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Climate refugia implications of warming and land-intensive mitigation under overshoot

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Supplementary material for this article is available online

Abstract

Biodiversity loss is expected to escalate with every increment of global warming. Simultaneously, land-intensive climate change mitigation strategies, such as afforestation and bioenergy, may further compound biodiversity loss. So far, the magnitude of these two drivers has not been compared in the context of temperature overshoot, meaning the temporary exceedance of a targeted global warming limit. By combining spatial data on climate refugia (areas sheltering biodiversity from climate change), bioenergy cropland, and forestation for multiple cost-effective scenarios with varying levels of climate action and overshoot, we illustrate how both warming and mitigation affect today's climate refugia across five integrated assessment models. Decisive climate action, compatible with limiting warming to 1.5 °C, reduces the combined loss of today's climate refugia due to warming and mitigation-related land-use change by more than 50% compared to current climate policies, outweighing potentially negative implications of mitigation at the global level by limiting the magnitude and duration of warming above 1.5 °C. We observe notable differences across regions and the considered model frameworks. Overshoot implications strongly depend on the underlying biodiversity recovery assumptions.

1. Introduction

Biodiversity loss is expected to escalate with every increment of global warming [1, 2]. Land-intensive climate change mitigation strategies, such as afforestation and the use of bioenergy plantings may further compound biodiversity loss. This duality of drivers of biodiversity loss in the context of climate change raises the question of how these compare in magnitude. Existing studies show mixed results. Several studies cautioned that negative biodiversity implications of land-intensive mitigation via afforestation [3] and bioenergy with [4] or without [5] carbon capture and storage might outweigh positive conservation effects of mitigated warming. More recent studies corroborate that land-intensive mitigation partly comes with negative impacts for biodiversity conservation, while still indicating net benefits

[6, 7] globally. Some studies emphasize the role of temporal dynamics, where land-based mitigation may bring net harm over shorter evaluation periods, while the benefit of avoided climate change outweighs negative mitigation effects over longer periods [8, 9]. Regional implications may strongly deviate from global mean estimates [6, 7, 9].

An important, so far largely underexplored, aspect concerns biodiversity implications under potential temperature overshoot, defined as temporary exceedance of a target warming level, which is reversed by achieving net negative CO_2 emissions [10, 11]. Overshoot management is gaining attention as it would be needed to limit long-term climate risks [12, 13]. First steps have been made to assess warming-related overshoot implications for biodiversity [11, 14]. However, comparative evidence on warming-related and mitigation-related biodiversity implications in the context of overshoot scenarios is still largely lacking [10].

Here, we illustrate and compare the scale of warming and mitigation-related implications for today's climate refugia (climate shelters for biodiversity at the current level of global warming of 1.3 °C—see methods and table 1) in existing decarbonisation scenarios with varying levels of overshoot or peak-and-decline warming. Various definitions of climate refugia exist, which suit different analytical use cases [15–17]. Our study assesses the future climatic suitability of *in situ* macro-refugia. We critically examine the role of two stylized climate refugia recovery assumptions and dynamics after peak warming. We focus on land-intensive mitigation as this is a main driver of land-use change in the assessed scenarios and thus critical for biodiversity (supplementary information SI(A)). Beyond our illustrative analysis, we discuss other important determinants of biodiversity implications in the context of overshoot.

Table 1. Overview of the climate refugia and related recovery concept of this study.

Concept	Description
Today's climate refugia	Today's climate refugia represent areas (grid cells) where terrestrial biodiversity (comprising roughly 135 000 species of fungi, plants, invertebrates, and vertebrates) can persist at the current level of global warming of around 1.3 °C (for at least 11 out of 21 considered regional climate model projections).
'Loss' of climate refugia	Today's climate refugia areas (at grid cell level) are considered lost to global warming when the regional climate (for at least 11 out of 21 considered regional climate model projections) becomes unsuitable for more than 25% of the species initially present. Unless otherwise specified, today's climate refugia areas are considered 'lost' to mitigation-related land-use change when allocated for forestation or bioenergy cropland.
Recovery of climate refugia	Today's climate refugia areas, which lose climatic suitability due to global warming, may become climatically suitable again if global warming declines. In such cases, initially present species may repopulate these areas (grid cells). The degree to which this is possible depends on species' ability to recover from warming, which we illustrate through two extreme cases: no recovery or full and instant recovery (acknowledging that there is likely only limited recovery over the assessed timescales).

2. Methods

2.1. Analysis overview

We considered and combined the following existing datasets as inputs to our analysis: spatial data on climate refugia areas; spatial land use data on forestation (afforestation, reforestation, and forest restoration) and bioenergy cropland for various already existing, cost-effective mitigation pathways and from five different model frameworks; spatial data on the world administrative boundaries at country and territory level; scenario-based global warming data; and contextual data on the suitability of land for forestation and bioenergy cropland.

First, we compared the warming-related and mitigation-related 'losses' of today's climate refugia side-by-side. We denote 'loss' that fully or partly stems from land-intensive mitigation with quotation marks to highlight the illustrative nature of this precautionary estimate (section 2.5). We also estimated the combined climate refugia 'loss' of these two drivers. In doing this, we tested different refugia recovery assumptions (defined below) after peak warming in peak-and-decline scenarios (supplementary information SI(B)). Second, we compared which of the two impact drivers (warming loss or land allocation) dominate at country or territory level and explored how insights align or differ across the five considered model frameworks. Lastly, we illustrated differences in land allocation within climate refugia at 1.5 °C of global warming before versus after overshoot.

2.2. Climate refugia

Climate refugia are crucial shelters for biodiversity in the context of climate change, making their protection an important component of conservation strategies [15, 16, 18–20]. Climate refugia can lose their insulating function if climate velocity accelerates and climate conditions become unsuitable under overshoot for sheltered species [20]. Evidence suggests that some species could partly cope with overshoot by temporarily migrating to other places (tracking their suitable climate niches) and repopulating previously inhabited areas if they become climatically suitable again—recovery would, however, only be feasible over long time periods and only for certain species [15, 20–22].

The here used climate refugia data are based on previous analyses [23–25], building on the Wallace Initiative. Climate refugia are defined as areas (grid cells) in which at least 75% of the initially present terrestrial species (fungi, plants, invertebrates, and vertebrates) retain a suitable climate space under a given warming level, requiring pattern consensus of at least 11 out of 21 considered regional climate model projections (based on CMIP5). This spatial dataset (10 arcmin spatial resolution) comprises around 135 000 species across taxa, showing the potential future change in species' climatically suitable ranges under global median surface temperature levels (GSAT) from 1 °C to 4.5 °C, relative to the preindustrial level (1850–1900). Information on individual species models was aggregated to indicate remaining cross-taxa species richness per grid cell and warming level. The global species distribution is based on the MaxENT model [24, 26, 27]. The dataset implies that the relationship between present-day regional climatic conditions and observed species distribution would remain stable under future climate change. The input dataset shows climate refugia locations and extent at 0.5 °C increments of global warming. We used linear interpolation to generate climate refugia maps at 0.01 °C increments of global warming (this should not be interpreted as reflecting the level of precision of the underlying data), based on the available climate refugia maps.

Here, we focus on *in situ* climate refugia, meaning that we do not track potential shifts in the location of climate refugia, based on species dispersal rates. Instead, we explore potential refugia recovery in the context of peak-and-decline warming trajectories (table 1 and section 2.5). A dedicated assessment of refugia recovery from land-use changes is beyond the scope of this study. In this analysis, 'today's climate refugia' refers to the global climate refugia extent at 1.3 °C of warming, corresponding to the current state of global warming. Altered regional climate conditions after overshoot are currently not captured in the underlying dataset.

Note that other definitions of refugia exist in the literature which deviate from this study's approach, e.g. focusing primarily on *ex situ* instead of *in situ* refugia, looking at the micro-scale instead of the macro-scale, or identifying past glacial refugia rather than projecting future refugial suitability under anthropogenic climate change [15, 16].

2.3. Scenario-based forestation and bioenergy cropland

As in Prütz *et al* [14], data on future deployment of forestation and bioenergy cropland for several combinations of the shared socioeconomic pathways (SSPs) and representative concentration pathways (RCPs) [28–30] are retrieved from the models AIM-SSP/RCP Ver2018 [31] at 30 arcmin spatial resolution, GCAM-Demeter-LU [32] at 3 arcmin spatial resolution, GLOBIOM [33–35] at 5 arcmin spatial resolution, IMAGE 3.0.1 [36] at 30 arcmin resolution, and from the REMIND-MAgPIE integrated assessment modelling framework (REMIND 1.6 coupled with MAgPIE 3.0) [30, 37] at 30 arcmin spatial resolution.

For AIM, GLOBIOM, IMAGE, and REMIND-MAgPIE, this land use data is based on the original SSP quantification [37–40]. For GCAM, the data is based on the 2020 quantification [32]. A variable for bioenergy cropland is directly available in the model datasets. The net increase in managed and unmanaged forest cover per grid cell between 2010 and a given future timestep is used as a proxy for forestation—comprising afforestation, reforestation, and natural restoration—as the datasets do not contain explicit information on these forest-based mitigation options. This proxy may also capture natural forest regrowth or expansion on abandoned agricultural land, which is not necessarily linked to active mitigation efforts. For GCAM, we used 2020 as base year when estimating the net increase in managed and unmanaged forest cover per grid cell since no data for 2010 is available. Implications and caveats of this forestation estimation approach have been described in Prütz *et al* [14].

Biodiversity considerations are increasingly incorporated in more recent IAM-based scenario development (e.g. by quantifying scenario implications for the biodiversity intactness index BII or by actively protecting biodiversity hotspots) [41–43], compared to the scenario data assessed in this study.

The evaluated scenarios are cost-effective, meaning that the mitigation costs of achieving a given climate policy objective are minimized. Assumptions on land-use change regulations differ across the assessed socioeconomic pathways, with strong regulations in SSP1 (characterizing a world that develops sustainably), moderate regulations in SSP2 (a pathway following historical socioeconomic development patterns), and limited regulations in SSP3 (characterized by high regional rivalry) [29]. Differences in individual models concerning their assumptions and representation of land allocation processes are further described in Popp *et al* [30] and in the individual modelling studies underlying the SSPs [32, 37–40]. Land-use change dynamics per model and considered scenario are shown in supplementary information SI(A).

2.4. Scenario data processing

We used nearest-neighbour resampling to resample the forestation and bioenergy cropland data to 10 arcmin to match the spatial resolution of the climate refugia dataset, while preserving numerical properties. We matched the spatial SSP-RCP land use datasets with corresponding scenario-based global warming (GSAT), as reported in the AR6 Scenarios Database, based on the climate emulator MAGICCv7.5.3 [44, 45]. The AR6 global warming data and the land use dataset used from AIM and GCAM are based on slightly different but similar model versions [31, 32, 44]. Warming curves per model and scenario are shown in supplementary information SI(B).

The assessed scenarios comprise a 1.5 °C-scenario (RCP1.9), a 2 °C-scenario (RCP2.6), a scenario stabilizing above 2 °C (RCP3.4), and one substantially exceeding 2 °C (RCP4.5). The 1.5 °C-scenario and the 2 °C-scenario imply a peak-and-decline trajectory of global warming, and therefore form the basis of our overshoot-focused analysis. RCP4.5 is used to illustrate climate refugia implications of a trajectory that roughly aligns with current global climate policies. The current policies scenario is used as a reference case to contrast with the potential biodiversity benefits of ambitious climate action, consistent with the assessed peak-and-decline scenarios. The used IAM scenario data and climate refugia maps are matched based on GSAT [24, 44].

2.5. Analysis of global climate refugia 'loss'

We contrasted warming-related loss and mitigation-related'loss' of today's climate refugia by exploring both impact drivers separately. For this comparison, we deliberately did not consider areal overlap of the two drivers (section 3.1 and figure 1(a)). Secondly, we explored the combined effect of warming-related loss of today's climate refugia and mitigation-related 'loss' (considering areal overlap) (section 3.2 and figure 1(b)).

Warming-related loss is here defined as the relative reduction of today's global climate refugia for a given scenario-based future warming level, compared to today's climate refugia extent (table 1). Due to the uncertain response of species to warming reversal in the context of peak-and-decline scenarios, we worked with two different refugia recovery assumptions. The first assumption implies no recovery after peak warming and holds the climate refugia extent constant after scenario peak warming. While unrealistic over the timescales considered here, the second assumption implies full recovery once warming starts to decline [22]. In scenarios where global warming is lowered below 1.3 °C towards the end of the century, we capped refugia recovery at 100% of the baseline climate refugia extent. We stress the illustrative character of the two recovery assumptions. Especially full recovery is likely impossible in less than century timescales [22]. We used these two recovery assumptions to map the maximum impact space and note that climate refugia response to peak-and-decline warming would fall somewhere between these two extreme cases—until 2100, likely only very limited recovery [22, 46]. We do not provide a central recovery assumption, as doing so might imply a level of confidence not supported by the underlying data.

Mitigation-related 'loss' is estimated as the share of today's climate refugia allocated for forestation or bioenergy cropland, based on the considered SSP-RCP scenarios at different time steps. For the main analysis, we assume that all mitigation-related land-use change in climate refugia leads to negative biodiversity outcomes. This precautionary assumption is considered appropriate as it safeguards against underestimating potential biodiversity loss to support robust risk-hedging in conservation planning. Implications of this assumption are described in the discussion.

Complementary results with alternative assumptions concerning level of warming and the land-use change effect are presented and discussed in supplementary information SI(C). Note that we focus on future implications of today's climate refugia, starting in 2030. Past or current land use-related impacts (positive or negative) on climate refugia are not within the scope of this analysis—in the assessed scenarios, most land-use change occurs after 2030 (supplementary information SI(A)).

2.6. Analysis of regional variations in climate refugia 'loss'

To identify potential regional variations in the warming-related versus the mitigation-related biodiversity implications, we compared which of these two drivers dominate at the country or territory level across the five considered model frameworks. The results are shown for the focus scenario SSP2-26 in 2100 (since this scenario is available for all five model frameworks), assuming full and instant refugia recovery once warming starts to decline again (section 3.3). The magnitude of warming-related climate refugia loss and mitigation-related climate refugia 'loss' are assessed separately, meaning that areal overlap of the two impact drivers is not considered. For the assessment of model consensus (figure 2(a)), at least three out of the five considered models needed to agree on which of the two drivers results in larger climate refugia 'loss' per administrative region. We imposed a lower bound threshold of 5% to highlight model

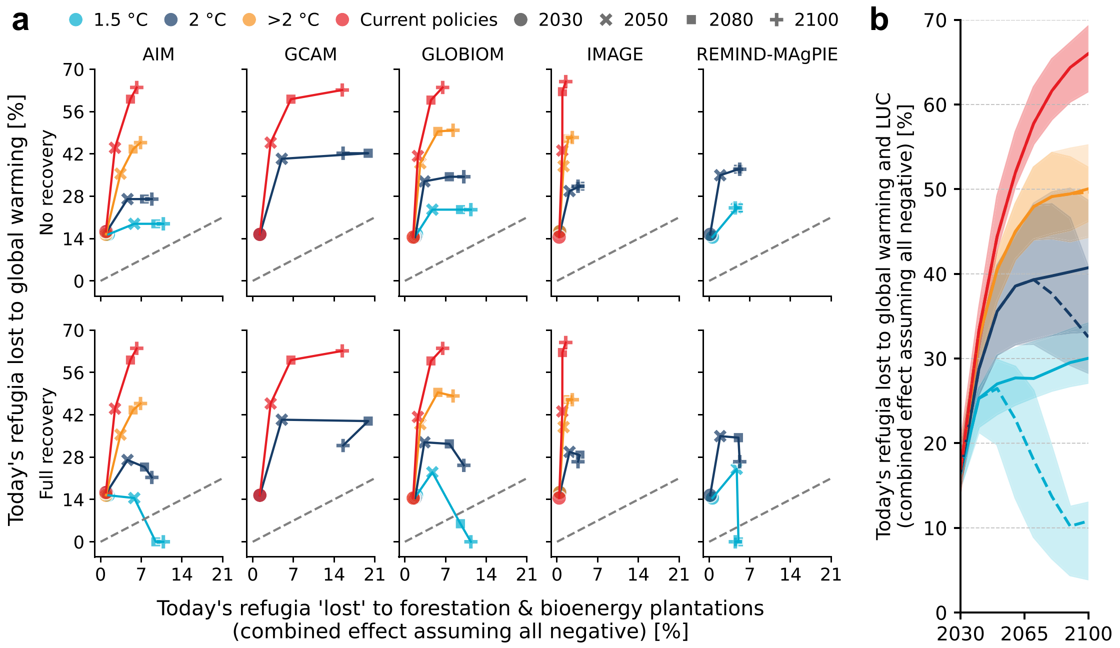

Figure 1. Overview of warming effect and land-intensive mitigation effect on today's global climate refugia across scenarios and models. Panel (a) shows the magnitude of warming-related climate refugia loss (y-axis) and mitigation-related climate refugia 'loss' (x-axis) separately (areal overlap of the two impact drivers not considered). Colored lines represent the scenario-based, decomposed evolution of relative climate refugia 'loss' over time (2030–2100). Above the dashed grey line, the warming effect on climate refugia is larger than the land-use change effect and vice versa. The top row implies no refugia recovery, whereas the bottom row implies full and instant refugia recovery after peak warming in the context of peak-and-decline scenarios. Scenarios are based on SSP2. Columns show results for individual model frameworks. Panel (b) shows the magnitude of combined warming and mitigation-related climate refugia 'loss' (considering areal overlap of the two drivers). LUC refers to land-use change for forestation and bioenergy cropland. Lines show the median estimate and shading shows the 5–95 percentile-range across the five considered model frameworks and across SSP1-3. Solid lines imply no refugia recovery after peak warming, whereas dashed lines imply full and instant recovery. Median estimates for global warming were used in this figure. Not all variables are available for all model-scenario combinations. Complementary results with alternative assumptions are shown in supplementary information SI(C).

consensus concerning more substantial implications, excluding administrative regions for which both considered 'losses' are below this threshold. Results for alternative lower bound thresholds and for a case in which not all mitigation-related land-use change in climate refugia leads to negative biodiversity outcomes are shown in the supplementary information SI(D). Model-specific land allocation patterns are presented in supplementary information SI(E).

2.7. Analysis of climate refugia land allocation before and after overshoot

To illustrate differences in land allocation within climate refugia at 1.5 °C before and after overshoot (section 3.4), we focused on the two illustrative scenarios in our considered scenario set that overshoot 1.5 °C by at least 0.1 °C and return to 1.5 °C of global warming within this century (2020–2100). These two scenarios are based on SSP1-19 from the GLOBIOM model, and the REMIND-MAgPIE model framework. For both scenarios, we overlaid global climate refugia (at 1.5 °C) with forestation and bioenergy areas and compared the difference in overlap at 1.5 °C before and after overshoot. Full and instant refugia recovery is assumed in this case.

3. Results

3.1. Global effects comparison

Across all considered model frameworks and scenarios, we find that the magnitude of warming-related climate refugia loss is larger than the 'loss' induced by land-intensive mitigation if we assume no refugia recovery (figure 1(a), top row). We observe similar warming-related climate refugia losses across the considered model frameworks. Differences in mitigation-related land allocation within today's climate refugia are more pronounced but show a similar global pattern. More ambitious scenarios can substantially reduce the warming-related climate refugia loss, however, at the expense of increased land allocation for land-intensive mitigation within today's climate refugia (see section 3.2 for the integrated effect).

We also find that the warming-related climate refugia loss arises markedly faster than the mitigation-related 'loss'. By 2030, around 16% (17 Mkm^2) of today's climate refugia would be lost due to warming across all assessed scenarios (main analysis), whereas the mitigation-related 'loss' does not reach this level even towards the end of the 21st century, except for the 2 °C-scenario modelled in GCAM (figure 1(a)).

In the scenario aligned with the expected warming outcome of current climate policies (SSP2-45), more than 60% of today's climate refugia would be lost due to warming by 2100, whereas the mitigation-related 'loss' ranges between 2%–15% (6% median 'loss') across the considered model frameworks. For the scenario compatible with limiting warming to less than 2 °C (SSP2-26), the warming-related loss in 2100 is substantially reduced and roughly halved (29% median loss) across the five considered model frameworks compared to current policies. The mitigation-related 'loss' in 2100 in this 2 °C-scenario increases compared to the current policies scenario, ranging between 4%–16% (9% median 'loss'), corresponding to an area loss of 4–16 Mkm^2 (9 Mkm^2 median 'loss').

For two considered peak-and-decline scenarios (SSP2-19 and SSP2-26), the underlying assumptions concerning refugia recovery are crucial for the ratio between the two impact drivers. If we assume full refugia recovery (though highly unlikely over the timescales considered here), the warming-related loss is partly reversed after peak warming, meaning that the magnitudes of warming-related loss and mitigation-related 'loss' converge. For the 1.5 °C-scenario (SSP2-19), the mitigation-related 'loss' even becomes larger than the warming-related loss towards the end of the century. However, mitigation still avoids much higher warming-related climate refugia loss in the first place (figure 1(b)). Implications of this illustrative global analysis and the underlying assumptions about mitigation-related 'loss' and refugia recovery after peak warming are examined further under discussion.

3.2. Integrated global picture

The integrated 'loss' of today's climate refugia due to both impact drivers is shown in figure 1(b), which accounts for the fact that warming-related and mitigation-related climate refugia 'losses' overlap in some regions. We show that by 2100, ambitious climate action compatible with 1.5 °C of global warming would more than halve the combined 'loss' of today's climate refugia (implied 'loss' 30% median estimate), compared to the expected climate refugia 'loss' under current policies (66% median estimate), even if no recovery after peak warming is assumed. With full and instant refugia recovery after peak warming, the disparity in biodiversity outcomes between current policies and ambitious climate action would become even larger (implied climate refugia 'loss' for the 1.5 °C-scenario with recovery in 2100: 11% median estimate). This integrated analysis of both drivers underlines the value of strong climate change mitigation, which reduces overall climate refugia 'loss', despite larger land allocation within refugia.

We find that mitigation-related 'losses' may be even smaller when only assuming 'losses' in areas where mitigation-related land-use change is likely harmful, while assuming no 'losses' in potentially suitable areas or areas of unclear effect direction (supplementary information SI(C)).

3.3. Model consensus at sub-global level

We find that in most countries and territories, the warming-related climate refugia loss is larger than the mitigation-related 'loss', despite assumed refugia recovery after peak warming and fully negative land-related mitigation effects (figure 2). However, we identify several administrative regions for which at least three-of-five model frameworks agree that mitigation-related 'loss' would be larger than the warming-related loss (figure 2(a)). Results depend on the imposed minimum 'loss' thresholds as shown in supplementary information SI(D).

Despite the partial agreement (figure 2(a)), we observe distinct results across the five considered models at the administrative level (figures 2(b)–(f)). Warming-related climate refugia losses at country and territory level are similar across the five models—differences stem from slightly different median warming in the assessed 2 °C-scenario across the individual model frameworks (supplementary information SI(B)). The mitigation-related 'loss' of today's climate refugia differs more substantially between model frameworks due to distinct land allocation patterns [14] (supplementary information SI(E)). Complementary results for a case in which not all mitigation-related land-use change in climate refugia lead to negative biodiversity outcomes are shown in supplementary information SI(D).

3.4. Post- versus pre-overshoot

In the assessed 1.5 °C-scenarios with overshoot, overshoot starts in the early-2030s and ends in the early-2070s (figure 3(a)). Warming in both scenarios peaks at around 1.65 °C, implying relatively low overshoot of 0.15 °C [44], at which around 11% of the total 1.5 °C-refugia area would be temporarily lost, while 89% would still remain but under increased climatic stress.

While the assessed scenarios show distinct regional land allocation patterns within climate refugia, our analysis shows a pronounced increase in mitigation-related land allocation within climate refugia at 1.5 °C of global warming after an overshoot, compared to before. These results are illustrative to showcase that ecosystems would not only need to cope with and recover from overshoot but also deal with altered mitigation-related land use within climate refugia, implying that a world at 1.5 °C after overshoot is different from a world at 1.5 °C before overshoot, with increasing differences at higher levels of overshoot. In reality, many additional factors are at play, determining the impact of land use and land-use change and species' ability to cope with and recover from overshoot.

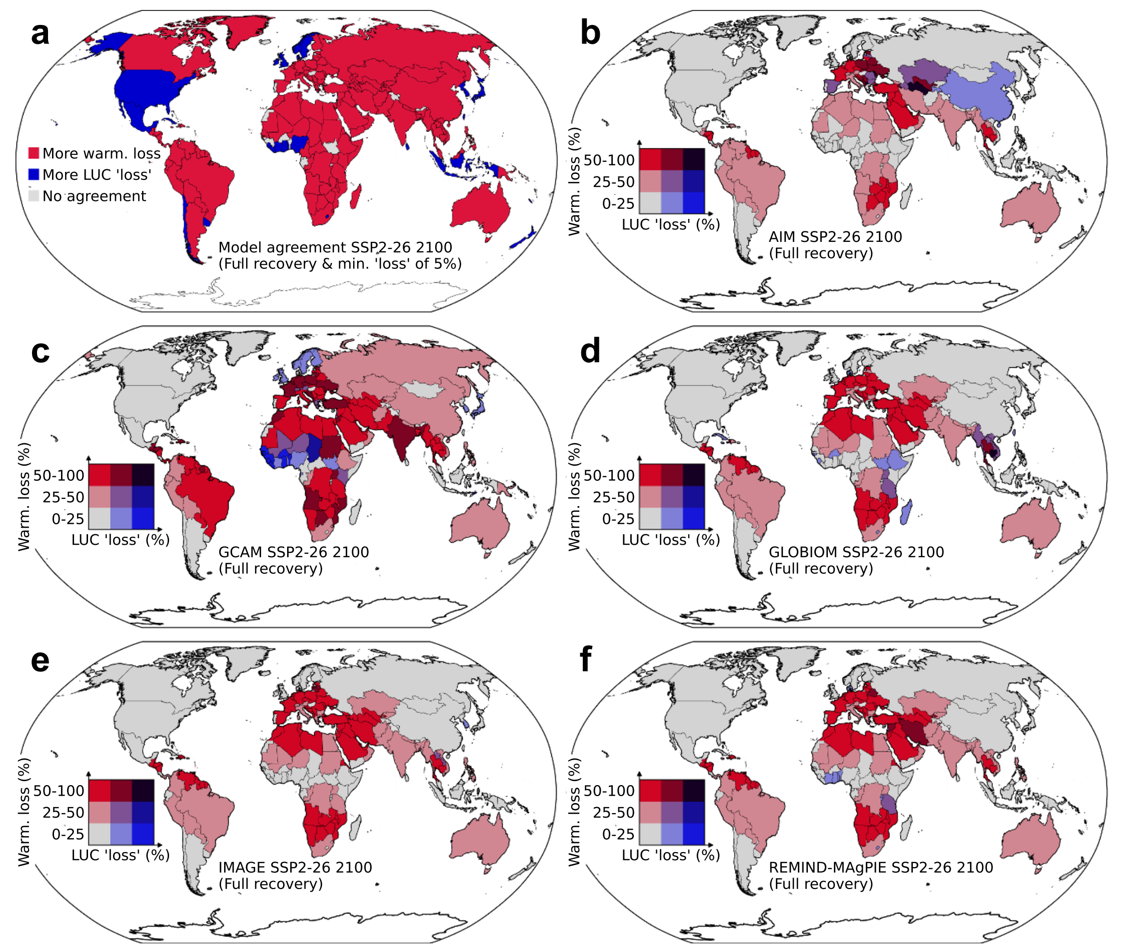

Figure 2. Dominance of warming effect versus land-intensive mitigation effect on today's climate refugia across administrative boundaries. Panel (a) shows model consensus per administrative region on whether more of today's climate refugia is 'lost' due to global warming [median warming estimate] (red) or due to mitigation-related land-use change (LUC) (blue) for the five considered model frameworks. Model consensus is given if at least three-of-five models agree on the dominant effect for a given administrative region. Results are shown for climate refugia 'loss' of at least 5%, excluding countries or territories in which both impact drivers are below this lower bound threshold. Panels (b)–(f) show the relative climate refugia 'loss' across administrative boundaries due to warming or mitigation-related land-use change based on three bins: 0%–25% 'loss', 25%–50% 'loss', and 50%–100% 'loss', based on the five considered model frameworks. Since bins represent ranges, effects that fall into the same bin may still differ in size. All panels are based on SSP2-26 in 2100. Full and instant recovery of climate refugia is assumed after peak warming in the context of a peak-and-decline warming trajectory. All panels compare the climate refugia 'loss' across administrative boundaries for the two drivers separately, meaning that areal overlap of the two impact drivers is not considered. Results for alternative thresholds and assumptions are shown in supplementary information SI(D). Model-specific land allocation patterns are presented in supplementary information SI(E). Basemaps were generated in Cartopy using Natural Earth data. World administrative boundaries are based on [47].

4. Discussion and conclusion

To date, very few studies have discussed potential future biodiversity impacts in the context of peak-and-decline warming scenarios [10, 11, 46]. Our study contributes to this nascent body of literature by combining and contrasting multi-model evidence of warming and mitigation-related climate refugia impacts of such peak-and-decline scenarios. Implications and limitations, as well as entry points for future work, are discussed below.

4.1. Warming versus land-intensive mitigation

Our assessment suggests that warming-related climate refugia loss would be larger and arise substantially faster than mitigation-related 'loss'. This is true across all considered scenarios and model frameworks when assuming no refugia recovery in peak-and-decline scenarios. This holds despite our precautionary assumption that spatial overlap between land-intensive mitigation and climate refugia would imply only negative effects for biodiversity. However, in peak-and-decline scenarios compatible with long-term warming of 1.5 °C, mitigation-related climate refugia 'loss' could become larger than the warming-related loss if we assume refugia recovery after peak warming. For the illustrative comparison of warming-related and mitigation-related implications, we looked at the two drivers side-by-side. It needs to be noted that global warming affects climate refugia across scale, even if the effects are too small to result in refugia loss. In contrast, mitigation-related

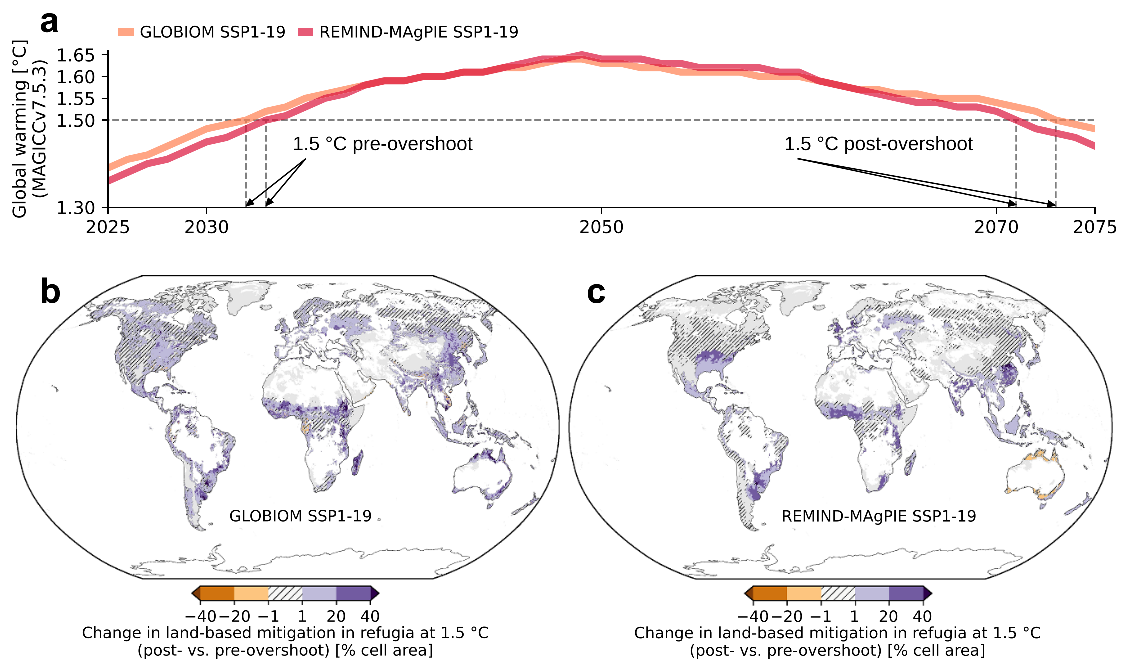

Figure 3. Change in land-intensive climate change mitigation within climate refugia at 1.5 °C before and after overshoot of 1.5 °C. Panel (a) shows the start and end points of overshoot for the two considered scenarios. Panels (b) and (c) show the difference in land-based mitigation within climate refugia at 1.5 °C before versus after overshoot for SSP1-19, based on the GLOBIOM model and the REMIND-MAgPIE model framework respectively. Increases in land-based mitigation within climate refugia at 1.5 °C after overshoot are shown in purple, decreases are shown in orange, and relative change below ±1% is hatched (panels (b), (c)). Change in land allocation per grid cell is shown relative to the total grid cell area. Climate refugia at 1.5 °C are shown in grey, representing a stylized case in which climate refugia location and extent would be the same after an overshoot compared to before (panels (b), (c)). Basemaps were generated in Cartopy using Natural Earth data.

land allocation would be more spatially confined, affecting only parts of climate refugia. In reality, warming and mitigation-related implications would not arise in isolation but partly overlap, as shown by our integrated analysis of the combined effect.

4.2. Ambitious action versus current policies

Our integrated analysis of the combined warming and mitigation effect shows that ambitious climate action compatible with 1.5 °C of global warming reduces today's climate refugia 'loss' by more than 50% (in 2100), compared to the current policy trajectory, even if we assume no refugia recovery after peak warming. With recovery, biodiversity benefits of ambitious climate action become even larger.

The here-tested recovery assumptions are used to delimit the maximum impact space. However, until 2100, only very little and gradual recovery may be expected [11, 12, 22]. Beyond warming, there may also be recovery from mitigation-related land allocation, e.g. when land uses are reversed or changed again. This is partly the case in the GCAM-based below 2 °C-scenario. While beyond the scope of our analysis, future studies may explore levels of mitigation-related recovery and compare implications to warming-related recovery.

4.3. Precautionary versus optimistic approach

In addition to the beneficial effects of mitigated warming, carefully implemented land-based mitigation measures can at least partly support biodiversity rather than disturb it. This can be achieved by prioritizing reforestation or natural restoration on degraded lands rather than afforestation and bioenergy plantations in pristine ecosystems, including grasslands and savannas [21, 48–53]. To complement our precautionary analysis with a more nuanced case, we show that mitigation-related 'losses' would be smaller when only assuming 'losses' in areas where mitigation-related land-use change is likely harmful, while assuming no 'losses' in potentially suitable areas or areas of unclear effect direction [54, 55]. In this more optimistic case, the difference in size between the warming-related loss and the mitigation-related 'loss' becomes even more pronounced. Integrated climate refugia 'losses' from both impact drivers are slightly reduced across all scenarios, however, without altering the pattern observed in the precautionary analysis.

4.4. Regional versus global pattern

As for the global level, we show that in most countries and territories, the warming-related loss of today's climate refugia is larger than the mitigation-related land allocation within today's climate refugia for our tested 2 °C-scenario, however, with a few exceptions. Our findings can inform future scenario modelling in refining mitigation-related land allocation patterns to design scenarios that are more sensitive to biodiversity. Careful selection of land-based climate mitigation strategies, their mode of implementation, and deployment sites can not only avoid negative climate refugia implications but actively support climate refugia conservation, e.g. through improving habitat connectivity or by actively designing future climate refugia [20, 21].

4.5. After versus before overshoot

We show how mitigation-related land allocation of climate refugia areas is markedly higher in a 1.5 °C world after an overshoot compared to before. This finding is partly a feature of continuously scaled land-intensive mitigation that, over time, would also arise in a stabilization scenario without overshoot. However, the necessity to achieve net negative emissions to reverse warming in an overshoot context comes with higher dependence on land-intensive forestation and bioenergy with carbon capture and storage compared to scenarios that avoid overshoot [12, 44, 53, 56]—unless portfolios of less land-intensive carbon dioxide removal options or marine-based approaches are leveraged [57], as partly done in more recent integrated modelling efforts [58, 59]. More generally, our illustrative analysis shows that ecosystems would not only need to recover from overshoot but also deal with altered mitigation-related land use within climate refugia, implying that a world at 1.5 °C after overshoot is different from a world at 1.5 °C before overshoot.

4.6. Limitations and outlook

To what extent individual species can recover and repopulate areas that become climatically suitable again after an overshoot is highly uncertain [11, 53] and contingent on an array of factors beyond the scope of our analysis, as outlined in the following. A prerequisite for species' ability to track their suitable climate niche during overshoot is the connectivity of ecosystems to allow for migration [21]. In this regard, land-based mitigation could be an enabler or barrier, depending on the mode of implementation, as highlighted above. Importantly, different species have distinct abilities to track their climate niche during overshoot, with higher dispersal rates among birds and long-lived mammals compared to short-lived insects or plants [15, 26, 46]. These distinct abilities to cope with overshoot threaten ecosystem composition and, therefore, stability [60]. Even if some species can successfully recover, important species-interdependencies such as predator-prey or plant-pollinator relationships may be lost [21, 23, 61]. Further, land-intensive mitigation efforts to limit overshoot may also alter ecosystem composition, as different species within and across taxa may differ in their ability to cope with the effects of forestation or bioenergy cropland expansion. Future research may assess such divergent species responses to both overshoot and land-intensive mitigation to refine our understanding of potential future climate refugia changes and species' ability to recover.

Another important aspect concerning potential refugia recovery pertains to altered and continuously changing regional climate conditions after overshoot compared to a world that avoids overshoot [10, 12], meaning that climatically suitable areas may be continuously shifted to other locations. In addition, land-intensive mitigation via forestation and bioenergy plantations also directly impacts local climate [62–64], which may affect the suitability of climate refugia for species. Lastly, overshoot is linked to more intense and frequent climate extremes and may induce stronger land-intensive adaptation such as human resettlement—both of which can increase the pressure on species and their ability to recover [11, 53].

In light of these different factors and related uncertainties, we stress the illustrative nature of our assessment of biodiversity implications in the context of peak-and-decline scenarios and highlight that only limited recovery can be expected over the timescales considered here. More research on this mitigation-biodiversity-overshoot nexus is required. Our discussion has outlined several dynamics that remain uncertain as entry points for future work. Despite these uncertainties, one thing is clear: constraining overshoot by cutting emissions as much as possible is our best chance to limit climate-related biodiversity loss.

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Data availability statement

The global and regional data outputs are made available at: https://doi.org/10.5281/zenodo.15497447.

Climate refugia data can be made available upon reasonable request.

Non-spatial scenario data from the AR6 Scenarios Database are available at: https://doi.org/10.5281/zenodo.7197970.

Land use data from AIM-SSP/RCP Ver2018 are available at: http://doi.org/10.18959/20180403.001.

Land use data from GCAM-Demeter are available at: https://doi.org/10.25584/data.2020-07.1357/1644253.

Land use data from GLOBIOM are available at: https://doi.org/10.5281/zenodo.15964077.

Land use data from IMAGE 3.0.1 are available at: https://doi.org/10.5281/zenodo.17046335.

Land use data from REMIND-MAgPIE 1.6-3.0 are available at: https://doi.org/10.5281/zenodo.17047534.

Data on the constrained reforestation potential map are available at: www.naturebase.org.

Data on the constrained biomass plantation map are available at: https://doi.org/10.5281/zenodo.14514051.

World administrative boundaries data are available at: https://geonode.wfp.org/layers/geonode%3Awld_bnd_adm0_wfp.

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Conflict of interest

The authors declare no competing interests.

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References

[1] Urban M C 2024 Climate change extinctions *Science* **386** 1123–8

[2] Pörtner H O, Roberts D C, Adams H, Adler C, Aldunce P and Ali E 2023 Summary for policymakers *Climate Change 2022—Impacts Adaptation Vulnerability* (Cambridge University Press) pp 3–34

[3] Putz F E and Redford K H 2009 Dangers of carbon-based conservation *Glob. Environ. Change* **19** 400–1

[4] Powell T W R and Lenton T M 2013 Scenarios for future biodiversity loss due to multiple drivers reveal conflict between mitigating climate change and preserving biodiversity *Environ. Res. Lett.* **8** 025024

[5] Hof C, Voskamp A, Biber M F, Böhning-Gaese K, Engelhardt E K, Niamir A, Willis S G and Hickler T 2018 Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity *Proc. Natl Acad. Sci.* **115** 13294–9

[6] Ohashi H *et al* 2019 Biodiversity can benefit from climate stabilization despite adverse side effects of land-based mitigation *Nat. Commun.* **10** 5240

[7] Hirata A, Ohashi H, Hasegawa T, Fujimori S, Takahashi K, Tsuchiya K and Matsui T 2024 The choice of land-based climate change mitigation measures influences future global biodiversity loss *Commun. Earth Environ.* **5** 259

[8] Newbold T 2018 Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios *Proc. R. Soc. B* **285** 20180792

[9] Hanssen S V, Steinmann Z J N, Daioglou V, Čengić M, Van Vuuren D P and Huijbregts M A J 2022 Global implications of crop-based bioenergy with carbon capture and storage for terrestrial vertebrate biodiversity *GCB Bioenergy* **14** 307–21

[10] Meyer A L S and Trisos C H 2023 Ecological impacts of temperature overshoot: the journey and the destination *One Earth* **6** 1614–7

[11] Meyer A L S, Bentley J, Odoulami R C, Pigot A L and Trisos C H 2022 Risks to biodiversity from temperature overshoot pathways *Phil. Trans. R. Soc. B* **377** 20210394

[12] Schleussner C-F *et al* 2024 Overconfidence in climate overshoot *Nature* **634** 366–73

[13] Möller T, Högner A E, Schleussner C-F, Bien S, Kitzmann N H, Lamboll R D, Rogelj J, Donges J F, Rockström J and Wunderling N 2024 Achieving net zero greenhouse gas emissions critical to limit climate tipping risks *Nat. Commun.* **15** 6192

[14] Prütz R *et al* 2026 Biodiversity implications of land-intensive carbon dioxide removal *Nat. Clim. Change* **16** 1–9

[15] Ashcroft M B 2010 Identifying refugia from climate change *J. Biogeogr.* **37** 1407–13

[16] Keppel G, Van Niel K P, Wardell-Johnson G W, Yates C J, Byrne M, Mucina L, Schut A G, Hopper S D and Franklin S E 2012 Refugia: identifying and understanding safe havens for biodiversity under climate change *Glob. Ecol. Biogeogr.* **21** 393–404

[17] Morelli T L *et al* 2016 Managing climate change refugia for climate adaptation *PLoS One* **11** e0159909

[18] Rillig M C 2025 Global change refugia could shelter species from multiple threats *Nat. Rev. Biodivers.* **1** 10–11

[19] Heller N E and Zavaleta E S 2009 Biodiversity management in the face of climate change: a review of 22 years of recommendations *Biol. Conserv.* **142** 14–32

[20] Keppel G, Stralberg D, Morelli T L and Bátori Z 2024 Managing climate-change refugia to prevent extinctions *Trends Ecol. Evol.* **39** 800–8

[21] IPCC 2023 Terrestrial and freshwater ecosystems and their services *Climate Change 2022—Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* 1st edn (Cambridge University Press) (https://doi.org/10.1017/9781009325844)

[22] Price J and Forstenhäusler N 2025 *D2.5 Biodiversity impacts of overshoot* (PROVIDE) (available at: https://www.provide-h2020.eu/wp-content/uploads/PROVIDE_D2.5_Biodiversity_final.pdf)

[23] 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 °C rather than 2 °C *Science* **360** 791–5

[24] Warren R, Price J, VanDerWal J, Cornelius S and Sohl H 2018 The implications of the United Nations Paris agreement on climate change for globally significant biodiversity areas *Clim. Change* **147** 395–409

[25] Warren R *et al* 2013 Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss *Nat. Clim. Change* **3** 678–82

[26] Price J, Warren R and Forstenhäusler N 2024 Biodiversity losses associated with global warming of 1.5–4 °C above pre-industrial levels in six countries *Clim. Change* **177** 47

[27] Phillips S J, Anderson R P and Schapire R E 2006 Maximum entropy modeling of species geographic distributions *Ecol. Model.* **190** 231–59

[28] Rogelj J *et al* 2018 Scenarios towards limiting global mean temperature increase below 1.5 °C *Nat. Clim. Change* **8** 325–32

[29] Riahi K *et al* 2017 The shared socioeconomic pathways and their energy, land use, and greenhouse gas emissions implications: an overview *Glob. Environ. Change* **42** 153–68

[30] Popp A *et al* 2017 Land-use futures in the shared socio-economic pathways *Glob. Environ. Change* **42** 331–45

[31] AIM 2018 AIM-SSP/RCP gridded emissions and land-use data Ver2018 (https://doi.org/10.18959/20180403.001)

[32] Chen M, Vernon C R, Graham N T, Hejazi M, Huang M, Cheng Y and Calvin K 2020 Global land use for 2015–2100 at 0.05° resolution under diverse socioeconomic and climate scenarios *Sci. Data* **7** 320

[33] Havlík P *et al* 2014 Climate change mitigation through livestock system transitions *Proc. Natl Acad. Sci.* **111** 3709–14

[34] Havlík P *et al* 2011 Global land-use implications of first and second generation biofuel targets *Energy Policy* **39** 5690–702

[35] IBF-IIASA. Global biosphere management model (GLOBIOM) documentation 2023—version 1.0 2023 (available at: https://pure.iiasa.ac.at/18996) (Accessed 12 May 2025)

[36] PBL 2025 IMAGE framework version overview (available at: https://models.pbl.nl/image/IMAGE_framework_version_overview#IMAGE_3.0.1)

[37] Kriegler E *et al* 2017 Fossil-fueled development (SSP5): an energy and resource intensive scenario for the 21st century *Glob. Environ. Change* **42** 297–315

[38] Fujimori S, Hasegawa T, Masui T, Takahashi K, Herran D S, Dai H, Hijioka Y and Kainuma M 2017 SSP3: AIM implementation of shared socioeconomic pathways *Glob. Environ. Change* **42** 268–83

[39] Fricko O *et al* 2017 The marker quantification of the shared socioeconomic pathway 2: a middle-of-the-road scenario for the 21st century *Glob. Environ. Change* **42** 251–67

[40] van Vuuren D P *et al* 2017 Energy, land-use and greenhouse gas emissions trajectories under a green growth paradigm *Glob. Environ. Change* **42** 237–50

[41] van Vuuren D *et al* 2026 The scenario model intercomparison project for CMIP7 (ScenarioMIP-CMIP7) *Geosci. Model Dev.* **19** 2627–56

[42] Soergel B *et al* 2024 Multiple pathways towards sustainable development goals and climate targets *Environ. Res. Lett.* **19** 124009

[43] Soergel B *et al* 2021 A sustainable development pathway for climate action within the UN 2030 Agenda *Nat. Clim. Change* **11** 656–64

[44] Byers E *et al* 2022 AR6 scenarios database *Zenodo* (https://doi.org/10.5281/zenodo.5886912)

[45] IPCC 2023 Climate change *2021—The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* 1st edn (Cambridge University Press) (https://doi.org/10.1017/9781009157896)

[46] Hayman G, Huntingford C, Kelley D, Price J, Jevrejeva S, Jacobs Z, Popova K, Findlay H S, Pritchard H and Taylor I 2024 *Global consequences of climate overshoot pathways: Annex 5 - Natural system impacts of overshoot pathways* (available at: https://www.gov.uk/government/publications/global-consequences-of-climate-overshoot-pathways)

[47] World Food Programme 2019 World administrative boundaries—countries and territories (available at: https://public.opendatasoft.com/explore/dataset/world-administrative-boundaries/information/)

[48] Veldman J W, Overbeck G E, Negreiros D, Mahy G, Le Stradic S, Fernandes G W, Durigan G, Buisson E, Putz F E and Bond W J 2015 Tyranny of trees in grassy biomes *Science* **347** 484–5

[49] Veldman J W, Overbeck G E, Negreiros D, Mahy G, Le Stradic S, Fernandes G W, Durigan G, Buisson E,

Putz F E and Bond W J 2015 Where tree planting and forest expansion are bad for biodiversity and ecosystem services *BioScience* **65** 1011–8

[50] Griscom B W *et al* 2017 Natural climate solutions *Proc. Natl Acad. Sci.* **114** 11645–50

[51] Di Sacco A *et al* 2021 Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits *Glob. Change Biol.* **27** 1328–48

[52] Seddon N, Turner B, Berry P, Chausson A and Girardin C A J 2019 Grounding nature-based climate solutions in sound biodiversity science *Nat. Clim. Change* **9** 84–87

[53] Anderson C M, Weber C L, Fabricius C, Glew L, Opperman J J, Pacheco P, Pendleton L H, Thau D, Vermeulen S J and Shaw M R 2020 Planning for change: conservation-related impacts of climate overshoot *BioScience* **70** 115–8

[54] Fesenmyer K A *et al* 2025 Addressing critiques refines global estimates of reforestation potential for climate change mitigation *Nat. Commun.* **16** 4572

[55] Braun J, Werner C, Gerten D, Stenzel F, Schaphoff S and Lucht W 2025 Multiple planetary boundaries preclude biomass crops for carbon capture and storage outside of agricultural areas *Commun. Earth Environ.* **6** 1–14

[56] Riahi K *et al* (eds) 2022 IPCC climate *Change 2022 Mitigation Climate Change contribution Work Group III Sixth Assessment Report Intergovernmental Panel Climate Change* (Cambridge University Press)

[57] Rodriguez Mendez Q, Creutzig F and Fuss S 2025 Deep uncertainty in carbon dioxide removal portfolios *Environ. Res. Lett.* **20** 054013

[58] Riahi K *et al* 2026 Mitigation benchmarks from the 2025 community update of global emissions pathways *Research Square* (https://doi.org/10.21203/rs.3.rs-8891091/v1)

[59] Van Vuuren D P *et al* 2026 The scenario model intercomparison project for CMIP7 (ScenarioMIP-CMIP7) *Geosci. Model. Dev.* **19** 2627–56

[60] Albrich K, Rammer W and Seidl R 2020 Climate change causes critical transitions and irreversible alterations of mountain forests *Glob. Change Biol.* **26** 4013–27

[61] Warren I I R J and Bradford M A 2014 Mutualism fails when climate response differs between interacting species *Glob. Change Biol.* **20** 466–74

[62] Wang J, Li W, Ciais P, Lzx L, Chang J, Goll D, Gasser T, Huang X, Devaraju N and Boucher O 2021 Global cooling induced by biophysical effects of bioenergy crop cultivation *Nat. Commun.* **12** 7255

[63] Moustakis Y, Nützel T, Wey H-W, Bao W and Pongratz J 2024 Temperature overshoot responses to ambitious forestation in an Earth system model *Nat. Commun.* **15** 8235

[64] Prütz R, Fuss S, Lück S, Stephan L and Rogelj J 2024 A taxonomy to map evidence on the co-benefits, challenges, and limits of carbon dioxide removal *Commun. Earth Environ.* **5** 1–11