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Biodiversity–productivity relationships are key to nature-based climate solutions

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The global impacts of biodiversity loss and climate change are interlinked, but the feedbacks between them are rarely assessed. Areas with greater tree diversity tend to be more productive, providing a greater carbon sink, and biodiversity loss could reduce these natural carbon sinks. Here, we quantify how tree and shrub species richness could affect biomass production on biome, national and regional scales. We find that GHG mitigation could help maintain tree diversity and thereby avoid a 9–39% reduction in terrestrial primary productivity across different biomes, which could otherwise occur over the next 50 years. Countries that will incur the greatest economic damages from climate change stand to benefit the most from conservation of tree diversity and primary productivity, which contribute to climate change mitigation. Our results emphasize an opportunity for a triple win for climate, biodiversity and society, and highlight that these co-benefits should be the focus of reforestation programmes.

Climate change and biodiversity loss are two major environmental challenges in this era of global change[1]. Although the tight linkages between them have been recognized[2,3], the vast majority of attention has been paid to one unidirectional relationship—climate change as a cause and biodiversity loss as a consequence. Climate change is projected to become an increasingly important driver of biodiversity loss[4,5] and its interaction with other major drivers such as land-use change will indirectly accelerate its impacts on biodiversity[6] further. For example, in terrestrial systems, most species ranges are predicted to shrink dramatically, even for a rise in global temperature below 2 °C[4,7]. Besides, some land-based measures of climate change mitigation have detrimental side-effects on ecosystems[4,8], because of substantial land conversions such as large-scale bioenergy crop production and afforestation with monocultures[9]. There is now recognition of the need for nature-based solutions, which involve working with nature to address societal challenges such as climate change[10–13]. Better management and restoration of natural ecosystems, such as forests, coastal lands and peatlands, could produce multiple benefits to society including the conservation of biodiversity and sequestration of carbon[2,3,10–15]. In response, the United Nations (UN) has declared the present decade (2021–2030) the Decade on Ecosystem Restoration (www.decadeonrestoration.org) to ensure ecosystem services are sustained, such as the removal of carbon from the atmosphere. However, natural climate solutions are currently missing biodiversity as part of the equation: that is, although biodiversity is often seen as a target for conservation, it is not yet widely appreciated as a powerful contributor to climate stabilization[11,13,16].

Forest productivity is often higher in species-rich forests, which absorb more carbon than species-poor forests such as tree monocultures[17–19]. Moreover, communities with more species are better able to sustain their productivity in the face of global environmental change, indicating a synergistic interaction between biodiversity and climate change[16]. Thus, conserving biodiversity, and particularly the diversity of tree species, may have a previously unquantified contribution to global climate change mitigation[13]. Biodiversity loss is increasingly recognized as a driver that can amplify climate risks and the associated economic risks[20]. However, it is still challenging to quantitatively incorporate the effects of diversity change on carbon storage—which often arise from local scale species interactions[21]—into global scale models[22,23] that assess how land-use changes and vegetation dynamics will drive future climate change[24]. Here, we assess how biodiversity effects on climate change—the ecological and marginal economic benefits of having more species in an ecosystem—might accumulate on larger scales relevant to policy[8,25].

We assess how efforts to mitigate climate change can reduce climate impacts on the diversity of woody plant species (hereafter, tree diversity), which, in turn, can safeguard the ability of forests to store carbon (Fig. 1). To assess this potential on the global scale, we quantified future shifts in species richness on the local scale (that is, 30 arcsec, total number of grids ≈ 115 million; Fig. 2) by combining multiple methods of ecological modelling (Methods).

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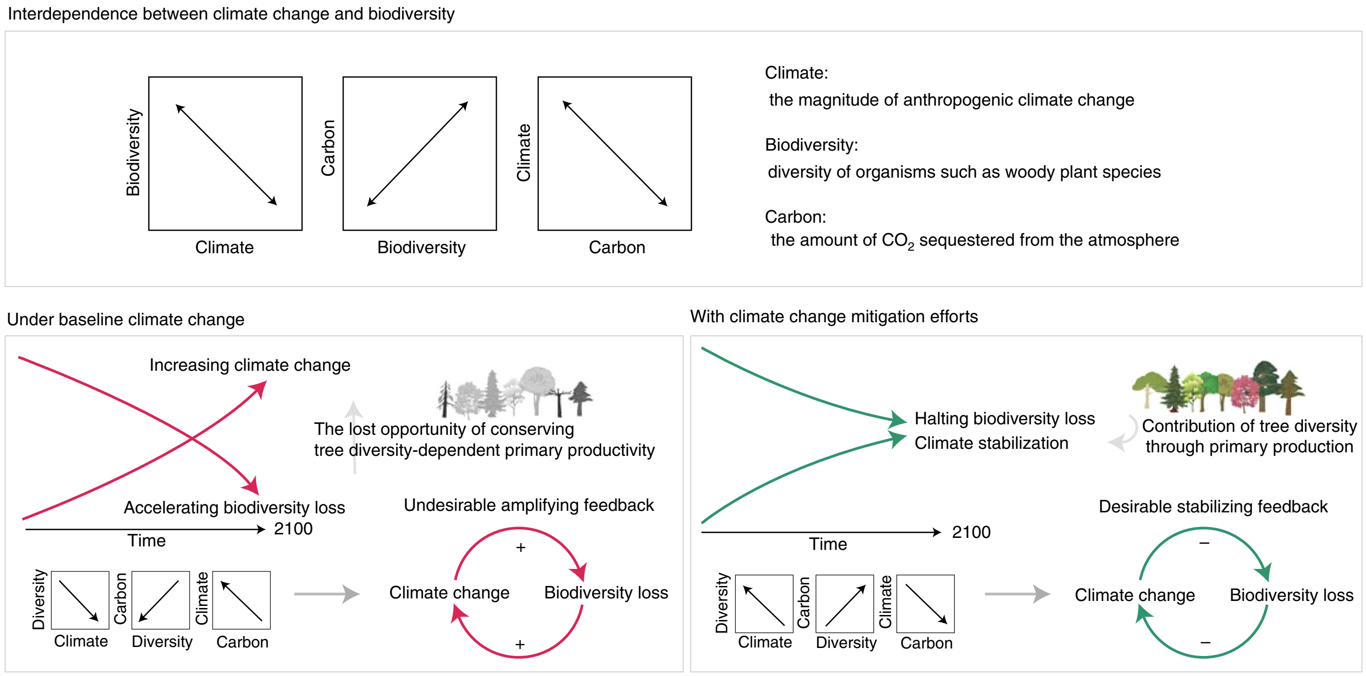

Fig. 1 | Schematic diagram of a possible pathway to biodiversity-based climate solutions. There is much emphasis on the undesirable feedbacks where climate change drives biodiversity loss (magenta arrows feedback). Here, we highlight the contribution of an underutilized positive feedback in which biodiversity-dependent productivity could contribute to climate change mitigation (green arrows feedback). The conservation and restoration of tree diversity could enhance this feedback and promote the desirable pathway whereby forest biodiversity contributes to climate change mitigation.

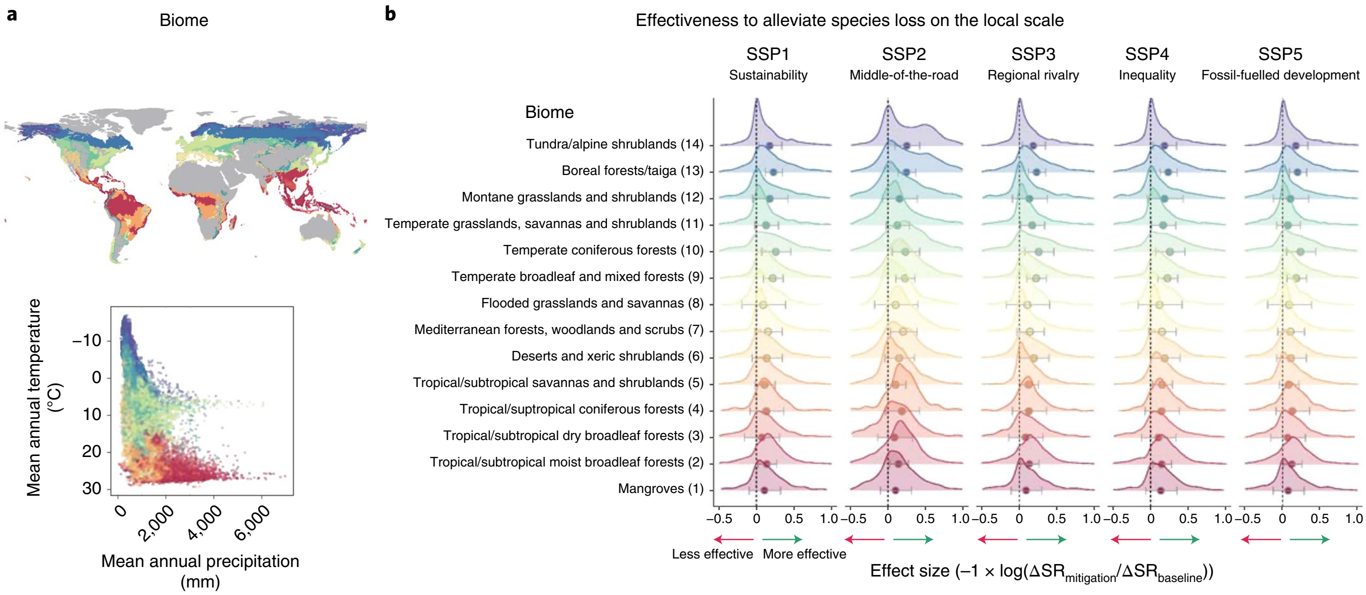

Fig. 2 | Biome-level projections in alleviating the loss of tree diversity from 2005 to the 2070s. a, Map of biomes where trees are present and the distribution of coarse grids (on the spatial scale of 30 arcmin) within each biome along temperature and precipitation gradients (annual means for the period 1970–2000). Colours of the points of each biome correspond to those shown in **b**. **b**, Ridge density plots showing the effect sizes of an effective climate change mitigation policy on ΔSR, calculated as mean α diversity change within each of the coarse grids between 2005 and the 2070s ($n=32,670$ grids). Results are shown for the five SSPs. Ensembled results across the three GCMs are shown; the points and horizontal bars indicate means and their 95% confidence intervals, respectively. When the effect sizes in each biome were converted into percentage changes, the consequences of mitigation efforts corresponded to approximately 3.0–61.3% reductions in local tree species loss compared with the respective baseline scenario. Outliers are not shown for density plots. Results for each GCM are shown in Extended Data Fig. 3. Numbers after biome names correspond to those used in Figs. 3 and 4, and Extended Data Figs. 3, 4 and 6.

We combined these local scale estimates of species richness changes with local scale estimates of proportional changes in primary productivity in response to richness changes[17]—a parameter estimated within forests, which reflects the strength of local tree diversity effects on productivity after accounting for climate and soil covariates. Then, by further multiplying these estimates by net primary

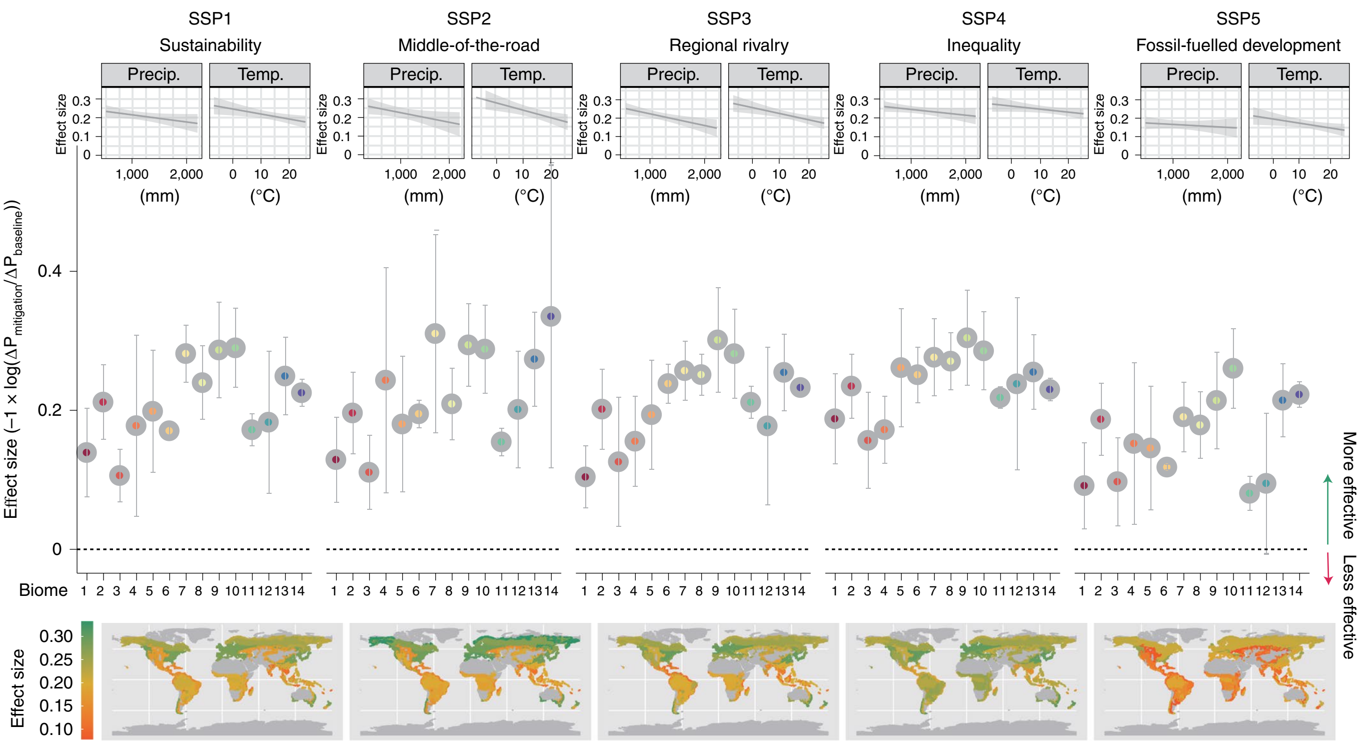

Fig. 3 | Biome-level projections in the effect of a climate change mitigation to alleviate the loss of tree diversity-dependent ΔP from 2005 to the 2070s. The effect sizes of ΔP were calculated on the local scale (on the spatial scale of 30 arcsec) in 14 biomes that include trees ($n = {\sim}115$ million grids). Results are shown for the five SSPs. Ensembled results for the effect size across the three GCMs are shown; the points and vertical bars indicate means and their 95% confidence intervals, respectively. Colours of the points and numbers of each biome correspond to those shown in Fig. 2. When the effect sizes in each biome were converted into percentage changes, the consequences of mitigation efforts corresponded to approximately 8.8–38.9% reductions in productivity loss compared with the respective baseline scenario. Results for each GCM are shown in Extended Data Fig. 4. Insets show the relations of the effect sizes with climate (annual mean temperature (temp.; °C) and precipitation (precip.; mm)); all significant at $P < 0.001$. Small maps are to visualize the effect sizes of each biome. Maps of the effect sizes on the coarse grid scale are shown in Extended Data Fig. 5.

productivity (NPP; Pg C yr^{-1}) derived from Moderate Resolution Imaging Spectroradiometer (MODIS) imagery[26], we quantified how proportional changes in local species richness could affect changes in biomass production (that is, tree diversity-dependent productivity) on the local scale. Finally, we aggregated these changes in local productivity to produce large-scale estimates of changes in productivity (due to changes in tree diversity resulting from climate change) on biome, national and regional scales (Figs. 3–5). Note that, among many primary producer species, we especially focused on tree and shrub species (hereafter jointly referred to as trees) in different biomes. As some of them are present also in non-forested biomes, our global analyses extend to woody species in all terrestrial biomes (all 14 biomes defined by the World Wildlife Fund; www.worldwildlife.org/biomes). On a regional scale, we focused on the subregion categories of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES: ipbes.net/regional-assessments)[7].

Our analyses used five Shared Socioeconomic Pathways (SSPs) reflecting different plausible projections of land-use change[27]. The underlying allocation scheme, based on an integrated assessment model, implements climate change mitigation in the form of a globally uniform carbon tax on GHG emissions from the agriculture, land-use and energy sectors[27]. Using a scenario matrix architecture, we compared two future scenarios: high-emission baseline versus mitigation scenario[28]. The mitigation scenario assumes levels of GHG emissions will stabilize the global mean temperature rise relative to preindustrial times to less than 2 °C by the end of the twenty-first century. The baseline scenario assumes a continued increase in GHG emissions, and thus also the global mean surface temperature continues to rise. We relied on three general circulation models (GCMs) to consider two different representative concentration pathways (RCPs) in each of the five SSPs[27]. Thus, we considered a wide range of future land allocation and climate conditions[28]. We quantified how efforts to mitigate climate change could alleviate species loss (ΔSR) and thereby avoid biodiversity-dependent productivity loss (ΔP) on the local scale as log ratios, with zero corresponding to the true absence of the effect (Methods).

We found that, in many biomes, climate change mitigation could substantially reduce the global loss of tree diversity that would otherwise be expected to result from an unabated continuation of climate change (Fig. 2). This, in turn, is expected to reduce the loss of productivity that would otherwise be expected to result from biodiversity loss (Fig. 3). Climate change mitigation is estimated to curtail productivity losses by approximately 9–39% compared with the baseline scenario of unabated warming (Fig. 3). The alleviated loss of tree diversity and the resultant conservation of biodiversity-dependent productivity are especially substantial in colder and drier biomes compared with warmer and wetter biomes, probably because species in these biomes are often close to the edge of their climatic niche[29]. Losing one species may have a disproportionate impact in ecosystems where only a limited number of species are filling niche space and functional redundancy is thus low. Among these biomes, cold areas in particular are expected to gain species in a warmer future, due to the poleward migration of species. However, the poor dispersal ability of trees (coupled with the pace of climate change and land-use change) generally makes it difficult for species to track their environmental optimum under

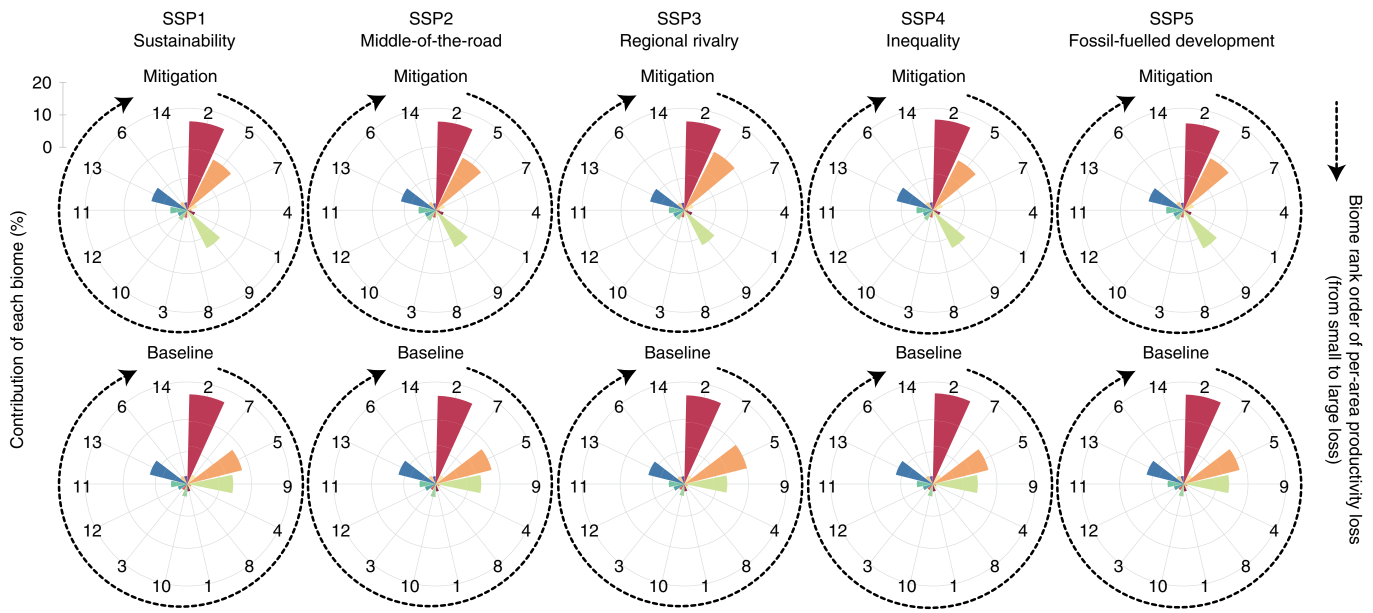

Fig. 4 | Biome-level sums in the effect of a climate change mitigation to alleviate the loss of tree diversity-dependent ΔP from 2005 to the 2070s. Radar charts showing the proportional contribution of productivity loss resulting from species loss in each biome to global productivity loss under the mitigation (top) and baseline (bottom) scenarios (%). Colours and numbers of each biome correspond to those shown in Fig. 2. The order of biomes in each radar chart is based on the per-area productivity loss of each biome (clockwise; from small to large loss), which is indicated by the black dotted arrow. Mean values across the three GCMs are shown for the five SSPs. Results of ΔP in each biome for each GCM are shown in Extended Data Fig. 6.

anthropogenic warming[28,30]. Further, warming could alter the strength of the diversity–productivity relationship, though this has not yet been well studied in forests. A possibility is that, if conditions become less limiting due to climatic warming, the productivity of individual trees might increase, potentially offsetting the negative impacts of species decline on primary productivity. Owing to these and other possibilities, the responses of tree diversity and associated productivity in a changing climate can vary by region[31]. Variable responses among biomes are also seen for the absolute impacts of losing diversity in different biomes of the world. While the per-area loss of biodiversity-dependent productivity tended to be small in warmer biomes such as tropical and subtropical forests, their gross contribution to global productivity loss was considerable due to their high absolute productivity and the extent of these biomes (Fig. 4). The analysis conducted on the IPBES subregional scale also illustrates the spatially heterogeneous effectiveness of climate change mitigation efforts in safeguarding forest productivity (Fig. 5). This heterogeneity in the responses among regions is partly due to variation in the extent to which biodiversity is conserved when climate change is mitigated (Fig. 2 and Extended Data Figs. 1–3). Furthermore, substantial land-use changes may be required for stringent mitigation efforts, especially under the scenarios of high demand for bioenergy consumption[32], which could have detrimental effects on biodiversity in some regions[4,28]. Overall, although the estimations were variable among GCMs and SSPs (Extended Data Figs. 1–7), tree diversity in most biomes and subregions would benefit from additional efforts to reduce GHG emissions. Overall, climate change mitigation efforts conserve the diversity of woody plant species and primary productivity, which contributes to carbon storage in terrestrial ecosystems.

To gain further insights at the national level, the scale on which many policy decisions are made, we aggregated the regional heterogeneity into country-level estimates and considered how tree diversity effects on productivity at the country level relate to the economic value of avoiding carbon emissions. Here, we obtained the absolute country-wide estimate of reductions in productivity loss due to climate mitigation efforts. We compared these estimates with the country-level social cost of carbon (CSCC; US\$ (t CO_2)$^{-1}$), which is the marginal damage expected to occur in a particular country as a consequence of additional CO_2 emissions produced anywhere in the world[33]. We found that countries with a high CSCC, which have the greatest incentive to mitigate climate change to avoid its economic damages, also tend to be the countries where climate change mitigation could greatly help maintain primary productivity by safeguarding tree diversity, regardless of model and scenario (Fig. 6a and Extended Data Fig. 8). Thus, countries with both large CSCC and productivity conservation potential, which especially include but are not limited to those with a large land area (Fig. 6b,c and Extended Data Fig. 9), have a great incentive to focus their efforts on stabilizing climate by safeguarding tree diversity as a potent nature-based climate solution[10], in addition to reducing the emissions from industry and the energy sector[34]. For instance, the United States and China—the two biggest emitters of carbon—are estimated to experience some of the biggest economic damages due to anthropogenic global warming[33], indicating a great responsibility and opportunity to mitigate emissions by maintaining tree diversity. Brazil has the largest potential to benefit in multiple ways from climate mitigation efforts (outliers in Fig. 6a; also see Extended Data Fig. 9). In contrast, Canada and Russia are expected to experience only small economic damages or may even benefit from climatic warming[33]. Nonetheless, as the largest forested countries in the world, their contributions are a vital part in considering biodiversity-dependent productivity as a nature-based solution, particularly as they also have experienced the largest loss of tree cover in recent years[35]. Moreover, India and Indonesia—which bear some of the greatest social costs of carbon pollution even though they are not among the top emitters of carbon[33]—have pledged to restore large areas of natural forests[14]. Such efforts offer opportunities for the international community to internalize the global climate externality and help achieve global pathways to stabilize climate while also conserving biodiversity. Although restoring natural forests and their biodiversity will not fully compensate for GHG

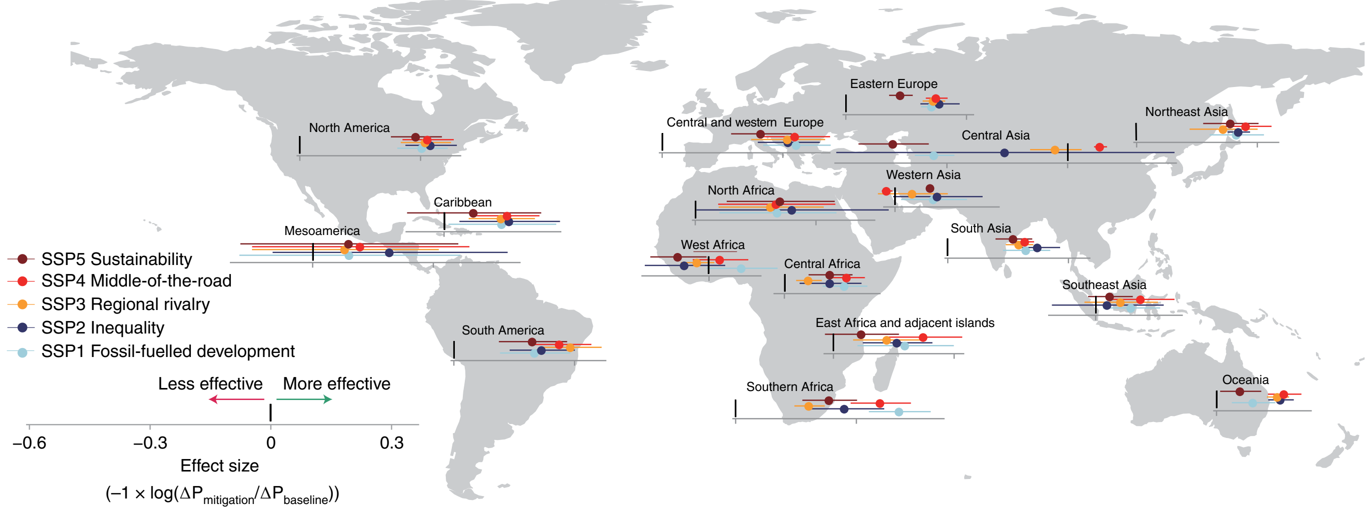

Fig. 5 | Subregion-level projections in the effect of a climate change mitigation to alleviate the loss of tree diversity-dependent ΔP from 2005 to the 2070s. The effect sizes of ΔP were calculated on the local scale (on the spatial scale of 30 arcsec cells; n = ~115 million grids) for 17 subregions (based on the IPBES[7]). Results are shown for the five SSPs. Ensembled results across the three GCMs are shown; the points and horizonal bars indicate means and their 95% confidence intervals, respectively. Vertical black bars indicate zero values of the effect size in each subregion (see scale at the bottom left). Results for each GCM are shown in Extended Data Fig. 7.

emissions, this strategy could be developed to form clear national and international targets[13].

We estimate that the possible conservation of biodiversity-dependent annual productivity by means of climate change mitigation corresponds to approximately 4.9–6.7% of the present total NPP in the terrestrial areas analysed (Fig. 6d). This substantial contribution emphasizes that biodiversity conservation is not only a target in and of itself, but can also be a critical part of the solution to the ongoing climate crisis. Our results indicate that ambitious efforts to mitigate climate change—at both the national and global levels—have a substantial potential to help societies reduce the externalized cost of carbon. Although decarbonizing the economy and relying on nature for carbon storage are both seen as important but parallel options[34], our results quantitatively show that they are tightly connected. Still, many reforestation programmes and policies focus on monocultures[11,14], which misses the potential contribution of tree diversity to carbon sequestration we highlight here. We stress the value of restoring and conserving diverse natural forests, which harbour great plant, animal and microbial biodiversity, provide a variety of ecosystem services[36], and contribute to climate stabilization[11,14]. Carbon-based forest management has been suggested as a way forward[37], but an estimated 45% of national level commitments to restore forests propose monocultures of trees profitable for businesses[14]. Planting vast expanses of monocultures will preclude the opportunity for a triple win for nature, climate and society that can arise by fostering tree biodiversity (Fig. 1).

Sustainable forest management has been emphasized in many policy contexts[38], including UN frameworks[39–41], and can provide a natural climate solution pathway[10]. While sustainable forest management emphasizes the importance of biodiversity conservation as an objective[3,36], climate policy has, to date, largely ignored the dependence of primary productivity on biodiversity and the contribution of tree diversity to carbon storage[16,19,31]. Despite this gap, reports produced by the UN Convention on Biological Diversity have repeatedly supported the use of biodiversity and ecosystem services as part of an overall strategy to help mitigate climate change and the associated risks to society[41,42]. Since 2009, this UN framework has mentioned the potential of increasing biodiversity in forests, emphasizing the positive effects on ecosystem productivity and carbon storage[41]. Yet most strategies so far have focused on avoiding further land conversion and expanding forested areas[14]. In addition to considering the spatial extent of forests, their status and quality—for example, in an extreme comparison, whether they are mono-species plantation or species-diverse old-growth stands—deserves further consideration[11,13,14,16]. A dual focus on both the quantity (area) and the quality (biodiversity) of forest ecosystems could help support climate stabilization. We therefore emphasize the great value of biologically diverse forests[16,17,19,36], both planted and restored.

The projections we make contain several sources of uncertainty, which future research could help resolve. For example, we focus on a limited subset of woody species to represent the tree diversity in the forests around the globe (Extended Data Fig. 10). Most species on Earth are still poorly described, which makes estimating their present and future ranges challenging[5]. Our estimates are thus probably conservative because they are based on well-documented species, whereas poorly described species, which often have narrow geographical ranges and small population sizes, are more prone to climate-driven extinction[43]. Given the disproportionately large contributions by some rare species to ecosystem functioning[44], our approximation of biodiversity-dependent productivity could be seen as a lower bound estimate. Although modelling the spatial distributions of rare species, which generally have a limited number of occurrence data, is challenging, analytical approaches are developing rapidly to foster the conservation of poorly described species[45]. These emerging methods will help to improve future estimates of biodiversity change and its consequences for the supply of ecosystem services.

Another source of uncertainty is that new combinations of species are likely to emerge under a changing climate[3], which may alter interactions between species[29] and probably influence the magnitude of diversity–productivity relationships[31]. Although the dispersal ability of each tree species is explicitly considered in our analysis, it is highly likely that novel combinations of species will emerge in the future, resulting from idiosyncratic events (for example, exceptional long-distance dispersal[46]) and human influences (for example, climate-suitable planting and assisted migration[12,31]). Furthermore, our results should be interpreted with care because responses at the biome level were not necessarily consistent across socioeconomic pathways (Fig. 3). This was especially true when summarized on

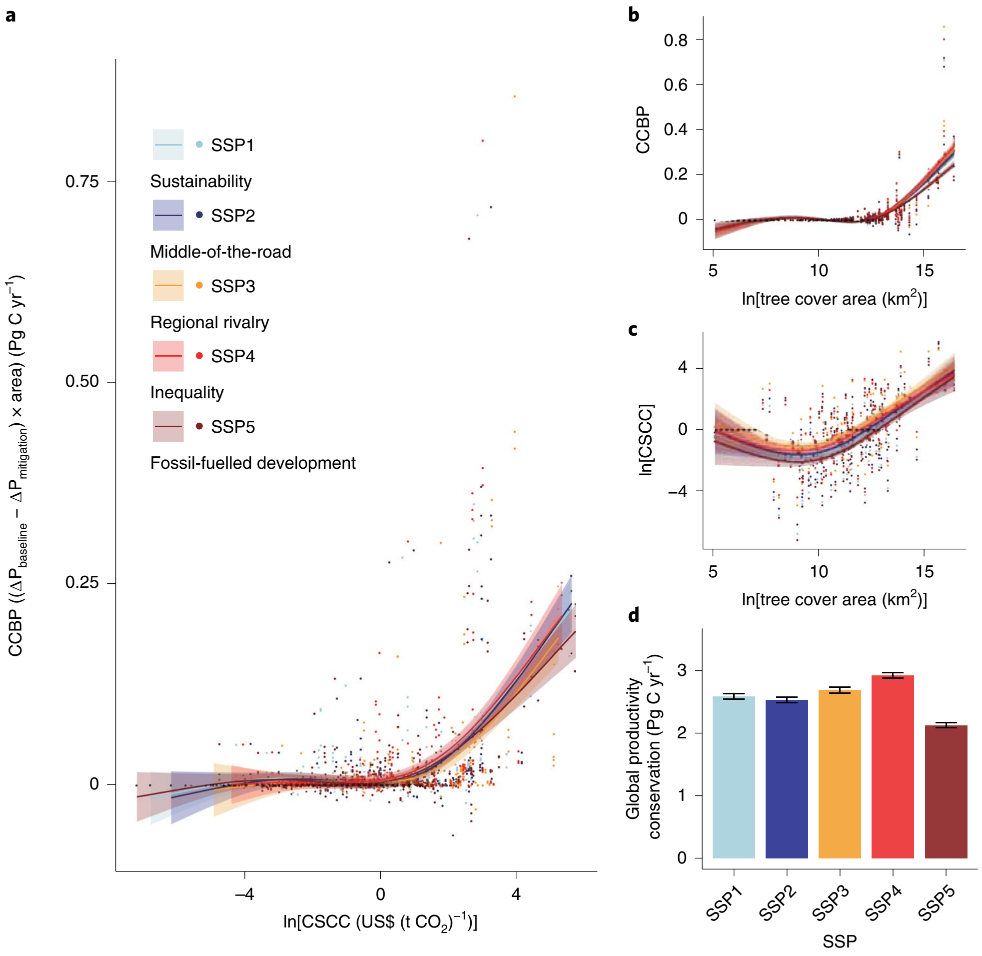

Fig. 6 | Country-level outcomes of a climate change mitigation to conserve tree diversity-dependent productivity. a, The relationship between the CSCC[33], which is the marginal damages expected to occur in a particular country as a consequence of additional CO_2 emissions, and the country-level conservation of biodiversity-dependent productivity (CCBP; the differences in local productivity changes, ΔP, between the two scenarios aggregated for each country). The largest value (outlier) of CCBP is Brazil for all SSPs. Results for each GCM are shown in Extended Data Fig. 8. **b**,**c**, The relationships of the terrestrial area analysed for each country with the CCBP (**b**) and the CSCC (**c**). The lines and shaded areas are the estimates based on a generalized additive mixed model and their 95% confidence intervals, respectively. Results are shown for the five SSPs. **d**, The sum of productivity conservation across countries for the five SSPs (mean ± standard error across three GCMs). These estimates corresponded to 4.9–6.7% of total NPP in the terrestrial areas analysed.

large scales such as at the level of the IPBES[7] subregions (Fig. 5): large variability was especially identified in Western/Central Asian and West African subregions, where the outcomes of climate change mitigation policy ranged from negative to positive. In this study, we did not separate the individual influences of different climate mitigation practices (for example, reforestation, bioenergy production and low-carbon energy use) on biodiversity and primary productivity, but doing so could help identify drivers underlying such inconsistent responses in the future. For example, if mitigation goals were achieved by afforestation in formerly non-forested lands such as peatlands and grasslands, then this could have unintended negative impacts on biodiversity and the productivity of these ecosystems[47]. Another consideration is that the ability of forests to increase the uptake of carbon in the short term (for example, over the next decade) cannot be linearly translated into the ability of forests to halt climate warming over a 50–100-year time horizon. This is because complex biogeochemical and biophysical processes—for instance, surface exchange of energy and water vapour and sensible heat flux, resulting from compositional and structural changes in forests—might not directly parallel the effects of carbon uptake rates on climate[48,49]. Carbon storage in deadwood and soil—critical drivers of terrestrial carbon dynamics[19,50]—was also not considered in this study. Finally, in our estimates of the change in social cost from conserving species and productivity (Fig. 6), we did not fully account for management and opportunity costs. Nonetheless, our estimates provide a first global assessment of the contribution of biodiversity in forests to climate change mitigation on which future refinements can build.

We advocate for the protection and restoration of biologically diverse forests because they can make a substantial contribution to climate change mitigation[16,19], helping to avoid irreversible change to the Earth system[1]. Nature-based solutions are among the fastest[2] and most cost-effective policy options[10,11]. As such, there is an enthusiasm for relying on trees and forests to recapture carbon[37]. Now, it is urgently necessary to accurately assess this potential to guide the ongoing efforts such as the Intergovernmental Panel on Climate Change[51]. Here we identify an important backbone for these considerations—tree diversity—as a missing piece of the nature-based climate solution puzzle. By buying time[4], climate mitigation efforts are essential to help both people and biodiversity adapt to climate change[12]. Our emphasis on biodiversity-dependent climate change mitigation is thus also important for ecosystem-based adaptation[3]. However, a nature-based approach is only one option[15,52] along with others that are necessary, including substantial reductions in energy emissions and the transition to renewable sources of energy[34]. Although challenging, reducing the adverse impacts of climate change on species in ecosystems is important (Fig. 2), as they serve as a massive sink and storehouse of carbon (Figs. 3–5), thereby contributing to climate stabilization (the desirable pathway to stabilizing feedback between climate change mitigation and biodiversity conservation in Fig. 1). Solving one environmental problem may help address the other, whereas failing to address either problem may lead to the further deterioration of both biodiversity and climate crises. Here we show an opportunity to create a triple win for climate, nature and society by simultaneously protecting and leveraging the ecosystem benefits contributed by the biodiversity of the world's forests.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-021-01062-1.

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Methods

Our workflow of how to estimate proportional changes in species richness and forest productivity as well as absolute changes in NPP on the local scale is visualized in Supplementary Figs. 1 and 2. We refer to the Supplementary Information for a full description of the methods, and provide only a succinct summary of our approach here.

Species distribution modelling. Spatially explicit observations of tree and shrub species (hereafter referred to as trees) were available from a previous study[28]. Also see Supplementary Table 1 for the protocol of our species distribution modelling, which relied on climate and land-use variables. Note that the modelling was previously conducted at a spatial resolution of 30 arcmin (hereafter, coarse grids). Here we extended the modelling to a resolution of 30 arcsec (hereafter, fine grids) to improve our approximation of biodiversity-dependent productivity (see below). However, the modelling for species distributions on the fine scale was possible only for the present period, because future land-use variables were available only on the scale of coarse grids. We sampled one occurrence record per grid for all species at both spatial resolutions. To avoid the effect of model inaccuracy from small sample size, we limited our analysis to species that had occurrence records of 30 and more[53]. These resulted in 1,755 and 934 target tree species at a spatial resolution of fine and coarse grids, respectively. See Supplementary Data 1 for the list of these target species.

For the present period, we obtained a dataset of 19 bioclimatic variables, calculated from monthly minimum temperature, maximum temperature and precipitation at the resolution of fine grids downloaded from the WorldClim 1.4 (www.worldclim.org)[54]. Then, we obtained land-use variables at a resolution of fine grids from the MODIS land cover type for the year 2005 (glcf.umd.edu/data/lc; accessed April 2018). We used land cover classes from the global vegetation classification scheme of the International Geosphere-Biosphere Programme (www.igbp.net) as a categorical variable in our models of species distribution. One of the five land-use types (cropland, pasture, forest, other natural lands and settled land) was assigned to each of the fine grids. For future scenarios, we focused on a mitigation scenario and a high-emission baseline scenario based on the RCPs: the mitigation scenario aimed to stabilize climate change by the end of the twenty-first century, whereas the baseline scenario assumed increasing GHG emissions and thus climate change over time[28]. We set the target period for analyses as the 2070s. We used future climatic variables based on three GCMs included in the Coupled Model Intercomparison Project Phase 5 experiment: MIROC-ESM-CHEM[55], HadGEM2-ES[56,57] and GFDL-CM3 (ref. [58]), downloaded from the WorldClim 1.4 (www.worldclim.org)[54]. All 19 bioclimatic variables for the future were calculated using the same method as for the current climate. We estimated changes in future land use under the mitigation and baseline scenarios[27] with AIM/CGE[59], a computable general equilibrium model representing the entire global economy. AIM/CGE implements climate change mitigation in the form of a global uniform carbon tax on GHG emissions from the agriculture, land-use and energy sectors. The allocation of land by sector for 17 regions is formulated as a multinomial logit function to reflect differences in substitutability across land rent, and regional land use is further downscaled to the scale of coarse grids based on spatially explicit attainable yields[60]. In this study, we relied on the SSPs framework[61]. The SSPs are based on five narratives describing how socioeconomic factors may change over the next century, considering changes in population, gross domestic product, energy, emissions and land use: challenges to adaptation and mitigation are both low (SSP1: sustainability) or both high (SSP3: regional rivalry); low challenges to mitigation are combined with high challenges to adaptation (SSP4: inequality); high challenges to mitigation are combined with low challenges to adaptation (SSP5: fossil-fuelled development); intermediate challenges exist for both adaptation and mitigation (SSP2: middle-of-the-road). Also, refer to Supplementary Table 2 for these narratives. The SSPs employ a concept called scenario matrix architecture, which has a two-dimensional space comprising combinations of socioeconomic patterns, represented by the SSPs, and climate change mitigation levels, represented by RCPs. For our mitigation scenarios, we used each SSP, combined with the RCP with the lowest radiative forcing level. SSPs 1, 2, 4 and 5 were combined with RCP2.6. SSP3 was combined with RCP3.4 because the SSP3–RCP2.6 combination was found to be incompatible[61]. We used the high-emission baseline condition in each SSP for the baseline scenario, assuming the absence of additional climate policy and efforts. Given that land-use scenarios explicitly incorporated areas for bioenergy crops and afforestation for GHG mitigation activity, which did not exist in land-use data in the current condition, bioenergy crops and afforestation were merged into cropland and forests, respectively.

Using these variables, we employed Maxent v3.3 (ref. [62]) for predicting the current and future probability of occurrence of target species. First, by using the five land-use and 19 bioclimatic variables, we generated all possible combinations of these explanatory variables. We then excluded explanatory variables showing collinearity. We selected the most parsimonious combination of explanatory variables based on the corrected Akaike information criterion[63]. Among the final models developed for all species, we discarded those with poor performance for subsequent analyses based on tenfold cross-validation, as follows. We used models with Boyce index[64] >0 based on the 95% confidence interval for the subsequent analyses. To obtain a map of suitable habitat for each species under the current conditions, the average value of the relative probability of occurrence calculated by the tenfold cross-validation was converted into a binary map. We applied the average of the 90% sensitivity threshold to minimize the false-negative fractions and to avoid underestimating the suitable habitat area[65]. For future scenarios, we explicitly included a species' ability to disperse and track the shifting climate[28] by considering dispersal traits[66]. Here dispersal distance per generation was estimated from the formula based on earlier work[66]. Based on this approach, we obtained habitat maps for individual species. The possible changes in areas hospitable to species under different future scenarios were described earlier[28]: briefly, the losses of suitable habitats due to the combined effects of climate and land use were estimated to be smaller in the mitigation scenario than in the baseline scenario (for example, approximately 17–28% and 22–36% for the mitigation and baseline scenario, respectively, across a wide range of organism groups).

Species richness and productivity estimation. We projected spatial distributions of individual species for the year 2005 and the 2070s at a spatial resolution of 30 arcmin (coarse grids; $n=32{,}670$). For both estimates, we obtained the total number of species present in each coarse grid (γ diversity). For the former year, we also projected spatial distributions of individual species at the spatial resolution of 30 arcsec (fine grids; $n=115{,}426{,}714$). Based on these projections, we calculated changes in species richness on the scale of fine grids (α diversity) from 2005 to the 2070s for different scenarios of climate and land-use change. We first obtained species–area and endemics–area relationships (SARs and EARs, respectively) for 2005 that were unique to each of the coarse grids. If all fine grids were forested, a coarse grid had 3,600 fine grids. These relationships were used to estimate α diversity in the year 2005 ($n=32{,}670$ grids; each coarse grid had a unique mean value of α diversity). Note that it was infeasible to directly estimate the temporal changes in γ diversity because future spatial distributions were estimated only for a subset of species present in the 2005 data (that is, widespread common species). Instead, we used the number of these common species that went extinct from or immigrated into a given coarse grid by the 2070s for estimating the number of other subordinate species (which were excluded in the Maxent analysis for the period of 2070s because of limited occurrence on the scale of 30 arcmin) that went co-extinct or co-immigrated.

To implement this, we first ran two spatially explicit simulations for species co-extinction and co-immigration. In an artificial landscape with 3,600 homogeneous grids, we randomly drew between 5 and 80 species with total occurrence between 500 and 180,000 individuals, based on a lognormal species abundance distribution with randomly assigned parameters μ and σ of species abundance distributions reported in different biomes[67–69]. To consider many possibilities of spatial patterns of tree individuals in different biomes, we randomly assigned individuals of each species to each of the 3,600 grids. For each of these artificial meta-communities, we calculated mean α diversity (number of species per grid), γ diversity (number of species per landscape), Whittaker's multiplicative β diversity and Shannon's evenness (across the grids)[69]. We also constructed SARs for estimating species richness on the smallest spatial scale. Here we defined common species as abundant species that had an abundance rank of 25% and above. For co-extinction simulation, we randomly made some (up to half) of these common species extinct from a meta-community. Other rare species that were present in the same grid with these extinct common species were also forced to extinction, assuming that these grids became no longer habitable for any species. For co-immigration simulations, we assumed that an artificial meta-community resulted from additional immigration of both common and rare species. We again randomly assigned some (up to half) of the species as common and removed them from the meta-community to construct a pre-immigration meta-community. We also removed individuals of other species that were present in the same grid with these common species, assuming that these grids became newly hospitable in a post-immigration meta-community. We repeated the above co-extinction and co-immigration simulations 25,000 times each. Based on the results from these artificial landscapes, we used extreme gradient boosting (XGBoost)[70] to obtain machine learning regressions for predicting the number of species co-extinct and co-immigrated based on other information described above.

We applied these regressions to the results of species distribution modelling (see Supplementary Fig. 2 for a schematic diagram). By comparing the number of widespread common species in each coarse grid between the 2005 and the 2070s, we obtained the number of common species extinct or immigrated. This information was combined with our XGBoost regressions to obtain the potential number of subordinate species co-extinct and co-immigrated in each coarse grid. When we observed extinctions of some species for the 2070s in a given coarse grid, we converted this total number of species lost into a proportion of habitats that was required for losing these species based on the unique EAR[71]. When we observed immigration by some species for the 2070s in a coarse grid, then we converted this total number of species gained into a proportion of habitat that was required to gain these species based on the unique SAR[71]. By multiplying these proportional changes in the habitable area for the period of the 2070s with species richness values on the scale of fine grids, which were derived from the unique SARs in the year 2005, we obtained the values of α diversity in the 2070s. In some coarse grids, it was not possible to obtain unique SARs or EARs for reasons such as low γ diversity. In such a case, we assumed that proportional changes in the habitable areas between the two periods were estimated by relying on an empirical SAR with the slope value of 0.3 in log–log space[72,73]. Based on the changes in γ diversity, we estimated the values of α diversity in the 2070s. Note that, like the year 2005, each of the coarse grids in the period of the 2070s also had a single unique value of α diversity ($n = 32,670$).

We calculated proportional changes in α diversity from the year 2005 to the period of the 2070s (%) and converted them into proportional changes in forest productivity (%) based on parameters of the elasticity of substitution (θ), which we estimated for forest biomes worldwide[17]. The elasticity of substitution can be used to estimate forest productivity based on proportional changes in tree species richness (that is, α diversity). The values of the elasticity of substitution were originally estimated based on forest inventory datasets collected on the local spatial scale[17]. For avoiding a potential mismatch due to scaling issues[23,74], we estimated the changes in productivity on the scale of fine grids. We used an NPP dataset estimated using the MODIS imagery[26] for the year 2005 (note, in the terrestrial biomes analysed here, total NPP was approximately 43.78 Pg C yr^{-1}). We obtained NPP values on the scale of fine grids. Here we assumed that all fine grids in a given coarse grid showed the equivalent changes in productivity on a proportional scale, reflecting the mean change in α diversity expected to occur in that coarse grid. Based on these estimations, we have obtained absolute changes in forest productivity (kg C m^{-2} yr^{-1}) for different scenarios of climate/land-use change on the scale of fine grids. Note that our analyses for tree diversity and productivity changes were conducted for the grids where tree species were observed in the present period and θ values were available (resulting in the analysis of ~115 million fine grids); thus, the results are also shown for non-forested biomes.

Data analyses. We summarized our results on different spatial scales from local to global. Here, the fine grids are defined as the local scale. We also focused on the scales of countries and biomes. Terrestrial biome categories are based on the 14 terrestrial ecoregions used by the World Wildlife Fund (www.worldwildlife.org). We have obtained information for areas and names of individual countries from Natural Earth (www.naturalearthdata.com). To be relevant for global policy, we have summarized results also on the scale of the subregion used in the IPBES (www.ipbes.net/regional-assessments). For some territories and nations that are not explicitly classified into regional categories, we assigned their subregions based on their geographical locations.

To quantify the effect sizes of mitigation efforts on conservation of species and productivity, we calculated the reductions in local scale ΔSR and ΔP as a log ratio scale, which assumes that zero corresponds to no difference between the two scenarios. Estimates based on the baseline and mitigation scenarios were used for the denominator (control; $\Delta SR_{\mathrm{baseline}}$ and $\Delta P_{\mathrm{baseline}}$) and numerator (treatment; $\Delta SR_{\mathrm{mitigation}}$ and $\Delta P_{\mathrm{mitigation}}$), respectively. To facilitate interpretation, we multiplied -1 by the effect sizes and thereby positive and negative values, respectively, indicate a more and less effective climate change mitigation policy in reducing species loss and the associated productivity loss (see a schematic diagram in Supplementary Fig. 3). To ensemble results across the three GCMs, we obtained global means and the associated 95% confidence intervals for each SSP scenario. We repeated the above calculations at the biome, IPBES subregion and countryscale. For biome-level analyses, we used a mixed-effects meta-regression with the effect size as a response variable, the GCMs as a random effect and climate conditions (mean annual temperature or precipitation of biomes) as a moderator.

Then, we focused on the relationship between the CSCC (US\$ (t CO$_2$)$^{-1}$ (ref. [33]), estimated for each of the SSPs) and the country-level reduction in forest productivity loss under a given SSP. Here we were interested in the country-level loss of productivity (absolute changes within each country), instead of the productivity loss per area that can give the average estimates of local productivity changes within a focal area (for example, proportional changes within each country). We thus summed up the differences between $\Delta P_{\mathrm{baseline}}$ and $\Delta P_{\mathrm{mitigation}}$ within each country and multiplied these values by the area of each country (Pg C yr^{-1}). For each of the individual combinations of SSPs and GCMs, we relied on a generalized additive model with the CSCC as an explanatory variable. To ensemble results across the GCMs, we used a generalized additive mixed model with the GCMs as a random effect and the CSCC as an explanatory variable. We additionally checked if the results were affected by land area, using the generalized additive mixed models. Lastly, we summed up the reduction in productivity loss across all countries, under each of the SSPs and GCMs. This gave us the estimate of global productivity conservation, corresponding to the value, global $\sum (\Delta P_{\mathrm{baseline}} - \Delta P_{\mathrm{mitigation}})$.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The source data underlying figures (Supplementary Data 1–6) are archived in the Dryad repository: https://doi.org/10.5061/dryad.vq83bk3s2.

Code availability

The code that supports the findings of this study is available from the corresponding author upon reasonable request.

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Author contributions

A.S.M. designed the study with critical inputs from F.I., R.S. and T.N. H.O. and T.M. analysed species distributions, and A.S.M. and K.O. contributed to the

following analyses. J.C., A.G. and A.S.M. developed a conceptual diagram of biodiversity-dependent climate solutions. H.O. and T.N. contributed to developing the protocol of species distribution modelling. W.T. contributed to developing land-use data. A.S.M., L.E.D., A.G., R.S. and F.I. prepared drafts to have further discussions among all authors. A.J.W., J.C., Y.H., P.B.R. and M.L. provided substantial inputs on drafts and revisions of the paper.

Competing interests

The authors declare no competing interests.

Additional information

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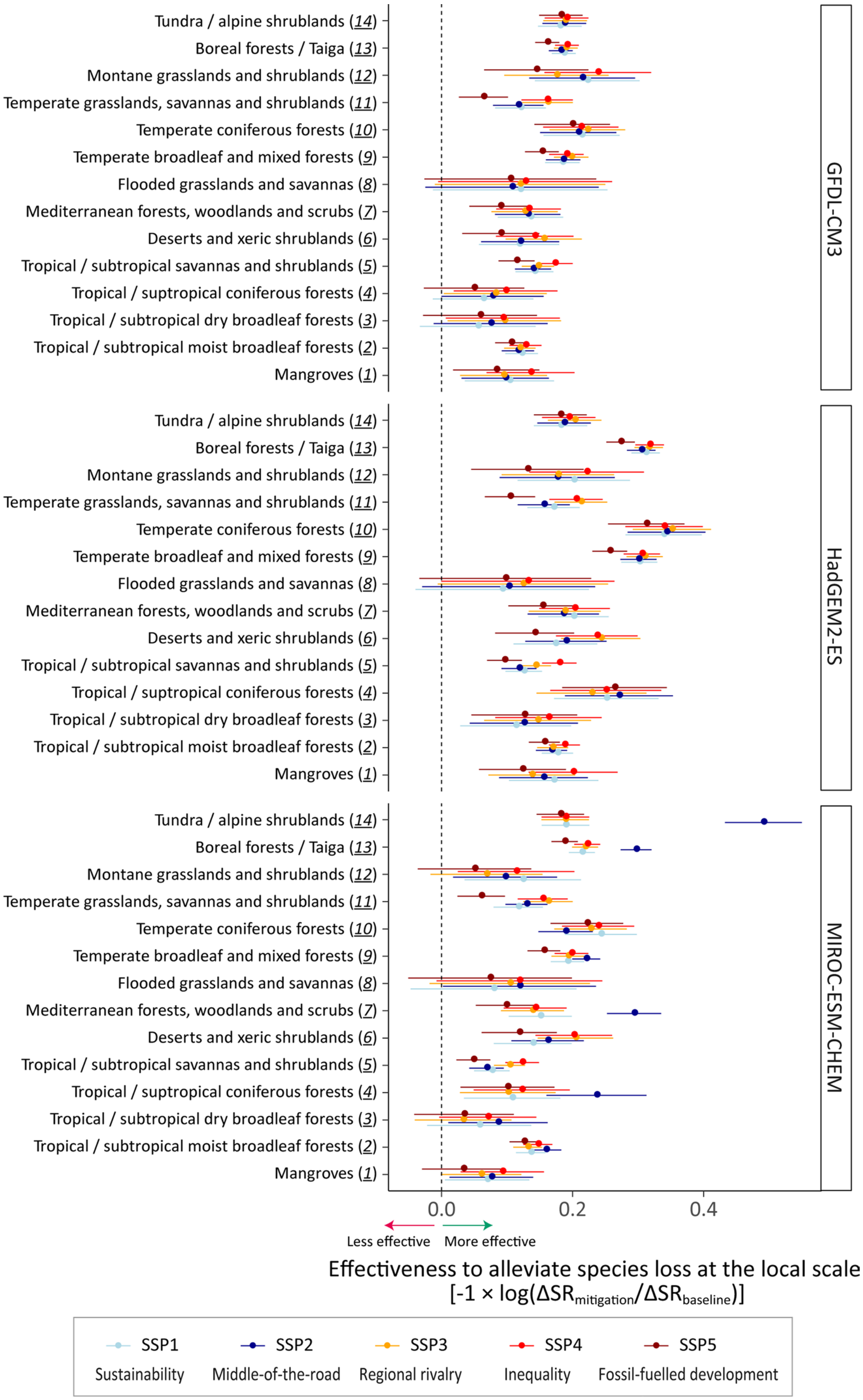
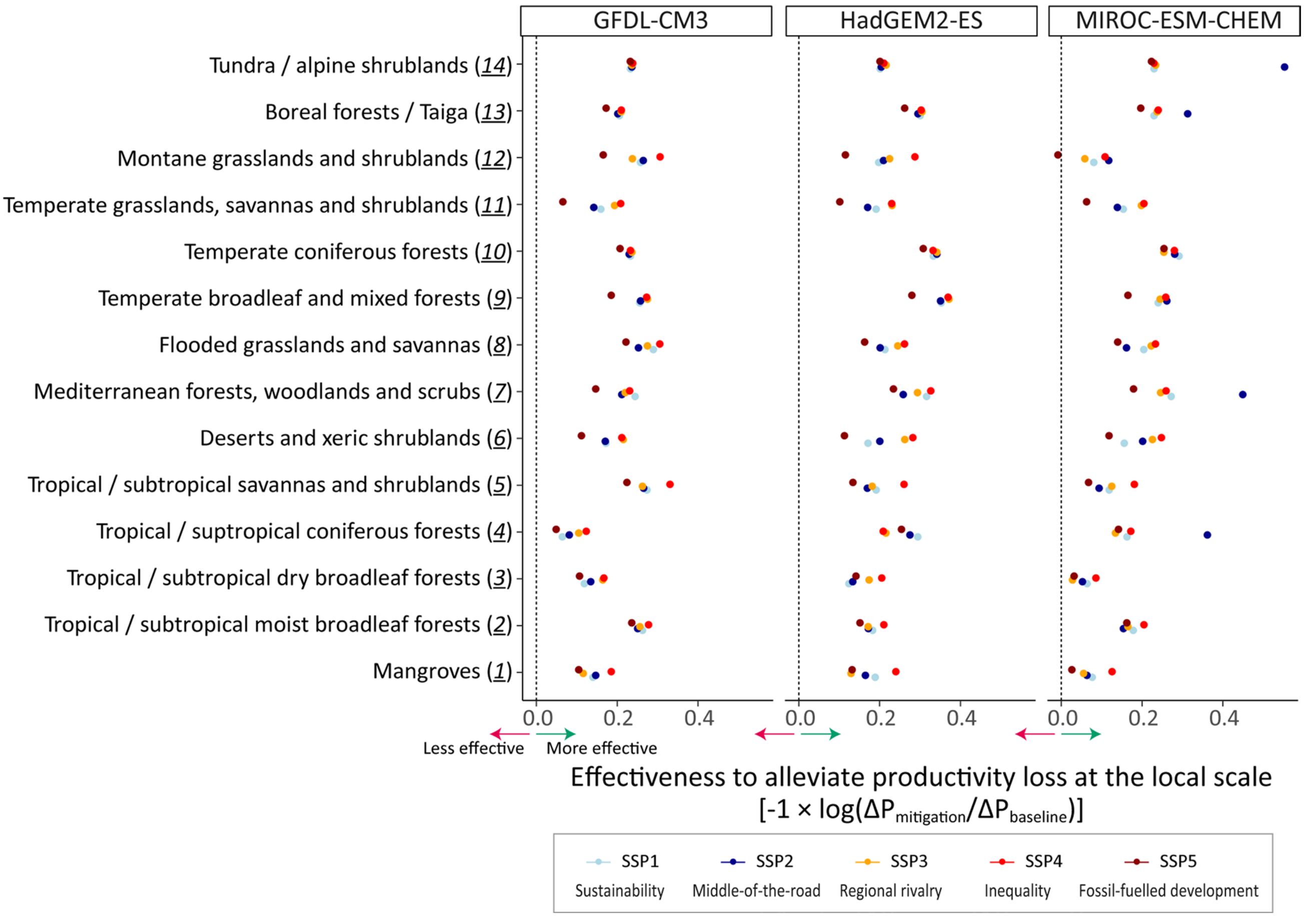
Extended Data Fig. 1 | Maps showing the projected changes in tree diversity under the mitigation scenarios from 2005 to 2070s. The proportional changes (%) in mean α-diversity (remaining species richness estimated at the fine grid-scale) are shown within each of the coarse grids (n = 32,670 grids). Results are shown for the five Shared Socioeconomic Pathways (SSPs) and the three Global Climate Models (GCMs).

Extended Data Fig. 2 | Maps showing the projected changes in tree diversity under the baseline scenarios from 2005 to 2070s. The proportional changes (%) in mean α-diversity (remaining species richness estimated at the fine grid-scale) are shown within each of the coarse grids (n = 32,670 grids). Results are shown for the five Shared Socioeconomic Pathways (SSPs) and the three Global Climate Models (GCMs).

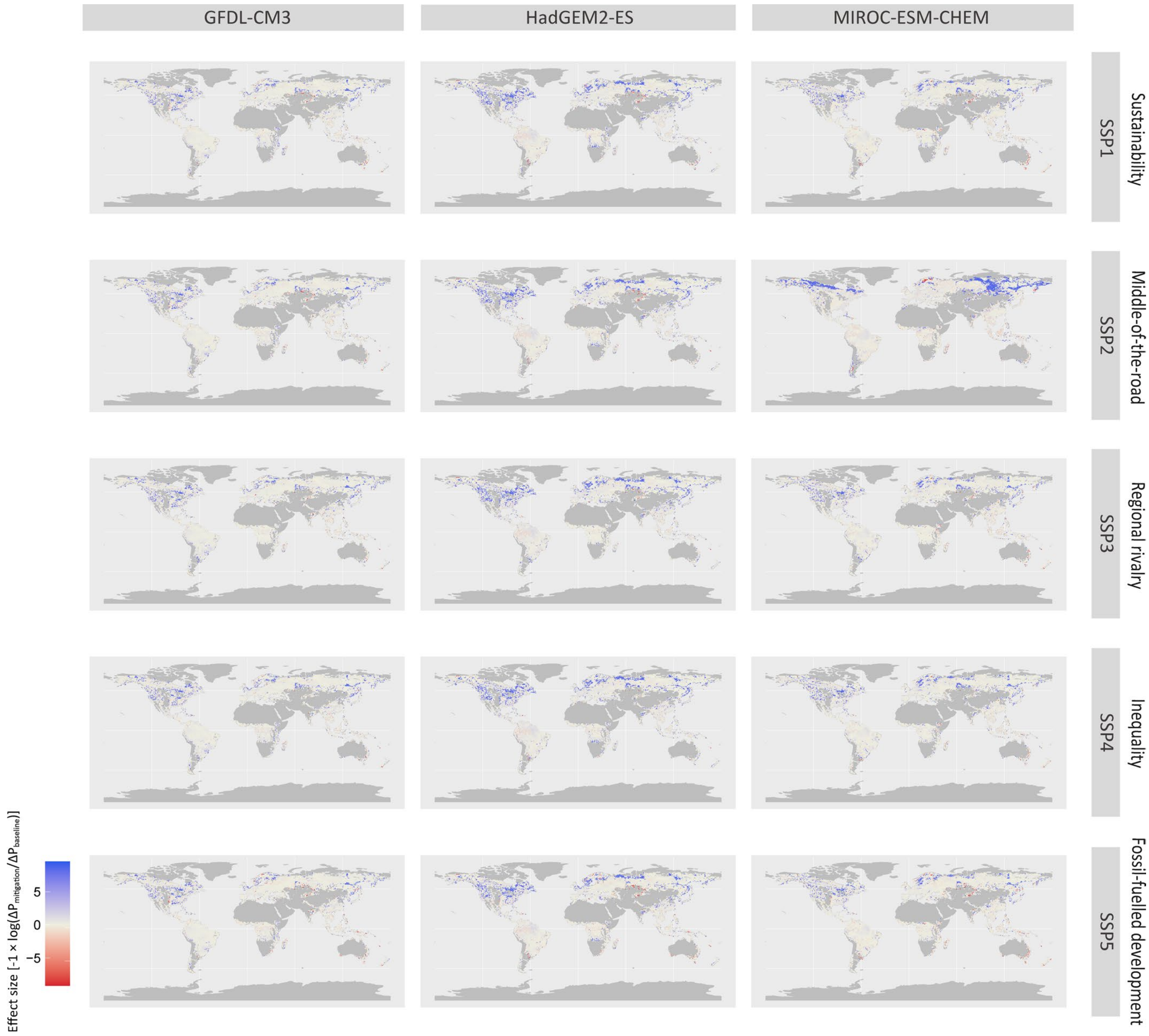


Extended Data Fig. 3 | See next page for caption.

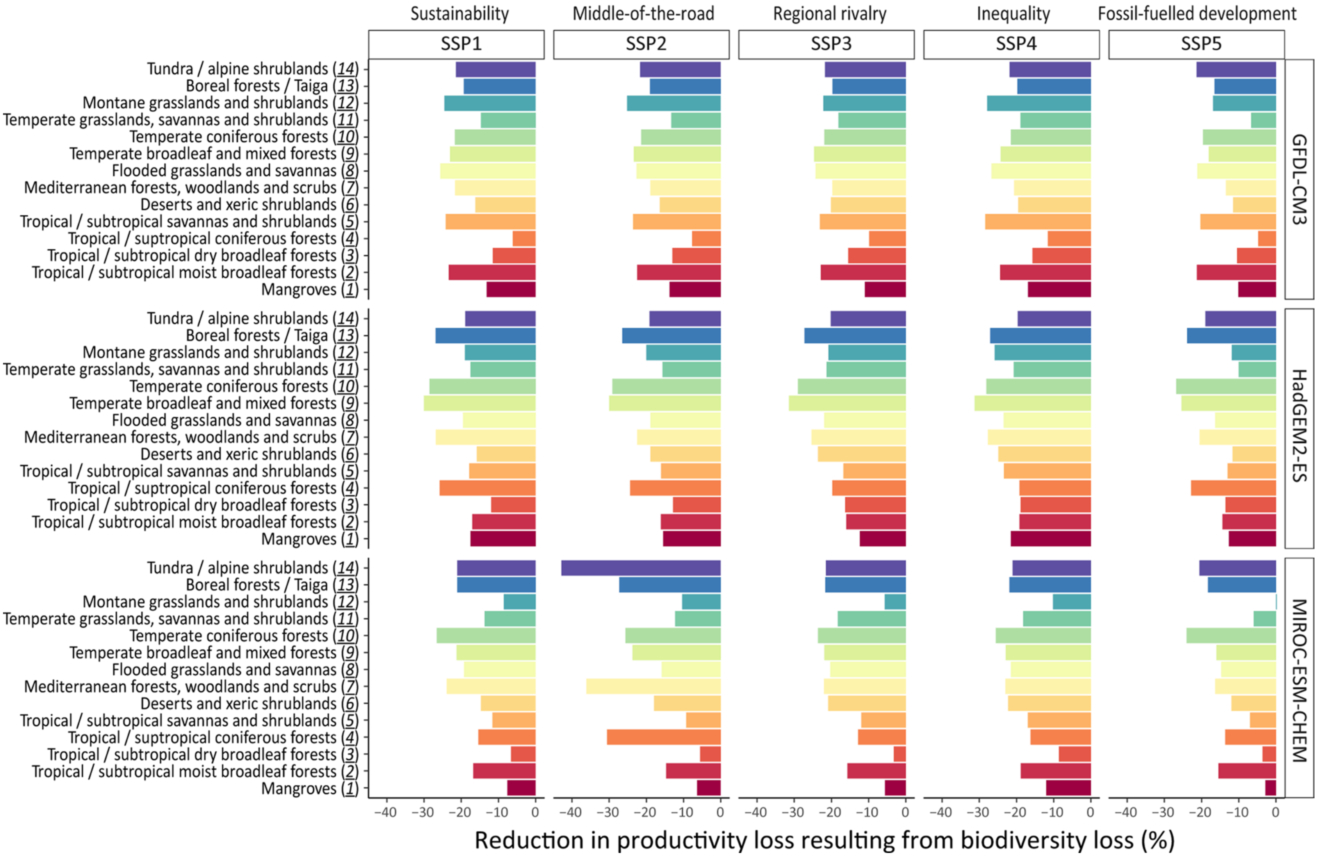
Extended Data Fig. 3 | Biome-level projections in the effects of a climate change mitigation to alleviate the loss of tree diversity (ΔSR) from 2005 to 2070s. The effect sizes [inverse of log(mitigation/baseline)] of ΔSR were estimated based on mean α-diversity values within each of the coarse grids (the total number of the coarse grids = 32,670). The effect size is shown as a log ratio scale; zero corresponds to the true absence of the outcome. Positive and negative values of effect size indicate more and less effectiveness of mitigation policy, respectively (green and red arrow, respectively). The points and horizontal bars indicate means and their 95% confidence intervals, respectively. Results are shown for the five Shared Socioeconomic Pathways (SSPs: SSP1, sustainability; SSP2, middle-of-the-road; SSP3, regional rivalry; SSP4, inequality; SSP5, fossil-fuelled development) and the three Global Climate Models (GCMs). Results are also provided as Supplementary Data 2.



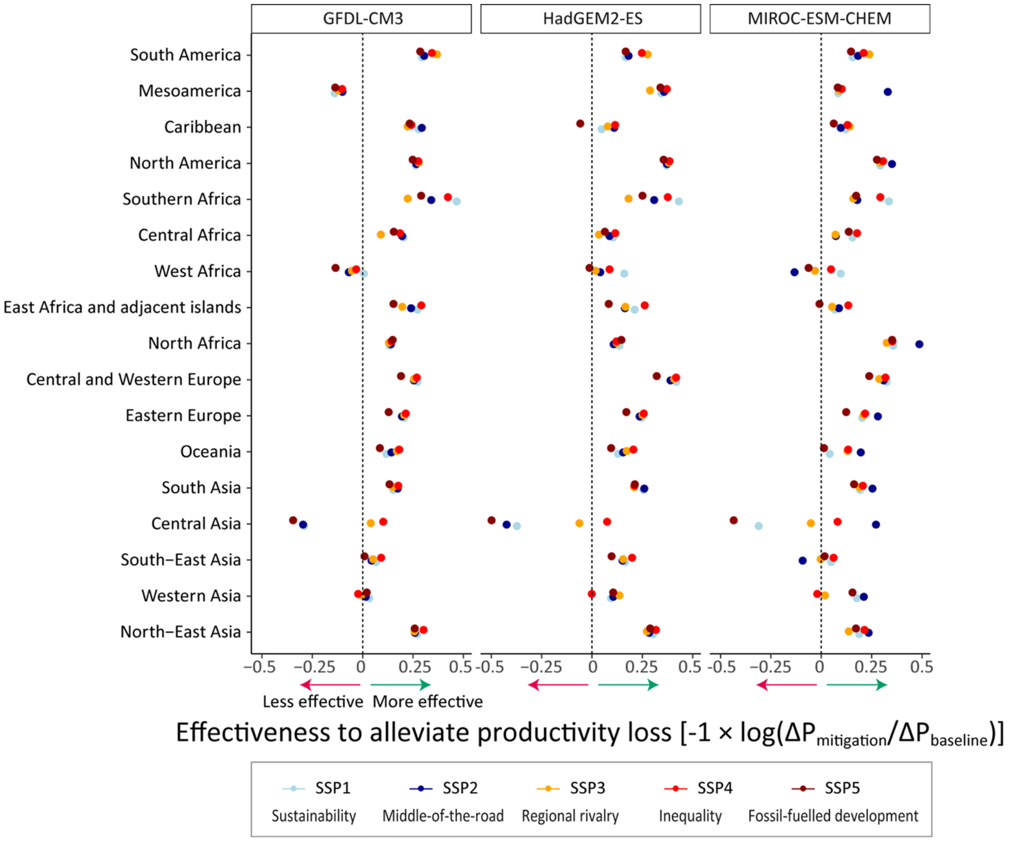
Extended Data Fig. 4 | Biome-level projections in the effects of a climate change mitigation to alleviate the loss of tree diversity-dependent productivity (ΔP) from 2005 to 2070s. The effect sizes [inverse of log(mitigation/baseline)] of ΔP were estimated at the local scale (at the 30 arcseconds; the total number of grids = ~ 115 million for each scenario). The effect size is shown as a log ratio scale; zero corresponds to the true absence of the outcome. Positive and negative values of effect size indicate more and less effectiveness of mitigation policy, respectively (green and red arrows, respectively). All points indicate mean effect size. Results are shown for the five Shared Socioeconomic Pathways (SSPs) and the three Global Climate Models (GCMs). See Supplementary Data 3 for the values of means and the associated 95% confidence intervals of the effect sizes.



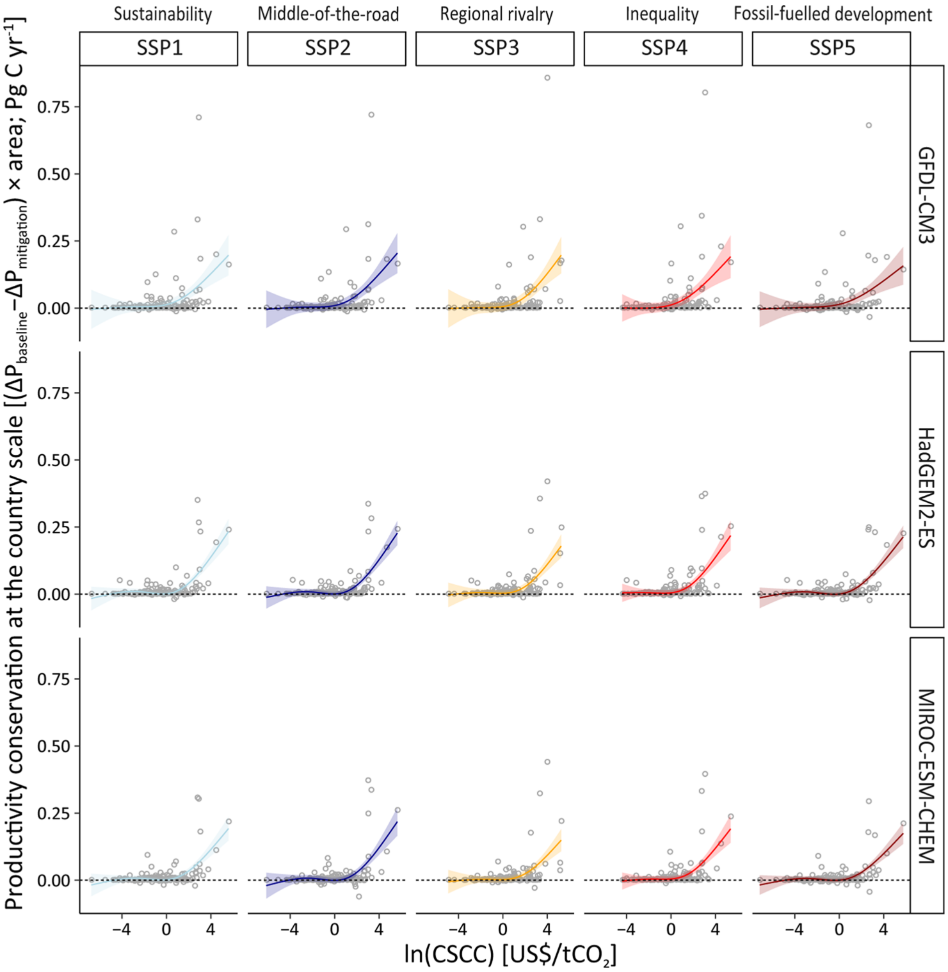
Extended Data Fig. 5 | Maps showing the effects of a climate change mitigation to alleviate the loss of tree diversity-dependent productivity (ΔP) from 2005 to 2070s. The effect sizes [inverse of log(mitigation/baseline)] of ΔP were estimated at the local scale (at the 30 arcsec; the total number of fine grids ~ 115 million for each scenario). Positive and negative values of effect size indicate more and less effectiveness of mitigation policy, respectively. In these maps, means of the effect sizes within each of the coarse grids (n = 32,670 coarse grids) are shown. Results are shown for the five Shared Socioeconomic Pathways (SSPs) and the three Global Climate Models (GCMs). Files to produce these maps are provided as Supplementary Data 4.



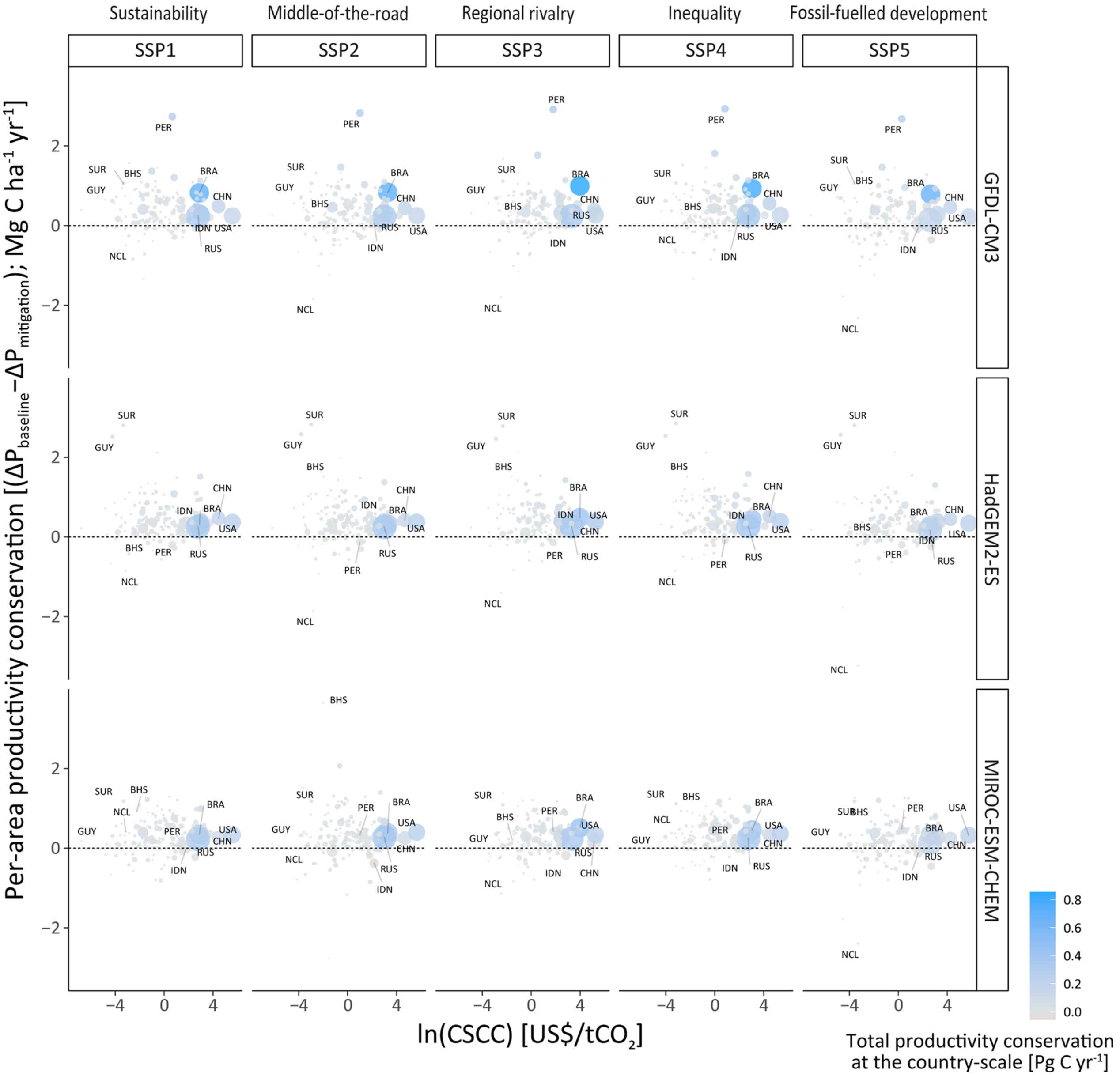
Extended Data Fig. 6 | Biome-level sums in alleviating the loss of tree diversity-dependent productivity (ΔP) from 2005 to 2070s. Proportional reductions (%) in ΔP are summarised for each of 14 different biomes. Negative values indicate the relative magnitude of reduction in productivity loss by the implementation of additional climate mitigation policy compared to the estimates based on business-as-usual scenario. Results are shown for the five Shared Socioeconomic Pathways (SSPs) and the three Global Climate Models (GCMs).



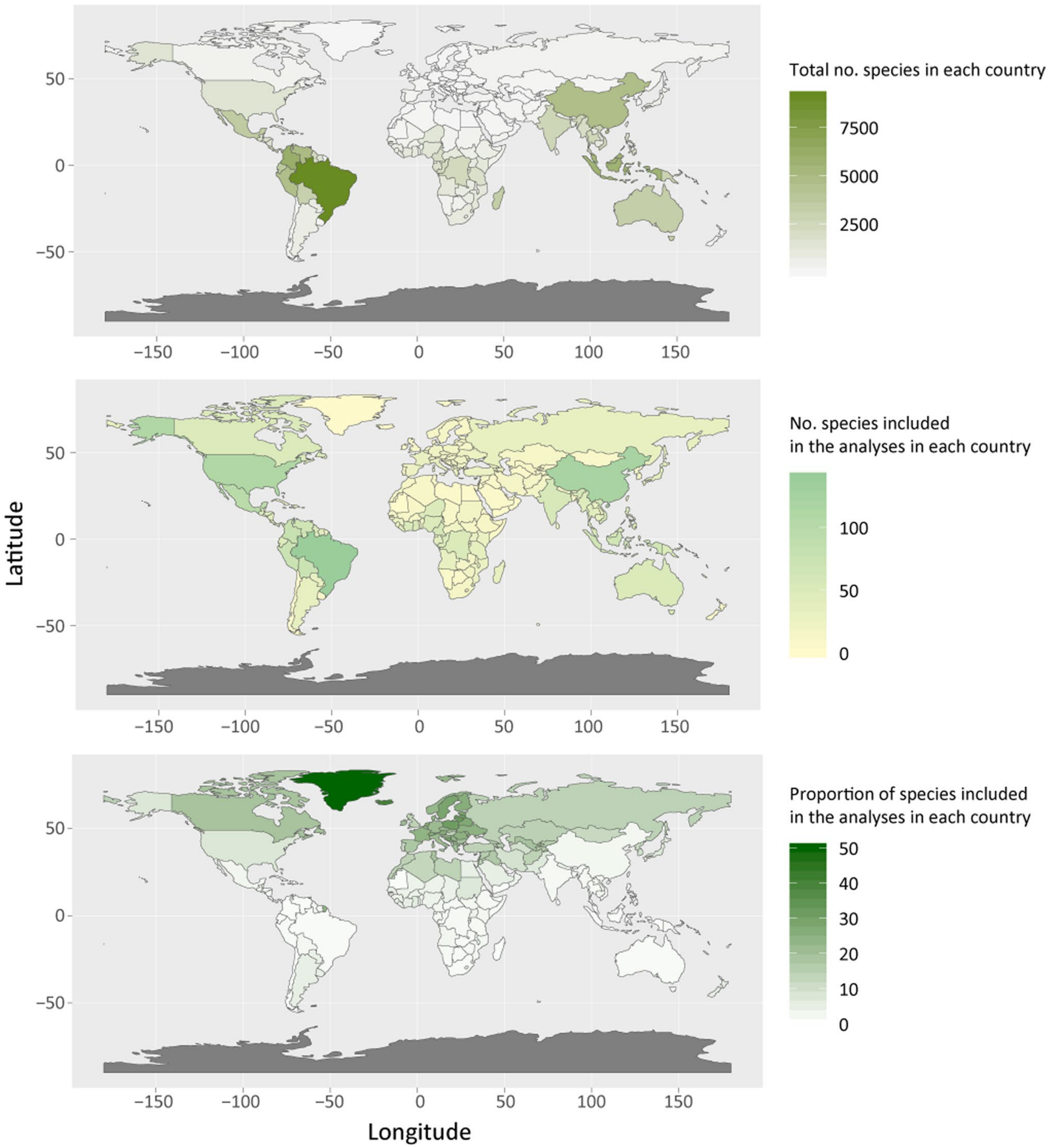
Extended Data Fig. 7 | Subregion-level projections in the effects of a climate change mitigation to alleviate the loss of tree diversity-dependent productivity (ΔP) from 2005 to 2070s. The effect sizes [inverse of log(mitigation/baseline)] of ΔP were estimated at the local scale (at the 30 arcseconds; the total number of grids = ~ 115 million for each scenario). The effect size is shown as a log ratio scale; zero corresponds to the true absence of the outcome. Positive and negative values of effect size indicate more and less effectiveness of mitigation policy, respectively (green and red arrows, respectively). The points indicate means. Subregions are based on the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services; IPBES; https://www.ipbes.net/regional-assessments). Results are shown for the five Shared Socioeconomic Pathways (SSPs) and the three Global Climate Models (GCMs). See Supplementary Data 5 for the values of means and the associated 95% confidence intervals of the effect sizes.



Extended Data Fig. 8 | The relationships between the country-level social cost of carbon (CSCC[33]) and the country-level conservation of tree diversity-dependent productivity. The lines and shaded areas are the estimates based on a generalized additive mixed model and their 95% confidence intervals, respectively. Results are shown for the five Shared Socioeconomic Pathways (SSPs) and the three Global Climate Models (GCMs). See Supplementary Data 6 for the values of means and the associated 95% confidence intervals of the effect sizes [inverse of log(mitigation/baseline)] of climate change mitigation policy to alleviate the loss of tree diversity-dependent productivity for each country.



Extended Data Fig. 9 | The relationships between the country-level social cost of carbon (CSCC[33]) and the country-level per-area conservation of tree diversity-dependent productivity. The size of circles is proportional to the forested area of each country. The colors of circles correspond to the country-level sum of productivity conservation shown in Extended Data Figure 8 (see the color scale at the bottom right). Results are shown for the five Shared Socioeconomic Pathways (SSPs) and the three Global Climate Models (GCMs). Names of major and outlier countries are shown beside the symbols; ISO 3166-1 alpha-3 code is used to indicate countries.



Extended Data Fig. 10 | Tree species analysed. The maps showing the total number of tree species reported in each country[75], and the number of the target species (those analysed in the present study) and the proportion (%) of these target species within the total number of species reported in each country[75].

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Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Datasets used for species distribution modelling are summarized in Supplementary Table S1: ODMAP protocol. Changes in forest productivity (%) along species richness changes were based on parameters of the elasticity of substitution (θ), of Liang et al. 2016, Science (DOI:10.1126/science.aaf8957). Data were obtained from the website of the Global Forest Biodiversity Initiative (http://gfbinitiative.com/data/). For net primary productivity, we used a dataset estimated using the MODIS imagery (https://lpdaac.usgs.gov/products/mod17a3hv006/).
Data analysis	We used the “tidyverse”, “metafor”, “lmerTest”, “effects”, “ARPobservation”, “maptools”, sf”, “raster”, “vegan”, “mobsim", and “xgboost” packages of the R software version 3.5.1 and 4.0.3.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The source data underlying figures are archived in the Dryad repository: https://doi.org/10.5061/dryad.vq83bk3s2. The additional data that support the findings of this study are available from the corresponding author upon reasonable request.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Our workflow of how to estimate proportional changes in species richness and forest productivity as well as absolute changes in net primary productivity at the local scale is visualized in Figures S1 and S2. We conducted species distribution modelling to estimate future changes in tree species richness. These projections of the proportional changes were converted to the proportional changes in net primary productivity. Our projections of tree diversity-dependent productivity were based at the spatial resolution of 30 arcseconds. We aggregated our estimations at biome, national, and regional scales. Furthermore, we compared the country-level estimates of tree diversity-dependent productivity with the country-level social cost of carbon. Our analyses used five shared socioeconomic pathways (SSPs) reflecting different plausible projections of land-use change, and we relied on the mitigation and baseline scenario to estimate the effectiveness of a climate change mitigation policy. For future climate projections, we used climatic variables based on three global climate models.
Research sample	Datasets used for species distribution modelling are summarized in Supplementary Table S1: ODMAP protocol. Changes in forest productivity (%) along species richness changes were based on parameters of the elasticity of substitution (θ), of Liang et al. 2016, Science (DOI:10.1126/science.aaf8957). Data were obtained from the website of the Global Forest Biodiversity Initiative (http://gfbinitiative.com/data/). For net primary productivity, we used a dataset estimated using the MODIS imagery (https://lpdaac.usgs.gov/products/mod17a3hv006/).
Sampling strategy	Our workflow of how to estimate proportional changes in species richness and forest productivity as well as absolute changes in net primary productivity at the local scale is visualized in Figures S1 and S2. Protocols of species distribution modelling are summarized in Supplementary Table S1: ODMAP protocol.
Data collection	Datasets used for species distribution modelling are summarized in Supplementary Table S1: ODMAP protocol. Changes in forest productivity (%) along species richness changes were based on parameters of the elasticity of substitution (θ), of Liang et al. 2016, Science (DOI:10.1126/science.aaf8957). Data were obtained from the website of the Global Forest Biodiversity Initiative (http://gfbinitiative.com/data/). For net primary productivity, we used a dataset estimated using the MODIS imagery (https://lpdaac.usgs.gov/products/mod17a3hv006/).
Timing and spatial scale	We estimated changes in tree diversity-dependent productivity at the local scale (i.e., 30 arcseconds, the total number of grids ~ 115 million) from 2005 to 2007s. Our analyses were extended to all terrestrial biomes, where tree or shrub species were observed.
Data exclusions	We excluded terrestrial areas, where no tree or shrub species were observed. Also, we focused on a limited subset of woody species to represent the tree diversity in the forests around the globe (Extended Data Fig. 10).
Reproducibility	The study is based on the existing data of species occurrence and forest productivity estimations. No original experiments were carried out.
Randomization	To consider the uncertainties of future projections, we used three different climate models for each scenario. We then obtained grand means and the associated 95% confidence intervals. Results for each global climate model are also provided as Extended Data Figures and Supplementary Data.
Blinding	No original experiments were carried out.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging