Climate and parameter sensitivity and induced uncertainties in carbon stock projections for European forests (using LPJ-GUESS 4.0)

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Abstract

Understanding uncertainties and sensitivities of projected ecosystem dynamics under environmental change is of immense value for research and climate change policy. Here, we analyze sensitivities (change in model outputs per unit change in inputs) and uncertainties (changes in model outputs scaled to uncertainty in inputs) of vegetation dynamics under climate change, projected by a state-of-the-art dynamic vegetation model (LPJ-GUESS v4.0) across European forests (the species *Picea abies*, *Fagus sylvatica* and *Pinus sylvestris*), considering uncertainties of both model parameters and environmental drivers. We find that projected forest carbon fluxes are most sensitive to photosynthesis-, water- and mortality-related parameters, while predictive uncertainties are dominantly induced by environmental drivers and parameters related to water and mortality. The importance of environmental drivers for predictive uncertainty increases with increasing temperature. Moreover, most of the interactions of model inputs (environmental drivers and parameters) are between environmental drivers themselves or between parameters and environmental drivers. In conclusion, our study highlights the importance of environmental drivers not only as contributors to predictive uncertainty in their own right, but also as modifiers of sensitivities and thus uncertainties in other ecosystem processes. Reducing uncertainty in mortality related processes and accounting for environmental influence on processes should therefore be a focus in further model development.

1. Introduction

Terrestrial ecosystem models have emerged in the last three decades as a central tool for decision making and basic research on vegetation ecosystems (Cramer et al., 2001; Fisher et al., 2018; IPCC, 2014; Smith et al., 2001; Snell et al., 2014). Projections from different vegetation models, however, often disagree on important details, for example regarding the observable past (Bastos et al., 2020) or the future carbon uptake of forest ecosystems (Huntzinger et al., 2017; Krause et al., 2019). Among the possible reasons for such differences is the uncertainty in climate scenarios (Saraiva et al., 2019), model structural uncertainty (Bugmann et al., 2019; Oberpriller et al., 2021; Prestele et al., 2016), initial condition uncertainty (Dietze, 2017b) as well as uncertainty about the model parametrization (Grimm, 2005), which in turn make models' projections themselves uncertain (Dietze, 2017a). It is widely appreciated that understanding which exact factors drive these uncertainties is of immense value for directing research (Tomlin, 2013), but also to interpret and understand projections (Dietze et al., 2018). For example, the IPCC started in its Fifth Assessment Report to systematically analyze uncertainties and attribute them to model inputs (IPCC, 2014) similar to other predictive sciences (e.g. nuclear reactor safety (Chauliac et al., 2011), energy assessment for buildings (Tian et al., 2018) or policy analysis (Maxim and van der Sluijs, 2011)).

The two main tools to propagate uncertainties in model inputs (drivers, parameters, and model structure) to model outputs are sensitivity analysis (SA) and uncertainty analysis (UA) (Cariboni et al., 2007; Caswell, 2019; Saltelli, 2002; Saltelli et al., 2008). The key difference between these two methods is that an UA considers the magnitude of uncertainty in the model inputs (e.g. parameters, typically determined via expert elicitations and previous studies (Matott et al., 2009)), while a SA is agnostic about the magnitudes of uncertainty in different inputs, and simply calculates the change in the output per unit or percentual change of the respective input (Jørgensen and Bendoricchio, 2001). This difference aside, both methods share the goal of identifying inputs with a high influence on model outputs, with the underlying idea that better constraining these will increase robustness and reliability of model projections (Balaman, 2019).

Although the benefits for understanding model behavior and predictive uncertainties are obvious, relatively few SAs and UAs have been applied to complex ecosystem models and especially the widely used dynamic global vegetation models (DGVMs) that project terrestrial ecosystem responses to climate change or land management (see, e.g., Courbaud et al., 2015; Cui et al., 2019; Huber et al., 2018; Reyer et al., 2016; S. Tian et al., 2014; Wang et al., 2013). A reason for this is arguably the complex structure of most DGVMs (Fer et al., 2018), which makes SAs and UAs computationally demanding and difficult to interpret, especially when performing state-of-the-art global SAs and UAs that compute sensitivities and uncertainties across the entire parameter space (Saltelli et al., 2008) rather than just locally around a reference parameter set (see e.g., Hamby, 1994). Moreover, several studies highlight that sensitivities and uncertainties of DGVMs also exist with respect to environmental drivers (Barman et al., 2014; Wu et al., 2017, 2018), especially solar radiation (Barman et al., 2014; Wu et al., 2018), temperature (Barman et al., 2014) and precipitation (Wu et al., 2017), and it is reasonable to expect that there can be interactions between parameter and environmental sensitivities, meaning that certain parameters are more sensitive in some environments than in others. It therefore seems important to investigate parametric sensitivities in conjunction with their environmental sensitivities in one combined analysis.

In this study, we concentrate on a well-established and widely applied DGVM, the Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) (Gerten et al., 2004; Sitch et al., 2003; B. Smith et al., 2001). Three previous SAs or UAs for the LPJ family identified the intrinsic quantum efficiency of CO_2 uptake (*alpha_C3*) and the photosynthesis scaling parameter (from leaf to canopy) (*alpha_a*) as the main contributors of sensitivity for net primary production (NPP) (about 50-60% of the overall sensitivity, Zaehle et al., 2005; Pappas et al., 2013) or foliage projective cover (Jiang et al., 2012). Additionally, these previous studies show that LPJ-GUESS projections of NPP and vegetation carbon pools showed high sensitivity to tree structure-related (sapwood to heartwood turnover rate, longevity of trees, Pappas et al., 2013; Wramneby et al., 2008; Zaehle et al., 2005), establishment-related (maximum sapling establishment rate, minimum forest floor photosynthetically active radiation for tree establishment, Jiang et al., 2012; Wramneby et al., 2008; Zaehle et al., 2005), mortality-related (threshold for growth suppression mortality, Pappas et al., 2013) and water-related parameters (minimum canopy conductance not associated with photosynthesis, maximum daily transpiration, Pappas et al., 2013; Zaehle et al., 2005). Regarding uncertainties, strong impacts on LPJ-GUESS projections of NPP and vegetation carbon pools (FPC for Jiang et al., 2012) were found for photosynthesis related parameters (Jiang et al., 2012; Zaehle et al., 2005), but also for water-related (minimum canopy conductance not associated with photosynthesis, Zaehle et al., 2005) as well as structure-related parameters (tree leaf to sapwood area ratio, crown area to height function Jiang et al., 2012), whereas soil hydrology parameters were not identified as very sensitive in earlier studies.

Since the publication of these studies, however, the structure of the LPJ-GUESS model changed substantially. The most important changes are the inclusion of the nitrogen cycle (Smith et al., 2014) and new management modules (Lindeskog et al., 2021). Since these changes, no study has systematically examined how model sensitivities and uncertainties were affected by the new model structure. Moreover, previous SAs and UAs ignored management parameters, which, however, are expected to have large impacts on carbon pools and fluxes (Lindeskog et al., 2021).

A further limitation of most previous studies for LPJ-GUESS and other models (e.g. Mäkelä et al., 2020) is that they either analyzed sensitivities and uncertainties to parameter changes, or to changes in the environmental drivers, but not both. As discussed earlier, however, there are good reasons to expect that the sensitivity of parameters will change if environmental drivers change. Given that previous sensitivity analyses used different choices for these boundary conditions (different sensitivities for the climate scenarios and sites in Jiang et al., 2012; for different elevations in Pappas et al., 2013; different sites in Wramneby et al., 2008), this not only limits the comparability between studies, but also questions the generality of the results for all climatic conditions. Only Jiang et al. (2012) combined parameter and driver sensitivities, but used for the latter only a number of fixed climate scenarios instead of a range of possible values, which prohibits a systematic joint analysis. Moreover, it would be interesting to compare the relative importance of drivers and parameters for the predictive uncertainty of model simulations and how these change between environmental zones (here we use the classification of Metzger et al., 2005) and thus on an environmental gradient. When sensitivities or uncertainties of parameters belonging to a specific process increase on an environmental gradient, this indicates that the process itself becomes more important on the gradient (Saltelli, 2002). By comparing such changes to existing ecological hypotheses, we can test if model sensitivities and thus process descriptions are in line with ecological expectations.

To answer these questions, we analyzed sensitivities and uncertainties in LPJ-GUESS for 200 randomly distributed sites across Europe (see Appendix A1.1). We address the issue of interactions between environmental and parametric sensitivities by simultaneously investigating uncertainty in environmental drivers (precipitation, temperature, solar radiation, CO_2, nitrogen deposition) with parametric uncertainty in the most important processes (photosynthesis, establishment, nitrogen, water cycle, mortality, disturbance/management, and growth) for dynamic climate change from 2001-2100 and steady climate from 2100-2200. We simulated the most abundant tree species in Europe (*Fagus sylvatica*, *Pinus sylvestris* and *Picea abies*) individually and in mixed stands, as these species are suffering from climate change (e.g. Buras et al., 2018; Walentowski et al., 2017) and could benefit from mixed stands (e.g. Pretzsch et al., 2015). To test climate change impacts, we randomly sampled climate projections within the boundaries of RCP2.6 and RCP8.5. Thereby, our key objectives were to understand the sensitivities and uncertainties of LPJ-GUESS due to environmental drivers and parameters. We were especially interested in 1) overall sensitivities and uncertainties across European forests, 2) uncertainties per environmental zone and 3) uncertainties on a temperature gradient. Moreover, we investigated, 4) if and how environmental conditions change the uncertainties of environmental processes.

2. Methods and Material

2.1. The LPJ-GUESS vegetation model

LPJ-GUESS is a process-based ecosystem model that simulates vegetation growth, vegetation dynamics and biogeography as well as biogeochemical (e.g. nitrogen and carbon) and water cycles (Lindeskog et al., 2013; Olin et al., 2015; Smith et al., 2014). Ecosystem dynamic processes in the model include establishment, growth, mortality, and competition for light, space and soil resources. To simulate these processes, the model combines time steps on different scales from daily (e.g. phenological and photosynthesis processes) to yearly (e.g. allocation of net primary production to tree carbon components) basis. LPJ-GUESS includes forest gap dynamics succession of cohorts (each represented by an average individual) of different plant functional types (PFTs) or species. Each PFT/species has a unique parameter set.

In this study, we use a model version that was slightly modified from Lindeskog et al. (2021), which is based on the LPJ-GUESS 4.0 version, with a re-parameterization for spruce (*Picea abies*), pine (*Pinus sylvestris*) and beech (*Fagus sylvatica*) (see Appendix A1.2 for *Pin. syl.* and *Pic. abi.*). To account for the stochastic components of establishment, mortality and patch destroying disturbances, LPJ-GUESS simulates several replicate patches (25 for the simulation with the reference parametrization and 1 for each simulation in the SA and UA) representing "snapshots" of the grid-cell. In this model version, fire is based on the BLAZE model (Rabin et al., 2017). Thereby annually burned area is generated based on fire weather and fuel continuity and distributed to monthly intervals based on climatology (Giglio et al., 2010). Tree mortality is then estimated by computing firelines based on weather and converted into height-dependent survival probabilities (see Haverd et al., 2014) depending on empirical biome specific parameters.

A first set of key parameters from our expert elicitation (see below) for **establishment** are the bioclimatic limits (i.e. minimum growing degree days (*gdd5min_est*), minimum 20-year coldest month (*tcmin_est*), maximum 20-year coldest month (*tcmax_est*) and minimum forest photoactive radiation at forest floor (*parff_min*)), which build the environmental envelope for establishment. Given the bioclimatic limits are fulfilled, at regular intervals new PFTs are established (here: 1 year) given enough space, light, soil water and photoactive radiation at forest floor is available for establishment (B. Smith et al., 2001). Moreover, each of our three investigated species has a maximum establishment rate (*est_max*) (B. Smith et al., 2001).

Structure of trees in the model is mainly linked to the simulated growth of trees, which is triggered by allocating all net primary production (NPP) besides a reproduction debt of 10% (*reprfrac*) to tree components thereby satisfying mechanical (e.g. allometric eq. for the relationship between height and diameter with allometric parameters (*k_allom2, k_allom3) (e.g. Huang et al., 1992)*, the relationship between tree leaf to sapwood area (*k_latosa*) (e.g. Robichaud & Methven, 1992), the relationship between crown area and height (*k_rp*) (packing constraint, Zeide, 1993), the maximum crown area (*crownarea_max*) and leaf longevity (*leaflong*)) and functional balance as well as demographic constraints (Sitch et al., 2003). Each living tissue is assigned a turnover rate transferring sapwood into heartwood (*turnover_sap*) and leaves (*turnover_leaf*) and fine roots (turnover_root) to litter. Investment into above and belowground growth is influenced by the resource stress as individuals are competing for light, space, nitrogen and water. Competition for light is determined by the photosynthetic response and light extinction in the canopy. Competition for space (*self-thinning*) is represented in the model via allometric equations between crown area and stem diameter (Sitch et al., 2003). Competition for nitrogen and water is determined by tree individual demand for nitrogen and water and soil availability of nitrogen and water and the PFT-specific root profile. Competition between species will favor certain life-history strategies in particular situations, for example shade-tolerant (e.g. *Fagus sylvatica* and *Picea abies*) or intermediate-shade tolerant (e.g. *Pinus sylvestris*) growth responses, and dynamically changing root-to-shoot ratios.

Tree mortality (natural or via harvest) in the model responds to growth efficiency (ratio of annual NPP to leaf area) being too low over a 5-year period, e.g. due to light competition, maximum longevity of a PFT or changes in environmental conditions (e.g. tolerance to drought (*drought_tolerance*) changes water uptake) exceeding the species suitable range. Light competition is modeled using the foliage projective cover (FPC), defined as the area of ground by foliage directly above it, using Beer's Law (B. Smith et al., 2011). The resulting shading mortality is distributed proportional to species' FPC growth in the respective year due to their biomass increase. Mortality is modeled inversely proportional to the growth efficiency (with a given species-specific threshold (*greff_min*), e.g. Waring (1983)). Moreover, negative NPP of a species kills all individuals of the respective cohort. Background mortality probability increases with tree age, reaching one at the maximum longevity (*longevity*). Mortality has also a stochastic component. Natural disturbances are implemented in the model as process-based wildfires (with a given fire resistance for each species (*fireresist*)) and as patch-destroying disturbances (e.g. windthrow and landslides) with the same yearly occurrence probability for all patches (inverse of *distinterval*). Additional mortality arises from forest management activities, determined by thinning intensity (percentage of all trees cut, *thinning_intensity*) and cutting intervals (*cut_interval*), which can be set for each species individually. For a more detailed description of the management module and the additional management parameters see Lindeskog et al. (2021).

Nitrogen input is implemented in the model through nitrogen deposition (prescribed) and biological nitrogen fixation. The latter is simulated empirically as a linear function with intercept (*nfix_a*) and slope (*nfix_b*) of the five-year averaged actual evapotranspiration (Cleveland et al., 1999). The resulting amount of nitrogen accumulates in the ecosystem equally over the year and directly adds to the available mineral soil nitrogen pool. When nitrogen is in living tissue, a fraction (*nrelocfrac*) is re-translocated before leaf- and root shedding.

Photosynthesis is modeled as a function of absorbed photosynthetically active radiation, temperature (optimum temperature range for photosynthesis determined by *pstemp_low and pstemp_high*, Larcher, 1983), intercellular CO_2 (i.e. non-water stressed ratio of intercellular to ambient CO_2 (*lambda_max*)), and canopy conductance thereby considering a species-specific respiration coefficient (*respcoeff*) (B. Smith et al., 2001) and nitrogen availability. The photosynthesis scheme is a modified version of the Farquhar photosynthesis model, but instead of prescribed values for the Rubisco capacity it is optimized for maximum net CO_2 assimilation at the canopy level (Smith et al., 2014).

Water availability for plants is based on precipitation and snowmelt in the two-layer soil hydrology submodule (for details see Hickler et al., 2004; Smith et al., 2001). Vegetation transpiration and evaporation (with a maximum evapotranspiration rate (*emax*)) from bare ground and leaves reduce water availability as well as runoff from saturated soil (Sitch et al., 2003). Water vapor exchange by the vegetation canopy is calculated on a daily basis within the photosynthesis scheme (e.g. minimum canopy conductance not associated with photosynthesis (*gmin*)). The water supply and transpirative demand are calculated on a daily basis and converted into a drought-stress coefficient. Given this coefficient, the investment in roots at the costs of leaves is calculated.

2.2. Simulation setup

We selected 200 study sites (see Appendix A1.1) spatially and environmentally stratified over Europe by applying random stratified sampling (using the R package splitstackshape Mahto, 2019) with longitudinal and latitudinal coordinates as well as mean precipitation, solar radiation and temperature as categories based on IPSL-CM5 Earth System Model CMIP5 (Dufresne et al., 2013) climate data. We chose 200 sites as a compromise between the high computational demand of running LPJ-GUESS multiple times for all sites and a good spatial as well as environmental coverage of Europe. For these sites, we performed simulations for each of the three most common species in Europe (*Fagus sylvatica*, *Pinus sylvestris* and *Picea abies)* as monospecific stands and additionally all three species together as mixed stands.

The simulation period was from 1861 to 2199. To start the simulations with equilibrium C pools and fluxes, we spun up LPJ-GUESS vegetation and soil carbon and nitrogen pools to pre-industrial equilibrium by recycling the 1861 to 1900 climate, the 1861 CO_2 concentration (Meinshausen et al., 2011) and nitrogen deposition. For the transient and future simulation runs, we used the bias-corrected monthly IPSL-CM5 Earth System Model CMIP5 (Dufresne et al., 2013). From this data set, we extracted temperature, precipitation, number of wet days per month, and incoming solar radiation from 1861 to 2099 for RCP4.5 as base scenario and RCP2.6/RCP8.5 as lower/upper boundaries for the climate ranges (see below). In addition to these data, monthly nitrogen deposition was extracted from Lamarque et al. (2013) and soil texture data from Batjes (2005). All these driving data had a spatial resolution of 0.5°x 0.5°. We recycled detrended data from 2090-2099 for all environmental drivers except CO_2 and nitrogen deposition and used these as potential stable climates for the 2100-2199 period.

2.3. Selection of parameters and drivers and their ranges

The a priori selection of the most influential parameters that can be specified in the parameter file and their ranges was based on our expert knowledge (following the SHELF expert elicitation protocol, see Gosling, 2018) and a literature review. The resulting eleven (= 33%) parameters common for all species and 22 (= 20%) species-specific parameters (see Table 1) were grouped to the specific processes they contribute most to (Table 1, Grouping).

From the environmental drivers of the model, we selected incoming solar radiation, temperature, precipitation, atmospheric CO_2 and nitrogen deposition for our analysis. To obtain uncertainties for temperature, precipitation and solar radiation, we calculated the mean deviations of RCP8.5/RCP2.6 to our base scenario RCP4.5 plus/minus one standard deviation as maximal/minimal per site. As the CO_2 data is global and not site-specific, we calculated ranges from the global data set

(RCP2.6 as minimum, RCP8.5 as maximum) averaged over time and plus/minus a standard deviation. For nitrogen deposition, we used RCP6.0 as maximum and RCP2.6 as minimum with the same procedure as for the other drivers.

2.5. Sensitivity analysis and uncertainty analysis

LPJ-GUESS predicts a substantial number of output variables, which could all be examined regarding their sensitivities and uncertainties. Here, we concentrate on carbon outputs (**gross primary production GPP**, **total standing biomass TSB** and **net biome productivity NBP**), because of forests' role for carbon cycling (Bonan, 2008), their large contribution to the land carbon sink (Pugh et al., 2019) and the economic importance of tree growth for forest owners (Pearce, 2001).

Sensitivities and uncertainties were calculated by Monte-Carlo sampling from the assumed multivariate parameter and climate uncertainty. For the monospecific / mixed simulations, we drew respectively 10.000 / 50.000 parameter and climate combinations randomly from the prespecified uncertainty ranges, and ran the model based on these combinations for each of the 200 sites. Note, that for mixed simulations, for each simulation we individually drew parameter combinations for each species, i.e. the same parameter could be different for different species. In total, this means that 200 x (50.000 + 3 x 10.000) = 16 million LPJ-GUESS simulations were run.

We quantified sensitivity and uncertainty indices by running multiple linear regressions with the model output averaged over time as response, and parameters and drivers as well as their second order interactions as predictors. With 200 sites, each having three monospecific and one mixed stands setup, we overall ran 200x (3 +1) = 800 linear regressions. This analysis corresponds to a global SA/UA in the context of regression analysis and has been applied to other system models (e.g. Sobie, 2009). The estimated effects from the regression can be interpreted as sensitivities, as the effect of a unit change of the driver on the response (model output) is estimated. By scaling the predictors to the range [-0.5, 0.5], we obtained the corresponding uncertainties. To check whether we missed non-linear effects, we additionally applied a random forest and extracted the variable importance (following Augustynczik et al., 2017, see Appendix A1.3.). To calculate mean sensitivities/uncertainties for each species, we averaged site-specific sensitivities over all sites with an average annual biomass production greater than 2 tC/ha. We have chosen this threshold because smaller values indicate that the environment is not suitable for the species, however, for each site at least one species was able to establish. For the mixed stands, we first averaged the three species-specific sensitivities/uncertainties per site and then averaged over all sites. Mean percentual sensitivities were calculated by dividing by the mean model output, while mean uncertainty contributions were calculated by dividing by the entire uncertainty budget. Thereby, positive values mean that the respective output increases with increasing parameter values, while negative values mean that it decreases.

It is important to note that uncertainties and sensitivities have different interpretations, and which of these two is more relevant strongly depends on the purpose. The calculated percental sensitivities can be interpreted as percentage change in the corresponding output, when changing a parameter value 1% in the prespecified range. The calculated uncertainties per parameter/driver can be interpreted as relative proportion of the overall uncertainty budget coming from environmental drivers and parameters. For scenario-analysis, e.g. comparing different cut intervals of forests, sensitivities provide a direct estimate of the model response, e.g. how much biomass changes when the cut interval is changed. For a comparison of different model forecasts, uncertainties are usually more relevant. If a reduction of uncertainty via a model-data comparison is the purpose, both measures are important, as parameters with high sensitivities can contribute more or less predictive uncertainty, depending on their input uncertainty.

3. Results

3.1. Mean sensitivities over Europe

Regardless of the output variable, LPJ-GUESS was most sensitive to photosynthesis-related parameters (*respcoeff*, *lambda_max*), parameters controlling the wood turnover (*turnover_sap*) and tree allometry (*k_rp*), water-related parameters (*emax*), mortality-related parameters (*greffmin*) and environmental drivers (temperature, CO_2 and solar radiation) (Fig. 1). When looking at differences in the strength of sensitivities for different outputs, TSB was most sensitive to the respiration coefficient (*respcoeff*), the growth suppression mortality threshold (*greff_min*) and solar radiation while NBP projections showed negative sensitivity to wood turnover rates (*turnover_sap*) and *longevity* and positive sensitivity to temperature, CO_2 and the ratio of intercellular to ambient CO_2 (*lambda_max*). GPP was negatively sensitive to the respiration coefficient (*respcoeff*), growth suppression mortality threshold (*greffmin)*, tree allometry (*k_rp)* and temperature and positive to CO_2, solar radiation and the maximum transpiration rate (*emax*). Establishment and nitrogen showed the smallest sensitivities for all three carbon-related projections (Fig.1). Note also that NBP had higher percentual sensitivities than GPP and TSB.

Mixed stands were less sensitive to changes in parameters than mono-specific stands (Fig. 1). For monospecific simulations, species sometimes showed different magnitudes and even directions of sensitivities, especially *Fag. syl.* was more strongly affected by bioclimatic limits and *Pin. syl.* showed higher sensitivity to environmental drivers (temperature and solar radiation) than the other species. Moreover, TSB and GPP are negatively sensitive to temperature except for Fag. syl. For NBP, the direction of sensitivities changes between species for the non-water-stressed ratio of intercellular to ambient CO_2 *(lambdamax)*, the respiration coefficient (*respcoeff)*, the root turnover (*turnoverroot)*, an allometric constant (*krp)* and the maximum evapotranspiration rate (*emax)*.

3.2. Mean uncertainties over Europe

Looking at uncertainties, we found that environmental drivers contributed most of all processes/drivers to the predictive uncertainty (Fig 2), regardless of the considered model output. For TSB projections, CO_2, solar radiation and temperature contributed substantial uncertainty (Fig. 2a). Additionally, large uncertainty contributions arose from growth suppression mortality thresholds (*greffmin*) and the respiration coefficient (*lambda_max*). Uncertainty in NBP projections was substantially affected by model parameters (*longevity* (Mortality process), *tcmax_est* (Establishment process), *turnover_sap* (Tree structure process), *greffmin* (Mortality process) and *emax* (Water process)), additionally to the high contributions of temperature and CO_2 (Fig. 2b). For GPP projections, solar radiation and CO_2 contributed most to climate induced uncertainty, while the threshold for growth suppression mortality (*greffmin)* and maximum evaporation rate (*emax)* contributed most to parameter induced uncertainty (Fig. 2c). Notably, also nitrogen-fixation induced uncertainty was substantial (7-9%) for TSB and GPP. Most tree structure related parameters except the sapwood to heartwood turnover rate (*turnoversap)* and the fraction of NPP allocated to reproduction (*repfrac*) contributed only small uncertainties (Fig. 2). Uncertainty contributions analyzed by a random forest are similar to linear regression results (see Appendix 1.3.).

By analyzing uncertainty contributions on a species level, a more diverse picture emerged. *Fag. syl.* was more affected by temperature and less by solar radiation than the other species. Additionally, we found that uncertainty contributions of environmental drivers were substantially higher for mixed than for mono-specific stands.

3.3. Geographic variation in uncertainties of TSB across Europe

To project the uncertainties of TSB (for GPP and NBP see Appendix 1.4.) into the European environmental space, we filtered stands according to environmental zones, then calculated mean uncertainties per environmental zone and aggregated these per process.

The broad pattern of TSB uncertainty contributions for all three monospecific and mixed stands remains similar in all environmental zones. On average across all environmental zones, stands and species about 45% of the uncertainty was due to environmental drivers, 15% due to mortality-, 14% due to photosynthesis-, 12% due to structure-, 7% due to water- and 7% due to nitrogen-related parameters (Fig. 3).

For the individual environmental zones, however, there were subtle differences. In the Mediterranean mountain (MDN) and Pannonian (PAN) zone, environmental driver induced uncertainty was higher than on average especially for monospecific stands (Fig. 3). In the Boreal (BOR), Atlantic central (ATC), and Atlantic north (ATN) zone, tree structure- related uncertainty increased compared to the average pattern (Fig. 3). In the Atlantic central (ATC) and Atlantic north (ATN) zones nitrogen related uncertainty increased for all species and stands (Fig. 3).

To examine this spatial pattern further, we investigated the change of uncertainties across a temperature gradient. To this end, we aggregated the uncertainties per site and process/driver and then fitted a linear regression with the process/driver as predictor and the aggregated uncertainties as dependent variables.

For TSB, we found that increasing mean annual temperature increased the uncertainty contributions of environmental drivers, water- and establishment-parameters, while the uncertainty due to nitrogen- and tree structure- related parameters decreased (Fig. 4a). Thereby, the uncertainty contributions of environmental drivers (≈0.4%/°C) increased the most (measured in percentage points per °C) and uncertainty contributions of nitrogen fixation decreased most (≈ -0.5%/°C). Mortality and photosynthesis stayed approximately constant on the gradient (Fig. 4b).

Looking in more detail at the environmental drivers, temperature (≈+0.75%/°C) as well as CO_2 (≈ +0.2%/°C) and precipitation (≈ +0.25%/°C) induced uncertainty increased with mean annual temperature, while the uncertainty contribution of solar radiation (≈ -0.75%/°C) decreased with mean annual temperature (Fig. 4c). Nitrogen deposition induced uncertainty contributions stayed approximately constant on a mean annual temperature gradient.

The above geographical and correlative observations of changing uncertainties across Europe receive further support when looking at the interactions between uncertainties of different drivers/parameters (Fig. 5). Interaction indices were calculated by averaging the interactions found in the linear regression over all sites and species (Fig. 5b). Moreover, to investigate the overall influence on other parameters or drivers we summed the absolute individual interaction indices of each parameter with each other (Fig. 5a).

We found that environmental drivers (temperature, solar radiation, CO_2 and precipitation) had the highest sum of interactions for TSB (Fig. 5a). Moreover, the respiration coefficient (*respcoeff)*, the growth suppression mortality threshold (*greffmin*), longevity, the sapwood to heartwood turnover rate (*turnover_sap*) and maximum evaporation rate (*emax*) had a lower, but still high sum of interactions (Fig. 5a). Establishment and nitrogen related parameters had only a few weak interactions (Fig. 5). Strong interaction effects occurred mostly with environmental drivers (Fig. 5b). A main part of these interactions was between the different environmental drivers themselves (solar radiation- CO_2 and solar radiation- CO_2). Additionally, we found interactions of parameters and environmental drivers (temperature-sapwood to hardwood turnover (*turnover_sap)*, temperature – threshold for growth suppression mortality (*greffmin)* and temperature-respiration coefficient (*respcoeff)* (Fig. 5b)) and moderate parameter-parameter interactions (*longevity* (Mortality process) - *greffmin* (Mortality process), *respcoeff*

(Water process) – *longevity* (Mortality process) (Fig. 5b)). Similar patterns were present for the other two carbon outputs (see Appendix A1.4.).

4. Discussion

In this study, we analyzed sensitivities and uncertainties of the LPJ-GUESS vegetation model due to environmental driver and parameter variations across European forests. We found that the model is most sensitive to relative (percentage) changes in photosynthesis-related parameters, structure-related parameters controlling the wood turnover and tree allometry, water-related parameters, mortality-related parameters, and environmental drivers (Fig.1), irrespective of the considered output variable. When considering the different uncertainties (i.e. the entire plausible range) in these parameters and the environmental inputs, we found that environmental drivers and parameters controlling evapotranspiration, background mortality and nitrogen cycling contribute most to predictive uncertainty (Fig. 2). When correlated against a temperature gradient and thus geographically from north to south, uncertainty contributions to TSB increased for environmental drivers and decreased for tree structure and nitrogen-related parameters (Fig. 3, 4). Interactions between the uncertainty contributions were mainly between different drivers or between model parameters and drivers, whereas only a few parameter-parameter interactions were present (Fig. 5).

Our finding that average sensitivities of carbon-related projections across European forests were highest for photosynthesis-related parameters amplifies the evidence from earlier studies (Pappas et al., 2013; Zaehle et al., 2005), although we have used different parameter ranges. In addition, the finding about high sensitivity of LPJ-GUESS to parameters controlling tree structure and especially carbon turnover (*turnover_sap*) (Fig. 1) is in line with results reported for a previous version of LPJ-GUESS (Pappas et al., 2013) and its important role for carbon allocation in trees found in empirical studies (e.g. Herrero de Aza et al., 2011). The finding that carbon-related projections are very sensitive to mortality-related parameters (*greffmin*) is also supported by previous studies on the sensitivity of vegetation models and underlines the importance of improving mortality submodules for generating precise projections of vegetation dynamics (Bugmann et al., 2019; Hardiman et al., 2011). Moreover, sensitivities in mixed stands were lower than in mono-specific stands for NBP and GPP (Fig. 1) (in line Wramneby et al., 2008). The reason for that imbalance may be that other species can dampen and even benefit from non-optimal life-history strategies of an individual species (Loehle, 2000). Another reason might be, that for mixed simulations we sampled parameters for each species individually, which reduces the influence of each parameter on stand-level carbon projections.

We found that uncertainty contributions of environmental drivers were comparable to the uncertainty contributions of all parameters together (Figs. 2-5, see also Snell et al., 2018 for the FLMs model, but see Petter et al., 2020, who found that most uncertainty is induced by the choice of the forest model). Especially high uncertainty contributions arose from temperature (negative effect for TSB, GPP positive for NBP), CO_2 (positive effect for all variables) and solar radiation (positive effect for all variables). These results are supported by the earlier studies on the effect of environmental drivers in DGVMs (Barman et al., 2014; Wu et al., 2017, 2018). The positive effect of CO_2 could be explained by increased water-use efficiency and the CO_2 fertilization effect (also found for other DGVMs Keenan et al., 2011; Galbraith et al., 2010), which in LPJ-GUESS is an emerging property of the formulation of photosynthesis and respiration (see Hickler et al., 2008). However, empirical studies do not find such an effect (Körner, 2006), which could be link to the fact that LPJ-GUESS does not model phosphor cycling which could be the limiting nutrient (for a DVGM study see Fleischer et al., 2019). We speculate that the negative effect of temperature (also found for multiple DGVMs, see Galbraith et al., 2010) arises from decreased photosynthetic efficiency and increased respiration rates with higher temperatures (see the empirical study of Gustafson et al., 2018, here confirmed by the negative relationship between temperature and the respiration coefficient). This effect, however, differed in magnitude and direction between tree species (Fig. 2) - while there was a strong effect for *Pic. abi.* and *Pin. syl.*, *Fag. syl.* was less affected, which could be a sign of its higher resistance to increasing drought (Buras and Menzel, 2019; Tegel et al., 2014; but see Charru et al., 2010). From the parameters, especially water-, nitrogen- and mortality-related parameters contributed a substantial amount of uncertainty. The uncertainty contributions from mortality parameters (Bugmann et al., 2019, for a variety of DGVMs) and water (Pappas et al., 2013, with different parameter ranges for LPJ-GUESS) were already highlighted by earlier studies.

4.1. Geographical and environmental patterns in sensitivities and uncertainties

Several of our results suggest that environmental context influences the sensitivity of LPJ-GUESS model parameters. First, we found changing uncertainties across different vegetation zones (Fig. 3) and on an environmental gradient (Fig. 4) and that most interactions occurred with environmental drivers (Fig. 5). Moreover, uncertainty contributions analyzed by a random forest were similar to the linear regression results, but assign higher importance to environmental drivers (see Appendix A1.3). All these findings indicate that environmental context can change the importance of different processes in the model, which is in line with the biological expectation that the environment affects the physiology of organisms directly and thus indirectly the fitness and biotic interactions (e.g. Seebacher & Franklin, 2012; Tylianakis et al., 2008), and that environmental responses can be particularly nonlinear (e.g. Burkett et al., 2005) or show higher order interactions.

Interestingly, our results of decreased uncertainty contributions of structure- related parameters and increased contributions of environmental drivers on the temperature gradient (Fig. 4) also seem in line with the stress-gradient hypothesis (Maestre et al., 2009), an empirically-observed pattern which states that in stressful environments, positive interactions should occur more often than in benign environments (e.g. Callaway, 2007). For the ecosystem that we consider, we interpret increasing temperature as increasing stress (e.g. Ruiz-Pérez and Vico, 2020), and structure as the best indicator for competitive interactions as the structure dictates resource allocation (e.g. bigger crown, but identical stem diameter leads to more photosynthesis; more sapwood to heartwood turnover requires less NPP). With this interpretation, one would conclude that under increasing stress, the importance of competition-related parameters decreases in the model, as expected from the stress-gradient hypothesis. We acknowledge that a fair amount of interpretation is needed to arrive at this conclusion, and we do not claim that this result lends evidence to the empirical discussion about the generality of the stress-gradient hypothesis, but we find it noteworthy that such a large-scale pattern emerges in the model from lower-level processes, without having been imposed (see also Levin, 1992).

4.2. Associated uncertainties of previous changes in model structure and implications for future model development

The management and the nitrogen cycling module are the most recent improvements of the LPJ-GUESS model (Smith et al., 2014; Lindeskog et al., 2021). Compared to previous sensitivity and uncertainty analysis, the high contributions of the nitrogen fixation to the predictive uncertainty of TSB and GPP (Fig. 2 a,c) are novel, though not surprising, as nitrogen is an important factor for the productivity of most temperate and boreal ecosystems (Vitousek and Howarth, 1991). The main reason why few earlier studies report those uncertainties is that vegetation models have only recently begun to integrate nitrogen cycling and limitation (e.g. B. Smith et al., 2014). The management module showed only small uncertainties, which could be due to the narrow parameter ranges for the cut interval and thinning intensity reflecting typical forest owners' choices. As forest owners usually try to maximize their profits (Johansson, 1986; but see Brazee and Amacher, 2000) and thus biomass production, low sensitivities of the management module are not surprising. A more suitable and important test case and application of the management module is a historical reconstruction of foliage projective cover data or similar outputs of the LPJ-GUESS model.

Our study helps to guide the model application, discussion of uncertainties and model development of LPJ-GUESS and other DGVMs. First, future model applications and model comparisons should focus on mortality as these processes contributes high uncertainties for carbon-related projections (see Fig. 1-3). Thereby, it should be investigated if these uncertainties stem from the intra-specific variability of the parameters itself (Bolnick et al., 2011), parameters are just not identifiable (see Marsili-Libelli et al., 2014), or if a model data comparison could reduce uncertainties in the parameters (e.g. Hartig et al., 2011). Using time series inventory data might help as it is informative for constraining mortality modules (Cailleret et al., 2020). Second, small sensitivities of establishment related parameters are surprising as we know that not all three investigated species can effortlessly establish across all of Europe, e.g. Fag. syl. can only establish on locations with no extreme drought and heat and no extreme winter frosts (Bolte et al., 2007). Thus, either we missed important parameters of this module, or the parametrization of the model needs to be updated. Third, when introducing new processes or coupling with other models (e.g. Forrest et al., 2020) calculating interactions helps to get a first impression where these new processes influence other model processes and potentially detect missing links. Moreover, future model applications can interpret their results with regard to the sensitivities in different factors (Saltelli et al., 2019) and discuss uncertainties and the causing factors, when used in policy advice (Laberge, 2013).

4.3. Limitations

We caution that our results regarding the importance of different factors for predictive uncertainties (but not sensitivities) depend on the a priori defined uncertainty range of the contributing factors (see Wallach & Genard, 1998), as well as on several other technical choices in our study. For determining uncertainty ranges of the drivers, we used RCP scenarios; however, these were not created as probabilistic min / max ranges. For the model parameters, we relied on expert guesses, reducing subjectivity as far as possible by following the SHELF expert elicitation protocol (Gosling, 2018). Future studies could include more experts and their opinion on parameter distributions to reduce variability in this protocol. As the model is sensitive to parameters and environmental drivers, and because these influence each other, we treated them in a combined sensitivity and uncertainty analysis (Saltelli et al., 2019), however, when interpreting it should be kept in mind that the one group relates to uncertainties in the model, while the other is external, so the two are conceptually very different. A certain ambiguity also arises from the definition of the indicators: here, we calculated sensitivities and uncertainties by capturing only linear components and second-order interactions, and we may therefore miss highly non-linear (and in particular hump-shaped) responses in LPJ-GUESS (Roux et al., 2021). However, our comparison to uncertainties calculated with random forest variable importance, a method that would also capture nonlinearities, did not reveal any qualitative differences in the ranking of parameter importance (Appendix A1.3). Overall, while we acknowledge that a certain amount of subjectivity exists in the choice of input uncertainty and calculation of indices, we believe that our results are quantitatively robust to those choices.

Moreover, we acknowledge that LPJ-GUESS is known to be sensitive to the scaling parameters *alpha_a* and *alpha_C3* (Pappas et al., 2013; Zaehle et al., 2005), which we have omitted from our analysis. These parameters, however, are not accessible in the parameter input file. Instead, they are hard coded in the model's source code and therefore a normal user would not change them. We argue that these parameters should thus be counted towards the more general and here neglected contribution of structural uncertainty (i.e. the uncertainty regarding the functional form of processes or even to entire modules) to the joint model uncertainty. Several previous studies suggest that the sensitivity of vegetation models to structural changes can be large, often larger than to parameters (e.g. Bugmann et al., 2019), and it would certainly be useful (although very complicated) to explore these uncertainties together with the here considered factors in a joint analysis. In the present study, however, we considered only the parameters that would be accessible to normal LPJ-GUESS users, and neglect structural uncertainty that could be explored by changing the source code.

5. Conclusions

Our findings highlight the relative importance of parametric uncertainties in different processes and their interactions with uncertainties in environmental drivers for carbon projections with LPJ-GUESS. Our results demonstrate that environmental context changes uncertainty contributions of other processes across the European environmental gradient. The pattern of decreasing importance of competition towards the warmer areas is in line with the stress-gradient hypothesis, which posits that the importance of competition decreases with increasing environmental stress. Our findings improve our understanding of forest ecosystem models, enable pathways for future ecosystem model development and thus builds a basis for more realistic projections. In the future, parametric uncertainties could be reduced by model-data fusion (e.g. Trotsiuk et al., 2020) of LPJ-GUESS, concentrating on the parameters contributing most uncertainty in each geographic region (Fig. 3). Reducing uncertainties in the drivers is more difficult. To some extent, environmental drivers are themselves influenced by the vegetation (Strengers et al., 2010), so model-data fusion on a fully coupled model including feedback loops between vegetation and climate, as well as a general improvement of climate models, could reduce driver uncertainty to some degree. Effectively, however, much of the uncertainty in this section arises from potential greenhouse gas emission trajectories, for which a probabilistic assignment is difficult due to their dependency on human decision-making.

Appendix A

A1.1 Site selection

We sampled 200 sites geographically and environmentally stratified over Europe and thereby avoided sites near the sea. The corresponding sites with the average temperature (Fig. A1) covers most of European climates and vegetation zones.

A1.2. Re-parametrization for better fit to observed data

There are several technical and methodological reasons requiring a re-parametrization of LPJ-GUESS for our study. First, most of European forests are managed and species are planted far outside of their natural distribution. Second, the introduction of the nitrogen cycle (Smith et al., 2014) changed the model structure and thus parameters require an adjustment. Third, the productivity of trees in managed forests did not fit to the reported inventory data (Fig. A2). To account for all these issues, we adjusted the parametrization of (Hickler et al., 2012) to allow species growing according to their actual (i.e., caused by forest management) distribution instead of their natural distribution.

Especially *Picea abies* and *Pinus sylvestris* are planted far outside their natural distribution (Figure S2). In particular we adjusted bioclimatic limits, drought tolerances, longevity, leaf turnover, disturbance intervals and allometry for these species.

A1.3. Random forest results

To check the consistency of the results obtained via linear regressions, we compare them to variable importance of random forest. The variable importance measures additionally non-linear effects and thus, should be able to deal with non-linear models like DGVMs. We calculated the variable importance the same way as we did for the linear regression by fitting a random forest with all parameters against the sum of differences between model outputs with default values and model outputs with sampled parameters. As our parameters were sampled from a uniform distribution with no correlation between the individual parameters, random forest variable importance can be compared to linear regression results.

The ranking is very similar to the ranking of the parameters and environmental drivers obtained via linear regression (Fig. A3). There is, however, a difference in the magnitude of the uncertainty induced by drivers, which is higher compared to linear regression (Fig A3). The higher uncertainty due to drivers is thus a nonlinear effect and stresses our conclusion that environmental conditions change the uncertainty contributions of other parameters.

A1.4. Interactions of GPP and NBP

Interactions of gross primary production (Fig. A4 a,b) and net biome production (Fig. A4c,d) are similar to the interactions of total standing biomass. These interactions are mostly between environmental drivers and environmental drivers or between environmental drivers and parameters (Fig. A4). Some strong interactions are between parameters and parameters, however, in such interactions there are always parameters included having strong interactions with environmental drivers (Fig. A4).

High sums of strong interactions arise from temperature, precipitation, solar radiation, greffmin, emax and respcoeff (Fig. A4a,b).

Code and Data Availability

LPJ-GUESS development is managed and the code maintained in a permanent repository at Lund University, Sweden. Source code is made available on request. The model version presented in this paper is identified by the permanent revision number r10207 in the code repository. There is no DOI associated with the code. Code to perform the sensitivity and uncertainty analysis can be found on zenodo under https://zenodo.org/record/5873672#.YebgTmAxnYU. Results from the LPJ-GUESS runs are available under https://zenodo.org/record/4670295#.YKIkI-tCRqs.

Author contribution

JO and FH conceived and designed the study and wrote a first draft. JO implemented the case studies, ran the experiments, and analyzed the results. CH, AK and PA advised regarding running the LPJ-GUESS model. CH, AR and AK determined the prior ranges for the parameters. All authors contributed to discussing and interpreting the results, and to the preparation of the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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References

Augustynczik, A. L. D., Hartig, F., Minunno, F., Kahle, H.-P., Diaconu, D., Hanewinkel, M., and Yousefpour, R.: Productivity of Fagus sylvatica under climate change – A Bayesian analysis of risk and uncertainty using the model 3-PG, Forest Ecology and Management, 401, 192–206, https://doi.org/10.1016/j.foreco.2017.06.061, 2017.

Barman, R., Jain, A. K., and Liang, M.: Climate-driven uncertainties in modeling terrestrial gross primary production: a site level to global-scale analysis, 20, 1394–1411, https://doi.org/10.1111/gcb.12474, 2014.

Bastos, A., O'Sullivan, M., Ciais, P., Makowski, D., Sitch, S., Friedlingstein, P., Chevallier, F., Rödenbeck, C., Pongratz, J., Luijkx, I. T., Patra, P. K., Peylin, P., Canadell, J. G., Lauerwald, R., Li, W., Smith, N. E., Peters, W., Goll, D. S., Jain, A. k., Kato, E., Lienert, S., Lombardozzi, D. L., Haverd, V., Nabel, J. E. M. S., Poulter, B., Tian, H., Walker, A. P., and Zaehle, S.: Sources of Uncertainty in Regional and Global Terrestrial CO2 Exchange Estimates, 34, e2019GB006393, https://doi.org/10.1029/2019GB006393, 2020.

Batjes, N. H.: ISRIC-WISE global data set of derived soil properties on a 0.5 by 0.5 degree grid (ver. 3.0), 24, 2005.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C., and Vasseur, D. A.: Why intraspecific trait variation matters in community ecology, Trends in Ecology & Evolution, 26, 183–192, https://doi.org/10.1016/j.tree.2011.01.009, 2011.

Bolte, A., Czajkowski, T., and Kompa, T.: The north-eastern distribution range of European beech a review, Forestry, 80, 413–429, https://doi.org/10.1093/forestry/cpm028, 2007.

Bonan, G. B.: Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests, Science, 320, 1444–1449, https://doi.org/10.1126/science.1155121, 2008.

Brazee, R. J. and Amacher, G. S.: Duality and Faustmann: Implications for the Evaluation of Landowner Behavior, Forest Science, 46, 132–138, https://doi.org/10.1093/forestscience/46.1.132, 2000.

Bugmann, H., Seidl, R., Hartig, F., Bohn, F., Brůna, J., Cailleret, M., François, L., Heinke, J., Henrot, A.-J., Hickler, T., Hülsmann, L., Huth, A., Jacquemin, I., Kollas, C., Lasch-Born, P., Lexer, M. J., Merganič, J., Merganičová, K., Mette, T., Miranda, B. R., Nadal-Sala, D., Rammer, W., Rammig, A., Reineking, B., Roedig, E., Sabaté, S., Steinkamp, J., Suckow, F., Vacchiano, G., Wild, J., Xu, C., and Reyer, C. P. O.: Tree mortality submodels drive simulated long-term forest dynamics: assessing 15 models from the stand to global scale, 10, e02616, https://doi.org/10.1002/ecs2.2616, 2019.

Buras, A. and Menzel, A.: Projecting Tree Species Composition Changes of European Forests for 2061–2090 Under RCP 4.5 and RCP 8.5 Scenarios, Front. Plant Sci., 9, https://doi.org/10.3389/fpls.2018.01986, 2019.

Buras, A., Schunk, C., Zeiträg, C., Herrmann, C., Kaiser, L., Lemme, H., Straub, C., Taeger, S., Gößwein, S., Klemmt, H.-J., and Menzel, A.: Are Scots pine forest edges particularly prone to drought-induced mortality?, Environ. Res. Lett., 13, 025001, https://doi.org/10.1088/1748-9326/aaa0b4, 2018.

Burkett, V. R., Wilcox, D. A., Stottlemyer, R., Barrow, W., Fagre, D., Baron, J., Price, J., Nielsen, J. L., Allen, C. D., Peterson, D. L., Ruggerone, G., and Doyle, T.: Nonlinear dynamics in ecosystem response to climatic change: Case studies and policy implications, Ecological Complexity, 2, 357–394, https://doi.org/10.1016/j.ecocom.2005.04.010, 2005.

Cailleret, M., Bircher, N., Hartig, F., Hülsmann, L., and Bugmann, H.: Bayesian calibration of a growth-dependent tree mortality model to simulate the dynamics of European temperate forests, 30, e02021, https://doi.org/10.1002/eap.2021, 2020.

Callaway, R. M.: Positive Interactions and Interdependence in Plant Communities, Springer Netherlands, https://doi.org/10.1007/978-1-4020-6224-7, 2007.

Cariboni, J., Gatelli, D., Liska, R., and Saltelli, A.: The role of sensitivity analysis in ecological modelling, Ecological Modelling, 203, 167–182, https://doi.org/10.1016/j.ecolmodel.2005.10.045, 2007.

Caswell, H.: Introduction: Sensitivity Analysis – What and Why?, in: Sensitivity Analysis: Matrix Methods in Demography and Ecology, edited by: Caswell, H., Springer International Publishing, Cham, 3–12, https://doi.org/10.1007/978-3-030-10534-1_1, 2019.

Charru, M., Seynave, I., Morneau, F., and Bontemps, J.-D.: Recent changes in forest productivity: An analysis of national forest inventory data for common beech (Fagus sylvatica L.) in north-eastern France, Forest Ecology and Management, 260, 864–874, https://doi.org/10.1016/j.foreco.2010.06.005, 2010.

Chauliac, C., Aragonés, J.-M., Bestion, D., Cacuci, D. G., Crouzet, N., Weiss, F.-P., and Zimmermann, M. A.: NURESIM – A European simulation platform for nuclear reactor safety: Multi-scale and multi-physics calculations, sensitivity and uncertainty analysis, Nuclear Engineering and Design, 241, 3416–3426, https://doi.org/10.1016/j.nucengdes.2010.09.040, 2011.

Cleveland, C. C., Townsend, A. R., Schimel, D. S., Fisher, H., Howarth, R. W., Hedin, L. O., Perakis, S. S., Latty, E. F., Fischer, J. C. V., Elseroad, A., and Wasson, M. F.: Global patterns of terrestrial biological nitrogen (N2) fixation in natural ecosystems, 13, 623–645, https://doi.org/10.1029/1999GB900014, 1999.

Courbaud, B., Lafond, V., Lagarrigues, G., Vieilledent, G., Cordonnier, T., Jabot, F., and de Coligny, F.: Applying ecological model evaludation: Lessons learned with the forest dynamics model Samsara2, Ecological Modelling, 314, 1–14, https://doi.org/10.1016/j.ecolmodel.2015.06.039, 2015.

Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. A., Brovkin, V., Cox, P. M., Fisher, V., Foley, J. A., Friend, A. D., Kucharik, C., Lomas, M. R., Ramankutty, N., Sitch, S., Smith, B., White, A., and Young-Molling, C.: Global response of terrestrial ecosystem structure and function to CO2 and climate change: results from six dynamic global vegetation models, 7, 357–373, https://doi.org/10.1046/j.1365-2486.2001.00383.x, 2001.

Cui, E., Huang, K., Arain, M. A., Fisher, J. B., Huntzinger, D. N., Ito, A., Luo, Y., Jain, A. K., Mao, J., Michalak, A. M., Niu, S., Parazoo, N. C., Peng, C., Peng, S., Poulter, B., Ricciuto, D. M., Schaefer, K. M., Schwalm, C. R., Shi, X., Tian, H., Wang, W., Wang, J., Wei, Y., Yan, E., Yan, L., Zeng, N., Zhu, Q., and Xia, J.: Vegetation Functional Properties Determine Uncertainty of Simulated Ecosystem Productivity: A Traceability Analysis in the East Asian Monsoon Region, GLOBAL BIOGEOCHEM. CYCLES, 33, 668–689, https://doi.org/10.1029/2018GB005909, 2019.

Dietze, M. C.: Ecological Forecasting, Princeton University Press, 284 pp., 2017a.

Dietze, M. C.: Prediction in ecology: a first-principles framework, 27, 2048–2060, https://doi.org/10.1002/eap.1589, 2017b.

Dietze, M. C., Fox, A., Beck-Johnson, L. M., Betancourt, J. L., Hooten, M. B., Jarnevich, C. S., Keitt, T. H., Kenney, M. A., Laney, C. M., Larsen, L. G., Loescher, H. W., Lunch, C. K., Pijanowski, B. C., Randerson, J. T., Read, E. K., Tredennick, A. T., Vargas, R., Weathers, K. C., and White, E. P.: Iterative near-term ecological forecasting: Needs, opportunities, and challenges, Proc Natl Acad Sci USA, 115, 1424–1432, https://doi.org/10.1073/pnas.1710231115, 2018.

Dufresne, J.-L., Foujols, M.-A., Denvil, S., Caubel, A., Marti, O., Aumont, O., Balkanski, Y., Bekki, S., Bellenger, H., Benshila, R., Bony, S., Bopp, L., Braconnot, P., Brockmann, P., Cadule, P., Cheruy, F., Codron, F., Cozic, A., Cugnet, D., de Noblet, N., Duvel, J.-P., Ethé, C., Fairhead, L., Fichefet, T., Flavoni, S., Friedlingstein, P., Grandpeix, J.-Y., Guez, L., Guilyardi, E., Hauglustaine, D., Hourdin, F., Idelkadi, A., Ghattas, J., Joussaume, S., Kageyama, M., Krinner, G., Labetoulle, S., Lahellec, A., Lefebvre, M.-P., Lefevre, F., Levy, C., Li, Z. X., Lloyd, J., Lott, F., Madec, G., Mancip, M., Marchand, M., Masson, S., Meurdesoif, Y., Mignot, J., Musat, I., Parouty, S., Polcher, J., Rio, C., Schulz, M., Swingedouw, D., Szopa, S., Talandier, C., Terray, P., Viovy, N., and Vuichard, N.: Climate change projections using the IPSL-CM5 Earth

System Model: from CMIP3 to CMIP5, Clim Dyn, 40, 2123–2165, https://doi.org/10.1007/s00382-012-1636-1, 2013.

Fer, I., Kelly, R., Moorcroft, P. R., Richardson, A. D., Cowdery, E. M., and Dietze, M. C.: Linking big models to big data: efficient ecosystem model calibration through Bayesian model emulation, 15, 5801–5830, https://doi.org/10.5194/bg-15-5801-2018, 2018.

Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C., Farrior, C. E., Holm, J. A., Hurtt, G. C., Knox, R. G., Lawrence, P. J., Lichstein, J. W., Longo, M., Matheny, A. M., Medvigy, D., Muller-Landau, H. C., Powell, T. L., Serbin, S. P., Sato, H., Shuman, J. K., Smith, B., Trugman, A. T., Viskari, T., Verbeeck, H., Weng, E., Xu, C., Xu, X., Zhang, T., and Moorcroft, P. R.: Vegetation demographics in Earth System Models: A review of progress and priorities, 24, 35–54, https://doi.org/10.1111/gcb.13910, 2018.

Fleischer, K., Rammig, A., De Kauwe, M. G., Walker, A. P., Domingues, T. F., Fuchslueger, L., Garcia, S., Goll, D. S., Grandis, A., Jiang, M., Haverd, V., Hofhansl, F., Holm, J. A., Kruijt, B., Leung, F., Medlyn, B. E., Mercado, L. M., Norby, R. J., Pak, B., von Randow, C., Quesada, C. A., Schaap, K. J., Valverde-Barrantes, O. J., Wang, Y.-P., Yang, X., Zaehle, S., Zhu, Q., and Lapola, D. M.: Amazon forest response to CO2 fertilization dependent on plant phosphorus acquisition, Nat. Geosci., 12, 736–741, https://doi.org/10.1038/s41561-019-0404-9, 2019.

Forrest, M., Tost, H., Lelieveld, J., and Hickler, T.: Including vegetation dynamics in an atmospheric chemistry-enabled general circulation model: linking LPJ-GUESS (v4.0) with the EMAC modelling system (v2.53), Geosci. Model Dev., 13, 1285–1309, https://doi.org/10.5194/gmd-13-1285-2020, 2020.

Galbraith, D., Levy, P. E., Sitch, S., Huntingford, C., Cox, P., Williams, M., and Meir, P.: Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change, 187, 647–665, https://doi.org/10.1111/j.1469-8137.2010.03350.x, 2010.

Gerten, D., Schaphoff, S., Haberlandt, U., Lucht, W., and Sitch, S.: Terrestrial vegetation and water balance—hydrological evaluation of a dynamic global vegetation model, Journal of Hydrology, 286, 249–270, https://doi.org/10.1016/j.jhydrol.2003.09.029, 2004.

Giglio, L., Randerson, J. T., van der Werf, G. R., Kasibhatla, P. S., Collatz, G. J., Morton, D. C., and DeFries, R. S.: Assessing variability and long-term trends in burned area by merging multiple satellite fire products, 7, 1171–1186, https://doi.org/10.5194/bg-7-1171-2010, 2010.

Gosling, J. P.: SHELF: The Sheffield Elicitation Framework, in: Elicitation: The Science and Art of Structuring Judgement, edited by: Dias, L. C., Morton, A., and Quigley, J., Springer International Publishing, Cham, 61–93, https://doi.org/10.1007/978-3-319-65052-4_4, 2018.

Grimm, V.: Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology, 310, 987–991, https://doi.org/10.1126/science.1116681, 2005.

Gustafson, E. J., Miranda, B. R., and Sturtevant, B. R.: Can Future CO2 Concentrations Mitigate the Negative Effects of High Temperature and Longer Droughts on Forest Growth?, 9, 664, https://doi.org/10.3390/f9110664, 2018.

Hamby, D. M.: A review of techniques for parameter sensitivity analysis of environmental models, Environ Monit Assess, 32, 135–154, https://doi.org/10.1007/BF00547132, 1994.

Hardiman, B. S., Bohrer, G., Gough, C. M., Vogel, C. S., and Curtis, P. S.: The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest, 92, 1818–1827, https://doi.org/10.1890/10-2192.1, 2011.

Hartig, F., Calabrese, J. M., Reineking, B., Wiegand, T., and Huth, A.: Statistical inference for stochastic simulation models – theory and application, 14, 816–827, https://doi.org/10.1111/j.1461-0248.2011.01640.x, 2011.

Haverd, V., Smith, B., Nieradzik, L. P., and Briggs, P. R.: A stand-alone tree demography and landscape structure module for Earth system models: integration with inventory data from temperate and boreal forests, 11, 4039–4055, https://doi.org/10.5194/bg-11-4039-2014, 2014.

Herrero de Aza, C., Turrión, M. B., Pando, V., and Bravo, F.: Carbon in heartwood, sapwood and bark along the stem profile in three Mediterranean Pinus species, Annals of Forest Science, 68, 1067, https://doi.org/10.1007/s13595-011-0122-y, 2011.

Hickler, T., Smith, B., Sykes, M. T., Davis, M. B., Sugita, S., and Walker, K.: USING A GENERALIZED VEGETATION MODEL TO SIMULATE VEGETATION DYNAMICS IN NORTHEASTERN USA, Ecology, 85, 519–530, https://doi.org/10.1890/02-0344, 2004.

Hickler, T., Smith, B., Prentice, I. C., Mjöfors, K., Miller, P., Arneth, A., and Sykes, M. T.: CO2 fertilization in temperate FACE experiments not representative of boreal and tropical forests, 14, 1531–1542, https://doi.org/10.1111/j.1365-2486.2008.01598.x, 2008.

Hickler, T., Vohland, K., Feehan, J., Miller, P. A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T. R., Cramer, W., Kühn, I., and Sykes, M. T.: Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model, 21, 50–63, https://doi.org/10.1111/j.1466-8238.2010.00613.x, 2012.

Huang, S., Titus, S. J., and Wiens, D. P.: Comparison of nonlinear height–diameter functions for major Alberta tree species, https://doi.org/10.1139/x92-172, 1992.

Huber, N., Bugmann, H., and Lafond, V.: Global sensitivity analysis of a dynamic vegetation model: Model sensitivity depends on successional time, climate and competitive interactions, Ecological Modelling, 368, 377–390, https://doi.org/10.1016/j.ecolmodel.2017.12.013, 2018.

Huntzinger, D. N., Michalak, A. M., Schwalm, C., Ciais, P., King, A. W., Fang, Y., Schaefer, K., Wei, Y., Cook, R. B., Fisher, J. B., Hayes, D., Huang, M., Ito, A., Jain, A. K., Lei, H., Lu, C., Maignan, F., Mao, J., Parazoo, N., Peng, S., Poulter, B., Ricciuto, D., Shi, X., Tian, H., Wang, W., Zeng, N., and Zhao, F.: Uncertainty in the response of terrestrial carbon sink to environmental drivers undermines carbon-climate feedback predictions, 7, 4765, https://doi.org/10.1038/s41598-017-03818-2, 2017.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp, 2014.

Jiang, Y., Zhuang, Q., Schaphoff, S., Sitch, S., Sokolov, A., Kicklighter, D., and Melillo, J.: Uncertainty analysis of vegetation distribution in the northern high latitudes during the 21st century with a dynamic vegetation model, 2, 593–614, https://doi.org/10.1002/ece3.85, 2012.

Johansson, P. O.: The economics of forestry and natural resources, 1986.

Jørgensen, S. E. and Bendoricchio, G.: Fundamentals of Ecological Modelling, Elsevier, 544 pp., 2001.

Keenan, T., Serra, J. M., Lloret, F., Ninyerola, M., and Sabate, S.: Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO2 matters!, 17, 565–579, https://doi.org/10.1111/j.1365-2486.2010.02254.x, 2011.

Körner, C.: Plant CO2 responses: an issue of definition, time and resource supply, New Phytol, 172, 393–411, https://doi.org/10.1111/j.1469-8137.2006.01886.x, 2006.

Krause, A., Haverd, V., Poulter, B., Anthoni, P., Quesada, B., Rammig, A., and Arneth, A.: Multimodel Analysis of Future Land Use and Climate Change Impacts on Ecosystem Functioning, 7, 833–851, https://doi.org/10.1029/2018EF001123, 2019.

Laberge, Y.: Simulating nature: a philosophical study of computer-simulation uncertainties and their role in climate science and policy advice, Journal of Applied Statistics, 40, 919–920, https://doi.org/10.1080/02664763.2012.749047, 2013.

Lamarque, J.-F., Dentener, F., McConnell, J., Ro, C.-U., Shaw, M., Vet, R., Bergmann, D., Cameron-Smith, P., Dalsoren, S., Doherty, R., Faluvegi, G., Ghan, S. J., Josse, B., Lee, Y. H., MacKenzie, I. A., Plummer, D., Shindell, D. T., Skeie, R. B., Stevenson, D. S., Strode, S., Zeng, G., Curran, M., Dahl-Jensen, D., Das, S., Fritzsche, D., and Nolan, M.: Multi-model mean nitrogen and sulfur deposition from the Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP): evaluation of historical and projected future changes, 13, 7997–8018, https://doi.org/10.5194/acp-13-7997-2013, 2013.

Larcher, W.: Ökophysiologische Konstitutionseigenschaften von Gebirgspflanzen, 96, 73–85, https://doi.org/10.1111/j.1438-8677.1983.tb03223.x, 1983.

Levin, S. A.: The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture, 73, 1943–1967, https://doi.org/10.2307/1941447, 1992.

Lindeskog, M., Arneth, A., Bondeau, A., Waha, K., Seaquist, J., Olin, S., and Smith, B.: Implications of accounting for land use in simulations of ecosystem carbon cycling in Africa, 4, 385–407, https://doi.org/10.5194/esd-4-385-2013, 2013.

Lindeskog, M., Smith, B., Lagergren, F., Sycheva, E., Ficko, A., Pretzsch, H., and Rammig, A.: Accounting for forest management in the estimation of forest carbon balance using the dynamic vegetation model LPJ-GUESS (v4.0, r9710): implementation and evaluation of simulations for Europe, 14, 6071–6112, https://doi.org/10.5194/gmd-14-6071-2021, 2021.

Loehle, C.: Strategy Space and the Disturbance Spectrum: A Life-History Model for Tree Species Coexistence., 156, 14–33, https://doi.org/10.1086/303369, 2000.

Maestre, F. T., Callaway, R. M., Valladares, F., and Lortie, C. J.: Refining the stress-gradient hypothesis for competition and facilitation in plant communities, 97, 199–205, https://doi.org/10.1111/j.1365-2745.2008.01476.x, 2009.

Mahto, A.: splitstackshape: Stack and Reshape Datasets After Splitting Concatenated Values, 2019.

Mäkelä, J., Minunno, F., Aalto, T., Mäkelä, A., Markkanen, T., and Peltoniemi, M.: Sensitivity of 21st century simulated ecosystem indicators to model parameters, prescribed climate drivers, RCP scenarios and forest management actions for two Finnish boreal forest sites, 17, 2681–2700, https://doi.org/10.5194/bg-17-2681-2020, 2020.

Marsili-Libelli, S., Beck, M. B., Brunner, P., Croke, B., Guillaume, J., Jakeman, A., Jakeman, J., Keesman, K. J., and Stigter, H.: Practical identifiability analysis of environmental models, in: Proceedings - 7th International Congress on Environmental Modelling and Software: Bold Visions for Environmental Modeling, iEMSs 2014, Accepted: 2015-12-10T22:27:43ZLast Modified: 2020-05-19, 2014.

Matott, L. S., Babendreier, J. E., and Purucker, S. T.: Evaluating uncertainty in integrated environmental models: A review of concepts and tools, 45, https://doi.org/10.1029/2008WR007301, 2009.

Maxim, L. and van der Sluijs, J. P.: Quality in environmental science for policy: Assessing uncertainty as a component of policy analysis, Environmental Science & Policy, 14, 482–492, https://doi.org/10.1016/j.envsci.2011.01.003, 2011.

Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M. L. T., Lamarque, J.-F., Matsumoto, K., Montzka, S. A., Raper, S. C. B., Riahi, K., Thomson, A., Velders, G. J. M., and van Vuuren, D. P. P.: The RCP greenhouse gas concentrations and their extensions from 1765 to 2300, Climatic Change, 109, 213, https://doi.org/10.1007/s10584-011-0156-z, 2011.

Metzger, M. J., Bunce, R. G. H., Jongman, R. H. G., Mücher, C. A., and Watkins, J. W.: A climatic stratification of the environment of Europe, 14, 549–563, https://doi.org/10.1111/j.1466-822X.2005.00190.x, 2005.

Oberpriller, J., Cameron, D. R., Dietze, M. C., and Hartig, F.: Towards robust statistical inference for complex computer models, 24, 1251–1261, https://doi.org/10.1111/ele.13728, 2021.

Olin, S., Schurgers, G., Lindeskog, M., Wårlind, D., Smith, B., Bodin, P., Holmér, J., and Arneth, A.: Modelling the response of yields and tissue C : N to changes in atmospheric CO_2 and N management in the main wheat regions of western Europe, 12, 2489–2515, https://doi.org/10.5194/bg-12-2489-2015, 2015.

Pappas, C., Fatichi, S., Leuzinger, S., Wolf, A., and Burlando, P.: Sensitivity analysis of a process-based ecosystem model: Pinpointing parameterization and structural issues, 118, 505–528, https://doi.org/10.1002/jgrg.20035, 2013.

Pearce, D. W.: The Economic Value of Forest Ecosystems, Ecosystem Health, 7, 284–296, https://doi.org/10.1046/j.1526-0992.2001.01037.x, 2001.

Petter, G., Mairota, P., Albrich, K., Bebi, P., Brůna, J., Bugmann, H., Haffenden, A., Scheller, R. M., Schmatz, D. R., Seidl, R., Speich, M., Vacchiano, G., and Lischke, H.: How robust are future projections of forest landscape dynamics? Insights from a systematic comparison of four forest landscape models, Environmental Modelling & Software, 134, 104844, https://doi.org/10.1016/j.envsoft.2020.104844, 2020.

Prestele, R., Alexander, P., Rounsevell, M. D. A., Arneth, A., Calvin, K., Doelman, J., Eitelberg, D. A., Engström, K., Fujimori, S., Hasegawa, T., Havlik, P., Humpenöder, F., Jain, A. K., Krisztin, T., Kyle, P., Meiyappan, P., Popp, A., Sands, R. D., Schaldach, R., Schüngel, J., Stehfest, E., Tabeau, A., Meijl, H. V., Vliet, J. V., and Verburg, P. H.: Hotspots of uncertainty in land-use and land-cover change projections: a global-scale model comparison, 22, 3967–3983, https://doi.org/10.1111/gcb.13337, 2016.

Pretzsch, H., del Río, M., Ammer, Ch., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D. I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Vanhellemont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., and Bravo-Oviedo, A.: Growth and yield of mixed versus pure stands of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) analysed along a productivity gradient through Europe, Eur J Forest Res, 134, 927–947, https://doi.org/10.1007/s10342-015-0900-4, 2015.

Pugh, T. A. M., Lindeskog, M., Smith, B., Poulter, B., Arneth, A., Haverd, V., and Calle, L.: Role of forest regrowth in global carbon sink dynamics, PNAS, 116, 4382–4387, https://doi.org/10.1073/pnas.1810512116, 2019.

Rabin, S. S., Melton, J. R., Lasslop, G., Bachelet, D., Forrest, M., Hantson, S., Kaplan, J. O., Li, F., Mangeon, S., Ward, D. S., Yue, C., Arora, V. K., Hickler, T., Kloster, S., Knorr, W., Nieradzik, L., Spessa, A., Folberth, G. A., Sheehan, T., Voulgarakis, A., Kelley, D. I., Prentice, I. C., Sitch, S., Harrison, S., and Arneth, A.: The Fire Modeling Intercomparison Project (FireMIP), phase 1: experimental and analytical protocols with detailed model descriptions, Geosci. Model Dev., 10, 1175–1197, https://doi.org/10.5194/gmd-10-1175-2017, 2017.

Reyer, C. P. O., Flechsig, M., Lasch-Born, P., and van Oijen, M.: Integrating parameter uncertainty of a process-based model in assessments of climate change effects on forest productivity, Climatic Change, 137, 395–409, https://doi.org/10.1007/s10584-016-1694-1, 2016.

Robichaud, E. and Methven, I. R.: The applicability of the pipe model theory for the prediction of foliage biomass in trees from natural, untreated black spruce stands, https://doi.org/10.1139/x92-148, 1992.

Roux, S., Buis, S., Lafolie, F., and Lamboni, M.: Cluster-based GSA: Global sensitivity analysis of models with temporal or spatial outputs using clustering, Environmental Modelling & Software, 140, 105046, https://doi.org/10.1016/j.envsoft.2021.105046, 2021.

Ruiz-Pérez, G. and Vico, G.: Effects of Temperature and Water Availability on Northern European Boreal Forests, 3, 34, https://doi.org/10.3389/ffgc.2020.00034, 2020.

Saltelli, A.: Sensitivity Analysis for Importance Assessment, 22, 579–590, https://doi.org/10.1111/0272-4332.00040, 2002.

Saltelli, A., Ratto, M., Andres, T., Campolongo, F., Cariboni, J., Gatelli, D., Saisana, M., and Tarantola, S. (Eds.): Global sensitivity analysis: the primer, John Wiley, Chichester, England ; Hoboken, NJ, 292 pp., 2008.

Saltelli, A., Aleksankina, K., Becker, W., Fennell, P., Ferretti, F., Holst, N., Li, S., and Wu, Q.: Why so many published sensitivity analyses are false: A systematic review of sensitivity analysis practices, Environmental Modelling & Software, 114, 29–39, https://doi.org/10.1016/j.envsoft.2019.01.012, 2019.

Saraiva, S., Meier, H. E. M., Andersson, H., Höglund, A., Dieterich, C., Gröger, M., Hordoir, R., and Eilola, K.: Uncertainties in Projections of the Baltic Sea Ecosystem Driven by an Ensemble of Global Climate Models, Front. Earth Sci., 6, https://doi.org/10.3389/feart.2018.00244, 2019.

Seebacher, F. and Franklin, C. E.: Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology, Philos Trans R Soc Lond B Biol Sci, 367, 1607–1614, https://doi.org/10.1098/rstb.2012.0036, 2012.

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., and Venevsky, S.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, Glob. Change Biol., 9, 161–185, https://doi.org/10.1046/j.1365-2486.2003.00569.x, 2003.

Smith, B., Prentice, I. C., and Sykes, M. T.: Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space, 10, 621–637, https://doi.org/10.1046/j.1466-822X.2001.t01-1-00256.x, 2001.

Smith, B., Samuelsson, P., Wramneby, A., and Rummukainen, M.: A model of the coupled dynamics of climate, vegetation and terrestrial ecosystem biogeochemistry for regional applications, Tellus A: Dynamic Meteorology and Oceanography, 63, 87–106, https://doi.org/10.1111/j.1600-0870.2010.00477.x, 2011.

Smith, B., Wårlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., and Zaehle, S.: Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model, 11, 2027–2054, https://doi.org/10.5194/bg-11-2027-2014, 2014.

Snell, R. S., Huth, A., Nabel, J. E. M. S., Bocedi, G., Travis, J. M. J., Gravel, D., Bugmann, H., Gutiérrez, A. G., Hickler, T., Higgins, S. I., Reineking, B., Scherstjanoi, M., Zurbriggen, N., and Lischke, H.: Using dynamic vegetation models to simulate plant range shifts, 37, 1184–1197, https://doi.org/10.1111/ecog.00580, 2014.

Snell, R. S., Elkin, C., Kotlarski, S., and Bugmann, H.: Importance of climate uncertainty for projections of forest ecosystem services, Reg Environ Change, 18, 2145–2159, https://doi.org/10.1007/s10113-018-1337-3, 2018.

Sobie, E. A.: Parameter Sensitivity Analysis in Electrophysiological Models Using Multivariable Regression, Biophysical Journal, 96, 1264–1274, https://doi.org/10.1016/j.bpj.2008.10.056, 2009.

Strengers, B. J., Müller, C., Schaeffer, M., Haarsma, R. J., Severijns, C., Gerten, D., Schaphoff, S., Houdt, R. van den, and Oostenrijk, R.: Assessing 20th century climate–vegetation feedbacks of land-use change and natural vegetation dynamics in a fully coupled vegetation–climate model, 30, 2055–2065, https://doi.org/10.1002/joc.2132, 2010.

Tegel, W., Seim, A., Hakelberg, D., Hoffmann, S., Panev, M., Westphal, T., and Büntgen, U.: A recent growth increase of European beech (Fagus sylvatica L.) at its Mediterranean distribution limit contradicts drought stress, Eur J Forest Res, 133, 61–71, https://doi.org/10.1007/s10342-013-0737-7, 2014.

Tian, S., Youssef, M. A., Amatya, D. M., and Vance, E. D.: Global sensitivity analysis of DRAINMOD-FOREST, an integrated forest ecosystem model: GLOBAL SENSITIVITY ANALYSIS OF DRAINMOD-FOREST, Hydrol. Process., 28, 4389–4410, https://doi.org/10.1002/hyp.9948, 2014.

Tian, W., Heo, Y., de Wilde, P., Li, Z., Yan, D., Park, C. S., Feng, X., and Augenbroe, G.: A review of uncertainty analysis in building energy assessment, Renewable and Sustainable Energy Reviews, 93, 285–301, https://doi.org/10.1016/j.rser.2018.05.029, 2018.

Tomlin, A. S.: The role of sensitivity and uncertainty analysis in combustion modelling, Proceedings of the Combustion Institute, 34, 159–176, https://doi.org/10.1016/j.proci.2012.07.043, 2013.

Trotsiuk, V., Hartig, F., Cailleret, M., Babst, F., Forrester, D. I., Baltensweiler, A., Buchmann, N., Bugmann, H., Gessler, A., Gharun, M., Minunno, F., Rigling, A., Rohner, B., Stillhard, J., Thürig, E., Waldner, P., Ferretti, M., Eugster, W., and Schaub, M.: Assessing the response of forest productivity to climate extremes in Switzerland using model–data fusion, 26, 2463–2476, https://doi.org/10.1111/gcb.15011, 2020.

Tylianakis, J. M., Didham, R. K., Bascompte, J., and Wardle, D. A.: Global change and species interactions in terrestrial ecosystems, 11, 1351–1363, https://doi.org/10.1111/j.1461-0248.2008.01250.x, 2008.

Vitousek, P. M. and Howarth, R. W.: Nitrogen limitation on land and in the sea: How can it occur?, Biogeochemistry, 13, 87–115, https://doi.org/10.1007/BF00002772, 1991.

Walentowski, H., Falk, W., Mette, T., Kunz, J., Bräuning, A., Meinardus, C., Zang, C., Sutcliffe, L. M. E., and Leuschner, C.: Assessing future suitability of tree species under climate change by multiple methods: a case study in southern Germany, 60, 101–126, https://doi.org/10.15287/afr.2016.789, 2017.

Wallach, D. and Genard, M.: Effect of uncertainty in input and parameter values on model prediction error, Ecological Modelling, 105, 337–345, https://doi.org/10.1016/S0304-3800(97)00180-4, 1998.

Wang, F., Mladenoff, D. J., Forrester, J. A., Keough, C., and Parton, W. J.: Global sensitivity analysis of a modified CENTURY model for simulating impacts of harvesting fine woody biomass for bioenergy, Ecological Modelling, 259, 16–23, https://doi.org/10.1016/j.ecolmodel.2013.03.008, 2013.

Waring, R. H.: Estimating Forest Growth and Efficiency in Relation to Canopy Leaf Area, in: Advances in Ecological Research, vol. 13, edited by: MacFadyen, A. and Ford, E. D., Academic Press, 327–354, https://doi.org/10.1016/S0065-2504(08)60111-7, 1983.

Wramneby, A., Smith, B., Zaehle, S., and Sykes, M. T.: Parameter uncertainties in the modelling of vegetation dynamics—Effects on tree community structure and ecosystem functioning in European forest biomes, Ecological Modelling, 216, 277–290, https://doi.org/10.1016/j.ecolmodel.2008.04.013, 2008.

Wu, Z., Ahlström, A., Smith, B., Ardö, J., Eklundh, L., Fensholt, R., and Lehsten, V.: Climate Data Induced Uncertainty in Model-Based Estimations of Terrestrial Primary Productivity, Environ. Res. Lett., 12, 064013, https://doi.org/10.1088/1748-9326/aa6fd8, 2017.

Wu, Z., Boke-Olén, N., Fensholt, R., Ardö, J., Eklundh, L., and Lehsten, V.: Effect of climate dataset selection on simulations of terrestrial GPP: Highest uncertainty for tropical regions, PLOS ONE, 13, e0199383, https://doi.org/10.1371/journal.pone.0199383, 2018.

Zaehle, S., Sitch, S., Smith, B., and Hatterman, F.: Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics, 19, https://doi.org/10.1029/2004GB002395, 2005.

Zeide, B.: Analysis of Growth Equations, Forest Science, 39, 594–616, https://doi.org/10.1093/forestscience/39.3.594, 1993.

Zhang, H., Yuan, W., Dong, W., & Liu, S. (2014). Seasonal patterns of litterfall in forest ecosystem worldwide. *Ecological Complexity*, *20*, 240–247. https://doi.org/10.1016/j.ecocom.2014.01.003

Tables

Table 1: The model inputs investigated in the sensitivity analysis can be group in a) common parameters b) species-specific parameters and c) drivers. The ranges for the parameters have been determined from experts and literature, default parameter values that changed from Hickler et al. (2012) due to the reparameterization are explained in Appendix A1.2 .* denotes an averaging over sites.

a) Common Paramaters

Grouping	Parameter	Explanation	Unit	Default Value	Min. Value	Max. Value	-	-	-	-	-	-	Literature sources
Mortality / Management	distinterval	average return time for generic patch-destroying disturbances	year	920	200	1000	-	-	-	-	-	-	-
Nitrogen	nfix_a	First term in N fixation eqn	-	0,102	0,102	0,367	-	-	-	-	-	-	-
Nitrogen	nfix_b	Second term in N fixation eqn	-	0,624	0,764	0,624	-						Cleveland et. al, 1999
Nitrogen	nrelocfrac	Fraction of N retranslocated prior to leaf and root shedding	-	0,5	0,1	0,8	-	-	-	-	-	-	-
Photosynthesis/Light	lambda_max	Non-water-stressed ratio of intercellular to ambient CO2 pp	-	0,8	0.6	0.8	-	-	-	-	-	-	Pappas et al. 2013
Structure/Phenology	reprfrac	Fraction of NPP allocated to reproduction	-	0,1	0,05	0,3	-	-	-	-	-	-	-
Structure/Phenology	turnover_root	Rate of fine root turnover	1/year	0,7	0,65	0,75	-	-	-	-	-	-	-
Structure/Phenology	crownarea_max	maximum crown area	mm^2	40	20	60	-	-	-	-	-	-	-
Structure/Phenology	k_allom2	height =kallom2* ~diameter ^(kallom3)	-	60	30	80	-	-	-	-	-	-	-
Structure/Phenology	k_rp	crown area = kallom1~*height^(k_rp)	-	1,6	1,3	1,6	-	-	-	-	-	-	-
Water	emax	Maximum evapotranspiration rate	mm/day	5	2	6	-	-	-	-	-	-	Köstner 2000

b) Species-specific Paramaters

Group	Parameter	Explanation	Unit	Default Value	Min. Value	Max. Value	Default Value	Min. Value	Max. Value	Default Value	Min. Value	Max. Value	Literature sources
-	-	-	-		*Pinus sylvestris*			*Picea abies*			*Fagus sylvatica*		-
Establishment	parff_min	Min forest floor PAR for grass growth/tree estab	J/m^2/day	2500000	1500000	3500000	1000000	750000	1600000	1000000	750000	1600000	-
Establishment	gdd5min_est	Min GDD on 5 deg C base for establishment	°C day	500	250	700	350	300	700	1300	1050	1450	-
Establishment	tcmin_est	Min 20-year coldest month mean temp for establishment	°C	-29	-100	-15	-29	-100	-15	-6.5	-8	-5	-
Establishment	tcmax_est	Max 20-year coldest month mean temp for establishment	°C	5.5	-1.0	6	3	-2	6	7	5	8	Schilbasiki et al 2017
Establishment	est_max	Max sapling establishment rate	1/m^2/year	0,2	0,1	0,25	0,1	0,05	0,2	0,2	0,05	0,25	-
Establishment	alphar	Shape parameter for recruitment-juv growth rate relationship	-	10	4	15	4	2	5	2	0.8	5	-
Mortality / Management	longevity	Expected longevity under lifetime non-stressed conditions (yr)	year	500	300	900	300	200	1000	400	250	650	-
Mortality / Management	fireresist	fire resistance	-	0,4	0,05	0,7	0,1	0,05	0,8	0,1	0,05	0,8	-
Mortality / Management	cutinterval	Time until trees are cut	year	90	40	140	90	60	120	105	80	140	-
Mortality / Management	greff_min	Threshold for growth suppression mortality	kgC/m^2/yr	0,21	0,07	0,26	0,135	0,03	0,19	0,02	0,001	0,13	Pappas et al. 2013
Mortality / Management	drought_tolerance	Implements drought-limited establishment plus water uptake, from 0: total to 1: not at all drought-limited	-	0,25	0,1	0,4	0,48	0,2	0,65	0,39	0,2	0,49	-
Mortality / Management	thinning_intensity	percentage of treshold crowncoverage that is kept after thinning	-	0,9	0,45	1	0,9	0,5	1	0,9	0,55	1	-
Photosynthesis/Light	respocoeff	Respiration coefficient	-	1	0,8	2,2	1	0,8	2,2	1	0,5	1,5	-
Photosynthesis/Light	pstemp_low	Approx lower range of temp optimum for photosynthesis	°C	10	6,75	15	10	6,75	14	15	8	20	Renwick et al. 2019;Pallandt-Vermeulen et al. 2015
Photosynthesis/Light	pstemp_high	Approx higher range of temp optimum for photosynthesis (deg C)	°C	25	16	30	25	16	30	25	20	30	Zhang et al 2014
Structure/Phenology	cton_leaf_min	minimum leaf C:N ratio	-	31,90	27,32	38,37	38,37	31,9	43,16	24,06	22,7	27,19	-
Structure/Phenology	sla	Specific leaf area	m^2/kgC	8,56	7,812	9,3	11,52	8,7	15,1	43,08	28,33	48,23	Mencuccini, M., Bonosi, L., 2001.; Pallandt-Vermeulen et al. 2015; Xiao et. al. 2006
Structure/Phenology	turnover_sap	Rate of sapwood turnover	fraction/year	0,085	0,05	0,1	0,065	0,04	0,09	0,085	0,05	0,1	-
Structure/Phenology	k_latosa	Tree leaf to sapwood xs area ratio	-	3000	1800	5200	4000	2500	7000	5000	2500	8000	-
Structure/Phenology	k_allom2	height =kallom2* ~diameter ^(kallom3)	-	30	15	60	Values from common Parameters			Values from common Parameters			Zhang et al 2014
Structure/Phenology	k_chillb	Coefficient in equation for budburst chilling time requirement	-	100	80	800	100	80	800	600	250	800	-
Water	gmin	minimum canopy conductance not assoc with photosynthesis	mm/s	0,3	0,22	0,38	0,3	0,22	0,38	0,5	0,42	0,58	Pappas et al 2013;

c) Drivers

Environmental Drivers	insol	Mean deviations solar radiation from standard scenario RCP 4.5 per site	W/m^2	RCP 4.5	-63,9*	65,2*	-	-	-	-	-	-	-
Environmental Drivers	temp	Mean deviations temperature from standard scenario RCP 4.5 per site	°C	RCP 4.5	-5,40*	5,82*	-	-	-	-	-	-	-
Environmental Drivers	prec	Mean deviations precipitation from standard scenario RCP 4.5 per site	mm/month	RCP 4.5	-6,18*	6,27*	-	-	-	-	-	-	-
Environmental Drivers	co2	Mean deviations co2 from standard scenario RCP 4.5 per site	ppm	RCP 4.5	-95,4	237	-	-	-	-	-	-	-
Environmental Drivers	ndep	Mean deviations nitrogen deposition from standard scenario RCP 4.5 per site	g/mm^2/year	RCP 4.5	5,30E-07*	-4,22E-07*	-	-	-	-	-	-	-

Figures

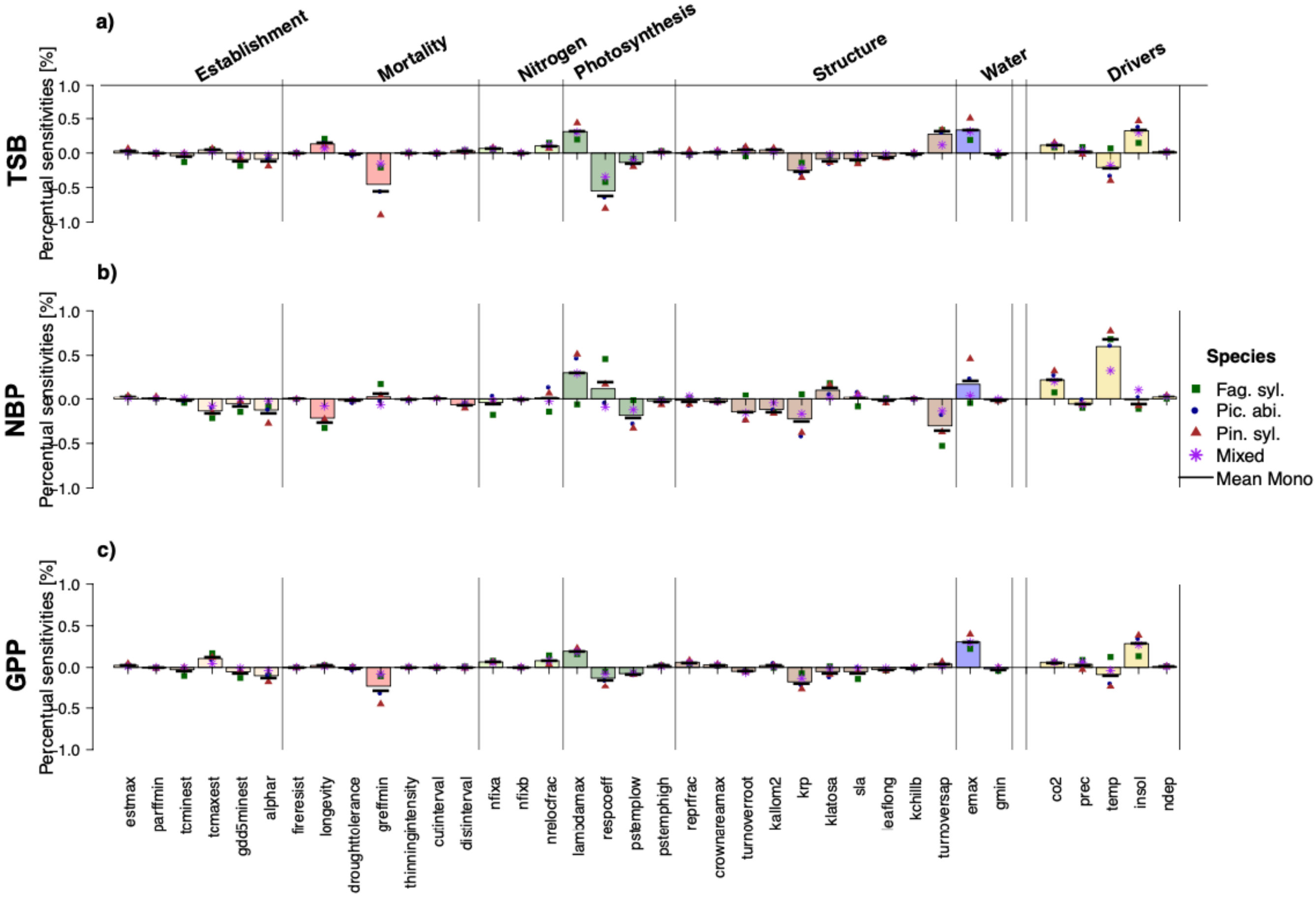

Fig.1: Relative sensitivities (percent output change per percent parameter change) of the individual parameters and environmental drivers regarding a) total standing biomass, b) net biome productivity and c) gross primary production. Sensitivities were not substantially different between *Fag. syl.* (green squares), *Pic. abi.* (blue circles) and *Pin. syl.* (red triangles), but parameter sensitivities were stronger for mono-specific stands than mixed stands (purple asterisks). The height of the bar reflects the mean over mono and mixed stands. Positive values for points and bars indicate a positive and negative values a negative relationship with the corresponding output.

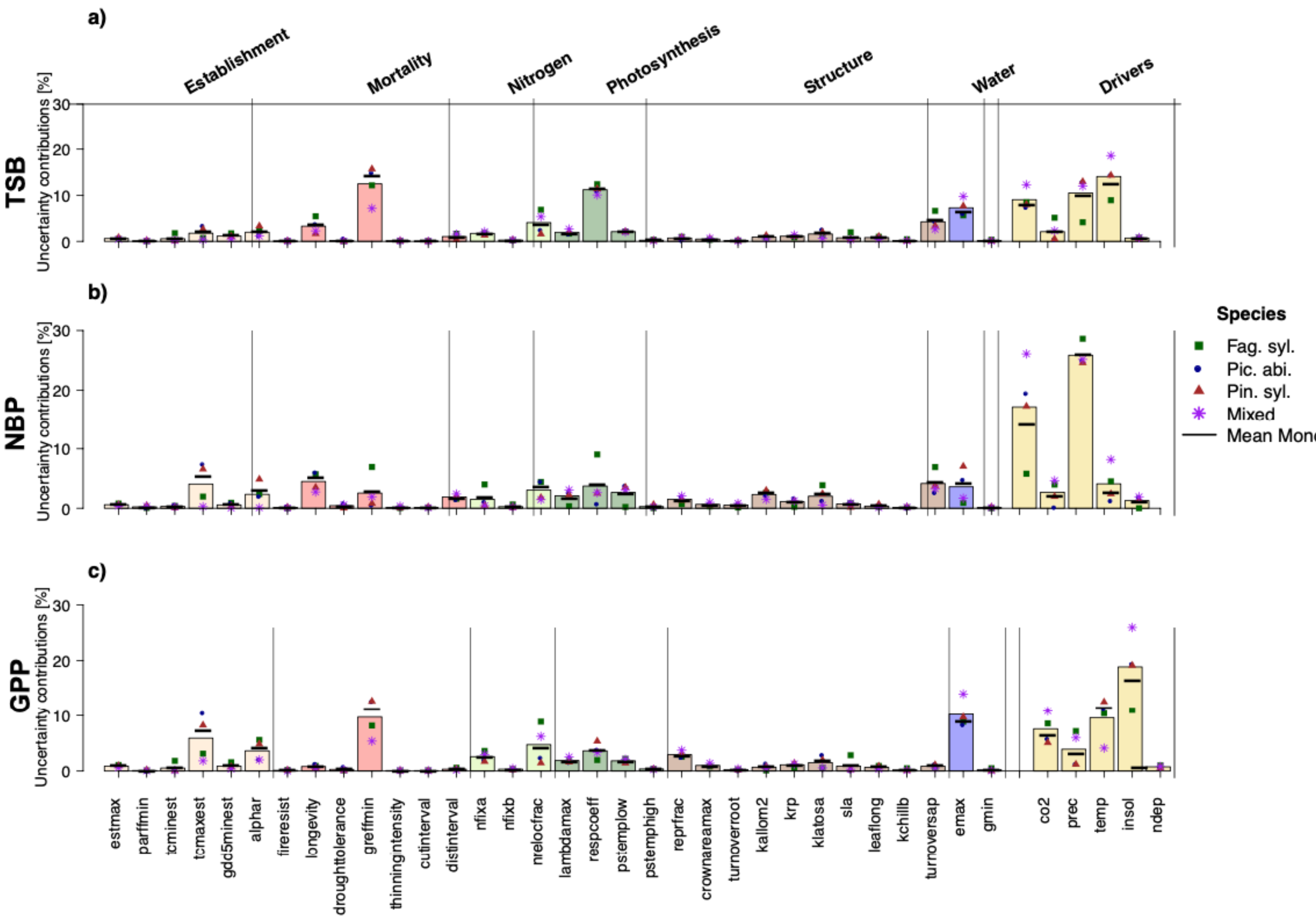

Fig. 2: Uncertainty contributions in percent of the individual parameters and environmental drivers regarding a) total standing biomass, b) net biome productivity and c) gross primary production showed no strong differences between *Fag. syl.* (green squares), *Pic. abi.* (blue circles) and *Pin. syl.* (red triangles) and were stronger for mono-specific stands than mixed stands (purple asterisks). The height of the bars reflects the mean over mono and mixed stands. Positive values for points and bars indicate a positive and negative values a negative relationship with the corresponding output.

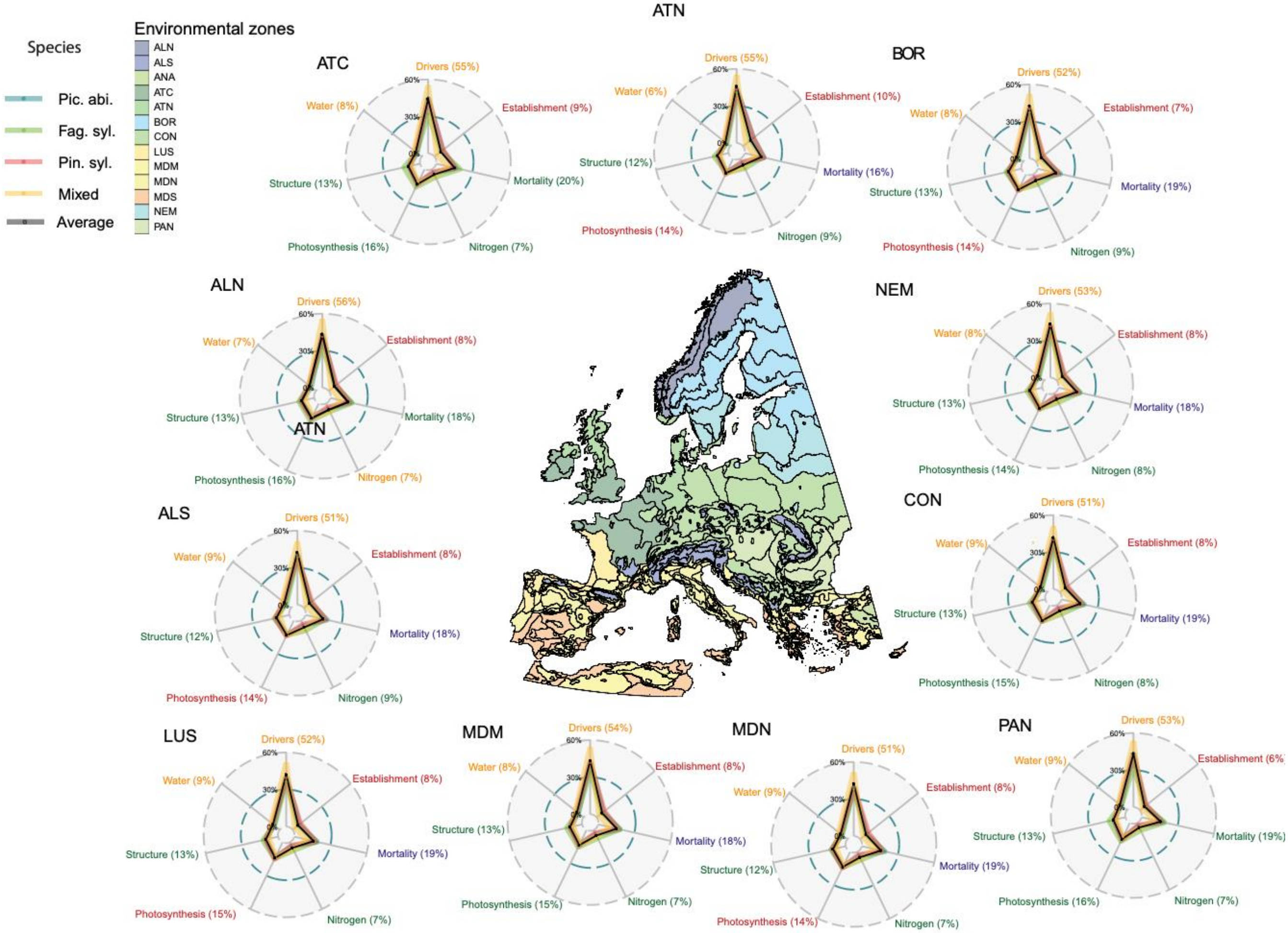

Fig. 3: The aggregated relative uncertainties of total standing biomass per environmental zone (with more than five sites) show a higher importance of drivers in the south than in the north. The environmental zones are from Metzger et al. (2005): ALN–Alpine North; ALS – Alpine South; ANA - Anatolian; ATC – Atlantic Central; ATN– Atlantic North; BOR–Boreal; CON–Continental; LUS – Lusitanian; MDM – Mediterranean Mountains; MDN – Mediterranean North; MDS – Mediterranean South; NEM – Nemoral; PAN – Pannonian. For each environmental zones the color and percentage value of the process label indicates which simulation setup (monospecific with corresponding species or mixed) has contributed most uncertainty and how much.

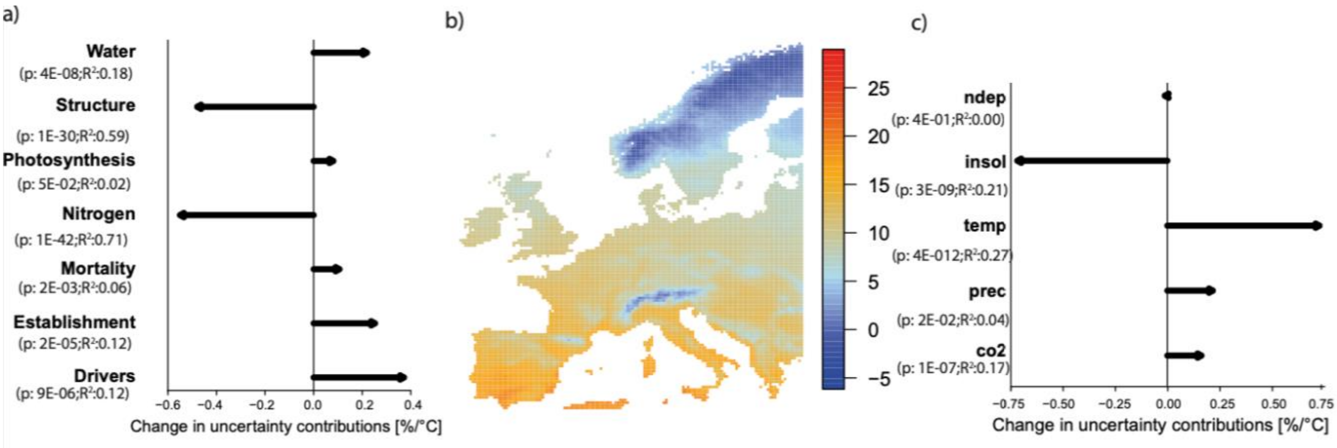

Fig. 4: The uncertainty contributions to total standing biomass projections of parameters and environmental drivers change across a mean annual temperature gradient across Europe from north to south (with p-values and R^2 for the processes/drivers). With increasing temperature, the importance of drivers and establishment became higher for total standing biomass, while the uncertainty contributions from nitrogen and structure declined (4a). The uncertainty contributions due to temperature increased on the temperature gradient and the contributions from solar radiation decreased (4c).

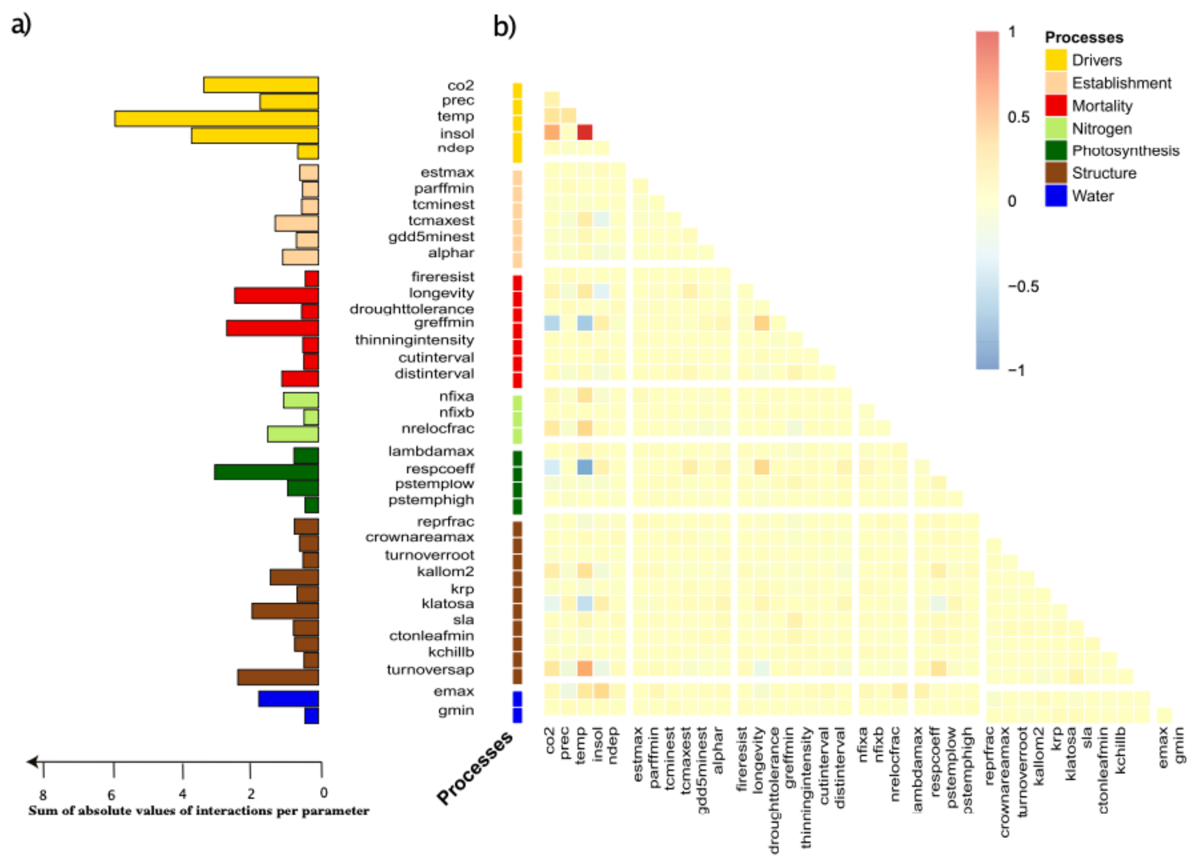

Fig. 5: The induced uncertainty of environmental drivers, mortality- and photosynthesis-related parameters changed the most depending on other parameters (Fig. 5a). Strong individual interactions between parameters and environmental drivers in monospecific projections of total standing biomass were rare (Fig. 5b). If strong interactions occurred, these were mainly between two environmental drivers or environmental drivers and parameters and only rarely between two parameters (Fig. 5b).

Tables Appendix A

Table *A*1: Differences in parametrization of Hickler et al. 2012 and our study for the investigated species (Fag. syl., Pic. Abi. and Pin. Syl)

Parameters	***Fag_syl***		***Pic_abi***		***Pin_syl***	
	Hickler et al. 2012	**Our study**	**Hickler et al. 2012**	**Our study**	**Hickler et al. 2012**	**Our study**
drought_tolerance	0.3	0.3	0.43	0.48	0.25	0.25
fireresist	0.1	0.1	0.1	0.1	0.2	0.4
leaflong	0.5	0.5	4	7	2	4
turnover_leaf	1	1	0.33	0.1429	0.5	0.25
turnover_sap	0.085	0.085	0.05	0.065	0.065	0.085
est_max	0.05	0.1	0.05	0.1	0.2	0.2
alphar	3	10	2	4	6	10
parff_min	1.250.000	1.000.000	1.250.000	1.000.000	2.500.000	2.500.000
tcmin_surv (minimum 20-year coldest month mean temperature for survival)	-3.5	-7.5	-30	-30	-30	-30
tcmin_est (min. 20-year coldest month mean temperature for establishment)	-3.5	-6.5	-29	-29	-30	-29
tcmax_est (max. 20-year coldest month temperature for establishment)	6	7	-1.5	3	-1	5.5
twmin_est (minimum warmest month mean temperature for establishment)	5	-1000	5	-1000	5	8
k_chillb	600	600	100	100	100	100

sla	43?	43.08	11?	11.52	8?	8.56
k_allom2	40	60	40	60	40	60
wooddens	200	293	200	185	200	211
longevity	500	400	500	300	500	500
ga (aerodynamic conductance)	0.04	0.04	0.14	0.14	0.14	0.14
gdd5min_est	1500	1300	600	350	500	500

Figures Appendix A

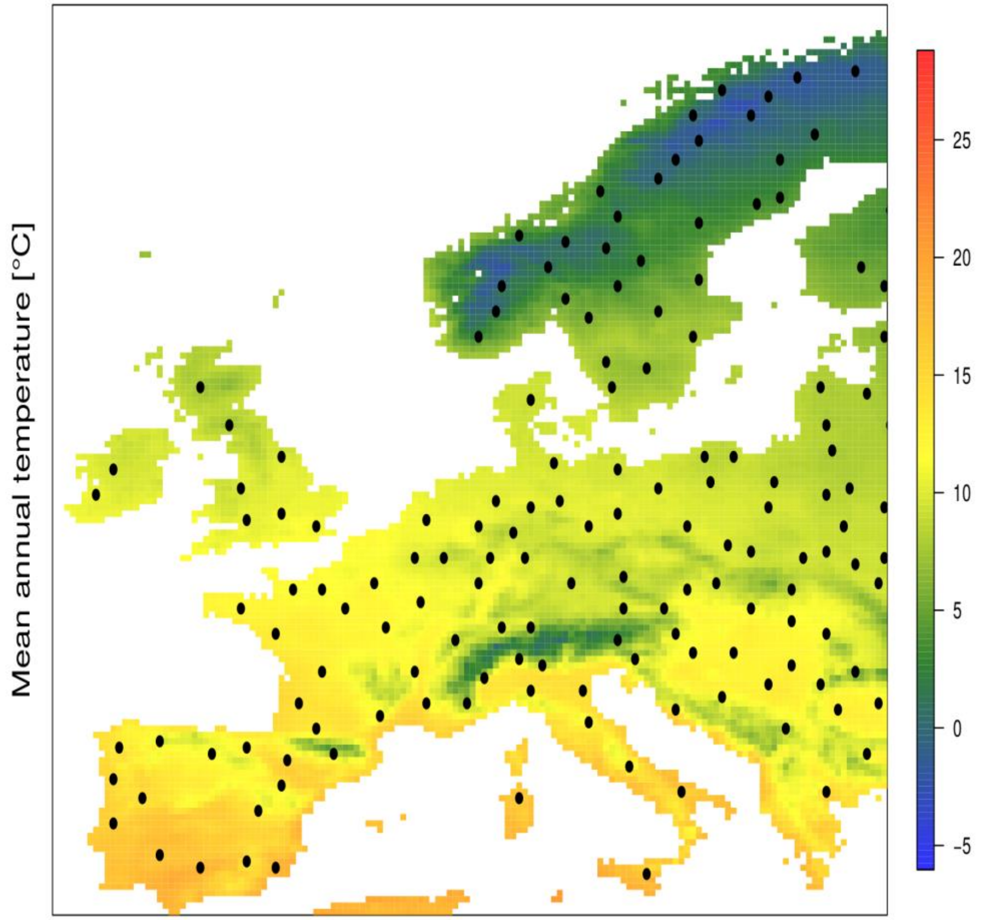

Fig. A1: Our 200 sampled sites geographically and environmentally stratified over Europe cover the most important countries, climate and temperature zones.

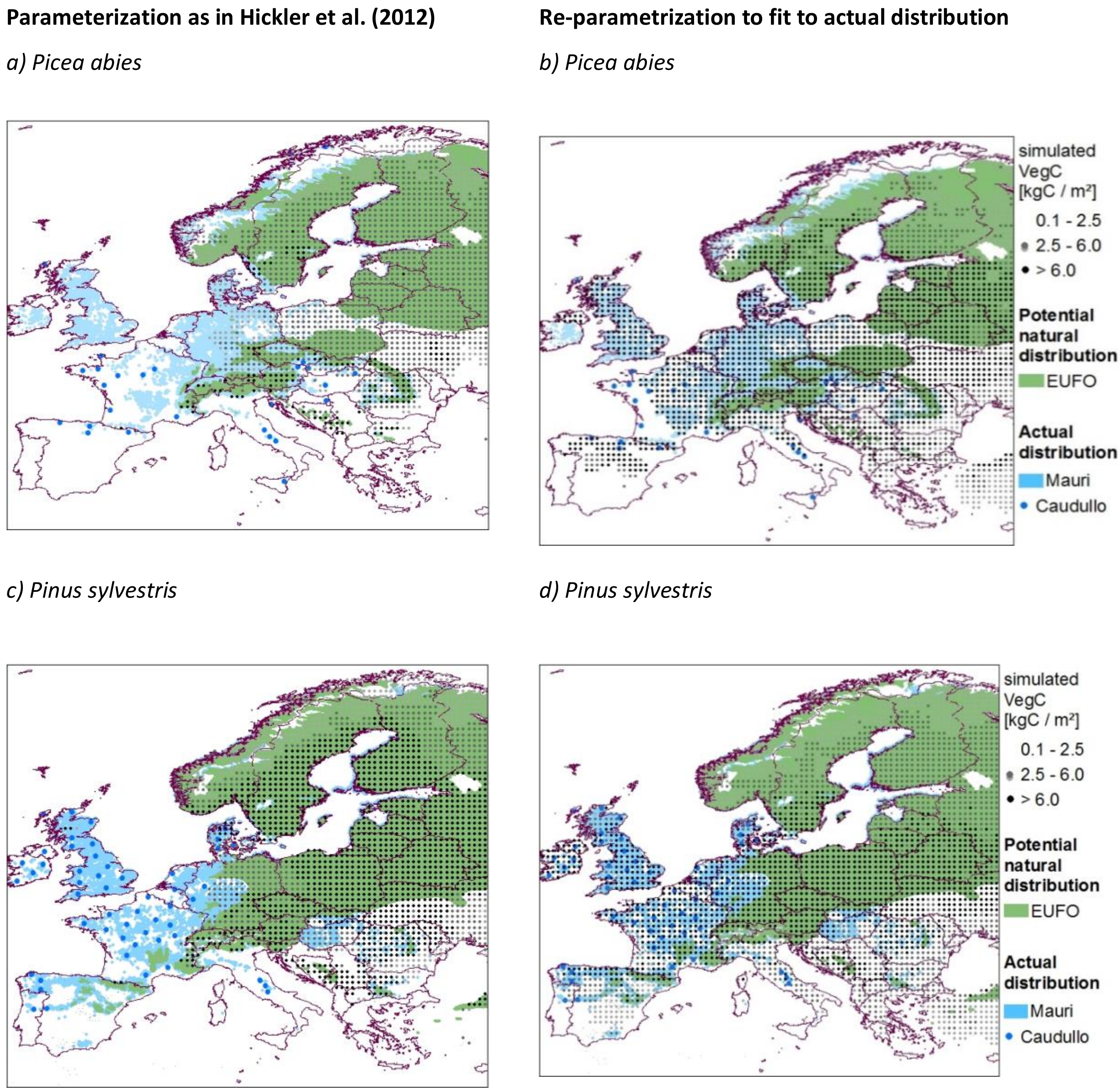

Fig. A2: Simulated (black points), observed (blue) and natural distributions (green) of the adjusted parametrization (b, d) compared to applying the parametrization from Hickler et al., 2012 (a, c) for Picea abies and Pinus sylvestris. EUFO = EUFROGEN, 2008 and 2013, Mauri =(Mauri et al., 2017), Caudullo =(Caudullo, 2017). The simulations were run from 1600 to 2010 without management and without competition between species. The plotted biomasses were averages over the last 20 years.

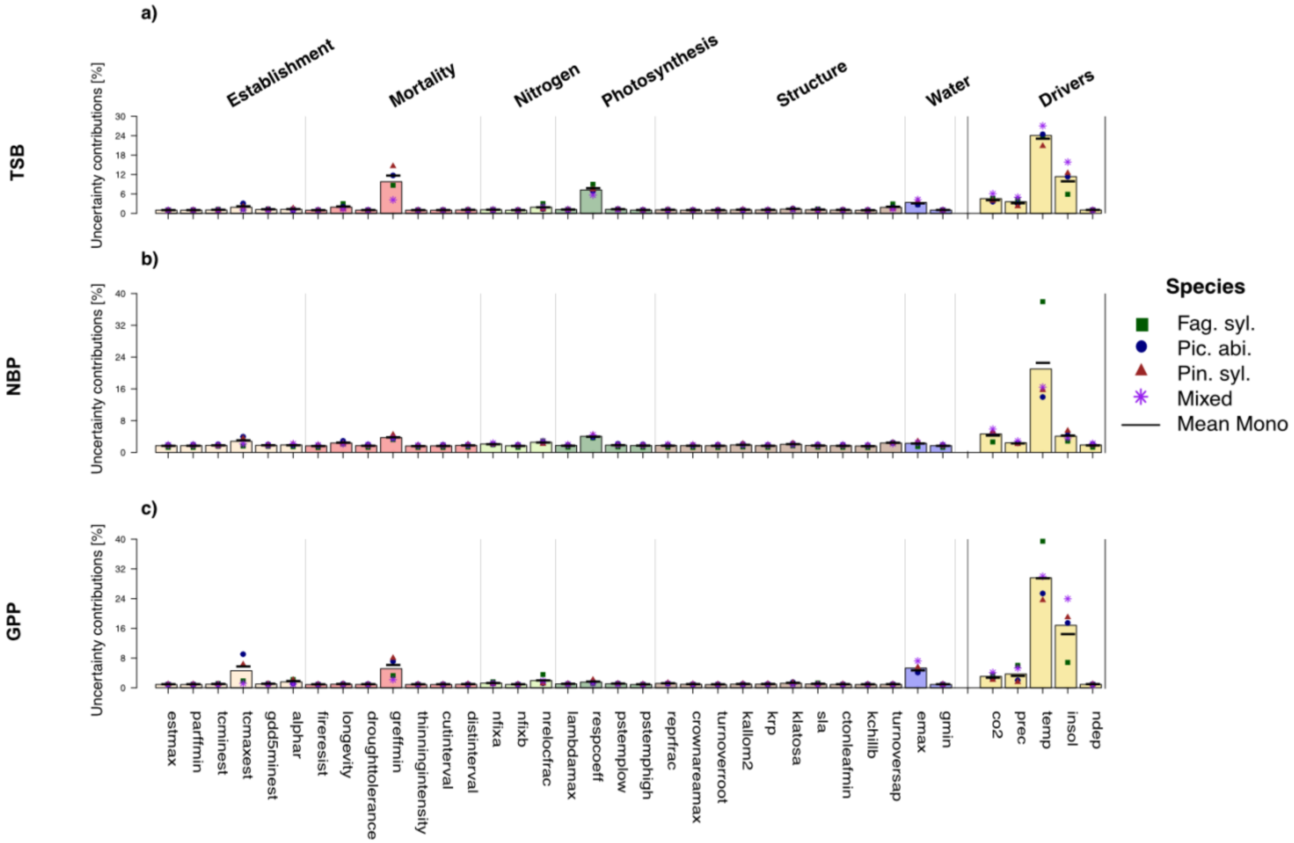

Fig. A3: Results of the random forest uncertainty contributions. The uncertainties due to environmental drivers are higher than the uncertainties due parameters compared to linear regression, but the ranking of parameters is similar to linear regression results.

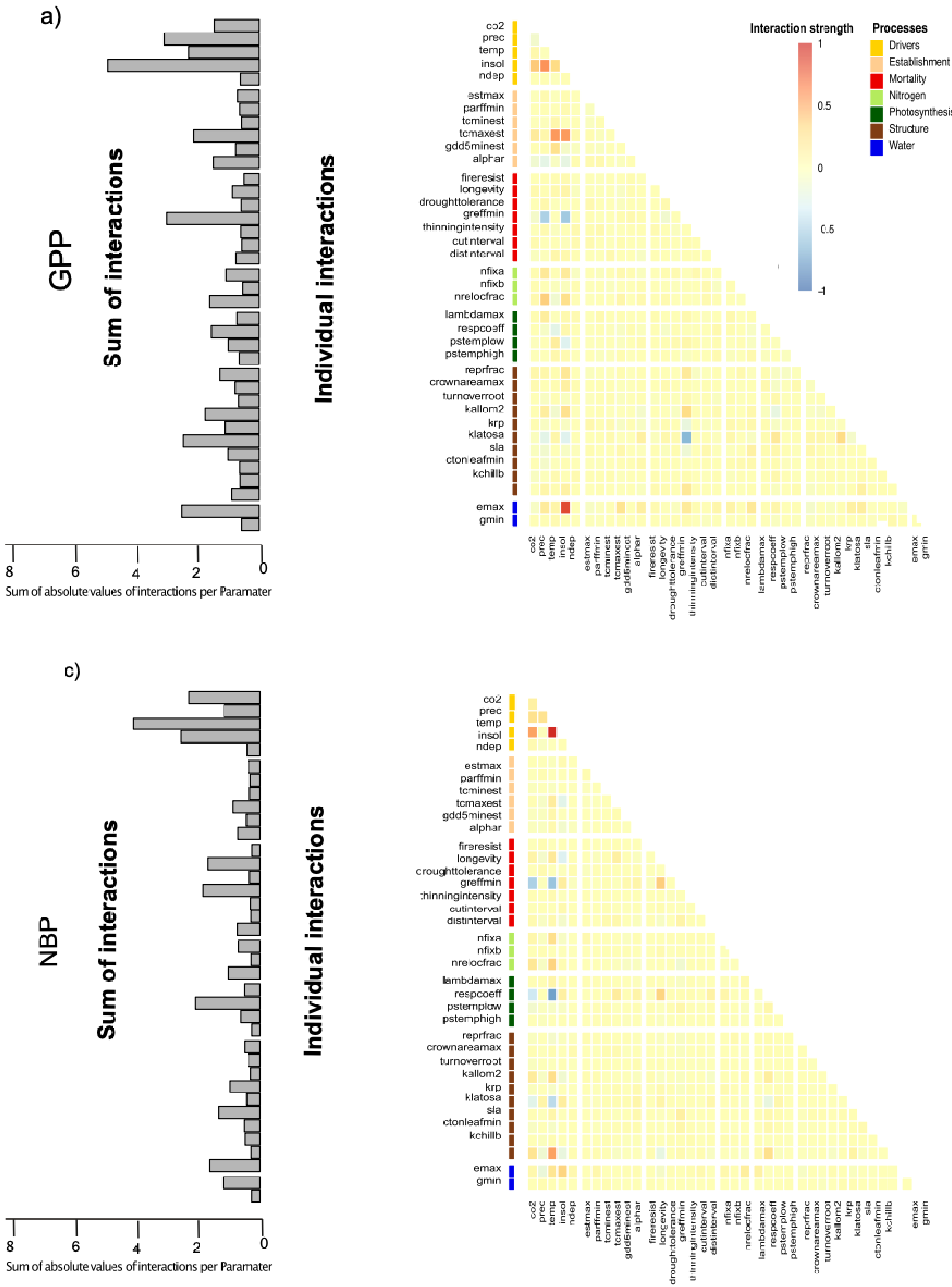
a)
GPP
Sum of interactions
Individual interactions
Interaction strength
1
0.5
0
-0.5
-1
Processes
Drivers
Establishment
Mortality
Nitrogen
Photosynthesis
Structure
Water
co2
prec
temp
insol
ndep
estmax
parffmin
tcminest
tcmaxest
gdd5minest
alphar
fireresist
longevity
droughttolerance
greffmin
thinningintensity
cutinterval
distinterval
nfixa
nfixb
nrelocfrac
lambdamax
respcoeff
pstemplow
pstemphigh
reprfrac
crownareamax
turnoverroot
kallom2
krp
klatosa
sla
ctonleafmin
kchillb
emax
gmin
8
6
4
2
0
Sum of absolute values of interactions per Paramater
c)
NBP
Sum of interactions
Individual interactions
8
6
4
2
0
Sum of absolute values of interactions per Paramater

Fig. A4: Interactions of uncertainty contributions of GPP and total standing biomass are similar to net biome productivity with most interactions arising from environmental drivers.