Change Biol.* **11** 1–16

Reichstein M *et al* 2007 Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites *Geophys. Res. Lett.* **34** L01402.262

Ryan M G and Law B E 2005 Interpreting, measuring and modeling soil respiration *Biogeochemistry* **73** 3–27

Sutton M A *et al* 2008 Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration *Glob. Change Biol.* **14** 2057–63

Thornton P E *et al* 2002 Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests *Agric. Forest Meteorol.* **113** 185–222

Valentini R *et al* 2000 Respiration as the main determinant of carbon balance in European forests *Nature* **404** 861–5

Wand M P and Jones M C 1995 *Kernel Smoothing* (London: Chapman & Hall)

White J D, Running S W and Thornton P 1999 Impact of growing season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern deciduous forest *Int. J. Biometeorol.* **42** 139–45

Xiao J and Moody A 2004 Trends in vegetation activity and their climatic correlates: China 1982 to 1998 *Int. J. Remote Sens.* **25** 5669–89

Xiao J, Zhuang Q, Liang E, McGuire A D, Moody A, Kicklighter D W and Melillo J M 2009 Twentieth century droughts and their impacts on terrestrial carbon cycling in China *Earth Interact.* **13** 1–31

Yi C 2008 Momentum transfer within canopies *J. Appl. Meteorol. Climatol.* **47** 262–75

Zeng N, Qian H, Munoz E and Iacono R 2004 How strong is carbon cycle-climate feedback under global warming? *Geophys. Res. Lett.* **31** L20203

Zeng N, Qian H, Roedenbeck C and Heimann M 2005 Impact of 1998–2002 midlatitude drought and warming on terrestrial ecosystem and the global carbon cycle *Geophys. Res. Lett.* **32** L22709

Zhou T, Yi C, Bakwin P S and Zhu L 2008 Links between global CO_2 variability and climate anomalies of biomes *Sci. China* D **51** 740–7