

Resilience of Amazon forests emerges from plant trait diversity

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Climate change threatens ecosystems worldwide, yet their potential future resilience remains largely unquantified¹. In recent years many studies have shown that biodiversity, and in particular functional diversity, can enhance ecosystem resilience by providing a higher response diversity^{2–5}. So far these insights have been mostly neglected in large-scale projections of ecosystem responses to climate change⁶. Here we show that plant trait diversity, as a key component of functional diversity, can have a strikingly positive effect on the Amazon forests' biomass under future climate change. Using a terrestrial biogeochemical model that simulates diverse forest communities on the basis of individual tree growth⁷, we show that plant trait diversity may enable the Amazon forests to adjust to new climate conditions via a process of ecological sorting, protecting the Amazon's carbon sink function. Therefore, plant trait diversity, and biodiversity in general, should be considered in large-scale ecosystem projections and be included as an integral part of climate change research and policy.

Ecological resilience has been defined as the ability of an ecosystem to absorb environmental impacts and still provide the goods and services of the initial state^{2,8}. Thereby, the species composition of the ecosystem may adjust to new conditions, enabling species that had a lesser functional role to become functionally dominant and vice versa⁹. The functional role of a species is determined by its functional traits¹⁰, and the existence of different roles implies a diversity of those traits in the community. This functional diversity, as one aspect of biodiversity, is thought to increase the response diversity of an ecosystem and, hence, ecosystem resilience³. According to this idea, tropical forests should be highly resilient ecosystems since they harbour a high plant trait diversity^{11–14} and could therefore be highly resilient, potentially ensuring the continued provisioning of their globally important ecosystem services¹⁵ in the face of environmental pressures.

Current findings support this hypothesis^{5,16}, based on experimental or observational studies of forest plots covering years to decades. To approach this hypothesis at regional and centennial timescales, we used a new dynamic global vegetation model (DGVM) that accounts for individual tree-based competition and plant trait diversity, called LPJmL-FIT (Lund-Potsdam-Jena managed Lands with Flexible Individual Traits⁷). LPJmL-FIT uses plant trait diversity to better represent tropical forests' biodiversity, enabling biodiversity–ecosystem functioning relationships to be investigated. In contrast to standard LPJmL and most other DGVMs which simulate forests based on few average tree growth strategies at the biome level in a simplistic competition scheme⁶,

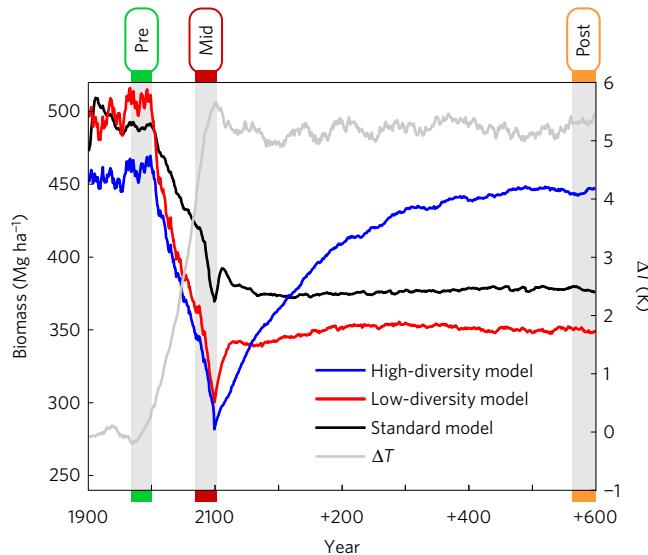


Figure 1 | Simulated rainforest biomass under climate change and different plant trait diversity. Annual biomass over 800 simulation years for 400 ha of Ecuadorian rainforest (longitude: 77.75° W; latitude: 1.25° S, Supplementary Fig. 10) from three different versions of the vegetation model LPJmL under a severe climate change scenario (RCP 8.5 HadGEM2). ΔT : annual temperature difference to the mean temperature of pre-impact time (1971–2000) in K. For different model versions see Methods.

LPJmL-FIT simulates individual competing trees which form a diverse community of growth strategies⁷ as observed in the field. More specifically, the model diversifies four key leaf traits and one stem trait according to their globally observed ranges and trade-offs (Methods and Supplementary Methods 1 and 2). The trade-offs are in line with general ecological concepts of leaf and stem economics found to explain a large part of the global variability of crucial plant traits and how they affect tree growth and survival—and hence, forest productivity and biomass^{17–20} (Methods and Supplementary Method 3). Our modelling approach opens a multi-dimensional trait space from which parameter value combinations are chosen for tree saplings at establishment. Initially, all parameter combinations from this trait space are equally likely at each study site. During tree growth and succession, competition dynamics under given environmental conditions determine which trait values and which combinations of these are successful and dominate the local tree community. Therefore, a change of environmental conditions can

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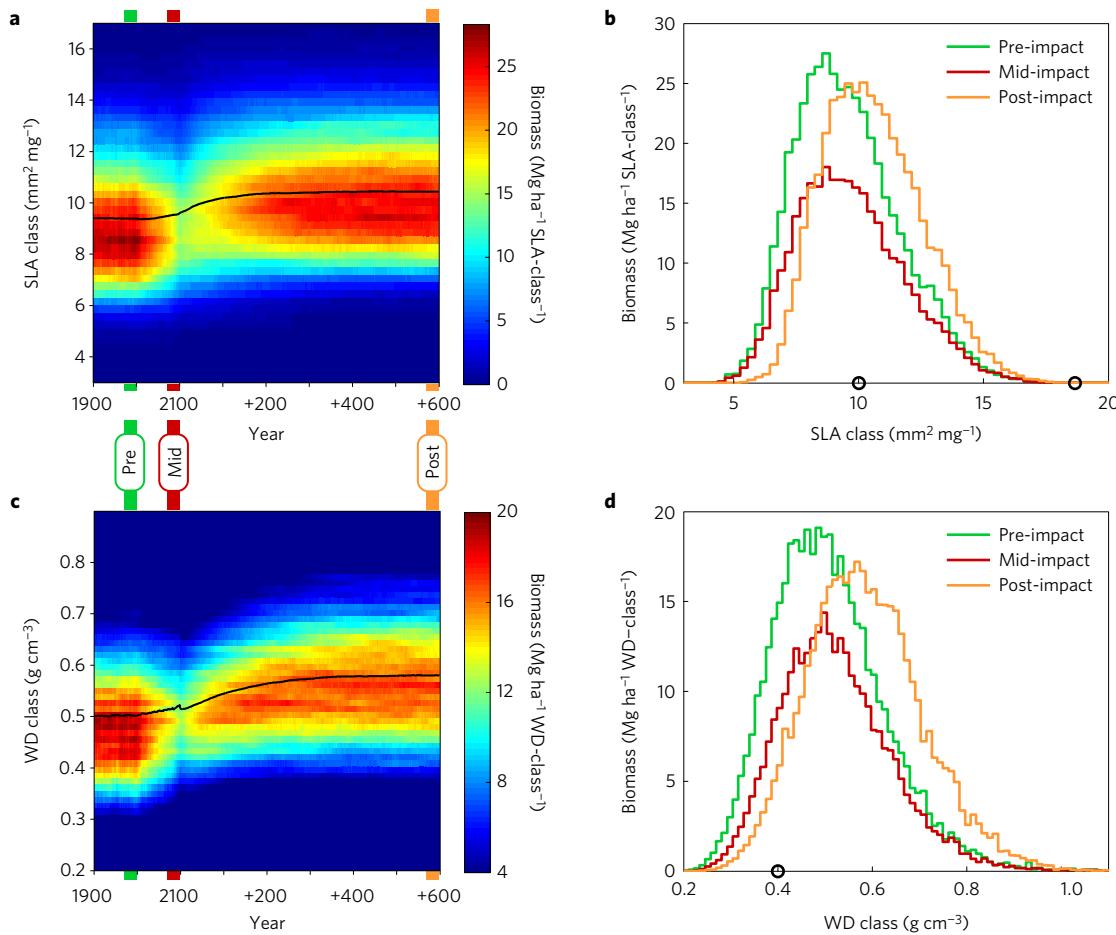


Figure 2 | Climate-change-induced plant trait shifts lead to biomass recovery. Biomass-weighted plant trait distributions of the high-diversity model (see Fig. 1 and Methods). **a,c**, Annual biomass contribution of individual trees assigned to classes of specific leaf area (SLA) and wood density (WD), respectively. The black line shows the mean of the respective trait distribution. **b,d**, Mean biomass contribution of SLA classes (**b**) and WD classes (**d**) for pre-, mid- and post-impact time (Methods). Black circles on the x-axes indicate the fixed trait values used in the low-diversity and standard model (Methods).

lead to changes in competition dynamics, ultimately changing the community composition of the simulated forest.

Here we investigated how plant trait diversity affects the ecological resilience of rainforest under climate change at an experimental site in Ecuador (Methods), for which LPJmL-FIT successfully reproduced observed plant trait distributions⁷ stored in the global plant trait database TRY²¹ (Supplementary Figs 1 and 2; Supplementary Note 1 and Supplementary Method 4). We focused on biomass resilience as one of the most important and measurable proxies for ecological resilience and defined it as the change of biomass between two points in time. We applied two climate change scenarios depicting intermediate and severe greenhouse gas emissions over the twenty-first century (representative concentration pathways²² (RCP) 4.5 and 8.5 applied to the Global Circulation Model (GCM) HadGEM2²³; Methods, Supplementary Notes 2 and 3). We focused on this range of climate scenarios because of its high potential to produce climate-change-induced impacts on the simulated forest. The objective was to assess whether the higher plant trait diversity in LPJmL-FIT leads to higher biomass resilience under climate change compared to the traditional modelling approach. Therefore, we compared the results of the default LPJmL-FIT model (hereafter high-diversity model) with the results of two other LPJmL versions. One is a low-diversity version of LPJmL-FIT (hereafter low-diversity model) and the other is the standard version of LPJmL²⁴ (hereafter standard model). Both of these functionally reduced versions use the same

two distinct tropical tree types (deciduous and evergreen trees) as plant functional types (PFT), but differ in the plant competition scheme. Whereas the standard model simulates plant competition between two average individuals of each PFT, the low-diversity model uses the gap model approach of LPJmL-FIT (Supplementary Method 1). This allows the effects of the competition schemes and plant trait diversity on simulated biomass to be disentangled. Distributions of leaf and stem traits over time are displayed for the high-diversity model to provide a mechanistic explanation for the influence of plant trait composition and height structure on the development of forest biomass under climate change. To show that the identified mechanisms apply to large spatial scales, we extended the experiment to the Amazon basin.

At the experimental site in Ecuador, biomass recovered after a climate-change-induced (RCP 8.5) decline in the high-diversity model (Fig. 1; for results under RCP 4.5 see Supplementary Fig. 3). From pre-impact time (1971–2000) to mid-impact time (2071–2100), biomass decreased by 31% (from 455 to 314 Mg ha⁻¹) due to year-round higher mean air temperatures (+5.3 K), stronger seasonality, a more severe dry season (Fig. 1 and Supplementary Figs 4 and 5), and thus increased plant transpiration at the site (Supplementary Fig. 6). While the climate remains in its mid-impact state (Methods), biomass recovered logically and levelled off in post-impact time (571–600 years after mid-impact time) at 5% below pre-impact time (431 Mg ha⁻¹, Fig. 1), meaning a biomass resilience of 95% between these points in time. Under the same

experimental settings, the low-diversity and the standard model did not show biomass recovery (Fig. 1). The absence of biomass resilience in these two model versions is consistent with other PFT-based DGVMs which also simulated a potential risk for Amazon biomass loss under a wide range of climate change scenarios of comparable severity²⁵. The qualitatively different behaviour of the high-diversity model implies that plant trait diversity enabled the future forest to recover its biomass under new climate states.

The pre-impact forest composition in the high-diversity model resulted from ecological sorting under the pre-impact climate. This community can be characterized by the underlying distributions of its key traits (Fig. 2a,c), namely specific leaf area (SLA; leaf area per unit leaf mass) and wood density (WD; wood mass per unit wood volume), which were previously validated against field data⁷ (Supplementary Figs 1 and 2 and Supplementary Note 1). SLA as a measure of leaf thickness or leaf density is closely connected to phenology and growth efficiency, whereas WD is linked to height growth and mortality⁷. The biomass-weighted distributions of these traits were stable until climate change intensified over the twenty-first century (Fig. 2). Under this stress, the abundance of canopy trees above 30 m was considerably reduced in mid-impact time, whereas medium-sized trees accumulated (Fig. 3a). The model agrees with real observations, where large exposed canopy trees which contribute most to forest biomass²⁶ are more sensitive to drought than smaller trees²⁷ as water stress reduces tree growth and increases mortality²⁸. Initially, the death of large trees increased light in the understory, providing regeneration opportunities for younger tree individuals whose traits were better suited to the new climate conditions (Figs 2 and 3). As a result, the tree community of the high-diversity model then showed a clear shift in its plant trait composition (Fig. 2). This shift improved the carbon balance and survival rates of individual trees, in return causing biomass and height structure recovery.

The simulated increase in mean SLA of 11% (Fig. 2a,b) lowered the community-level leaf construction costs per leaf area and, via trade-offs, the leaf longevities as well as the photosynthetic capacities per leaf area⁷. Producing cheaper leaves enabled newly established trees to save carbon for, for example, height growth, while at the same time reducing costs of leaf abscission under drought events. This outweighed the negative effects of generally higher leaf turnover due to lower leaf longevities and photosynthetic capacities. Therefore, higher SLAs improved the carbon balance of the new tree generation under warmer and drier conditions, which increased tree survival rates. The simulated increase in mean WD of 16% (Fig. 2c,d) was a response to increased drought-induced tree mortality (Fig. 3b), resulting in a more open forest with less competition for light. This environment enabled trees with higher WDs, and thus lower height growth rates, to be competitive. At the same time, higher WDs decreased drought-induced tree mortality⁷, in return enhancing tree survival rates. In combination, the shifts in SLA and WD increasingly contributed to the logistic recovery of total forest biomass after mid-impact time (Figs 1 and 2). Because trees are slow-growing and long-lived, there was a time lag of several hundred years between the trait shifts (Fig. 2) on the one hand and the 95% recovery of biomass (Fig. 1) and the 94% recovery of height structure (Fig. 3) on the other.

Reducing plant trait diversity to two discrete tree types (PFT1 and PFT2, Methods), in contrast, disabled a gradual shift of plant traits, preventing better suited trait combinations from becoming established (Supplementary Figs 7 and 8). Therefore, the PFT-based models (low-diversity and standard model) did not show biomass recovery. Consistently, post-impact trees in the low-diversity model failed to reach the same heights as in pre-impact time (Supplementary Fig. 9). Being less suited for post-impact time climate, the two distinct tree types performed less well, leading to lower individual heights and total forest biomass.

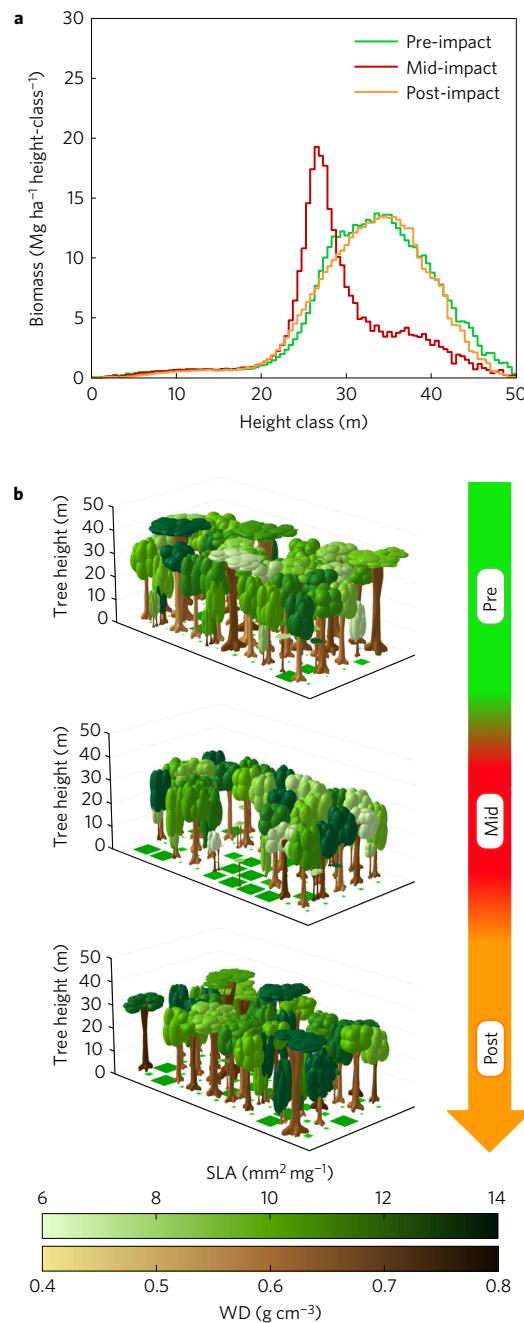


Figure 3 | Forest height structure recovers with biomass. **a**, Mean biomass contribution of tree height classes for pre-, mid- and post-impact time (Methods). **b**, Visualization of model output (also see Supplementary Movie 1) showing 0.5 ha of the 400 ha of Ecuadorian rainforest in a selected year during pre-, mid-, and post-impact time, respectively (top to bottom). Different crown (stem) colours denote different SLA (WD) values of individual trees. Crown size, stem diameter and tree height are scaled by model output. Green squares indicate tree gaps covered by herbaceous plants.

Extending the experiment to the Amazon basin (area shown in Supplementary Fig. 10), we found that biomass resilience emerged from plant trait diversity at large scales. As for the experimental site in Ecuador, we used the percentage ratio of post- and pre-impact biomass in each grid cell as the proxy for biomass resilience across the Amazon basin (Methods). We defined forest areas as resilient when they showed a biomass resilience of at least 50% per grid cell. By comparing the size of resilient areas between the high- and

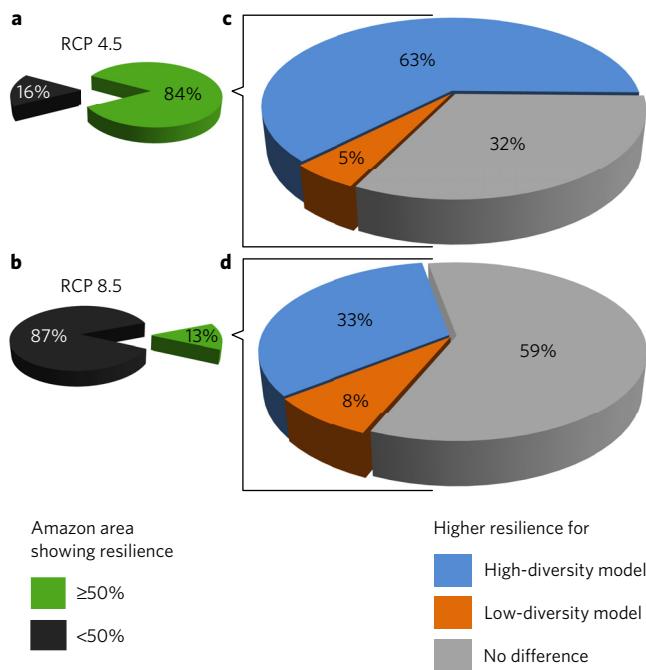


Figure 4 | Effect of plant trait diversity on biomass resilience of the Amazon basin. **a,b**, Amazon area showing at least 50% biomass resilience under RCP 4.5 (**a**) and RCP 8.5 (**b**). **c,d**, Significant contributions (Methods) of the high-diversity and low-diversity model to biomass resilience within the resilient area shown in **a,b**, respectively. Insignificant differences between the two model versions are shown in grey.

low-diversity model, we quantified the influence of trait diversity in the Amazon simulations. Under RCP 4.5 (RCP 8.5), 410 million ha (63 million ha) of the 487 million ha Amazon forests were resilient in at least one model in the grid cell-wise comparison (Fig. 4a,b and Supplementary Fig. 11). 63% (33%) of this area showed significantly higher biomass resilience (Methods) in the high-diversity model, whereas 32% (59%) showed no significant difference between the two model versions (Fig. 4c,d and Supplementary Figs 11 and 12). In contrast, only 5% (8%) of the area showed significantly higher biomass resilience in the low-diversity model. In those rare cases, one PFT of the low-diversity model was by chance well-suited to post-impact climate, showing a higher performance than a diverse forest (Supplementary Discussion 1). Overall, our findings imply that, independent of the climate scenario and regarding the total Amazon basin, the high-diversity model is always more resilient, even though the positive contribution of plant trait diversity to biomass resilience is limited by climate change intensity.

With our simulations we provide first evidence that plant trait diversity might act as an insurance against climate change impacts across large spatio-temporal scales by maintaining biomass resilience. Although about 1% of the Amazon tree species are found to make up 50% of its biomass today²⁹, we show here that this functional dominance could shift in the future. This shift in functional dominance is made possible by tree types which contribute little to forest biomass under the current climate, but which are better suited to novel climate conditions in the future. Considering the possible plasticity of traits within the lifetime of plants in future studies might result in even faster shifts of functional dominance and biomass recovery in forests, possibly enhancing biomass resilience. So far trait-based DGVMs such as LPJmL-FIT or aDGVM³⁰ are the only process-based modelling tools available for scaling up, quantifying and evaluating effects of functional diversity on ecosystem functioning at large spatio-temporal scales. Therefore, our study complements the existing body of knowledge on the importance of

functional diversity for ecosystem resilience^{11–13,31}. We argue that the relation of plant trait diversity and biomass resilience should be an integral part of ecosystem projections evaluating the future status of (tropical) forests as a carbon source or sink. Plant trait diversity, and therefore biodiversity, should be recognized as an effective means to mitigate climate change in management strategies, rather than reducing it to a co-benefit of ecosystem conservation. Given that the scientific community, policy makers, stakeholders and the general public rely on results of DGVMs, especially for climate change projections, our results may stimulate a new debate on the value of biodiversity for climate change mitigation.

Methods

Methods and any associated references are available in the online version of the paper.

Received 2 September 2015; accepted 25 July 2016;
published online 29 August 2016

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Acknowledgements

We would like to thank H. J. Schellnhuber, W. Lucht, S. Rahmstorf, A. Rammig, F. Langerwisch, A. Schlums (Potsdam Institute for Climate Impact Research) and

Ü. Niinemets (Estonian University of Life Sciences) for helpful comments that improved the manuscript. The research leading to these results has received partial funding from the European Union Seventh Framework Programme (FP7/2007–2013) under grant agreement no 283093—The Role Of Biodiversity In climate change mitigatioN (ROBIN). J.H. acknowledges funding from the Helmholtz Alliance ‘Remote Sensing and Earth System Dynamics’. The study has been supported by the TRY initiative on plant traits (<http://www.try-db.org>). The TRY initiative and database is hosted, developed and maintained by J. Kattge and G. Bönicke (Max Planck Institute for Biogeochemistry, Jena, Germany). TRY is/has been supported by DIVERSITAS, IGBP, the Global Land Project, the UK Natural Environment Research Council (NERC) through its program QUEST (Quantifying and Understanding the Earth System), the French Foundation for Biodiversity Research (FRB), and GIS ‘Climat, Environnement et Société France.

Author contributions

B.S., W.v.B., A.B., K.T., M.P.-C. and L.P. conceived the experiments, B.S. and W.v.B. performed the experiments and analysed the data, J.H. contributed material/analysis tools. B.S., W.v.B., A.B., K.T., M.P.-C., L.P. and J.J. co-wrote the paper.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to B.S.

Competing financial interests

The authors declare no competing financial interests.

Methods

LPJmL-FIT. LPJmL-FIT⁷ is a recent version of the dynamic global vegetation model LPJmL (standard LPJmL) with enhanced plant trait diversity. Standard LPJmL is a process-based model with 9 plant functional types (PFTs) for natural vegetation^{24,32–34}, 12 crop functional types and managed grass³². Each PFT parameter specifies the influence on physiology, carbon allocation and mortality risk. Parameter values may differ between but never within a PFT in standard LPJmL. LPJmL-FIT has the same model approach for physiology, but diversifies selected parameters by allowing for the observed value range of those parameters⁷. Physiological and morphological trade-offs found to explain a large part of the variability of global plant traits and connected plant performances^{17,19} ensure realistic parameter combinations and are based on statistical analyses of plant trait data from the TRY data base²¹. The light and water competition scheme in LPJmL-FIT follows the gap model approach of LPJ-GUESS³⁵ and simulates individual trees. LPJmL-FIT assigns those trees individual parameter combinations by diversifying the plant traits SLA (leaf area per unit leaf mass, mm² mg⁻¹), LL (average lifespan of leaves, in months), the maximum carboxylation rate of the RUBISCO enzyme per leaf area at 25 °C ($V_{cmax,area}^{25^\circ}$, μmol CO₂ m⁻² s⁻¹), a model internal parameter accounting for the level of water stress at which leaf abscission occurs ($wscal_{min}$), and wood density (WD, wood dry mass per unit of green volume, g cm⁻³). For the maximum range of each trait in question please see Supplementary Table 1. The trait regression functions in LPJmL-FIT were described in the Supplementary Information of Sakschewski *et al.*⁷ (formulae 1–5).

Simulation set-up and data analysis. Vegetation was simulated with three versions of the DGVM LPJmL: standard LPJmL with two tropical tree PFTs²⁴; LPJmL-FIT with high trait diversity of tropical trees⁷; and LPJmL-FIT with low trait diversity of tropical trees parameterized as the two tropical PFTs of standard LPJmL (those two PFTs are called ‘tropical broadleaved evergreen tree’ and ‘tropical broadleaved rain-green tree’, and their main difference in parameterization is the phenology strategy²⁴). Distributions of leaf and stem traits over time (Figs 2 and 3 and Supplementary Figs 7–9) refer to the two versions of LPJmL-FIT and are represented by the individual tree traits SLA, WD and tree height (in m), which are divided into distinct classes and weighted by the specific biomass contribution of each class in each year. Simulations are carried out for 400 ha of an experimental site in the Ecuadorian rainforest (latitude 1.25° S, longitude 77.75° W) where LPJmL-FIT had been previously validated against TRY data⁷, and for the whole Amazon basin. The Amazon basin³⁶ is simulated on 1946 0.5° grid cells. For each of those grid cells (roughly 2,500 km² in size), 1 ha of forest is simulated as a representative area, to stay within computational capabilities. All climate input data refers to the Global Circulation Model (GCM) HadGEM2²³ following a medium and high (RCP 4.5, RCP 8.5; ref. 22) climate change scenario from the 5th IPCC Assessment Report (IPCC AR5; ref. 37; Supplementary Method 5). Under RCP 4.5 (RCP 8.5) the Amazon basin shows an increase of mean annual temperature of 3.26 K (6.24 K) and a decrease of mean annual precipitation of 2.95% (10.37%) between pre- and mid-impact time (Supplementary Fig. 13). For all DGVM experiments the atmospheric CO₂ level was kept constant at values of the year 1901 (291 ppm) to quantify solely the effects of plant trait diversity on biomass development under climate change (Supplementary Method 6). Simulations are carried out for the time period 1900–2100, followed by 600 additional simulation years. From the year 2100 onwards the DGVM is forced with the GCM climate data of the time span 2071–2100 (mid-impact time) shuffled for 600 additional simulation years.

Output weighted by biomass. We investigate the temporal development of aboveground forest biomass because it is a widely used indicator of ecosystem

functioning³⁸. Forest phenotype composition and forest structure over time are represented by individual tree traits, namely SLA, WD and tree height (in m), which are divided into distinct classes and weighted by the specific biomass contribution of each class in each year.

Overlap of biomass-weighted trait distributions is calculated as:

$$\text{overlap} = \frac{\sum_{i=1}^n (\text{class}_{\text{pre},i} + \text{class}_{\text{post},i} - |\text{class}_{\text{pre},i} - \text{class}_{\text{post},i}|)}{\sum_{i=1}^n (\text{class}_{\text{pre},i} + \text{class}_{\text{post},i})} \quad (1)$$

with

$$0 \leq \text{overlap} \leq 1$$

where n is the number of trait classes, and $\text{class}_{\text{pre}}$ and $\text{class}_{\text{post}}$ represent the biomass contribution of the biomass-weighted trait classes for the pre- and post-impact time, respectively.

Resilience. Percentage biomass resilience is defined as:

$$\text{resilience} = \frac{\text{biomass}_{\text{post}}}{\text{biomass}_{\text{pre}}} \times 100 \quad (2)$$

where $\text{biomass}_{\text{post}}$ and $\text{biomass}_{\text{pre}}$ are the mean biomass of post- and pre-impact time, respectively. Data points are defined to have a significant difference in biomass resilience (Supplementary Fig. 11, black dots) when their corresponding standard deviation intervals [$\text{res}_{\text{min}}, \text{res}_{\text{max}}$] do not intersect with the angle bisection (see Supplementary Fig. 11), with res_{min} and res_{max} defined as:

$$\text{res}_{\text{min}} = \frac{\text{biomass}_{\text{post}} - \sigma \text{biomass}_{\text{post}}}{\text{biomass}_{\text{pre}} + \sigma \text{biomass}_{\text{pre}}} \quad (3)$$

$$\text{res}_{\text{max}} = \frac{\text{biomass}_{\text{post}} + \sigma \text{biomass}_{\text{post}}}{\text{biomass}_{\text{pre}} - \sigma \text{biomass}_{\text{pre}}} \quad (4)$$

where $\text{biomass}_{\text{pre/post}}$ and $\sigma \text{biomass}_{\text{pre/post}}$ are the mean and standard deviation of the biomass of pre- and post-impact time, respectively. For grid cells in which this criterion is not fulfilled, the effect of plant trait diversity on resilience in the two model versions is not unambiguously verifiable (Supplementary Fig. 11, grey dots).

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