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Earth System Dynamics
Discussions

ESD Reviews: Evidence of multiple inconsistencies between representations of terrestrial and marine ecosystems in Earth System Models

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Abstract. Terrestrial and marine ecosystems interact with other Earth system components through different biosphere-climate feedbacks that are very similar among ecosystem types. Despite these similarities, terrestrial and marine systems are often treated relatively separately in Earth System Models (ESM). In these ESM, the ecosystems are represented by a set of biological processes that are able to influence the climate system by affecting the chemical and physical properties of the environment. While most of the climate-relevant processes are shared between ecosystem types, model representations of terrestrial and marine ecosystems often differ. This raises the question whether inconsistencies between terrestrial and marine ecosystem models exist and potentially skew our perception of the relative influence of each ecosystem on climate. Here we compared the terrestrial and marine modules of 17 Earth System Models in order to identify inconsistencies between the two ecosystem types. We sorted out the biological processes included in ESM regarding their influence on climate into three types of biosphere-climate feedbacks (i.e. the biogeochemical pumps, the biogeophysical mechanisms and the gas and particle shuttles), and critically compare their representation in the different ecosystem modules. Overall, we found multiple evidences of unjustified differences in process representations between terrestrial and marine ecosystem models within ESM. These inconsistencies may lead to wrong predictions about the role of biosphere in the climate system. We believe that the present comparison can be used by the Earth system modeling community to increase consistency between ecosystem models. We further call for the development of a common framework allowing the uniform representation of climate-relevant processes in ecosystem modules of ESM.

1 Introduction

Terrestrial and marine ecosystems have been mostly independently studied (Steele, 1991; Raffaelli et al., 2005; Menge et al., 2009). The separate development of terrestrial and marine ecosystem models led to important differences in their conceptual-

https://doi.org/10.5194/esd-2020-55
Preprint. Discussion started: 3 August 2020

ization and complexity. For instance, the vegetation models consider CO_2 as one of the main limiting factors for plant growth and therefore include a detailed representation of photosynthesis (reviewed in Rogers et al., 2017), while nutrient limitation is still ignored or simplistic in most of the models (Fisher et al., 2014). Conversely, the marine ecosystem models estimate growth of primary producers based on nutrient and light limitations, and ignore the processes behind carbon uptake (reviewed in Laufkotter et al., 2015). These differences can originate from intrinsic differences between terrestrial and marine habitats (e.g. physical environment gaseous vs liquid), but can also be unjustified (e.g. nutrient limitation, Elser et al., 2007). Since the development of Earth System Models (ESM) in which both terrestrial and marine models are combined, it is not clear whether inconsistencies (i.e. unjustified differences) between terrestrial and marine ecosystem models exist and potentially skew our perception of the relative influence of each ecosystem on climate regulations. For instance, the absence of nutrient limitation in terrestrial models may lead to qualitatively different responses of marine and terrestrial ecosystems to elevated CO_2, although the response may be similar in reality.

In ESM, marine and terrestrial ecosystems are mechanistically represented by different biological processes that can both respond to and influence climate. These climate-biosphere feedbacks involve biogeochemical and biogeophysical mechanisms (e.g. Hungate and Hampton, 2012; Hense et al., 2017; Bonan and Doney, 2018) that are, in many cases, similar for terrestrial and marine ecosystems. Terrestrial and marine ecosystems are both involved in biogeochemical cycles (e.g. carbon cycle, Heimann and Reichstein (2008); Bloom et al. (2016); Worden et al. (2015); nitrogen cycle, McNeill and Unkovich (2007); Gruber and Galloway (2008); Canfield et al. (2010); Zehr and Kudela (2011); phosphorous cycle, Filippelli (2002)) and biogeophysical feedbacks (e.g. albedo/light absorption, Dickinson and Hanson (1979); Frouin and Iacobellis (2002); Park et al. (2015); Alkama and Cescatti (2016); Zeng et al. (2017); momentum, Jöhnk et al. (2008); Sonntag and Hense (2011); Alkama and Cescatti (2016); Zeng et al. (2017); aerosol emissions, Andreae and Crutzen (1997); Meir et al. (2006)). However, the representation of these mechanisms differs between terrestrial and marine modules of Earth System Models (see Fisher et al. (2014) for a review of the terrestrial ecosystem models and Hense et al. (2017) for a review of the marine modules of ESM). Improving consistency in the representation of the biosphere-climate feedbacks between the two types of ecosystem in ESM is necessary to understand the central role that the biosphere plays in the earth system.

Although the biosphere in ESM is constituted by the combination of terrestrial and marine ecosystems, previous comparative studies were focusing on one or the other ecosystem model individually (e.g. Schwalm et al., 2010; Huntzinger et al., 2012; Cabré et al., 2015; Laufkotter et al., 2015; Fisher et al., 2014). To our knowledge, there is no study that critically evaluates whether marine and terrestrial models represent the processes occurring in both ecosystem types in a consistent way. Therefore, the present study aims to compare, for the first time, the terrestrial and marine modules of Earth System Models in order to identify inconsistencies between the two ecosystem types. Inconsistencies refer to unjustified differences in the representation of particular processes between ecosystem models. They cover: 1) the representation of a process in one model and its absence of representation in the second model, 2) different levels of complexity in the representation of a given process between models and 3) different modeling approaches used to represent the same process. Note that most of the inconsistencies identified in the present study correspond to the first category (i.e. presence of a process in one ecosystem model and not in the other).

The absence of important climate relevant processes in terrestrial (or marine) modules can offset the benefit of an accurate representation of the corresponding processes in marine (or terrestrial) ecosystem modules.

We review and critically compare the terrestrial and marine modules of 17 Earth System Models that have been applied to the CMIP5 and CMIP6 experiments (Table 1, Taylor et al., 2012; Eyring et al., 2016). These 17 ESM included 15 and 16 distinct terrestrial and marine ecosystem models, respectively (Table 1). The different climate-relevant processes included in these ESM were listed and sorted regarding their function and their influence on climate (Table 2).

2 The biosphere – climate feedbacks

We present here a detailed description of the main biosphere-climate feedbacks, thereby differentiating the biogeochemical and the biogeophysical influence of biosphere on climate. The term climate refers to multiple aspects of the climatic system, such as average temperature, humidity and seasonality. Here we focus mainly on the effect of biosphere on surface and atmospheric temperature. We provide a detailed comparison of how biosphere-climate feedbacks are represented in terrestrial and marine ecosystem modules of current ESM in the next section.

Hense et al. (2017) described the biogeochemical and biogeophysical influence of the biosphere on climate for marine ecosystems by three main mechanisms: the biogeochemical pumps, the biogeophysical mechanisms and the gas and particles shuttles. In the following we also apply these three mechanisms to terrestrial systems.

The biogeochemical pumps influence the cycles of multiple chemical elements, including carbon, through the biosphere. The growth of organisms depends on chemical elements and ions that are thus removed from the environment and stored in the organic matter before being released during exudation, excretion, respiration and remineralization of dead organic matter (Luo and Weng, 2011; Worden et al., 2015). The processes involved in the uptake, storage and release of these elements are thus important for the biogeochemical cycles and affect the climate by modifying the concentration of these elements in the environment, such as carbon in the atmosphere (Heimann and Reichstein, 2008; Monroe et al., 2018). Both terrestrial and marine ecosystems are involved in the biogeochemical pumps. For instance, terrestrial ecosystems were responsible for the net uptake of 3.2 giga tons of carbon (GtC) per year over the period 2009-2018 (Friedlingstein et al., 2019). In the same study they estimated that the ocean contributed to the uptake of 2,5 GtC per year, with approximately 90% of this uptake due to the biological pump (2.25 GtC per year) and the remaining by the solubility pump (Sarmiento and Gruber, 2006; Boyd et al., 2019). This corresponds to 29 and 20% of the human CO_2 emissions for terrestrial and marine ecosystems respectively. Besides carbon, terrestrial and marine ecosystems are also involved in the cycle of nitrogen (McNeill and Unkovich, 2007; Gruber and Galloway, 2008; Canfield et al., 2010; Zehr and Kudela, 2011), phosphorus (Filippelli, 2002), iron (Boyd and Ellwood, 2010; Hutchins and Boyd, 2016; Tagliabue et al., 2017; Wu et al., 2019), sulfur (Turner et al., 2016; Wasmund et al., 2017), silicon (Struyf et al., 2009) and oxygen (Walker, 1980). These elements can directly affect climate or be coupled to carbon via stoichiometric ratios and affect the climate indirectly (Elser et al., 2010; Meunier et al., 2017; Zhu et al., 2020). Terrestrial ecosystems play also a crucial role on the water cycle and marine ecosystems influence the carbonate cycle (Ridgwell and Zeebe, 2005).

https://doi.org/10.5194/esd-2020-55
Preprint. Discussion started: 3 August 2020

The biogeophysical mechanisms include the influence of the biosphere on its surrounding physical environment. Organisms modify the optical, mechanical and thermal properties of the environment, both on land and ocean. On land, vegetation influences surface albedo, roughness and evapotranspiration, and, as a consequence, wind speed, surface temperature and humidity (e.g. Hollinger et al., 2010; THOM, 1971; Fisher et al., 2014; Zeng et al., 2017). The different biogeophysical impacts of vegetation can influence climate in opposite directions. For instance, the recent increase in leaf area index (LAI) following the rise of atmospheric CO_2 led to a decrease in albedo, causing higher surface temperature (Betts, 2000). Conversely, the increase in LAI enhances transpiration which cools the surface via the latent heat flux (Shen et al., 2015). Altogether, the biogeophysical mechanisms have buffered climate change globally during the past 30 years (Zeng et al., 2017). In oceans, phytoplankton communities are also influencing surface albedo, temperature distribution, air-sea gas exchange, turbulent viscosity and vertical mixing (Frew et al., 1990; Sathyendranath et al., 1991; Sonntag and Hense, 2011; Katija and Dabiri, 2009). Indeed, due to surface distribution, phytoplankton, especially reflective species (e.g. coccolithophores) and positively buoyant species (e.g. filamentous cyanobacteria), influence surface albedo (Kahru et al., 1993; Tyrrell et al., 1999; Frouin and Iacobellis, 2002; Jung and Moon, 2019) and also trap the heat at the surface of the ocean, impacting sea surface temperature and ocean circulation globally (e.g. Paulsen et al., 2018).

Finally, the biosphere emits gas and particles into the atmosphere and thus influences the concentrations of green house gases and aerosols, impacting radiative forcing, cloud formation and light transmission through the atmosphere. Some processes involved in the gas and particle shuttle mechanisms are also influencing the biogeochemical pumps and the biogeophysical mechanisms. However, we distinguish this biosphere-climate feedback from the other to account for the direct influence of biosphere on atmospheric composition and properties. Marine and terrestrial ecosystems emit greenhouse gases, including CO_2, water vapor, methane and nitrous oxide, into the atmosphere (Meir et al., 2006; Rap et al., 2013; Stocker et al., 2013). Photosynthesis, autotrophic and heterotrophic respiration drive the exchanges of CO_2 between the atmosphere and biosphere (e.g. Heimann and Reichstein, 2008). On land, the exchange of water from plant to atmosphere is also essential for the water cycle and water vapor concentration in the atmosphere (e.g. Davin and de Noblet-Ducoudre, 2010). The emission of methane (CH_4) by the biosphere occur mainly in anoxic region of the soil, typically in wetland, during the decomposition of organic matter (see Dean et al., 2018, for a review of the different biologic methane sources and sinks), but also, to a lesser extent, in the ocean (Valentine, 2011). Finally, nitrous oxide (N_2O) is produced during nitrification and denitrification processes by bacteria in soil and ocean. N_2O is a greenhouse gas at least 200 times more potent than CO_2 (Gruber and Galloway, 2008; Myhre et al., 2014; Battaglia and Joos, 2018), and is also involved in the depletion of ozone (Myhre et al., 2014).

Besides greenhouse gases, significant quantities of aerosols are emitted by the biosphere. Aerosols affect climate as they influence cloud formation and properties, and also scatter the incoming beam solar radiation (Novakov and Penner, 1993; Andreae and Crutzen, 1997). The scattering of solar radiation could further affect climate by promoting plant growth which benefit from diffuse radiations (Rap et al., 2018). Biosphere-emitted aerosols, called biogenic volatile organic compounds (BVOC), include a variety of chemical substances as well as cells and organic fragments emitted by both kind of ecosystems Meir et al. (2006). One of the main BVOC produced by marine ecosystems is the dimethyl sulphide (DMS). DMS emission into the atmosphere may promote cloud formation, increasing albedo and cooling down the surface temperature (e.g. Charlson et al.

https://doi.org/10.5194/esd-2020-55
Preprint. Discussion started: 3 August 2020

(1987) but see Quinn and Bates (2011)). On land, the emission of BVOCs may lead to more complex climate responses. Indeed, some BVOC may promote ozone formation and thus increase greenhouse effect, while others may form cloud condensation nuclei and increase albedo (Peñuelas and Staudt, 2010).

The three mechanisms described above are able to affect climate in different directions by either buffering or accentuating changes in the climatic conditions. For instance, contemporary climate change affects biological processes which can reciprocally accelerate (i.e positive feedback) or dampen (i.e. negative feedback) climate change. A good example of a negative feedback mechanism is enhanced vegetation carbon uptake following the increase in atmospheric CO_2 concentration that may buffer human induced CO_2 emissions and thus surface temperature (Canadell and Raupach, 2008). On the other hand, the increase in temperature is expected to enhance soil bacterial metabolism and may therefore increase natural CO_2 and methane production by micro-organisms (Montzka et al., 2011; Dean et al., 2018), increasing further more atmospheric temperature (i.e. positive feedback). These two examples highlight the central role of the biosphere on climate regulation and the necessity to accurately represent biosphere-climate feedbacks on both land and ocean to predict future (and past) climate change.

2.1 Comparative review of terrestrial and marine ecosystem models in ESM

To compare terrestrial and marine ecosystem models, we listed all the climate-relevant processes that are involved in the biosphere-climate feedbacks described in the previous section. We focused on the processes that were present at least in one of the 15 terrestrial ecosystem models and 16 marine ecosystem models we reviewed. Based on this list, we compared how the different biosphere-climate feedbacks are considered in terrestrial and marine ecosystem modules of current ESM (Table 2).

Overall, inconsistencies exist among terrestrial and marine ecosystem models of ESM regarding the biogeochemical, the biogeophysical and, to a lesser extent, the gas and particle shuttle mechanisms (Table 2, Fig. 2). In the next paragraphs, we describe these inconsistencies among ecosystem modules in ESM by providing a detailed comparison of each process, as well as its potential influence on - and its response to - climate.

2.1.1 Biogeochemical processes

The biogeochemical pump, including the carbon cycle, is the mechanism represented with the most diverse processes in terrestrial and marine modules of Earth System Models. However, terrestrial and marine models show important differences (Table 2, Fig. 2), due to the way they were initially developed. Because terrestrial ecosystem models were initially based on the carbon cycle, the processes of photosynthesis, respiration, phenology, mortality and soil respiration (i.e. C remineralization in Table 2) are represented in the 15 terrestrial modules. The net primary production is calculated in each model from the balance of photosynthesis and respiration, each of these processes being represented by a set of physiological traits interacting with the environment (Fig. 1).

Besides carbon, the representation of other important elements such as nitrogen, phosphorus and iron in terrestrial ecosystem models is rather sparse compared to marine models, while the different ecosystem types are similar in terms of N and P limitation (Elser et al., 2007). Nitrogen is an essential element of protein, including the photosynthetic enzymes such as Rubisco, the enzyme that fixes carbon from the atmosphere into carbohydrates. Phosphorus is also important for plant physiology as it is part of the composition of nucleid acid, lipid and bioenergetic molecules such as ATP (Wright et al., 2004). For that reason, the terrestrial modules used for the CMIP6 experiments include nitrogen limited carboxylation capacity of the plants. The last generation of land surface models incorporate a representation of the phosphorous cycle as well (Fisher and Koven, 2020). However, these land surface models are not integrated in ESM and the representation of the phosphorus cycle is still needed in most of the terrestrial ecosystem models within ESM.

In contrast, the development of marine ecosystem models was initially based on the cycles of limiting nutrients for phytoplankton growth. In the simplest models, only one element was explicitly modeled and the concentrations of others such as carbon were calculated using a fixed ratio (i.e. the Redfield ratio, Redfield, 1934). However, the ratios of the main nutrients and elements (N, C, P, Si, Fe) vary among phytoplankton groups and with the environmental conditions (Rhee.G.Yull, 1978; Goldman et al., 1979; Geider and La Roche, 2002; Quigg et al., 2003). Therefore, the use of a fixed ratio among elements constrains the predictions within a narrow range of potential ecosystem responses that may not represent the current states of marine ecosystems. Some recent marine ecosystem models (e.g. BFMv5.2, Vichi et al., 2015) thus included variable ratios that are influenced by the environmental conditions (i.e. the availability of the different elements in the environment). Nevertheless, the explicit carbon cycle representation is still lacking in most of the models and the processes of photosynthesis and cell respiration are ignored (Table 2, Fig. 1).

Another difference between terrestrial and marine models in Earth System Models is the representation of trophic interactions (Table 2, Fig. 2). In terrestrial models, only plants and soil microorganisms are represented while higher trophic levels are ignored. Although it has been traditionally assumed that trophic interactions had a limited effect on large scale climate, recent studies underline the potential strong influence of grazers and higher trophic levels on ecosystem carbon uptake and storage (e.g. Schmitz et al., 2018). For instance, the disturbance induced by elephants enhance aboveground biomass, and thus carbon storage, in African tropical forest (Berzaghi et al., 2019). Grazers may also influence climate by changing the biogeophysical properties of the ecosystem. For instance, larger animals grazing on boreal ecosystem limit shrub height and density, cooling down air temperature by increasing summer albedo (Te Beest et al., 2016), or protect the permafrost from thawing (Beer et al., 2020).

Most of the marine models reviewed here considered zooplankton, heterotrophic organisms that feed on primary producers. Zooplankton has been implemented in marine ecosystem models because they exert a strong grazing pressure on phytoplankton, impeding or buffering phytoplankton bloom formation (Prowe et al., 2012). Zooplankton and higher trophic levels in general, play also an important role in carbon removal (Davison et al., 2013; Steinberg and Landry, 2017), nutrient distribution and recycling (Vanni, 2002; Schmitz et al., 2010). However, the representation of the trophic chains in marine models remains very simple. Complex trophic interactions can strongly influence carbon storage by marine ecosystems. For instance, Wilmers et al. (2012) showed that the presence of sea otters increases the carbon fixation by kelp by a factor of 10 due to their predation pressure on kelp grazers. A better understanding of the importance of trophic complexity and length on carbon cycle and on climate is needed to properly judge the necessity to include them in Earth System Models.

There are also several justified differences between terrestrial and marine ecosystem which are represented in ESM (Table 2). Terrestrial and marine ecosystem models differ in the representation of processes involved in the water cycle and silicate cycle.

https://doi.org/10.5194/esd-2020-55
Preprint. Discussion started: 3 August 2020

The role of the biosphere on the carbon cycle is central and has been considered in terrestrial and marine models of ESM. Both ecosystem models are based on the growth of photosynthetic primary producers (i.e. net primary production, NPP). However, important differences exist in the representation of growth and its implication for the carbon cycle among ecosystem types.

In terrestrial ecosystem models, NPP corresponds to the difference between the carbon fixed by photosynthesis and the carbon released by respiration. Photosynthesis has been modeled using three different approaches in terrestrial ecosystem models (Arora, 2002; Fisher et al., 2014): the biochemical approach, the light use efficiency approach and the carbon assimilation approach. Most of the modules reviewed here followed the biochemical approach to represent photosynthesis (a). In this approach, the rate of CO_2 assimilation is limited by i) the rate of carboxylation by Rubisco, ii) electron transport which depends on light and iii) the transport of photosynthetic products (Farquhar et al., 1980; Collatz et al., 1992). Note that the transport of photosynthetic products is sometimes ignored in the present modules (a). In the biochemical approach, the assimilation of carbon by photosynthesis is closely linked to stomatal conductance that control intercellular CO_2 concentration and water exchange with the atmosphere. A part of the carbon fixed by photosynthesis is re-emitted to the atmosphere through respiration. In all the models, respiration is divided into maintenance respiration and growth respiration. The growth respiration is a fixed proportion of the NPP, while the maintenance respiration, considered at the organ level (i.e. leaf, stem, root), can depend on temperature, nitrogen content and the rate of carboxylation (a).

In marine models (b), the growth of primary producers ignore the processes of photosynthesis and respiration. NPP depends on light, nutrients and temperature (b). Most of the modules do not explicitly consider carbon, and thus deduce carbon assimilation by applying a stochiometric ratio. For that reason, respiration cannot be properly estimated because the ratio of elements in phytoplankton is considered constant. Only one model that explicitly represents the carbon cycle accounts for respiration by phytoplankton (BFMv5.2).

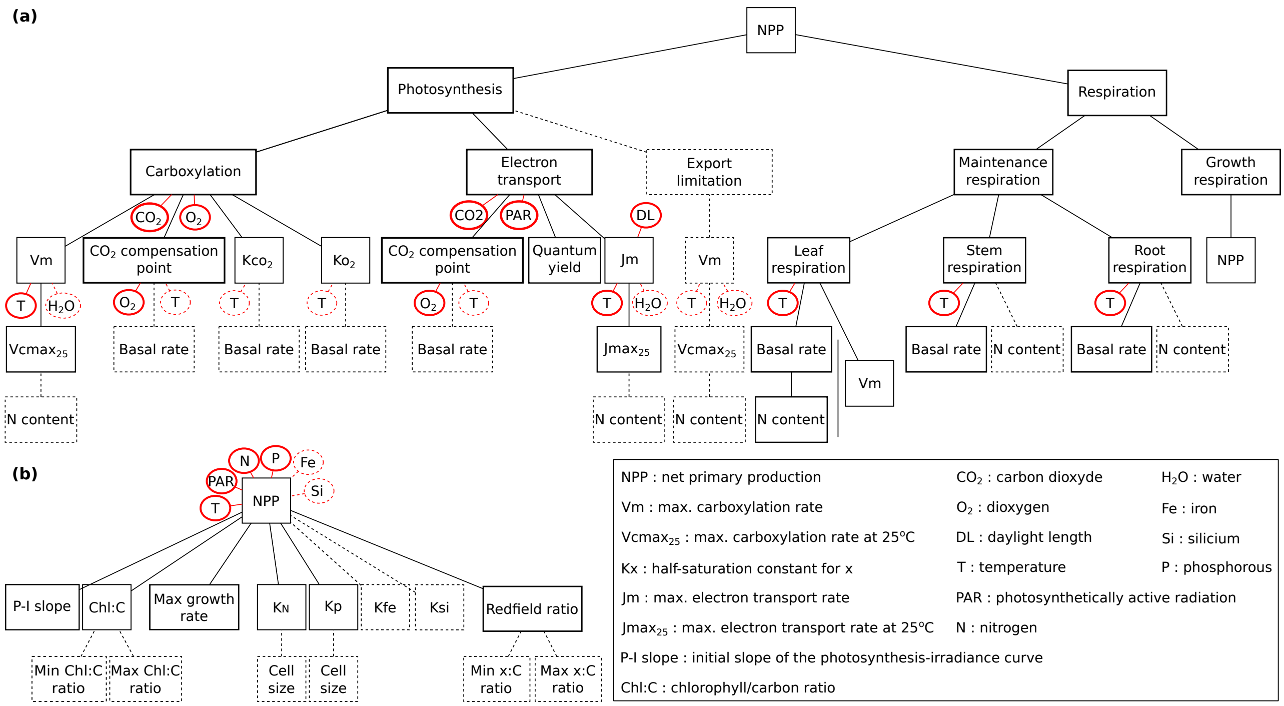


Figure 1. Box 1: Differences in the representation of primary producers' carbon growth between terrestrial and marine ecosystem modules of ESM. The text present the main approaches used to model carbon assimilation in terrestrial and marine ecosystem modules. The diagrams detail the different biological traits and processes (boxes) considered in the calculation of primary producers' growth in most of the terrestrial (a) and marine (b) ecosystem modules of ESM. From the bottom to the top, the black lines indicate the influence of different traits on the trait/process above. The influence of the environmental conditions are indicated in red. The traits and environmental factors considered in only few modules are represented by dotted lines and boxes.

https://doi.org/10.5194/esd-2020-55
Preprint. Discussion started: 3 August 2020

These differences rely on biological singularity of terrestrial and marine ecosystems. Water is an essential and limiting element for terrestrial plant growth and is tightly linked to carbon uptake. Similarly, silicon is an important constituent of the shell of an abundant phytoplankton group (i.e. the diatoms). Diatoms are often considered in marine ecosystem models because their silicate shell influence particle sinking from the surface to the deep ocean, and thus influence carbon storage in the ocean. For these reasons, these differences among ecosystem models are not part of the inconsistencies we identified in the previous paragraphs.

2.1.2 Biogeophysical processes

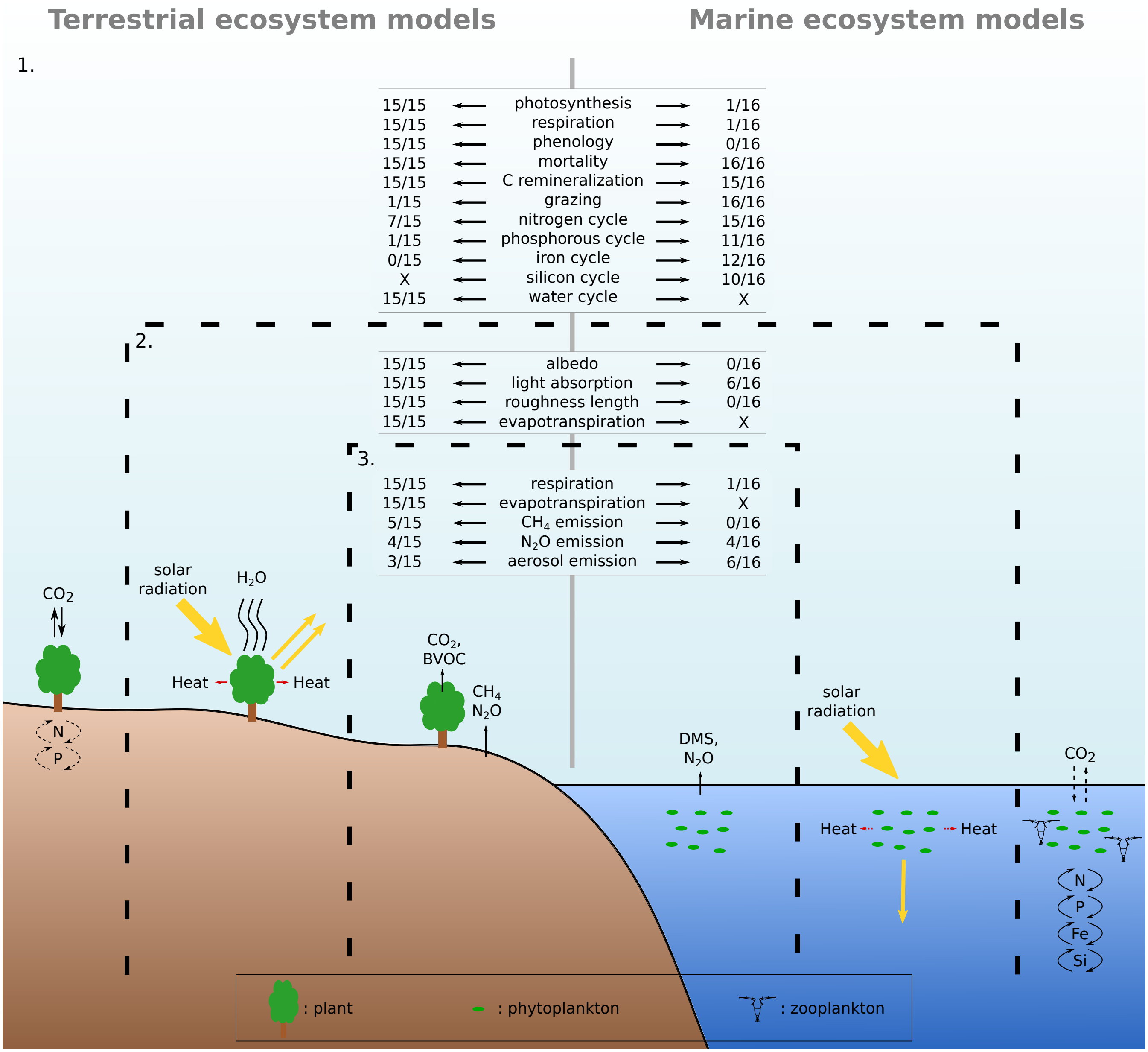
The biogeophysical influence of the biosphere is unequally considered in terrestrial and marine models of Earth system models (Table 2, Fig. 2). In terrestrial modules, there is a good representation of vegetation albedo, light absorption, evapotranspiration and roughness length. For instance, the calculation of vegetation albedo often considered multiple leaf traits such as absorbance, transmittance, surface and orientation (e.g. Kowalczyk et al., 2013). Global changes, including deforestation, could have a strong impact on the biogeophysical characteristics of land ecosystems (Davin and de Noblet-Ducoudre, 2010). The effect of the biogeophysical changes associated with deforestation may counteract the effects of biogeochemical changes (i.e. lower CO_2 fixation by vegetation), at least in certain regions (mostly at high latitude) (Claussen et al., 2001).

In contrast to terrestrial models, the representation of the biogeophysical mechanisms in marine modules of ESM is scarce (Table 2, Fig. 2). Only the light absorption by phytoplankton is considered in 6 of the 16 modules reviewed here, modifying the heat distribution in the water column. All other biophysical mechanisms are ignored. Models including light absorption by phytoplankton obtained contrasted results. They simulated either an average cooling of the surface ocean (Mignot et al., 2013; Paulsen et al., 2018) due to the increase of intra-annual surface temperature variation with light absorption, while others predicted an increase of sea surface temperature when biologically induced heating is considered (Lengaigne et al., 2009; Patara et al., 2012). This feedback mechanism may become more important in the future (Hense et al., 2013), because higher temperature could increase surface buoyant phytoplankton (cyanobacteria) abundance and thus enhance light absorption. For instance, climate change in the Arctic might be amplified by 20% due to higher light absorption that results from an increase in plankton density caused by warmer water (Park et al., 2015). Further ESM including light absorption by plankton are therefore needed to reduce prediction uncertainties and better predict climate change. The influence of other biogeophysical mechanisms in the ocean (i.e. surface albedo, air-sea gas exchange, turbulent viscosity and vertical mixing) are more difficult to evaluate because they are less studied and will thus not be discussed further.

2.1.3 Gas and particles emission processes

Terrestrial and marine ecosystem models are rather similar in their representation of gas and particle shuttles. Both ecosystem modules only sparsely consider the role of the biosphere on greenhouse gas and aerosol atmospheric concentration, except CO_2 and water vapor in terrestrial ecosystem models (Table 2, Fig. 2).

The ecosystem models mainly differ with regard to CO_2 emissions. While CO_2 emission back to the atmosphere through plant and soil respiration is well considered in terrestrial ecosystem models, the influence of marine biota on dissolved and



Terrestrial ecosystem models	1.	Marine ecosystem models
15/15	photosynthesis	1/16
15/15	respiration	1/16
15/15	phenology	0/16
15/15	mortality	16/16
15/15	C remineralization	15/16
1/15	grazing	16/16
7/15	nitrogen cycle	15/16
1/15	phosphorous cycle	11/16
0/15	iron cycle	12/16
X	silicon cycle	10/16
15/15	water cycle	X

Terrestrial ecosystem models	2.	Marine ecosystem models
15/15	albedo	0/16
15/15	light absorption	6/16
15/15	roughness length	0/16
15/15	evapotranspiration	X

Terrestrial ecosystem models	3.	Marine ecosystem models
15/15	respiration	1/16
15/15	evapotranspiration	X
5/15	CH_4 emission	0/16
4/15	N_2O emission	4/16
3/15	aerosol emission	6/16

Figure 2. General scheme summarizing the representation of the different biosphere-climate feedbacks in terrestrial and marine ecosystem modules of current ESM. The different processes are sorted into the biogeochemical pumps (1), the biogeophysical mechanisms (2) and the gas and particle shuttles (3). The ratio of the number of modules in which each process is present on the total number of reviewed module (15 terrestrial distinct terrestrial ecosystem modules and 16 distinct marine ecosystem modules) is indicated for each ecosystem model type.

atmospheric CO_2 is poorly represented (Table 2, Fig. 2). The great majority of the models do not explicitly consider the processes of photosynthesis and respiration (Fig. 1). We now know that the reaction norm of photosynthesis and respiration to temperature are different and that organisms adapt and both rates change with higher temperature (Padfield et al., 2016; Schaum et al., 2017; Barton et al., 2020). The resulting net exchange of carbon between atmosphere and marine biota is thus sensitive to temperature. By ignoring photosynthesis and respiration processes, marine models may fail to properly predict the influence of phytoplankton on the carbon cycle, and thus on atmospheric CO_2 concentration under changing climatic conditions.

CH_4 emissions are considered only in 5 of the 15 terrestrial modules and in none of the marine modules (Table 2, Fig. 2). Knowing that the large majority of CH_4 is produced by terrestrial ecosystems (Dean2018) and that soil production is predicted to increase under future conditions (Montzka et al., 2011; Dean et al., 2018), CH_4 emissions in terrestrial modules of ESM are still underrepresented. Ocean methane production is assumed to be small compared to terrestrial ones (Valentine, 2011), thus the absence of methane emission in marine ecosystem models of current ESM may be justified. Nevertheless, the CH_4 emission by coastal ecosystems might also grow under future climatic conditions (Al-Haj and Fulweiler, 2020) and further evaluation of their role in global CH_4 emissions will be needed to judge the necessity to include them in ESM.

N_2O production is represented in a quarter of the terrestrial and marine modules of current ESM (Table 2, Fig. 2). While the estimations of N_2O emissions are still rather uncertain (from 3,3 to 9 Tg N y^{-1} for terrestrial ecosystems and from 1,8 to 9,45 Tg N y^{-1} for marine ecosystems, Ciais et al., 2014), it has been shown that N_2O plays an important role in the past and ongoing climate change (Schilt et al., 2010; Stocker et al., 2013). Furthermore, climate change is affecting biologically mediated N_2O emissions (Stocker et al., 2013; Martinez-Rey et al., 2014) and also the overall impact of N_2O on climate. Increasing temperature may enhance the transport of N_2O from its source location (Earth surface) to its sink location (stratosphere), reducing both the lifetime of N_2O and its global warming potential (Kracher et al., 2016). ESM represent the adequate tools to study such complex feedbacks between biosphere, atmosphere and climate. However, it necessitates a good representation of the processes behind N_2O emissions that is currently missing in many current ESM (in both terrestrial and marine modules and despite their consistency regarding this particular process).

The emission of aerosols is represented in the form of biogenic volatile organic compound (BVOC, 3/15 modules) in terrestrial ecosystems and dimethyl sulphide (DMS, 6/16 modules) in marine ones (Table 2, Fig. 2). The fact that there is consistent evidence that DMS decreases atmospheric temperature (e.g. Charlson et al. (1987); McCoy et al. (2015) but see Quinn and Bates (2011)) may explain the slightly higher number of marine modules representing volatile production than terrestrial ones in ESM. Future changes of DMS-fluxes may be stronger under ocean acidification as suggested by Six et al. (2013) and Schwinger et al. (2017). However, only one marine ecosystem module considered the pH dependency of DMS production so far (PISCESv2-gas module of CNRM-ESM2.1, Séférian et al., 2019).

Similarly, BVOC production is sparsely presented in terrestrial modules of ESM (Table 2, Fig. 2). Current knowledge indicates that the influence of terrestrial aerosols on climate is highly variable and depends on the type of emitted substances (see Peñuelas and Staudt, 2010). Nevertheless, a recent study estimated that aerosol-climate feedbacks could be strong enough to moderate the CO_2-related atmospheric temperature increase (Scott et al., 2018). Further studies are needed to identify the most important aerosols emitted by terrestrial ecosystems in order to facilitate their integration in ESM. The future inclusion of BVOC emission in ESM may be further considered knowing that the production of BVOC by vegetation is predicted to increase under climate change (Laothawornkitkul et al., 2009; Peñuelas and Staudt, 2010; Zhao et al., 2017).

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3 Discussion and Conclusions

The present review highlights important inconsistencies in the representation of the main biosphere-climate feedbacks between terrestrial and marine ecosystem models within ESM. The main processes related to the carbon cycle (i.e. photosynthesis and respiration) are still implicitly represented in marine models, while nutrient limitation of growth is only scarcely considered in terrestrial ones. Major differences also occur in the representation of biophysical mechanisms. Light absorption only is partially considered in marine ecosystem models while terrestrial ecosystem models represent adequately the influence of vegetation on land surface biogeophysics (i.e. albedo, roughness length, evapotranspiration and light absorption). Conversely, emission of non-CO_2 gases and particles by the biosphere into the atmosphere is consistently represented, even if scarcely, in terrestrial and marine modules of ESM.

Inconsistencies in ecosystem representation can lead to wrong predictions about the role of the biosphere in the climate system. The relative importance of terrestrial and marine ecosystems on climate regulation might be inaccurately perceived because predictions result from different models representing various processes with different complexity levels. As an example, terrestrial ecosystems models currently include a wider range of biosphere-climate feedbacks than marine models (Fig. 2), leading to the potential overweighting of the influence of terrestrial ecosystem on climate compared to marine ones. Future predictions could be further biased by the lack of mechanistic representation of particular processes in one or the other ecosystem model. While human activities are predicted to bring atmospheric green-house gas concentration above 750ppm CO_2 equivalent and temperature above +4°C in the worst-case scenario (RCP8.5, IPCC, 2014), the response of biosphere to these changes and the subsequent feedbacks on climate can be underestimated in marine models due to the lack of explicit representation of photosynthesis and respiration (Fig. 1). Conversely, the predicted increase of CO_2 uptake by terrestrial ecosystem following the increase in atmospheric CO_2 and temperature might be overestimated due to the lack of representation of nutrient limitation on plant growth (Zaehle et al., 2015; Wieder et al., 2015; Terrer et al., 2019).

Nevertheless, there is the potential to reduce inconsistencies in the representation of terrestrial and marine ecosystems in ESM in the near future. We believe that more collaboration among terrestrial and marine scientific communities can strongly improve the representation of the biosphere in ESM. By identifying the major inconsistencies that currently exist among ecosystem modules in ESM, the present work provides a solid basis toward future consistency in biosphere representation. Modelers could further benefit from the development of a common framework allowing to i) identify the important processes involved in the different biosphere-climate feedbacks and ii) standardize their inclusion in both terrestrial and marine ecosystem models of ESM. Such general framework is still missing and thus urgently needed. Finally, the development of combined databases joining both terrestrial and marine organisms could help to remove current inconsistencies in the representation of these organisms in ESM. The reliability of model predictions depends on the use of accurate parameter values for the different mathematical equations used to represent diverse biological processes. Estimation of parameters at a global scale rely on the development of worldwide large data bases (e.g. the TRY data base for plants, Kattge et al., 2011) which are currently scarce especially for marine ecosystems.

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Altogether, we argue that increasing consistency between ecosystem modules of ESM enables to extend their ability to predict future climate. While human activities strongly impact the biosphere, improving our understanding and representation of the biosphere-climate feedbacks in both terrestrial and marine ecosystem models is crucial to make reliable predictions and build efficient management policies.

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Competing interests. The authors declare that they have no conflict of interest.

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References

Al-Haj, A. N. and Fulweiler, R. W.: A synthesis of methane emissions from shallow vegetated coastal ecosystems, Global Change Biology, 26, 1–18, https://doi.org/10.1111/gcb.15046, 2020.

Alkama, R. and Cescatti, A.: Climate change: Biophysical climate impacts of recent changes in global forest cover, Science, 351, 600–604, https://doi.org/10.1126/science.aac8083, 2016.

Andreae, M. O. and Crutzen, P. J.: Atmospheric aerosols: Biogeochemical sources and role in atmospheric chemistry, Science, 276, 1052–1058, https://doi.org/10.1126/science.276.5315.1052, 1997.

Arora, V. K.: Modeling vegetation as a dynamic component in soil-vegetation-atmosphere transfer schemes and hydrological models, Reviews of Geophysics, 40, 3–1–3–26, https://doi.org/10.1029/2001RG000103, 2002.

Aumont, O., Ethé, C., Tagliabue, A., Bopp, L., and Gehlen, M.: PISCES-v2: An ocean biogeochemical model for carbon and ecosystem studies, Geoscientific Model Development, 8, 2465–2513, https://doi.org/10.5194/gmd-8-2465-2015, 2015.

Barton, S., Jenkins, J., Buckling, A., Schaum, C. E., Smirnoff, N., Raven, J. A., and Yvon-Durocher, G.: Evolutionary temperature compensation of carbon fixation in marine phytoplankton, Ecology Letters, 23, 722–733, https://doi.org/10.1111/ele.13469, 2020.

Battaglia, G. and Joos, F.: Marine N2O emissions from nitrification and denitrification constrained by modern observations and projected in multimillennial global warming simulations, Global Biogeochemical Cycles, 32, 92–121, https://doi.org/10.1002/2017GB005671, 2018.

Beer, C., Zimov, N., Olofsson, J., Porada, P., and Zimov, S.: Protection of permafrost soils from thawing by increasing herbivore density, Scientific reports, 10, 1–10, https://doi.org/10.1038/s41598-020-60938-y, 2020.

Bentsen, M., Bethke, I., Debernard, J. B., Iversen, T., Kirkevåg, A., Seland, Ø., Drange, H., Roelandt, C., Seierstad, I. A., Hoose, C., and Kristjánsson, J. E.: The Norwegian Earth System Model, NorESM1-M – Part 1: Description and basic evaluation, Geoscientific Model Development Discussions, 5, 2843–2931, https://doi.org/10.5194/gmdd-5-2843-2012, 2012.

Berzaghi, F., Wright, I. J., Kramer, K., Oddou-Muratorio, S., Bohn, F. J., Reyer, C. P., Sabaté, S., Sanders, T. G., and Hartig, F.: Towards a new generation of trait-flexible vegetation models, Trends in Ecology and Evolution, 35, 191–205, https://doi.org/10.1016/j.tree.2019.11.006, 2019.

Betts, R. A.: Offset of the potential carbon sink from boreal forestation by decreases in surface albedo, Nature, 408, 187–190, https://doi.org/10.1038/35041545, 2000.

Bloom, A. A., Exbrayat, J. F., Van Der Velde, I. R., Feng, L., and Williams, M.: The decadal state of the terrestrial carbon cycle: Global retrievals of terrestrial carbon allocation, pools, and residence times, Proceedings of the National Academy of Sciences of the United States of America, 113, 1285–1290, https://doi.org/10.1073/pnas.1515160113, 2016.

Bonan, G. B. and Doney, S. C.: Climate, ecosystems, and planetary futures: The challenge to predict life in Earth system models, Science, 359, https://doi.org/10.1126/science.aam8328, 2018.

Boyd, P. W. and Ellwood, M. J.: The biogeochemical cycle of iron in the ocean, Nature Geoscience, 3, 675–682, https://doi.org/10.1038/ngeo964, http://dx.doi.org/10.1038/ngeo964, 2010.

Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A., and Weber, T.: Multi-faceted particle pumps drive carbon sequestration in the ocean, Nature, 568, 327–335, https://doi.org/10.1038/s41586-019-1098-2, 2019.

Cabré, A., Marinov, I., and Leung, S.: Consistent global responses of marine ecosystems to future climate change across the IPCC AR5 earth system models, Climate Dynamics, 45, 1253–1280, https://doi.org/10.1007/s00382-014-2374-3, 2015.

Canadell, J. G. and Raupach, M. R.: Managing forests for climate change mitigation, Science, 320, 1456–1457, https://doi.org/10.1126/science.1155458, 2008.

Canfield, D. E., Glazer, A. N., and Falkowski, P. G.: The evolution and future of earth's nitrogen cycle, Science, 330, 192–196, https://doi.org/10.1126/science.1186120, 2010.

Charlson, R. J., Lovelock, J. E., Andreae, M. O., and Warren, S. G.: Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate, Nature, 326, 655–661, https://doi.org/10.1038/326655a0, 1987.

Cherchi, A., Fogli, P. G., Lovato, T., Peano, D., Iovino, D., Gualdi, S., Masina, S., Scoccimarro, E., Materia, S., Bellucci, A., and Navarra, A.: Global mean climate and main patterns of variability in the CMCC-CM2 coupled model, Journal of Advances in Modeling Earth Systems, 11, 185–209, https://doi.org/10.1029/2018MS001369, 2019.

Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., and Heimann, M.: Carbon and other biogeochemical cycles, in: Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, pp. 465–570, Cambridge University Press, 2014.

Clark, D. B., Mercado, L. M., Sitch, S., Jones, C. D., Gedney, N., Best, M. J., Pryor, M., Rooney, G. G., Essery, R. L. H., Blyth, E., Boucher, O., Harding, R. J., and Cox, P. M.: The Joint UK Land Environment Simulator (JULES), Model description – Part 2: Carbon fluxes and vegetation, Geoscientific Model Development Discussions, 4, 641–688, https://doi.org/10.5194/gmdd-4-641-2011, 2011.

Claussen, M., Brovkin, V., and Ganopolski, A.: Biophysical versus biogeochemical feedbacks of large-scale land cover change, Geophysical Research Letters, 28, 1011–1014, https://doi.org/10.1029/2000GL012471, 2001.

Collatz, G. J., Ribas-Carbo, M., and Berry, J. A.: Coupled photosynthesis-stomatal conductance model for leaves of C4 plants, Functional Plant Biology, 19, 519–538, https://doi.org/10.1071/PP9920519, 1992.

Collins, W. J., Bellouin, N., Doutriaux-Boucher, M., Gedney, N., Halloran, P., Hinton, T., Hughes, J., Jones, C. D., Joshi, M., Liddicoat, S., Martin, G., O'Connor, F., Rae, J., Senior, C., Sitch, S., Totterdell, I., Wiltshire, A., and Woodward, S.: Development and evaluation of an Earth-System model - HadGEM2, Geoscientific Model Development, 4, 1051–1075, https://doi.org/10.5194/gmd-4-1051-2011, 2011.

Cox, P. M.: Description of the "TRIFFID" dynamic global vegetation model, Hadley Centre. Technical Note 24, p. 17, 2001.

Danabasoglu, G., Lamarque, J., Bacmeister, J., Bailey, D., DuVivier, A., Edwards, J., Emmons, L., Fasullo, J., Garcia, R., Gettelman, A., Hannay, C., Holland, M., Large, W., Lauritzen, P., Lawrence, D., Lenaerts, J., Lindsay, K., Lipscomb, W., Mills, M., Neale, R., Oleson, K., Otto-Bliesner, B., Phillips, A., Sacks, W., Tilmes, S., Kampenhout, L., Vertenstein, M., Bertini, A., Dennis, J., Deser, C., Fischer, C., Fox-Kemper, B., Kay, J., Kinnison, D., Kushner, P., Larson, V., Long, M., Mickelson, S., Moore, J., Nienhouse, E., Polvani, L., Rasch, P., and Strand, W.: The Community Earth System Model version 2 (CESM2), Journal of Advances in Modeling Earth Systems, 2, 1–35, https://doi.org/10.1029/2019ms001916, 2020.

Davin, E. L. and de Noblet-Ducoudre, N.: Climatic impact of global-scale deforestation: Radiative versus nonradiative processes, Journal of Climate, 23, 97–112, https://doi.org/10.1175/2009JCLI3102.1, 2010.

Davison, P. C., Checkley Jr, D. M., Koslow, J. A., and Barlow, J.: Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean, Progress in Oceanography, 116, 14–30, https://doi.org/10.1016/j.pocean.2013.05.013, 2013.

Dean, J. F., Middelburg, J. J., Röckmann, T., Aerts, R., Blauw, L. G., Egger, M., Jetten, M. S., de Jong, A. E., Meisel, O. H., Rasigraf, O., Slomp, C. P., in't Zandt, M. H., and Dolman, A. J.: Methane feedbacks to the global climate system in a warmer world, Reviews of Geophysics, 56, 207–250, https://doi.org/10.1002/2017RG000559, 2018.

Dickinson, R. E. and Hanson, B.: Vegetation-albedo feedbacks, 29, 180–186, https://doi.org/10.1029/GM029p0180, 1979.

Dunne, J. P., John, J. G., Shevliakova, S., Stouffer, R. J., Krasting, J. P., Malyshev, S. L., Milly, P. C., Sentman, L. T., Adcroft, A. J., Cooke, W., Dunne, K. A., Griffies, S. M., Hallberg, R. W., Harrison, M. J., Levy, H., Wittenberg, A. T., Phillips, P. J., and Zadeh, N.: GFDL's ESM2 global coupled climate-carbon earth system models. Part II: Carbon system formulation and baseline simulation characteristics, Journal of Climate, 26, 2247–2267, https://doi.org/10.1175/JCLI-D-12-00150.1, 2013.

Elser, J. J., Bracken, M. E., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B., and Smith, J. E.: Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems, Ecology Letters, 10, 1135–1142, https://doi.org/10.1111/j.1461-0248.2007.01113.x, 2007.

Elser, J. J., Fagan, W. F., Kerkhoff, A. J., Swenson, N. G., and Enquist, B. J.: Biological stoichiometry of plant production: Metabolism, scaling and ecological response to global change, New Phytologist, 186, 593–608, https://doi.org/10.1111/j.1469-8137.2010.03214.x, 2010.

Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J., and Taylor, K. E.: Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization, Geoscientific Model Development, 9, 1937–1958, https://doi.org/10.5194/gmd-9-1937-2016, 2016.

Farquhar, G. D., von Caemmerer, S., and Berry, J. A.: A biochemical model of photosynthetic CO2 assimilation in leaves of C3 species, Planta, 149, 78–90, https://doi.org/10.1007/BF00386231, 1980.

Filippelli, G. M.: The global phosphorus cycle, Phosphates: Geochemical, Geobiological and Materials Importance, 48, 391–426, https://doi.org/10.2138/rmg.2002.48.10, 2002.

Fisher, J. B., Huntzinger, D. N., Schwalm, C. R., and Sitch, S.: Modeling the Terrestrial Biosphere, Annual Review of Environment and Resources, 39, 91–123, https://doi.org/10.1146/annurev-environ-012913-093456, 2014.

Fisher, R. A. and Koven, C. D.: Perspectives on the future of Land Surface Models and the challenges of representing complex terrestrial systems, Journal of Advances in Modeling Earth Systems, 12, https://doi.org/10.1029/2018MS001453, 2020.

Frew, N. M., Goldman, J. C., Dennett, M. R., and Johnson, A. S.: Impact of phytoplankton-generated surfactants on air-sea gas exchange, Journal of Geophysical Research: Oceans, 95, 3337–3352, https://doi.org/10.1029/JC095iC03p03337, 1990.

Friedlingstein, P., Jones, M., O'Sullivan, M., Andrew, R., Hauck, J., Peters, G., Peters, W., Pongratz, J., Sitch, S., and Le Quéré, C.: Global carbon budget 2019, Earth System Science Data, 11, 1783–1838, 2019.

Frouin, R. and Iacobellis, S. F.: Influence of phytoplankton on the global radiation budget, Journal of Geophysical Research Atmospheres, 107, 5–1–5–10, https://doi.org/10.1029/2001JD000562, 2002.

Galbraith, E. D., Kwon, E. Y., Gnanadesikan, A., Rodgers, K. B., Griffies, S. M., Bianchi, D., Sarmiento, J. L., Dunne, J. P., Simeon, J., Slater, R. D., Wittenberg, A. T., and Held, I. M.: Climate variability and radiocarbon in the CM2Mc earth system model, Journal of Climate, 24, 4230–4254, https://doi.org/10.1175/2011JCLI3919.1, 2011.

Geider, R. J. and La Roche, J.: Redfield revisited: variability of C / N / P in marine microalgae and its biochemical basis, European Journal of Phycology, 37, 1–17, https://doi.org/10.1017/S0967026201003456, 2002.

Gibelin, A. L., Calvet, J. C., Roujean, J. L., Jarlan, L., and Los, S. O.: Ability of the land surface model ISBA-A-gs to simulate leaf area index at the global scale: Comparison with satellites products, Journal of Geophysical Research Atmospheres, 111, 1–16, https://doi.org/10.1029/2005JD006691, 2006.

Goldman, J. C., McCarthy, J. J., and Peavey, D. G.: Growth rate influence on the chemical composition of phytoplankton in oceanic waters, Nature, 279, 210–215, https://doi.org/10.1038/279210a0, 1979.

Gruber, N. and Galloway, J. N.: An Earth-system perspective of the global nitrogen cycle, Nature, 451, 293–296, https://doi.org/10.1038/nature06592, 2008.

Hajima, T., Watanabe, M., Yamamoto, A., Tatebe, H., Noguchi, A., Abe, M., Ohgaito, R., Ito, A., Yamazaki, D., Ito, A., Takata, K., Ogochi, K., and Watanabe, S.: Description of the MIROC-ES2L Earth system model and evaluation of its climate – biogeochemical processes and feedbacks, Geosci. Model Dev. Discuss., 5, 1–73, https://doi.org/10.5194/gmd-2019-275, 2019.

Heimann, M. and Reichstein, M.: Terrestrial ecosystem carbon dynamics and climate feedbacks, Nature, 451, 289–292, https://doi.org/10.1038/nature06591, 2008.

Hense, I., Meier, H. E. M., and Sonntag, S.: Projected climate change impact on Baltic Sea cyanobacteria, Climatic Change, 119, 391–406, https://doi.org/10.1007/s10584-013-0702-y, 2013.

Hense, I., Stemmler, I., and Sonntag, S.: Ideas and perspectives: Climate-relevant marine biologically driven mechanisms in Earth system models, Biogeosciences, 14, 403–413, https://doi.org/10.5194/bg-14-403-2017, 2017.

Hollinger, D. Y., Ollingerw, S. V., Richardsonw, A. D., Meyersz, T. P., Dail, D. B., Martinw, M. E., Scott, N. A., Arkebauerk, T. J., Baldocchi, D. D., Clark, K. L., Curtis, P. S., Davis, K. J., Desai, A. R., Dragonikk, D., Goulden, M. L., Gu, L., Katulzzz, G. G., Pallardy, S. G., Pawu, K. T., Schmid, H. P., Stoy, P. C., Suyker, A. E., and Verma, S. B.: Albedo estimates for land surface models and support for a new paradigm based on foliage nitrogen concentration, Global Change Biology, 16, 696–710, https://doi.org/10.1111/j.1365-2486.2009.02028.x, 2010.

Hungate, B. A. and Hampton, H. M.: Ecosystem services: Valuing ecosystems for climate, Nature Climate Change, 2, 151–152, https://doi.org/10.1038/nclimate1398, 2012.

Huntzinger, D. N., Post, W. M., Wei, Y., Michalak, A. M., West, T. O., Jacobson, A. R., Baker, I. T., Chen, J. M., Davis, K. J., Hayes, D. J., Hoffman, F. M., Jain, A. K., Liu, S., McGuire, A. D., Neilson, R. P., Potter, C., Poulter, B., Price, D., Raczka, B. M., Tian, H. Q., Thornton, P., Tomelleri, E., Viovy, N., Xiao, J., Yuan, W., Zeng, N., Zhao, M., and Cook, R.: North American Carbon Program (NACP) regional interim synthesis: Terrestrial biospheric model intercomparison, Ecological Modelling, 232, 144–157, https://doi.org/10.1016/j.ecolmodel.2012.02.004, 2012.

Hutchins, D. A. and Boyd, P. W.: Marine phytoplankton and the changing ocean iron cycle, Nature Climate Change, 6, 1072–1079, https://doi.org/10.1038/nclimate3147, 2016.

Ilyina, T., Six, K. D., Segschneider, J., Maier-Reimer, E., Li, H., and Núñez-Riboni, I.: Global ocean biogeochemistry model HAMOCC: Model architecture and performance as component of the MPI-Earth system model in different CMIP5 experimental realizations, Journal of Advances in Modeling Earth Systems, 5, 287–315, https://doi.org/10.1029/2012MS000178, 2013.

Inatomi, M., Ito, A., Ishijima, K., and Murayama, S.: Greenhouse gas budget of a cool-temperate deciduous broad-leaved forest in Japan estimated using a process-based model, Ecosystems, 13, 472–483, https://doi.org/10.1007/s10021-010-9332-7, 2010.

IPCC: 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.)]., vol. 1, Cambridge University Press, Geneva, Switzerland, 2014.

Ito, A. and Oikawa, T.: A simulation model of the carbon cycle in land ecosystems (Sim-CYCLE): A description based on dry-matter production theory and plot-scale validation, Ecological Modelling, 151, 143–176, https://doi.org/10.1016/S0304-3800(01)00473-2, 2002.

Ji, D. and Dai, Y.: The Common Land Model (CoLM) Technical Guide, Bulletin of the American Meteorological Society, 84, 1–60, https://doi.org/10.1175/BAMS-84-8-1013, 2010.

Ji, D., Wang, L., Feng, J., Wu, Q., Cheng, H., Zhang, Q., Yang, J., Dong, W., Dai, Y., Gong, D., Zhang, R. H., Wang, X., Liu, J., Moore, J. C., Chen, D., and Zhou, M.: Description and basic evaluation of Beijing Normal University Earth System Model (BNU-ESM) version 1, Geoscientific Model Development, 7, 2039–2064, https://doi.org/10.5194/gmd-7-2039-2014, 2014.

Jöhnk, K. D., Huisman, J., Sharples, J., Sommeijer, B., Visser, P. M., and Stroom, J. M.: Summer heatwaves promote blooms of harmful cyanobacteria, Global Change Biology, 14, 495–512, https://doi.org/10.1111/j.1365-2486.2007.01510.x, 2008.

Jung, H.-C. and Moon, B.-K.: Impacts of albedo and wind stress changes due to phytoplankton on ocean temperature in a coupled global ocean-biogeochemistry model, Journal of the Korean earth science society, 40, 392–405, https://doi.org/10.5467/jkess.2019.40.4.392, 2019.

Kahru, M., Leppanen, J. M., and Rud, O.: Cyanobacterial blooms cause heating of the sea surface, Marine Ecology Progress Series, 101, 1–8, https://doi.org/10.3354/meps101001, 1993.

Katija, K. and Dabiri, J. O.: A viscosity-enhanced mechanism for biogenic ocean mixing, Nature, 460, 624–626, https://doi.org/10.1038/nature08207, 2009.

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H., Violle, C., Harrison, S. P., Van Bodegom, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., Atkin, O., Bahn, M., Baker, T. R., Baldocchi, D., Bekker, R., Blanco, C. C., Blonder, B., Bond, W. J., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender-Bares, J., Chambers, J. Q., Chapin, F. S., Chave, J., Coomes, D., Cornwell, W. K., Craine, J. M., Dobrin, B. H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W. F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G. T., Fyllas, N. M., Gallagher, R. V., Green, W. A., Gutierrez, A. G., Hickler, T., Higgins, S. I., Hodgson, J. G., Jalili, A., Jansen, S., Joly, C. A., Kerkhoff, A. J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J. M., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T. D., Leishman, M., Lens, F., Lenz, T., Lewis, S. L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M. D., Manning, P., Massad, T., Medlyn, B. E., Messier, J., Moles, A. T., Müller, S. C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V. G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W. A., Patiño, S., Paula, S., Pausas, J. G., Peñuelas, J., Phillips, O. L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J. F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S. J., Yguel, B., Zaehle, S., Zanne, A. E., and Wirth, C.: TRY - a global database of plant traits, Global Change Biology, 17, 2905–2935, https://doi.org/10.1111/j.1365-2486.2011.02451.x, 2011.

Kawamiya, M., Kishi, M. J., and Suginohara, N.: An ecosystem model for the North Pacific embedded in a general circulation model Part I: Model description and characteristics of spatial distributions of biological variables, Journal of Marine Systems, 25, 129–157, https://doi.org/10.1016/S0924-7963(00)00012-9, 2000.

Kowalczyk, E. A., Wang, Y. P., and Law, R. M.: The CSIRO Atmosphere Biosphere Land Exchange (CABLE) model for use in climate models and as an offline model, CSIRO Marine and Atmospheric Research Paper, 13, 1–42, https://doi.org/1921232390, 2006.

Kowalczyk, E. A., Stevens, L., Law, R. M., Dix, M., Wang, Y. P., Harman, I. N., Haynes, K., Srbinovsky, J., Pak, B., and Ziehn, T.: The land surface model component of ACCESS: Description and impact on the simulated surface climatology, Australian Meteorological and Oceanographic Journal, 63, 65–82, https://doi.org/10.22499/2.6301.005, 2013.

Kracher, D., Reick, C. H., Manzini, E., Schultz, M. G., and Stein, O.: Climate change reduces warming potential of nitrous oxide by an enhanced Brewer-Dobson circulation, Geophysical Research Letters, 43, 5851–5859, https://doi.org/10.1002/2016GL068390, 2016.

Laothawornkitkul, J., Taylor, J. E., Paul, N. D., and Hewitt, C. N.: Biogenic volatile organic compounds in the Earth system: Tansley review, New Phytologist, 183, 27–51, https://doi.org/10.1111/j.1469-8137.2009.02859.x, 2009.

Laufkotter, C., Vogt, M., Gruber, N., Aita-Noguchi, M., Aumont, O., Bopp, L., Buitenhuis, E., Doney, S. C., Dunne, J., Hashioka, T., Hauck, J., Hirata, T., John, J., Le Quere, C., Lima, I. D., Nakano, H., Seferian, R., Totterdell, I., Vichi, M., and Volker, C.: Drivers and uncertainties of future global marine primary production in marine ecosystem models, Biogeosciences, 12, 6955–6984, https://doi.org/10.5194/bg-12-6955-2015, 2015.

Law, R. M., Ziehn, T., Matear, R. J., Lenton, A., Chamberlain, M. A., Stevens, L. E., Wang, Y. P., Srbinovsky, J., Bi, D., Yan, H., and Vohralik, P. F.: The carbon cycle in the Australian Community Climate and Earth System Simulator (ACCESS-ESM1) - Part 1: Model description and pre-industrial simulation, Geoscientific Model Development, 10, 2567–2590, https://doi.org/10.5194/gmd-10-2567-2017, 2017.

Lawrence, D. M., Oleson, K. W., Flanner, M. G., Thornton, P. E., Swenson, S. C., Lawrence, P. J., Zeng, X., Yang, Z., Levis, S., and Sakaguchi, K.: Parameterization improvements and functional and structural advances in version 4 of the Community Land Model, Journal of Advances in Modeling Earth Systems, 3, https://doi.org/10.1029/2011MS00045, 2011.

Lawrence, D. M., Fisher, R. A., Koven, C. D., Oleson, K. W., Swenson, S. C., Bonan, G., Collier, N., Ghimire, B., van Kampenhout, L., and Kennedy, D.: The Community Land Model version 5: Description of new features, benchmarking, and impact of forcing uncertainty, Journal of Advances in Modeling Earth Systems, https://doi.org/10.1029/2018MS001583, 2019.

Lengaigne, M., Madec, G., Bopp, L., Menkes, C., Aumont, O., and Cadule, P.: Bio-physical feedbacks in the Arctic Ocean using an Earth system model, Geophysical Research Letters, 36, 1–5, https://doi.org/10.1029/2009GL040145, 2009.

Luo, Y. and Weng, E.: Dynamic disequilibrium of the terrestrial carbon cycle under global change, Trends in Ecology and Evolution, 26, 96–104, https://doi.org/10.1016/j.tree.2010.11.003, 2011.

Martinez-Rey, J., Bopp, L., Gehlen, M., Tagliabue, A., and Gruber, N.: Oceanic N2O emissions in the 21st century, Biogeosciences Discussions, 11, 16 703–16 742, https://doi.org/10.5194/bgd-11-16703-2014, 2014.

Mauritsen, T., Bader, J., Becker, T., Behrens, J., Bittner, M., Brokopf, R., Brovkin, V., Claussen, M., Crueger, T., Esch, M., Fast, I., Fiedler, S., Fläschner, D., Gayler, V., Giorgetta, M., Goll, D. S., Haak, H., Hagemann, S., Hedemann, C., Hohenegger, C., Ilyina, T., Jahns, T., Jimenéz-de-la Cuesta, D., Jungclaus, J., Kleinen, T., Kloster, S., Kracher, D., Kinne, S., Kleberg, D., Lasslop, G., Kornblueh, L., Marotzke, J., Matei, D., Meraner, K., Mikolajewicz, U., Modali, K., Möbis, B., Müller, W. A., Nabel, J. E., Nam, C. C., Notz, D., Nyawira, S. S., Paulsen, H., Peters, K., Pincus, R., Pohlmann, H., Pongratz, J., Popp, M., Raddatz, T. J., Rast, S., Redler, R., Reick, C. H., Rohrschneider, T., Schemann, V., Schmidt, H., Schnur, R., Schulzweida, U., Six, K. D., Stein, L., Stemmler, I., Stevens, B., von Storch, J. S., Tian, F., Voigt, A., Vrese, P., Wieners, K. H., Wilkenskjeld, S., Winkler, A., and Roeckner, E.: Developments in the MPI-M Earth System Model version 1.2 (MPI-ESM1.2) and its response to increasing CO2, Journal of Advances in Modeling Earth Systems, 11, 998–1038, https://doi.org/10.1029/2018MS001400, 2019.

McCoy, D. T., Burrows, S. M., Wood, R., Grosvenor, D. P., Elliott, S. M., Ma, P. L., Rasch, P. J., and Hartmann, D. L.: Natural aerosols explain seasonal and spatial patterns of Southern Ocean cloud albedo, Science Advances, 1, https://doi.org/10.1126/sciadv.1500157, 2015.

McNeill, A. and Unkovich, M.: The nitrogen cycle in terrestrial ecosystems, Nutrient Cycling in Terrestrial Ecosystems, pp. 37–64, https://doi.org/10.1007/978-3-540-68027-7_2, 2007.

Meir, P., Cox, P., and Grace, J.: The influence of terrestrial ecosystems on climate, Trends in Ecology and Evolution, 21, 254–260, https://doi.org/10.1016/j.tree.2006.03.005, 2006.

Menge, B. A., Chan, F., Dudas, S., Eerkes-Medrano, D., Grorud-Colvert, K., Heiman, K., Hessing-Lewis, M., Iles, A., Milston-Clements, R., Noble, M., Page-Albins, K., Richmond, E., Rilov, G., Rose, J., Tyburczy, J., Vinueza, L., and Zarnetske, P.: Terrestrial ecologists ignore aquatic literature: Asymmetry in citation breadth in ecological publications and implications for generality and progress in ecology, Journal of Experimental Marine Biology and Ecology, 377, 93–100, https://doi.org/10.1016/j.jembe.2009.06.024, 2009.

Meunier, C. L., Boersma, M., El-Sabaawi, R., Halvorson, H. M., Herstoff, E. M., Van de Waal, D. B., Vogt, R. J., and Litchman, E.: From elements to function: Toward unifying ecological stoichiometry and trait-based ecology, Frontiers in Environmental Science, 5, https://doi.org/10.3389/fenvs.2017.00018, 2017.

Mignot, J., Swingedouw, D., Deshayes, J., Marti, O., Talandier, C., Séférian, R., Lengaigne, M., and Madec, G.: On the evolution of the oceanic component of the IPSL climate models from CMIP3 to CMIP5: A mean state comparison, Ocean Modelling, 72, 167–184, https://doi.org/10.1016/j.ocemod.2013.09.001, 2013.

Monroe, J. G., Markman, D. W., Beck, W. S., Felton, A. J., Vahsen, M. L., and Pressler, Y.: Ecoevolutionary dynamics of carbon cycling in the anthropocene, Trends in Ecology and Evolution, 33, 213–225, https://doi.org/10.1016/j.tree.2017.12.006, 2018.

Montzka, S. A., Dlugokencky, E. J., and Butler, J. H.: Non-CO2 greenhouse gases and climate change, Nature, 476, 43–50, https://doi.org/10.1038/nature10322, 2011.

Moore, J. K., Lindsay, K., Doney, S. C., Long, M. C., and Misumi, K.: Marine ecosystem dynamics and biogeochemical cycling in the community earth system model [CESM1(BGC)]: Comparison of the 1990s with the 2090s under the RCP4.5 and RCP8.5 scenarios, Journal of Climate, 26, 9291–9312, https://doi.org/10.1175/JCLI-D-12-00566.1, 2013.

Myhre, G., Shindell, D., and Pongratz, J.: Anthropogenic and natural radiative forcing, in: Stocker, Thomas (ed.) : Climate change 2013 : the physical science basis; Working Group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change., pp. 659–740, Cambridge University Press, https://doi.org/10.1017/CBO9781107415324.018, 2014.

Naudts, K., Ryder, J., McGrath, M. J., Otto, J., Chen, Y., Valade, A., Bellasen, V., Berhongaray, G., Bönisch, G., Campioli, M., Ghattas, J., De Groote, T., Haverd, V., Kattge, J., MacBean, N., Maignan, F., Merilä, P., Penuelas, J., Peylin, P., Pinty, B., Pretzsch, H., Schulze, E. D., Solyga, D., Vuichard, N., Yan, Y., and Luyssaert, S.: A vertically discretised canopy description for ORCHIDEE (SVN r2290) and the modifications to the energy, water and carbon fluxes, Geoscientific Model Development, 8, 2035–2065, https://doi.org/10.5194/gmd-8-2035-2015, 2015.

Novakov, T. and Penner, J. E.: Large contribution of organic aerosols to cloud-condensation-nuclei concentrations, Nature, 365, 823–826, https://doi.org/10.1038/365823a0, 1993.

Oke, P. R., Griffin, D. A., Schiller, A., Matear, R. J., Fiedler, R., Mansbridge, J., Lenton, A., Cahill, M., Chamberlain, M. A., and Ridgway, K.: Evaluation of a near-global eddy-resolving ocean model, Geoscientific Model Development, 6, 591–615, https://doi.org/10.5194/gmd-6-591-2013, 2013.

Oleson, K. W., Lawrence, D. M., Bonan, G. B., Drewniak, B., Huang, M., Koven, C. D., Levis, S., Li, F., Riley, W. J., and Subin, Z. M.: Technical Description of version 4.5 of the Community Land Model (CLM)(NCAR Technical Note No. NCAR/TN-503+ STR). Citeseer, National Center for Atmospheric Research, PO Box, 3000, 2013.

Padfield, D., Yvon-Durocher, G., Buckling, A., Jennings, S., and Yvon-Durocher, G.: Rapid evolution of metabolic traits explains thermal adaptation in phytoplankton, Ecology Letters, 19, 133–142, https://doi.org/10.1111/ele.12545, 2016.

Palmer, J. R. and Totterdell, I. J.: Production and export in a global ocean ecosystem model, Deep-Sea Research Part I: Oceanographic Research Papers, 48, 1169–1198, https://doi.org/10.1016/S0967-0637(00)00080-7, 2001.

Park, J. Y., Kug, J. S., Bader, J., Rolph, R., and Kwon, M.: Amplified Arctic warming by phytoplankton under greenhouse warming, Proceedings of the National Academy of Sciences of the United States of America, 112, 5921–5926, https://doi.org/10.1073/pnas.1416884112, 2015.

Patara, L., Vichi, M., Masina, S., Fogli, P. G., and Manzini, E.: Global response to solar radiation absorbed by phytoplankton in a coupled climate model, Climate Dynamics, 39, 1951–1968, https://doi.org/10.1007/s00382-012-1300-9, 2012.

Paulsen, H., Ilyina, T., Jungclaus, J., Six, K., and Stemmler, I.: Light absorption by marine cyanobacteria affects tropical climate mean state and variability, Earth System Dynamics, 9, 1283–1300, https://doi.org/10.5194/esd-9-1283-2018, 2018.

Peñuelas, J. and Staudt, M.: BVOCs and global change, Trends in Plant Science, 15, 133–144, https://doi.org/10.1016/j.tplants.2009.12.005, 2010.

Prowe, A. E. F., Pahlow, M., Dutkiewicz, S., Follows, M., and Oschlies, A.: Top-down control of marine phytoplankton diversity in a global ecosystem model, Progress in Oceanography, 101, 1–13, https://doi.org/10.1016/j.pocean.2011.11.016, 2012.

Quigg, A., Finkel, Z. V., Irwin, A. J., Rosenthal, Y., Ho, T.-Y., Reinfelder, J. R., Schofield, O., Morel, F. M. M., and Falkowski, P. G.: The evolutionary inheritance of elemental stoichiometry in marine phytoplankton, Nature, 425, 291–294, https://doi.org/10.1038/nature01953, 2003.

Quinn, P. K. and Bates, T. S.: The case against climate regulation via oceanic phytoplankton sulphur emissions, Nature, 480, 51–56, https://doi.org/10.1038/nature10580, 2011.

Raffaelli, D., Solan, M., and Webb, T. J.: Do marine and terrestrial ecologists do it differently?, Marine ecology progress series, 304, 283–289, https://www.jstor.org/stable/24869863, 2005.

Rap, A., Scott, C. E., Spracklen, D. V., Bellouin, N., Forster, P. M., Carslaw, K. S., Schmidt, A., and Mann, G.: Natural aerosol direct and indirect radiative effects, Geophysical Research Letters, 40, 3297–3301, https://doi.org/10.1002/grl.50441, 2013.

Rap, A., Scott, C. E., Reddington, C. L., Mercado, L., Ellis, R. J., Garraway, S., Evans, M. J., Beerling, D. J., MacKenzie, A. R., Hewitt, C. N., and Spracklen, D. V.: Enhanced global primary production by biogenic aerosol via diffuse radiation fertilization, Nature Geoscience, 11, 640–644, https://doi.org/10.1038/s41561-018-0208-3, 2018.

Redfield, A. C.: On the proportions of organic derivatives in sea water and their relation to the composition of plankton, https://doi.org/citeulike-article-id:11236440, 1934.

Reick, C. H., Raddatz, T., Brovkin, V., and Gayler, V.: Representation of natural and anthropogenic land cover change in MPI-ESM, Journal of Advances in Modeling Earth Systems, 5, 459–482, https://doi.org/10.1002/jame.20022, 2013.

Rhee.G.Yull: Effects of N : P atomic ratios and nitrate limitation on algal growth , cell composition , and nitrate uptake, Limnology and Oceanography, 23, 10–25, http://www.jstor.org/stable/2835687, 1978.

Ridgwell, A. and Zeebe, R. E.: The role of the global carbonate cycle in the regulation and evolution of the Earth system, Earth and Planetary Science Letters, 234, 299–315, https://doi.org/10.1016/j.epsl.2005.03.006, 2005.

Rogers, A., Medlyn, B. E., Dukes, J. S., Bonan, G., Von Caemmerer, S., Dietze, M. C., Kattge, J., Leakey, A. D. B., Mercado, L. M., and Niinemets, Ü.: A roadmap for improving the representation of photosynthesis in Earth system models, New Phytologist, 213, 22–42, https://doi.org/10.1111/nph.14283, 2017.

Sarmiento, J. L. and Gruber, N.: Ocean biogeochemical dynamics, Princeton University Press, 2006.

Sathyendranath, S., Gouveia, A. D., Shetye, S. R., Ravindran, P., and Platt, T.: Biological control of surface temperature in the Arabian Sea, Nature, 349, 54–56, 1991.

Sato, H., Itoh, A., and Kohyama, T.: SEIB-DGVM: A new Dynamic Global Vegetation Model using a spatially explicit individual-based approach, Ecological Modelling, 200, 279–307, https://doi.org/10.1016/j.ecolmodel.2006.09.006, 2007.

Schaum, C. E., Barton, S., Bestion, E., Buckling, A., Garcia-Carreras, B., Lopez, P., Lowe, C., Pawar, S., Smirnoff, N., Trimmer, M., and Yvon-Durocher, G.: Adaptation of phytoplankton to a decade of experimental warming linked to increased photosynthesis, Nature Ecology and Evolution, 1, 1–7, https://doi.org/10.1038/s41559-017-0094, 2017.

Schilt, A., Baumgartner, M., Schwander, J., Buiron, D., Capron, E., Chappellaz, J., Loulergue, L., Schüpbach, S., Spahni, R., Fischer, H., and Stocker, T. F.: Atmospheric nitrous oxide during the last 140,000years, Earth and Planetary Science Letters, 300, 33–43, https://doi.org/10.1016/j.epsl.2010.09.027, 2010.

Schmitz, O. J., Hawlena, D., and Trussell, G. C.: Predator control of ecosystem nutrient dynamics, Ecology Letters, 13, 1199–1209, https://doi.org/10.1111/j.1461-0248.2010.01511.x, 2010.

Schmitz, O. J., Wilmers, C. C., Leroux, S. J., Doughty, C. E., Atwood, T. B., Galetti, M., Davies, A. B., and Goetz, S. J.: Animals and the zoogeochemistry of the carbon cycle, Science, 362, https://doi.org/10.1126/science.aar3213, 2018.

Schwalm, C. R., Williams, C. A., Schaefer, K., Anderson, R., Arain, M. A., Baker, I., Barr, A., Black, T. A., Chen, G., Chen, J. M., Ciais, P., Davis, K. J., Desai, A., Dietze, M., Dragoni, D., Fischer, M. L., Flanagan, L. B., Grant, R., Gu, L., Hollinger, D., Izaurralde, R. C., Kucharik, C., Lafleur, P., Law, B. E., Li, L., Li, Z., Liu, S., Lokupitiya, E., Luo, Y., Ma, S., Margolis, H., Matamala, R., McCaughey, H., Monson, R. K., Oechel, W. C., Peng, C., Poulter, B., Price, D. T., Riciutto, D. M., Riley, W., Sahoo, A. K., Sprintsin, M., Sun, J., Tian, H., Tonitto, C., Verbeeck, H., and Verma, S. B.: A model-data intercomparison of CO2 exchange across North America: Results from the North American Carbon Program site synthesis, Journal of Geophysical Research: Biogeosciences, 115, https://doi.org/10.1029/2009JG001229, 2010.

Schwinger, J., Tjiputra, J., Goris, N., Six, K. D., Kirkevåg, A., Seland, Ø., Heinze, C., and Ilyina, T.: Amplification of global warming through pH dependence of DMS production simulated with a fully coupled Earth system model, Biogeosciences, 14, 3633–3648, https://doi.org/10.5194/bg-14-3633-2017, 2017.

Scott, C. E., Arnold, S. R., Monks, S. A., Asmi, A., Paasonen, P., and Spracklen, D. V.: Substantial large-scale feedbacks between natural aerosols and climate, Nature Geoscience, 11, 44–48, https://doi.org/10.1038/s41561-017-0020-5, 2018.

Séférian, R., Delire, C., Decharme, B., Voldoire, A., David Salas, Y. M., Chevallier, M., Saint-Martin, D., Aumont, O., Calvet, J. C., Carrer, D., Douville, H., Franchistéguy, L., Joetzjer, E., and Sénési, S.: Development and evaluation of CNRM Earth system model-CNRM-ESM1, Geoscientific Model Development, 9, 1423–1453, https://doi.org/10.5194/gmd-9-1423-2016, 2016.

Séférian, R., Nabat, P., Michou, M., Saint-Martin, D., Voldoire, A., Colin, J., Decharme, B., Delire, C., Berthet, S., Chevallier, M., Sénési, S., Franchisteguy, L., Vial, J., Mallet, M., Joetzjer, E., Geoffroy, O., Guérémy, J. F., Moine, M. P., Msadek, R., Ribes, A., Rocher, M., Roehrig, R., Salas-y Mélia, D., Sanchez, E., Terray, L., Valcke, S., Waldman, R., Aumont, O., Bopp, L., Deshayes, J., Éthé, C., and Madec, G.: Evaluation of CNRM Earth System Model, CNRM-ESM2-1: Role of Earth System Processes in Present-Day and Future Climate, Journal of Advances in Modeling Earth Systems, 11, 4182–4227, https://doi.org/10.1029/2019MS001791, 2019.

Sellar, A. A., Jones, C. G., Mulcahy, J. P., Tang, Y., Yool, A., Wiltshire, A., O'Connor, F. M., Stringer, M., Hill, R., Palmieri, J., Woodward, S., de Mora, L., Kuhlbrodt, T., Rumbold, S. T., Kelley, D. I., Ellis, R., Johnson, C. E., Walton, J., Abraham, N. L., Andrews, M. B., Andrews, T., Archibald, A. T., Berthou, S., Burke, E., Blockley, E., Carslaw, K., Dalvi, M., Edwards, J., Folberth, G. A., Gedney, N., Griffiths, P. T., Harper, A. B., Hendry, M. A., Hewitt, A. J., Johnson, B., Jones, A., Jones, C. D., Keeble, J., Liddicoat, S., Morgenstern, O., Parker, R. J., Predoi, V., Robertson, E., Siahaan, A., Smith, R. S., Swaminathan, R., Woodhouse, M. T., Zeng, G., and Zerroukat, M.: UKESM1: Description and evaluation of the U.K. Earth System Model, Journal of Advances in Modeling Earth Systems, 11, 4513–4558, https://doi.org/10.1029/2019MS001739, 2019.

Shen, M., Piao, S., Jeong, S. J., Zhou, L., Zeng, Z., Ciais, P., Chen, D., Huang, M., Jin, C. S., Li, L. Z., Li, Y., Myneni, R. B., Yang, K., Zhang, G., Zhang, Y., and Yao, T.: Evaporative cooling over the Tibetan Plateau induced by vegetation growth, Proceedings of the National Academy of Sciences of the United States of America, 112, 9299–9304, https://doi.org/10.1073/pnas.1504418112, 2015.

Six, K. D., Kloster, S., Ilyina, T., Archer, S. D., Zhang, K., and Maier-Reimer, E.: Global warming amplified by reduced sulphur fluxes as a result of ocean acidification, Nature Climate Change, 3, 975–978, https://doi.org/10.1038/nclimate1981, 2013.

Sonntag, S. and Hense, I.: Phytoplankton behavior affects ocean mixed layer dynamics through biological-physical feedback mechanisms, Geophysical Research Letters, 38, 1–6, https://doi.org/10.1029/2011GL048205, 2011.

Steele, J. H.: Can ecological theory cross the land-sea boundary?, Journal of Theoretical Biology, 153, 425–436, https://doi.org/10.1016/S0022-5193(05)80579-X, 1991.

Steinberg, D. K. and Landry, M. R.: Zooplankton and the ocean carbon cycle, Annual Review of Marine Science, 9, 413–444, https://doi.org/10.1146/annurev-marine-010814-015924, 2017.

Stocker, B. D., Roth, R., Joos, F., Spahni, R., Steinacher, M., Zaehle, S., Bouwman, L., Xu-Ri, and Prentice, I. C.: Multiple greenhouse-gas feedbacks from the land biosphere under future climate change scenarios, Nature Climate Change, 3, 666–672, https://doi.org/10.1038/nclimate1864, 2013.

Struyf, E., Smis, A., van Damme, S., Meire, P., and Conley, D. J.: The global biogeochemical silicon cycle, Silicon, 1, 207–213, https://doi.org/10.1007/s12633-010-9035-x, 2009.

Swart, N. C., Cole, J. N., Kharin, V. V., Lazare, M., Scinocca, J. F., Gillett, N. P., Anstey, J., Arora, V., Christian, J. R., Hanna, S., Jiao, Y., Lee, W. G., Majaess, F., Saenko, O. A., Seiler, C., Seinen, C., Shao, A., Sigmond, M., Solheim, L., Von Salzen, K., Yang, D., and Winter, B.: The Canadian Earth System Model version 5 (CanESM5.0.3), Geoscientific Model Development, 12, 4823–4873, https://doi.org/10.5194/gmd-12-4823-2019, 2019.

Tagliabue, A., Bowie, A. R., Boyd, P. W., Buck, K. N., Johnson, K. S., and Saito, M. A.: The integral role of iron in ocean biogeochemistry, Nature, 543, 51–59, https://doi.org/10.1038/nature21058, 2017.

Taylor, K. E., Stouffer, R. J., and Meehl, G. A.: An overview of CMIP5 and the experiment design, Bulletin of the American Meteorological Society, 93, 485–498, https://doi.org/10.1175/BAMS-D-11-00094.1, 2012.

Te Beest, M., Sitters, J., Ménard, C. B., and Olofsson, J.: Reindeer grazing increases summer albedo by reducing shrub abundance in Arctic tundra, Environmental Research Letters, 11, 1–13, https://doi.org/10.1088/1748-9326/aa5128, 2016.

Terrer, C., Jackson, R. B., Prentice, I. C., Keenan, T. F., Kaiser, C., Vicca, S., Fisher, J. B., Reich, P. B., Stocker, B. D., and Hungate, B. A.: Nitrogen and phosphorus constrain the CO2 fertilization of global plant biomass, Nature Climate Change, 9, 684–689, https://doi.org/10.1038/s41558-019-0545-2, 2019.

THOM, A.: Momentum absorption by vegetation, Quarterly Journal of the Royal Meteorological Society, 097, 414–428, https://doi.org/10.1256/smsqj.41403, 1971.

Turner, B. L., Condron, L. M., France, C. A. M., Lehmann, J., Solomon, D., Peltzer, D. A., and Richardson, S. J.: Sulfur dynamics during long-term ecosystem development, Biogeochemistry, 128, 281–305, https://doi.org/10.1007/s10533-016-0208-6, 2016.

Tyrrell, T., Holligan, P. M., and Mobley, C. D.: Optical impacts of oceanic coccolithophore blooms, Journal of Geophysical Research: Oceans, 104, 3223–3241, https://doi.org/10.1029/1998jc900052, 1999.

Valentine, D. L.: Emerging Topics in Marine Methane Biogeochemistry, Annual Review of Marine Science, 3, 147–171, https://doi.org/10.1146/annurev-marine-120709-142734, 2011.

https://doi.org/10.5194/esd-2020-55
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Vanni, M. J.: Nutrient cycling by animals in freshwater ecosystems, Annual Review of Ecology and Systematics, 33, 341–370, https://doi.org/10.1146/annurev.ecolsys.33.010802.150519, 2002.

Vichi, M., Lovato, T., Lazzari, P., Cossarini, G., Gutierrez Mlot, E., Mattia, G., Masina, S., McKiver, W., Pinardi, N., Solidoro, C., Tedesco, L., and Zavatelli, M.: The Biogeochemical Flux Model (BFM) Equation Description and User Manual, 5, 1–104, 2015.

Walker, J. C. G.: The oxygen cycle, in: The natural environment and the biogeochemical cycles, pp. 87–104, Springer, 1980.

Wasmund, K., Mußmann, M., and Loy, A.: The life sulfuric: microbial ecology of sulfur cycling in marine sediments, Environmental microbiology reports, 9, 323–344, https://doi.org/10.1111/1758-2229.12538, 2017.

Watanabe, S., Hajima, T., Sudo, K., Nagashima, T., Takemura, T., Okajima, H., Nozawa, T., Kawase, H., Abe, M., Yokohata, T., Ise, T., Sato, H., Kato, E., Takata, K., Emori, S., and Kawamiya, M.: MIROC-ESM 2010: Model description and basic results of CMIP5-20c3m experiments, Geoscientific Model Development, 4, 845–872, https://doi.org/10.5194/gmd-4-845-2011, 2011.

Wieder, W. R., Cleveland, C. C., Smith, W. K., and Todd-Brown, K.: Future productivity and carbon storage limited by terrestrial nutrient availability, Nature Geoscience, 8, 441–444, https://doi.org/10.1038/ngeo2413, 2015.

Wilmers, C. C., Estes, J. A., Edwards, M., Laidre, K. L., and Konar, B.: Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests, Frontiers in Ecology and the Environment, 10, 409–415, https://doi.org/10.1890/110176, 2012.

Worden, A. Z., Follows, M. J., Giovannoni, S. J., Wilken, S., Zimmerman, A. E., and Keeling, P. J.: Rethinking the marine carbon cycle: Factoring in the multifarious lifestyles of microbes, Science, 347, https://doi.org/10.1126/science.1257594, 2015.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R.: The worldwide leaf economics spectrum, Nature, 428, 821–827, https://doi.org/10.1038/nature02403, 2004.

Wu, B., Amelung, W., Xing, Y., Bol, R., and Berns, A. E.: Iron cycling and isotope fractionation in terrestrial ecosystems, Earth-Science Reviews, 190, 323–352, https://doi.org/10.1016/j.earscirev.2018.12.012, 2019.

Yool, A., Popova, E. E., and Anderson, T. R.: MEDUSA-2.0: An intermediate complexity biogeochemical model of the marine carbon cycle for climate change and ocean acidification studies, Geoscientific Model Development, 6, 1767–1811, https://doi.org/10.5194/gmd-6-1767-2013, 2013.

Yukimoto, S., Yoshimura, H., Hosaka, M., Sakami, T., Tsujino, H., Hirabara, M., Tanaka, T. Y., Deushi, M., Obata, A., Nakano, H., Adachi, Y., Shindo, E., Yabu, S., Ose, T., and Kitoh, A.: Meteorological Research Institute-Earth System Model Version 1 (MRI-ESM1), Technical Reports, 64, 88, https://doi.org/10.11483/mritechrepo.64, 2011.

Zaehle, S., Jones, C. D., Houlton, B., Lamarque, J. F., and Robertson, E.: Nitrogen availability reduces CMIP5 projections of twenty-first-century land carbon uptake, Journal of Climate, 28, 2494–2511, https://doi.org/10.1175/JCLI-D-13-00776.1, 2015.

Zehr, J. P. and Kudela, R. M.: Nitrogen cycle of the open ocean: From genes to ecosystems, Annual Review of Marine Science, 3, 197–225, https://doi.org/10.1146/annurev-marine-120709-142819, 2011.

Zeng, Z., Piao, S., Li, L. Z., Zhou, L., Ciais, P., Wang, T., Li, Y., Lian, X., Wood, E. F., Friedlingstein, P., Mao, J., Estes, L. D., Myneni, R. B., Peng, S., Shi, X., Seneviratne, S. I., and Wang, Y.: Climate mitigation from vegetation biophysical feedbacks during the past three decades, Nature Climate Change, 7, 432–436, https://doi.org/10.1038/nclimate3299, 2017.

Zhao, D. F., Buchholz, A., Tillmann, R., Kleist, E., Wu, C., Rubach, F., Kiendler-Scharr, A., Rudich, Y., Wildt, J., and Mentel, T. F.: Environmental conditions regulate the impact of plants on cloud formation, Nature Communications, 8, 1–8, https://doi.org/10.1038/ncomms14067, 2017.

Zhu, Q., Riley, W. J., Iversen, C. M., and Kattge, J.: Assessing impacts of plant stoichiometric traits on terrestrial ecosystem carbon accumulation using the E3SM land model, Journal of Advances in Modeling Earth Systems, 12, https://doi.org/10.1029/2019ms001841, 2020.

Table 1. List of the 17 earth system models reviewed in this study. For each ESM, the names of the terrestrial ecosystem module and the marine ecosystem module are indicated as well as the CMIP phase for which the model has been applied and the main references. A total of 15 different terrestrial ecosystem models and 16 marine ecosystem models are considered.

Earth system model	Terrestrial eco. mod.	Marine eco. mod.	CMIP	References
ACCESS-ESM1.5	CABLE Casa-CNP	WOMBAT	CMIP5	Law et al. (2017); Kowalczyk et al. (2006); Oke et al. (2013)
BNU-ESM	CoLM	iBGC	CMIP5	Ji et al. (2014); Ji and Dai (2010); Galbraith et al. (2011)
CanESM5	CLASS CTEM	CMOC	CMIP6	Swart et al. (2019)
CESM1	CLM4.5	BEC	CMIP5	Oleson et al. (2013); Moore et al. (2013)
CESM2	CLM5	MARBL	CMIP6	Danabasoglu et al. (2020); Lawrence et al. (2019); Moore et al. (2013)
CMCC-ESM2	CLM4.5	BFMv5.1	CMIP6	Cherchi et al. (2019); Oleson et al. (2013); Vichi et al. (2015)
CNRM-ESM1	ISBA	PISCESv2	CMIP5	Séférian et al. (2016); Gibelin et al. (2006); Aumont et al. (2015)
CNRM-ESM2.1	ISBA	PISCESv2-gas	CMIP6	Séférian et al. (2019); Gibelin et al. (2006); Aumont et al. (2015); Martinez-Rey et al. (2014)
GFDL-ESM2M/ESM2G	LM3	TOPAZ2m	CMIP5	Dunne et al. (2013)
HadGEM2	MOSES - TRIFFID	Diat-HadOCC	CMIP5	Collins et al. (2011); Cox (2001); Palmer and Totterdell (2001)
IPSL-CM5	ORCHIDEE	PISCESv2	CMIP6	Naudts et al. (2015); Aumont et al. (2015)
MIROC-ESM	SEIB-DVGM	NPZD	CMIP5	Watanabe et al. (2011); Sato et al. (2007); Kawamiya et al. (2000)
MIROC-ES2L	VISIT-e	OECO-v2	CMIP6	Hajima et al. (2019); Ito and Oikawa (2002); Inatomi et al. (2010)
MPI-ESM1.2	JSBACH3.2	HAMOCC6	CMIP6	Mauritsen et al. (2019); Reick et al. (2013); Ilyina et al. (2013)
MRI-ESM1	HAL	unnamed	CMIP5	Yukimoto et al. (2011)
NorESM1	CLM4	HAMOCC5	CMIP5	Bentsen et al. (2012); Lawrence et al. (2011); Ilyina et al. (2013)
UKESM1	JULES	MEDUSA	CMIP6	Sellar et al. (2019); Clark et al. (2011); Yool et al. (2013)

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Preprint. Discussion started: 3 August 2020

Table 2. List of climate-relevant processes and their consideration in the terrestrial (T) and marine (M) modules of the different ESM. The processes are sorted according to their role in the biogeochemical pumps (column 3), the biogeophysical mechanisms (column 4) and the gas and particle shuttles (column 5). The * for N source and sink of the CoLM module indicates that the processes are included but have been turned-off for the CMIP5 experiments. The - indicate that the given process is not relevant for terrestrial or marine ecosystem.

Module	Eco.	Photosynthesis	Respiration	Phenology	Mortality	C remineralization	Grazing	N source and sink	P source and sink	Fe source and sink	Si source and sink	H_2O source and sink	Albedo	Light absorption	Roughness length	Evapotranspiration	Respiration	Evapotranspiration	CH_4 production	N_2O production	Aerosol production
CABLE Casa-CNP	T	x	x	x	x	x		x	x		-	x	x	x	x	x	x	x			
CoLM	T	x	x	x	x	x		*			-	x	x	x	x	x	x	x			
CLASS CTEM	T	x	x	x	x	x					-		x	x	x	x	x	x	x		
CLM4.5	T	x	x	x	x	x		x			-	x	x	x	x	x	x	x	x	x	x
CLM5	T	x	x	x	x	x		x			-	x	x	x	x	x	x	x	x	x	x
ISBA	T	x	x	x	x	x					-	x	x	x	x	x	x	x			
LM3	T	x	x	x	x	x					-	x	x	x	x	x	x	x			
MOSES – TRIFFID	T	x	x	x	x	x					-	x	x	x	x	x	x	x			
ORCHIDEE	T	x	x	x	x	x	x				-	x	x	x	x	x	x	x			
SEIB-DVGM	T	x	x	x	x	x					-	x	x	x	x	x	x	x			
VISIT-e	T	x	x	x	x	x		x			-	x	x	x	x	x	x	x	x	x	
JSBACH3.2	T	x	x	x	x	x		x			-	x	x	x	x	x	x	x			
HAT	T	x	x	x	x	x					-	x	x	x	x	x	x	x			
CLM4	T	x	x	x	x	x		x			-	x	x	x	x	x	x	x		x	
JULES	T	x	x	x	x	x		x			-	x	x	x	x	x	x	x	x		x
WOMBAT	M				x	x	x	x		x		-				-		-			
iBGC	M				x	x			x			-				-		-			
CMOC	M	x			x	x	x	x				-				-		-			
BEC	M				x	x	x	x	x	x	x	-		x		-		-			
MARBL	M				x	x	x	x	x	x	x	-		x		-		-			
BFMv5.1	M		x		x	x	x	x	x	x	x	-		x		-	x	-			
PISCESv2	M				x	x	x	x	x	x	x	-		x		-		-			
PISCESv2-gas	M				x	x	x	x	x	x	x	-		x		-		-		x	x
TOPAZ2m	M				x	x	x	x	x	x	x	-		x		-		-			
Diat-HadOCC	M				x	x	x	x		x	x	-				-		-			x
NPZD	M				x	x	x	x				-				-		-			
OECO-v2	M				x	x	x	x	x	x		-				-		-		x	x
HAMOCC6	M				x	x	x	x	x	x	x	-				-		-		x	x
unnamed	M				x	x	x	x	x			-				-		-			
HAMOCC5	M				x	x	x	x	x	x	x	-				-		-		x	x
MEDUSA	M				x	x	x	x		x	x	-				-		-			x