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Effect of climate change, CO₂ trends, nitrogen addition, and land-cover and management intensity changes on the carbon balance of European grasslands

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3

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5

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28

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30

31 **Abstract**

32

33 Several lines of evidence point to European managed grassland ecosystems being a sink of
34 carbon. In this study, we apply ORCHIDEE-GM a process-based carbon cycle model that
35 describes specific management practices of pastures and the dynamics of carbon cycling in
36 response to changes in climatic and biogeochemical drivers. The model is used to simulate
37 changes in the carbon balance (i.e., Net Biome Production, NBP) of European grasslands over
38 1991-2010 on a 25 km × 25 km grid. The modeled average trend of NBP is 1.8 - 2.0 g C m⁻²
39 yr⁻² during the past two decades. Attribution of this trend suggests management intensity as
40 the dominant driver explaining NBP trends in the model (36% - 43% of the trend due to all
41 drivers). A major change in grassland management intensity has occurred across Europe
42 resulting from reduced livestock numbers. This change has ‘inadvertently’ enhanced soil C
43 sequestration and reduced N₂O and CH₄ emissions by 1.2 - 1.5 Gt CO₂-equivalent, offsetting
44 more than 7% of greenhouse gas emissions in the whole European agricultural sector during
45 the period 1991-2010. Land-cover change, climate change and rising CO₂ also make positive
46 and moderate contributions to the NBP trend (between 24% and 31% of the trend due to all
47 drivers). Changes in nitrogen addition (including fertilization and atmospheric deposition) is
48 found to have only marginal net effect on NBP trends. However, this may not reflect reality
49 because our model has only a very simple parameterization of nitrogen-effects on
50 photosynthesis. The sum of NBP trends from each driver is larger than the trend obtained
51 when all drivers are varied together, leaving a residual - non-attributed - term (22% - 26% of
52 the trend due to all drivers) indicating negative interactions between drivers.

53 **Introduction**

54

55 Grassland is not a natural vegetation type in Europe. Europe's grasslands were created and
56 managed to feed livestock for producing meat and dairy products (so-called pasture). These
57 grasslands are mowed for forage production and grazed by ruminant animals, often within the
58 same farm, although in regions of intensive livestock production, animals are also fed
59 substantial additional amounts of crop feedstuff products. Meanwhile, nitrogen-rich mineral
60 and organic fertilizers (manure/slurry) are commonly applied to European grasslands to
61 sustain meat and dairy production. The frequency and intensity of these agricultural practices,
62 combined with climate change, are expected to strongly impact the carbon (C) balance of
63 grasslands in Europe (Soussana *et al.*, 2007).

64 The annual C balance of managed grassland ecosystems (also called net biome production,
65 *NBP*; here using the definition proposed by Schulze & Heimann, 1998; Buchmann & Schulze,
66 1999; and Chapin *et al.*, 2006) must account for not only the fluxes of CO₂ exchanged with
67 the atmosphere (net ecosystem production, *NEP*), but also the land-atmosphere CO₂ fluxes
68 caused by lateral carbon import and export due to management and other processes (e.g., C
69 export to rivers and groundwater). *NEP* is determined by the difference between net primary
70 productivity (*NPP*) and ecosystem-level heterotrophic respiration (R_h). *NPP*, indicating the C
71 incorporated into plant biomass, is known to be sensitive to climate (Melillo *et al.*, 1993),
72 atmospheric CO₂ concentration (e.g., Ainsworth & Long, 2005) and nitrogen availability (Le
73 Bauer & Treseder, 2008; Xia & Wan, 2008). R_h is also controlled by climate (Rustad *et al.*,
74 2001) as well as by organic C and nitrogen availability, and micro-environmental conditions
75 (soil physical and chemical properties such as clay content, pH, etc), while organic C input to

76 R_h (including above and belowground litter) is determined both by NPP, and by C input (as
77 manure) and exported as harvested biomass or ingested by grazing animals.

78 The amount of C exported from a grassland ecosystem depends on the grass consumed by
79 ruminant livestock. According to the FAOstat agricultural statistics, during the period 1991-
80 2010, a more than 17% reduction of livestock numbers occurred across Europe. This reduced
81 the requirement for grass forage; at the same time grassland potential productivity was
82 increasing (Chang *et al.*, 2015a). These changes affected the ecosystem C balance, decreasing
83 C export and increasing litter-fall to soils. Meanwhile, according to the harmonized high
84 resolution land-cover change data set *HILDA* (Fuchs *et al.*, 2013), the grassland area
85 increased by 3.7% in the 30 European countries of the EU28 plus Norway and Switzerland.
86 This figure includes concurrent loss and creation of grasslands by 5.8% and 9.5% of total
87 grassland area in 1991, respectively, but with significant regional differences (EEA, 2005, pp.
88 47-53). The stronger relative reduction of livestock numbers compared to that of grassland
89 area suggests an overall trend towards less intensive pasture usage.

90 A significant net C sequestration (a positive NBP of $15 \pm 7 \text{ g C m}^{-2} \text{ yr}^{-1}$) by grassland
91 ecosystems of the 30 European countries during the period 1961-2010 was estimated in a
92 previous study, using the process-based biogeochemical model ORCHIDEE-GM, which has
93 an explicit and rather detailed representation of grassland management (Chang *et al.*, 2015b).
94 ORCHIDEE-GM simulates a significant *increase* of NBP with time during the past five
95 decades (NBP linear trend of $0.25 \pm 0.08 \text{ g C m}^{-2} \text{ yr}^{-2}$, $P = 0.26$) with the rate of increase being
96 much larger after 1990 ($1.83 \pm 0.30 \text{ g C m}^{-2} \text{ yr}^{-2}$, $P = 0.07$) than before that date (-0.25 ± 0.15
97 $\text{g C m}^{-2} \text{ yr}^{-2}$, $P = 0.55$). This acceleration of C sequestration can be attributed to changes in
98 climate, CO_2 concentration, nitrogen atmospheric deposition, land-cover change, and to
99 changes in management drivers, e.g., fertilization and decreasing grazing intensity, through

100 decreased livestock numbers (Chang *et al.*, 2015b). Yet, the quantitative contribution of these
101 drivers and their interactions, to the observed NPP and NBP trends are not clearly understood.

102 In this study, we use the ORCHIDEE-GM Version 2.1 managed grassland model to analyze
103 the overall trend of NBP of European grasslands during the past two decades. We separate the
104 effects of changes in management, i.e., grassland management intensity (including
105 abandonment, grazing intensity decrease or intensification, and change in fertilizer usage),
106 and new grassland establishment (land-cover change) from the effects of observed external
107 drivers, i.e., climate change, rising CO₂ and nitrogen deposition.

108

109 **Material and methods**

110

111 *Model description*

112

113 ORCHIDEE is a process-based ecosystem model for simulating carbon cycling in
114 ecosystems, and water and energy fluxes from site-level to global scale (Krinner *et al.*, 2005;
115 Ciais *et al.*, 2005; Piao *et al.*, 2007). ORCHIDEE-GM (Chang *et al.*, 2013) is a version of
116 ORCHIDEE specifically developed to study grassland management. It incorporates a
117 grassland module from the PaSim model (Reido *et al.*, 1998; Vuichard *et al.*, 2007a,b; Graux
118 *et al.*, 2011). ORCHIDEE-GM Version 1 was evaluated and some of its parameters calibrated
119 using eddy covariance NEE and biomass measurements from 11 European grassland sites
120 representative of a range of management practices. The model simulated the average NBP of
121 these managed grasslands as $37 \pm 30 \text{ g C m}^{-2} \text{ yr}^{-1}$, $P < 0.01$; Chang *et al.*, 2013). At
122 continental scale, ORCHIDEE-GM Version 2.1 was first applied over Europe to calculate the
123 spatial pattern, long-term evolution and interannual variability of potential productivity
124 (potential productivity is the productivity resulting from the optimal management regime that
125 maximizes livestock densities; Chang *et al.*, 2015a). Chang *et al.* (2015a) further added a new
126 parameterization to describe an adaptive management strategy whereby farmers react to a
127 climate-driven change of previous-year productivity. Though a full nitrogen cycle is not
128 included in ORCHIDEE-GM, the positive effect of nitrogen addition on grass photosynthesis,
129 and thus on subsequent ecosystem carbon balances, is parameterized with a simple empirical
130 function calibrated from literature estimates (Chang *et al.*, 2015a). In a recent study,
131 ORCHIDEE-GM Version 2.1 was used to simulate long-term NBP changes over European
132 grasslands during the past five decades, indicating an enhancement of the C sink over the

133 period 1991-2010 (with an NBP increasing rate of $1.83 \pm 0.30 \text{ g C m}^{-2} \text{ yr}^{-2}$, $P = 0.07$; Chang *et*
134 *al.*, 2015b).

135

136 *Simulation set-up*

137

138 Five drivers were considered for their impact on modeled NBP trend: 1) climate change, 2)
139 rising global CO₂ concentration, 3) changes of nitrogen addition (including fertilization and
140 atmospheric deposition), 4) land-cover change related to new grassland establishment and 5)
141 the changes in grassland management intensity, through the observed reduction of ruminant
142 livestock density (Chang *et al.*, 2015b). These drivers were prescribed in ORCHIDEE-GM.
143 Harmonized climate forcing data were taken from the ERA-WATCH reanalysis for the period
144 1901–2010, at a spatial resolution of 25 km × 25 km (Beer *et al.*, 2014). Global atmospheric
145 CO₂ concentration was from the combination of ice core records and atmospheric
146 observations assembled by Keeling *et al.* (2009 and update). Yearly gridded mineral fertilizer
147 and manure nitrogen application rates for grasslands in the European Union (EU27) were
148 estimated by the CAPRI model (Leip *et al.*, 2011, 2014) based on combined information from
149 different data sources such as Eurostat, FAOstat and OECD, and spatially dis-aggregated
150 using the methodology described by Leip *et al.* (2008). Gridded atmospheric nitrogen
151 deposition rates for Europe from the European Monitoring & Evaluation Program (EMEP)
152 data set were downloaded from the EU-PF7 GHG-Europe project (data available at
153 <http://gaia.agraria.unitus.it/ghg-europe/data/others-data>) with the decadal means linearly
154 interpolated to annual values.

155 Maps of changing grassland management intensity at 25 km resolution were constructed to
156 drive the model with yearly changes in relative management intensity (fraction of extensively

157 versus intensively managed grasslands) from 1961 to 2010, constrained by the total forage
158 requirement of grass-fed livestock numbers (see Chang *et al.*, 2015b for a detailed explanation
159 of the calculation of the forage requirement and the diagnostic of the fraction of animals that
160 receive complementary crop feed products). These maps were incorporated into the *HILDA*
161 land-cover data set (Fuchs *et al.*, 2013) to form enhanced historic land-cover maps delineating
162 grassland management intensity and land-cover transitions (Chang *et al.*, 2015b). Here if a
163 fraction of grasslands in a 25 km grid cell is converted into another biome, it is no longer
164 counted in the simulated NBP of grasslands, even though ORCHIDEE-GM simulates the C
165 balance of the new biome. If a fraction of new grassland is created in a grid cell it is
166 incorporated into the NBP by calculating at each time step the C balance of soils from the
167 previous ecosystem to which new litter input from grassland is added.

168 The management intensity maps used above are constrained by the total forage requirement of
169 grass-fed livestock numbers converted from the metabolizable energy (ME) requirement. The
170 calculation of ME requirement depends on animal performance data such as liveweight and
171 average daily milk production for each animal category (see Supporting Information Text S1
172 from Chang *et al.*, 2015b), and a typical energy density of the feed suggested by IPCC (2006)
173 is applied to convert energy requirement to forage requirement for the whole period 1961-
174 2010. An assumption underlying the above calculations is that both ruminant diet composition
175 (i.e., the fraction of arable crop-feed, crop by-products, and grass forage) and feed conversion
176 efficiency (i.e., the animals' efficiency at converting feed mass into increases of the desired
177 animal products such as meat and milk; referred to as FCE hereafter) are kept constant during
178 the period 1961-2010. However, feedstuffs (including arable crop and crop by-products used
179 to feed farm animals) have varied in the past, and FCE is changing due to the improved and
180 balanced feeding practices and improved breeding which enable more of the feed to go to
181 meat and milk production rather than to maintenance of the animals (Bouwman *et al.*, 2005).

182 By applying a simple feed model (Ciais *et al.*, 2007), grain-feed consumption per ruminant
183 animal (including maize and other cereal grain used as feedstuff) is estimated to have been
184 increasing rapidly over the past two decades (see Supporting Information Text S1 for detail),
185 which indicates a possible decrease in the fraction of grass forage in ruminant diet (i.e., a
186 decline in grass-based feed consumption per ruminant animal; here, grass-based feed includes
187 fresh grass, hay and silage) during the same period. However, the fraction of grass-based feed
188 in the ruminant diet cannot be calculated simply by subtracting feedstuff fractions in ruminant
189 diet, because 1) the feedstuffs considered in this study are not complete; and 2) the simple
190 feed model developed by Ciais *et al.* (2007) is purely diagnostic (based on animal and
191 production data and a set of rules) thus it cannot produce by itself an increasing share of crop-
192 based feed (unless it is in the input data). In addition, data on the past development of FCE do
193 not exist for all European countries.

194 Given: 1) the increasing grain-feed consumption per ruminant livestock, and 2) the possible
195 growth of FCE (Bouwman *et al.*, 2005), we can make a new assumption to account for their
196 impact on changes in total grass forage requirement and further on changes in grassland
197 management intensity during the two most recent decades. The above two facts together are
198 assumed to be fully responsible for the increase in meat and milk productivities of ruminant
199 livestock after 1991, which implies the meat and milk productivities of ruminant livestock are
200 kept constant in the calculation of the ME requirement (dashed lines in Fig. S1 as an example
201 of beef cattle and cows). The new estimate of ME requirement is then used to calculate the
202 observed grass-fed livestock numbers (dashed lines in Fig. S2), and further, to establish the
203 new maps of changing grassland management intensity considering changes in crop-based
204 feed per animal and FCE. The newly calculated observed grass-fed livestock numbers show a
205 stronger decline (-25% in Livestock Units, LU) compared to the ones that do not consider the
206 increase in crop-based feed consumption per animal and the growth in FCE (-18% in LU).

207 These new management intensity maps were also incorporated into the *HILDA* land-cover
208 data set (Fuchs *et al.*, 2013) to form a new version (Version 2) of the enhanced historic land-
209 cover maps delineating grassland management intensity. The original maps with constant
210 ruminant diet composition and FCE from Chang *et al.* (2015b) will be referred as Version 1
211 hereafter.

212 To assess the contribution of each of the five drivers (management intensity, land-cover
213 change that forms new grasslands, climate change, rising CO₂ and changes in nitrogen
214 addition) and possible interactions between them, we generated a series of ORCHIDEE-GM
215 factorial simulations where one driver remains fixed while the others vary during the period
216 1991-2010. The simulation protocol is shown in Fig. 1. For the spin-up and the historic
217 simulation (before 1991), the simulation was carried out exactly as detailed by Chang *et al.*
218 (2015b) so that carbon stocks and fluxes in the starting year are already out of equilibrium,
219 accounting for previous management, climate, nitrogen and CO₂ history. ORCHIDEE-GM
220 was then run on each grid point at 25 km resolution during the period 1991-2010 forced by
221 increasing CO₂, observed climate variability and nitrogen addition, with the adaptive
222 management change algorithm described by Chang *et al.* (2015a), gridded land-cover change
223 and annual changes in grassland management, but with constant ruminant diet composition
224 and FCE (Version 1). The simulation with all drivers varying defines the control experiment
225 (E_{CTL}). All the factorial sensitivity simulations are carried out for the period 1991-2010,
226 starting from the same state (year 1991) as in E_{CTL} (e.g., soil and vegetation carbon pools,
227 optimal animal stocking rates (S_{opt}), and management intensity maps). In each factorial
228 simulation ($E1$ to $E5$; Fig. 1), one of the five drivers is held constant at its value in year 1991,
229 while all other drivers vary as in the control run. In the case of the “constant climate” driver
230 ($E1$), in order to keep interannual variability, we cycled the climate fields from years 1991 to
231 1995 in a loop. Another set of simulations (Set-2, indicated with a prime, viz: E_{CTL}' and $E1'$ to

232 *E5'*) were conducted with the same protocol described above, but using the grassland
233 management intensity maps Version 2. Differences between the two sets of simulations allow
234 us to assess the contribution of each of the five drivers over the full range of uncertainty due
235 to the time-variable ruminant diet composition and FCE. All results from simulation Set-2
236 (i.e., using Version 2 of the historic management and land-cover change maps; E_{CTL}' and EI'
237 to *E5'*) will be marked “in Set-2”.

238

239 *Trends in the drivers during past two decades*

240

241 During the period 1991-2010, mean annual temperature increased in Europe. The fastest rates
242 were found in southern Spain and southeastern Europe (Bulgaria and Romania), where the
243 warming rate was 0.7 °C per decade (Fig. S3a). Concurrently, total annual precipitation
244 increased in many regions of Europe, but a decline in precipitation occurred in the west of
245 Ireland, north of Spain, southern France, and the west of Italy and Austria (Fig. S3b).

246 Large amount of nitrogen fertilizer (more than 60 kg N ha⁻¹ yr⁻¹ typically) have been applied
247 to grassland in Germany, the Netherlands, Belgium, Luxembourg, France and Ireland,
248 whereas application rates have remained low in other regions (mostly less than 40 kg N ha⁻¹
249 yr⁻¹; see Fig. S1 of Chang *et al.*, 2015a). A decrease in nitrogen fertilization during the period
250 1991-2000 is present in the gridded nitrogen addition maps used as input to ORCHIDEE-GM
251 (Fig. S3c). According to the European Monitoring & Evaluation Programme (EMEP) data set
252 cited above, atmospheric nitrogen deposition rates for Europe increased over part of western
253 Europe during the period 1991-2000, but decreased over eastern Europe for the same period
254 (Fig. S3d).

255 According to the *HILDA* land-cover data set, the area of grassland remained fairly stable
256 during the period 1991-2000 in northern and western Europe, but increased in Portugal, Spain,
257 Italy and eastern Europe countries; it decreased in Slovenia (Fig. S3e). In parallel, a decline in
258 the area of grassland in the Czech Republic is shown in this satellite-derived data set, but this
259 may not be real, because an extension in pasture during the period 1990-2000 may be
260 expected due to government policies to keep farmland managed as pasture wherever possible
261 (EEA, 2005). Ruminant livestock numbers have been reduced by 17% during the period
262 1991-2010 in Europe (EU28 plus Norway and Switzerland; FAOstat). Large reductions took
263 place in eastern European countries (Fig. S3f) in response to the major political changes
264 which happened in the early 1990s. The reduction in ruminant livestock numbers as well as
265 the change in grassland area during the past two decades has mainly driven a transition from
266 intensively managed grasslands to more extensively managed ones (Fig. S3g). This transition
267 is even more severe (Fig. S3h) when the lower grass forage requirement is considered (i.e.,
268 less grass-fed livestock numbers; dashed line in Fig. S2), i.e., the possible decrease of grass-
269 feed fraction in ruminant diet (given the increasing grain-feed consumption per ruminant
270 animal; Fig. S4c) and the growth in FCE (Bouwman *et al.*, 2005).

271

272 *Carbon balance of European grasslands*

273

274 The net ecosystem production (NEP) is defined hereafter as the difference between gross
275 primary production (GPP) and ecosystem respiration (R_{eco}) as suggested by Chapin *et al.*
276 (2006):

$$277 \quad NEP = GPP - R_{eco} \quad (1)$$

278 where R_{eco} is the respiration of all organisms including autotrophic respiration (R_a) by primary
279 producers and heterotrophic respiration (R_h) by heterotrophic organisms (microbes in animals'
280 digestive systems, and microbes in soils). Since net primary production (NPP) is defined as
281 GPP minus R_a , NEP thus can also be expressed as:

$$282 \quad NEP = NPP - R_h \quad (2)$$

283 R_h simulated by ORCHIDEE-GM is defined by heterotrophic respiration caused by grazing
284 animals (microbes living in animals' digestive systems) and by soil microbes. A positive NEP
285 value indicates a net removal (sink) of atmospheric CO₂. Note that in ORCHIDEE-GM there
286 is no explicit representation of microbial biomass but rather the model uses first order kinetics
287 to represent the decomposition of organic matter (Krinner *et al.*, 2005).

288 NBP denotes the total rate of C accumulation (or loss) from ecosystems at large spatial scales
289 (e.g., a grid cell of 25 km or a region), and is defined by:

$$290 \quad NBP = NEP + C_{input} - C_{export} \quad (3)$$

291 where C_{input} is the flux of C entering the grassland ecosystem through manure and/or slurry
292 application, and C_{export} is the total C lost from the grassland ecosystem through plant biomass
293 export (mowing), and CH₄ emissions by grazing animals. C_{export} through milk production and
294 animal body-mass increase is not determined and will be neglected for the calculation of NBP,
295 which has only marginal effect on the NBP estimate (Chang *et al.*, 2015b). It must be noted
296 that C lost through dissolved organic (DOC) and carbonate-borne inorganic (carbonate-borne
297 DIC) leaching to rivers is not determined and will also be neglected for this study in the
298 estimation of NBP, whereas biogenic DIC (formed by CO₂ from soil respiration, including R_a
299 by root and R_h by heterotrophic organisms; Kindler *et al.*, 2011) has been implicitly accounted
300 for in the simulated R_a and R_h fluxes to the atmosphere.

301

302 *Attribution method of NBP trends*

303

304 The net effect of a factor or driver x , is defined as the difference of NBP trend between the
305 control simulation and each factorial simulation, Δ_x , as:

$$306 \quad \Delta_x = \dot{NBP}_{CTL} - \dot{NBP}_x \quad (4)$$

307 where \dot{NBP}_{CTL} is the NBP linear trend during 1991-2010 from the control simulation where all
308 drivers including x are varied, and \dot{NBP}_x is the NBP linear trend of simulation x where only
309 this driver remains fixed. Therefore, $\Delta_{climate}$, Δ_{CO_2} , $\Delta_{nitrogen}$, Δ_{LCC} and $\Delta_{management}$ are here the
310 individual effects of changes in climate, CO₂, nitrogen fertilization, grassland area (new
311 grasslands produced from land-cover change; LCC) and in management intensity on the NBP
312 linear trend. The sum of individual effects can be less than or more than the effect of all the
313 factors taken together, due to non-linear interactions, and a residual, non-attributed, is defined
314 as $\Delta_{residual}$. The same attribution method was also used to determine the effect of each factor
315 on the trends of NEP (which can be divided into NPP and R_h), C_{input} and C_{export} .

316

317 **Results**

318

319 *Trends in NBP and in its component*

320

321 During the past two decades, NBP of European grasslands simulated by ORCHIDEE-GM
322 has increased at mean rate of 1.8 to 2.0 (in Set-2) $\text{g C m}^{-2} \text{yr}^{-2}$ (Table 1). Given a decline of
323 carbon input from organic fertilizers (C_{input} ; Table 1 and Fig. 2b), this increasing NBP must
324 come from an enhanced CO_2 fixation (NEP) and/or the reduction of carbon exported as forage
325 and CH_4 emissions by grazing animals (C_{export} ; Table 1 and Fig. 2b). The trend in NEP is
326 derived from the trend of NPP minus the one in R_h (Table 1 and Fig. 2a). A more intense
327 increase in NBP ($2.0 \text{ g C m}^{-2} \text{yr}^{-2}$) found in simulation Set-2 mainly resulted from the faster
328 decrease of C_{export} (with a rate of $-1.2 \text{ g C m}^{-2} \text{yr}^{-2}$; Table 1) caused by the stronger decrease in
329 total forage requirement when accounting for the possible decrease of grass-feed fraction in
330 ruminant diet and the growth in FCE.

331

332 *Attribution of NBP trends to different drivers*

333

334 All drivers considered in this study have the overall effect of increasing NBP (positive trend)
335 for the whole European grassland ecosystem, during the period 1991-2010 (Table 1; Fig. 3).
336 The key result is that changes in grassland management intensity make the largest
337 contribution to the average NBP trend, namely: 0.65 - 0.88 (in Set-2) $\text{g C m}^{-2} \text{yr}^{-2}$, about 36% -
338 43% (in Set-2) of the trend due to all drivers. Management intensity changes alone are

339 estimated to have enhanced soil carbon stocks by 164 - 214 (in Set-2) Tg C in 20 years over
340 1.3×10^6 km² grassland (i.e., 0.23 - 0.30 (in Set-2) Mg CO₂ ha⁻¹ yr⁻¹ when converted to the C
341 sequestration per hectare of grassland). Newly established grassland (increase of grassland
342 area) caused a comparable but lower NBP positive trend of 0.48 (in Set-2) - 0.51 g C m⁻² yr⁻²
343 (24% (in Set-2) - 28% of the trend due to all drivers). The increase in NBP attributed to
344 increasing CO₂ and climate change is 0.54 (in Set-2) - 0.55 g C m⁻² yr⁻² (27% (in Set-2) - 30%
345 of the trend due to all drivers) and 0.54 (in Set-2) - 0.56 g C m⁻² yr⁻² (27% (in Set-2) - 31% of
346 the trend due to all drivers) respectively. The net effect of changes of nitrogen addition is only
347 marginal (2% of the trend due to all drivers). The sum of NBP trends attributed to each driver
348 is larger than the overall NBP trend caused by all drivers, leaving a residual term (about 22%
349 (in Set-2) - 26% of the trend due to all drivers). This residual is due to negative interactions
350 between the effects of the different drivers.

351 Trends of grassland management intensity are also the largest factor explaining C_{export} trends
352 (Table 1). Less intensively managed grassland (Figs S3g and S3h) tends to reduce C_{export}
353 because average stocking rates decrease, which enhances NBP by higher litter-fall and soil
354 carbon storage. Climate change and rising CO₂ concentration both have a positive effect on
355 NEP trends, by enhancing NPP in excess of R_h , but they also tend to increase C_{export} due to a
356 higher NPP being available for forage. Grassland establishment (land-cover change from
357 cropland/forest to grassland) has a moderate and positive effect on NEP, however, because R_h
358 decreases more than NPP (Table 1). This lower R_h in newly established grassland is due to the
359 usually lower soil carbon storage of the source land cover, which is usually cropland (Post &
360 Kwon, 2000; Guo & Gifford, 2002). This result depends on the source ecosystem and on the
361 simulation by ORCHIDEE of its soil C stock. In ORCHIDEE, croplands are harvested so that
362 only a small fraction of biomass returns to the soil; this tends to make soil C stocks lower than
363 those in grasslands.

364

365 *Spatial distribution of NBP trend and its attribution*

366

367 Figure 4 shows the spatial distribution of the simulated trends in NBP across European
368 grasslands during 1991-2010 from simulation Set-1 (the spatial pattern from simulation Set-2
369 is very similar to that of simulation Set-1). The simulated trend of NBP is positive over 80%
370 of European grasslands. After aggregation into the major agricultural regions defined in Table
371 S1 (for details see Olesen & Bindi, 2002), the largest positive NBP trends appear over
372 northeastern, and eastern (Figs 3 and 4) Europe, where decreasing management intensity and
373 grassland establishment are the major causes of positive NBP trends. Positive NBP trends
374 larger than $2.0 \text{ g C m}^{-2} \text{ yr}^{-2}$ were also found in the British Isles and southeastern Europe,
375 where changes in grassland management intensity play the most important role in explaining
376 positive NBP trends. In the British Isles climate change has the largest positive effect
377 compared to other regions of Europe (Figs 3 and 5a). It is noteworthy that in the British Isles,
378 the sum of the five effects is 49% (in Set-2) - 50% larger than the NBP trend obtained in the
379 control simulation (NBP_{CTL}), suggesting a strong negative effect due to their interactions (Fig.
380 3). Not all the regions show an increasing NBP, and we obtained a decline of NBP (negative
381 trend) in northwest Germany, France, Spain and southwest Romania (Fig. 4). A moderate
382 NBP increase was simulated in alpine regions attributed to the effect of rising CO_2 and
383 changes in management intensity.

384 Within the five drivers considered in this study, changes in management intensity (mainly
385 changing from intensively managed grasslands to extensively managed ones; Chang *et al.*,
386 2015b) is clearly a major factor causing NBP to increase in those regions where it did (e.g.,
387 the British Isles, alpine regions, and eastern EU countries; Figs 3 and 5d). It caused

388 simultaneously a decline in NEP which forced NBP to decrease (Fig. 6b), but caused an even
389 stronger reduction of C_{export} , which compensates for decreased NEP and results in a net
390 positive trend in NBP (Fig. 6d). Grassland establishment diagnosed from high resolution land-
391 cover change satellite data has a positive effect on NBP trends over regions where an increase
392 of grassland area happened (Portugal, northeastern, southeastern and eastern European
393 countries, except the Czech Republic; Fig. S3e), but also can have a negative effect on NBP
394 trends, as in Finland (Fig. 5c), because the soil C stock of the source ecosystem (forest in
395 Finland) is larger than that of grassland and during 2001-2010 the newly established grassland
396 in Finland was mainly converted from forest. Regionally, climate change can have either a
397 positive or a negative effect on NBP trends (Fig. 5a), mainly through its effect on NEP. This
398 effect can be seen from the similar spatial patterns of NEP trends and NBP trends due to
399 climate change (Fig. 6a). The difference between NBP and NEP trend patterns are located in
400 the most productive grasslands such as in Denmark, the Netherlands, and Belgium, where
401 enhanced C_{export} offsets or even exceeds the effects of enhanced NEP, thus causing a neutral,
402 or negative, effect of climate change on NBP in those regions. Rising CO₂ concentration has a
403 moderate and positive effect all over Europe, whereas changes in nitrogen fertilization only
404 have a marginal effect on NBP trends (Fig. 5b).

405

406 Discussion

407

408 In this study, we attributed the NBP trend over European grasslands to its driving factors
409 through a series of simulations of the ORCHIDEE-GM model separately quantifying the
410 effect of each factor. In summary, four of the five factors considered in this study (except
411 nitrogen addition) resulted into an overall positive effect on the NBP trend, but with different
412 spatial patterns, magnitudes and mechanisms.

413 Climate change during the past two decades was simulated to cause an increase in NBP over
414 European grassland as a whole, by increasing NPP more than R_h (Table 1). However, the
415 effect of recent climate trends can be positive or negative in different regions (Fig. 6a). For
416 example, climate change induced a positive trend of NBP in the Nordic countries and the
417 British Isles, likely from temperature warming, which enhances plant growth and extends the
418 growing-season length in cold environments (Fig. S5). Our modeled positive effect of climate
419 change on productivity (NPP) in the British Isles is consistent with the increasing
420 aboveground live biomass from 1982 to 2006 derived from remote sensing products, which
421 shows positive correlation with annual mean temperature (Xia *et al.*, 2014). In regions where
422 productivity is limited by water stress (Le Houerou *et al.*, 1988; Knapp *et al.*, 2001; Nippert *et*
423 *al.*, 2006), a decline in precipitation by more than 75 mm yr⁻¹ per decade (such as in north
424 Spain, southern France and northeastern Italy, Fig. S3b) or a strong warming by more than 0.7
425 °C per decade (such as in Romania and north Bulgaria) cause drought conditions that reduce
426 productivity and furthermore reduce NBP (Fig. 6a).

427 Elevated CO₂ concentration has the dual effect of increasing leaf photosynthesis and reducing
428 stomatal conductance, thus indirectly increasing soil moisture in unsaturated soils. These
429 effects increase water-use efficiency (Rötter & van de Geijn, 1999) and reduce the

430 consumption of soil moisture by plant transpiration (Soussana & Luescher, 2007). In our
431 simulation, rising CO₂ concentration causes a 4.5% increase in grassland water-use efficiency
432 (defined as the ratio of GPP to transpiration) during the two most recent decades. This
433 increase is calculated from the simulation E1 in which the climate of 1991-1995 is recycled,
434 but CO₂ concentration rises (Fig. 1). Increases in productivity of temperate grassland
435 stimulated by rising CO₂ concentration has been observed in FACE experiments (e.g.,
436 BioCON and Swiss FACE; Ainsworth *et al.*, 2003; Ainsworth & Long, 2005) and also been
437 simulated by ORCHIDEE-GM (Chang *et al.*, 2015a). In a separate test, ORCHIDEE-GM
438 simulated an increase in aboveground dry matter production of C3 grass of 10.7% under
439 elevated CO₂ of 550 ppm (Chang *et al.*, 2015), which is close to that from FACE experiments,
440 e.g., the increase of 10.5% observed by Ainsworth & Long (2005). However, trends and
441 variability in temperature and precipitation, as well as nitrogen limitation, will all interact
442 with the effects of elevated CO₂ in the future to determine actual changes in grassland
443 productivity in response to CO₂ (Jones & Donnelly, 2004; Soussana & Luescher, 2007). The
444 residual effect on NBP trends found in this study (Table 1, Fig. 3) may be partly attributed to
445 these interactions.

446 Application of nitrogen to grassland improves soil nitrogen availability, leading to higher
447 nitrogen concentration in plant leaves, thus enhancing plant growth and productivity (Frink *et*
448 *al.*, 1999). ORCHIDEE-GM accounts for the positive effect of nitrogen addition on
449 photosynthesis (Chang *et al.*, 2015a). However, the effect of nitrogen addition remains
450 marginal, because: 1) the rates of change in nitrogen addition (including fertilization and
451 atmospheric deposition) are small over most European grasslands (within $\pm 6\%$ per decade,
452 Fig. S5b); or 2) nitrogen addition rate is already high throughout the period (e.g., over 100 kg
453 N ha⁻¹ yr⁻¹ in the south of Ireland, France, the Netherlands and eastern Germany; Fig. S6a) in
454 the regions with higher rates of change (more than 6% per decade, Fig. S6b). As a result, the

455 net effect of changes in nitrogen addition (including fertilization and atmospheric deposition)
456 on NBP trends is found to be only marginal. However, this finding may not reflect reality,
457 since our model has only a very simple parameterization of the effects of nitrogen on
458 photosynthesis (Chang *et al.*, 2015a). In fact, omitting nitrogen addition from our model could
459 also have effect on allocation (Poorter *et al.*, 2012), and possibly affect soil organic
460 decomposition and hence heterotrophic respiration (see review by Janssens *et al.*, 2010 for
461 forest).

462 Note that in our simulations, climate change, rising CO₂ concentration and changes in
463 nitrogen addition all impact NBP trends only through their indirect effect on NPP. The NPP
464 change (increase/decrease) will cause a trend of fresh organic C availability to the three soil
465 carbon pools of ORCHIDEE-GM, thus affecting R_h . In our model, R_h depends on the soil
466 organic C formed during the historical period (pre-1991), and on soil temperature and
467 moisture trends. Overall R_h tracks the NPP change, but with a lag. As a result, the
468 nonsynchronous evolution of NPP and R_h causes the NEP trend (and further the NBP trend).
469 However, several other processes that could affect R_h are omitted from our model: 1) the
470 dependence of R_h not only on soil organic C availability, but also on microbes which are
471 assumed to be the direct producer of R_h and whose activity can be temperature dependent
472 (Allison *et al.*, 2010); 2) the priming effect that emphasizes that increased inputs of fresh C
473 (e.g., increased NPP due to climate change, rising CO₂ and nitrogen addition) could stimulate
474 soil microbes to decompose old soil organic matter (Kuzyakov *et al.*, 2000; Kuzyakov, 2010);
475 although an experiment on grassland soil in central France suggested high nutrient availability
476 might reduce the priming effect, thus increase the mean residence time of soil C (Fontaine *et al.*
477 *et al.*, 2011); 3) elevated CO₂ might affect soil microbial community structure (e.g., Janus *et al.*,
478 2005; Carney *et al.*, 2007; Guenet *et al.*, 2012) and possibly enzyme activities (though
479 conflicting effects have been reported; Freeman *et al.*, 2004), might further impact soil

480 organic C decomposition. The soil microbial community structure could alter the temperature
481 sensitivity of R_h (Bradford *et al.*, 2008), and the enzyme activities that are directly responsible
482 for R_h . We need better models of soil C cycling and the representation of these microbial
483 mechanisms should be a high priority in future model development. The CLM microbial
484 model (Wieder *et al.*, 2013) shows one way forward.

485 To avoid the negative side-effects of some farming practices, since 1962 the European Union
486 (EU) has provided various incentives to farmers through the Common Agricultural Policy
487 (European CAP). In 1984 the European Community introduced milk production quotas that
488 contributed to a reduction in the dairy cow population in Europe. This was followed in 1991
489 by the Nitrates Directive (91/676/EEC) that restricted the application of animal manure in
490 “nitrate vulnerable zones” (46.7% of EU-27 land area in 2012; European Commission, 2013)
491 to a maximum of 170 kg N ha⁻¹ yr⁻¹, effectively capping livestock density in pastures at some
492 1.7 livestock units (LU) per hectare (Annex 1 in Webb *et al.*, 2011). In 1992, the incentives of
493 CAP shifted from price support to direct aid payments to farmers who withdraw land from
494 production and further limit stocking levels. As a result of these policies, the livestock
495 numbers in Europe have decreased. In addition, major political changes in eastern and central
496 Europe also resulted in wet grasslands being abandoned (Joyce, 2014). The European-wide
497 livestock numbers declined by more than 17% during the period 1991-2010 (FAOstat),
498 reducing the requirement for grass forage and for the grassland C balance, less forage means
499 less C export and thus increasing NBP. Our simulation is forced by the observed decrease of
500 grass-fed livestock numbers (decline by 18% - 25% (in Set-2); Figs S1 and S2) in each
501 European region, and takes into account the NBP response to a less intensive grassland
502 management through its constraint that the total forage requirement of grass-fed livestock
503 must be satisfied by grass NPP (cut and grazed). Without harvest by mowing or grazing,
504 grasslands with less animals can have higher leaf area index (LAI), thus higher NPP than

505 more intensively managed ones (Joyce, 2014; also see Chang *et al.*, 2015b). In this study, we
506 simulated an annual mean LAI of extensively managed grassland 26% higher than that of
507 intensively managed grassland over Europe (data averaged for the period 1991-2010). The
508 extra C taken up would be accumulated in soil as litter instead of being exported as forage.
509 Litter has a relatively longer turnover time than forage (most forage C is consumed then
510 returned to atmosphere within one year). As a result, the changes in grassland management in
511 Europe, characterized by changing from intensively to extensively managed grassland (Fig.
512 S2; Figs S3f, g and h) are able to cause enhanced sequestration of C in soil (NBP increase).
513 Furthermore, during the transition from intensively to extensively managed grassland,
514 nitrogen accumulated in managed grassland soils (e.g., due to fertilization) may maintain a
515 high productivity (i.e., NPP) for some years. This residual effect of nitrogen fertilization on
516 productivity was not taken into account because the nitrogen-effects on photosynthesis in
517 ORCHIDEE-GM (Chang *et al.*, 2015a) will immediately stop when grassland is converted to
518 extensive management. In this case, our model may underestimate the NPP increase caused
519 by decline in management intensity, and further underestimate the positive trend of NEP and
520 NBP in the control simulation (NBP_{CTL}). It implies the effect of changes in management
521 intensity in reality could be even larger than that estimated here (given by Eqn 4: $NBP_{CTL} -$
522 $NBP_{management}$; about 36% - 43% (in Set-2) of the trend due to all drivers). Thus again, fully
523 accounting for the nitrogen cycle is required to produce better estimates of the grassland C
524 balance and its trend. Nevertheless, a large portion of the NBP trend (36% - 43% of the trend
525 due to all drivers) can be attributed to the reduction of grassland management intensity in
526 Europe, that is probably caused by changes in policy and socio-economic influences. As far
527 as we are aware this is the first instance of a modeling study revealing the impact of policy on
528 the C balance of European grasslands.

529 ORCHIDEE-GM estimates an average NBP of 19 to 21 (in Set-2) ± 7 gC m⁻² yr⁻¹ in the most
530 recent two decades -- a cumulative C sink of 1.8 to 1.9 (in Set-2) ± 0.7 gigatonnes (Gt) CO₂
531 over about 1.3×10^6 km² for European grasslands during 1991-2010 (EU28 plus Norway and
532 Switzerland). This amount offsets about 10% of total greenhouse gases (GHGs) emissions in
533 the whole agricultural sector during this period (a total of 17.3 Gt CO₂ equivalent from 1991-
534 2010 including CO₂, CH₄ and N₂O emissions; data from FAOstat). With respect to European
535 grassland ecosystems, changes in grassland management alone were estimated to have
536 enhanced the soil C sequestration during the 20-year period studied by 0.60 - 0.79 (in Set-2)
537 Gt CO₂ and to have simultaneously reduced CH₄ and N₂O emissions by 0.42 – 0.48 (in Set-2)
538 Gt CO₂-equivalent and by 0.22 - 0.27 (in Set-2) Gt CO₂-equivalent respectively, offsetting 7%
539 - 9% (in Set-2) of GHG emissions in the whole agricultural sector during this period, making
540 a substantial contribution to climate change mitigation (Ripple *et al.*, 2014).

541 The C sequestration enhanced by changes in grassland management alone (0.23 - 0.30 Mg
542 CO₂ ha⁻¹ yr⁻¹) is close to the C sequestration potential from optimizing grazing management
543 for rangeland estimated by Henderson *et al.* (2015), which is 0.17 – 0.32 Mg CO₂ ha⁻¹ yr⁻¹ (to
544 be consistent in regions considered by Henderson *et al.* (2015), values in western Europe and
545 in eastern Europe and Russia were used), but higher than that for pasture in the same
546 estimation (0.03 – 0.05 Mg CO₂ ha⁻¹ yr⁻¹). It is noteworthy that the area of amenable grassland
547 in Henderson *et al.*, 2015 is only 13% of grassland area in our simulation. Our estimation is
548 also within the range of the global mean C sequestration potential due to grazing management
549 (per hectare bases) reported by Lal (2004; 0.18 - 0.55 Mg CO₂ ha⁻¹ yr⁻¹) and Smith *et al.*
550 (2008; 0.11-0.81 Mg CO₂ ha⁻¹ yr⁻¹), while the value from Smith *et al.* (2008) considered a
551 broader range of practices (grazing, fertilization and fire). Furthermore, the differences
552 between our estimate and that from literature above should be kept in mind: 1) in this study,
553 the C sequestration enhanced by changes in management intensity accounts for climate

554 change, rising CO₂ and a simple management change constrained simply by historic grass
555 forage requirement; 2) Henderson *et al.* (2015) estimated C sequestration potential that could
556 be achieved by optimizing grazing management based on assumed grazing management
557 scenarios, and considered climate change at 0.5° resolution; 3) the C sequestration potential
558 estimated by Lal (2004) and Smith *et al.* (2008) are data-based (e.g., based on a small number
559 of field studies), but didn't include the climate and CO₂ perturbation (i.e., they did not use
560 gridded simulations accounting for climate gradients across a domain). Thus our estimate and
561 the previous estimates above could be quite complementary allowing a better view to be
562 developed of the role of grassland management on the C balance and further on GHG
563 mitigation.

564 Soil carbon stocks increased because of decreased management intensity in our control
565 simulation (originating from the combination of reduced ruminant livestock numbers and the
566 changes in grassland area, where only the new grasslands creation were considered; Fig. S3e
567 to h). Carbon sequestration efficiency due to changes of ruminant livestock density can thus
568 be calculated as the ratio between NBP trend due to changes in management ($\Delta_{management}$, see
569 '*Attribution method of NBP trends*' for detail) and trend of livestock density (Table 2). Here,
570 $\Delta_{management}$ is the individual effect of changes in grassland management intensity on the NBP
571 linear trend; livestock density over grassland is calculated as the ratio of grass-fed livestock
572 numbers to grassland area; and carbon sequestration efficiency due to changes of ruminant
573 livestock density measures how much extra C can be sequestered in grassland soil per each
574 LU reduction of livestock numbers. Averaged over European grasslands, a unit LU reduction
575 of livestock numbers is able to enhance soil C sequestration by 1016 (in Set-2) - 1131 kg C
576 per year (i.e., with carbon sequestration efficiency of 1016 (in Set-2) - 1131 kg C LU⁻¹ yr⁻¹).
577 This reduction indicates a substantial contribution to GHG mitigation (Ripple *et al.*, 2014).
578 High sequestration efficiency was found in the Nordic countries, the British Isles, alpine

579 regions, southeastern and eastern regions, suggesting grassland ecosystems in these regions
580 can benefit more, with regards to GHG mitigation, from each unit of livestock numbers
581 reduction. However, the sequestration efficiency in the Nordic countries, the British Isles, and
582 alpine regions from the simulation Set-1 are not given, and should be neglected because the
583 too-low trends in livestock density (e.g., lower than $-0.2 \text{ LU km}^{-2} \text{ yr}^{-1}$) might cause
584 unrealistically high sequestration efficiency. Grassland ecosystems in western, Mediterranean,
585 and northeastern regions of Europe can also benefit from livestock number reduction of
586 moderate magnitude.

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590

591 **Reference:**

- 592 Ainsworth EA, Davey PA, Hymus GJ, *et al.* (2003) Is stimulation of leaf photosynthesis by
593 elevated carbon dioxide concentration maintained in the long term? A test with *Lolium*
594 *perenne* grown for 10 years at two nitrogen fertilization levels under Free Air CO₂
595 Enrichment (FACE). *Plant Cell and Environment*, **26**, 705-714.
- 596 Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO₂
597 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis,
598 canopy. *New Phytologist*, **165**, 351-371.
- 599 Allison SD, Wallenstein MD, Bradford MA (2010) Soil-carbon response to warming
600 dependent on microbial physiology. *Nature Geoscience*, **3**, 336-340.
- 601 Beer C, Weber U, Tomelleri E, Carvalhais N, Mahecha M, Reichstein M (2014) Harmonized
602 European Long-Term Climate Data for Assessing the Effect of Changing Temporal
603 Variability on Land-Atmosphere CO₂ Fluxes. *Journal of Climate*, **27**, 4815-4834.
- 604 Bouwman AF, Van der Hoek KW, Eickhout B, Soenario I (2005) Exploring changes in world
605 ruminant production systems. *Agricultural Systems*, **84**, 121-153.
- 606 Bradford MA, Davies CA, Frey SD, *et al.* (2008) Thermal adaptation of soil microbial
607 respiration to elevated temperature. *Ecology Letters*, **11**, 1316-1327.
- 608 Buchmann N, Schulze ED (1999) Net CO₂ and H₂O fluxes of terrestrial ecosystems. *Global*
609 *Biogeochemical Cycles*, **13**, 751-760.
- 610 Carney KM, Hungate BA, Drake BG, Megonigal JP (2007) Altered soil microbial community
611 at elevated CO₂ leads to loss of soil carbon. *Proceedings of the National Academy of*
612 *Sciences of the United States of America*, **104**, 4990-4995.

613 Chang JF, Ciais P, Viovy N, Vuichard N, Sultan B, Soussana J-F (2015b) The greenhouse
614 gas balance of European grasslands. *Global Change Biology*, doi:10.1111/gcb.12998.

615 Chang JF, Viovy N, Vuichard N, *et al.* (2013) Incorporating grassland management in
616 ORCHIDEE: model description and evaluation at 11 eddy-covariance sites in Europe.
617 *Geoscientific Model Development*, **6**, 2165-2181.

618 Chang JF, Viovy N, Vuichard N, *et al.* (2015a) Modeled changes in potential grassland
619 productivity and in ruminant livestock density in Europe over 1961-2010. *PLoS One*,
620 **10**, e0127554, doi: 10.1371/journal.pone.0127554.

621 Chapin FS, III, Woodwell GM, Randerson JT, *et al.* (2006) Reconciling carbon-cycle
622 concepts, terminology, and methods. *Ecosystems*, **9**, 1041-1050.

623 Ciais P, Bousquet P, Freibauer A, Naegler T (2007) Horizontal displacement of carbon
624 associated with agriculture and its impacts on atmospheric CO₂. *Global
625 Biogeochemical Cycles*, **21**, GB2014, doi:10.1029/2006GB002741.

626 Ciais P, Reichstein M, Viovy N, *et al.* (2005) Europe-wide reduction in primary productivity
627 caused by the heat and drought in 2003. *Nature*, **437**, 529-533.

628 EEA (European Environment Agency) (2005) The European environment – State and outlook.
629 576 pp. pp. 49

630 European Commission (2013) Commission Staff Working Document Accompanying the
631 document Report From The Commission To The Council And The European
632 Parliament on the implementation of Council Directive 91/676/EEC concerning the
633 protection of waters against pollution caused by nitrates from agricultural sources
634 based on Member State reports for the period 2008-2011 {COM(2013) 683 final}

635 European Common Agricultural Policy (CAP) <http://ec.europa.eu/agriculture/cap-post-2013/>

636 FAOstat (2013) <http://faostat3.fao.org>

637 Fontaine S, Henault C, Aamor A, *et al.* (2011) Fungi mediate long term sequestration of
638 carbon and nitrogen in soil through their priming effect. *Soil Biology & Biochemistry*,
639 **43**, 86-96.

640 Freeman C, Kim SY, Lee SH, Kang H (2004) Effects of elevated atmospheric CO₂
641 concentrations on soil microorganisms. *Journal of Microbiology*, **42**, 267-277.

642 Frink CR, Waggoner PE, Ausubel JH (1999) Nitrogen fertilizer: Retrospect and prospect.
643 *Proceedings of the National Academy of Sciences of the United States of America*, **96**,
644 1175-1180.

645 Fuchs R, Herold M, Verburg PH, Clevers JGPW (2013) A high-resolution and harmonized
646 model approach for reconstructing and analysing historic land changes in Europe.
647 *Biogeosciences*, **10**, 1543-1559.

648 Graux AI, Gaurut M, Agabriel J, Baumont R, Delagarde R, Delaby L, Soussana J-F (2011)
649 Development of the Pasture Simulation Model for assessing livestock production
650 under climate change. *Agriculture Ecosystems & Environment*, **144**, 69-91.

651 Guenet B, Lenhart K, Leloup J, *et al.* (2012) The impact of long-term CO₂ enrichment and
652 moisture levels on soil microbial community structure and enzyme activities.
653 *Geoderma*, **170**, 331-336.

654 Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: a meta analysis. *Global*
655 *Change Biology*, **8**, 345-360.

- 656 Henderson BB, Gerber PJ, Hilinski TE, *et al.* (2015) Greenhouse gas mitigation potential of
657 the world's grazing lands: Modeling soil carbon and nitrogen fluxes of mitigation
658 practices. *Agriculture, Ecosystems & Environment*, **207**, 91-100.
- 659 Janus LR, Angeloni NL, McCormack J, Rier ST, Tuchman NC, Kelly JJ (2005) Elevated
660 atmospheric CO₂ alters soil microbial communities associated with trembling aspen
661 (*Populus tremuloides*) roots. *Microbial Ecology*, **50**, 102-109.
- 662 Jones MB, Donnelly A (2004) Carbon sequestration in temperate grassland ecosystems and
663 the influence of management, climate and elevated CO₂. *New Phytologist*, **164**, 423-
664 439.
- 665 Joyce CB (2014) Ecological consequences and restoration potential of abandoned wet
666 grasslands. *Ecological Engineering*, **66**, 91-102.
- 667 Keeling RF, Piper SC, Bollenbacher AF, Walker JS (2009) Atmospheric CO₂ records from
668 sites in the SIO air sampling network. In Trends: A Compendium of Data on Global
669 Change. Carbon Dioxide Information Analysis Center, Oak Ridge National
670 Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., U.S.A. doi:
671 10.3334/CDIAC/atg.035.
- 672 Kindler R, Siemens J, Kaiser K, *et al.* (2011) Dissolved carbon leaching from soil is a crucial
673 component of the net ecosystem carbon balance. *Global Change Biology*, **17**, 1167-
674 1185.
- 675 Knapp AK, Briggs JM, Koelliker JK (2001) Frequency and extent of water limitation to
676 primary production in a mesic temperate grassland. *Ecosystems*, **4**, 19-28.

677 Krinner G, Viovy N, de Noblet-Ducoudre N, *et al.* (2005) A dynamic global vegetation model
678 for studies of the coupled atmosphere-biosphere system. *Global Biogeochemical*
679 *Cycles*, **19**, GB1015, doi: 10.1029/2003GB002199.

680 Kuzyakov Y (2010) Priming effects: Interactions between living and dead organic matter. *Soil*
681 *Biology & Biochemistry*, **42**, 1363-1371.

682 Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of
683 priming effects. *Soil Biology & Biochemistry*, **32**, 1485-1498.

684 Lal R (2004) Soil carbon sequestration to mitigate climate change. *Geoderma*, **123**, 1-22.

685 Le Bauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in
686 terrestrial ecosystems is globally distributed. *Ecology*, **89**, 371-379.

687 Le Houerou HN, Bingham RL, Skerbek W (1988) Relationship between the variability of
688 primary production and the variability of annual precipitation in world arid lands.
689 *Journal of Arid Environments*, **15**, 1-18.

690 Leip A, Britz W, Weiss F, de Vries W (2011) Farm, land, and soil nitrogen budgets for
691 agriculture in Europe calculated with CAPRI. *Environmental Pollution*, **159**, 3243-
692 3253.

693 Leip A, Marchi G, Koeble R, Kempen M, Britz W, Li C (2008) Linking an economic model
694 for European agriculture with a mechanistic model to estimate nitrogen and carbon
695 losses from arable soils in Europe. *Biogeosciences*, **5**, 73-94.

696 Leip A, Weiss F, Lesschen JP, Westhoek H (2014) The nitrogen footprint of food products in
697 the European Union. *Journal of Agricultural Science*, **152**, S20-S33.

698 Melillo JM, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL (1993)
699 Global climate-change and terrestrial net primary production. *Nature*, **363**, 234-240.

700 Nippert JB, Knapp AK, Briggs JM (2006) Intra-annual rainfall variability and grassland
701 productivity: can the past predict the future? *Plant Ecology*, **184**, 65-74.

702 Nitrates Directive (91/676/EEC) <http://eur-lex.europa.eu/>

703 Olesen JE, Bindi M (2002) Consequences of climate change for European agricultural
704 productivity, land use and policy. *European Journal of Agronomy*, **16**, 239-262.

705 Piao S, Friedlingstein P, Ciais P, de Noblet-Ducoudré N, Labat D, Zaehle S (2007) Changes
706 in climate and land use have a larger direct impact than rising CO₂ on global river
707 runoff trends. *Proceedings of the National Academy of Sciences of the United States of*
708 *America*, **104**, 15242-15247.

709 Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to
710 leaves, stems and roots: meta-analyses of interspecific variation and environmental
711 control. *New Phytologist*, **193**, 30-50.

712 Post WM, Kwon KC (2000) Soil carbon sequestration and land-use change: processes and
713 potential. *Global Change Biology*, **6**, 317-327.

714 Riedo M, Grub A, Rosset M, Fuhrer J (1998) A pasture simulation model for dry matter
715 production, and fluxes of carbon, nitrogen, water and energy. *Ecological Modelling*,
716 **105**, 141-183.

717 Ripple WJ, Smith P, Haberl H, Montzka SA, McAlpine C, Boucher DH (2014)
718 COMMENTARY: Ruminants, climate change and climate policy. *Nature Climate*
719 *Change*, **4**, 2-5.

- 720 Rotter R, Van de Geijn SC (1999) Climate change effects on plant growth, crop yield and
721 livestock. *Climatic Change*, **43**, 651-681.
- 722 Rustad LE, Campbell JL, Marion GM, *et al.* (2000) A meta-analysis of the response of soil
723 respiration, net nitrogen mineralization, and aboveground plant growth to
724 experimental ecosystem warming. *Oecologia*, **126**, 543-562.
- 725 Schulze ED, Heimann M (1998) Carbon and water exchange of terrestrial systems, in: Asian
726 change in the context of global change, vol. 3, IGBP Series, edited by: Galloway, J. N.
727 and Melillo, J., Cambridge University Press, Cambridge, 145–161.
- 728 Smith P, Martino D, Cai Z, *et al.* (2008) Greenhouse gas mitigation in agriculture.
729 *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 789-813.
- 730 Soussana JF, Allard V, Pilegaard K, *et al.* (2007) Full accounting of the greenhouse gas (CO₂,
731 N₂O, CH₄) budget of nine European grassland sites. *Agriculture Ecosystems &*
732 *Environment*, **121**, 121-134.
- 733 Soussana JF, Luescher A (2007) Temperate grasslands and global atmospheric change: a
734 review. *Grass and Forage Science*, **62**, 127-134.
- 735 Vuichard N, Ciais P, Viovy N, Calanca P, Soussana J-F (2007a) Estimating the greenhouse
736 gas fluxes of European grasslands with a process-based model: 2. Simulations at the
737 continental level. *Global Biogeochemical Cycles*, **21**, GB1005,
738 doi:10.1029/2005GB002612
- 739 Vuichard N, Soussana J-F, Ciais P, *et al.* (2007b) Estimating the greenhouse gas fluxes of
740 European grasslands with a process-based model: 1. Model evaluation from in situ
741 measurements. *Global Biogeochemical Cycles*, **21**, GB1004,
742 doi:10.1029/2005GB002611.

743 Webb J, Sorensen P, Velthof GL, *et al.* (2011) Study on variation of manure N efficiency
744 throughout Europe. AEA Technology plc, Didcot, 114 pp.

745 Wieder WR, Bonan GB, Allison SD (2013) Global soil carbon projections are improved by
746 modelling microbial processes. *Nature Climate Change*, **3**, 909-912.

747 Xia J, Liu S, Liang S, Chen Y, Xu W, Yuan W (2014) Spatio-Temporal Patterns and Climate
748 Variables Controlling of Biomass Carbon Stock of Global Grassland Ecosystems from
749 1982 to 2006. *Remote Sensing*, **6**, 1783-1802.

750 Xia J, Wan S (2008) Global response patterns of terrestrial plant species to nitrogen addition.
751 *New Phytologist*, **179**, 428-439.

752

753 **Supporting Information Legends**

754 Text S1. The changes in feedstuffs for ruminants.

755 Table S1. Major agricultural regions in Europe (Olesen & Bindi, 2002).

756 Figure S1. The evolution of meat productivity of beef cattle and milk productivity of cows in
757 Europe. Data are averaged for EU28 plus Norway and Switzerland. Solid lines indicate the
758 productivities derived from FAOstat; dashed lines are the constant productivities of ruminant
759 livestock in the new calculation of ME requirement assuming that the growth in feed
760 conversion efficiency is consistent with the increase of meat and milk productivities of
761 ruminant livestock after 1991.

762 Figure S2. Grass-fed livestock numbers in each of major agricultural regions and their
763 evolution during the period 1961-2010. The numbers were converted to livestock unit (LU)
764 based on the calculation of metabolizable energy (ME) requirement of each type of animal
765 with variable (i.e., the growth in feed conversion efficiency is consistent to the increase of
766 meat and milk productivities of ruminant livestock after 1991; dashed lines) or constant (solid
767 lines) feed conversion efficiency.

768 Figure S3. Spatial distribution of the changing rate (linear trends) during the period 1991-
769 2010 in: (a) mean annual temperature, (b) total annual precipitation, (c) nitrogen fertilization,
770 (d) atmospheric nitrogen deposition, (e) grassland area, (f) ruminant livestock numbers and
771 (g) in fraction of intensively managed grassland in total grassland area with constant feed
772 conversion efficiency (FCE) or (h) with assumed changes in FCE. The changing rate in (c)
773 nitrogen fertilization and (d), atmospheric nitrogen deposition are estimated for the period
774 1991-2000, because in the database they are assumed to be constant from 2000 till 2010.
775 Temperature and precipitation were from ERA-WATCH reanalysis climate forcing data at a
776 spatial resolution of 25 km (Beer *et al.*, 2014). Gridded mineral fertilizer and manure nitrogen

777 application rate was estimated by the CAPRI model (Leip *et al.*, 2011, 2014), based on
778 combined information from official and harmonized data sources such as Eurostat, FAOstat
779 and OECD, and spatially dis-aggregated using the methodology described by Leip *et al.*
780 (2008); grassland area was extracted from the HILDA data set (Fuchs *et al.*, 2013); ruminant
781 livestock numbers were taken from FAOstat with annual country-averaged statistical data on
782 major ruminant livestock numbers for dairy cows, beef cattle, sheep and goats; livestock
783 species are converted to livestock unit (LU) based on the calculation of metabolizable energy
784 requirement (see Supplementary Information Text S1 of Chang *et al.*, 2015); fraction of
785 intensively managed grassland in total grassland area is as established by Chang *et al.* (2015),
786 constrained by the total forage requirement (derived from metabolizable energy requirement)
787 of grass-fed livestock numbers.

788 Figure S4. Temporal evolution of (a) total feedstuff products, (b) farm animal numbers, and
789 (c) feedstuff for ruminant and grain-feed consumption per head of ruminant during the last
790 five decades. For the feedstuffs, cereal grains include maize and other cereals; other crop
791 products and by-products included cakes of cereals and oilseeds, brans, and pulses; grain for
792 cattle was the residual grain-feed for cattle after being distributed successively to poultry and
793 pigs using the simple feed model (Ciais *et al.*, 2007). To keep data consistency, the figure
794 shows the total quantities from 23 countries of Europe, where data from Croatia, Czech
795 Republic, Estonia, Latvia, Lithuania, Slovakia, and Slovenia were not included in due to the
796 short period of data availability.

797 Figure S5. Shift in seasonal evolution of grassland GPP during the last two decades in the
798 Nordic countries and the British Isles. The monthly mean GPP of grassland was simulated by
799 ORCHIDEE-GM, aggregated and averaged over each region according to the area and the
800 management intensity (extensively or intensively managed) of grassland in the enhanced
801 historic land-cover maps delineating grassland management intensity (Version 1; see main

802 text section '*Simulation set-up*' for detail). Decadal averages of monthly GPP (for the period
803 1991-2000 and 2001-2010 respectively) were used. GPP: gross primary production.

804 Figure S6. (a) mean nitrogen addition rate over European grassland (including fertilization
805 and atmospheric deposition) and (b) its normalized changing rate during the period 1991-
806 2000. The normalized changing rate of nitrogen addition is calculated as the ratio of changing
807 rate (linear trend) to mean nitrogen addition rate.

808 **Tables**

809 Table 1. Trends in NBP and its components over European grasslands during the period 1991-2010, and the effects of the drivers on these trends.

	Linear trends		Effect of the drivers on the trends				
	(g C m ⁻² yr ⁻²)	Climate forcing	Atmospheric CO ₂ concentration	Nitrogen addition	Grassland area	Grassland management	Residual
<i>NBP</i>	1.8 / 2.0'	0.6 / 0.5'	0.5	0.0	0.5	0.6 / 0.9'	0.5 / 0.4'
<i>NEP</i>	2.0 / 1.9'	0.9	0.8 / 0.7'	0.0	0.5	-0.1	0.1 / 0.0'
<i>C_{export}</i>	-0.1 / -0.4'	0.3	0.2	0.0	-0.1	-0.9 / -1.2'	-0.3 / -0.4'
<i>C_{input}</i>	-0.2 / -0.3'	0.0	0.0	0.0	0.0	-0.2	0.0
<i>NPP</i>	4.7 / 5.0'	2.7	2.0 / 1.9'	0.0	-0.2	0.7 / 1.0'	0.4
<i>R_h</i>	2.7 / 3.1'	1.8	1.2	0.0	-0.7	0.8 / 1.1'	0.3 / 0.4'

810 Note: Values without a prime (') are the results from the simulation Set-1 accounting for the constant ruminant diet composition and feed
811 conversion efficiency; Values with a prime (') are the results from the simulation Set-2 accounting for the varied ruminant diet composition and
812 feed conversion efficiency (section 'Simulation set-up'); when results from the two sets of simulations are the same, only one value will be
813 shown. NEP, net ecosystem production; *C_{export}*, carbon exported from grassland ecosystem as forage and CH₄ emission; *C_{input}*, carbon input by
814 organic fertilizer application; NPP, net primary production; *R_h*, heterotrophic respiration. NEP is defined as the difference between NPP and *R_h*,
815 indicating the CO₂ sequestration from atmosphere.

816 Table 2. Carbon sequestration efficiency due to the changes in livestock density over
 817 European grasslands.

Regions	$\Delta_{management}$ g C m ⁻² yr ⁻²	Trends in livestock density LU km ⁻² yr ⁻¹	C sequestration efficiency kg C LU ⁻¹ yr ⁻¹
Nordic	0.14 / 0.19'	-0.01 / -0.21'	-* / 1612'
British Isles	1.24 / 1.75'	-0.17 / -0.87'	-* / 2013
Western	0.36 / 0.55'	-0.46 / -0.75'	795 / 734'
Mediterranean	0.25 / 0.41'	-0.42 / -0.51'	605 / 795'
Alpine	0.48 / 0.75'	-0.16 / -0.49'	-* / 1539'
North eastern	0.90 / 1.53'	-1.07 / -1.77'	839 / 860'
Sourth eastern	1.82 / 1.95'	-0.96 / -1.08'	1884 / 1810'
Eastern	2.22 / 2.82'	-1.58 / -2.12'	1398 / 1330'
Total	0.65 / 0.88'	-0.58 / -0.87'	1131 / 1016'

818 * Carbon sequestration efficiency is not given due to the too-low trends in both NBP and/or
 819 livestock density.

820 Note: Values in the $\Delta_{management}$ column are the individual effects of changes in grassland
 821 management intensity on the NBP linear trend; Livestock density over grassland is calculated
 822 as the ratio of grass-fed livestock numbers to grassland area. Values without the prime (')
 823 indicate the results from the simulation Set-1 accounting for the constant ruminant diet
 824 composition and feed conversion efficiency; Values with the prime (') indicate the results
 825 from the simulation Set-2 accounting for the varied ruminant diet composition and feed
 826 conversion efficiency (section '*Simulation set-up*' and Supporting information Text S1 for
 827 detail).

828

829 **Figure legends**

830 Figure 1. Illustration of the simulation protocol and the five factors used as input data for
831 various simulations. E_{CTL} : control simulation with all factors varied; E1–E5: the factorial
832 sensitivity simulations started from the same state (at the end of 1990) as in E_{CTR} , but with
833 one of the five drivers being held constant to the value of year 1991 or cycled in a loop with
834 the climate fields from years 1991 to 1995 (in gray background). The NBP trend during
835 1991-2010 from simulation E_{CTL} , and E1–E5 is expressed as NBP_{CTL} , $NBP_{climate}$, NBP_{CO_2} ,
836 $NBP_{nitrogen}$, NBP_{LCC} , and $NBP_{management}$ respectively.

837 Figure 2. Changes in the components of NBP ((a) NPP and R_h , (b) C_{export} and C_{input}) across
838 European grasslands during the period 1991-2010. NPP: net primary production; R_h :
839 heterotrophic respiration; C_{export} : carbon exported from grassland ecosystem as forage; C_{input} :
840 carbon input by organic fertilizer application. Results are derived from simulation Set-1
841 considering constant ruminant diet composition and feed conversion efficiency.

842 Figure 3. The NBP trends of grassland ecosystems and the effect of each driver considered in
843 this study. The figure shows the results for all the grassland in Europe and for grassland in
844 each major agricultural region (region 1 to 8 as shown in the figure; also see Table S1 for
845 detail). NBP_{CTL} is the NBP trend during 1991-2010 from the control simulation; $\Delta_{climate}$, Δ_{CO_2} ,
846 $\Delta_{nitrogen}$, Δ_{LCC} and $\Delta_{management}$ are the individual effects of climate change, rising CO_2
847 concentration, changes in nitrogen addition, in land cover (grassland area) and in grassland
848 management intensity respectively to the NBP trend. The sum of individual effects can be less
849 than, or more than, the effect of all the factors taken together, due to non-linear interactions,
850 and the residual is defined as $\Delta_{residual}$. Bars filled with solid color indicate the trends and the
851 effects from the simulation Set-1 accounting for the constant ruminant diet composition and
852 feed conversion efficiency; bars filled with parallel lines indicate the trends and the effects
853 from the simulation Set-2 accounting for the varied ruminant diet composition and feed

854 conversion efficiency (section ‘*Simulation set-up*’ and Supporting Information Text S1 for
855 detail).

856 Figure 4. The spatial distribution of linear trends in NBP during the period 1991-2010 derived
857 from simulation Set-1 considering constant ruminant diet composition and feed conversion
858 efficiency.

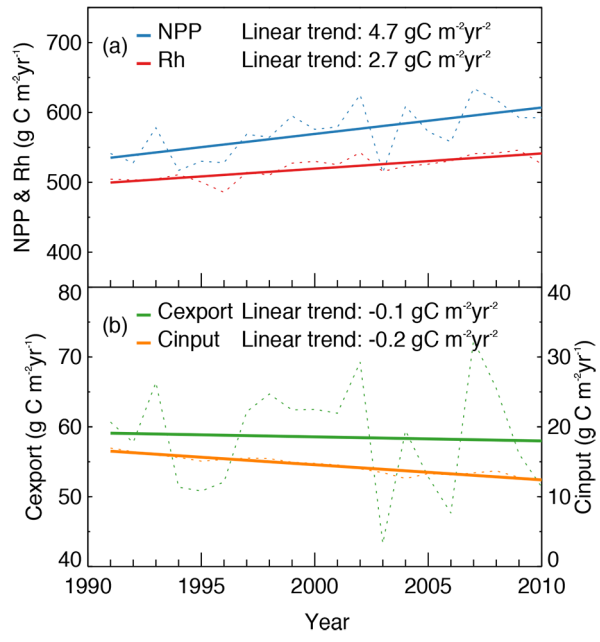
859 Figure 5. Spatial distribution of the trends in NBP due to: (a) climate change, (b) changes in
860 nitrogen fertilization, (c) changes in grassland area, and (d) in grassland management
861 intensity. Grassland management intensity in this study is given by the fraction of extensively
862 versus intensively managed grasslands; the transition between them (i.e., changes in grassland
863 management intensity) is constrained by the total forage requirement of grass-fed livestock
864 numbers (see Chang *et al.*, 2015b for detailed). Results are derived from simulation Set-1
865 considering constant ruminant diet composition and feed conversion efficiency.

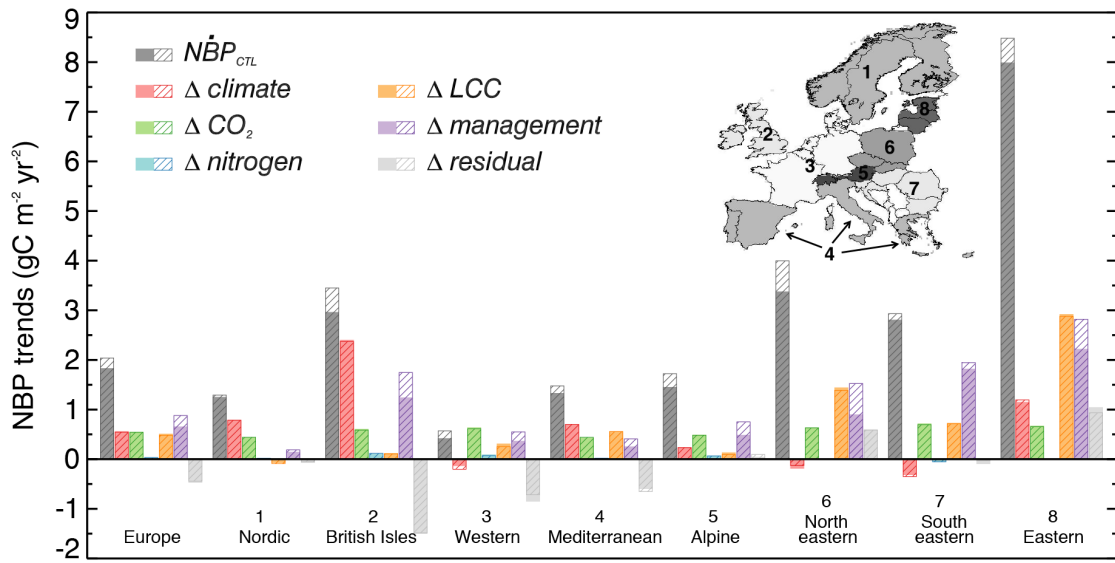
866 Figure 6. Spatial distribution of the trends in: (a and b) NEP and (c and d) C_{export} due to (a
867 and c) climate change and (b and d) changes in grassland management intensity. Grassland
868 management intensity in this study is given by the fraction of extensively versus intensively
869 managed grasslands; the transition between them (i.e., changes in grassland management
870 intensity) is constrained by the total forage requirement of grass-fed livestock numbers (see
871 Chang *et al.*, 2015b for details). Results are derived from simulation Set-1 considering
872 constant ruminant diet composition and feed conversion efficiency.

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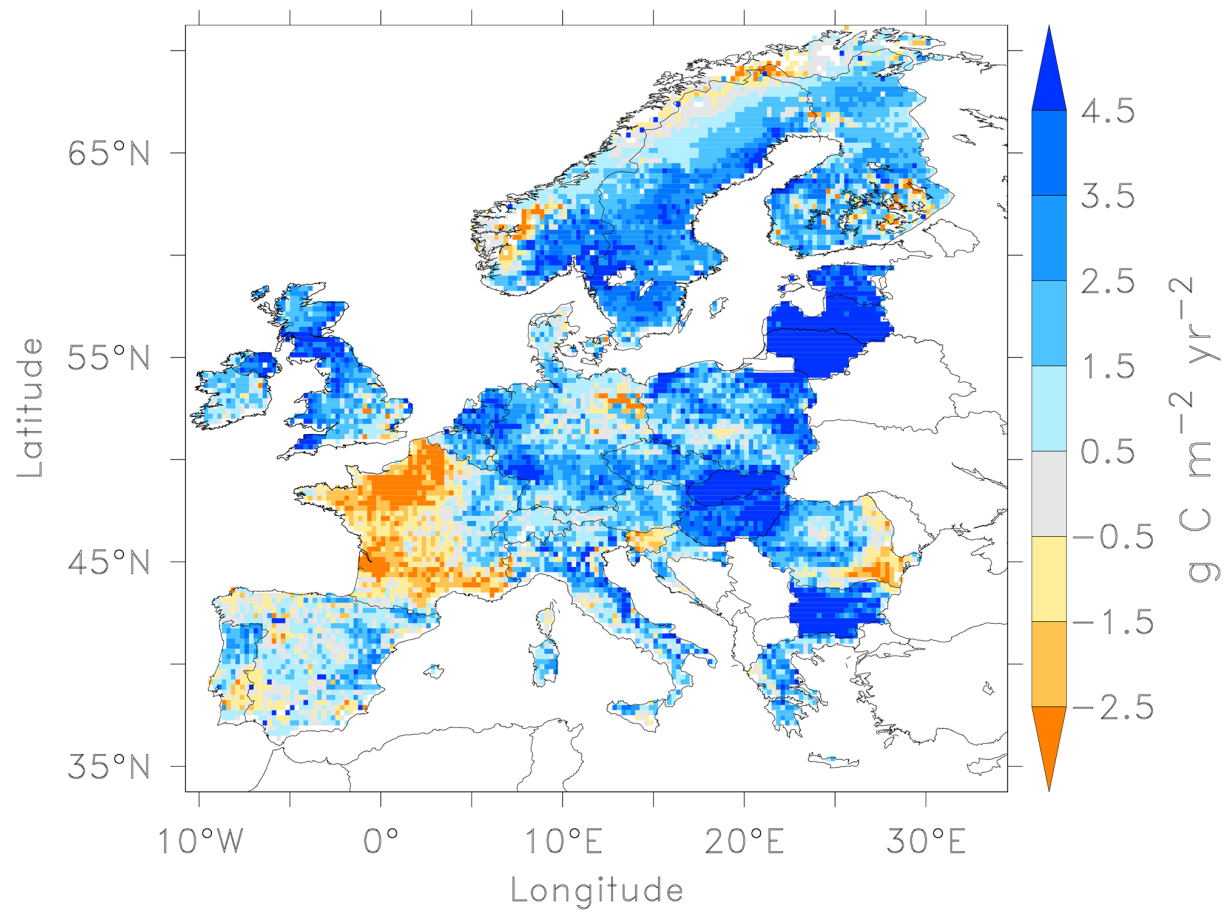
	Climate forcing	Atmospheric CO ₂ concentration	Nitrogen addition	Grassland area	Grassland management	NBP trend
E_{CTL}	1991-2010	1991-2010	1991-2010	1991-2010	1991-2010	NBP_{CTL}
E1	1991-1995	1991-2010	1991-2010	1991-2010	1991-2010	NBP_{climate}
E2	1991-2010	1991	1991-2010	1991-2010	1991-2010	NBP_{CO2}
E3	1991-2010	1991-2010	1991	1991-2010	1991-2010	NBP_{nitrogen}
E4	1991-2010	1991-2010	1991-2010	1991	1991-2010	NBP_{LCC}
E5	1991-2010	1991-2010	1991-2010	1991-2010	1991	NBP_{management}

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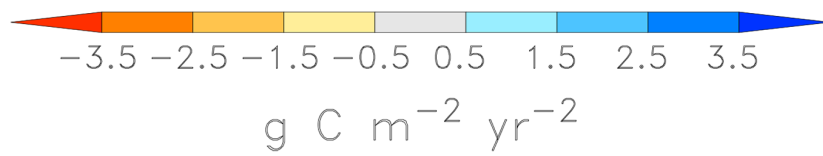
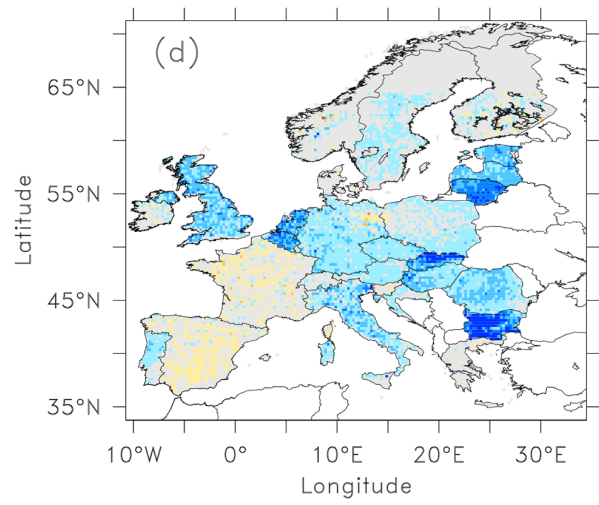
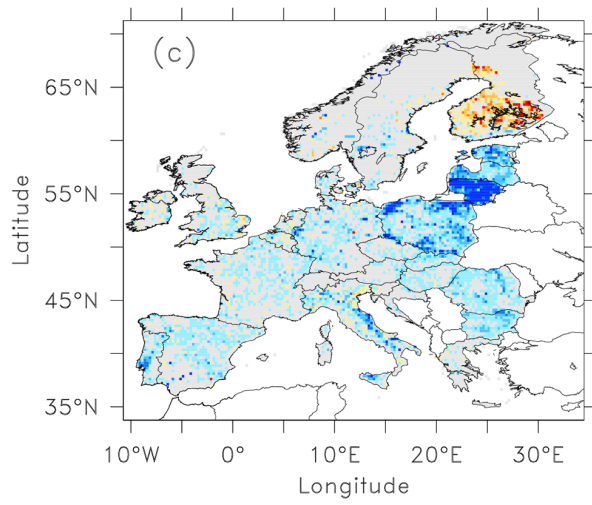
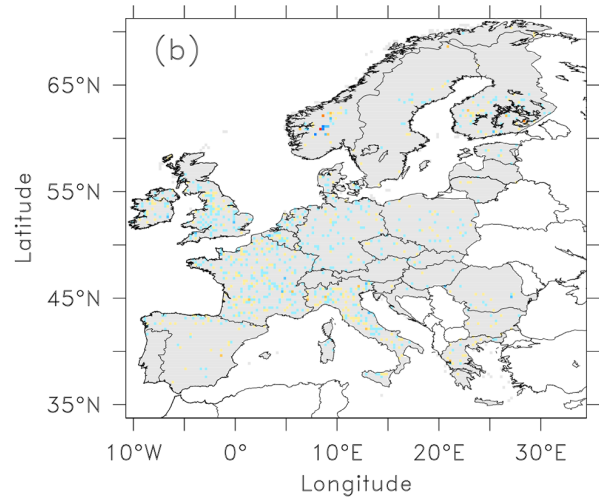
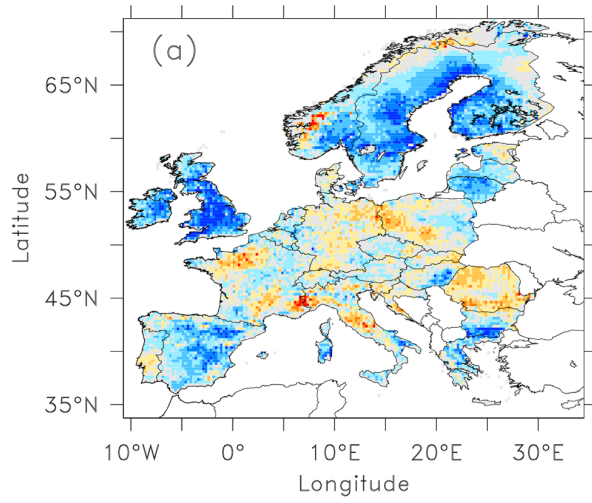




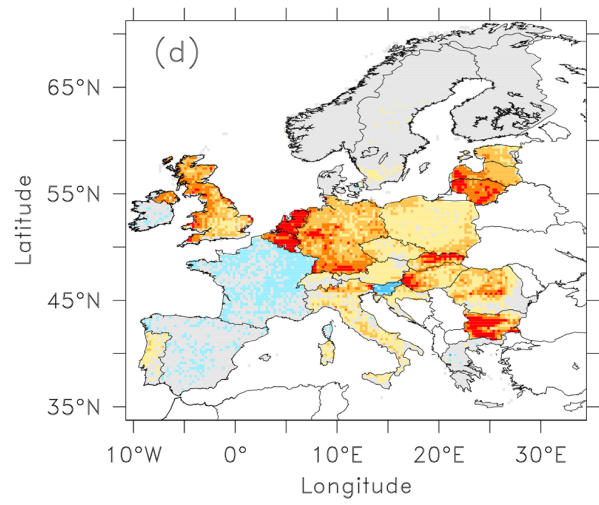
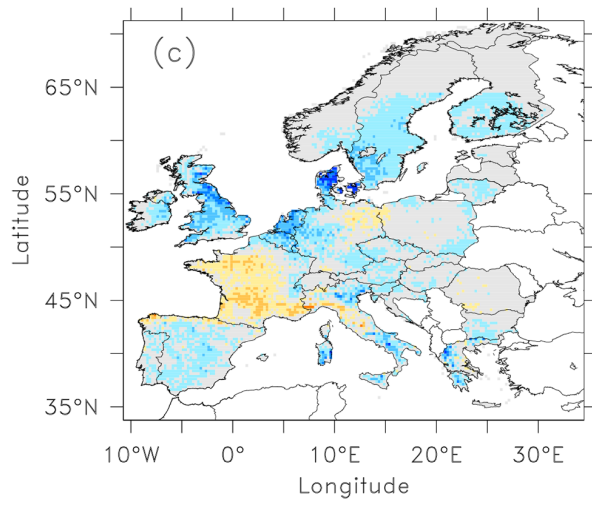
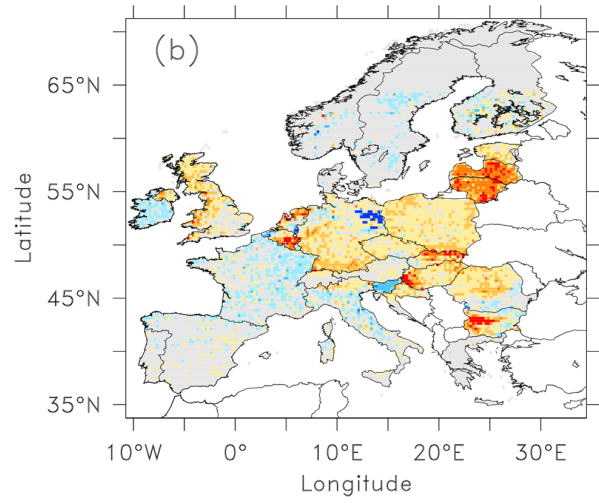
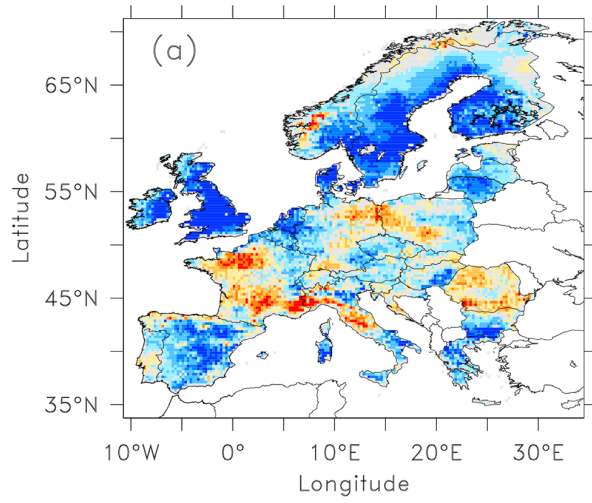
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$\text{g C m}^{-2} \text{ yr}^{-2}$