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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Abstract

Several lines of evidence point to European managed grassland ecosystems being a sink of carbon. In this study, we apply ORCHIDEE-GM a process-based carbon cycle model that describes specific management practices of pastures and the dynamics of carbon cycling in response to changes in climatic and biogeochemical drivers. The model is used to simulate changes in the carbon balance (i.e., Net Biome Production, NBP) of European grasslands over 1991-2010 on a 25 km × 25 km grid. The modeled average trend of NBP is 1.8 - 2.0 g C m^{-2} yr^{-2} during the past two decades. Attribution of this trend suggests management intensity as the dominant driver explaining NBP trends in the model (36% - 43% of the trend due to all drivers). A major change in grassland management intensity has occurred across Europe resulting from reduced livestock numbers. This change has 'inadvertently' enhanced soil C sequestration and reduced N$_2$O and CH$_4$ emissions by 1.2 - 1.5 Gt CO$_2$-equivalent, offsetting more than 7% of greenhouse gas emissions in the whole European agricultural sector during the period 1991-2010. Land-cover change, climate change and rising CO$_2$ also make positive and moderate contributions to the NBP trend (between 24% and 31% of the trend due to all drivers). Changes in nitrogen addition (including fertilization and atmospheric deposition) is found to have only marginal net effect on NBP trends. However, this may not reflect reality because our model has only a very simple parameterization of nitrogen-effects on photosynthesis. The sum of NBP trends from each driver is larger than the trend obtained when all drivers are varied together, leaving a residual - non-attributed - term (22% - 26% of the trend due to all drivers) indicating negative interactions between drivers.

Introduction

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

The annual C balance of managed grassland ecosystems (also called net biome production, *NBP*; here using the definition proposed by Schulze & Heimann, 1998; Buchmann & Schulze, 1999; and Chapin *et al*., 2006) must account for not only the fluxes of CO_2 exchanged with the atmosphere (net ecosystem production, *NEP*), but also the land-atmosphere CO_2 fluxes caused by lateral carbon import and export due to management and other processes (e.g., C export to rivers and groundwater). NEP is determined by the difference between net primary productivity (NPP) and ecosystem-level heterotrophic respiration (R_h). NPP, indicating the C incorporated into plant biomass, is known to be sensitive to climate (Melillo *et al*., 1993), atmospheric CO_2 concentration (e.g., Ainsworth & Long, 2005) and nitrogen availability (Le Bauer & Treseder, 2008; Xia & Wan, 2008). R_h is also controlled by climate (Rustad *et al*., 2001) as well as by organic C and nitrogen availability, and micro-environmental conditions (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 ± 7 g C m^{-2} 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 ± 0.08 g C m^{-2} yr^{-2}, P = 0.26) with the rate of increase being

96   much larger after 1990 (1.83 ± 0.30 g C m^{-2} yr^{-2}, P = 0.07) than before that date (-0.25 $\pm$ 0.15

97   g C m^{-2} 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 CO_2 and nitrogen deposition.

108

Material and methods

Model description

ORCHIDEE is a process-based ecosystem model for simulating carbon cycling in ecosystems, and water and energy fluxes from site-level to global scale (Krinner *et al.*, 2005; Ciais *et al.*, 2005; Piao *et al.*, 2007). ORCHIDEE-GM (Chang *et al.*, 2013) is a version of ORCHIDEE specifically developed to study grassland management. It incorporates a grassland module from the PaSim model (Reido *et al.*, 1998; Vuichard *et al.*, 2007a,b; Graux *et al.*, 2011). ORCHIDEE-GM Version 1 was evaluated and some of its parameters calibrated using eddy covariance NEE and biomass measurements from 11 European grassland sites representative of a range of management practices. The model simulated the average NBP of these managed grasslands as 37 ± 30 g C m^{-2} yr^{-1}, $P < 0.01$; Chang *et al.*, 2013). At continental scale, ORCHIDEE-GM Version 2.1 was first applied over Europe to calculate the spatial pattern, long-term evolution and interannual variability of potential productivity (potential productivity is the productivity resulting from the optimal management regime that maximizes livestock densities; Chang *et al.*, 2015a). Chang *et al.* (2015a) further added a new parameterization to describe an adaptive management strategy whereby farmers react to a climate-driven change of previous-year productivity. Though a full nitrogen cycle is not included in ORCHIDEE-GM, the positive effect of nitrogen addition on grass photosynthesis, and thus on subsequent ecosystem carbon balances, is parameterized with a simple empirical function calibrated from literature estimates (Chang *et al.*, 2015a). In a recent study, ORCHIDEE-GM Version 2.1 was used to simulate long-term NBP changes over European 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 ± 0.30 g C m^{-2} 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 CO_2 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 CO_2 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 CO_2 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 CO_2 history. ORCHIDEE-GM

220   was then run on each grid point at 25 km resolution during the period 1991-2010 forced by

221   increasing CO_2, 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 *E1′*

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 ^{o}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   $NEP = GPP - R_{eco}$ (1)

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

$$NEP = NPP - R_h \qquad (2)$$

R_h simulated by ORCHIDEE-GM is defined by heterotrophic respiration caused by grazing animals (microbes living in animals' digestive systems) and by soil microbes. A positive NEP value indicates a net removal (sink) of atmospheric CO_2. Note that in ORCHIDEE-GM there is no explicit representation of microbial biomass but rather the model uses first order kinetics to represent the decomposition of organic matter (Krinner *et al.*, 2005).

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

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

where C_{input} is the flux of C entering the grassland ecosystem through manure and/or slurry application, and C_{export} is the total C lost from the grassland ecosystem through plant biomass export (mowing), and CH_4 emissions by grazing animals. C_{export} through milk production and animal body-mass increase is not determined and will be neglected for the calculation of NBP, which has only marginal effect on the NBP estimate (Chang *et al.*, 2015b). It must be noted that C lost through dissolved organic (DOC) and carbonate-borne inorganic (carbonate-borne DIC) leaching to rivers is not determined and will also be neglected for this study in the estimation of NBP, whereas biogenic DIC (formed by CO_2 from soil respiration, including R_a by root and R_h by heterotrophic organisms; Kindler *et al.*, 2011) has been implicitly accounted for in the simulated R_a and R_h fluxes to the atmosphere.

301

Attribution method of NBP trends

303

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

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

where $\dot{NBP}_{CTL}$ is the NBP linear trend during 1991-2010 from the control simulation where all drivers including x are varied, and $\dot{NBP}_x$ is the NBP linear trend of simulation x where only this driver remains fixed. Therefore, $\Delta_{climate}$, Δ_{CO2}, $\Delta_{nitrogen}$, Δ_{LCC} and $\Delta_{management}$ are here the individual effects of changes in climate, CO_2, nitrogen fertilization, grassland area (new grasslands produced from land-cover change; LCC) and in management intensity on the NBP linear trend. The sum of individual effects can be less than or more than the effect of all the factors taken together, due to non-linear interactions, and a residual, non-attributed, is defined as $\Delta_{residual}$. The same attribution method was also used to determine the effect of each factor 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) g C m^{-2} 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 g C m^{-2} yer^{-2}) found in simulation Set-2 mainly resulted from the faster

328 decrease of C_{export} (with a rate of -1.2 g C m^{-2} 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) g C m^{-2} 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 km^2 grassland (i.e., 0.23 - 0.30 (in Set-2) Mg CO_2 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 CO_2 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 CO_2 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.

Spatial distribution of NBP trend and its attribution

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

Within the five drivers considered in this study, changes in management intensity (mainly changing from intensively managed grasslands to extensively managed ones; Chang *et al*., 2015b) is clearly a major factor causing NBP to increase in those regions where it did (e.g., 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 CO_2 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

Discussion

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

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

Elevated CO_2 concentration has the dual effect of increasing leaf photosynthesis and reducing stomatal conductance, thus indirectly increasing soil moisture in unsaturated soils. These 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 CO_2 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 CO_2 concentration rises (Fig. 1). Increases in productivity of temperate grassland

435 stimulated by rising CO_2 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 CO_2 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 CO_2 in the future to determine actual changes in grassland

443 productivity in response to CO_2 (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 ±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 CO_2 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 CO_2 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*

477   *al.*, 2011); 3) elevated CO_2 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 ($N\dot{B}P_{CTL}$). It implies the effect of changes in management

521   intensity in reality could be even larger than that estimated here (given by Eqn 4: $N\dot{B}P_{CTL}$ -

522    $N\dot{B}P_{management}$; 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 fas

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) $\pm$ 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) $\pm$ 0.7 gigatonnes (Gt) CO_2

531   over about 1.3×10^6 km^2 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 CO_2 equivalent from 1991-

534   2010 including CO_2, CH_4 and N_2O 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 CO_2 and to have simultaneously reduced CH_4 and N_2O emissions by 0.42 – 0.48 (in Set-2)

538   Gt CO_2-equivalent and by 0.22 - 0.27 (in Set-2) Gt CO_2-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   CO_2 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 CO_2 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 CO_2 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 CO_2 ha^{-1} yr^{-1}) and Smith *et al*.

550   (2008; 0.11-0.81 Mg CO_2 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 CO_2 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^o 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 CO_2 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 sequestrated 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 LU km^{-2} 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.

590

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752

Supporting Information Legends

Text S1. The changes in feedstuffs for ruminants.

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

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

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

Figure S3. Spatial distribution of the changing rate (linear trends) during the period 1991-
2010 in: (a) mean annual temperature, (b) total annual precipitation, (c) nitrogen fertilization,
(d) atmospheric nitrogen deposition, (e) grassland area, (f) ruminant livestock numbers and
(g) in fraction of intensively managed grassland in total grassland area with constant feed
conversion efficiency (FCE) or (h) with assumed changes in FCE. The changing rate in (c)
nitrogen fertilization and (d), atmospheric nitrogen deposition are estimated for the period
1991-2000, because in the database they are assumed to be constant from 2000 till 2010.
Temperature and precipitation were from ERA-WATCH reanalysis climate forcing data at a
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.

Tables

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
NBP	1.8 / 2.0'	0.6 / 0.5'	0.5	0.0	0.5	0.6 / 0.9'	0.5 / 0.4'
NEP	2.0 / 1.9'	0.9	0.8 / 0.7'	0.0	0.5	-0.1	0.1 / 0.0'
C$_{export}$	-0.1 / -0.4'	0.3	0.2	0.0	-0.1	-0.9 / -1.2'	-0.3 / -0.4'
C$_{input}$	-0.2 / -0.3'	0.0	0.0	0.0	0.0	-0.2	0.0
NPP	4.7 / 5.0'	2.7	2.0 / 1.9'	0.0	-0.2	0.7 / 1.0'	0.4
R$_h$	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 CH$_4$ 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 CO$_2$ 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 $N\dot{B}P_{CTL}$, $N\dot{B}P_{climate}$, $N\dot{B}P_{CO2}$,

836 $N\dot{B}P_{nitrogen}$, $N\dot{B}P_{LCC}$, and $N\dot{B}P_{management}$ 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). $N\dot{B}P_{CTL}$ is the NBP trend during 1991-2010 from the control simulation; $\Delta_{climate}$, Δ_{CO2},

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.

873

	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	$N\dot{B}P_{CTL}$
E1	1991-1995	1991-2010	1991-2010	1991-2010	1991-2010	$N\dot{B}P_{climate}$
E2	1991-2010	1991	1991-2010	1991-2010	1991-2010	$N\dot{B}P_{CO2}$
E3	1991-2010	1991-2010	1991	1991-2010	1991-2010	$N\dot{B}P_{nitrogen}$
E4	1991-2010	1991-2010	1991-2010	1991	1991-2010	$N\dot{B}P_{LCC}$
E5	1991-2010	1991-2010	1991-2010	1991-2010	1991	$N\dot{B}P_{management}$

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