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The response of the terrestrial biosphere to urbanization: land cover conversion, climate, and urban pollution

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Abstract

Although urban areas occupy a relatively small fraction of land, they produce major disturbances of the carbon cycle through land use change, climate modification, and atmospheric pollution. In this study we quantify effects of urban areas on the carbon cycle in Europe. Among urbanization-driven environmental changes, which influence carbon sequestration in the terrestrial biosphere, we account for: 1) proportion of land covered by impervious materials, 2) local urban meteorological conditions, 3) urban CO_2-dome, and 4) elevated atmospheric nitrogen deposition. We use the terrestrial ecosystem model BIOME-BGC to estimate fluxes of carbon exchange between the biosphere and the atmosphere in response to these urban factors.

We analysed these four urbanization-driven changes individually, setting up our model in such a way that only one of the four was active at a time. From these model simulations we found that fertilization effects from the CO_2-dome and the atmospheric nitrogen deposition made the strongest positive contributions to the carbon uptake (0.023 Pg/year and 0.039 Pg/year, respectively), whereas, the impervious urban land and local urban meteorological conditions resulted in a reduction of carbon uptake (–0.006 Pg/year and –0.007 Pg/year, respectively). The synergetic effect of the four urbanization-induced changes was an increase of the carbon sequestration in Europe of 0.056 Pg/year.

1 Introduction

Urban population is growing at a much faster rate than the Earth's total population and this leads to the growth of urban areas and often to an increase of urban pollution. As urban areas continue to grow the potential carbon sink on land is shrinking because vegetated land is replaced by land covered with impervious materials (buildings, roads, parking lots, etc.). Although urban areas occupy a small land fraction of about 2–3% of the Earth's surface (WRI, 1998), they are sources of about 90% of anthropogenic

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carbon dioxide (CO_2) globally. In Europe, about 70% of nitrogen dioxide emissions are attributed to traffic (USGS, 1999) and, thus, to urbanized land. At the same time, due to high energy consumption and often lack of evaporation, a warmer and drier microclimate is maintained within urban areas. All consequences of urban development mentioned above have a great potential to influence the carbon cycle and to cause irreversible damage to the surrounding land ecosystems.

Attempts to quantify the role of urban areas on the global carbon budget have focused largely on emissions inventories and carbon sequestration in urban ecosystems. Earlier studies focused on different but single aspects of urbanization and its effects on our environment such as land use modifications (USGS, 1999), global climate change (Jones et al., 1990; Kukla et al., 1986; Parker, 2004; Wood, 1988), climate modifications at regional and local scales (Lamptey et al., 2005; Trusilova et al., 2008), and atmospheric pollution (ESA, 2004; Idso et al., 2001; Koerner and Klopatek, 2002; WRI, 1998). It was found that the enrichment of atmospheric CO_2 results in an increased Net Primary Productivity (NPP) of plants (Dewees and Saxena, 1995; Hollinger et al., 1999; Idso and Kimball, 2001). Significant fertilisation effects of atmospheric nitrogen were described in the work of Churkina et al. (2007). However, little research was done on investigating the synergetic effects of these two and the urban climate on the land biosphere. One of the major difficulties in quantifying such synergetic effects is that urbanization affects the environment on different scales: from local (land use change) and regional (urban climate) to continental (high concentrations of CO_2 and nitrogen compounds).

In this study we quantify synergetic effects of local-, regional- and continental-scale changes driven by urbanization on the terrestrial biosphere in Europe. We use a biogeochemical terrestrial ecosystem model BIOME-BGC to estimate responses in the net carbon flux to the urbanization-driven changes in land cover, climate, atmospheric CO_2 concentrations, atmospheric deposition of nitrogen that comes from oxides of nitrogen (NO_x) produced during combustion, and the synergetic effect of all these four changes together. We chose to include only nitrogen and CO_2 fertilisation effects in our

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simulations because those are direct effects which are well represented by a variety of process-based biosphere models.

Effects on vegetation caused by urban ozone, a major component of smog, were not included into model simulations because:

1. urban ozone affects urban vegetation locally due to its short lifetime of 1–2 days and
2. mechanisms of these effects are not well understood and are poorly represented in biosphere models.

2 Materials and methods

2.1 Model

The terrestrial ecosystem model BIOME-BGC (Running, 1994; Running and Coughlan, 1988; Running and Gower, 1991; Running and Hunt, 1991; Thornton, 1998; Thornton et al., 2002) was used to estimate carbon fluxes from vegetation to the atmosphere. The model simulates daily carbon, nitrogen, and water cycles through land ecosystems. This process-based model is driven by daily meteorological data such as maximum and minimum daily temperature, precipitation, vapour pressure deficit, and solar radiation. The land surface is parameterized using a digital elevation map, soil texture data, land cover classification including eight plant functional types, atmospheric CO_2 concentrations and the atmospheric deposition of nitrogen. Each plant functional type is described by ecophysiological parameters.

For this study we defined urban land as in the *Corine Land Cover 2000* database (CLC2000, http://terrestrial.eionet.europa.eu/CLC2000): urban land includes areas mainly occupied by dwellings and buildings including their connected areas (associated lands, road network, and parking-lots), rail networks, airport installations, river and sea port installations, industrial livestock rearing facilities, construction sites, man-made

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waste dump sites, urban parks, sport and leisure facilities. For the model simulations all urban areas were parameterized as vegetation-free surfaces. As the CLC2000 urban land mask has resolution of 250 m, this data was upscaled to the model resolution of 0.25 degrees.

Effects of urban pollution and climate changes were indirectly included in the simulations as "urban effects". This was done by introducing a relevant change into the input data of the model:

1. urban land fraction as percentage of barren land in the land-use map,
2. changes in temperature and precipitation in the meteorological input dataset for representing urban climate,
3. local elevated urban CO_2 concentrations, and
4. elevated atmospheric nitrogen due to human activities.

2.2 The model simulations

The model domain for this study covers most of Europe, 15 W–45 E 30 N–60 N, with a spatial resolution of 0.25 degrees for the land surface data and meteorological fields. The meteorological dataset was generated with the regional climate model REMO (Jacob and Podzun, 1997) for multi-decadal atmospheric modelling for Europe (Chen et al., 2007; Feser et al., 2001). These data were aggregated to a daily time step and included minimum and maximum daily temperature, daily precipitation, downward shortwave solar radiation, and air relative humidity.

The map of land cover classes was made based on the USGS global land cover product (Global Land Cover Characterization from US Geological Survey).

2.2.1 Spinup simulation

Carbon and nitrogen state variables of the BIOME-BGC model represent amounts of carbon or nitrogen stored in simulated plant and soil pools. Unless variables for the

initialization of the model's state variables are available from measurements, model simulations are required for their initialization (spinup run). In the spinup run, the model is run to a steady state to obtain the size of the ecosystem's carbon and nitrogen pools under the assumption of the ecosystem being in equilibrium with the long-term climate. In this simulation the CO_2 concentration was set to a preindustrial level of 283 ppm (Fig. 1), the annual nitrogen atmospheric deposition was set to a constant of 2 kg N/ha, the highest pre-industrial estimate reported by Holland et al. (1999). The meteorological data of 1958–1977 were replicated throughout the simulation. The spinup run was done for each grid cell of the model domain independently (there is no spatial dependence between model grid cells), until the carbon balance of the ecosystem reached its equilibrium state.

2.2.2 Transient simulation

After the spinup simulation, the model simulations were performed for 1800–1957 with repeated meteorological data from 1958–1977, atmospheric nitrogen deposition gradually rising (Galloway et al., 2004), and with the increasing annual mean atmospheric CO_2 supplied by the CARBOEUROPE-IP project (http://www.carboeurope.org/). The atmospheric CO_2 concentration (Fig. 1) represents a smooth change in the well mixed atmosphere and was used as the background value for all model simulations. The carbon dioxide concentration within the model was updated annually using the same background value for all grid cells. The state variables from model simulations ending in 1957 were used as starting point for model simulations from 1958 to 2003 that include different urban effects. These are described below.

2.2.3 Simulation of urbanization-driven changes

In order to isolate effects of individual urbanization-driven changes on the terrestrial net ecosystem exchange of carbon during the time from 1958 to 2003, six model simulations were performed. Model drivers for each simulation were set up in such a way

that they represented none, one, or all urbanization effects (Table 1).

The NOU-simulation was the reference model run, which included no changes due to urbanization. Each of UMET, ULAND, UAND, and UCO2 simulations included one of the urbanization-driven changes such as urban land, urban climate bias, elevated carbon dioxide, and atmospheric nitrogen, respectively. The UALL simulation represented a synergetic effect of all individual urban–related changes of the terrestrial biosphere.

For the *baseline NOU-simulation* the atmospheric nitrogen deposition was fixed at the level of 1958, the atmospheric CO_2 concentration was set at the level of 294.8 ppm (year 1958) assuming no rise throughout the simulation. The NOU-land-cover map, which includes no urban land, was used. No additional urban change was introduced to the meteorological dataset of the model.

ULAND-simulation included urban land as non-vegetated/barren surfaces. The data on the fractional urban cover in Europe was derived from the updated urban mask (Trusilova et al., 2008) at a spatial resolution of 10 km. This map was then upscaled to a spatial resolution of 0.25 degrees as the fraction of urban land in each model grid cell (Fig. 2). The ecosystem carbon fluxes of the ULAND simulation were calculated with the model setup as in the NOU simulation with the only difference being that a part of these fluxes proportional to the fraction of urban land was subtracted.

UMET-simulation. Quantitative estimates of the effects of urban land on the local climate were taken from the study of Trusilova et al. (2008), who analysed differences in near-surface temperature and precipitation between an undisturbed (without urban land) and a present day atmospheric circulation in Europe. The extracted maps of urbanization-induced changes for temperature and precipitation were added to the input data of meteorological fields for the BIOME-BGC model.

UCO2-simulation. Near the surface, large urban clusters often are "hot spots" of intensive CO_2 release from diffuse sources of anthropogenic origin (transport network, industrial emissions etc.). A localized, human-induced increase in CO_2 concentrations in urban and exurban environments is called "CO_2-dome". In previous studies, urban CO_2 was reported to be higher by 8% to 129% than CO_2 concentrations in rural areas

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depending on season and location (Table 2). Data on the magnitude of the CO_2-dome were available for a few European cities only and did not cover all urban areas of the domain.

Taking into account the reported magnitude of the CO_2 dome for selected cities, we assumed that the larger urbanized areas produce higher CO_2 concentrations in proportion to their size. Using this assumption, a map of differences between urban and rural CO_2 concentrations (ΔCO_2) was calculated from the fraction of urban land. The urban increase of CO_2 concentrations was set proportionally to the urban land fraction in the model grid (Fig. 3).

The $\Delta CO_2$was then used as an additional model input and included into the calculation of total input CO_2 concentration for each grid cell as:

$$\text{Input\_}CO_2[i, j] = \text{Background\_}CO_2 \times (1 + \Delta CO_2[i, j]), \quad (1)$$

where Input_CO_2 is the CO_2 concentration value for a grid cell $[i, j]$, and Background_CO_2 is the input annual background carbon dioxide concentration (the same value for all grid cells throughout the simulation).

UAND-simulation. In contrast to the NOU-simulation, the data on dry atmospheric nitrogen deposition for the UAND-simulation corresponds to the year 2003. As the model was run from 1958 to 2003, the nitrogen deposition was gradually interpolated from the value at the beginning of the simulation (Fig. 4a) to the value in the end of the simulation (Fig. 4b) for each model pixel. This yielded an additional input of 8.86 Tg of nitrogen over 46 years in the model domain.

The *UALL-simulation* was performed with all four urbanization-driven changes included: the CO_2-dome, the rising nitrogen deposition, fraction of urban land, and the urbanization-induced changes in local climate. As the BIOME-BGC model simulates interactions of carbon, nitrogen, and water cycles, including all four urban factors represented the synergetic effect of urban pollution, land use, and local climate on the carbon sequestration of European land ecosystems.

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3 3 Analysis of model mutput

In order to quantify responses of the land ecosystems we analysed the following carbon fluxes calculated by the BIOME-BGC model: Net Ecosystem Exchange (NEE), Gross Primary Production (GPP), and Total Ecosystem Respiration (TER). The latter was calculated as a sum of heterotrophic respiration, plant growth respiration, and maintenance respiration.

We calculated differences in modelled carbon fluxes from each of the simulations ULAND-, UMET-, UCO2-, and UAND- and the baseline NOU-simulation. We used these differences as quantitative estimates of the sensitivity of the carbon fluxes to the respective urbanization-driven change. The flux difference between the UALL and NOU simulations was interpreted as the response of the biosphere to all counteracting urban changes together.

We calculated the total difference in the GPP, TER, and NEE over the model domain as the sum over differences in individual pixels:

$$C\,(\mathrm{FLX},\mathrm{sim}) = \frac{1}{N}\sum_{t}\sum_{i}\sum_{j}\left(\mathrm{Area}_{i,j} * \left(\mathrm{flx}\,(\mathrm{FLX},\mathrm{sim})_{i,j} - \mathrm{flx}\,(\mathrm{FLX},\mathrm{NOU})_{i,j}\right) * \Delta t\right),$$

where

FLX	GPP, TER or NEE flux in the simulation sim
sim=ULAND | UMET | UAND | UCO2 | UALL	simulation
i, j	coordinates of a model grid cell
$\mathrm{flx(FLX, sim)}_{i,j}$	flux FLX of the grid sell i, j in the simulation sim, [Pg m^{-2} year^{-1}]
Δt	time interval over which the total amount of carbon is averaged, [year]
N	total number of simulated years (N=46)
$\mathrm{Area}_{i,j}$	area of grid cell i, j, [m^2]
C(FLX,sim)	total amount of carbon attributed to the flux FLX in the simulation sim

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4 Results and discussion

Model simulations were performed according to the six setups described above. Modelled GPP, NEE, and TER fluxes from simulations ULAND, UMET, UCO2, UAND, and UALL were analysed in relation to the baseline simulation NOU. The differences between each U* simulation and the baseline were interpreted as a quantitative measure of the effect of the respective urbanization-induced change on biosphere.

4.1 Land cover

The conversion of vegetated land to urban caused a reduction of GPP (Fig. 5a1), TER (not shown) and NEE (Fig. 5a2) over perturbed land. The average reduction of the NEE flux over simulated period was –0.006 Pg/year in Europe (model domain). This reduction accounted for 0.3% of the yearly average NEE from the relevant area. This is the maximum over estimate of carbon release, because it is based on the assumption that urban areas are barren. In reality, a blend of land cover types such as trees, grasses, barren, and impervious surfaces is typical for urban areas. To account for the heterogeneity of urban vegetation and its role in the carbon cycle we would have to use very precise maps of urban land cover on the spatial resolution of 1–10 m. This heterogeneity also involves a wider set of model set-ups in order to represent the full variety of urban ecosystems and, thus, would generate large uncertainties in carbon flux estimates. An estimation of total reduction of net primary production (NPP) in the southeastern US was made by Milesi et al. (2003). Using a remote sensing based methodology, the authors found that an increase in urban development of 1.9% over 1990–2000 resulted in a reduction of NPP by 0.4% over the region. However, in the present study we focused on a general estimate of the urban effects on the European carbon cycle and, thus, used a rather simplified representation of urban land as barren surfaces.

The fraction of urban area covered by vegetation was estimated to be between 52 and 78 percent depending on a city's climate zone and corresponding potential veg-

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etation (Nowak, 1996). This result was based on the estimates from 48 cities in the USA. The vegetation fraction in European urban areas was estimated from data on 17 cities (Lavalle et al., 2002) and accounted for 29 per cent. In this study we assumed that urban areas had no vegetation and therefore are a source rather than a sink of carbon; 2.8% of the total land in the model domain was urban.

4.2 Climate

Conversion of vegetated to urban land leads to a reduction of the diurnal temperature range, and changes in precipitation (Trusilova et al., 2008). Trusilova et al. (2008) showed that this conversion reduced diurnal temperature range in European cities on average by –1.26±0.71°C in summer and by –0.73±0.54°C in winter. At the same time the land conversion increased urban precipitation in winter by +0.09±0.16 mm day^{-1} and reduced in summer by –0.05±0.22 mm day^{-1}. However, patterns of precipitation change over Europe were heterogeneous: while urban areas in Southern Europe experienced dry summers, cities in Western and Northern Europe were exposed to increased rainfall in winter months.

The response of GPP and TER fluxes to these changes in climate was spatially heterogeneous. In most areas of reduced precipitation; GPP (Fig. 5b1) and TER flux (growth respiration and heterotrophic respiration components) were reduced. However, the photosynthetic productivity was higher in areas with enhanced precipitation and increased temperature and resulted in local peaks of GPP (Fig. 5b1). The range for GPP changes was (–0.22±0.41) kg m^{-2} year^{-1} and for TER (–0.20±0.40) kg m^{-2} year^{-1}. Since the areas of GPP reduction were larger in extent, they dominated the overall average change in carbon balance –0.007 Pg/year over Europe. This could partly be explained by the high sensitivity of the BIOME-BGC model to the soil water availability; the reduced amount of precipitation leads to drying of soils and to the reduction in photosynthetic productivity of plants. The overall effect of climatic changes on carbon balance of Europe was negative and the enhanced release of carbon from land ecosystems.

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4.3 Urban CO_2

An increase in carbon uptake of (+0.01±0.01) kg m^{-2} year^{-1} over large areas, with the highest values up to 0.10 g m^{-2} year^{-1}, were found in Central Europe where densely urbanized areas are located (Fig. 5c1,c2). In densely urbanized areas an increase in atmospheric CO_2 concentrations was up to 129 per cent as compared to the background value over rural land. Effects of CO_2 concentration on plants productivity were previously addressed in several studies. For example, Griffin et al. (2001) found that elevated CO_2 produces significant changes in major cellular organelles of plants and lead to enhanced plant productivity. Taub et al. (2000) found that plants respond to the higher CO_2 by increased thermotolerance of high-temperature stress; and that effect may have a substantial impact (increase) on productivity. Our simulations showed an average increment of carbon sink of 0.023 Pg/year that was dominated by an increase in GPP. This estimate reflects pure CO_2 fertilization effect on ecosystems in urban and suburban ecosystems. This positive effect may be counterbalanced by negative effects of cities' pollution on ecosystem productivity, such as urban ozone and urban dust effects on plants, and effects of air pollution on the surface energy budget.

4.4 Effects of elevated nitrogen deposition

The sensitivity of the GPP flux to the additional atmospheric nitrogen deposition was the highest among all analysed urban changes (+0.164 Pg/year). The additional nitrogen to the soils enhanced the microbial activity and lead to the higher heterotrophic respiration component of TER (+0.125 Pg/year). The total net carbon flux (NEE) increased over the whole modelled domain by 0.039 Pg/year. This result is based on the model assumption that temperate and boreal vegetation is nitrogen limited (Vitousek et al., 2002). An increasing deposition of nitrogen from the atmosphere serves as a fertiliser for European ecosystems. Of all individual urbanization-driven changes studied here, nitrogen deposition has the most significant impacts on the total carbon balance. The role of atmospheric nitrogen deposition

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on the European carbon balance as a fertiliser is however debatable because agricultural land, which occupies a considerable proportion of Europe. In 1997 arable land together with permanent cropland and pasture covered 44% of EU15 (EUROSTAT, http://ec.europa.eu/agriculture/envir/report/en/terr_en/report.htm). Agricultural land receives high loads of nitrogen directly as chemical fertilizer and therefore insensitive to the increasing deposition of nitrogen from atmosphere. In this study, we only looked at the effects of atmospheric nitrogen deposition assuming no additional nitrogen-fertilisers are applied on agricultural land. On the other hand, the fraction of agricultural land was declining, while fraction of forests was increasing in the last 50 years. The European forests are currently young and are in the re-growth stage. The total forest area of 30 European countries has increased by 6% between 1950 and 1990 (Nabuurs et al., 2003). The productivity of regrowing forests is especially sensitive to the increasing atmospheric nitrogen deposition (Churkina et al., 2007).

4.5 Synergetic effects

When all four urbanization-induced changes were applied at once, the biosphere responded with a 0.056 Pg/year increase of carbon sink. This increase in NEE resulted from an increase in GPP (+0.044 Pg/year) and a reduction in TER (–0.013 Pg/year). As the vegetation was replaced by barren land the amount of the potential carbon source through growth respiration was reduced, however, in the whole model domain, the reduction of carbon sink due to urban land use and climate was compensated by an increase of carbon sink due to fertilisation by simultaneously increasing atmospheric CO_2 and nitrogen deposition.

The synergetic effect of the urbanization-driven changes considered here led to a stronger increase of carbon sink than any of them individually (Fig. 6), because atmospheric CO_2 and soil nitrogen availability co-limit productivity of land ecosystems. This finding is confirmed by field studies where nitrogen availability was shown to be a constraint to CO_2-induced stimulation of plant growth (Oren et al., 2001; Reich et al., 2006). Our results were also in accordance with results from several modelling

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studies (Churkina et al., 2007; Lloyd, 1999) where numerical models were employed to simulate response of biosphere carbon cycle on the continental level. Low availability of nitrogen in the soils suppresses the positive physiological response of plant growth to elevated CO_2. Anthropogenic increase in nitrogen deposition enhances availability of nitrogen in soil and thus the response of plants to increasing atmospheric CO_2. Increase in atmospheric nitrogen deposition has been shown to drive the sequestration of carbon by European forests (Magnani et al., 2007).

Relationships between the carbon sequestration rates, nitrogen input, and climate variables are nonlinear and due to this nonlinearity, the total effect on vegetation of all urbanization-related changes together was not equal to the sum of individual effects from individual changes.

5 Summary and outlook

In this study we analysed dynamics of carbon sink in Europe driven by urbanization-induced changes of land use, climate, concentrations of carbon dioxide and nitrogen deposition from the atmosphere. We used the BIOME-BGC terrestrial ecosystem model to calculate responses of the biosphere to the urban changes applied individually and all together. We did not include agricultural management such as field-fertilisation with nitrogen compounds in our simulations.

The land use and urban climate changes affected rather small land areas while the urban CO_2-dome and nitrogen pollution spread over larger areas. When all urban changes were applied at once, the synergetic effects were dominated by the fertilisation effects from the CO_2-dome and nitrogen pollution and led to a net increase of carbon sink in Europe.

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Table 1. Model setup for simulating different urbanization-driven changes of the terrestrial biosphere.

Simulation	Description	Disturbances			
		Urban land	Urban climate bias	Urban CO_2-dome	Atm. nitrogen deposition
NOU	Baseline simulation	No	No	No	No
ULAND	Effects of urban land (fraction)	Yes (urban land fr.)	No	No	No
UMET	Effects of urban warm and dry environment	No	Yes	No	No
UCO2	Effects of urban elevated CO_2 concentrations	No	No	Yes (urban CO_2)	No
UAND	Effects of elevated atm. nitrogen deposition	No	No	No	Yes
UALL	Synergetic effect of all four factors	Yes	Yes	Yes	Yes

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Table 2. Ratio of the urban CO_2 concentration increase relative to the rural CO_2 concentration as observed in several European cities.

Site	CO_2 dome intensity	Source of information
Rome, Italy	15%–23%	(Gratani and Varone, 2005)
Krakow, Poland	24%	(Zimnoch et al., 2004)
Paris, France	Up to 220%	(Widory and Javoy, 2003)
Copenhagen, Denmark	Up to 86%	(Soegaard and Moller-Jensen, 2003)

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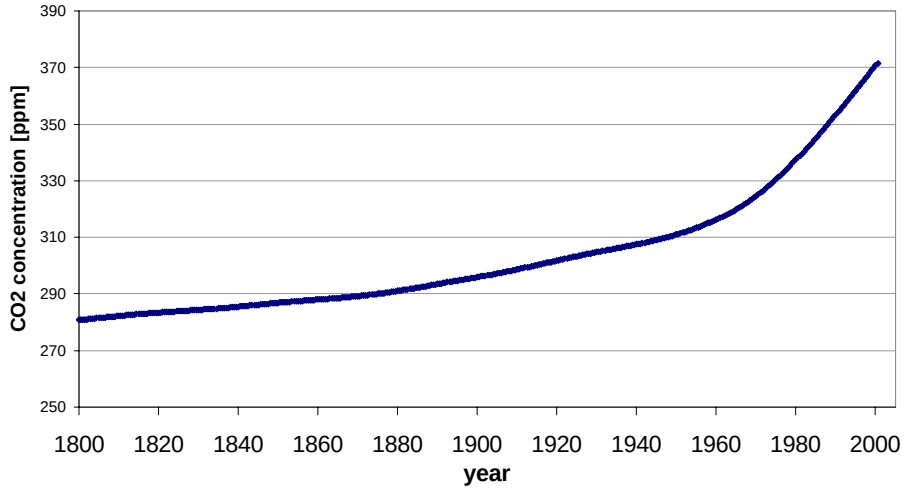

Fig. 1. Background atmospheric CO_2 concentration [ppm] rise used in simulations with the BIOME-BGC model. For each year, one concentration value is uniformly used for all model grid cells assuming that the atmosphere is well-mixed. Data source: CARBOEUROPE-IP database.

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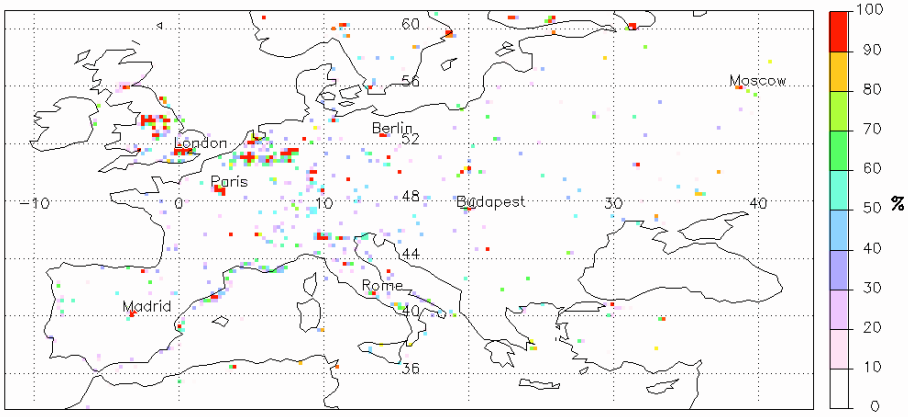

Fig. 2. Fraction of urban land [%] in grid cells of the model domain.

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The response of the terrestrial biosphere to urbanization

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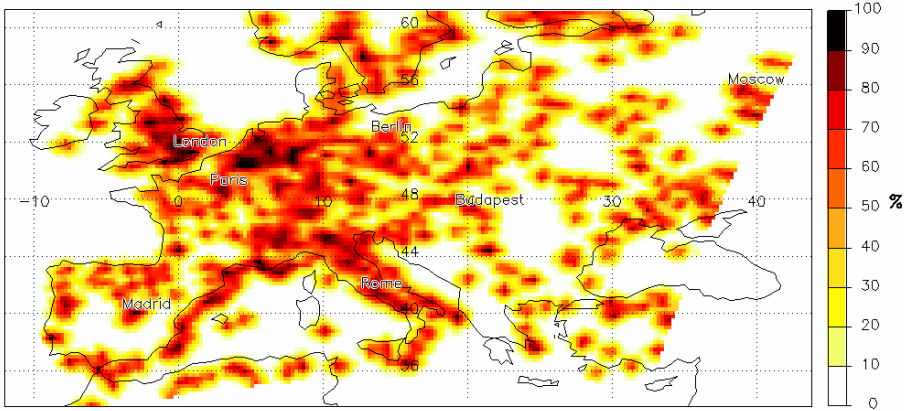

Fig. 3. The spatial distribution of differences [%] in carbon dioxide concentrations (ΔCO_2) between urban and rural land relative to the background CO_2 concentration.

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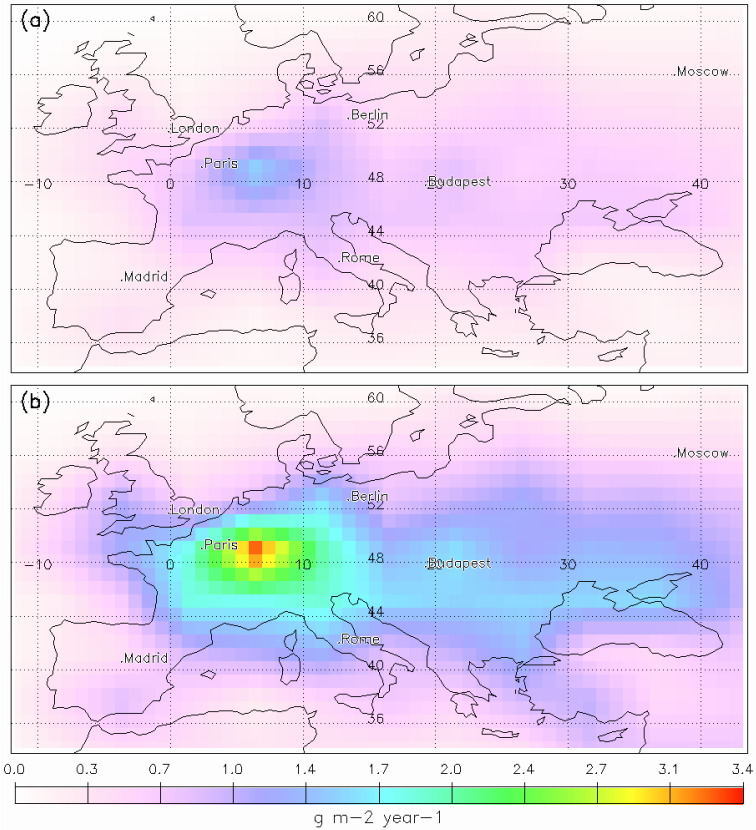

Fig. 4. Dry nitrogen atmospheric deposition [g m^{-2} $year^{-1}$] in 1958 **(a)** and 2003 **(b)**.

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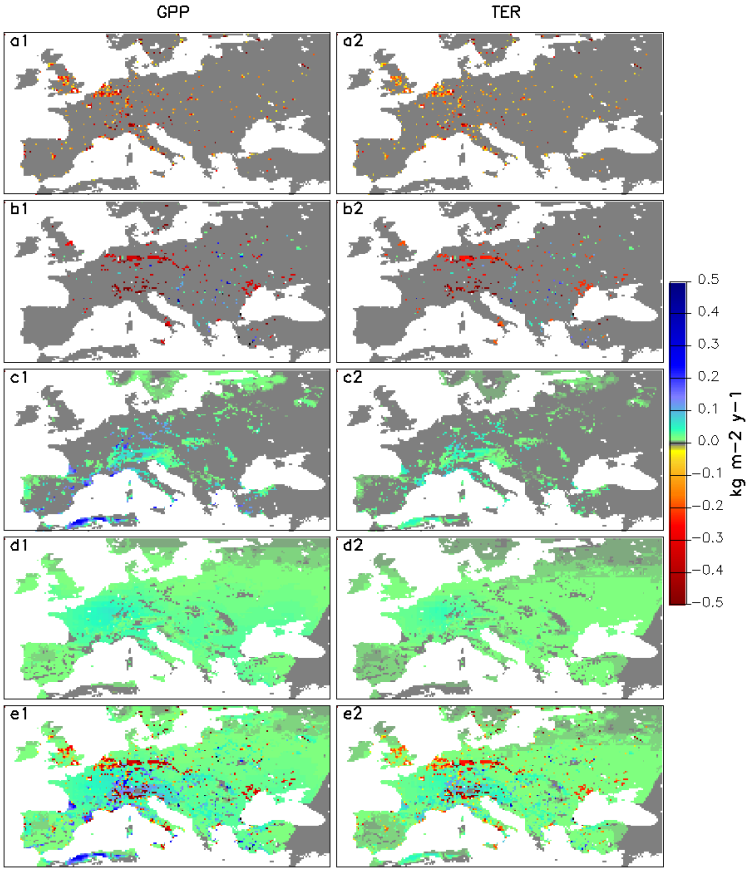

Fig. 5. Response of GPP (**a1,b1,c1,d1,e1**) and TER (**a2,b2,c2,d2,e2**) fluxes to different urbanization-driven changes: urban land (**a1,a2**), urban climate (**b1,b2**), urban CO_2 dome (**c1,c2**), elevated nitrogen deposition (**d1,d2**), and all mentioned changes together (**e1,e2**).

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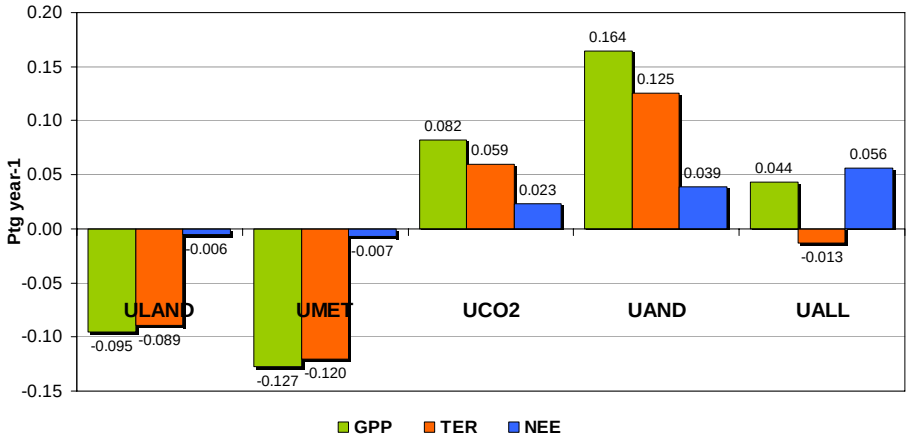

Fig. 6. Changes of carbon amount [Pg/year] exchanged between the biosphere and the atmosphere in response to different urban disturbances: urban land (ULAND), urban meteorological bias (UMET), urban CO_2-dome (UCO_2), anthropogenic nitrogen deposition (UAND), and composition of all four disturbances (UALL). Data are 46-year averages of BIOME-BGC model output over 1958–2003.

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