The role of local-scale heterogeneities in terrestrial ecosystem modeling

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Abstract The coarse-grained spatial representation of many terrestrial ecosystem models hampers the importance of local-scale heterogeneities. To address this issue, we combine a range of observations (forest inventories, eddy flux tower data, and remote sensing products) and modeling approaches with contrasting degrees of abstraction. The following models are selected: (i) Lund-Potsdam-Jena (LPJ), a well-established, area-based, dynamic global vegetation model (DGVM); (ii) LPJ-General Ecosystem Simulator, a hybrid, individual-based approach that additionally considers plant population dynamics in greater detail; and (iii) distributed in space-LPJ, a spatially explicit version of LPJ, operating at a fine spatial resolution (100 m × 100 m), which uses an enhanced hydrological representation accounting for lateral connectivity of surface and subsurface water fluxes. By comparing model simulations with a multivariate data set available at the catchment scale, we argue that (i) local environmental and topographic attributes that are often ignored or crudely represented in DGVM applications exert a strong control on terrestrial ecosystem response; (ii) the assumption of steady state vegetation and soil carbon pools at the beginning of simulation studies (e.g., under “current conditions”), as embedded in many DGVM applications, is in contradiction with the current state of many forests that are often out of equilibrium; and (iii) model evaluation against vegetation carbon fluxes does not imply an accurate simulation of vegetation carbon stocks. Having gained insights about the magnitude of aggregation-induced biases due to smoothing of spatial variability at the catchment scale, we discuss the implications of our findings with respect to the global-scale modeling studies of carbon cycle and we illustrate alternative ways forward.

1. Introduction

The Earth’s carbon balance and its variability under changing climatic conditions and anthropogenic disturbances are topics of great societal and scientific importance [e.g., Le Quéré et al., 2009, 2013; Regnier et al., 2013]. Terrestrial ecosystems often undergo state transitions imposed by climate variability, anthropogenic interventions, and/or natural disturbances [e.g., Bonan, 2008; Luo and Weng, 2011]. However, understanding and modeling these trajectories still remain very challenging [Levin et al., 1997; Hurtt et al., 1998; Schellnhuber, 1999; Landsberg, 2003; Moorcroft, 2006; Purves and Pacala, 2008; Evans et al., 2012; Pappas et al., 2013]. A bulk of numerical representations, with different degrees of abstraction, has been developed to mimic complex terrestrial ecosystem processes across different scales (see Martin [1993], Perry and Enright [2006], Jettsch et al. [2008], and Levis [2010], for extensive reviews). Dynamic global vegetation models (DGVMs) [Prentice et al., 2000; Quillet et al., 2010] are among the most widely used tools, not only in global carbon cycle research but also as integrated part of Earth system models [e.g., Cox et al., 2000; Prentice, 2012].

The embedded physical mechanisms and causalities allow DGVMs to operate across a wide range of spatial scales, e.g., from the footprint of eddy flux towers, where their performance is often assessed, to global-scale applications, where local parameterizations are extrapolated to larger domains. While the process-based framework of DGVMs makes them very appealing for analyzing future scenarios, any model-based inference is strongly conditioned on their underlying assumptions. Therefore, it is important to investigate whether the causal relations incorporated in these models mimic realistically the observed vegetation dynamics and whether the effects of a spatially heterogeneous vegetation are correctly reproduced. The importance of spatial heterogeneities has been recognized for ecosystem carbon budgets at the regional scale [Zhao and Liu, 2014; but see Hall et al., 2015], and when terrestrial carbon, energy, and water fluxes are
simulated with land surface models [e.g., Li et al., 2013; Melton and Arora, 2014], but has not yet been properly quantified for DGVMs.

In the present study, we combine a range of observations and modeling approaches for assessing the importance of spatial representation in forest-growth dynamics at the catchment scale. By analyzing the problem of terrestrial ecosystem modeling in a well-restricted domain, such as the catchment area, where multivariate data sets are available, rather than at the continental or global scale, where DGVMs often operate, a better assessment of the strengths and weaknesses of the models is expected. In addition, the regional and catchment scales represent scales at which management decisions are taken [e.g., Korzukhin et al., 1996; Mäkelä et al., 2000]. We focus on comparing different approaches for treating spatial vegetation heterogeneities. More specifically, three terrestrial ecosystem models with different degrees of abstraction and spatial representation of vegetation are applied: (i) Lund-Potsdam-Jena (LPJ) [Sitch et al., 2003], a well-established DGVM (section 2.1.1); (ii) LPJ-General Ecosystem Simulator (GUESS) [Smith et al., 2001], a hybrid approach that incorporates a mechanistic description of population dynamics into DGVMs (section 2.1.1); and (iii) distributed in space (D)-LPJ, that is presented for the first time in this study (section 2.1.2) and consists of a spatially explicit version of LPJ operating on a fine resolution grid, which is distributed in space and accounts for lateral water fluxes among the simulated grid cells through an enhanced hydrological representation. The experimental setup is designed to preserve commonly applied practices in each modeling approach (section 2.5).

By comparing model simulations with multiple observed variables, the following questions are addressed: (i) which is the role of landscape heterogeneity (e.g., local climate, and topography) in terrestrial ecosystem modeling? (ii) Does the simulated ecosystem response obtained averaging out subgrid heterogeneities, as is typically done in LPJ or LPJ-GUESS simulations (i.e., \( f(\overline{X}) \)), correspond to the mean simulated response of the system when spatial heterogeneities are explicitly taken into account, as done in D-LPJ simulations (i.e., \( f(X) \))? By answering these questions, we provide an explicit quantification of the potential biases in DGVMs applications, due to smoothing of local heterogeneities, induced by aggregation (\( f(\overline{X}) \) versus \( f(X) \)), as well as detailed explanations for their mismatch. In addition, building upon our findings at the catchment scale, we investigate implications for the modeling of global carbon cycle, where similar tools are often applied without scrutiny of underlying assumptions.

2. Methodology

2.1. Models

2.1.1. Ecosystem Models: LPJ and LPJ-GUESS

LPJ dynamic global vegetation model [Sitch et al., 2003] and LPJ-GUESS [Smith et al., 2001] are established terrestrial ecosystem models. Many studies have been published showing their skills in predicting potential natural vegetation and primary production at global and regional scales [e.g., Badeck et al., 2001; Hickler et al., 2004; Koca et al., 2006; Smith et al., 2008; Ahlström et al., 2012; Tang et al., 2012; Piao et al., 2013]. Both models are not spatially explicit but provide lumped, area-averaged representations (i.e., \( f(\overline{X}) \)), following the symbolism introduced in the previous section.

LPJ and LPJ-GUESS share the same process-oriented representation of plant physiology and ecosystem biogeochemistry but have different approaches for simulating the distribution of vegetation. In LPJ vegetation within a grid cell is described in terms of fractional coverage of different Plant Functional Types (PFTs), and each simulated PFT reflects average properties of the entire population (e.g., tree height and vegetation carbon pools; population-based approach). In LPJ-GUESS forest dynamics and local-scale vegetation heterogeneities are approximated following a gap-model approach [Bugmann, 2001] accounting for ecosystem demography: forest structure is represented by averaging several spatially independent patches (100 patches in the current model configuration) of PFTs with different age classes (cohorts; individual-based approach) [Smith et al., 2001]. The use of several replicated patches accommodates for the variability induced by stochastic processes, such as plant establishment and mortality.

Photonsynthesis, respiration, stomatal regulation, plant phenology, and soil biogeochemistry are simulated at the daily scale, while processes related to forest successional dynamics such as plant growth, establishment, and mortality are computed at the annual scale. Fire disturbances are disabled in the current study. Only a generic background mortality represented by stochastic disturbances (e.g., storms and diseases) is instead
Figure 1. Representation of the D-LPJ ecohydrological scheme. D-LPJ is based on an iterative coupling of the LPJ ecosystem model with the TOPKAPI-ETH hydrological model. LPJ provides an estimate of evapotranspiration fluxes (ETA; soil evaporation, evaporation from interception, and plant transpiration) to TOPKAPI-ETH which then feeds back to LPJ an estimate of the soil water content (SWC), snowpack (SP), and snowmelt (SM). Several iterations of the exchange variables (ETA and SWC, SP, and SM) are performed until convergence of estimated fluxes over the simulated area is achieved.

considered. Soil hydrological processes are modeled at the daily scale with a simple “bucket” hydrological model and do not consider lateral flows, as detailed in Geritne et al. [2004]. The meteorological forcings are daily values of precipitation, temperature, and radiation and annual values of CO$_2$ concentration. Instead of the commonly used generic PFTs, a species-based parameterization of European biomes, proposed by Hickler et al. [2012], is adopted. To better capture Swiss vegetation functioning, some plant physiological parameters are also adjusted, such that data from Swiss eddy covariance flux measurements are better simulated (see section 2.4.1 as well as the detailed discussion in supporting information Text S2). Detailed model descriptions of LPJ and LPJ-GUESS are provided in Sitch et al. [2003] and Smith et al. [2001], respectively.

Since vegetation grows dynamically in both LPJ and LPJ-GUESS, each model simulation starts with no vegetation (bare ground). An initialization period (equal to 500 years in our study) is used to spin-up the model and reach a state where carbon pools and vegetation cover are in equilibrium with the historical climatic conditions. The climate forcings used for spinning-up the model are constructed by repeating randomly years of the observed climate and using the preindustrial CO$_2$ levels. The use of a spin-up period to initialize vegetation and soil carbon pools represents a common and unavoidable step in DGVM applications [Pietsch and Hasenauer, 2006; Carvalhais et al., 2008; Williams et al., 2009].

2.1.2. Ecohydrological Scheme: D-LPJ
D-LPJ (“D” stands for distributed in space) is a novel ecohydrological scheme built upon state-of-the-art ecological and hydrological tools. It combines the LPJ process-based vegetation model, which mimics short- and long-term vegetation dynamics, with the TOPographic Kinematic APproximation and Integration (TOPKAPI-ETH) hydrological model, which mechanistically simulates soil and surface water dynamics. The coupling strategy incorporated in the D-LPJ scheme is illustrated in Figure 1.

TOPKAPI-ETH is a spatially explicit hydrological model that originates from the TOPKAPI rainfall-runoff model [Ciarapica and Todini, 2002; Liu and Todini, 2002]. The process-based framework of the model allows for a detailed spatial and temporal representation of the major hydrological processes at the catchment scale, accounting not only for runoff generation and routing but also for evapotranspiration, snow, and glacier dynamics (e.g., see Paschalis et al. [2014], for a recent application of TOPKAPI-ETH on catchment flood response). Spatial heterogeneity is represented by discretizing the domain as a fine resolution regular grid, while the temporal dynamics of the hydrological processes are solved at an hourly time step. The meteorological input variables are hourly values of precipitation and temperature and daily cloud cover transmissivity. The shortwave radiation fluxes are computed internally, accounting for topographic effects, based on clear-sky radiation [Bird and Hulstrom, 1981; Iqbal, 1983], sky view factor and terrain shading [Corripio, 2003], cloud cover transmissivity, and surface albedo. The spatially distributed nature of TOPKAPI-ETH facilitates a high-resolution representation of topography. Different computational elements are connected in the surface and in the subsurface according to topographic gradients. A kinematic wave approximation is applied to route water in the surface, subsurface, and channels [Liu and Todini, 2005]. Three soil layers are used for mimicking the vertical soil water dynamics; the first two (schematized as nonlinear
Table 1. Summary of the Model Configurations Used for the Numerical Experimentsa

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aModel settings are assigned based on typical practices, i.e., coarse resolution for LPJ and LPJ-GUESS and a spatially explicit representation for D-LPJ.

D-LPJ operates in a spatially explicit mode. Precipitation, temperature, and radiation fields are used to drive LPJ at a daily time step. The original hydrological module of LPJ is used for estimating soil and snow water dynamics only during the spin-up period. Once the spin-up period is completed, distributed fields of soil water content, snowmelt, and snowpack, computed with TOPKAPI-ETH, are provided as input to LPJ. When a simulation of LPJ is completed, distributed evapotranspiration fluxes (soil evaporation, plant transpiration, and evaporation from interception) are fed back to TOPKAPI-ETH (Figure 1). Several iterations are conducted until a convergence of the exchange state variables is achieved (evapotranspiration fluxes and soil water content; Figure S1). This information is exchanged at the end of the simulation period, i.e., 10 years in the present study. Contrary to the approach of using potential natural vegetation of LPJ and LPJ-GUESS, as well as of most DGVM applications, for obtaining the vegetation cover of the examined area, a land use map is imposed on D-LPJ in order to prescribe a realistic vegetation distribution over the simulated domain.

In summary, when compared to the original, area-averaged, lumped watershed representations of LPJ and LPJ-GUESS, D-LPJ includes (i) distributed vegetation cover based on the current land use map, (ii) spatially explicit topographic and meteorological attributes, defined on a fine resolution grid, and (iii) refined soil moisture dynamics computed with a spatially explicit hydrological module that solves the lateral connectivity of surface and subsurface water fluxes (see Table 1).

2.2. Case Study

The Kleine Emme basin is located in the central part of Switzerland, on the northern edge of the Alps (Figure 2). It covers about 477 km² with an average elevation of 1050 m above sea level (asl), ranging from 2329 m asl on the southern edge to 431 m asl at the catchment outlet (Littau; 47°4′0.1″N, 8°17′2.6″E). The long-term (from January 2000 to December 2009) precipitation and air temperature averaged over the entire catchment are 1650 mm yr⁻¹ and 7.7°C, respectively (Figure 3). The river flow is unregulated with a mean discharge at the outlet of about 1023 mm yr⁻¹. Most of the catchment area is covered by forest and grassland (Figure 4c).

2.3. Input Data

2.3.1. LPJ and LPJ-GUESS Input Variables

Assigning mean meteorological and topographic properties over a large area is a common practice for simulations with LPJ and LPJ-GUESS since they are typically used for regional- or global-scale applications with relatively coarse spatial resolution. Accordingly, daily values of spatially averaged meteorological variables (precipitation, temperature, and radiation) available in the Kleine Emme region, are used for the simulations with LPJ and LPJ-GUESS (see section 2.3.2 and Figure 3). Annual values of atmospheric CO₂ concentrations are derived from ice core reconstructions [Sitch et al., 2003; Frank et al., 2010] and the Mauna Loa record [Keeling et al., 2009]. Mean soil properties are also prescribed following the global soil map from Food and Agriculture Organization [1991].

2.3.2. D-LPJ Input Variables

For the hydrological component of D-LPJ, meteorological forcings as well as topographic, land cover, and soil data should be provided for each computational element, since TOPKAPI-ETH is spatially explicit. In the present model setup a regular grid of 100 m x 100 m resolution is used to account for spatial heterogeneity, resulting in a total of 47,707 computational elements over the Kleine Emme catchment.
Figure 2. The Kleine Emme catchment is located in the central part of Switzerland. Three stream gauges operate in the main river network (blue circles), and three meteorological stations (red circles) with high-quality temperature and radiation measurements are located close to the catchment boundaries.

Historical data are available from the Swiss meteorological service. Hourly precipitation and temperature gridded fields [Wüst et al., 2010], with 100 m × 100 m resolution, for the period January 2000 through December 2009, are used (Figure 3). Daily values of cloud transmissivity, uniformly distributed over the catchment, are estimated with a weather generator [Fatichi et al., 2011], comparing simulated clear-sky shortwave radiation with ground measurements from three radiometers in the catchment area (Figure 2). A detailed description of the meteorological products is provided in the supporting information (Text S1).

Topographic data are obtained by resampling a fine resolution (25 m × 25 m) digital terrain model of Switzerland to 100 m × 100 m resolution (Figure 4a). The Global Land Cover Product (GlobCover) [Bontemps et al., 2011] and the Swiss soil map [GEOSTAT, 2000] are used to assign spatially distributed land cover and soil properties (Figure 4).

Figure 3. Spatial distribution (100 m × 100 m resolution) of mean daily (a) precipitation, (b) temperature, and (c) radiation, averaged over the examined period (January 2000 to December 2009) for the Kleine Emme catchment. Inner plots illustrate the areal probability density function with the areal mean denoted by a continuous red line. D-LPJ simulations are driven with spatially explicit meteorological forcings, while area-averaged values are used for the simulations with LPJ and LPJ-GUESS.
The vegetation component of D-LPJ also operates in a spatially explicit mode with a 100 m × 100 m resolution regular grid but with a daily temporal resolution. Hourly precipitation and temperature fields are thus aggregated to daily scale and used for the D-LPJ simulations together with the radiation fields calculated by TOPKAPI-ETH (Figure 3). Annual values of atmospheric CO₂ concentrations, the same as for LPJ and LPJ-GUESS, are assumed to be uniformly distributed over the catchment area. In addition, spatially distributed fields of soil water content, snowmelt, and snowpack, computed using TOPKAPI-ETH, are used as inputs to D-LPJ after the spin-up period (Figure 4b).

A land use map, based on GlobCover, is imposed to constrain the occurrence of different vegetation types (Figure 4c). More specifically, generic land use classes (e.g., deciduous, evergreen, and mixed forest) are used to restrict the species distribution over the catchment. Evergreen species, for example, can only occur in computational elements where land use map indicates evergreen or mixed forest. This allows us to preserve the observed land use and to obtain a better spatial representation of the current vegetation cover.

2.4. Confirmation Data Sets
2.4.1. Eddy Covariance Flux Measurements
Eddy covariance (EC) flux measurements available from the Swiss FluxNet (http://www.swissfluxnet.ch), which is part of the international research network FluxNet [Baldocchi et al., 2001; Baldocchi, 2003], are incorporated in the analysis to refine the parameterization of carbon assimilation for vegetation in Switzerland. More specifically, we compare model simulations of LPJ with observations of carbon fluxes at five EC towers [Wolf et al., 2013]. Plant physiological parameters are adjusted to improve the representation of vegetation functioning in the Swiss environment (see supporting information Text S2). We use measurements from two forested areas: a deciduous forest (mostly dominated by European beech, *Fagus sylvatica*) in the Laegeren mountain (tower coordinates: 47°28′42.0″N and 8°21′51.8″E at 682 m asl; examined period: 2004–2009; Ahrends et al. [2009]; Zweifel et al. [2010, 2011]) and a subalpine coniferous forest in Davos (mostly covered by Norway spruce, *Picea abies*) in the Eastern Swiss Alps (tower coordinates: 46°48′55.2″N and 9°51′21.3″E at 1639 m asl; examined period: 2000–2005; Zweifel et al. [2010], Etzold et al. [2011]). In addition, EC data from three grassland sites are included in the analysis: Chamau (tower coordinates: 47°12′36.8″N and 8°24′37.6″E at 393 m asl; examined period: 2006–2008; Zeeman et al. [2010]), Fruebuel (tower coordinates: 47°6′57.0″N and 8°32′16.0″E at 982 m asl; examined period: 2006–2008; Zeeman et al. [2010]), and Oensingen (tower coordinates: 41°16′59.9″N, 7°43′59.9″E at 451 m asl; examined period: 2002–2003; Ammann et al. [2007, 2009]). A more detailed description of the use of EC flux measurements is provided in the supporting information (Text S2).
2.4.2. MODIS Products
Spatial and temporal dynamics of two variables, gross primary production (GPP) and leaf area index (LAI), from the Moderate Resolution Imaging Spectroradiometer (MODIS) [Huete et al., 2002] are used for a qualitative assessment of the models. The spatial resolution of these vegetation indices is $1 \times 1\, \text{km}^2$ while the temporal resolution is 8 days. The mismatch in the spatial resolution between MODIS and D-LPJ (100 m $\times$ 100 m), as well as the uncertainties related to these products [e.g., Tian et al., 2002; Kang et al., 2005; Heinsch et al., 2006; Pan et al., 2006; Zhao et al., 2006; Fang et al., 2012, 2013], hampers a quantitative evaluation of simulated vegetation metrics over the Kleine Emme area. Only a qualitative comparison of the spatial distributions and seasonality of GPP and LAI is therefore attempted, aiming at the visual comparison of long-term spatial patterns in the catchment and of the area-averaged seasonal dynamics. The implemented preprocessing procedures (e.g., quality control, temporal smoothing, and interpolation) of the raw MODIS data for the examined simulation period are detailed in the supporting information (Text S3).

2.4.3. Forest Inventory Data
The Swiss National Forest Inventory (NFI; http://www.lfi.ch) is a joint project of the Federal Office for the Environment and the Swiss Federal Institute for Forest, Snow, and Landscape Research. It records different vegetation variables related to the area, structure, and status of forests in Switzerland. The NFI database consists so far of three surveys: the first was conducted over the period from 1983 to 1985, the second one from 1993 to 1995, and the third one from 2004 to 2006. Inventory plots influenced by anthropogenic disturbances (e.g., plant cuttings and replanting) are excluded from our analysis. More details on the NFI are reported in the supporting information (Text S4). Here we focus on the rate of long-term changes in vegetation carbon stocks, $\Delta C_{\text{veg}}/\Delta t$, where $C_{\text{veg}}$ is the total vegetation carbon (i.e., carbon in the foliage, wood, and roots) and $\Delta t$ refers to the examined time period. Simulated values of $\Delta C_{\text{veg}}/\Delta t$ can be compared with the inventory-based estimates since forest plots with anthropogenic disturbances are excluded from our analysis. Changes in vegetation carbon stocks can be mainly attributed to the balance between vegetation growth and natural disturbances, assuming other components affecting the vegetation carbon balance (e.g., natural herbivory and emission of volatile organic compounds) to be of minor importance for the purpose of our study [Luyssaert et al., 2010].

2.4.4. River Discharge
We complement the validation data sets with measurements of river discharge distributed in the main river corridor (Figure 2). Hourly streamflow data from January 2000 through December 2009 at the catchment outlet at Littau (station coordinates: $47^\circ4'0.1''\text{N}, 8^\circ17'2.6''\text{E}$; elevation: 431 m asl) and at Werthenstein (station coordinates: $47^\circ2'5.6''\text{N}, 8^\circ4'6.4''\text{E}$; elevation: 595 m asl; draining area: 311 km$^2$) are provided by the Swiss Federal Office for the Environment. A cantonal station at Soerenberg (LU14; station coordinates: $46^\circ49'13.3''\text{N}, 8^\circ2'6.0''\text{E}$; elevation: 1150 m asl; draining area: 23 km$^2$) covering a period of January 2005 to December 2009 is also included in the analysis even though the station data is likely characterized by a lower quality (Figure 2). River discharge can be considered as an aggregated ecosystem property, encompassing both biotic (e.g., plant transpiration) and abiotic (e.g., evaporation and river routing) processes. Therefore, realistic simulation of streamflow reinforces our confidence about model consistency in reproducing the principal physical mechanisms determining the hydrological response of the catchment.

2.5. Experimental Design
The experimental approach is designed to respect the configurations that are commonly applied in each of the models we used. More specifically, the three examined models, namely, LPJ, LPJ-GUESS, and D-LPJ, are configured using either domain average or spatially explicit local-scale information ($f(\mathbf{X})$ and $f(\mathbf{x})$; Table 1). While, theoretically, both LPJ and LPJ-GUESS could have been used with a fine resolution configuration, e.g., by prescribing the current vegetation cover and using fine resolution climatic forcings, this would have been at odds with common applications carried out with these types of models. Furthermore, simplifications in process representation that can be acceptable at coarse spatial or temporal scales, are not valid at finer resolutions. For instance, the “bucket-type” hydrological representation, which ignores lateral water fluxes, can be a fair approximation at coarse spatial scales but typically fails at finer scales where lateral exchanges may be important [Li et al., 2013; G. Tang et al., 2014] (see also detailed discussion in section 4.4). Therefore, in order to preserve the assumptions applicable at the different scales, we use LPJ and LPJ-GUESS with coarse-scale boundary conditions and forcings, and D-LPJ with heterogeneous forcings at 100 m $\times$ 100 m resolution (Table 1). With this configuration, we investigate aggregation-induced biases ($f(\mathbf{X})$ versus $f(\mathbf{x})$).
comparing the three contrasting approaches for modeling vegetation dynamics. However, for the sake of completeness, the results of a full factorial experimental design (e.g., simulations of LPJ with fine resolution inputs and current land use information, as done for D-LPJ simulations) are included in the supporting information (Texts S5 and S6 and Figures S6–S11). In essence, as illustrated in Figure S1, the preliminary D-LPJ simulation (i.e., “iteration 0”; Figure S1) corresponds to a LPJ simulation which is forced with fine resolution inputs but lacks the mechanistic hydrological representation of TOPKAPI-ETH (Figure 1).

3. Results

3.1. Regionalizing the Parameterization of Vegetation

The parameterization proposed by Hickler et al. [2012] is used for a first comparison of vegetation carbon fluxes. However, a considerable mismatch is found between EC-based GPP and the simulated values (Figure S2). In this regard, the case of the evergreen forest in Davos is striking; the site is dominated by Norway spruce (Picea abies) with an observed mean annual GPP of about 1100 g C m$^{-2}$ yr$^{-1}$ [Etzold et al., 2011], while the simulated GPP with LPJ, using the original parameterization of Picea abies, is about 2000 g C m$^{-2}$ yr$^{-1}$ for the period 2000 to 2005 (Figure S2). This mismatch is not entirely surprising since the parameterization of LPJ, as well as that of LPJ-GUESS, is made envisioning global- or continental-scale applications (see Hickler et al. [2012], for the European continent). It is therefore expected that average parameter values, developed for example to describe vegetation properties in a 1° × 1° grid, will not be representative of the fine-scale heterogeneities encapsulated in the footprint of eddy flux towers [e.g., Pappas et al., 2013; Rogers, 2014]. Manual adjustments of some plant physiological properties are therefore applied to LPJ, LPJ-GUESS, and D-LPJ simulations, providing a more accurate representation of vegetation carbon fluxes for the Swiss environment (Figure S3). The supporting information (Text S2) provides a detailed description of the adjusted parameters and the rationale behind the modifications. After these modifications, the skill of the model in reproducing carbon fluxes for the Swiss FluxNet sites is significantly improved, enabling the model to achieve a coefficient of determination between daily simulated and observed GPP equal to 0.62, 0.71, 0.69, 0.69, and 0.53, respectively, in Chamau, Davos, Fruebuel, Laegeren, and Oensingen (see also Figure S3).

3.2. Confirming the Hydrological Consistency

Satisfactory results of river discharge are obtained with D-LPJ without significant calibration efforts. This model captures fairly well both the short-term and the seasonal dynamics of river flow in all the examined locations (Figure S4). The long-term water budget of the catchment is also realistically simulated, although evapotranspiration is slightly underestimated. For the period 2000–2009, out of the 1650 mm yr$^{-1}$ of precipitated water, 1170 mm yr$^{-1}$ is simulated as discharge at the outlet and around 480 mm yr$^{-1}$ as evapotranspiration, while the observed discharge at the outlet is 1023 mm yr$^{-1}$.

3.3. Bird’s-Eye View on Vegetation Indices

3.3.1. Vegetation Cover

The two implemented approaches for initialization of vegetation cover, i.e., potential natural vegetation for LPJ and LPJ-GUESS, as opposed to a constrained vegetation distribution based on current land cover for D-LPJ, lead to distinct results (Figure 5). The potential natural vegetation, obtained after the end of the spin-up period, varies significantly from the actual vegetation distribution in the area. In D-LPJ simulations, both evergreen and deciduous species have an important role in the overall vegetation carbon dynamics, reflecting the information of the current land use map in the area (Figure 5b). Since land cover information is not imposed in LPJ and LPJ-GUESS simulations, a considerable discrepancy occurs between the actual vegetation cover and the simulated potential natural vegetation over the Kleine Emme catchment (Figures 4c, 5d, and 5e, respectively). Both LPJ and LPJ-GUESS overestimate the proportional abundance of deciduous forest (Figures 5d and 5e). In addition, significant differences also occur when vegetation carbon stocks and their long-term dynamics are compared (Figures 5c–5e).

3.3.2. Spatial Dynamics of GPP and LAI

For both GPP and LAI, the spatially explicit nature of D-LPJ, accounting for current land cover as well as local topography and climatic conditions, allows for a reasonable representation of spatial heterogeneities (Figures 6a and 6b for GPP; and Figures 7a and 7b for LAI). Since LPJ and LPJ-GUESS are not spatially explicit, estimates of mean GPP and LAI over the examined area, computed using mean climate conditions, $\bar{f}(\mathbf{X})$, are compared with the area-averaged D-LPJ and MODIS estimates, $\bar{f}(\mathbf{X})$ (Figures 6c and 6d for GPP; and Figures 7c and 7d for LAI).
Figure 5. (a) Total vegetation carbon as simulated with D-LPJ, LPJ, and LPJ-GUESS for the spin-up (500 years) and the historical periods (10 years; shaded area). (b) Distribution of vegetation types over the catchment area, at the end of the simulation period, as estimated by D-LPJ (based on the current land cover map; Figure 4c). Long-term vegetation carbon dynamics over the Kleine Emme catchment, as obtained through the spin-up period, for simulations with (c) D-LPJ, (d) LPJ, and (e) LPJ-GUESS. Different plant types are grouped in major plant life forms, i.e., evergreen, deciduous, grass, and shrubs.

Visual similarities exist between GPP estimated by MODIS and D-LPJ (Figures 6a and 6b). The mean aggregated response over the catchment is comparable: about 970 g C m$^{-2}$ yr$^{-1}$ for MODIS, and about 1080 g C m$^{-2}$ yr$^{-1}$ for D-LPJ. However, MODIS fails, due to algorithmic limitations, to capture the high productivity of the grasslands located in the lowland valleys, while D-LPJ simulation provides a second peak in the GPP distribution, at around 1500 g C m$^{-2}$ yr$^{-1}$, highlighting such contribution to the overall GPP of the area (Figure 6e). The D-LPJ results cannot be considered an artifact of the model simulations since the high productivity of grasslands in Switzerland is confirmed by the Swiss FluxNet sites (see section 3.1). Conversely, uncertainties in MODIS product, related to the transfer of the absorbed radiation into carbon...
Figure 6. Spatial patterns of mean gross primary production (GPP) for the period 2000 through 2009, over the Kleine Emme catchment, as estimated by (a) MODIS, (b) D-LPJ, (c) LPJ, and (d) LPJ-GUESS as well as (e) a comparison of the spatial distribution among the four different estimates. The mean of each distribution is denoted by dashed lines. Note that since LPJ and LPJ-GUESS are not spatially explicit, a single value, representative for the entire catchment, is provided.

assimilation for grassland as well as frequent periods with cloud or snow cover in the catchment, may cause these discrepancies [e.g., Kang et al., 2005; Heinsch et al., 2006; Zhao et al., 2006].

The LPJ and LPJ-GUESS estimates of GPP are significantly different from those retrieved by MODIS and simulated by D-LPJ, i.e., $f(X) \neq \bar{f}(X)$. LPJ-GUESS gives a value of GPP of about 650 g C m$^{-2}$ yr$^{-1}$ (averaged over the simulated period), while the LPJ value is slightly higher (about 835 g C m$^{-2}$ yr$^{-1}$) but still considerably below the D-LPJ or MODIS values. This can be attributed to differences in vegetation composition as well as in local meteorological/hydrological conditions underlying D-LPJ, LPJ, and LPJ-GUESS simulations. In both LPJ and LPJ-GUESS simulations, deciduous forest is the dominant vegetation type over the area, while in D-LPJ simulations the current vegetation cover is preserved (Figure 5).

The coarse resolution of the MODIS product cannot capture some of the heterogeneities in the LAI patterns as simulated by D-LPJ (Figures 7a and 7b). The importance of local climate (particularly the spatial patterns of temperature and radiation, Figures 3b and 3c) in shaping the LAI dynamics is reflected in the D-LPJ
Figure 7. Spatial patterns of mean leaf area index (LAI) for the period 2000 through 2009, over the Kleine Emme catchment, as estimated by (a) MODIS, (b) D-LPJ, (c) LPJ, and (d) LPJ-GUESS as well as (e) a comparison of the spatial distribution among the four different estimates. The mean of each distribution is denoted by dashed lines. Note that since LPJ and LPJ-GUESS are not spatially explicit, a single value, representative for the entire catchment, is provided.

3.3.3. Temporal Dynamics of GPP and LAI

The seasonal dynamics of GPP simulated with D-LPJ are in good agreement with vegetation activity estimated with MODIS (Figure 8a). MODIS products capture greening phase dynamics with less uncertainty than its magnitude [e.g., Heinsch et al., 2006]. However, some source of error can still be present, for instance, related to data-processing algorithms and missing values. While the length of the growing season is fairly comparable between MODIS and D-LPJ estimates, a mismatch in the intraseasonal variability of LAI occurs (Figure 8b). The seasonal patterns of GPP and LAI as simulated by LPJ and LPJ-GUESS are also similar to the D-LPJ results, since the underlying phenology modules are identical in all three models and the effect of local climatic differences is smoothed out by averaging them over the entire domain (Figure S5).
3.4. Ant’s-Eye View on Carbon Stocks

Vegetation carbon dynamics, expressed as the rate of long-term changes in vegetation carbon stocks, denoted as $\Delta C_{\text{veg}}/\Delta t$, for the last 10 years of simulations with D-LPJ, LPJ, and LPJ-GUESS (i.e., 2000 to 2009), are significantly different when compared to estimates from the in situ forest inventory observations (Figure 9). In the spatial domain of the catchment, $\Delta C_{\text{veg}}/\Delta t$ values estimated by D-LPJ are close to zero for most of the grid cells except for few sites on the southwest part of the region where evergreen and mixed forest occur. Even for these cells, the values of $\Delta C_{\text{veg}}/\Delta t$ simulated by D-LPJ are much lower than the range of variability of the forest inventory sites, which exhibit values of the first and third quantiles around 100 and 400 g C m$^{-2}$ yr$^{-1}$, respectively (Figure 9b). This does not come as a surprise since it is the result of imposing in the simulations carried out with D-LPJ, LPJ, and LPJ-GUESS a spin-up period, as it is generally done in DGVM applications. The spin-up is designed to provide a state of vegetation in equilibrium with the prevailing environmental conditions. Therefore, in absence of significant climatic changes, the simulated changes in vegetation carbon stocks with D-LPJ, LPJ, and LPJ-GUESS are intrinsically low (practically close to zero, as shown by Figure 9b). Conversely, the observations obtained from the forest inventories give a mean rate of increase in vegetation carbon stocks of about 210 g C m$^{-2}$ yr$^{-1}$ in the examined forests (Figure 9b), because they represent measurements of actual and likely nonstationary conditions, which are influenced for example by environmental controls and natural disturbances. Discrepancies occur also when $\Delta C_{\text{veg}}/\Delta t$ values at the beginning of the spin-up period are compared with the inventory-based estimates. The slope of the vegetation carbon pools for the first 100 years of the spin-up, computed as the derivatives of the vegetation carbon stock accumulation over 10 year time windows (Figure 5a), varies in the range of 35–120, 15–135, and 25–65 g C m$^{-2}$ yr$^{-1}$ for LPJ, LPJ-GUESS, and D-LPJ, respectively, contrasting with the mean estimated changes in vegetation carbon stocks from the forest inventories which is considerably higher (210 g C m$^{-2}$ yr$^{-1}$; Figure 9b).

4. Discussion

The results presented in the previous sections provide a comprehensive evaluation of several approaches for modeling terrestrial ecosystems scrutinizing modeling assumptions and spatial aggregation rules. We explicitly quantified how the coarse spatial representations of DGVMs lead to aggregation-induced biases for the orographically complex landscape of the Kleine Emme catchment. Hereafter, we discuss the insights gained at the catchment scale which have possible implications for applying such modeling approaches at the regional and global scales.

4.1. Aggregating Landscape Heterogeneity: DGVMs, Gap Models, and Ecohydrological Schemes

Since LPJ, LPJ-GUESS, and D-LPJ apply an identical formulation to mimic biophysical and biochemical processes, discrepancies among the simulated vegetation dynamics can be attributed to three main reasons, further discussed in the following sections: (i) initialization with different vegetation cover, i.e., potential natural vegetation (LPJ and LPJ-GUESS) versus constrained vegetation distribution derived from current land cover information (D-LPJ); (ii) effects of local topography, climate, and hydrological representation, i.e., mean field approach of LPJ and LPJ-GUESS versus ecohydrological approach of D-LPJ;
Figure 9. (a) Spatial patterns of the rate of long-term changes in vegetation carbon stocks (denoted as $\Delta C_{\text{veg}}/\Delta t$) of forested areas in Kleine Emme as estimated by D-LPJ, and by the National Forest Inventories (NFI; black dots; filled symbols are used for increase, while open circles are used for decrease in total vegetation carbon). (b) Box plot of $\Delta C_{\text{veg}}/\Delta t$ values over the Kleine Emme region, based on LPJ-GUESS, LPJ, D-LPJ, and NFI. Grey dots correspond to $\Delta C_{\text{veg}}/\Delta t$ values either in each simulated grid cell (case of D-LPJ), or in each of the forest inventory plots (case of NFI). The areal mean is indicated with red circles.

4.1.1. The Importance of Actual Rather Than Potential Vegetation Cover

In agreement with other model- and data-based studies, the role of land use history cannot be easily neglected when fragmented landscapes, such as the Kleine Emme catchment, are simulated [Harmon, 2001; Barnes and Roderick, 2004; Hurtt et al., 2004; Gimmi et al., 2008, 2012; Williams et al., 2009]. Even though vegetation cover is initialized in the three approaches (LPJ, LPJ-GUESS, and D-LPJ), since the successional dynamics of vegetation are simulated starting from an unvegetated state, the imposition of a land use map allows for a better representation of the current state of the system. This was reflected in the D-LPJ results in terms of species distribution (Figure 5b), GPP (Figure 6b) and LAI (Figure 7b) dynamics. In addition, by comparing simulation results of LPJ using the current land cover map with the D-LPJ results (supporting information Text S5), the following additional conclusions can be drawn: (i) the role of land cover initialization is most relevant for the carbon fluxes (GPP; Figure S6) and (ii) the role of local climate, topography, and hydrological regime is predominant in controlling the leaf area pattern (Figure S7). These results highlight the importance of accounting for anthropogenic impacts on the land cover history within...
of the forest stand thus improving the area-averaged representation of most DGVMs [e.g., Bugmann by the individual-based approach. Mechanistic representations of forest demography using the gap model heterogeneities and hydrological regime, appears to be more influential, overcoming the variability induced topographic attributes, and soil water content spatiotemporal variability) that in mesoscale and fairly Nonetheless, they still fail in including local-scale heterogeneities (disturbances, meteorological and implemented here as well as in other ecohydrological models [e.g., Smith et al. 4.1.3. The Role of Forest Structure and Dynamics Different representations of the canopy (i.e., population-based versus individual-based approach; section 2.1.1) cause differences in simulated vegetation carbon dynamics (Figure 5). As already highlighted by Smith et al. [2001], the population-based model provides higher values of GPP and LAI in comparison to the individual-based approach (Figures 6e and 7e). This is due to differences in the light distribution throughout the canopy. In LPJ-GUESS the simulated forest stand is more heterogeneous, and light harvesting is less efficient because of leakages in the vegetation canopy, while the vertical homogeneity of LPJ allows to capture more radiation [Smith et al., 2001]. However, it is worth underlining that the variability of vegetation dynamics, induced by local-scale forest disturbances as well as climatic heterogeneities and hydrological regime, appears to be more influential, overcoming the variability induced by the individual-based approach. Mechanistic representations of forest demography using the gap model approach [Bugmann, 2001] are often introduced with the aim to account for the spatial heterogeneity of the forest stand thus improving the area-averaged representation of most DGVMs [e.g., Liu et al., 2011]. Nonetheless, they still fail in including local-scale heterogeneities (disturbances, meteorological and topographic attributes, and soil water content spatiotemporal variability) that in mesoscale and fairly
heterogeneous catchments, like Kleine Emme, appear to exert a strong signature in vegetation response (Figures 6 and 7).

4.2. Equilibrium Vegetation and the Rate of Carbon Sequestration

The concept of potential vegetation in equilibrium with historical climate conditions is often incorporated in DGVMs for the initialization of several of their state variables (e.g., vegetation, soil, and litter carbon pools). Given the daunting task of initializing every single variable for which often no information is available, a spin-up period, starting from an unvegetated state, is a convenient and unavoidable way for model initialization [Pietsch and Hasenauer, 2006; Carvalhais et al., 2008, 2010; Williams et al., 2009]. Our results provide a direct quantification of the implications of such a simplified assumption and are consistent with observations from an increasing number of studies indicating that many forest ecosystems are not in equilibrium but rather in a growing stage [e.g., Buchmann and Schulze, 1999; Liski et al., 2002; Clais et al., 2008; Keith et al., 2009; Luysaert et al., 2010]. This is particularly true for the highly productive Swiss forest [Gehrig-Fasel et al., 2007] where carbon sequestration is estimated to be 60% higher than an average forest of central Europe [SAEFL/WSL, 2005; Etzold et al., 2011]. The legacy of the place shapes the landscape in a much different way than what can be obtained using the potential vegetation hypothesis, i.e., assuming vegetation in equilibrium with historical climate. The history of local-scale disturbances controls ecosystem equilibrium or a lack thereof, thus influencing its response in terms of productivity and capacity to store carbon [e.g., Sprugel, 1991; Durrett and Levin, 1994; Körner, 2003; Gehrig-Fasel et al., 2007; Smith, 2014].

While the inventory-based estimate of $\Delta C_{reg}/\Delta t$ for our case study is about 210 g C m$^{-2}$ yr$^{-1}$, all the three models, LPJ, LPJ-GUESS, and D-LPJ, simulate a value at the end of the spin-up period which is close to zero (Figure 9). D-LPJ allows, however, for some variability, which makes the results more comparable to NFI estimates (Figure 9). Because LPJ-GUESS, in comparison to LPJ and D-LPJ, allows for generic disturbances, simulated as random events with predefined expected return periods, it can maintain a dynamic equilibrium by balancing between disturbance events and forest recovery leading to a more variable carbon balance dynamics (Figure 5a). However, while these patch-scale disturbances may lead to realistic simulations at the global or continental scales [e.g., Badeck et al., 2001; Smith et al., 2001; Hickler et al., 2004], our analysis demonstrates that they become questionable at basin mesoscales like that of our test case (Figure 9).

At these scales, approaches based on the specific local disturbance history should be applied.

Model simulations of terrestrial ecosystem functioning can therefore be significantly improved using a better description of the boundary conditions [Liu et al., 2011]. The increasing data availability through Earth observation programs [e.g., Pan et al., 2013; Butler, 2014] and advanced remote sensing techniques [Kerr and Ostrovsky, 2003; Hurtt et al., 2004; Antonarakis et al., 2014] provide already a rich amount of information, such as vegetation type, biomass, stand age class, phenology, leaf area index, and tree height [Lucas and Curran, 1999; Turner et al., 2004; Nightingale et al., 2004; Shugart et al., 2010], which can be conveniently used for model initialization. While enhancing model initialization with global scale-distributed observations comes without additional computational cost, it can improve significantly model simulations.

4.3. Vegetation Carbon Fluxes and Stocks: Toward a Better Model-Data Integration

Eddy covariance flux measurements and forest inventories are the two main strategies for tracing vegetation carbon fluxes and stocks, respectively. As eddy flux towers are becoming widespread worldwide [Baldocchi, 2014] and biosphere and atmosphere fluxes are getting widely accessible, many model-data comparisons are conducted for flux tower sites, mainly focusing on ecosystem level carbon fluxes (GPP [e.g., Schaefer et al., 2012] or net ecosystem exchange [e.g., Dietze et al., 2011]). At the same time, several tree census data sets are available worldwide [Anderson-Teixeira et al., 2014], offering a great potential for model-data integration [Lichstein et al., 2010]. However, few studies so far have compared model simulations with carbon stock measurements or demographic stand characteristics [e.g., Hurtt et al., 2004; Weng and Luo, 2011; Medvigy and Moorcroft, 2012; Antonarakis et al., 2014].

Model confirmation against vegetation carbon fluxes at eddy covariance flux tower sites does necessarily not imply a realistic simulation of vegetation carbon stock dynamics in areas with similar vegetation cover and environmental conditions. While D-LPJ performs fairly well in capturing the spatial (Figure 6) and temporal dynamics (Figure 8a) of vegetation carbon fluxes and shows a reasonable agreement with the Swiss FluxNet sites (Figure S3), remarkable differences occur when modeled and observed values of forest carbon stock changes are compared (Figure 9). Disturbances, aging, and turnover processes may have more significant contribution to the landscape’s carbon budget than the assimilated carbon through plant activity.
4.4. Broader Implications and Ways Forward

Organisms do not experience climate at coarse scales [Sears et al., 2011; Potter et al., 2013]. Thus, aggregation biases can be significant not only when past and current ecosystem dynamics are simulated but also when model projections under climate change scenarios are carried out [Trivedi et al., 2008]. When process-based models are used, and confidence on their results is based on their “physical correctness and consistency,” then the “physics” should be solved at appropriate scales with appropriate forcings. In this study we quantified the biases occurring in terrestrial ecosystem modeling when this is not done. Model complexity and process representation should therefore match with the adopted spatiotemporal representation, as well as with the quality and resolution of the available data [Costanza and Maxwell, 1994]. Advanced statistical tools, such as emulators, together with enhanced computing capabilities can provide viable options to cope with the additional computational burden [Neelin et al., 2010; Castelletti et al., 2012].

If solving processes at the appropriate scales is computationally too demanding, given the available resources, then statistical and/or top-down approaches may represent a conceptually better approximation of terrestrial ecosystem functioning. For instance, a statistical-dynamical approach [e.g., Giorgi and Avisser, 1997] can be incorporated in terrestrial ecosystem modeling using the empirical probability density function of local-scale attributes, thus describing the heterogeneity of the meteorological forcings in the examined domain or that of plant traits [Reich, 2014]. The potential of using well-established approaches from other disciplines dealing with spatial aggregation of complex nonlinear systems (e.g., population and community ecology [Auger et al., 2012; Chesson, 2012]), as well as organizing principles [e.g., Mäkelä et al., 2002; Whitfield, 2007; Dewar, 2010], is also worth of exploring.

5. Conclusions

Our study revealed that local-scale spatial heterogeneities, which are often ignored or at best crudely represented in terrestrial ecosystem models, exert a strong control on ecosystem response. Therefore, preservation of local environmental and topographic attributes, as proposed with the fine spatial resolution grid of the D-LPJ model, represents an important feature to achieve a more realistic representation of terrestrial ecosystem dynamics. In addition, we showed that model initialization, and therefore forest historical legacy, has a remarkable importance on carbon balance assessments and specifically on the capacity of the forest to store carbon. The assumption of steady state vegetation and soil carbon pools, incorporated in DGVMs for pragmatic reasons, is in contradiction with the current state of many forests, which are often far from an equilibrium and with different states of succession due to natural or anthropogenic disturbances. A realistic assessment of future carbon stocks cannot be separated from an accurate representation of these heterogeneities and local-scale trajectories. The light shed by this study on model limitations emphasizes the importance of solving biophysical and biogeochemical processes at the appropriate scales and with the appropriate boundary conditions.

References


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