



The importance of landscape diversity for carbon fluxes at the landscape level: small-scale heterogeneity matters

Katrin Premke,^{1,2*} Katrin Attermeyer,¹ Jürgen Augustin,² Alvaro Cabezas,¹ Peter Casper,³ Detlef Deumlich,⁴ Jörg Gelbrecht,¹ Horst H. Gerke,⁴ Arthur Gessler,^{2,5} Hans-Peter Grossart,^{3,6} Sabine Hilt,¹ Michael Hupfer,¹ Thomas Kalettka,⁷ Zachary Kayler,^{2,8} Gunnar Lischeid,^{7,9} Michael Sommer^{4,9} and Dominik Zak^{1,10}

Landscapes can be viewed as spatially heterogeneous areas encompassing terrestrial and aquatic domains. To date, most landscape carbon (C) fluxes have been estimated by accounting for terrestrial ecosystems, while aquatic ecosystems have been largely neglected. However, a robust assessment of C fluxes on the landscape scale requires the estimation of fluxes within and between both landscape components. Here, we compiled data from the literature on C fluxes across the air–water interface from various landscape components. We simulated C emissions and uptake for five different scenarios which represent a gradient of increasing spatial heterogeneity within a temperate young moraine landscape: (I) a homogeneous landscape with only cropland and large lakes; (II) separation of the terrestrial domain into cropland and forest; (III) further separation into cropland, forest, and grassland; (IV) additional division of the aquatic area into large lakes and peatlands; and (V) further separation of the aquatic area into large lakes, peatlands, running waters, and small water bodies. These simulations suggest that C fluxes at the landscape scale might depend on spatial heterogeneity and landscape diversity, among other factors. When we consider spatial heterogeneity and diversity alone, small inland waters appear to play a pivotal and previously underestimated role in landscape greenhouse gas emissions that may be regarded as C hot spots. Approaches focusing on the landscape scale will also enable improved projections of ecosystems' responses to perturbations, e.g., due to global change and anthropogenic activities, and

*Correspondence to: premke@igb-berlin.de

¹Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Chemical Analytic and Biogeochemistry, Berlin, Germany

²Leibniz Centre for Agricultural Landscape Research (ZALF), Institute of Landscape Biogeochemistry, Müncheberg, Germany

³Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Experimental Limnology, Berlin, Germany

⁴Leibniz Centre for Agricultural Landscape Research (ZALF), Institute of Soil Landscape, Stechlin, Müncheberg, Germany

⁵Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

⁶Institute of Biochemistry and Biology, Potsdam University, Potsdam, Germany

⁷Leibniz Centre for Agricultural Landscape Research (ZALF), Institute of Landscape Hydrology, Müncheberg, Germany

⁸USDA Forest Service, Northern Research Station, Lawrence Livermore National Laboratory, Livermore, California 94550, USA

⁹Institute of Earth and Environmental Sciences, Potsdam University, Potsdam, Germany

¹⁰Aarhus University, Department of Bioscience, Silkeborg, Denmark

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INTRODUCTION

Quantifying C fluxes at the landscape level integrates complex interactions between aquatic and terrestrial compartments and requires addressing the connectivity and interactions at the landscape level. A mechanistic understanding of ecosystem functions underlying the catena of C fluxes between land and water and between both and the atmosphere. This is crucial for comprehensively addressing the effects of climate and land use changes on regional and global C cycling. Whereas C cycling has received substantial attention in terrestrial,^{1,2} marine,³ and peatland⁴ science, the C fluxes through standing and fluvial waters remain a black box in the context of global C budgets.^{5,6}

To date, most landscape C budget studies have been based on eddy-flux measurements to determine CO₂ fluxes in essentially homogeneous ecosystems.⁷ Transferring such information to larger scales, such as the landscape scale, ignores the existing heterogeneity⁸ and does not consider smaller scale variability of fluxes.^{9–11} For example, the larger scale energy exchange processes determined using eddy-flux measurements only yield ‘smeared’ information averaged over a spatial footprint of several hundred to several thousand square meters.¹² By contrast, smaller scale soil-atmosphere gas exchange observed with, for example, flux chambers refer to much smaller surface areas of approximately one square meter or less. These measured C fluxes incorporate spatially small sections of an ecosystem and primarily focus on either terrestrial or aquatic landscape components. Only recently have C upscaling studies provided reliable calculations for linking terrestrial and aquatic ecosystems with each other based on small-scale ecosystem measurements extending to landscape or global scales.^{13–16} These analyses reveal that inland waters, while contributing little to the total surface area of the earth (0.8%), not only transports C but also constitute hotspots for C dynamics in the landscape.¹² In these waters, considerable amounts of organic carbon (OC) from terrestrial inputs (allochthonous C) underlie microbial transformation processes,^{13,17,18} are used in the aquatic food web,^{19,20} or escape transformation through burial in

aquatic sediments.²¹ Especially relevant to agricultural landscapes, is the increase in C stocks of aquatic systems that result from accelerated erosion and translocation of terrestrial C along with mineral particles that are deposited in topographic depressions such as ponds and lakes.²²

Inland waters show positive correlations between carbon dioxide (CO₂) emissions and allochthonous dissolved organic carbon (DOC) concentrations, e.g., in lake water from boreal regions.²³ Moreover, the annual burial of OC in the world’s inland waters⁶ has been estimated to equal the storage of OC in the oceans.²⁴ However, inland waters with large inputs of allochthonous C or with inputs of DIC from carbonate weathering are often supersaturated with CO₂, which means that these lakes are net sources of atmospheric CO₂^{25,26} and, hence, are net heterotrophic.²⁵ Thus, freshwater ecosystems may play an important but variable role in both regional and global C cycling.^{14,27}

A number of questions remain unresolved: How can the varying degree of heterogeneity on the landscape scale (terrestrial and aquatic ecosystems) be reflected in regional and global C fluxes? Landscapes differ in many ways, for example, with regards to the degree of variability, composition, and extent of different landscape elements. Agricultural moraine landscapes are prime examples of a heterogeneous landscape and are therefore useful for studying C dynamics at the landscape scale because they consist of a broad range of landscape elements. These include extended monocultures of cropland that differ substantially in their C dynamics. Currently, the estimation of C fluxes based on individual landscape elements is the subject of discipline oriented research (e.g., limnology and soil ecology). However, to gain a better understanding of the role that C fluxes play at the landscape scale requires interdisciplinary cooperation. Therefore, our multi-disciplinary team of scientists addressed the abovementioned questions through a short literature review and synthesis. We focused on estimating aquatic and terrestrial C emissions and uptake for different spatial heterogeneity scenarios within a temperate moraine landscape rich in water bodies and peatlands—both heavily altered by agriculture (Figure 1).

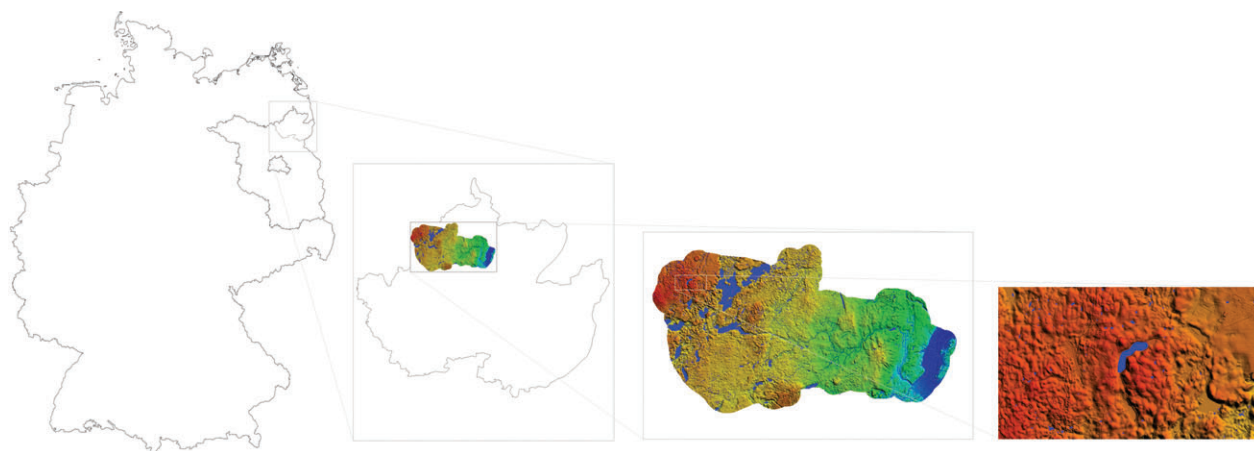


FIGURE 1 | The Quillow catchment (290 km²) in NE Germany: a 3D relief image derived from a high-resolution digital elevation model (DEM1); blue to red: increase in elevation from 15 to 125 m a.s.l.; inset: Germany, Quillow catchment, simulated area, landscape segment with a high density of lakes and kettle holes.

Components of C Fluxes at the Landscape Level

Landscapes can be viewed as spatially heterogeneous areas (herein referred to as components) encompassing terrestrial and aquatic domains. The global soil organic carbon (SOC) stock is ~4000 Tg C, one-third of which is retained in peatland soils. Substantial amounts of terrestrial C end up in freshwaters where 0.022 Gt C is buried and a substantial amount released to the atmosphere. Despite their high turnover and burial capacity, inland waters have been neglected in terrestrial C budgets to date. To completely assess C fluxes on a landscape scale requires the estimation of directly measured fluxes and/or C stock changes from both aquatic and terrestrial landscape components. Therefore, we provide as an example a detailed description of various aquatic and terrestrial landscape components present in a moraine agricultural landscape of NE Germany (except for reservoirs, despite their importance as landscape elements,²⁸ due to their absence in our study region), which we place within a conceptual framework that allows us to investigate in greater detail C fluxes from aquatic and terrestrial components. Carbon flux data for this case study were taken from the literature.

Large Lakes

Fewer than 0.07% of lakes worldwide have a surface area larger than 100 ha²⁹ and represent deeper, stratified systems with a total global area of 1.6%²⁴ (Table 1). Most of these large lakes are located in Nordic countries and the Russian Federation (World Resources 2000). For instance, the contribution of all

4784 lakes registered in north eastern Germany (Federal States of Brandenburg and Mecklenburg-Vorpommern, Figure 1), represents only 2.6% of the total area.

As already noted above, most inland lakes are supersaturated with CO₂ and are, therefore, net heterotrophic systems.¹⁰³ On the other hand, lake net heterotrophy can also arise solely from discharging groundwater supersaturated with CO₂.²⁶ The fact that CO₂ fluxes across the water–atmosphere interface are generally higher in colored lakes compared with clear water lakes,³⁰ however, demonstrates that DOC concentrations in lakes are related to the net CO₂ flux.²³ In addition, increasing concentrations of DOC and particulate organic carbon have recently been observed in many regions worldwide.¹³ Several mechanisms have been identified as: (1) an increase in soil pH resulting from rapidly declining anthropogenic acidification in large regions of Europe and North America;¹⁰⁴ (2) the rewetting of fens, drought-rewetting cycles,¹⁰⁵ and the CO₂ increase in the atmosphere;⁶ and (3) feedback mechanisms of increased concentrations of colored DOC affecting the heat budget and the stratification pattern of deeper lakes.¹⁰⁶

Small Inland Waters

Approximately, 277 million small standing water bodies (0.002–0.01 km²) make up 0.46% of the global land surface.¹⁰⁷ Most natural small water bodies are hydrogeomorphic systems that act as depressional wetlands and, thus, constitute effective OC traps in the landscape. OC enters these inland waters mainly in dissolved form¹⁰⁸ and originates

TABLE 1 | Global Surface Coverage, Carbon (C) Stock and C Emissions Data for the Different Aquatic and Terrestrial Ecosystems

Ecosystem	Global Surface Coverage %	Coverage of the Modeled Area %	OC Stock Globally Tg C	CO ₂ Efflux g CO ₂ -C m ⁻² year ⁻¹	CH ₄ Efflux g CH ₄ -C m ⁻² year ⁻¹
Large lakes (≥100 ha)	1.6	1.0	Nd	67.5 ± 26.1 –60.7 to 196	0.648 ± 0.213 0.036 to 3.00
Small inland waters (<100 ha)	0.46 ¹	9.6	Nd	261 ± 83.5 –1030 to 1892	1869 ± 1120 0 to 56,896
Running waters	~0.4	0.3	Nd	42.1 ± 8.5 6.07 to 66.8	nd
Peatlands ²	3	2.2	270–370	35.4 ± 49.5 –911 to 830	20.98 ± 8.60 –0.876 to 270
Croplands	12	54.2	40–130	75.1 ± 54.1 –22.5 to 613	–0.123 ± 0.057 –0.570 to 0.040
Grasslands	22	14.5	150–450	79.0 ± 85.6 –295 to 801	2.24 ± 1.93 0.030 to 8.00
Forest lands	30	18.1	790	–408.3 ± 65.7 –1107 to –73.0	–0.270 ± 0.045 –0.004 to –1.48

Data were generated from the literature (Ref 14,25,30–102). Mean ± standard error and range are given. Coverage of the modeled area gives the percentage of each compartment within the total modeled area used.

OC, organic carbon.

¹ Percentage only for water bodies <1 ha.

² Drained only.

from surrounding soils, especially from peatlands.¹⁰⁹ In addition, inorganic and organic C can reach the small standing waters as particulate detritus from their catchments, e.g., terrestrial litter and soil particles via erosion, which is greatly increased due to intensive agricultural land use practices. Moreover, small water bodies can be characterized by alternating wet–dry conditions. Typical examples of natural depressional wetlands are the glacially created kettle holes in northern Europe,¹¹⁰ prairie potholes in North America,¹¹¹ Mediterranean ponds in southern Europe and man-made ponds in Asia and South America, whereas the latter ones are primarily used for land management. Additionally, dammed artificial ponds, such as agricultural impoundments²⁴ and fishponds,¹¹² potentially act as sediment traps. Furthermore, CO₂ emissions from ponds can be very high and vary globally (Table 1).

Importantly, surface CO₂ concentrations are much higher in small water bodies than in large ones¹⁸ (Table 1), and oxygen concentrations tend to be lower in ponds and small lakes than in larger lakes.¹¹³ This condition may result in both enhanced CH₄³¹ and N₂O¹¹⁴ emissions and higher C sequestration in smaller water bodies.^{24,115}

Shallow lakes (>1 ha) are permanent water bodies that are sufficiently shallow (<5 m) to theoretically allow sufficient light penetration to support photosynthesis by higher plants over the entire basin. Shallow lakes do not maintain thermal stratification

(polymictic) and are larger than ponds, but their C fluxes and processing rates are similar (Table 1). Shallow lakes, however, may have high rates of internal OC production due to high nutrient loading.^{108,116} Pace and Prairie¹¹⁷ estimated the global gross primary production (GPP) of lakes as 650 Tg year⁻¹, which is likely an underestimate because the high GPP of small lakes was not considered. Still, this is only a minor fraction of the estimated total global GPP (100,000–150,000 Tg C year⁻¹).¹¹⁸

Peatlands

Worldwide peatlands, defined as wetlands with an organic soil layer of at least 30 cm, represent 3% of the global land surface. Most of the peatland area (80%) is situated in temperate-cold climates in the Northern Hemisphere in regions dominated by glacial shifts.¹¹⁹ A rather high proportion of peatlands, ~10–13% of the land area, can be found in the moraine landscape of NE Germany.¹²⁰ These peatlands typically connect terrestrial and aquatic ecosystems. Despite their small proportion, peatlands play a pivotal role within the global C cycle as well as in the global climate.¹²¹ Peatlands are estimated to store one-third of the world's soil C or between 270 and 370 Tg C.^{122,123} The site-specific organic C stock can reach 2200 t ha⁻¹ in the temperate zone.¹²⁴ Therefore, pristine peatlands are among the most important terrestrial long-term CO₂ sinks. Although 20% of all peatlands today are disturbed by

drainage, their annual global CO₂-C accumulation potential is still approximately 100 Tg.¹²⁵

However, the lowering of water tables by draining has allowed oxygen to penetrate the remaining peat, causing a rapid mineralization of the organic material accumulated over the millennia. This process is accompanied by a reduction in methane (CH₄) release as well as a drastic increase in the net CO₂ emissions due to respiration.^{123,126} Drainage causes the transformation of peatlands from a weak or moderate C sink to a strong C source. Consequently, total CO₂ emissions from degraded peatlands currently amount to ~800 Tg C year⁻¹.¹²⁵ Direct gas flux measurements of peatlands have revealed that net C losses vary from 100 to 13,000 g CO₂-C m⁻² year⁻¹, on average, 10 times higher than the CO₂-C sequestration rates.^{119,125} The climate impact increases drastically as a result of drainage. The decrease in CH₄ release, with its rather high global warming potential (GWP) of 28 as CO₂ equivalents, is overcompensated by a much higher net emission of CO₂, despite its low GWP of 1, and the conversion of peatlands to a source of nitrous oxide (GWP of 265 CO₂-equivalents, all referred to a 100-year time horizon).⁶

Croplands and Grasslands

Since the onset of agriculture, soils have lost 40,000–90,000 Tg C globally through cultivation.¹²⁷ Cropland ecosystems cover ~12% of the ice-free surface of the earth, and grasslands represent ~22%.¹²⁸ Croplands on mineral soils represent neither a net source nor sink of CO₂ as a first approximation, that is, the SOC stocks are assumed to be relatively constant.¹²⁹ However, as a result of their creation on former forest or grassland sites croplands can behave as a CO₂ source for a period up to 120 years.¹³⁰ On the other hand, they can also act as CO₂ sinks due to current land use activities such as fertilization, or to decades of deepening of the plough layer.¹³¹ The extent of the annual C stock changes is generally low; it varies between –80 g C m⁻² year⁻¹ (CO₂-C sink) and 130 g C m⁻² year⁻¹ (CO₂-C source).¹³² However, this topic remains controversial because methodological inaccuracies such as disregarding pretreatment C stock baselines or so-called equivalent soil masses might also be responsible for the alleged soil C stock changes.¹³³ In the long run, grassland on mineral sites are also neither soil C sinks nor soil C sources,¹³⁴ but there is an important difference with respect to the soil C stock: on an average, it is higher (11.8 kg C m⁻²) than in croplands (9 kg C m⁻²).¹³⁵ In addition, the soil C stock changes often last longer at higher loss or

accumulation rates (i.e., between –100 and 73 g C m⁻² year⁻¹).¹³⁴ The reason for this long-term C accumulation and hence higher soil C stocks is most likely that grasslands are currently much more widespread in areas of high rainfall and, particularly, lower temperatures than croplands.¹³⁶

Forest Lands

Forest ecosystems cover ~30% of the earth's land surface and are among the most important terrestrial C sinks globally, estimated to fix 30% of all CO₂ emitted from fossil fuels and deforestation worldwide.¹³⁷ In addition, forest biomes are the major reservoirs for terrestrial C storage both below and above ground.^{138,139} Forest soils account for one-third (~790 Tg C)¹³⁹ of the global terrestrial SOC¹⁴⁰ and for ~46% of the total C stocks;¹³⁹ even many old-growth forests still net sequester C.¹⁴¹ The annual net primary production (NPP) of forest ecosystems varies among tropical, temperate, and boreal biomes between ~70 and 1100 g C m⁻² year⁻¹;³² European forests have an average NPP of 520 ± 75 g C m⁻² year⁻¹.³³ CH₄ fluxes are low in forest soils, and forests are, in general, CH₄ sinks (Table 1). The average CH₄ sink strength of forest soils^{34,35} equals to 0.3 ± 0.3 g C m⁻² year⁻¹.

Landscape C Fluxes for Various Spatial Heterogeneity Scenarios: A Case Study

Whether the different types of landscape elements such as inland waters and forest land are C sinks or act as C sources to the atmosphere depends strongly on the connectivity of the aquatic systems with their terrestrial surroundings.^{26,27} As indicated above, it is important to consider each of the different landscape compartments when addressing C fluxes at the landscape level. We use a simulation approach designed to show that isolated perspectives on each landscape component will yield totally different results than an integrated view that includes all components of a diverse and heterogeneous landscape.

The main drivers controlling C fluxes at the landscape level might be scale dependent. To date, small-scale processes within landscapes have not been studied at a spatially relevant scale but, rather, for each landscape component separately. Thus, we still lack a basic understanding of the dependency of processes at small scales with those at the landscape scale. There is considerable uncertainty regarding whether landscape flux estimates, scaled up from smaller components of terrestrial and aquatic systems, can capture whole-landscape C fluxes. Therefore, to illustrate an improved concept we simulated

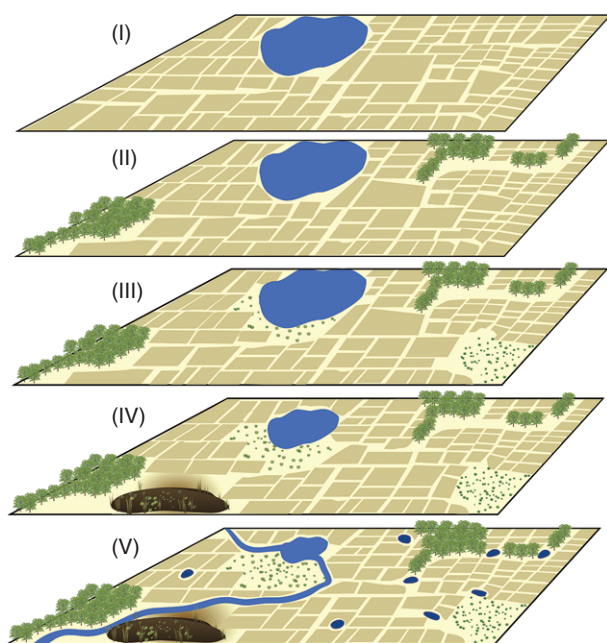


FIGURE 2 | Broad graphic representation of the land use scenarios S-I to S-V for the Quillow catchment based on the biotope mapping of the Federal States of Brandenburg and Mecklenburg-Vorpommern, GIS data (Landesamt für Umwelt, Naturschutz und Geologie, 1994). Scenarios show an increase in diversity and resolution: S-I forms a homogeneous landscape by using only cropland for the terrestrial domain and large lakes for the aquatic domain. S-II is the terrestrial area divided into croplands and forest lands. S-III is a further split of the terrestrial area into croplands, forest lands and grasslands. S-IV includes the partitioning of the aquatic domain into large lakes and peatlands, and in S-V, the aquatic area is further divided into large lakes, peatlands, rivers and small inland waters. For landscape compartment area percentages see Table 1. Peatlands are only considered drained because the area is known to host 95% of its peatlands in a drained state.

different scenarios of landscape spatial heterogeneity by compiling literature data from C effluxes (CO_2 and CH_4) measured across the air–water interface from different landscape components (Figures 1 and 2). Most studies we compiled here were done in boreal and temperate regions similar to the area where our simulation example is situated. Furthermore, most of the studies were made throughout the year and measurements were available for several years. Very few studies (<10) were done only on a single month. The literature review thus represents a good range of land-cover types and long-term datasets. Additionally, we also acknowledge that the literature data used for estimating fluxes of different landscape components might not be fully representative for the landscape assessed here. In the future, direct representative measurements of fluxes in landscape settings should be performed in order to

evaluate our estimates. We calculated the emissions and uptake under five different scenarios assuming increasing landscape diversity (diversity of different terrestrial and aquatic landscape components) and spatial resolution: (I) a homogeneous landscape with exclusively croplands for the terrestrial domain and large lakes for the aquatic domain; a more heterogeneous landscape, (II) with the terrestrial area separated into croplands and forest lands, (III) with the terrestrial area further separated into croplands, forest lands and grasslands, (IV) with the aquatic area additionally divided into large lakes and peatlands, and (V) with the aquatic area further subdivided into large lakes, peatlands, running water, and small lakes (Figure 2). This analysis is not a complete approach because it deals only with one element of landscape diversity and ignores scaling issues and interactions among landscape compartments. Our case study also lacks a representation of the underlying mechanism because it does not consider factors such as temperature, C quality, redox potential, or nutrient dynamics. In this analysis, C sequestration processes were not taken into account and lateral fluxes between landscape components were neglected. In addition, potential non-linear responses were neglected. Although we acknowledge that more mechanistic approaches must be established, we assume that as a first approximation, a more realistic representation of the heterogeneity of a landscape will greatly improve flux estimates.

We hypothesized that (1) increasing spatial heterogeneity will affect landscape C fluxes, primarily due to the inclusion of aquatic components; (2) ponds, small lakes, and peatlands influence the regional relevance of agricultural landscapes for C emissions or uptake at the landscape scale to a much greater extent than their relatively small areal proportion would suggest.

NE German Agricultural Lowlands as a Simulation Site

An ideal region for studying the impact of landscape diversity on C fluxes is the young moraine hummocky, agricultural landscape of the Quillow river catchment in NE Germany, which is rich in peatlands, lakes, and small water bodies (Figure 1). This region is located in the Uckermark and is part of a TERENO site area (TERrestrial ENvironmental Observation, Northeastern German Lowland Observatory, Figure 1).¹⁴² However, the majority of the landscape section we used for our case study is covered by croplands (~54% total by area), followed by forest lands (~18%) and grasslands (~15%; Figure 2, Table 1). A smaller proportion of the

investigated landscape is composed of inland waters (~13%), and most of the water bodies are rather shallow and small (~10%), tightly connected with the surrounding terrestrial systems through depression-focused recharge inside watersheds. All water bodies range in size from <0.1 ha to >1000 ha.

The soil landscapes of the Uckermark region show a complex pattern that is mainly influenced by relief and by the type of parent material (glacial tills with sandy outcrops).¹⁴³ Since medieval times, these soils have been strongly modified by intense erosion/deposition processes, mainly through tillage and water. As a consequence, strongly eroded soils are developed on hilltops and colluvial soils are found at footslope positions or around small depressions and hollows.^{144,145} These patterns are related to C transports¹⁴⁶ with lateral

fluxes toward topographic depressional wetlands, such as kettle holes, as reported for similar morainic landscapes in Canada.^{36,147}

Simulation Approach

The percentage of the major landscape components were retrieved based on GIS data on the spatial distribution of arable land, forest and grasslands. Then, we simulated five different scenarios with increasing diversity including an additional landscape for each subsequent scenario (Figure 2). These GIS-based calculated areas were linked to CO₂ and CH₄ fluxes from published data pertaining to the given landscape compartments (Table S1, Supporting Information) to yield estimates for the C fluxes of each landscape component. The various C flux scenarios

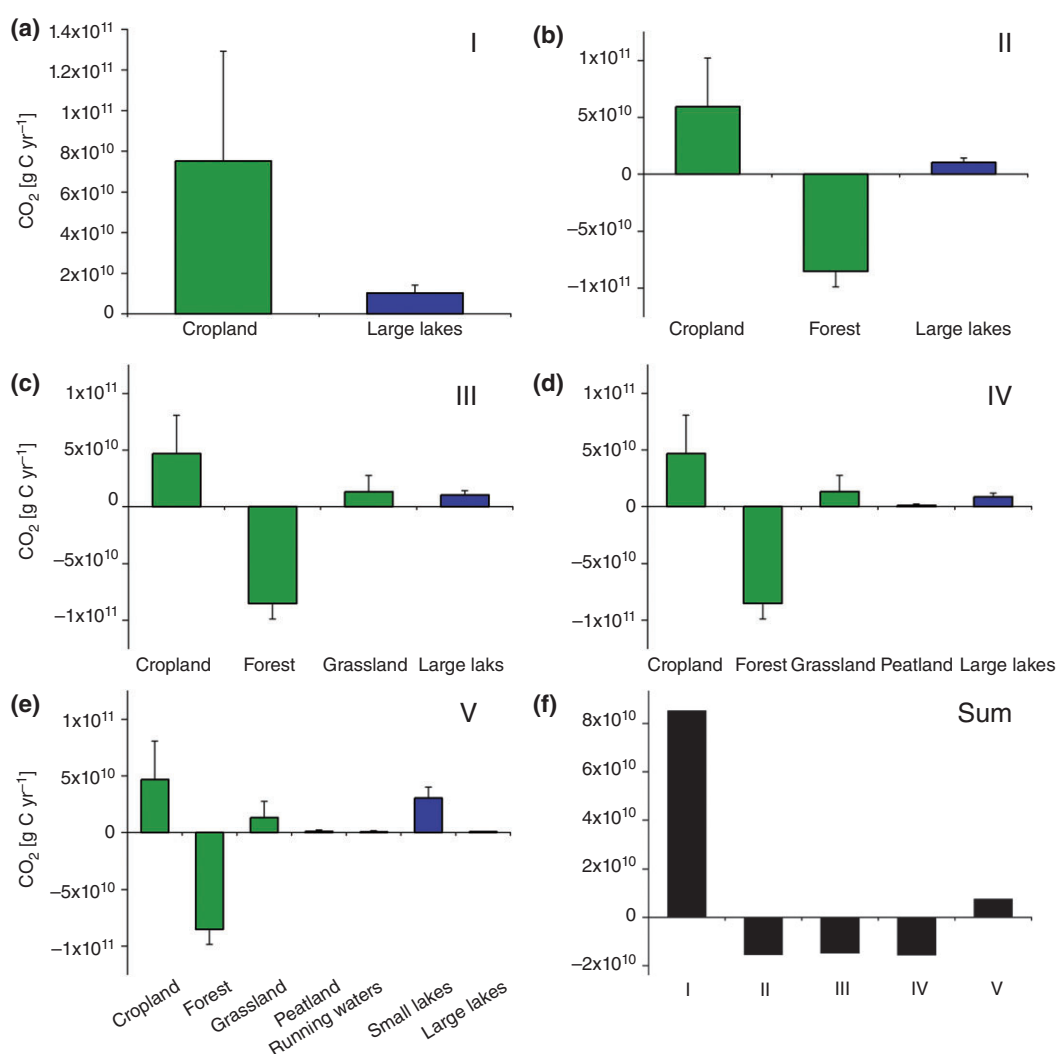


FIGURE 3 | Mean estimated CO₂-C and fluxes of the moraine landscape in NE Germany for the five different scenarios given (a–e). C-data based on the CO₂-C fluxes documented in Table S1. The estimates take the relative areal coverage (GIS data) of the individual categories in the catchment into account. (f) The total flux of the entire landscape for the different scenarios.

should simulate scaling effects by including an increasing diversity of the moraine landscape C fluxes in NE Germany (29,000 ha; E 13°46'29, N 53°28'94).

Scale Heterogeneity and Diversity of the Landscape

Diversity encompasses different meanings as ecological systems usually contain a mixture of several types of diversity.¹⁴⁸ Here, we solely focused on spatial diversity and resolution neglecting other mechanisms and processes. Estimated CO₂ fluxes change from a strong total landscape CO₂ efflux (S-I) driven by the high CO₂ emissions from croplands toward a net CO₂ uptake with increasing diversity (S-II, S-III, S-IV), mainly due to forest CO₂ uptake. However, the landscape with the highest heterogeneity in

landscape components (S-V, see figure 2) also revealed CO₂ emissions on the landscape scale (Figure 3f). In the literature, CO₂ data on croplands suggest landscape-scale C emissions. By including the forest component, as an ecosystem with a very large CO₂ uptake, the C fluxes change to a net C uptake at the landscape scale. As soon as small water bodies are included, e.g., in the scenario of the highest diversity (S-V), the overall landscape budget shifts from a C uptake to a C efflux. Thus, calculated fluxes of the simulated landscape among the various scenarios show that heterogeneity and diversity of the landscape are important controlling factors (Figures 2, 3, and 4).

In contrast, at the landscape scale, calculated CH₄ fluxes changed from a slight CH₄ uptake (S-I to S-II) to a substantial CH₄ efflux (Figure 4).

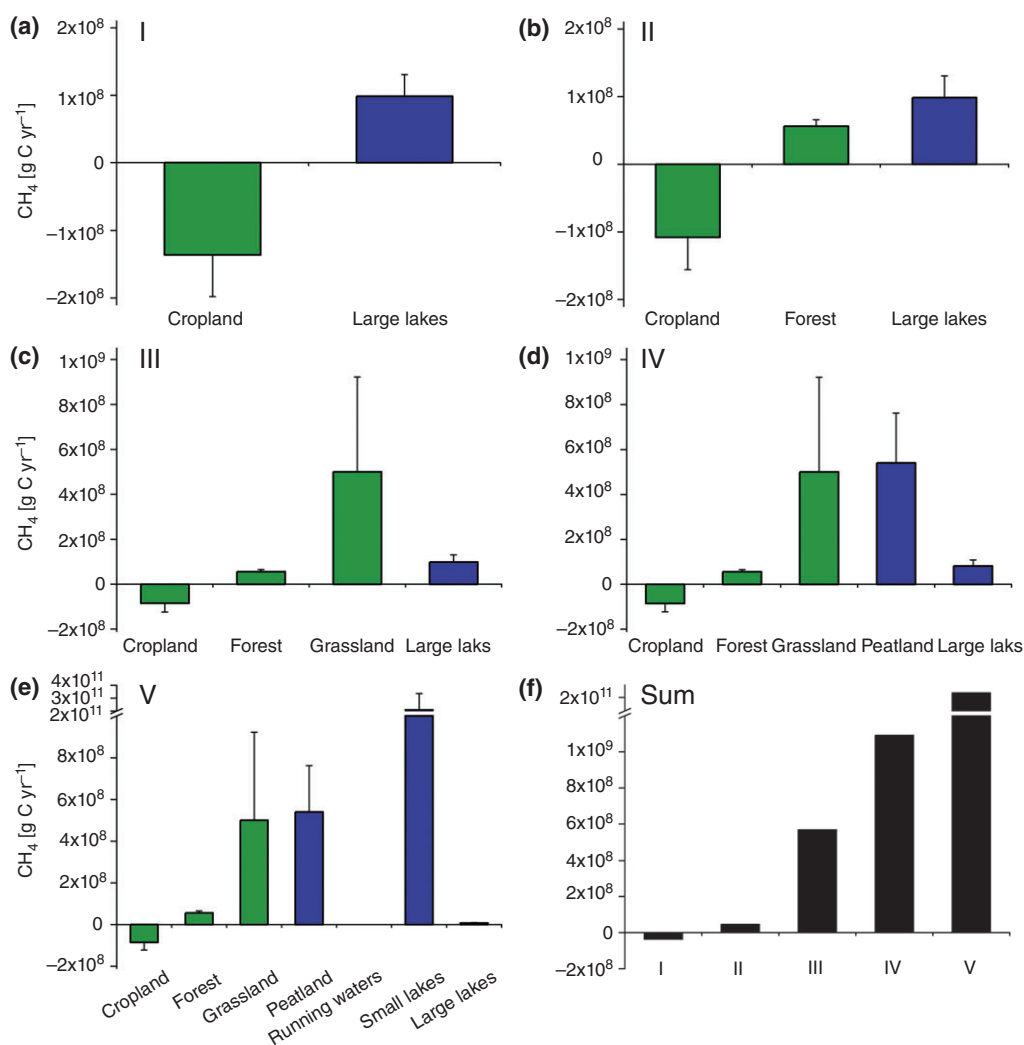


FIGURE 4 | Mean estimated and CH₄-C fluxes of the moraine landscape in NE Germany for the five different scenarios given (a–e). C-data based on the CH₄-C fluxes documented in Table S1. The estimates account for the relative areal coverage (GIS data) of the individual categories in the catchment. (f) The total flux of the entire landscape for the different scenarios.

Nevertheless, by including grasslands, the whole-landscape CH₄ efflux increased 12-fold (S-III, Figure 4(c) and (f)). A further increase in C efflux was observed upon increasing the landscape diversity by including peatlands (S-IV, Figure 4(d) and (f)). These C losses in form of CH₄ are very common for peatlands; for example, northern peatlands currently contribute ~3–5% of total global CH₄ emissions.¹⁴⁹ The flux of CH₄ plays the most important role in determining the climate impact of pristine peatland. Many drained peatlands suffer from inundation during wetter periods and release substantial amounts of CH₄ at those times. Some studies have shown that drained peatlands can release more CH₄ than native or intact peatlands under undrained conditions, mainly due to the high CH₄ release from drainage ditches.¹⁵⁰

Additionally, the influence of small inland waters on C emission estimations are more pronounced when considering the landscape's diversity (S-V) rather than the major, sole land use type (S-I). It is also important to keep in mind that additional factors can influence the reliability of the presented flux estimates. We did not intend to address all possible processes, e.g., we did not include issues of scaling, non-linearity and non-additive effects¹⁴⁸ even though these are important components to discuss further. For instance, in peatlands, the effect of water-table position on CH₄ efflux is highly non-linear. Consequently, an estimate of the C landscape flux which is based on mean water-table position and ignores such spatial and temporal variability may be strongly biased.¹⁵¹ An additional example is related to small water bodies, where C effluxes may be driven by allochthonous inputs from surrounding terrestrial areas. In such systems the size and spatial distribution of aquatic patches, as well as terrestrial–aquatic fluxes of dissolved and particulate organic carbon, will be important. Until today, these fluxes are highly uncertain and still unknown. However, we suggest that integrated flux measurement taking into account the high spatio-temporal variability of environmental drivers that affect fluxes and the transfer of carbon between compartments and along gradients should be performed in future for a more detailed assessment of landscape scale fluxes (Box 1).

CONCLUSIONS

Most C budget studies have focused either on aquatic or terrestrial research, in which C flux calculations are based on the researchers' own measurements and on additional literature data (e.g., terrestrial research

Box 1

SMALL WATER BODIES—IMPORTANT IMPLICATIONS AT THE LANDSCAPE SCALE

Most of the world's water bodies are shallow and small (≤ 1 ha),^{29,152} representing 1.8% ($>75,000$ km²) of the global surface area of standing inland water resources,²⁹ and their high perimeter-to-area and area-to-volume ratios facilitate strong coupling with their terrestrial catchments.^{107,153,154} Several analyses have shown that many aquatic processes, rates, and quantities per unit area are more intense and complex in small aquatic ecosystems than in larger lakes. Such small water bodies act as a littoral zone: the whole system comprises a biogeochemically active, terrestrial–aquatic interface where carbon dioxide (CO₂) and methane (CH₄) are exchanged with the atmosphere and where organic carbon from the surroundings is transferred into the system. High seasonal variability in many environmental variables, such as in water level fluctuations, substantial temperature changes, ice coverage, water color due to algal blooms, and macrophyte coverage, leads to extremely high spatio-temporal variability in physical, chemical, and biological variables. These rapid changes in environmental parameters indicate that they play an unexpectedly important role in global C cycling and greenhouse gas emissions and can be regarded as CO₂ hot spots.¹⁵⁵ Understanding carbon cycling through small inland water bodies will reduce the uncertainty in estimating the net ecosystem C exchange at the landscape scale.

for aquatic researchers and vice versa). Thus, there are still major knowledge gaps concerning the connectivity between aquatic and terrestrial C fluxes at the landscape scale. So far, only a few C flux studies at the landscape scale are available to bridge knowledge gaps between aquatic and terrestrial research.^{11,14,156}

The combination of this simplified GIS-based simulation approach as a landscape example with a literature review underpins the uncertainties in C flux calculations at the landscape level. This strategy also shows that small-scale patterns and spatial heterogeneity can affect the calculation of landscape scale fluxes, as portrayed in our example of the moraine landscape in NE Germany (Figure 5). As such, the



FIGURE 5 | (a) Image of the moraine landscape in NE Germany. Rape field with several small water bodies (kettle holes) embedded in the cropland (Image courtesy: G. Verch). (b) Instrumented kettle hole near Rittgarten, Uckermark. The kettle hole is part of the longer-term studies of the *LandScales* project (Image courtesy: Garabet Kazanjian).

occurrence of ponds, small lakes, and peatlands greatly increase the regional relevance of agricultural landscapes as sources of greenhouse gases. In the future, these calculated fluxes could help to identify which landscape components are the major drivers of net landscape C effluxes or C influxes.

Currently, small ecosystems are seldom integrated into whole landscape-based approaches. Accordingly, reliable high-quality and high-quantity

data for whole-landscape approaches are still lacking. A landscape-based approach to determine local and global C fluxes will face challenges related to actual research questions in aquatic and terrestrial biogeochemistry and ecology as well as to management options urgently needed for political decisions. For instance, catchment scale planning will support decision-making such as in changing hydrological regimes and potential higher greenhouse gas

emissions of small inland waters and bogs. Despite challenges, a landscape-based approach for calculating global C fluxes will be the most precise and beneficial path forward to counteract humane-induced climate change and the associated alterations of C fluxes.

Our literature review and the simulation exercise on the C fluxes of different aquatic and terrestrial

landscape components in NE Germany indicate that accounting for landscape diversity among different spatial scales improves our knowledge of spatial and temporal OC dynamics and estimates of C fluxes, especially at the landscape scale. Landscape-focused approaches will also improve the projected responses of ecosystems to perturbations, such as those due to global change and anthropogenic activities.

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