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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 4.0) across European forests addressing the effect 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 climatic drivers, and parameters related to water and mortality. The importance of climatic drivers for predictive uncertainty increases with increasing temperature and thus, from north to south across Europe, in line with the stress-gradient hypothesis, which proposes that environmental control dominates at the harsh end of an environmental gradient. In conclusion, our study highlights the importance of climatic 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.

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).

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Although different models usually agree in their essential projections for a given ecosystem, they often differ in essential details, for example regarding the future carbon uptake of forest ecosystems (Huntzinger et al., 2017; Krause et al., 2019). Among the reasons for such different results is the inherent uncertainty in climate scenarios (Saraiva et al., 2019), model structural uncertainty (Bugmann et al., 2019; Oberpriller et al., 2021; Prestele et al., 2016) as well as uncertainty about the model parametrization (Grimm, 2005), which in turn make models' projections themselves uncertain (Dietze, 2017). When considering the impact of these uncertainties for directing research (Tomlin, 2013), but also to interpret and understand projections (Dietze et al., 2018), it is of immense value to know which factors drive these uncertainties. 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 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 accounts for the different magnitudes 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 following the current state-of-the-art of running global SAs and UAs that compute sensitivities and uncertainties based on the entire parameter space (Saltelli et al., 2008) rather than just locally around a reference parameter set. Additionally, several studies highlight also the sensitivity and uncertainty of DGVMs to climatic 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), thereby investigating the effects of uncertainty in climatic change projections on model outcomes.

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

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LPJ family identified the intrinsic quantum efficiency of CO_2 uptake (*alpha_C3*) and the photosynthesis scaling parameter (from leaf to canopy) (*alpha_a*) (Jiang et al., 2012; Pappas et al., 2013; Zaehle et al., 2005) as the main contributors of sensitivity for net primary production (about 50-60% of the overall sensitivity). Additionally, LPJ-GUESS 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 impact was 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).

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, is that they either analyzed sensitivities and uncertainties to parameter changes, or to changes in the environmental drivers, but not both. There is strong evidence, however, that the sensitivity of parameters will change if climatic drivers change (different climate scenarios and sites in Jiang et al., 2012; different elevations in Pappas et al., 2013; different sites in Wramneby et al., 2008). 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 on an environmental gradient to assess if ecological principles also arise form model processes. Only Jiang et al. (2012) combined parameter and driver sensitivities but used fixed climate scenarios instead of a range of possible values for the driving variables, which, however, would be required for a probabilistic interpretation.

Here, we analyzed sensitivities and uncertainties in LPJ-GUESS for 200 randomly distributed sites across European forests (see Appendix A1.1). To quantify the impacts of environmental change, we investigated variation of environmental drivers (precipitation, temperature, solar radiation, CO_2, nitrogen deposition) simultaneously with parameters of the most important processes (photosynthesis, establishment, nitrogen, water cycle, mortality, disturbance/management and growth). To assess the impact of input uncertainties in environmental drivers, we performed the analysis for dynamic climate change from 2001-2100 and steady climate from 2100-2200 for the most common tree species in Europe (*Fagus sylvatica, Pinus sylvestris and Picea abies*) individually and in mixed stands based on randomly sampled climate projections within the

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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 and compared the resulting changes to empirical results.

2. Methods and Material

2.1. The LPJ-GUESS vegetation model

LPJ-GUESS is a process-based ecosystem model simulating 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 (even-aged and represented by same-size, averaged individuals) of different plant functional types (PFTs) or species. Each PFT/species has a unique parameter set. In this study, we use a re-parameterized version of Lindeskog et al. (2021) 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).

A first set of key parameters 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 (here: 1 year) new PFTs are established given enough space, light, soil water and photoactive radiation at forest floor 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 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

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(*leaflong*)) and functional balance as well as demographic constraints (Sitch et al., 2003). Each living tissue is assigned a turnover rate transferring litter or living sapwood into heartwood (*turnover_sap*) and a turnover rate for fine root (turnover_root). 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 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, 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. Background 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 population. Mortality probability increases with decreasing difference to the maximum longevity 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 with the same yearly occurrence probability for all patches (*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.

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 radiation, temperature (optimum temperature range for photosynthesis determined by *pstemp_low and pstemp_high*, Larcher, 1983), intercellular CO_2 (e.g. 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

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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. 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. 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 with longitudinal and latitudinal coordinates as well as mean precipitation, solar radiation and temperature as categories. We agreed on 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 with the most common species in Europe (*Fagus sylvatica*, *Pinus sylvestris* und *Picea abies)* as monospecific and 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 and data for atmospheric CO_2 concentration from Meinshausen et al. (2011). 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). 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 (following the SHELF expert elicitation protocol, see Gosling, 2018) was based on our expert knowledge and literature review. The resulting eleven parameters common for all species and 22 species-specific parameters (see Table 1) were grouped to the specific processes they contribute most to (Table 1, Grouping).

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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 concentrated on carbon outputs (**gross primary production GPP**, **total standing biomass TSB** and **net biome productivity NBP**), because of forests' role for carbon cycling, their large contribution to the land carbon sink (Pugh et al., 2019) and the economic importance of tree growth for forest owners.

Sensitivities and uncertainties were calculated by Monte-Carlo sampling from the assumed multivariate parameter and climate uncertainty. For the monospecific / mixed simulations, we drew 10.000 respectively 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, we individually drew parameter combinations for each 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 as response, and parameters and drivers as well as their second order interactions as predictors. 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 A1.2.). 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. 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 are 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. 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*). 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 were broadly similar in their sensitivities, although *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.

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

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substantially affected by model parameters (*longevity, tcmax_est, turnover_sap, greffmin* and *emax*), 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 *greffmin* and *emax* contributed most to parameter induced uncertainty (Fig. 2c). Notably, also nitrogen-fixation induced uncertainty was substantial for TSB and GPP.

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 across Europe

To project the uncertainties 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 tree monospecific and mixed stands remains similar in all environmental zones. On average 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 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 climatic 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 and pH 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 in the full dataset of simulated values (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 processes we summed the individual interaction indices of each parameter (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 similar sum of interactions (Fig. 5a). 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-*turnover_sap*, temperature-*greffmin* and temperature-*respcoeff* (Fig. 5b)) and moderate parameter-parameter interactions (*longevity*- *greffmin*, *respcoeff* – *longevity* (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 climatic 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 climate, we found that environmental drivers and parameters controlling evapotranspiration and background mortality contribute most to predictive uncertainty (Fig. 2). By investigating changes of uncertainties for TSB across Europe, we found that predictive uncertainty in northern regions was more strongly influenced by model parameters controlling structure and nitrogen fixation, while in southern regions environmental drivers contributed more uncertainty (Fig. 3). When correlated against a

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temperature gradient, uncertainty contributions to TSB increased for environmental drivers and decreased for tree structure and nitrogen-related parameters (Fig. 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), suggesting that climatic conditions moderate the effect of parameter-induced uncertainties, and not the other way around.

Our finding that average sensitivities of carbon-related outputs across European forests were highest for photosynthesis-related parameters amplifies the evidence of earlier studies (Pappas et al., 2013; Zaehle et al., 2005). 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 (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 forecasts of vegetation dynamics (Bugmann et al., 2019; Hardiman et al., 2011). High sensitivities to water-related parameters were not found in previous studies (Pappas et al., 2013), but are ecologically plausible. 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. 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 (but see Petter et al., 2020). From the parameters especially water-, nitrogen- and mortality-related parameters contributed a substantial amount of uncertainty. While the uncertainty contributions from mortality parameters were already highlighted by earlier studies (Bugmann et al., 2019), 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).

Environmental drivers contributed most uncertainty among the different groups of parameters/drivers (Figs. 2, 3, 4, 5). Especially high 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 climatic drivers in DGVMs (Barman et al., 2014; Wu et al., 2017, 2018). The positive effect of CO_2 is explained by the CO_2 fertilization effect (Keenan et al., 2011) and increased water-use efficiency. For the negative effect of temperature, this may arise from decreased photosynthetic efficiency and increased respiration rates with higher temperatures (Gustafson

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et al., 2018, confirmed by the negative relationship between temperature and the respiration coefficient). This effect, however, differed in magnitude between tree species (Fig. 2). While for *Pic. abi.* and *Pin. syl.* there was a strong effect, *Fag. syl.* was less affected, which is a sign of its higher resistance to increasing temperatures (Buras and Menzel, 2019).

The results for the different vegetation zones (Fig. 3) and the environmental gradient analysis (Fig. 4) indicated that environmental context changes the sensitivity of processes and the observation that most interactions occurred with environmental drivers (Fig. 5) confirms this. These findings stress that environmental conditions affect the physiology of organisms directly and thus indirectly the fitness and biotic interactions (e.g. Seebacher & Franklin, 2012; Tylianakis et al., 2008). The fact that uncertainty contributions analyzed by a random forest are similar to linear regression results but assign higher importance to environmental drivers suggests that environmental contributions are particularly nonlinear or show higher order interactions (see Appendix A1.3).

We also encountered agreement with different ecological principles and hypotheses in our results. First, we find several indicators that limiting factors change across environmental conditions. For example, nitrogen-induced uncertainty decreases with increasing temperatures (Fig. 4). Second, our results about changing uncertainty contributions on an environmental gradient also support the stress-gradient hypothesis (Maestre et al., 2009). This hypothesis states that in stressful environments positive interactions should occur more often than in benign environments and is highly supported by empirical studies (Callaway, 2007). The decrease of uncertainty contributions of structure- related parameters on the temperature gradient (Fig. 4) shows first evidence that the processes in an ecosystem model themselves mirror the hypothesis. Lastly, decreased sensitivity of mixed stands (Fig. 1) corresponds to higher resilience of mixed forests (Bauhus et al., 2017). All these findings suggest that ecological principles are emerging from lower-level processes (Levin, 1992) and that the processes reflecting these ecological principles are already modeled in DGVMs.

We caution that our results regarding the role 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). For the drivers, we used RCP scenarios; however, these were not created as probabilistic min / max ranges. For the model parameters, we had to rely on expert guesses. Here, we reduced subjectivity by following the SHELF expert elicitation protocol (Gosling, 2018). 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. 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.

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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 but hard coded and therefore a normal user does not interact with them. Thus, such parameters do arguably belong more to the model structure than to input parameters. When including such structural components in the analysis, we should also analyze sensitivity to the functional form or even to entire modules. It is, however, known that vegetation models are often more sensitive to functional forms than to parameters (e.g. Bugmann et al., 2019). To make the analysis comparable and useful for the normal LPJ-GUESS user, we restricted ourselves to more frequently changed parameters.

5. Conclusions

Our findings about the relative importance of different uncertainty contributions to carbon stocks and fluxes highlight which processes really matter for carbon projections with LPJ-GUESS. Moreover, we stress that environmental context changes uncertainty contributions of other processes and thereby find first indicators that several ecological principles (e.g. the gradient-stress hypothesis) are emerging from process descriptions. These 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 the most important climates, vegetation zones and countries of Europe.

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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. 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 total standing biomass

Interactions of gross primary production (Fig. A4a,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

Code to perform the sensitivity and uncertainty analysis can be found on github (https://github.com/JohannesOberpriller/SensitivityAnalysisLPJ).
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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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.

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a) Common Paramaters

Grouping	Parameter	Explanation	Unit	Default Value	Min. Value	Max. Value	-	-	-	-	-	-	Literature sources
Photosynthesis/Light	lambda_max	Non-water-stressed ratio of intercellular to ambient CO2 pp	-	0,8	0.6	0.8	-	-	-	-	-	-	Pappas et al. 2013
Water	emax	Maximum evapotranspiration rate	mm/day	5	2	6	-	-	-	-	-	-	Köstner 2000
Structure/Phenology	reprfrac	Fraction of NPP allocated to reproduction	-	0,1	0,05	0,3	-	-	-	-	-	-	-
Nitrogen	nfix_a	First term in N fixation eqn	-	0,102	0,102	0,367	-	-	-	-	-	-	-
Nitrogen	nfix_b	Second term in N fixation eqn	-	0,524	-0,754	0,524	-	-	-	-	-	-	Cleveland et. al, 1999
Nitrogen	nrelocfrac	Fraction of N retranslocated prior to leaf and root shedding	-	0,5	0,1	0,8	-	-	-	-	-	-	-
Structure/Phenology	turnover_root	Rate of fine root turnover	1/year	0,7	0,65	0,75	-	-	-	-	-	-	-
Mortality / Management	distinterval	average return time for generic patch-destroying disturbances	year	920	200	1000	-	-	-	-	-	-	-
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	-	-	-	-	-	-	-

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*		-
Mortality / Management	longevity	Expected longevity under lifetime non-stressed conditions (yr)	year	500	300	900	300	200	1000	400	250	650	-
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	-
Mortality / Management	fireresist	fire resistance	-	0,4	0,05	0,7	0,1	0,05	0,8	0,1	0,05	0,8	-
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;
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
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	-
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	-
Establishment	alphar	Shape parameter for recruitment-juv growth rate relationship	-	10	4	15	4	2	5	2	0,8	5	-
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
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
Structure/Phenology	k_latosa	Tree leaf to sapwood xs area ratio	-	3000	1800	5200	4000	2500	7000	5000	2500	8000	-
Mortality / Management	cutinterval	Time until trees are cut	year	90	40	140	90	60	120	105	80	140	-
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	-
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	-
Structure/Phenology	k_allom2	height =kallom2* ~diameter ^(kallom3)	-	30	15	60	Values from common Parameters			Values from common Parameters			Zhang et al 2014
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	-
Structure/Phenology	k_chillb	Coefficient in equation for budburst chilling time requirement	-	100	80	800	100	80	800	600	250	800	-
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	Schilbaslki et al 2017

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*	-	-	-	-	-	-	-

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Figures

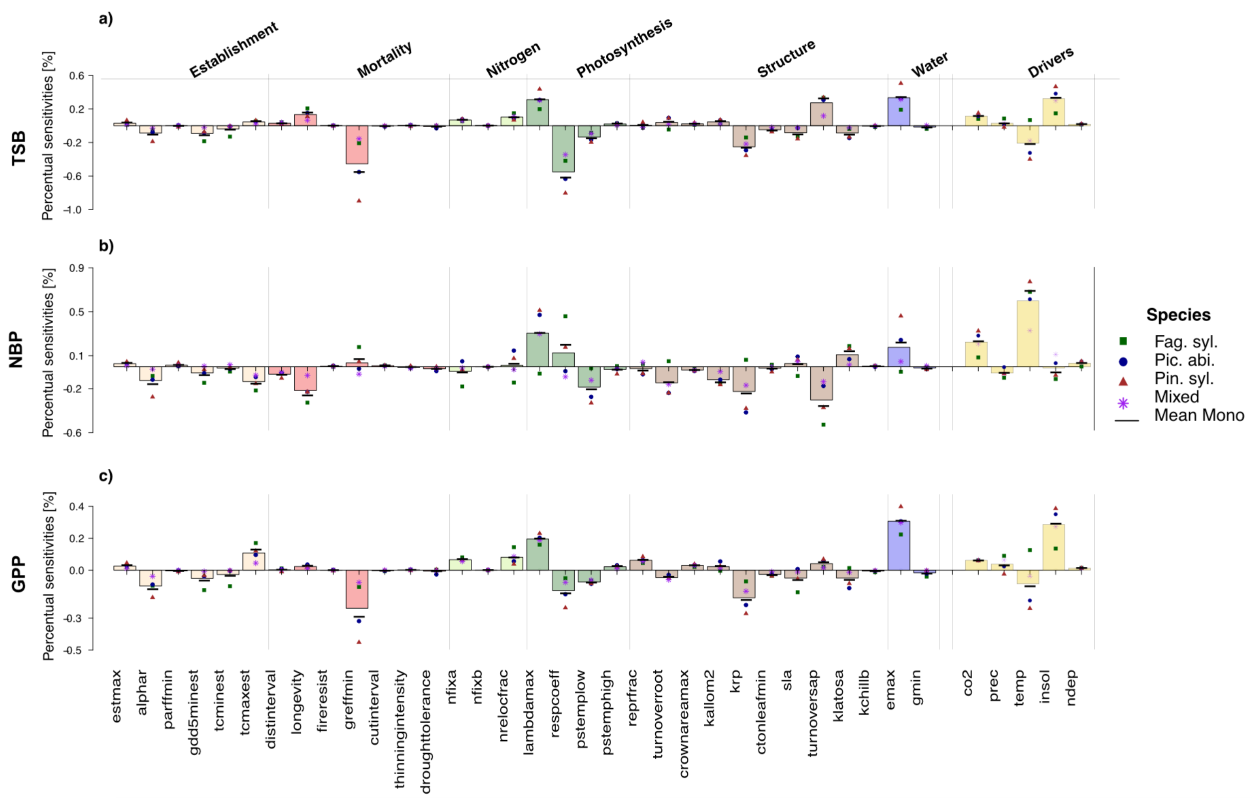

Fig.1: Relative sensitivities (percent output change per percent parameter change) of the individual parameters and environmental drivers regarding a) total standing biomass, b) net biome productivity and c) gross primary production. Sensitivities were not substantially different between *Fag. syl.* (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.

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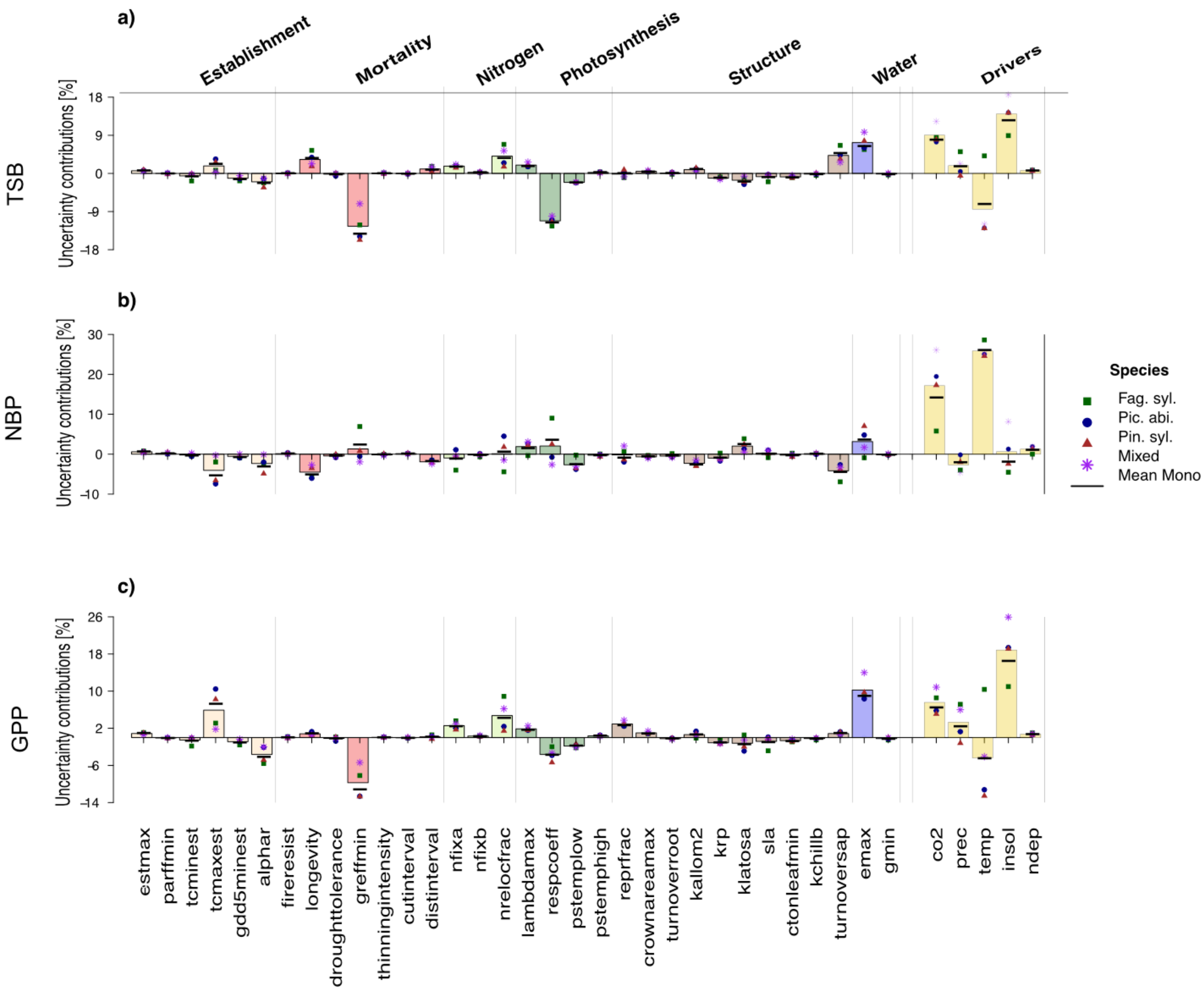

Fig. 2: Uncertainty contributions in percent of the individual parameters and environmental drivers regarding a) total standing biomass, b) net biome productivity and c) gross primary production showed no strong differences between *Fag. syl.* (green squares), *Pic. abi.* (blue circles) and *Pin. syl.* (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.

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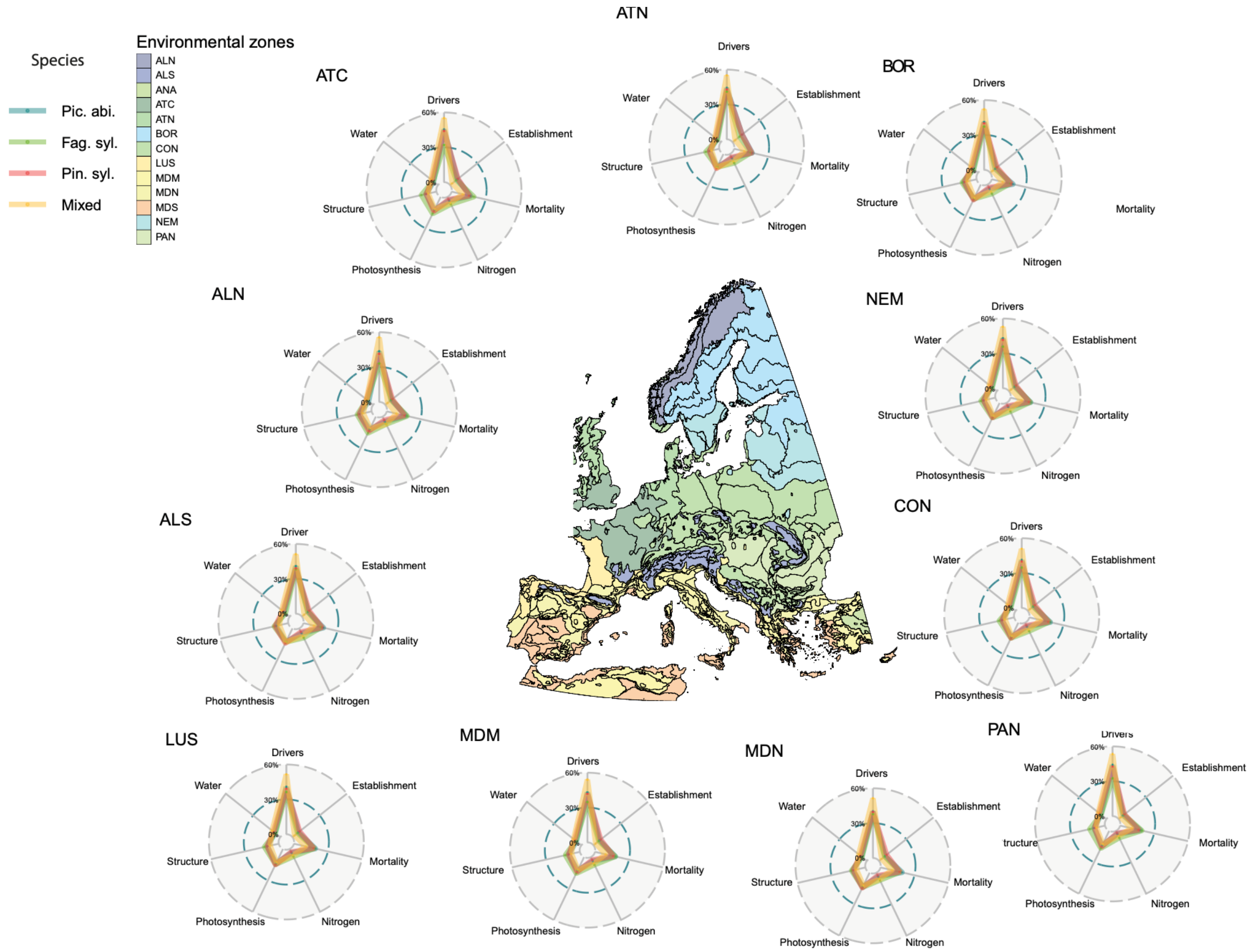

Fig. 3: The aggregated relative uncertainties of total standing biomass per environmental zone (with more than five sites) show a higher importance of drivers in the south than in the north. The environmental zones are from Metzger et al. (2005): ALN–Alpine North; ALS – Alpine South; ANA - Anatolian; 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.

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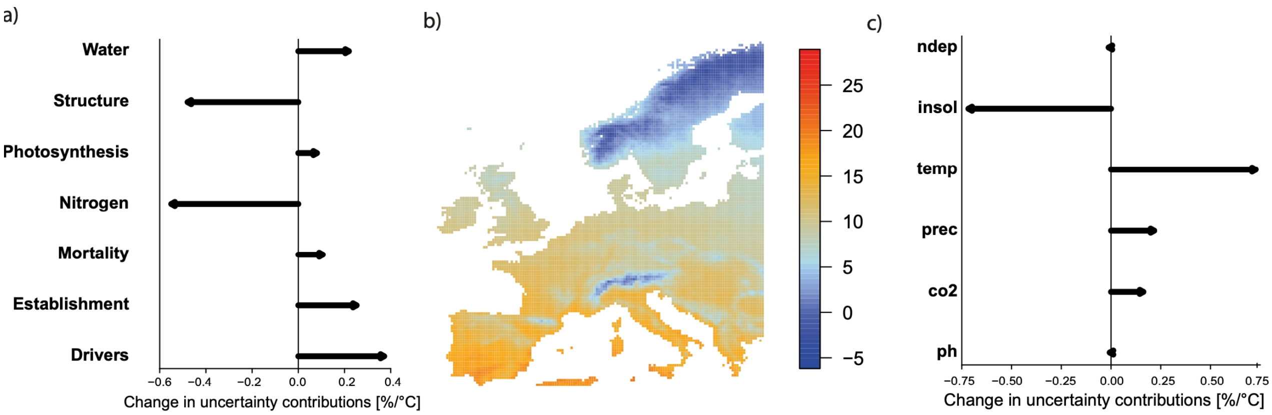

Fig. 4: The uncertainty contributions to total standing biomass projections of parameters and environmental drivers change across a mean annual temperature gradient across Europe from north to south. With increasing temperature, the importance of drivers and establishment became higher for total standing 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).

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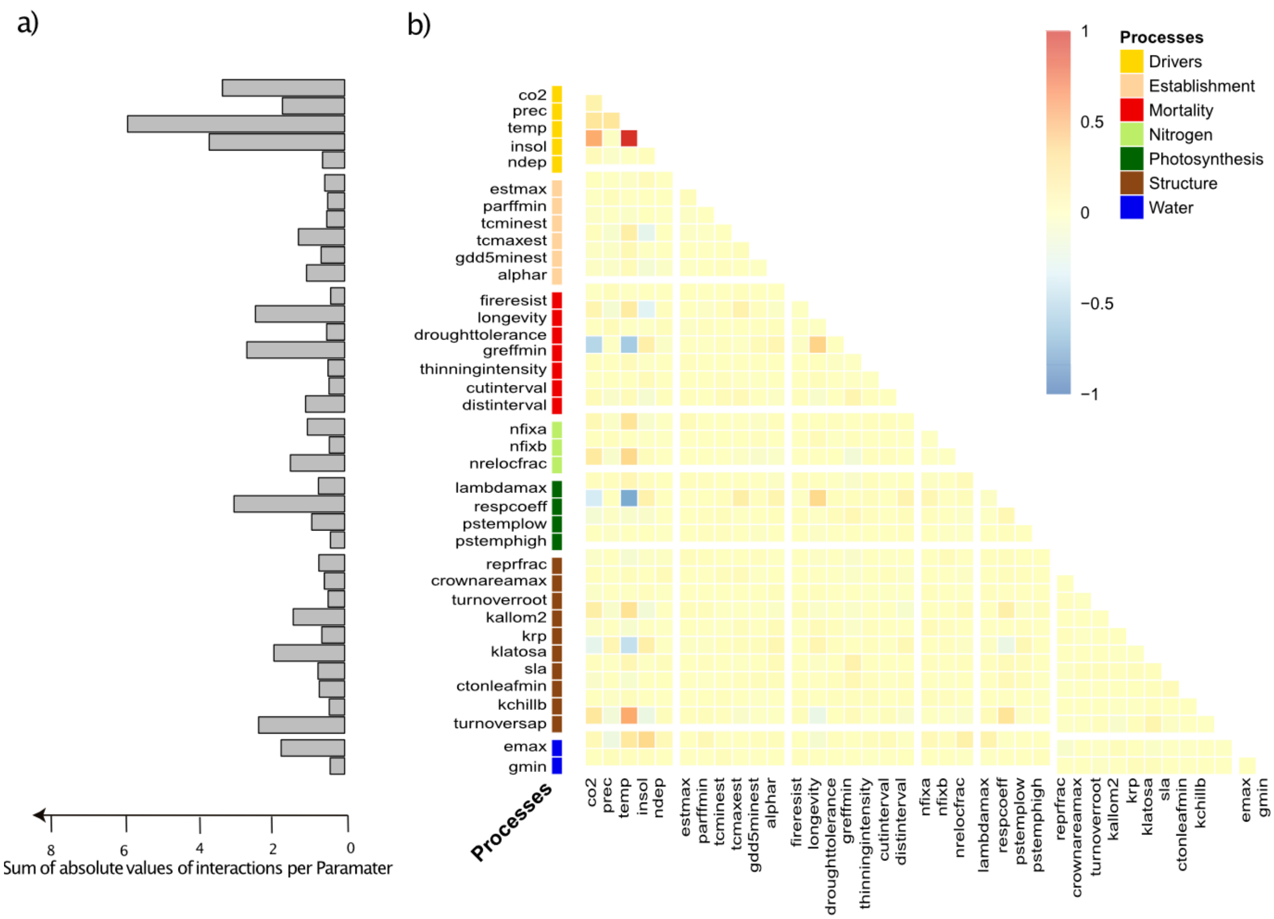

Fig. 5: The induced uncertainty of environmental drivers, mortality- and photosynthesis-related parameters changed the most depending on other parameters (Fig. 5a). Strong individual interactions between parameters and environmental drivers in monospecific projections of total standing biomass were rare (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).

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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

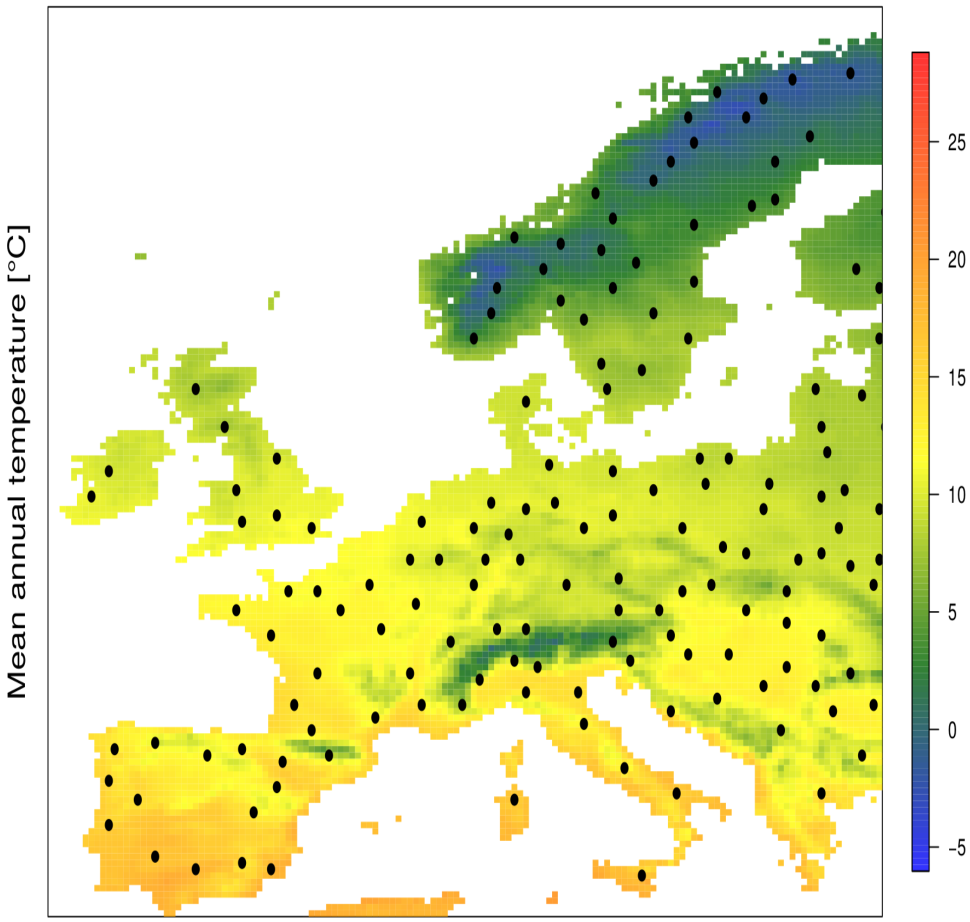

Fig. A1: Our 200 sampled sites geographically and environmentally stratified over Europe cover the most important countries, climate and temperature zones.

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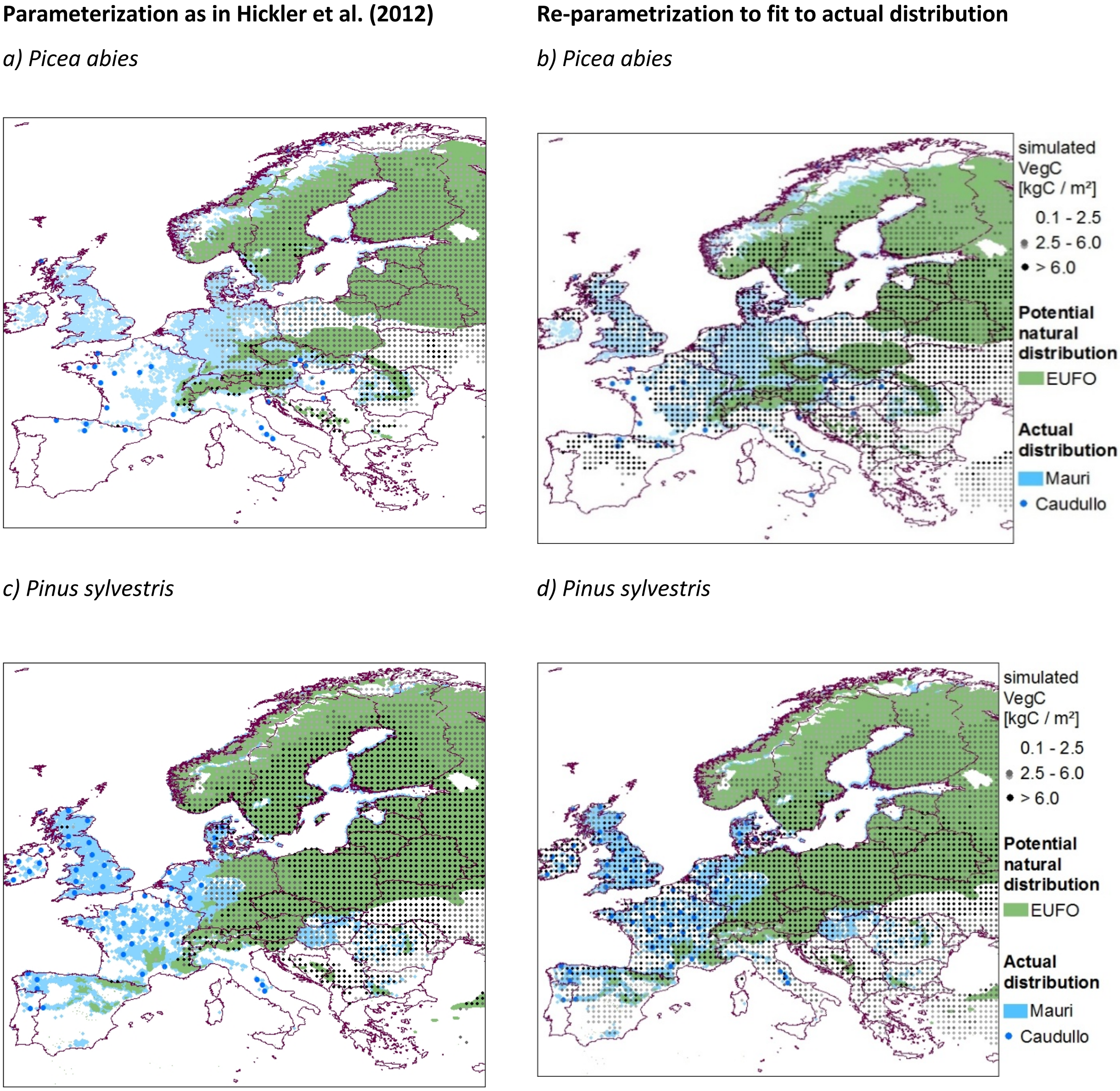

Fig. A2: Simulated (black points), observed (blue) and natural distributions (green) of the adjusted parametrization (b, d) compared to applying the parametrization from Hickler et al., 2012 (a, c) for Picea abies and Pinus sylvestris. EUFO = EUFROGEN, 2008 and 2013, Mauri =(Mauri et al., 2017), Caudullo =(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.

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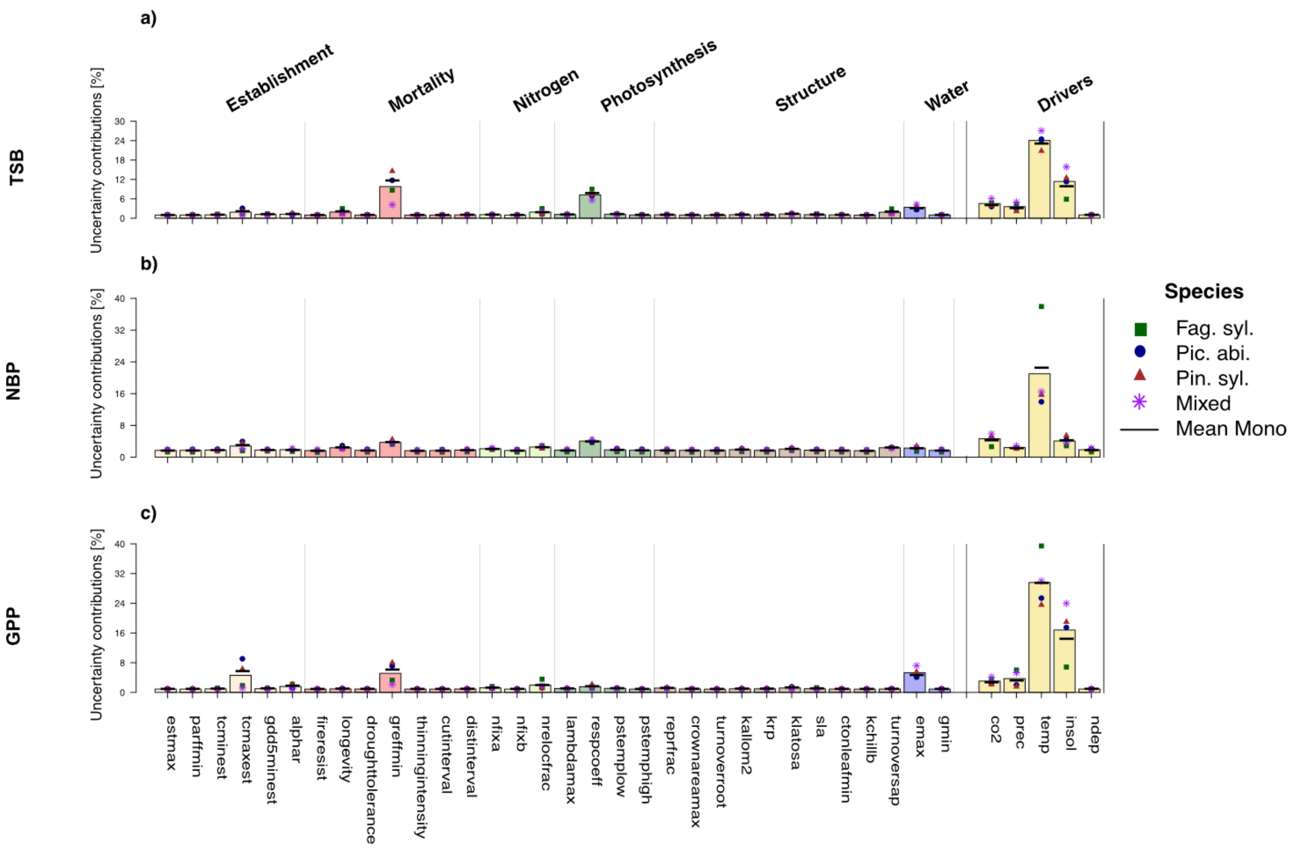

Fig. A3: Results of the random forest uncertainty contributions. The uncertainties due to environmental drivers are higher than the uncertainties due parameters compared to linear regression, but the ranking of parameters is similar to linear regression results.

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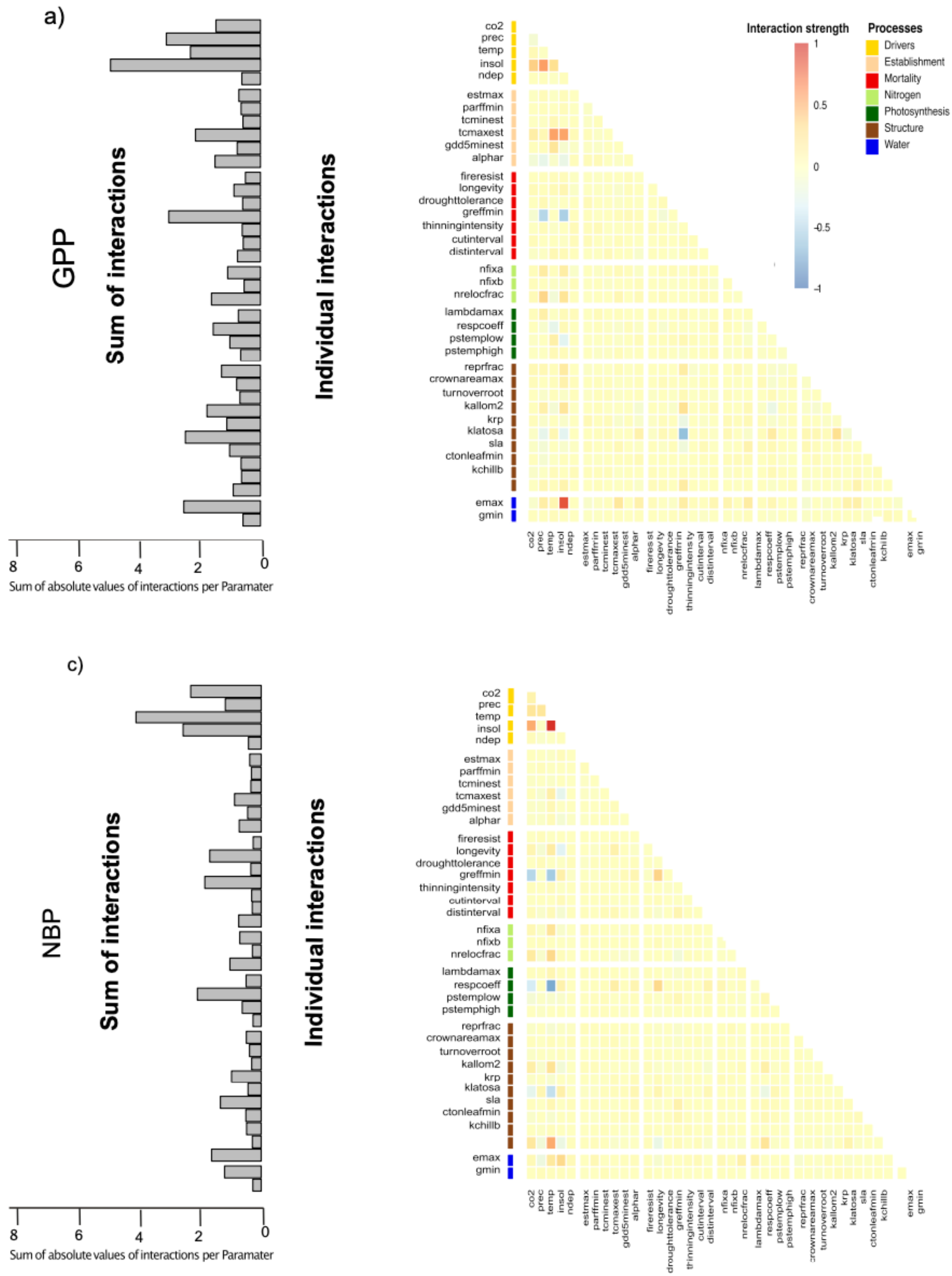

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Fig. A4: Interactions of uncertainty contributions of GPP and total standing biomass are similar to net biome productivity with most interactions arising from environmental drivers.