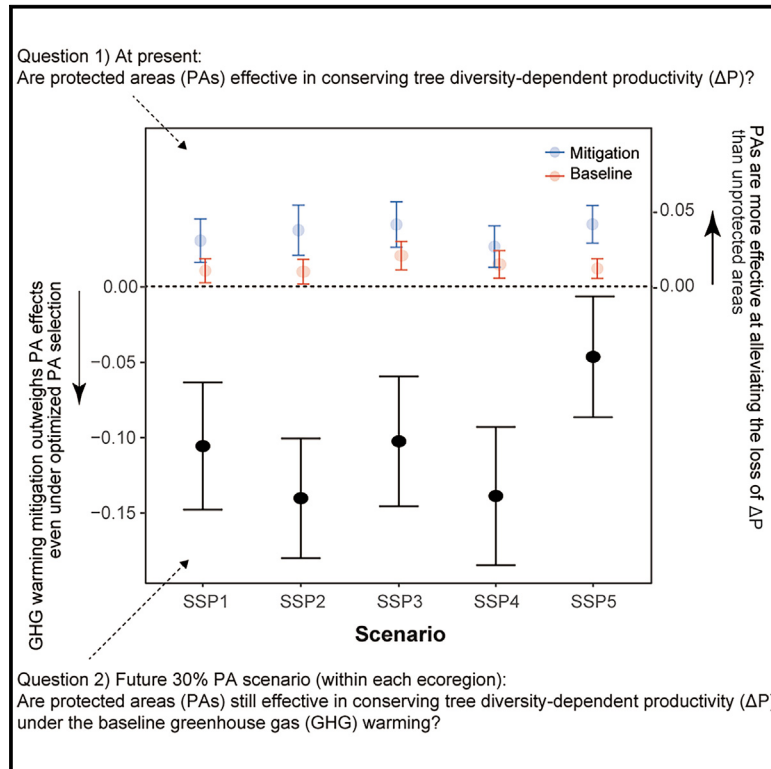


# Urgent climate action is needed to ensure effectiveness of protected areas for biodiversity benefits

## Graphical abstract



## Authors

Akira S. Mori, Andrew Gonzalez, Rupert Seidl, ..., Yann Hautier, Michel Loreau, Forest Isbell

## Correspondence

akkym@g.ecc.u-tokyo.ac.jp

## In brief

Biodiversity loss and climate change are interlinked challenges. This study shows that, while protected areas can preserve forest productivity and carbon capture through tree diversity, failing to mitigate climate change diminishes their effectiveness, especially in warmer biomes. Thus, mitigating climate change is crucial for conservation efforts aimed at achieving global biodiversity targets.

## Highlights

- Protected areas preserve tree productivity and carbon capture through biodiversity
- Anthropogenic climate change threatens effectiveness of this tree diversity effect
- Optimized protected areas still vulnerable without climate change mitigation
- Mitigating climate change is essential for achieving global biodiversity targets

Article

# Urgent climate action is needed to ensure effectiveness of protected areas for biodiversity benefits

Akira S. Mori,<sup>1,14,\*</sup> Andrew Gonzalez,<sup>2</sup> Rupert Seidl,<sup>3,4</sup> Peter B. Reich,<sup>5,6</sup> Laura Dee,<sup>7,8</sup> Haruka Ohashi,<sup>9</sup> Yann Hautier,<sup>10</sup> Michel Loreau,<sup>11,12</sup> and Forest Isbell<sup>13</sup>

<sup>1</sup>Research Center for Advanced Science and Technology, The University of Tokyo, 4-6-1 Komaba, Meguro, Tokyo 153-8904, Japan

<sup>2</sup>Department of Biology, Quebec Center for Biodiversity Science, McGill University, 1205 Dr. Penfield Avenue, Montreal, QC H3A 1B1, Canada

<sup>3</sup>Ecosystem Dynamics and Forest Management Group, School of Life Sciences, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

<sup>4</sup>Berchtesgaden National Park, Doktorberg 6, 83471 Berchtesgaden, Germany

<sup>5</sup>Institute for Global Change Biology and School for Environment and Sustainability, University of Michigan, 440 Church Street, Ann Arbor, MI 48109, USA

<sup>6</sup>Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA

<sup>7</sup>Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA

<sup>8</sup>Nature-Based Solutions Initiative, University of Colorado – Boulder, Boulder, CO, USA

<sup>9</sup>Department of Wildlife Biology, Forestry and Forest Products Research Institute, Forest Management Organization, Tsukuba, Ibaraki 305-8687, Japan

<sup>10</sup>Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, the Netherlands

<sup>11</sup>Theoretical and Experimental Ecology Station, CNRS, 2, route du CNRS, 09200 Moulis, France

<sup>12</sup>Institute of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China

<sup>13</sup>Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, USA

<sup>14</sup>Lead contact

\*Correspondence: [akkym@g.ecc.u-tokyo.ac.jp](mailto:akkym@g.ecc.u-tokyo.ac.jp)

<https://doi.org/10.1016/j.oneear.2024.08.003>

**SCIENCE FOR SOCIETY** Biodiversity loss and climate change are closely intertwined because changes in climate directly affect habitats, disturbance, and species distribution while biodiversity helps regulate the climate through processes like carbon capture. Yet, their connection is understated in policy discussions. Protected areas are crucial for preserving forest productivity and carbon capture, both of which depend on tree diversity. However, without efforts of climate change mitigation—such as reducing greenhouse gas emissions, enhancing carbon sequestration, and adopting sustainable land management—the effectiveness of these areas can be compromised. This could be true even if the goal of protecting 30% of land by 2030 under the Global Biodiversity Framework of the Convention on Biological Diversity is achieved. Our study highlights the importance of integrating climate change mitigation into conservation policies to maintain and enhance the ecosystem benefits that biodiversity provides to society.

## SUMMARY

The intertwined crises of biodiversity loss and climate change pose a significant sustainability challenge, threatening ecosystems and human well-being globally. Yet, the nuanced interplay between these challenges is often understated in policy dialogs. Global biodiversity targets, including 30% protection of the Earth's surface by 2030, may fall short without robust climate change mitigation. Here, we illustrate that conservation through protected areas can effectively preserve forest productivity and carbon capture, which depend on tree diversity. However, failing to mitigate climate change diminishes the effectiveness of these areas, especially in warmer biomes. Even with optimal protected area selection, preserving tree diversity-dependent productivity could be compromised without significant climate change mitigation. Our findings emphasize the need to integrate climate change mitigation into biodiversity conservation policies to ensure the success of the 30 × 30 targets and sustain the ecosystem benefits biodiversity provides to society.

## INTRODUCTION

Climate change and biodiversity loss are interconnected, dual environmental challenges of our time.<sup>1,2</sup> Their interconnectedness has been increasingly acknowledged across various sectors, including policy,<sup>3–6</sup> health,<sup>7–10</sup> business,<sup>11</sup> and academia.<sup>12–17</sup> The joint workshop by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and the Intergovernmental Panel on Climate Change emphasized the inseparable connection between climate and biodiversity for the future of human development.<sup>13</sup> Despite this knowledge,<sup>12,13,18</sup> there is an imbalance in attention given to these twin challenges in science and policy,<sup>2,19–22</sup> with climate change currently receiving more prominence on the international agenda.<sup>23</sup> The interdependence of climate change and biodiversity loss means that addressing one issue successfully cannot be achieved without considering the other.<sup>12</sup> Therefore, it is imperative to further recognize the importance of biodiversity conservation in effectively tackling climate change. In fact, a focus on biodiversity can provide nature-based solutions that support mitigation and adaptation actions.<sup>2,14,15,24,25</sup>

Currently, there is a scarcity of evidence quantifying the role of biodiversity as a modifier in mitigating climate change.<sup>2,26</sup> This is in contrast to the extensive body of evidence highlighting the impact of anthropogenic climate change on life on Earth.<sup>27–29</sup> Nonetheless, biodiversity is increasingly regarded as an important countermeasure in mitigating the ongoing climate crisis.<sup>12,15,30</sup> One of the strongest rationales for this lies in the positive relationship between plant diversity, primary productivity,<sup>31</sup> and thus carbon storage across different biomes.<sup>26,32–36</sup> The relationship provides the backbone of nature-based climate solutions, which are increasingly incorporated into international policies because of the potential environmental, social, and economic benefits.<sup>6,14,15</sup> In a recent study, we discovered substantial feedbacks between biodiversity and climate stabilization.<sup>12</sup> Specifically, our study demonstrated that, in terrestrial biomes, reducing the adverse impacts of climate change on tree diversity is crucial because diverse forests play a significant role in carbon sequestration, thereby contributing to further climate stabilization. This feedback loop holds significant implications at the global scale, suggesting that solving one environmental problem may help solve the other, whereas not addressing either problem would further degrade both biodiversity and climate.<sup>12</sup>

The Kunming-Montreal Global Biodiversity Framework (GBF) includes 23 action targets aimed at protecting and restoring biodiversity and fostering its benefits by 2050.<sup>37</sup> However, the current targets of the GBF, including the climate-focused Target 8, do not consider the potential changes in the distribution of biodiversity and its future contribution to humanity under different climatic conditions. These targets implicitly assume an equilibrium, which needs to be rectified by considering the potential disequilibrium between climate and ecological systems.<sup>38</sup> Even if global targets, such as protecting 30% of lands and waters for all ecoregions by 2030 (Target 3), are achieved based on target metrics, the absence of adequate measures to address anthropogenic climate change could undermine the climate impacts of these conservation efforts. More specifically, anthropogenic climate change could disrupt habitat conditions

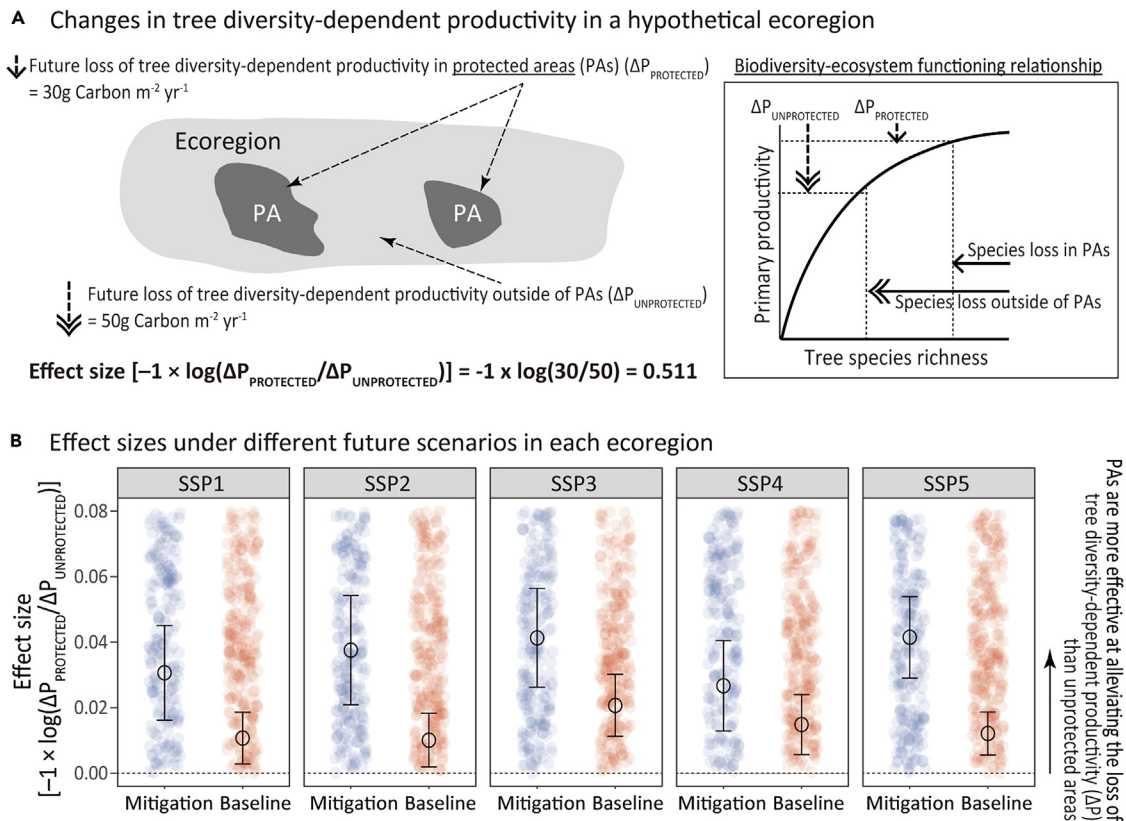
for many taxa, especially for most plants as sessile organisms, resulting in long-term climate extinction debts<sup>39</sup> in these protected areas (PAs).

Despite the growing recognition of the importance of considering climate velocity in the design of PAs,<sup>17,40–43</sup> there has been a notable absence of explicit evaluations regarding the impact of diverse climate scenarios on the benefits derived from biodiversity in terms of ecosystem functions and services. In this context, we aim to elucidate the intricate intersections between biodiversity and climate.<sup>13</sup> We here revisit previous assessments of potential losses in forest productivity that are dependent on tree species richness (hereafter called tree diversity-dependent productivity [ $\Delta P$ ]),<sup>12</sup> and introduce a pioneering perspective by scrutinizing both existing and prospective expansions of PAs under diverse future scenarios. Indeed, this quantitative approach is of paramount importance to address the growing demands for achieving multiple objectives in selecting PAs that could contribute to enhanced equity in our society.<sup>17,43</sup>

Here, we relied on the model used in our prior work,<sup>12</sup> which estimated the effects of possible future climate change and associated land-use changes on tree diversity<sup>44</sup> and the resulting forest productivity<sup>33</sup> at fine spatial resolution (30 arc-seconds;  $n = \sim 115$  million grid cells). The study considered two contrasting greenhouse gas (GHG) emission scenarios—baseline and mitigation—in the form of representative concentration pathways (RCPs), along with five different shared socio-economic pathways (SSPs). The baseline scenario represents a business-as-usual trajectory, and we explored how deviating from this pathway can help conserve  $\Delta P$ , thereby supporting nature-based climate solutions.<sup>12</sup> Building upon this model, we here examined the consequences for  $\Delta P$  inside and outside of PAs (Figure 1A) under different future scenarios. In the context of the aim of the GBF to increase the area under protection, we examined the present and future optimized allocation of PAs to quantify the effect of conserving biodiversity on global efforts to mitigate climate change. By conducting this forward-looking assessment, we quantified the potential synergies and antagonisms between climate change and biodiversity change. Specifically, we found that conservation through PAs can effectively preserve  $\Delta P$ . Yet, we also found that failing to mitigate climate change diminishes the effectiveness of these areas, including a scenario with optimal PA selection. Our findings emphasize the need to integrate climate change mitigation into biodiversity conservation policies to ensure and sustain the ecosystem benefits biodiversity provides to society.

## RESULTS AND DISCUSSION

We found that existing PAs in different terrestrial ecoregions worldwide have been designated in locations that also effectively conserve tree species in the future. They thus reduce the potential loss of  $\Delta P$  compared to unprotected areas, irrespective of the societal pathways (SSP scenarios) considered (Figures 1B and S1). There is thus a potential opportunity to protect places that may be a win-win for conserving both biodiversity and productivity. While the role of existing PAs in alleviating the loss of forest productivity in the future (PA effect, quantified as



**Figure 1. Effectiveness of PAs in alleviating the loss of  $\Delta P$**

(A) Illustration of our analytical approach using a hypothetical ecoregion with two PAs. The estimated future loss of forest productivity (based on a relationship between tree species richness and primary productivity) was compared between PAs (dark gray areas) and unprotected areas (light gray areas), yielding the effect size of biodiversity conservation on forest-based climate regulation (inverse of  $\log(\Delta P_{\text{PROTECTED}}/\Delta P_{\text{UNPROTECTED}})$ ).

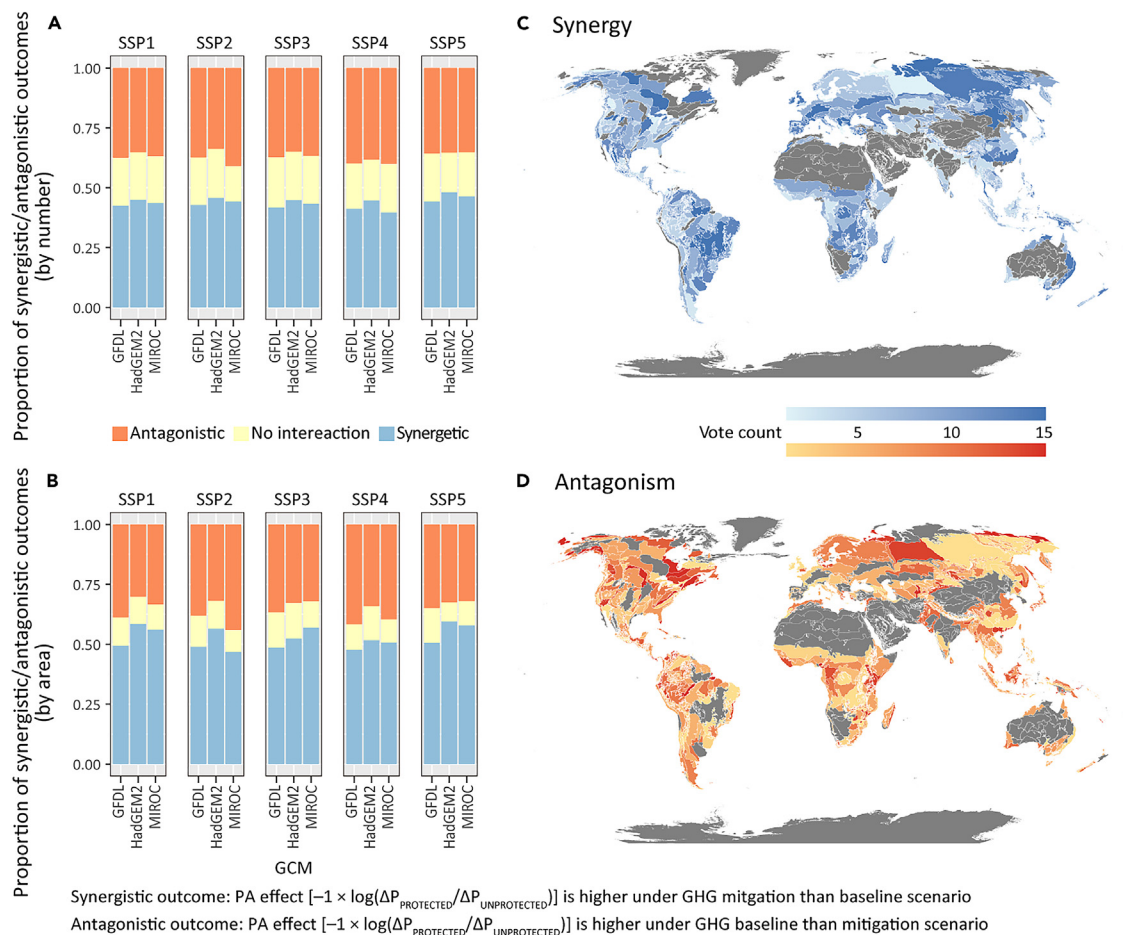
(B) Effect sizes for each ecoregion (colored points), considering different climate scenarios based on the two emission scenarios (mitigation and baseline) and the five shared socioeconomic pathways (SSPs). Positive values indicate that PAs are more effective at alleviating the loss of  $\Delta P$  under climate change compared to unprotected areas. For visual interpretation, only values between  $-1$  and  $1$  are shown (covering 95.5% of the data; refer to Figure 3 for complete results). Open circles and bars indicate means and 90% confidence intervals across all ecoregions, respectively.

$-\log(\Delta P_{\text{PROTECTED}}/\Delta P_{\text{UNPROTECTED}})$  varies substantially across ecoregions (Figures S2 and S3), the effectiveness of existing PAs tends to increase under the mitigation scenario compared to the baseline scenario (Figures 1B and S1). This variability among the scenarios can be attributed to multiple plausible factors, likely reflecting the differing potential and impacts of the GHG mitigation efforts.<sup>45</sup> When quantifying this effect using the baseline emissions scenario as a control ( $-\log(\Delta P_{\text{MITIGATION}}/\Delta P_{\text{BASELINE}})$ ), we also found that  $\Delta P$  is conserved more effectively under the mitigation scenario, particularly in areas currently under official protection at both the global (Figure S4) and ecoregion scales (Figure S5). Additionally, when we incorporated another scenario involving random selection of PAs from 2005 to 2021 (see experimental procedures), we found that the actual, realized allocations of PAs has been more effective overall in reducing the loss of  $\Delta P$  in comparison to random selection of PAs, especially under the mitigation scenario (Figures S4 and S5). Taken together, our findings highlight that mitigating GHG warming can further enhance the positive impact of terrestrial PAs.

The effectiveness of PAs in mitigating the loss of  $\Delta P$  varied across different ecoregions, with the potential for both synergistic

and antagonistic consequences (Figure 2). To identify possible moderators that determine the effectiveness of PAs, we conducted a meta-regression analysis. Initially, we examined the time since establishment of PAs (PA age; Figure S6) and found little influence on the effect size ( $-\log(\Delta P_{\text{PROTECTED}}/\Delta P_{\text{UNPROTECTED}})$ ) (Figure S7). Subsequently, we delved into the interaction between biodiversity and climate change by examining climatic variables. The analysis revealed that the effect size ( $-\log(\Delta P_{\text{PROTECTED}}/\Delta P_{\text{UNPROTECTED}})$ ) significantly decreased with increasing mean annual temperature, mostly under the baseline scenarios of GHG emissions (Figure 3). In contrast, under the mitigation scenario, this change in effect size was only observed for SSP2. These results indicate that the failure to mitigate the impacts of climate change on biodiversity can reduce or even negate the effectiveness of PAs for conserving forest productivity, especially in warmer ecoregions. This would lead to a missed opportunity offered by nature-based climate solutions.

In warmer areas, biodiversity is particularly vulnerable to local extinction due to lagged responses to climate change, especially among plant species that are unable to disperse rapidly enough to keep pace with changing climate conditions.<sup>39,46</sup> This climate



**Figure 2. Interactions between conservation and climate change mitigation**

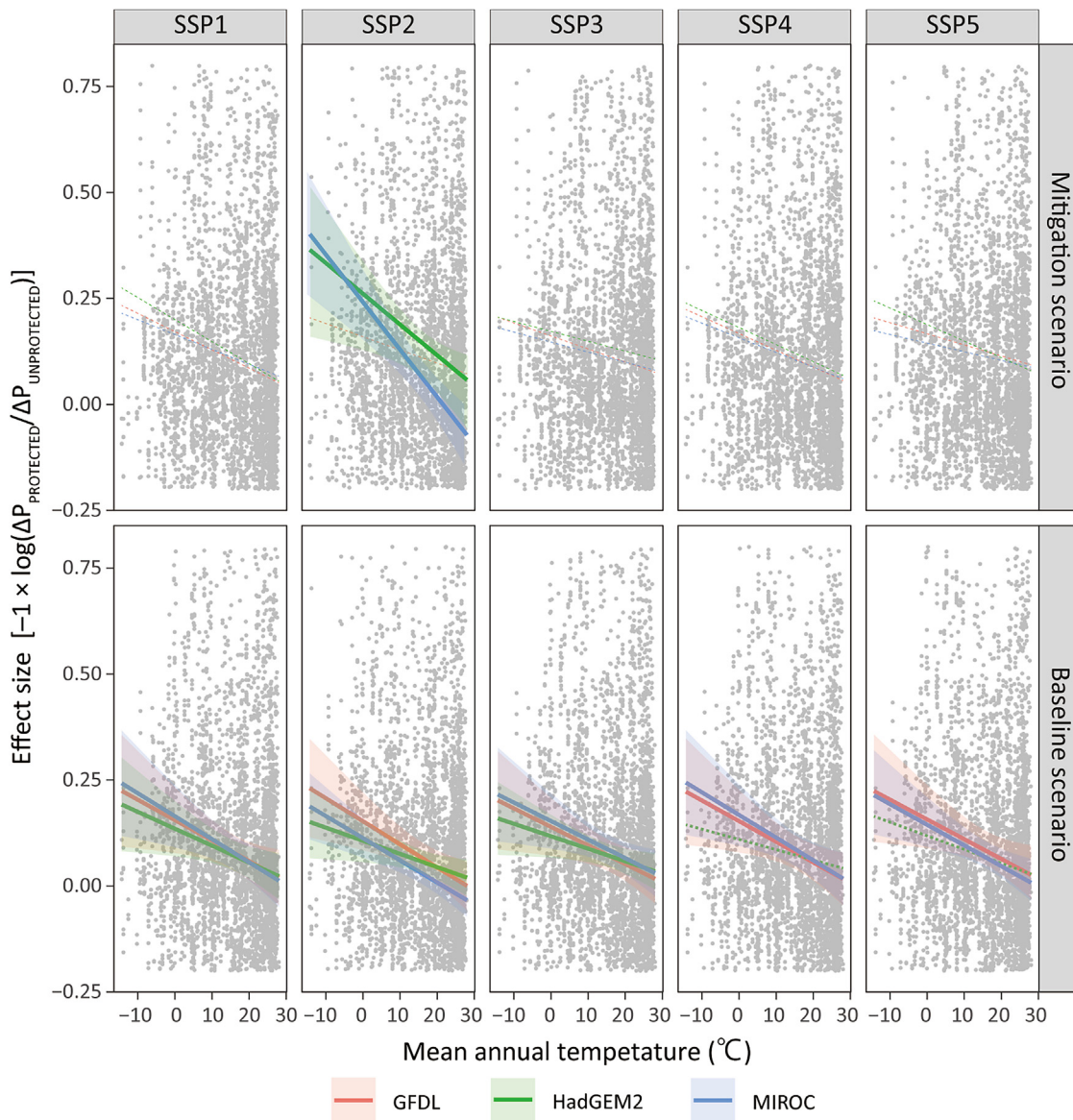
(A and B) Proportion of synergistic, neutral, and antagonistic outcomes in each ecoregion in terms of the effect of protected areas (PAs) and greenhouse gas (GHG) emission scenarios. Synergistic effects reflect that the PA effect on climate regulation (inverse of  $\log(\Delta P_{\text{PROTECTED}}/\Delta P_{\text{UNPROTECTED}})$ ) is significantly ( $p < 0.1$ ) higher under the GHG mitigation scenario than the baseline scenario of GHG emissions; antagonistic effects reflect the opposite signal. Results are shown for the five shared socioeconomic pathways (SSPs) based on the three global climate models (GCMs; MIROC, HadGEM2, and GFDL). The results are summarised by (A) number of ecoregions and by (B) area represented by these ecoregions. (C and D) The result of vote counts under the three GCMs and the five SSPs.

debt forces species to migrate into previously cooler areas in response to climate warming,<sup>47</sup> especially under baseline conditions where climatic stress most likely exceeds their tolerance.<sup>39,46</sup> Given that the thermophilization of plant communities has already been observed in many parts of the world,<sup>39,46,48,49</sup> our findings regarding the temperature effects, particularly prominent under the baseline scenario, align with expectations. Also, because these warmer areas are often prone to further land-use change, even under a scenario of climate change mitigation,<sup>50–52</sup> tree species in these areas could be more vulnerable than those in cooler areas. Urgent climate action is required to avoid a severe loss of the functional contributions of plant diversity to ecosystem productivity and carbon storage.

Another effect size ( $-\log(\Delta P_{\text{PROTECTED-BASELINE}}/\Delta P_{\text{UNPROTECTED-MITIGATION}})$ ) was calculated to further disentangle possible synergies and antagonisms between the efforts of biodiversity conservation (through PAs) and climate change mitigation. This allowed us to assess whether efforts

to mitigate the impacts of GHG warming outweigh the effectiveness of PAs (negative values of the effect size) or not (positive values of the effect size; see experimental procedures). While the effect size was both negative and positive among ecoregions, the global mean was significantly negative, regardless of the SSP (Figure 4A). This indicates that, in the absence of mitigation efforts, there will be a significant loss of 18.7%–24.5% in  $\Delta P$  within the existing areas under official protection compared to areas outside these reserves under a hypothetical future scenario where climate change mitigation will be implemented. Although there may still be some areas where conservation efforts can effectively preserve species and their contributions to ecosystem functioning, overall area-based conservation efforts cannot be successful without simultaneous efforts to avoid a business-as-usual pathway of anthropogenic warming.

This analysis was further extended in light of the GBF Target 3 of protecting 30% by 2030.<sup>37</sup> We hypothetically designated currently

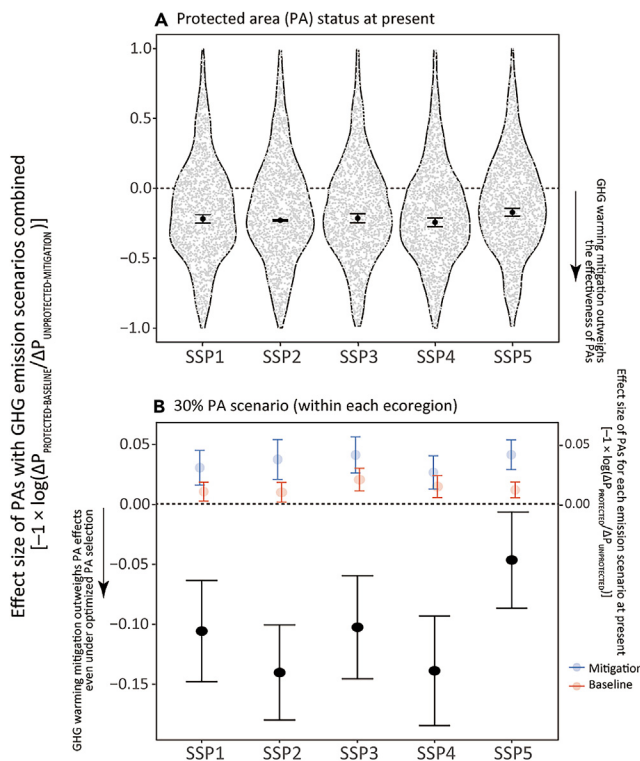


**Figure 3. Relationship between mean annual temperature and the effect size of PAs (inverse of  $\log(\Delta P_{\text{PROTECTED}}/\Delta P_{\text{UNPROTECTED}})$ ) at the ecoregion scale**

Solid lines and shaded areas represent the mean trend and 90% confidence intervals, respectively. If not significant ( $p > 0.1$ ), only dotted lines are shown. Gray dots indicate values for each ecoregion ( $n = 627$ ). The meta-regressions were conducted for different climate scenarios and models, separately. Climate scenarios were based on the two emission scenarios (mitigation and baseline) and the five SSPs, calculated using the three GCMs (MIROC, HadGEM2, and GFDL). There was no significant trend between mean annual precipitation and the effect size for all combinations of future climate scenarios, and, thus, results are not shown.

unprotected grids as protected (until reaching 30% within all ecoregions) to maximize the benefits of biodiversity in conserving forest productivity. Thirty-arcsecond grids that were expected to be minimally affected by climate change in terms of primary productivity were prioritized for protection within each ecoregion; that is, these selected grids represented the areas with the lowest adverse effects among all grids in each ecoregion (see experimental procedures). Here, we specifically examined whether mitigating GHG warming has a greater impact on  $\Delta P$  occurring outside of PA compared to the effect observed inside PAs under a baseline

scenario where warming proceeds without mitigation. Our analysis revealed that, even under the optimized designation of PAs with a quality assessment specifically aimed at maximizing productivity conservation (albeit with unrealistic exaggeration in extending the areas under protection), climate change mitigation remains a priority in order to avoid losing  $\Delta P$  (Figure 4B). This finding highlights the crucial need to address climate change; otherwise, existing and future efforts to conserve biodiversity and their benefits to society, including initiatives to foster other effective area-based conservation measures, could be in vain.



**Figure 4. Effectiveness of PAs in alleviating the loss of tree diversity-dependent productivity ( $\Delta P$ ) under different scenarios**

Results are shown for the five SSPs.

(A) The estimates of future loss of  $\Delta P$  were compared between protected and unprotected areas by combining different emission scenarios, leading to the effect size as a log response ratio (inverse of  $\log(\Delta P_{\text{PROTECTED-BASELINE}} / \Delta P_{\text{UNPROTECTED-MITIGATION}})$ ). The violin and point plots show values of each ecoregion, with black dots and bars representing means and 90% confidence intervals, respectively. Negative values indicate that GHG warming mitigation efforts, even without the contributions of PAs, have a greater impact on alleviating the loss of  $\Delta P$  compared to the effect observed inside PAs under a baseline scenario where warming proceeds without mitigation. The mean values of the log response ratios indicate an estimated 18.7–24.5% loss of  $\Delta P$  within existing PAs under the baseline scenario, as opposed to outside areas with another hypothetical climate mitigation effort.

(B) The analyses were extended to the optimized 30% protection within all ecoregions. The black dots and bars indicate means and 90% confidence intervals of the effect size as a log response ratio (inverse of  $\log(\Delta P_{\text{PROTECTED-BASELINE}} / \Delta P_{\text{UNPROTECTED-MITIGATION}})$ ), respectively. Same as above, negative values indicate that actions to counteract GHG warming are more effective at preserving  $\Delta P$  than what happens in PAs where no such actions are taken. Blue and red dots and bars represent means and 90% confidence intervals for the estimates at present (mitigation and baseline scenarios; Figure 1) and are displayed for visual comparison. The mean values of the log response ratios indicate an estimated 4.7%–15.0% loss of  $\Delta P$  within the optimized and expanded PAs under the baseline scenario compared to areas outside these reserves with another hypothetical future implementation of climate change mitigation efforts.

The results of this study have major implications for different GBF Targets and are also informative for related global initiatives. For instance, GBF Target 2 is for restoration. Even if ecosystem restoration is successful in terms of the targeted area-based measure (30% restoration), accelerated global warming could offset the outcomes of this effort. Recently, the

United Nations (UN) Decade on Ecosystem Restoration in 2021–2030 ([www.decadeonrestoration.org](http://www.decadeonrestoration.org)) was launched to ensure the continuity of ecosystem services, including carbon sequestration.<sup>5</sup> Likewise, there is increasing recognition of the importance of ecological restoration in achieving the combined benefits of carbon sequestration and biodiversity.<sup>53–56</sup> For many efforts to be fully effective, urgent action to mitigate the impacts of global climate change must be taken. Even though there already exist many important measures of mitigation—including nature-based solutions and geoengineering approaches—to achieve the challenging targets of GHG emission reduction and carbon neutrality,<sup>2,12,14,24,57–60</sup> these actions should coincide with global efforts to attain a nature-positive future. These actions include reconsidering our daily lifestyle, such as food habits and energy consumption<sup>61–63</sup>; changing business models to reduce remote impacts by supply chains<sup>64–66</sup>; and adopting international policy that disincentivizes actions of climate change mitigation at the expense of local biodiversity.

Undoubtedly, uncertainties remain in the assessment of the interactions between climate change and biodiversity conservation. First, the effectiveness of PAs for biological conservation varies substantially across regions,<sup>42,67</sup> which may partly explain why both synergistic and antagonistic consequences were observed. Further, the effectiveness of PAs to conserve the productivity of tree communities decreases uniformly with increasing mean annual temperature under the baseline scenario of GHG emission. While warmer ecoregions were identified as more vulnerable, there might be other influencing factors that could not be revealed in this study. Moreover, there is still a lack of comprehensive data on biodiversity and ecosystem services, which can limit the accuracy of the model and its ability to make informed decisions.<sup>68</sup> While our future estimates of diversity-related changes in productivity are likely conservative, as we have shown previously,<sup>12</sup> the possible synergistic and antagonistic consequences of biodiversity conservation and climate change mitigation highlight the manifold possible interactions. Additionally, similar assessments should be conducted for different types of ecosystem functions and services beyond primary productivity and carbon sequestration so as to meet multiple objectives.<sup>17,43</sup> Many of them are supported by various organism groups beyond trees,<sup>35,69–72</sup> which are not assessed here, and PAs play an indispensable role in supporting them and their contributions to ecosystem functions and services. Last, our scenarios do not assume potential carbon dioxide enrichment and its fertilizing effects on trees, which could alter carbon storage by forests.<sup>73</sup> By acknowledging the uncertainties and limitations of the current assessment, future studies may build upon this work and refine its understanding of the complex interactions between biodiversity conservation and climate change mitigation.

## Conclusions

In conclusion, our study emphasizes the significance of taking action to halt biodiversity loss and ensure its continued benefits to humanity through nature-based solutions. We take a significant step beyond previous research by demonstrating that, while protecting and restoring biodiversity is essential to achieving global goals for climate action, the effectiveness of PAs in conserving forest productivity varies across ecoregions

and is vulnerable to the impacts of climate change, particularly in warmer regions. Failing to mitigate global warming could compromise the efficacy of PAs and the benefits of biodiversity conservation to people and the biosphere, even when the most extensive efforts of protecting 30% of the Earth are pursued. Therefore, it is essential to further examine how the efficacy of different conservation efforts and initiatives are inherently dependent upon climate change. The interdependence of climate change and biodiversity loss underscores the urgent need for integrated actions that recognize the complex relationships between the two issues.<sup>12,74</sup> Addressing these twin challenges in an integrated manner is crucial, as they cannot be solved effectively in isolation.

We have contributed new quantitative estimates of the interdependency between biodiversity loss and climate change. Even though IPBES<sup>75</sup> and another independent study<sup>76</sup> determined that climate change is not the largest direct threat to biodiversity per se (relative to land use and habitat loss), it could potentially become a serious threat to the benefits biodiversity provides to people in the long term. Because biodiversity loss and ecosystem collapse are two of the fastest-growing global risks over the next decade,<sup>11</sup> the functional roles of biodiversity,<sup>30–33,70,77–83</sup> which are increasingly recognized as critical for humanity,<sup>84</sup> must be conserved effectively through urgent, transformative actions at multiple scales.

## EXPERIMENTAL PROCEDURES

### Methodology

#### Species richness and productivity estimation

To quantify the effectiveness of the existing and the expanding terrestrial PAs, we extended our previous analysis of species richness and productivity estimates for the years 2005 and the 2070s.<sup>12</sup> We estimated tree richness by projecting the present and future spatial distribution of individual species at a spatial resolution of 30 arcseconds (fine grids;  $n = 115,426,714$ ) by combining the approach of species distribution modeling using MaxEnt v.3.3<sup>85</sup> and spatially explicit downscaling based on species-area and endemics-area relationships.<sup>86</sup> The projections were based on the potential future changes in both climate and land-use variables. Climatic variables were obtained at a resolution of 30 arcseconds from WorldClim data.<sup>87</sup> Land-use variables were obtained at the same resolution by combining the moderate-resolution imaging spectroradiometer (MODIS) land cover type data from 2005 ([glcf.umd.edu/data/lc](http://glcf.umd.edu/data/lc); as of February 19, 2018) with land-use allocation models<sup>88–90</sup> to estimate the changes in five land-use types (cropland, pasture, forest, other natural land, and settled land) for the period between 2005 and the 2070s. These estimations considered 1,754 tree species and, thus, cannot fully reflect the potential changes in all tree species existing worldwide. However, the models to estimate future spatial distributions of individual species at the fine grid scale carefully considered coextinction and co-immigration of rare species based on the explicitly simulated widespread species; thus, the estimations presented here can be deemed conservative.<sup>12</sup>

To estimate changes in  $\Delta P$ , the projected estimates of tree species richness were then merged with the parameters of elasticity of substitution, estimated for forest biomes worldwide.<sup>33</sup> The elasticity of substitution can be used to estimate forest productivity based on proportional changes in woody species richness (%). This made it possible to estimate the proportional changes in  $\Delta P$  (percent) between the two time points (i.e., 2005 and 2070s). Although assumed to be scale independent, we note that the values of the elasticity of substitution were originally estimated based on forest inventory datasets collected at a local spatial scale.<sup>33</sup> The estimated proportional changes in forest productivity (percent) at each fine grid were then converted to absolute changes in productivity ( $\text{g carbon m}^{-2} \text{ yr}^{-1}$ ) between 2005 and 2070s by relating them to a net primary productivity estimation derived from the MODIS imagery for the year 2005.<sup>91</sup> Full details of tree species richness and productivity estimation are described in Mori et al.<sup>12</sup>

In the previous study,<sup>12</sup> the changes in  $\Delta P$  from 2005 to 2070s ( $\Delta P$ ) were estimated for two future scenarios of predictor variables: a mitigation and high-emission baseline scenario based on RCPs. The mitigation scenario aimed to stabilize radiative forcing by the end of the 21st century, whereas the baseline scenario assumed increasing GHG emissions over time.<sup>44</sup> Future climatic variables were based on the global climate models (GCMs) included in the Fifth Coupled Model Inter-Comparison Project experiment: MIROC-ESM-CHEM (hereafter called MIROC), HadGEM2-ES (HadGEM2), and GFDL-CM3 (GFDL). These were downloaded from the WorldClim database.<sup>87</sup> The changes in land use under the mitigation and baseline scenarios were assessed with the AIM/CGE model,<sup>88</sup> which was further downscaled to high spatial resolution with the AIM/PLUM downscaling model.<sup>89</sup> Future land-use variables<sup>90</sup> based on the SSP framework<sup>45</sup> were used to estimate future distributions of tree species. In the present study, the SSPs were 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 (SSP1, sustainability; SSP2, middle of the road; SSP3, regional rivalry; SSP4, inequality; SSP5, fossil-fueled development). The SSPs employ a concept called scenario matrix architecture, which involves a two-dimensional space comprising socioeconomic patterns and climate mitigation levels defined by RCPs. A radiative forcing level of 2.6  $\text{W/m}^2$  was primarily used for the mitigation scenario. For SSP3, a 3.4  $\text{W/m}^2$  forcing level was used instead because there was no scenario for 2.6  $\text{W/m}^2$ . High-emission baseline conditions in each SSP were set for the baseline scenario, assuming the absence of additional climate policy and efforts—business-as-usual scenario. Additional details are described in Ohashi et al.<sup>44</sup>

Below is the additional data preparation for this study. Here, we primarily relied on the tidyverse,<sup>92</sup> data.table,<sup>93</sup> sf,<sup>94</sup> and geodata<sup>95</sup> packages of the R software.<sup>96</sup> To summarize the estimations of potential changes in  $\Delta P$  at the ecoregion scale, we used RESOLVE Ecoregions 2017 ([https://developers.google.com/earth-engine/datasets/catalog/RESOLVE\\_ECOREGIONS\\_2017](https://developers.google.com/earth-engine/datasets/catalog/RESOLVE_ECOREGIONS_2017), as of March 5, 2023).<sup>97</sup> Within each ecoregion, fine grids were allocated to either PAs or unprotected areas. Here, we used the World Database on Protected Areas ([https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDP&as\\_of=2023-03-05](https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDP&as_of=2023-03-05)),<sup>98</sup> which is a joint project between the UN Environment Program and the International Union for Conservation of Nature, managed by the UN Environment Program World Conservation Monitoring Center. According to its guideline, all sites with “proposed,” “established,” and “not reported” status were classified as “unprotected.” Contrastingly, sites with “designated” and “inscribed” status were categorized as “protected.” Last, to consider potential differences in climate sensitivity between ecoregions (see Data Analysis, we obtained mean annual temperature and precipitation values for each of the ecoregions by extracting data at a fine-grid spatial resolution from the WorldClim database.<sup>87</sup>

#### Data analysis

We primarily relied on the ARPObservation,<sup>99</sup> metafor,<sup>100</sup> reshape2,<sup>101</sup> tidyverse,<sup>92</sup> data.table,<sup>93</sup> ggforce,<sup>102</sup> and RColorBrewer<sup>103</sup> packages of the R software<sup>96</sup> for data organization, analyses, and visualization. This study’s primary aim was to compare the effectiveness of PAs to conserve  $\Delta P$  in the future; thus, we excluded ecoregions where comparison between protected and unprotected areas was not possible due to the lack of PAs or existence of very small PAs with limited coverage at the resolution of our analysis. Additionally, ecoregions that are not forested were also excluded. As a result, the focal analyses considered 627 of the 2017 RESOLVE terrestrial ecoregions.

To quantify the PA effect, we calculated the reductions in local-scale loss of productivity as a log-ratio scale, which assumes that zero corresponds to the true absence of the outcome. Estimates based on the protected and unprotected areas were used for the denominator ( $\Delta P_{\text{PROTECTED}}$ ) and numerator ( $\Delta P_{\text{UNPROTECTED}}$ ), respectively. By using the ARPObservation<sup>99</sup> package, we obtained log-response ratios and the associated 90% confidence intervals of all 627 ecoregions across different combinations of SSP scenarios and GCMs. Smaller values of the effect size indicated more avoidance of the loss of  $\Delta P$  and vice versa. To facilitate interpretation, we multiplied the effect sizes by  $-1$ , resulting in positive and negative values indicating higher and lower effectiveness of PAs in conserving forest productivity, respectively (Figure 1A). Subsequently, we used a meta-analytical approach considering the GCMs as a random effect; we used the metafor<sup>100</sup> package to obtain global means and the associated 90% confidence intervals for each SSP scenario



(Figures 1B and S1–S3). Note that, generally, there were substantially more unprotected areas than PAs, suggesting that the environmental variation in the unprotected areas was much larger. To address this potential confounding effect, we subsampled fine grids to ensure an equal number of grids for both PA and unprotected area statuses. We then obtained the effect size using the same methodology as described above and found that the results were minimally affected by this bias (Figure S1). We further checked whether the effect sizes were affected by the proportion of PAs within each ecoregion and found that the distribution of the effect sizes was funnel like Figure S2, indicating a lower sampling bias.

To test whether the actual locations of PAs has had better, equal, or worse outcomes than random placement of PAs, we reassigned the fine grids that were designated as “protected” after 2005 until the year 2022 as “unprotected.” From all unprotected fine grids (including those reassigned as “unprotected”), we randomly chose fine grids to be assigned as “protected” until reaching the same number of “protected” fine grids within each ecoregion. The baseline year of 2005 for this random PA selection was selected because the present estimations of species richness and associated forest productivity were done with the year 2005 as a basis.<sup>12,44</sup> As the Kunming-Montreal GBF is using 2010 as the baseline, careful interpretations are necessary. For this dataset of random PA selection, we calculated the effect sizes (log response ratio) of the PA effect in the same way as described previously. This allowed us to compare how the actual selection of PAs differed from random PA selection in terms of conserving  $\Delta P$  (Figure S4). Additionally, we carried out a meta-regression analysis, focusing on the time since the establishment of PAs (PA age). Given that our evaluation of the effect sizes (log response ratio) was conducted at the ecoregion level, where multiple PAs exist within a single ecoregion (Figure S6), it was not feasible to analyze individual PAs separately. Therefore, for this meta-regression, we used the mean establishment year within each ecoregion (Figure S7). Because many PAs were established in recent years (Figure S6), PA ages were skewed, and, thus, they were Box-Cox transformed to improve normality (note that we added the value of 1 to all PA ages, as this transformation does not allow the value of 0). We also conducted a meta-regression with the effect size as a response variable and climate conditions (mean annual temperature or precipitation in each ecoregion) as a covariate. This allowed us to identify how the PA effect changed along a climatic gradient (Figure 3). Note that there was no significant trend between mean annual precipitation and the effect size for all combinations of future climate scenarios, and, thus, results are not shown. These meta-regressions were performed using the `metafor`<sup>100</sup> package.

To assess the synergistic and antagonistic outcomes of conservation (PA effect) and climate change (GHG warming) in terms of future changes in  $\Delta P$ , we compared the effect sizes of the PA effect under the two emission scenarios (mitigation versus baseline) within each ecoregion. We achieved this by comparing the confidence intervals of the PA effect across the five SSPs and three GCMs (15 comparisons). The vote count for these comparisons was used to visualize the result for each ecoregion (Figure 2). To further test possible synergistic and antagonistic effects of PAs and GHG warming, we conducted a hypothetical calculation of their effect sizes using two extreme cases of conservation/emission conditions. That is, to obtain the log response ratio, PAs under the baseline scenario and unprotected areas under the mitigation scenario were used for the denominator ( $\Delta P_{\text{PROTECTED-BASELINE}}$ ) and numerator ( $\Delta P_{\text{UNPROTECTED-MITIGATION}}$ ), respectively. This made it possible to compare which factor (PA effect or GHG warming) outweighs the other (Figure 4A). For this effect size (multiplied by  $-1$ ), positive values indicate that PAs are still important in alleviating the loss of  $\Delta P$  even under the baseline emission scenario of GHG warming compared to unprotected areas under the mitigation scenario. In contrast, negative values indicate that GHG warming outweighs the effectiveness of PAs to conserve forest productivity. To facilitate understanding of the magnitude of these effect sizes, we also converted the log response ratio to a percentage scale.

The above combined assessment of the PA effect and GHG emission scenarios was further conducted for a possible future in which 30% of the land surface are protected (to be consistent with Target 3 of the Kunming-Montreal GBF<sup>37</sup>). To select fine grids that are not currently designated as PAs, we used an optimization method. Specifically, within each ecoregion, we assigned “unprotected” fine grids as “protected” until the total protected grids reached 30% within each ecoregion by prioritizing the fine grids with

smaller values of  $\Delta P$  (i.e., where the loss of forest productivity was expected to be smaller). That is, areas that are expected to be more effective at conserving  $\Delta P$  in the future were given priority to be additionally included as PAs. Because our model considered the influence of both climate and land-use changes,<sup>44</sup> these selected areas are expected to provide the most favorable conditions for tree species, thereby maximizing the conservation of their contributions to forest productivity within a given future scenario. Under this optimized PA selection, we calculated the effect size of the log response ratio using PAs under the baseline scenario and unprotected areas under the mitigation scenario as the denominator ( $\Delta P_{\text{PROTECTED-BASELINE}}$ ) and numerator ( $\Delta P_{\text{UNPROTECTED-MITIGATION}}$ ), respectively. Here, negative values indicate that GHG warming outweighs the effectiveness of PAs to conserve forest productivity even under the optimized PA selection; that is, despite the fact that  $\Delta P_{\text{UNPROTECTED-MITIGATION}}$  reflected the least effective fine grids in terms of alleviating the loss of  $\Delta P$  (as in unprotected areas), the mitigation scenario was identified to be more effective than  $\Delta P_{\text{PROTECTED-BASELINE}}$ , which included the most effective fine grids in the baseline GHG emission future (Figure 4B). Again, to facilitate understanding of the magnitude of these effect sizes, we converted the log response ratio to a percentage scale.

Last, the log response ratio (effect size) of the reductions in  $\Delta P$  was estimated by comparing baseline and mitigation scenarios of GHG emissions as the denominator ( $\Delta P_{\text{BASELINE}}$ ) and numerator ( $\Delta P_{\text{MITIGATION}}$ ), respectively, as done in a previous study.<sup>12</sup> After multiplying the effect sizes by  $-1$ , positive and negative values indicate more and less effectiveness of the climate mitigation policy in reducing the loss of  $\Delta P$ , respectively. To analyze the ensemble results across the three GCMs, we adopted a mixed effects meta-analytical approach, as done for the comparison between protected and unprotected areas, with GCMs as a random effect (Figure S4). Random PA selection was again conducted in the same way as described previously, and then the effect sizes across different scenarios of PA selection were compared (Figure S5).

## RESOURCE AVAILABILITY

### Lead contact

Information related to this manuscript can be obtained from the lead contact, Akira S. Mori ([akkym@g.ecc.u-tokyo.ac.jp](mailto:akkym@g.ecc.u-tokyo.ac.jp)).

### Materials availability

The data are primarily sourced from the previous study<sup>12</sup> and archived in the repository: <https://doi.org/10.5061/dryad.vq83bk3s2>. The additional data and codes associated with the present study are archived in the repository (<https://doi.org/10.5281/zenodo.10818449>; <https://github.com/AkiraSMori/BiodProd-ProtectArea/releases/tag/BiodProd-ProtectArea>).

### Data and code availability

The data are primarily sourced from the previous study<sup>12</sup> and archived in the repository: <https://doi.org/10.5061/dryad.vq83bk3s2>. Ecoregion data are from RESOLVE Ecoregions 2017 ([https://developers.google.com/earth-engine/datasets/catalog/RESOLVE\\_ECOREGIONS\\_2017](https://developers.google.com/earth-engine/datasets/catalog/RESOLVE_ECOREGIONS_2017)). PA data are from the World Database on Protected Areas (<https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDPA>). Additional data and codes associated with the present study are archived in the repository (<https://doi.org/10.5281/zenodo.10818449>; <https://github.com/AkiraSMori/BiodProd-ProtectArea/releases/tag/BiodProd-ProtectArea>).

## ACKNOWLEDGMENTS

A.S.M. was supported by the Ichimura New Technology Foundation, the Japan Society for the Promotion of Science (JSPS) Fund for the Promotion of Joint International Research (22KK0102), and the Advanced Studies of Climate Change Projection Grant by the Ministry of Education, Culture, Sports, Science and Technology, Japan (JPMXD0722678534). A.G. was supported by the Liber Ero Chair in Biodiversity Conservation. R.S. was funded by the European Research Council under the European Union’s Horizon 2020 Research and Innovation Program (grant agreement 101001905). M.L. was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41). F.I. was supported by the US National Science Foundation (DEB-1845334, DEB-1831944, and DEB-2021898). A.S.M. and H.O. were funded by the Environment Research

and Technology Development Fund of the Environmental Restoration and Conservation Agency of Japan (JPMEERF15S11400) and were supported by the supercomputer of Agriculture, Forestry and Fisheries Research Technology Center, Japan during the analysis.

#### AUTHOR CONTRIBUTIONS

A.S.M. designed the study, analyzed data, and prepared drafts, with critical input from all authors.

#### DECLARATION OF INTERESTS

The authors declare no competing interests.

#### SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.oneear.2024.08.003>.

Received: October 10, 2023

Revised: March 16, 2024

Accepted: August 8, 2024

Published: September 2, 2024

#### REFERENCES

- Elsen, P.R., Oakes, L.E., Cross, M.S., DeGemmis, A., Watson, J.E., Cooke, H.A., Darling, E.S., Jones, K.R., Kretser, H.E., Mendez, M., et al. (2023). Priorities for embedding ecological integrity in climate adaptation policy and practice. *One Earth* 6, 632–644. <https://doi.org/10.1016/j.oneear.2023.05.014>.
- Mori, A.S. (2020). Advancing nature-based approaches to address the biodiversity and climate emergency. *Ecol. Lett.* 23, 1729–1732. <https://doi.org/10.1111/ele.13594>.
- WHO (2011). *Our planet, our health, our future. In Human Health and the Rio Conventions: Biological Diversity, Climate Change and Desertification* (World Health Organization).
- UNDP (2012). *Biodiversity and Ecosystems Global Framework 2012 to 2020* (United Nations Development Programme).
- UN (2020). *United Nations Decade on Ecosystem Restoration 2021–2030*. [www.decadeonrestoration.org](http://www.decadeonrestoration.org).
- Cohen-Shacham, E., Walters, G., Janzen, C., and Maginnis, S. (2016). *Nature-based Solutions to Address Global Societal Challenges* (International Union for Conservation of Nature).
- Donovan, G.H., Gatzliolis, D., Longley, I., and Douwes, J. (2018). Vegetation diversity protects against childhood asthma: results from a large New Zealand birth cohort. *Nat. Plants* 4, 358–364. <https://doi.org/10.1038/s41477-018-0151-8>.
- Donovan, G.H., Prestemon, J.P., Gatzliolis, D., Michael, Y.L., Kaminski, A.R., and Dadvand, P. (2022). The association between tree planting and mortality: A natural experiment and cost-benefit analysis. *Environ. Int.* 170, 107609. <https://doi.org/10.1016/j.envint.2022.107609>.
- Iungman, T., Cirach, M., Marando, F., Pereira Barboza, E., Khomenko, S., Masselot, P., Quijal-Zamorano, M., Mueller, N., Gasparrini, A., Urquiza, J., et al. (2023). Cooling cities through urban green infrastructure: a health impact assessment of European cities. *Lancet* 401, 577–589. [https://doi.org/10.1016/S0140-6736\(22\)02585-5](https://doi.org/10.1016/S0140-6736(22)02585-5).
- Donovan, G.H., Gatzliolis, D., t Mannetje, A., Weinkove, R., Fyfe, C., and Douwes, J. (2021). An empirical test of the biodiversity hypothesis: Exposure to plant diversity is associated with a reduced risk of childhood acute lymphoblastic leukemia. *Sci. Total Environ.* 768, 144627. <https://doi.org/10.1016/j.scitotenv.2020.144627>.
- World Economic Forum (2023). *The Global Risks Report 2023* (World Economic Forum).
- Mori, A.S., Dee, L.E., Gonzalez, A., Ohashi, H., Cowles, J., Wright, A.J., Loreau, M., Hautier, Y., Newbold, T., Reich, P.B., et al. (2021). Biodiversity–productivity relationships are key to nature-based climate solutions. *Nat. Clim. Chang.* 11, 543–550. <https://doi.org/10.1038/s41558-021-01062-1>.
- Pörtner, H.O., Scholes, R.J., Agard, J., Archer, E., Arneeth, A., Bai, X., Barnes, D., Burrows, M., Chan, L., Cheung, W.L., et al. (2021). Scientific Outcome of the IPBES-IPCC Co-sponsored Workshop on Biodiversity and Climate Change (IPBES secretariat). <https://zenodo.org/record/5101125#.Yp8T1XbP1D8>.
- Seddon, N., Turner, B., Berry, P., Chausson, A., and Girardin, C.A.J. (2019). Grouping nature-based climate solutions in sound biodiversity science. *Nat. Clim. Chang.* 9, 84–87. <https://doi.org/10.1038/s41558-019-0405-0>.
- Archer, E., Obura, D., Leadley, P., Arneeth, A., Smith, P., and Mori, A.S. (2022). Establishing a climate target within the post-2020 Global Biodiversity Framework. *PLOS Clim.* 1, e0000106. <https://doi.org/10.1371/journal.pclm.0000106>.
- Pecl, G.T., Araujo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengard, B., et al. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355, eaai9214. <https://doi.org/10.1126/science.aai9214>.
- Voskamp, A., Fritz, S.A., Köcke, V., Biber, M.F., Nogueira Brockmeyer, T., Bertzy, B., Forrest, M., Goldstein, A., Henderson, S., Hickler, T., et al. (2023). Utilizing multi-objective decision support tools for protected area selection. *One Earth* 6, 1143–1156. <https://doi.org/10.1016/j.oneear.2023.08.009>.
- Dinerstein, E., Vynne, C., Sala, E., Joshi, A.R., Fernando, S., Lovejoy, T.E., Mayorga, J., Olson, D., Asner, G.P., Baillie, J.E.M., et al. (2019). A Global Deal For Nature: Guiding principles, milestones, and targets. *Sci. Adv.* 5, eaaw2869. <https://doi.org/10.1126/sciadv.aaw2869>.
- Legagneux, P., Casajus, N., Cazelles, K., Chevallier, C., Chevris, M., Guéry, L., Jacquet, C., Jaffré, M., Naud, M.J., Noisette, F., et al. (2018). Our House Is Burning: Discrepancy in Climate Change vs. Biodiversity Coverage in the Media as Compared to Scientific Literature. *Front. Ecol. Evol.* 5. <https://doi.org/10.3389/fevo.2017.00175>.
- Pettorelli, N., Graham, N.A.J., Seddon, N., Maria da Cunha Bustamante, M., Lowton, M.J., Sutherland, W.J., Koldewey, H.J., Prentice, H.C., and Barlow, J. (2021). Time to integrate global climate change and biodiversity science-policy agendas. *J. Appl. Ecol.* 58, 2384–2393. <https://doi.org/10.1111/1365-2664.13985>.
- Gonzalez, A., Vihervaara, P., Balvanera, P., Bates, A.E., Bayraktarov, E., Bellingham, P.J., Bruder, A., Campbell, J., Catchen, M.D., Cavender-Bares, J., et al. (2023). A global biodiversity observing system to unite monitoring and guide action. *Nat. Ecol. Evol.* 7, 1947–1952. <https://doi.org/10.1038/s41559-023-02171-0>.
- Mori, A.S., Suzuki, K.F., Hori, M., Kadoya, T., Okano, K., Uruguchi, A., Muraoka, H., Sato, T., Shibata, H., Suzuki-Ohno, Y., et al. (2023). Perspective: sustainability challenges, opportunities and solutions for long-term ecosystem observations. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 378, 20220192. <https://doi.org/10.1098/rstb.2022.0192>.
- Nature Editorial (2023). Will the world ever see another IPCC-style body? *Nature* 615, 7–8. <https://doi.org/10.1038/d41586-023-00572-6>.
- Seddon, N., Chausson, A., Berry, P., Girardin, C.A.J., Smith, A., and Turner, B. (2020). Understanding the value and limits of nature-based solutions to climate change and other global challenges. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 375, 20190120. <https://doi.org/10.1098/rstb.2019.0120>.
- Morecroft, M.D., Duffield, S., Harley, M., Pearce-Higgins, J.W., Stevens, N., Watts, O., and Whitaker, J. (2019). Measuring the success of climate change adaptation and mitigation in terrestrial ecosystems. *Science* 366, eaaw9256. <https://doi.org/10.1126/science.aaw9256>.

26. Isbell, F., Tilman, D., Polasky, S., and Loreau, M. (2015). The biodiversity-dependent ecosystem service debt. *Ecol. Lett.* *18*, 119–134. <https://doi.org/10.1111/ele.12393>.
27. Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., and Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecol. Lett.* *15*, 365–377. <https://doi.org/10.1111/j.1461-0248.2011.01736.x>.
28. Garcia, R.A., Cabeza, M., Rahbek, C., and Araújo, M.B. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science* *344*, 1247579. <https://doi.org/10.1126/science.1247579>.
29. Warren, R., Price, J., Graham, E., Forstenhaeusler, N., and VanDerWal, J. (2018). The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5 degrees C rather than 2 degrees C. *Science* *360*, 791–795. <https://doi.org/10.1126/science.aar3646>.
30. Hisano, M., Searle, E.B., and Chen, H.Y.H. (2018). Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. *Biol. Rev.* *93*, 439–456. <https://doi.org/10.1111/brv.12351>.
31. Tilman, D., Isbell, F., and Cowles, J.M. (2014). Biodiversity and ecosystem functioning. *Ann Rev Ecol Evol Syst* *45*, 471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>.
32. Mori, A.S. (2018). Environmental controls on the causes and functional consequences of tree species diversity. *J. Ecol.* *106*, 113–125. <https://doi.org/10.1111/1365-2745.12851>.
33. Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.D., McGuire, A.D., Bozzato, F., Pretzsch, H., et al. (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science* *354*, aaf8957. <https://doi.org/10.1126/science.aaf8957>.
34. O'Connor, M.I., Gonzalez, A., Byrnes, J.E.K., Cardinale, B.J., Duffy, J.E., Gamfeldt, L., Griffin, J.N., Hooper, D., Hungate, B.A., Paquette, A., et al. (2017). A general biodiversity-function relationship is mediated by trophic level. *Oikos* *126*, 18–31. <https://doi.org/10.1111/oik.03652>.
35. Duffy, J.E., Godwin, C.M., and Cardinale, B.J. (2017). Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* *549*, 261–264. <https://doi.org/10.1038/nature23886>.
36. Hua, F., Bruijnzeel, L.A., Meli, P., Martin, P.A., Zhang, J., Nakagawa, S., Miao, X., Wang, W., McEvoy, C., Peña-Arancibia, J.L., et al. (2022). The biodiversity and ecosystem service contributions and trade-offs of forest restoration approaches. *Science* *376*, 839–844. <https://doi.org/10.1126/science.abl4649>.
37. CBD (2022). Kunming-Montreal Global biodiversity framework: Draft decision submitted by the President. CBD/COP/15/L.25, Convention on Biological Diversity, Montreal, Canada, 2022, <https://www.cbd.int/doc/c/e6d3/cd1d/daf663719a03902a9b116c34/cop-15-l-25-en.pdf>
38. Felton, A.J., Shriver, R.K., Stenkovski, M., Bradford, J.B., Suding, K.N., and Adler, P.B. (2022). Climate disequilibrium dominates uncertainty in long-term projections of primary productivity. *Ecol. Lett.* *25*, 2688–2698. <https://doi.org/10.1111/ele.14132>.
39. Bertrand, R., Riofrío-Dillon, G., Lenoir, J., Drapier, J., de Ruffray, P., Gégout, J.C., and Loreau, M. (2016). Ecological constraints increase the climatic debt in forests. *Nat. Commun.* *7*, 12643. <https://doi.org/10.1038/ncomms12643>.
40. Brito-Morales, I., García Molinos, J., Schoeman, D.S., Burrows, M.T., Poloczanska, E.S., Brown, C.J., Ferrier, S., Harwood, T.D., Klein, C.J., McDonald-Madden, E., et al. (2018). Climate Velocity Can Inform Conservation in a Warming World. *Trends Ecol. Evol.* *33*, 441–457. <https://doi.org/10.1016/j.tree.2018.03.009>.
41. Daru, B.H., and Rock, B.M. (2023). Reorganization of seagrass communities in a changing climate. *Nat. Plants* *9*, 1034–1043. <https://doi.org/10.1038/s41477-023-01445-6>.
42. Nowakowski, A.J., Watling, J.I., Murray, A., Deichmann, J.L., Akre, T.S., Muñoz Brenes, C.L., Todd, B.D., McRae, L., Freeman, R., and Friskhoff, L.O. (2023). Protected areas slow declines unevenly across the tetrapod tree of life. *Nature* *622*, 101–106. <https://doi.org/10.1038/s41586-023-06562-y>.
43. Adams, V.M., Chauvenet, A.L., Stoudmann, N., Gurney, G.G., Brockington, D., and Kuempel, C.D. (2023). Multiple-use protected areas are critical to equitable and effective conservation. *One Earth* *6*, 1173–1189. <https://doi.org/10.1016/j.oneear.2023.08.011>.
44. Ohashi, H., Hasegawa, T., Hirata, A., Fujimori, S., Takahashi, K., Tsuyama, I., Nakao, K., Kominami, Y., Tanaka, N., Hijioka, Y., and Matsui, T. (2019). Biodiversity can benefit from climate stabilization despite adverse side effects of land-based mitigation. *Nat. Commun.* *10*, 5240. <https://doi.org/10.1038/s41467-019-13241-y>.
45. Riahi, K., van Vuuren, D.P., Kriegler, E., Edmonds, J., O'Neill, B.C., Fujimori, S., Bauer, N., Calvin, K., Dellink, R., Fricko, O., et al. (2017). The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Glob. Environ. Change* *42*, 153–168. <https://doi.org/10.1016/j.gloenvcha.2016.05.009>.
46. Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.C., and Gégout, J.C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature* *479*, 517–520. <https://doi.org/10.1038/nature10548>.
47. Burrows, M.T., Schoeman, D.S., Richardson, A.J., Molinos, J.G., Hoffmann, A., Buckley, L.B., Moore, P.J., Brown, C.J., Bruno, J.F., Duarte, C.M., et al. (2014). Geographical limits to species-range shifts are suggested by climate velocity. *Nature* *507*, 492–495. <https://doi.org/10.1038/nature12976>.
48. Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., Osinaga-Acosta, O., Malizia, L., Silman, M., Farfán-Ríos, W., et al. (2018). Widespread but heterogeneous responses of Andean forests to climate change. *Nature* *564*, 207–212. <https://doi.org/10.1038/s41586-018-0715-9>.
49. Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Fosaa, A.M., Gould, W.A., Hermanutz, L., Hofgaard, A., Jónsdóttir, I.S., Jorgenson, J.C., Lévesque, E., et al. (2015). Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. *Proc. Natl. Acad. Sci. USA* *112*, 448–452. <https://doi.org/10.1073/pnas.1410088112>.
50. Lambin, E.F., and Meyfroidt, P. (2011). Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl. Acad. Sci. USA* *108*, 3465–3472. <https://doi.org/10.1073/pnas.1100480108>.
51. Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., et al. (2011). Solutions for a cultivated planet. *Nature* *478*, 337–342. <https://doi.org/10.1038/nature10452>.
52. Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., and Foley, J.A. (2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proc. Natl. Acad. Sci. USA* *107*, 16732–16737. <https://doi.org/10.1073/pnas.0910275107>.
53. Cook-Patton, S.C., Leavitt, S.M., Gibbs, D., Harris, N.L., Lister, K., Anderson-Teixeira, K.J., Briggs, R.D., Chazdon, R.L., Crowther, T.W., Ellis, P.W., et al. (2020). Mapping carbon accumulation potential from global natural forest regrowth. *Nature* *585*, 545–550. <https://doi.org/10.1038/s41586-020-2686-x>.
54. Cook-Patton, S.C., Shoch, D., and Ellis, P.W. (2021). Dynamic global monitoring needed to use restoration of forest cover as a climate solution. *Nat. Clim. Chang.* *11*, 366–368. <https://doi.org/10.1038/s41558-021-01022-9>.
55. Kobayashi, Y., Seidl, R., Rammer, W., Suzuki, K.F., and Mori, A.S. (2022). Identifying effective tree planting schemes to restore forest carbon and biodiversity in Shiretoko National Park, Japan. *Restor. Ecol.* *31*, e13681. <https://doi.org/10.1111/rec.13681>.
56. Rey Benayas, J.M., Newton, A.C., Diaz, A., and Bullock, J.M. (2009). Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* *325*, 1121–1124. <https://doi.org/10.1126/science.1172460>.
57. Bui, M., Adjiman, C.S., Bardow, A., Anthony, E.J., Boston, A., Brown, S., Fennell, P.S., Fuss, S., Galindo, A., Hackett, L.A., et al. (2018). Carbon

- capture and storage (CCS): the way forward. *Energ Environ Sci* 11, 1062–1176. <https://doi.org/10.1039/c7ee02342a>.
58. Bellamy, R., and Osaka, S. (2020). Unnatural climate solutions? *Nat. Clim. Chang.* 10, 98–99. <https://doi.org/10.1038/s41558-019-0661-z>.
59. Martin, S., Bartlett, R., and Kim, M. (2020). Enhancing NDCs through Nature-Based Solutions (WWF). <https://www.worldwildlife.org/publications/enhancing-ndcs-through-nature-based-solutions>.
60. Girardin, C.A.J., Jenkins, S., Seddon, N., Allen, M., Lewis, S.L., Wheeler, C.E., Griscom, B.W., and Malhi, Y. (2021). Nature-based solutions can help cool the planet - if we act now. *Nature* 593, 191–194. <https://doi.org/10.1038/d41586-021-01241-2>.
61. Clark, M.A., Domingo, N.G.G., Colgan, K., Thakrar, S.K., Tilman, D., Lynch, J., Azevedo, I.L., and Hill, J.D. (2020). Global food system emissions could preclude achieving the 1.5 degrees and 2 degrees C climate change targets. *Science* 370, 705–708. <https://doi.org/10.1126/science.aba7357>.
62. Harwatt, H., Ripple, W.J., Chaudhary, A., Betts, M.G., and Hayek, M.N. (2020). Scientists call for renewed Paris pledges to transform agriculture. *Lancet Planet. Health* 4, e9–e10. [https://doi.org/10.1016/s2542-5196\(19\)30245-1](https://doi.org/10.1016/s2542-5196(19)30245-1).
63. Willett, W., Rockström, J., Loken, B., Springmann, M., Lang, T., Vermeulen, S., Garnett, T., Tilman, D., DeClerck, F., Wood, A., et al. (2019). Food in the Anthropocene: the EAT–Lancet Commission on healthy diets from sustainable food systems. *Lancet* 393, 447–492. [https://doi.org/10.1016/S0140-6736\(18\)31788-4](https://doi.org/10.1016/S0140-6736(18)31788-4).
64. Bocken, N.M., and Short, S.W. (2021). Unsustainable business models – Recognising and resolving institutionalised social and environmental harm. *J. Clean. Prod.* 372, 127828. <https://doi.org/10.1016/j.jclepro.2021.127828>.
65. Nystrom, M., Jouffray, J.B., Norstrom, A.V., Crona, B., Sogaard Jorgensen, P., Carpenter, S.R., Bodin, O., Galaz, V., and Folke, C. (2019). Anatomy and resilience of the global production ecosystem. *Nature* 575, 98–108. <https://doi.org/10.1038/s41586-019-1712-3>.
66. Poore, J., and Nemecek, T. (2018). Reducing food’s environmental impacts through producers and consumers. *Science* 360, 987–992. <https://doi.org/10.1126/science.aaq0216>.
67. Geldmann, J., Manica, A., Burgess, N.D., Coad, L., and Balmford, A. (2019). A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. *Proc. Natl. Acad. Sci. USA* 116, 23209–23215. <https://doi.org/10.1073/pnas.1908221116>.
68. Weiskopf, S.R., Harmáčková, Z.V., Johnson, C.G., Londoño-Murcia, M.C., Miller, B.W., Myers, B.J.E., Pereira, L., Arce-Plata, M.I., Blanchard, J.L., Ferrier, S., et al. (2022). Increasing the uptake of ecological model results in policy decisions to improve biodiversity outcomes. *Environ. Model. Software* 149, 105318. <https://doi.org/10.1016/j.envsoft.2022.105318>.
69. Duffy, J.E. (2009). Why biodiversity is important to the functioning of real-world ecosystems. *Front Ecol Environ* 7, 437–444. <https://doi.org/10.1890/070195>.
70. Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., Mace, G.M., Wardle, D.A., O’Connor, M.I., Duffy, J.E., et al. (2017). Linking the influence and dependence of people on biodiversity across scales. *Nature* 546, 65–72. <https://doi.org/10.1038/nature22899>.
71. Naeem, S., Chazdon, R., Duffy, J.E., Prager, C., and Worm, B. (2016). Biodiversity and human well-being: an essential link for sustainable development. *Proc. Biol. Sci.* 283, 20162091. <https://doi.org/10.1098/rspb.2016.2091>.
72. Naeem, S., Duffy, J.E., and Zavaleta, E. (2012). The functions of biological diversity in an age of extinction. *Science* 336, 1401–1406. <https://doi.org/10.1126/science.1215855>.
73. Jiang, M., Medlyn, B.E., Drake, J.E., Duursma, R.A., Anderson, I.C., Barton, C.V.M., Boer, M.M., Carrillo, Y., Castañeda-Gómez, L., Collins, L., et al. (2020). The fate of carbon in a mature forest under carbon dioxide enrichment. *Nature* 580, 227–231. <https://doi.org/10.1038/s41586-020-2128-9>.
74. Leadley, P., Gonzalez, A., Krug, C., Londoño-Murcia, M., Millette, K., Obura, D., Radulovici, A., Rankovic, A., Shannon, L., Archer, E., et al. (2022). Achieving global biodiversity goals by 2050 requires urgent and integrated actions. *One Earth* 5, 6. <https://doi.org/10.32942/one.10/hy7a2>.
75. IPBES (2019). *Global Assessment Report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (IPBES Secretariat).
76. Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D.E., Coscieme, L., Golden, A.S., Guerra, C.A., Jacob, U., Takahashi, Y., Settele, J., et al. (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Sci. Adv.* 8, eabm9982. <https://doi.org/10.1126/sciadv.abm9982>.
77. Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T.M., Bonin, C., Bruelheide, H., de Luca, E., et al. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526, 574–577. <https://doi.org/10.1038/nature15374>.
78. Mori, A.S., Lertzman, K.P., and Gustafsson, L. (2017). Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *J. Appl. Ecol.* 54, 12–27. <https://doi.org/10.1111/1365-2664.12669>.
79. Mori, A.S., Cornelissen, J.H.C., Fujii, S., Okada, K.I., and Isbell, F. (2020). A meta-analysis on decomposition quantifies afterlife effects of plant diversity as a global change driver. *Nat. Commun.* 11, 4547. <https://doi.org/10.1038/s41467-020-18296-w>.
80. Hautier, Y., Zhang, P., Loreau, M., Wilcox, K.R., Seabloom, E.W., Borer, E.T., Byrnes, J.E.K., Koerner, S.E., Komatsu, K.J., Lefcheck, J.S., et al. (2020). General destabilizing effects of eutrophication on grassland productivity at multiple spatial scales. *Nat. Commun.* 11, 5375. <https://doi.org/10.1038/s41467-020-19252-4>.
81. O’Connor, M.I., Mori, A.S., Gonzalez, A., Dee, L.E., Loreau, M., Avolio, M., Byrnes, J.E.K., Cheung, W., Cowles, J., Clark, A.T., et al. (2021). Grand challenges in biodiversity–ecosystem functioning research in the era of science–policy platforms require explicit consideration of feedbacks. *Proc. Biol. Sci. R Soc.* 288, 20210783. <https://doi.org/10.1098/rspb.2021.0783>.
82. Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., et al. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294, 804–808.
83. Loreau, M., Hector, A., and Isbell, F. (2022). *The Ecological and Societal Consequences of Biodiversity Loss* (Wiley–ISTE).
84. Isbell, F., Balvanera, P., Mori, A.S., He, J.S., Bullock, J.M., Regmi, G.R., Seabloom, E.W., Ferrier, S., Sala, O.E., Guerrero-Ramirez, N.R., et al. (2022). Expert perspectives on global biodiversity loss and its drivers and impacts on people. *Front Ecol Environ* 21, 94–103. <https://doi.org/10.1002/fee.2536>.
85. Phillips, S.J., Anderson, R.P., and Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>.
86. May, F., Gerstner, K., McGlinn, D.J., Xiao, X., and Chase, J.M. (2018). mobsim: An R package for the simulation and measurement of biodiversity across spatial scales. *Method Ecol Evol* 9, 1401–1408. <https://doi.org/10.1111/2041-210x.12986>.
87. Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978. <https://doi.org/10.1002/joc.1276>.
88. Fujimori, S., Hasegawa, T., and Masui, T. (2017). AIM/CGE V2.0: Basic Feature of the Model (Springer Nature Singapore). [https://doi.org/10.1007/978-981-10-3869-3\\_13](https://doi.org/10.1007/978-981-10-3869-3_13).

89. Hasegawa, T., Fujimori, S., Ito, A., Takahashi, K., and Masui, T. (2017). Global land-use allocation model linked to an integrated assessment model. *Sci. Total Environ.* 580, 787–796. <https://doi.org/10.1016/j.scitotenv.2016.12.025>.
90. Fujimori, S., Hasegawa, T., Ito, A., Takahashi, K., and Masui, T. (2018). Gridded emissions and land-use data for 2005–2100 under diverse socioeconomic and climate mitigation scenarios. *Sci. Data* 5, 180210. <https://doi.org/10.1038/sdata.2018.210>.
91. Running, S., Mu, Q., and Zhao, M.; MODAPS-SIPS (2015). MOD17A3H MODIS/Terra Gross Primary Productivity Yearly L4 Global 500m SIN Grid (NASA). <https://doi.org/10.5067/MODIS/MOD17A3H.006>.
92. Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., et al. (2019). Welcome to the Tidyverse. *J. Open Source Softw.* 4, 1686. <https://doi.org/10.21105/joss.01686>.
93. Dowle, M., and Srinivasan, A. (2023). data.table: Extension of 'data.frame'. <https://github.com/Rdatatable/data.table>
94. Pebesma, E.. sf: Simple Features for R. R package version 0.6-3. <https://github.com/r-spatial/sf>.
95. Hijmans, R.J. (2022). geodata: Download Geographic Data. <https://github.com/rspatial/geodata/>.
96. R Core Team (2024). R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing).
97. Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., et al. (2017). An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. *Bioscience* 67, 534–545. <https://doi.org/10.1093/biosci/bix014>.
98. UNEP-WCMC (2019). User Manual for the World Database on Protected Areas and World Database on Other Effective Area-Based Conservation Measures, p. 1.6. [https://resources.unep-wcmc.org/products/WCMC\\_CB007](https://resources.unep-wcmc.org/products/WCMC_CB007).
99. Pustejovsky, J.. ARPobservation: Simulating recording procedures for direct observation of behavior. R package version 1.1. <https://doi.org/10.32614/CRAN.package.ARPobservation>.
100. Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the metafor Package. *J. Stat. Softw.* 36, 1–48. <https://doi.org/10.18637/jss.v036.i03>.
101. Wickham, H. (2007). Reshaping data with the 'reshape' package. *J. Stat. Softw.* 21, 1–20. <https://doi.org/10.18637/jss.v021.i12>.
102. Pedersen, T.L. (2023). ggforce: Accelerating ggplot2. <https://github.com/thomasp85/ggforce>
103. Neuwirth, E.. RColorBrewer: ColorBrewer Palettes. <https://doi.org/10.32614/CRAN.package.RColorBrewer>.