

**Biodiversity and  
biomes under  
climatic change**

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# The role of plant functional trade-offs for biodiversity changes and biome shifts under scenarios of global climatic change

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## Abstract

The global geographic distribution of biodiversity and biomes is determined by species-specific physiological tolerances to climatic constraints. Current models implement empirical bioclimatic relationships to predict present-day vegetation patterns and to forecast biodiversity changes and biome shifts under climatic change. In this paper, we consider plant functional trade-offs and their interactions with climatic changes to forecast and explain biodiversity changes and biome shifts.

The Jena Diversity model (JeDi) simulates plant survival according to essential plant functional trade-offs, including eco-physiological processes such as water uptake, photosynthesis, allocation, reproduction and phenology. We apply JeDi to quantify biodiversity changes and biome shifts between present-day and a range of possible future climates from two scenarios (A2 and B1) and seven global climate models using metrics of plant functional richness and functional identity.

Our results show (i) a significant biodiversity loss in the tropics, (ii) an increase in biodiversity at mid and high latitudes, and (iii) a poleward shift of biomes. While these results are consistent with the findings of empirical approaches, we are able to explain them in terms of the plant functional trade-offs involved in the allocation, metabolic and reproduction strategies of plants.

We conclude that general aspects of plant physiological tolerances can be derived from plant functional trade-offs, which may provide a useful process- and trait-based alternative to bioclimatic relationships in order to address questions about the causes of biodiversity changes and biome shifts.

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# 1 Introduction

*The purpose of models is not to fit the data but to sharpen the question.*

S. Karlin

The Earth's climate determines the geographic distribution of vegetation physiog-  
5 nomy and therefore biomes through species-specific physiological tolerances to tem-  
perature, water availability and length of the growing season (Woodward, 1987).  
Species physiological tolerances are also hypothesized to explain the latitudinal gra-  
dient in biodiversity of increasing species richness from the poles towards the tropics  
(Currie et al., 2004; Reu et al., 2010).

10 The predominant approach to predict the global distribution of biodiversity and  
biomes is to derive empirical relationships between the climate and the number of  
species or presence (dominance) of characteristic plant functional types (PFTs) (Fran-  
cis and Currie, 2003; Holdridge, 1947; Whittaker, 1975; Box, 1981). These relation-  
ships are then used to forecast biodiversity changes and biome shifts under various  
15 climate change scenarios (Thuiller, 2003; Sommer et al., 2010; Scholze et al., 2006;  
Thomas et al., 2008). However, because empirically-derived bioclimatic relationships  
consider physiological tolerance processes only implicitly, two problems arise when  
these models are applied to changing environmental conditions: (i) there is no guar-  
antee that predictions are reliable, especially if future climates have no current analog  
20 (Williams et al., 2007), and (ii) it is often impossible to disentangle what aspects of  
the climate (i.e., temperature or precipitation, climatic mean or variability) are driving  
biodiversity change and biome shift (Carrara and Vázquez, 2010).

One alternative to empirical bioclimatic relationships is to define physiological toler-  
ances in terms of adaptations (or functional traits) allowing plants to tolerate climatic  
constraints (Bazzaz et al., 1997; Ackerly et al., 2000; Reich et al., 2003). For exam-  
25 ple, Tilman (1990) proposed functional trade-offs between growth, maintenance and  
reproduction as a mechanism for explaining species survival and coexistence in plant  
communities. The existence of trade-offs is a fundamental feature of the concept of

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plant growth strategies considering that there are no “super-plant” species. Given finite resources individual plant species must “choose” between growing fast or old, producing large or numerous seeds, or investing their carbon into storage or anti-predatory traits (Bazzaz et al., 1997). Because species must functionally trade off, similar climatic constraints have led to similar plant forms and functions independent of phylogenetic taxonomy (Schimper, 1898).

The Jena Diversity model (JeDi) is a global biogeography model that explicitly implements key fundamental functional trade-offs of plant survival (Kleidon and Mooney, 2000; Reu et al., 2010). The major difference of JeDi to other biogeography models is that characteristic PFTs emerge from the effects of climate (i.e., solar radiation, temperature, precipitation) and land surface processes on plant survival and reproduction given plant functional trade-offs (Reu et al., 2010); rather than being prescribed from empirical relationships. Therefore, to avoid confusion these “emergent PFTs” will hereafter be referred to as plant growth strategies (PGS).

Using JeDi we study the effects of possible future climates, represented by the simulations of seven different climate models of the 4th IPCC Assessment Report and two different scenarios (A2 and B1) (IPCC, 2007), on the success of individual PGS, and deduce regions with important shifts in biodiversity and/or biome. Our model allows us then to determine how specific plant functional trade-offs and changes in climate variables (e.g., rainfall and temperature) relate in the context of future biodiversity changes and biome shifts.

## 2 Methods

### 2.1 Definitions

We define a plant functional trait as the morphological, phenological or physiological characteristic of an organism affecting its ability to acquire and allocate resources (Violle et al., 2007). A plant growth strategy (PGS) is defined as the combination of

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several functional traits that determine its growth behavior and tolerance to climatic constraints. To quantify the assemblage of PGSs in a given region (grid-cell), we introduce two metrics: first, we define functional richness (FR) as the number of different PGS in a grid-cell. Second, we define functional identity (FI) as the mean vector of plant functional traits calculated among all PGS found in a grid-cell. Using measures of FR and FI, the JeDi model has been shown to reproduce the present-day global geographic distribution of biodiversity and biomes consistent with current biogeographic understanding (Reu et al., 2010).

## 2.2 Model description

*Model initialization:* A PGS in JeDi is a combination of twelve functional traits (model parameters, Table 1) affecting plant growth, life history, and eco-physiology. Each plant functional trait is associated with a model function that determines the costs and benefits associated to living in a certain climate. For example, under limited water availability, plants benefit from increased root growth, which implies, however, that fewer resources are available for other functions such as allocation to shoot growth or reproduction. Each simulation starts with 5000 randomly generated PGSs in grid-cells of one-degree resolution covering the worlds landmasses.

*Model simulation:* We simulated the life-cycle of these 5000 PGS at a daily time-step under the given climatic conditions of each grid-cell (see Sect. 2.3). The model simulates plant growth from fundamental eco-physiological processes: photosynthesis, respiration, resource allocation, phenology, and reproduction (Kleidon and Mooney, 2000). JeDi uses daily climatic inputs of solar and terrestrial radiation, as well as surface temperature and precipitation (Sheffield et al., 2006) and calculates land surface processes, such as infiltration, evaporation, root-water uptake, and surface runoff.

*Success criterion:* A PGS starts its life cycle with a fixed amount of seed carbon (t11, Table 1). A PGS is considered successful, if it was able to reproduce at least once during its life-time. Reproduction is considered successful when the plant was able to allocate its initial amount of seed carbon to its reproduction pool. The model

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assumes competitive interactions between PGS do not affect the success or failure of a PGS at the scale of a grid-cell.

*Analysis of model results:* We calculated FR and FI metrics in each grid-cell to quantify the magnitude and direction of the change between present-day and future climates.

### 2.3 Simulation setup

We ran JeDi using present-day climate data (Sheffield et al., 2006) for the period between 1960 and 1989. We looped over these 30 years of climate re-analysis until we reached 120 years, which is a sufficiently long time for the model to reach a steady-state (Kleidon and Mooney, 2000). These results are referred to as JeDi present-day simulation in the following.

We obtained the future climate data from seven global circulation models (GCMs): CCSM3, CSIRO MK3, ECHAM5, GFDL 2.1, IPSL CM4, PCM, UKMO HAD3 ([http://www-pcmdi.llnl.gov/ipcc/about\\_ipcc.php](http://www-pcmdi.llnl.gov/ipcc/about_ipcc.php)). We selected the SRES A2 (856 ppm  $p\text{CO}_2$  by 2100 AD) and B1 (549 ppm  $p\text{CO}_2$ ) scenarios developed for the 4th IPCC assessment report to account for the potential range of future climates (IPCC, 2007). We used an anomaly procedure to avoid confounding effects in our analysis due to differences in present-day climates simulated by different GCMs (Harrison et al., 1998). We superimposed the difference between the present-day climate and the future climate obtained in each GCM to the 30-year climate re-analysis described in the paragraph above. To do so, we calculated for each GCM the monthly climatic difference between the periods of 1960–1989 and 2070–2099. These monthly differences were then interpolated to a spatial resolution of one degree and disaggregated to a daily temporal resolution. Finally, we added the climate differences obtained from the different GCMs to the 30-year climate re-analysis using absolute values for temperature and terrestrial radiation, while scaling precipitation and solar radiation by the relative proportion of change to prevent negative values.

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For each of these 14 future climates (seven GCMs, 2 scenarios), JeDi was run similar to the present-day climate simulation, for 120 years looping over the 30 years of climate data. Outputs of each of these 14 simulations were used to create global maps of plant functional richness (FR) and functional identity (FI). These results are referred to as JeDi future climate simulations in the following.

## 2.4 Diversity change under climatic change

We extracted the FR of each grid-cell for JeDi present-day and future climate simulations. We calculated the change in FR for each grid-cell in relative terms, taking the difference between the present-day and the future climate divided by the FR of the present-day climate. The change in FR for each grid-cell is then the proportion of FR gain or loss with respect to the present-day climate. We averaged the FR change obtained after running JeDi for each IPCC scenario (A2 and B1) across the seven GCM future climates. To quantify the variation among these seven JeDi runs, we calculated the signal-to-noise ratio (prediction index; Murphy et al., 2004) for each grid-cell. We calculated the prediction index from the ratio between the mean and the standard deviation of FR change across the seven JeDi future climate simulations.

## 2.5 Biome shift under climatic change

We calculated the FI of each grid-cell as the vector:  $FI = [f_1, f_2, \dots, f_k]$ , where  $f$  is the mean of a functional trait across all PGS in one grid-cell and  $k$  is the number of traits ( $k = 12$ ; Table 1). For the present-day climate we derived the global distribution of biomes by clustering grid-cells according to their FI. For this purpose we used the  $k$ -means algorithm and the simple structure index to assess the quality of cluster separation (both implemented in the R packages *vegan* and *stats*). A detailed description of this procedure and its evaluation can be found in Reu et al. (2010). We used the same approach to derive the global distribution of biomes for the future climates. However, instead of repeating the full cluster analysis for each combination of GCM

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future climates and IPCC scenario, we used the cluster centers of biomes found for the present-day climate to initiate the  $k$ -means algorithm. With this approach we could track biome shifts in a consistent manner across the seven GCM future climates and scenarios. We obtained shifts in the geographic distribution of biomes from grid-cells that changed their biome membership between present-day and future climates. To quantify the sensitivity of a grid-cell changing its biome membership to GCM future climates, we calculated the fraction among the seven JeDi future climate simulations that predicted a biome shift.

## 2.6 Identifying plant functional trade-offs

We explored the trade-offs responsible for changes in FR and FI from the plant functional traits that were most responsive to changes in future climates. We selected regions of the world that considerably changed according to their FR and FI metrics. For these regions, we calculated the mean plant functional trait (Table 1) among the PSG of each grid-cell under the present-day climate and subtracted it from the mean plant functional trait under the future climates. Furthermore, we calculated the signal-to-noise ratio (i.e., prediction index) of the difference in mean plant functional traits across the seven JeDi future climate simulations. As a rule of thumb, a prediction index with an absolute value greater than two for a given plant functional trait indicated a fair agreement among the model runs (cf., Zaehle et al., 2005). Finally, to quantify the relative importance of a plant functional trade-off on FR changes we regressed changes in the respective plant functional trait to changes in FR and reported the  $R^2$ .

## 3 Results

### 3.1 Diversity change under climatic change

Figure 1 illustrates that diversity change under climatic change can broadly be classed into three major trends: (1) a loss of functional richness (FR) under future climates

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in the tropics, which host the highest FR under the present-day climate; (2) a gain of FR under future climates at mid and high latitudes; and (3) a gain of FR in regions that were not (or scarcely) vegetated under present-day conditions (e.g., hot and cold deserts like Northern Siberia, the Sahel and high mountains like the Tibetan Plateau).

5 These trends are similar under both, the A2 and B1 scenario, but the changes in FR are more pronounced under the A2 scenario (Fig. 1a, b), which also exhibits the more rapid climatic change. These findings were robust across the seven JeDi (GCM future climate) runs, showing a prediction index greater than two (Fig. 1c, d).

### 3.2 Biome shift under climatic change

10 In JeDi, biome shifts are determined by changes in the functional identity (FI) of a grid-cell that are large enough to shift this grid-cell in the trait value space closer to the centre of another biome cluster. In general, we find a poleward shift of all major biomes, which leads to a shrinking of the geographical extent of the boreal forest and tundra biomes (Fig. 2). The shifts are most pronounced in the transition zones between the temperate and the boreal forest, as well as between the boreal forest and polar/tundra biomes. In particular the temperate forest biome expanded significantly into the boreal forest biome. Finally, we found an expansion of biomes with intermediate biodiversity (grasslands, boreal forest, and savanna) into cold or hot desert regions (e.g., Sahel, Tibetan Plateau; Fig. 2). Despite significant FR losses in the tropical biome, its spatial distribution remained stable.

### 3.3 Identifying plant functional trade-offs

15 The highest FR loss occurs in the Amazon Basin and Central China. We furthermore found a FR increase and FI shift for the Sahel region. We selected these regions as case studies to further investigate the underlying plant functional trade-offs responsible for these changes in FR and FI. We found changes in the functional traits of “relative allocation to above-ground structure vs. leaves” (t07, Table 1, hereafter for the sake

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of brevity “allocation to above-ground structure”), “light use efficiency regulation” (t12, Table 1) and “seed size” (t11, Table 1) were the most strongly associated to changes in FR and FI (Table 2, Fig. 3). These results were robust across the seven JeDi future climate simulations as indicated by a prediction index greater than two (not shown).

## 4 Discussion

### 4.1 Diversity change under climatic change

We found an increase in FR at mid- and high-latitudes and a decrease at low latitudes (trend 1; results section). This general trend is consistent with projections by Sommer et al. (2010), who used empirical bioclimatic relationships to predict vascular plant species richness in 2100. The increase in FR we observed at higher latitudes and altitudes (trend 2 and trend 3; result section) is also consistent with previous observations, which reported a north- and up-ward expansion of species ranges due to increased temperatures and longer growing seasons (Walther et al., 2002; Parmesan and Yohe, 2003; Parmesan, 2006). However, empirical assessments for rapid biodiversity losses triggered by climatic change in the tropics remain scarce, perhaps because interactions with other environmental drivers like land-use change obscure or overwrite any association with climate (Sala et al., 2000). Nevertheless, several studies point towards substantial losses of biodiversity in the humid tropics under climatic change (Thomas et al., 2004; Brook et al., 2008; Asner et al., 2010). In particular, the low physiological tolerances and narrow geographic ranges predispose tropical species to extinction.

For specific regions like the Sahel and Central China Sommer et al. (2010) predicted a loss, increase, respectively of species richness, while we found a significant decrease in FR for Central China and an increase for the Sahel. We conducted a more detailed evaluation of these regions in the section “Identifying plant functional trade-offs”.

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## 4.2 Biome shift under climatic change

We found the largest biome shifts to occur at mid- and high-latitudes, while a smaller proportion of grid-cells changed in FI at lower latitudes (e.g., the tropics). Gonzalez et al. (2010) found a similar trend for biome shifts under 21st-century climates using the MC1 dynamic global vegetation model. The north-ward biome shift is consistent with observations by Walther et al. (2002) and Parmesan and Yohe (2003), who observed similar trends for the past decades.

The fate of the tropical biome, in particular the Amazon rainforest, is subject of ongoing debate (Malhi et al., 2009). Using the UKMO HAD3 GCM, Betts et al. (2004) found up to a 50% reduction of the fractional coverage of broadleaf trees between present-day and 2080 climates. Using the same climate scenario, we found a biome shift of the tropical forest into a savanna for the eastern portion of the Amazon Basin. However, this is not the case for the other six scenarios, and the apparent model disagreement in Fig. 2c (light green color intensity) in rainforest classification of the Eastern Amazon is mainly due to the simulation using the UKMO HAD3 climate change scenario. Although future climate projections for rainfall show the highest variation (uncertainty) across GCMs for this region, most grid-cells remained classified as tropical forest. It is worth noting that despite the decline in FR, the classification is maintained because the changes in FI change were not substantial enough to assign a large proportion of grid-cells to another biome cluster.

## 4.3 Identifying plant functional trade-offs

### 4.3.1 Amazon Basin

The decrease in FR for the Amazon Basin is mostly associated with changes in two functional traits: “allocation to above-ground structure” and “light use efficiency” (Table 2). Surviving PGS under future climates allocated less of their carbon to above-ground structure and were more efficient in using light for photosynthesis than those

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PGS survived under present-day climate (Fig. 3). These functional changes were associated with (1) a decrease in rainfall (up to 25%, however GCM dependent) and (2) an increase in mean annual temperature by 3–7 °C as is commonly predicted for this region under future climates.

5 One reason for this trend is that decreased rainfall leads to decreased net primary productivity and therefore plants invest less of their carbon to above-ground allocation in favor of other carbon pools (e.g., root growth, reproduction). This has been observed in an Amazonian drought experiment showing that wood allocation is the most sensitive pool of above-ground net primary productivity (Brando et al., 2008). Similarly,  
10 da Costa et al. (2010) reported a 30–50 % decrease in wood production over a 7-years experimental drought in Eastern Amazonia.

A second explanation is that under raising temperatures plants increase their autotrophic respiration according to a q10 relationship, which assumes the respiration rate to double for every 10 K warming (i.e.,  $q_{10} = 2$ ). In response to changing climate  
15 (and mainly warmer temperatures), the maintenance respiration costs of plants using light in a less efficient manner may therefore exceed their gross primary productivity, thus leading to a negative carbon balance (net primary productivity) and eventually carbon starvation. While empirical support for this carbon starvation causing observed Amazonian tree mortality (Phillips et al., 2009), and subsequently FR to decrease is  
20 scarce, modelling studies partially support this explanation (Cox et al., 2004).

Similar to other models used in global change research (Cox et al., 2000; Sitch et al., 2003; Krinner et al., 2005), JeDi assumes that, in tropical ecosystems, an increase in temperature stimulates plant respiration more than photosynthesis leading to an increase in the ratio between respiration and photosynthesis. While the response of  
25 respiration to temperature can be expected to follow a q10 relationship on shorter time-scales (Mahecha et al., 2010), acclimation of respiration rates on longer time-scales and under different climates are poorly understood (Ryan, 1991; Dewar et al., 1999; Reich, 2010). Individual PGS in JeDi do not acclimate to changing climate, and adaption on the community level (a change in FI) only occurs through changing

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vegetation composition. Modelling the interactions between maintenance respiration, plant acclimation and tree mortality may be important in understanding the importance of acclimation processes operating at longer-time scales. If a significant proportion of the PGS currently predicted to become extinct were able to acclimate at the rate of climatic change, we would expect to see a less dramatic FR loss of tropical functional richness.

### 4.3.2 Sahel

We found a strong biome shift and FR increase for the Sahel region (Figs. 1 and 2), which is mostly associated to the functional traits of “allocation to above-ground structure” and “light use efficiency regulation” (Table 2). Invading PGS under future climates allocated more of their carbon to above-ground productivity and were more efficient in using light for photosynthesis (i.e., woody encroachment, Fig. 3). This trend is associated with increased rainfall that allowed PGS to invest more assimilates into above-ground structure as well as afford higher respiration rates. In fact, these mechanisms are the inverse we discussed for the Amazon Basin. This explanation is supported by Hickler et al. (2005), who investigated the observed greening of the Sahel for the time period between 1982 to 1999 (Eklundh and Olsson, 2003) using the LPJ dynamic vegetation model. This greening trend is suggested to continue under IPCC climate warming scenarios (Hoerling et al., 2006). The Sahel is an example of regions where the future climate is predicted to become less constraining (e.g., becoming wetter or warmer), thus allowing plant FR to increase.

### 4.3.3 Central China

We found a strong decrease in FR (Fig. 1) and “allocation to above-ground structure” (Table 2) for Central China where rainfall is predicted to increase rather than decrease (IPCC, 2007). This result contradicts the findings of Sommer et al. (2010), who predicted an increase in species richness for that region. This somewhat counterintuitive

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result is associated with a change in the functional trait “seed size” (t11, Table 1) towards bigger seeds under future climates (Fig. 3).

If it is not the decrease in precipitation, what did cause the considerable loss of FR in Central China? In their original paper Kleidon and Mooney (2000) performed a complete sensitivity study of the JeDi model that revealed that “seed size” in combination with the number of wet days during the growing season can significantly impact the success of PGSs. This has been also observed under drought periods, where a seedlings chance of establishing successfully is likely to be affected by the quantity of metabolic reserves in the seed (Leishman and Westoby, 1994). Associated with the predicted increase in rainfall under future climates, intensity of precipitation is projected to increase for Central China, while the frequency of rain days is projected to decrease, especially during summer due to alterations to the South Asian summer monsoon (Kitoh et al., 2005). Increased rainfall variability in this case means more heavy rain events, but longer periods without rain. Under increased rainfall variability (or extended periods of drought despite an increase in the annual total of precipitation), plants must invest more assimilates into their seed pool in order to ensure survival of their off-springs.

We predicted seed size to positively affect seedling survival, however the magnitude of this effect on FR (Table 2) is additionally affected by the trade-off between seed size and seed number (Moles and Westoby, 2004). The seed size – number trade-off is important for ecosystem demography dynamics that are currently implemented into the JeDi model (Bohn et al., 2010). Nevertheless, our results confirm that seed size is an important plant functional trait in terms of plant’s life history (Westoby et al., 1992) that requires more attention in vegetation models that are applied to global change scenarios.

#### 4.4 Limitations of the JeDi model

At its current stage JeDi assumes, similar to empirical bioclimatic relationships, a steady-state equilibrium between climate and vegetation. For this reason, the transient dynamics of FR and FI change, involving migration and other time-lag effects,

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e.g. discussed in Jump and Peñuelas (2005) and Jones et al. (2009), remain underexplored. By considering solely the effect of climate (solar radiation, temperature, precipitation) on FR and FI, JeDi neglects other potentially important factors such as changes in ambient CO<sub>2</sub> levels, soil nutrients, fire regimes, species interactions and land-use, which may further alter our projections. Moreover, the FR as simulated by JeDi is a limited surrogate for real world plant species richness, because of different species likely being functionally redundant. Finally, the simulations of FR change do not consider potential adaptations of PGS to climatic change (e.g., via phenotypic plasticity).

## 5 Summary and conclusions

We predicted the effects of climatic change on global vegetation distribution using 14 climate change scenarios derived from 7 global climate models and 2 scenarios. At the global scale, we identified three major plant functional trade-offs potentially responsible for shifts in biome and biodiversity patterns. These encompass major aspects of plant growth strategies including trade-offs associated to resource allocation (allocation to above-ground structure and seeds), plant metabolism (light use efficiency and respiration) and their interactions with mean climate and its variability. To better understand the responses (or sensitivities) of these mechanisms to possible future climates, these trade-offs should be treated explicitly in vegetation models used in global change research. In addition, further empirical work on the presented trade-offs will help to reduce the uncertainties about their sensitivity to real world plant performance and survival.

While our projected major geographic shifts in vegetations distribution due to global warming scenarios obtained from the JeDi model are consistent with previous findings and observations, these patterns emerge from climatic constraints acting upon plant functional trade-offs rather than relying on empirically derived bioclimatic relationships as in previous studies.

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We showed that general aspects of plant physiological tolerances can be derived from plant functional trade-offs. Given its capacity to simulate global biodiversity and biome patterns based on process- and trait characteristics, we are confident that the JeDi model is a very promising alternative tool to address questions about the causes of biodiversity changes and biome shifts.

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**Table 1.** Description of the 12 plant functional traits used to define a plant growth strategy (PGS). All traits are associated to costs and benefits in terms of allocation, phenology and ecophysiology.

Model trait	Description of the effect on plant behavior	Cost	Benefit
t01	growth response time to soil moisture conditions	less time for C assimilation	tolerance to water shortage
t02	growth response time to temperature conditions	less time for C assimilation	tolerance to frost damage
t03	allocation to reproduction	less growth	increased reproduction
t04	allocation of assimilates to above-ground growth	C expenditure for maintenance	increased growth
t05	allocation of assimilates to below-ground growth	C expenditure for maintenance	increased growth
t06	allocation of assimilates to storage	less growth	tolerance to C shortage
t07	relative allocation to above-ground structure vs. leaves	less photosynthetic capacity	increased access to light
t08	relative allocation to below-ground structure vs. fine roots	less water uptake	increased access to water
t09	senescence response time to net productivity conditions	less time for C assimilation	tolerance to climatic variability
t10	relative senescence of leaves vs. roots	less growth	tolerance to climatic variability
t11	initial amount of assimilates ("seed size")	C expenditure for maintenance	increased seedling survival
t12	light use efficiency regulation*	increased respiration	increased photosynthetic capacity

\*Light use efficiency is the ratio of net primary productivity to absorbed photosynthetically active radiation, which is closely related to the nitrogen content of leaves.

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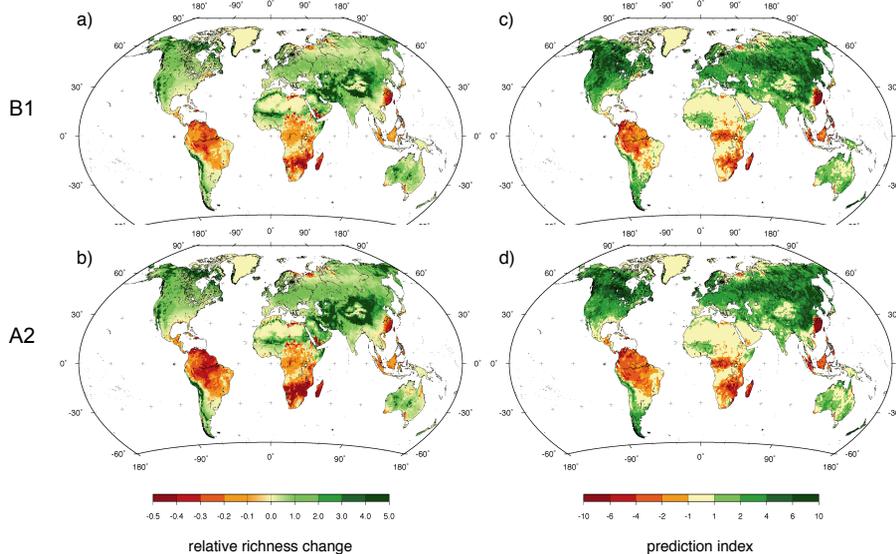
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**Fig. 1.** Mean shifts in the geographic variation of functional richness (FR) between present-day and future climate scenarios B1 (a) and A2 (b). FR increase and decrease is calculated relative to FR of present-day climates. The agreement among the seven JeDi future climate simulations is expressed as prediction index (c, d). An absolute value greater than 2 indicates a robust result across models.

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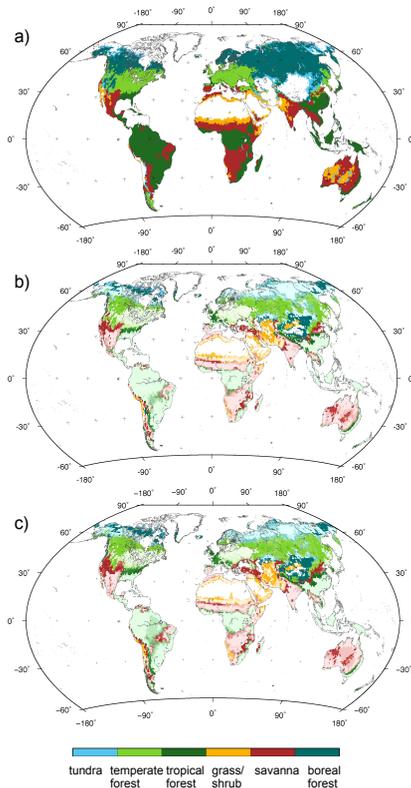
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**Fig. 2.** Biomes derived from functional identities (FI) for present-day (a), with biome descriptions identified from matching FI clusters and biomes according to their geographic correspondence. Biome shifts for B1 (b) and A2 (c) future climates. Grid-cells that are predicted to shift their biome membership are mapped in the color of their new biome. The color intensity indicates the proportion of agreement among the seven JeDi future climate simulations, with the lowest (highest) intensity indicating none (all seven) model(s) predicting a biome shift.

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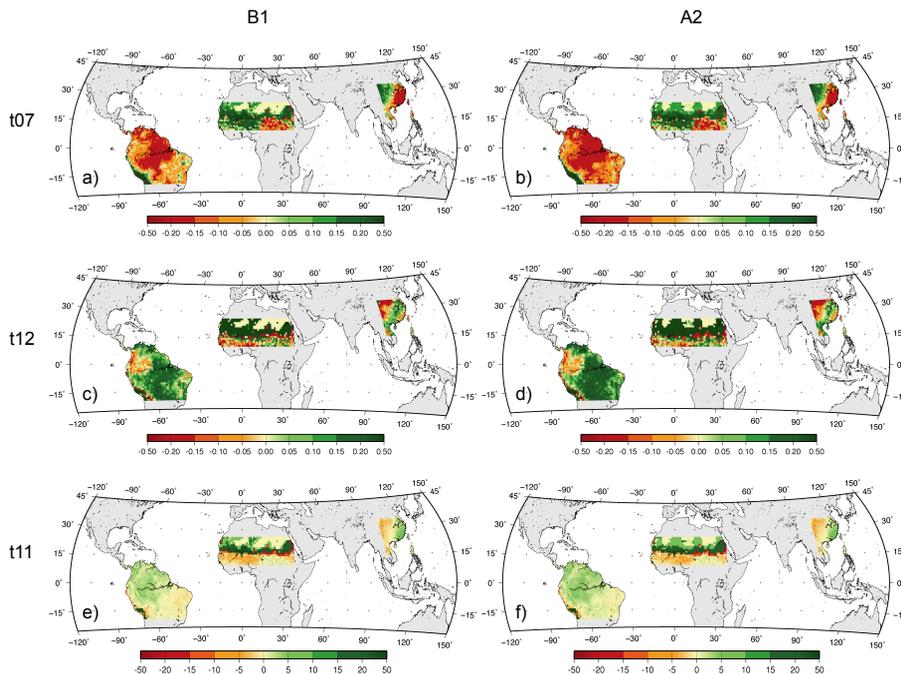
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**Fig. 3.** Mean shifts in the plant functional traits “allocation to above-ground structure” (t07; **a, b**), “light use efficiency regulation” (t12; **c, d**) and “seed size” (t11; **e, f**) between present-day and the climate scenarios (B1, A2). Values are expressed as the mean change in the respective plant functional trait across plant growth strategies (PGS) per grid-cell.

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