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# Biodiversity side effects of carbon-focused reforestation under Paris-aligned transformation pathways

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## Abstract

Large-scale afforestation/reforestation (AR) represents one of the most cost-effective approaches for carbon dioxide removal (CDR) and is therefore a central component of Paris-aligned land and energy transformation pathways. Using a dynamic land- and energy-system model, we assess the emergent biodiversity side effects and energy-system adjustments under varying scales of AR in Paris-aligned pathways. We show that increasing scales of AR markedly affect both the extent and pattern of habitat loss. While stringent climate action that avoids further conversion of forest and non-forest ecosystems offers substantial biodiversity co-benefits by reducing habitat loss, these benefits are largely offset at high levels of carbon-focused AR (>150 Mha) due to disproportionate losses of open habitats. Notably, we also find almost no effect of AR on energy-system transformations until 2050 and only limited effects of CDR from AR on long-term emissions. Our findings underline that near-term emission cuts remain critical for achieving the Paris Agreement and emphasise the need to shift from a dominant focus on large-scale tree planting to broader ecosystem restoration.

## 15 Main

16 Reaching the targets of the Paris Agreement requires deep and rapid decarbonisation across all sectors  
17 of the economy<sup>1,2</sup>. Most energy- and land-use transition pathways that align with these targets also rely  
18 on large-scale deployment of carbon dioxide removal (CDR) from the atmosphere to offset residual  
19 emissions and reach net-zero goals<sup>2,3</sup>. Among CDR options, afforestation/reforestation (AR) is widely  
20 regarded as one of the most cost-effective<sup>4-6</sup> and has therefore become a central component of many  
21 countries' Nationally Determined Contributions (NDCs), as well as of global programmes such as the  
22 Bonn Challenge and private sector net-zero commitments<sup>7,8</sup>.

23 When adapted to local conditions and based on native species, AR programmes may play a critical  
24 role in restoring important ecosystem functions and delivering substantial co-benefits for biodiversity  
25 by recreating former forest habitats<sup>9-11</sup>, in particular in many countries across Latin America, tropical  
26 Africa and Asia. However, ambitious AR deployment – often targeting land with low opportunity  
27 costs<sup>6</sup> – typically entails a large-scale conversion of open ecosystems into closed forest ecosystems.  
28 While increasing carbon uptake from the atmosphere, this transformation could also lead to notable  
29 trade-offs for biodiversity by fundamentally altering the habitat conditions for a broad variety of  
30 species that have adapted to and critically depend on open ecosystems<sup>12-14</sup>.

31 These open ecosystems are already under pressure. Over recent decades, agricultural intensification  
32 and land-use change have already caused steep declines especially in species adapted to open  
33 ecosystems, such as grasslands or savannas<sup>15,16</sup>. In Brazil, for example, non-forest ecosystems have the  
34 highest conservation risk indices<sup>17</sup>, while population declines of bird species across Europe and North  
35 America have been largest among those that prefer open habitats<sup>18,19</sup>. Many non-forest ecosystems on  
36 marginal lands are also being affected by land abandonment and woody encroachment<sup>20-22</sup>, a trend that  
37 could be further accelerated by ambitious AR programmes. This might not only have important  
38 consequences for local biodiversity, but a decline of contiguous open habitats, for instance, could also  
39 affect long-distance avian migration patterns<sup>23,24</sup>.

40 Several earlier studies have evaluated the sustainability constraints of large-scale AR deployment.  
41 Based on a literature review, Deprez et al.<sup>25</sup> identified emerging risks at scales of 100-300 Mha, while  
42 a more recent spatial analysis found a maximum reforestation potential of 195 Mha after the  
43 precautionary exclusion of problematic areas for AR<sup>26</sup>. However, neither study included quantitative  
44 analyses of the associated biodiversity implications of these proposed forest restoration potentials.  
45 Conversely, other research has examined the biodiversity consequences of land-use and energy system  
46 transformations suited for reaching ambitious climate targets, but did not quantify the emergent  
47 biodiversity side effects across different scales of AR deployment<sup>27,28</sup>. Moreover, changes in the  
48 energy system under Paris-aligned pathways that follow from more or less land-based CDR have not  
49 been put into relation to biodiversity side effects. Yet, a systematic assessment of biodiversity and  
50 energy systems responses at different levels of AR deployment is crucial in order to understand the

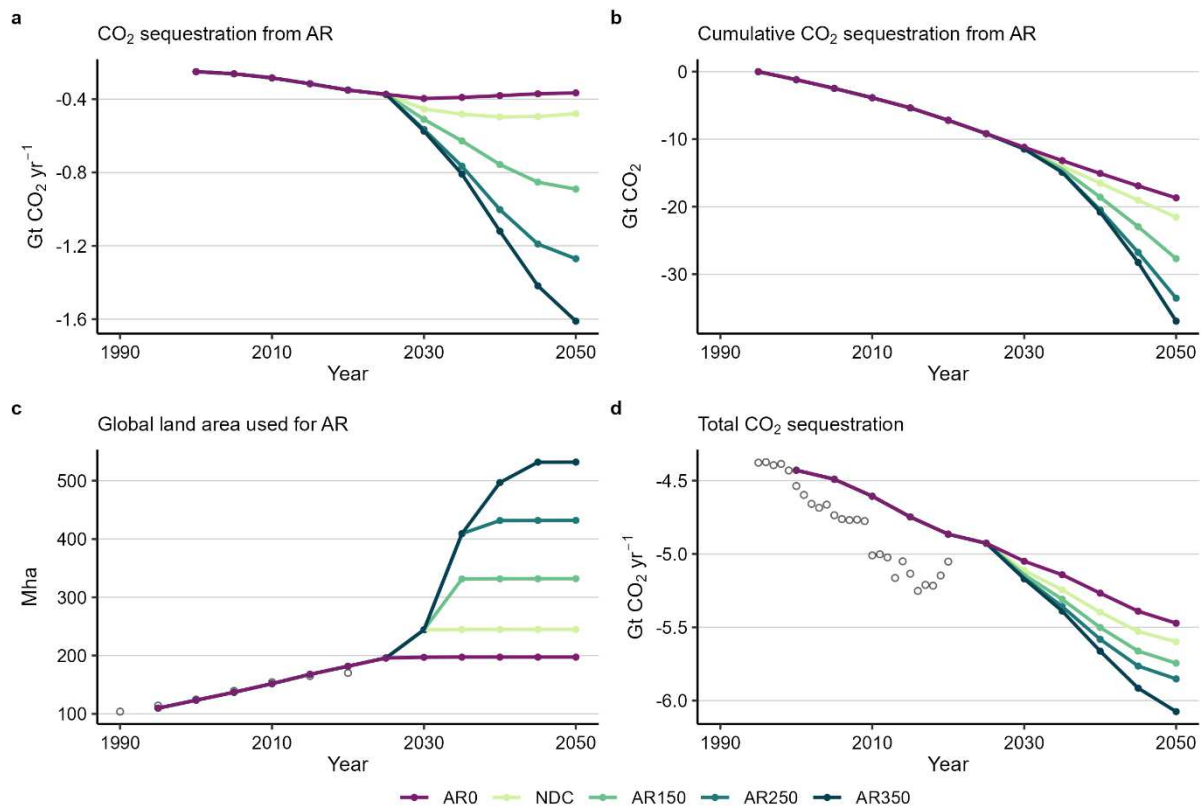
policy space, in which stringent climate change mitigation targets under the Paris Agreement can be reconciled with the biodiversity conservation goals under the Kunming-Montreal Global Biodiversity Framework (GBF).

Here, we provide a quantitative assessment of biodiversity outcomes in response to different levels of carbon-focused AR deployment. We also explore how the energy system would respond to different levels of AR deployment under stringent climate change mitigation in line with the Paris Agreement. Our analysis is based on the REMIND–MAGPIE integrated assessment modelling (IAM) framework, which combines a global economy and energy system model with a global land system model.<sup>29–31</sup>. REMIND and MAGPIE are continuously validated and have been widely used to study sustainable land-use and energy transformations<sup>30,32,33</sup>. To assess the impact of AR deployment on biodiversity at a high level of detail, we extend the REMIND-MAGPIE framework by including the Spatial Economic Allocation Landscape Simulator<sup>34</sup> (SEALS). SEALS downscales projected land-cover changes to a spatial resolution of 10 arc seconds (300 m × 300 m at the equator), using information on physical suitability, conversion eligibility, and empirically trained spatial adjacency relationships.

## Scenario Design

The primary objective of our scenario design is to isolate the effects of different levels of AR deployment on global energy system and land-use dynamics—and the associated biodiversity outcomes—under a stringent, Paris-aligned climate mitigation pathway. Core socioeconomic assumptions in our scenario set, including population and income growth, as well as projected food and energy demand, are based on the ‘middle-of-the-road’ shared socioeconomic pathway<sup>35</sup> (SSP2). All scenarios are designed to be consistent with the Paris Agreement, limiting the global mean temperature increase to ‘well-below’ 2° C throughout the 21<sup>st</sup> century and reaching 1.5° C by the end of the century with a 50 % probability. Accordingly, cumulative CO<sub>2</sub> emissions are constrained to not exceed a carbon budget of 750 GtCO<sub>2</sub> from 2020 onwards. In line with the overall carbon budget, we endogenously derive a uniform carbon price which applies to all GHG emissions in the land and energy systems, incentivising a decarbonisation of the energy system and, for instance, disincentivising the conversion of carbon-rich ecosystems to agricultural land. Furthermore, lignocellulosic second-generation bioenergy crops and residues are limited to 100 EJ yr<sup>-1</sup> to ensure sustainability and comparability across scenarios<sup>36</sup>.

Building on these shared assumptions, we explore a range of scenarios that differ in the total scale of AR deployment. In the AR150, AR250 and AR350 cases, AR deployment from 2020 onward is constrained to a global total of 150 Mha, 250 Mha and 350 Mha, respectively, with projected negative emissions of 0.9 GtCO<sub>2</sub> yr<sup>-1</sup>, 1.3 GtCO<sub>2</sub> yr<sup>-1</sup> and 1.6 GtCO<sub>2</sub> yr<sup>-1</sup> in 2050 (Figure 1). In the NDC scenario AR deployment after 2020 follows national pledges under countries’ ‘Nationally Determined



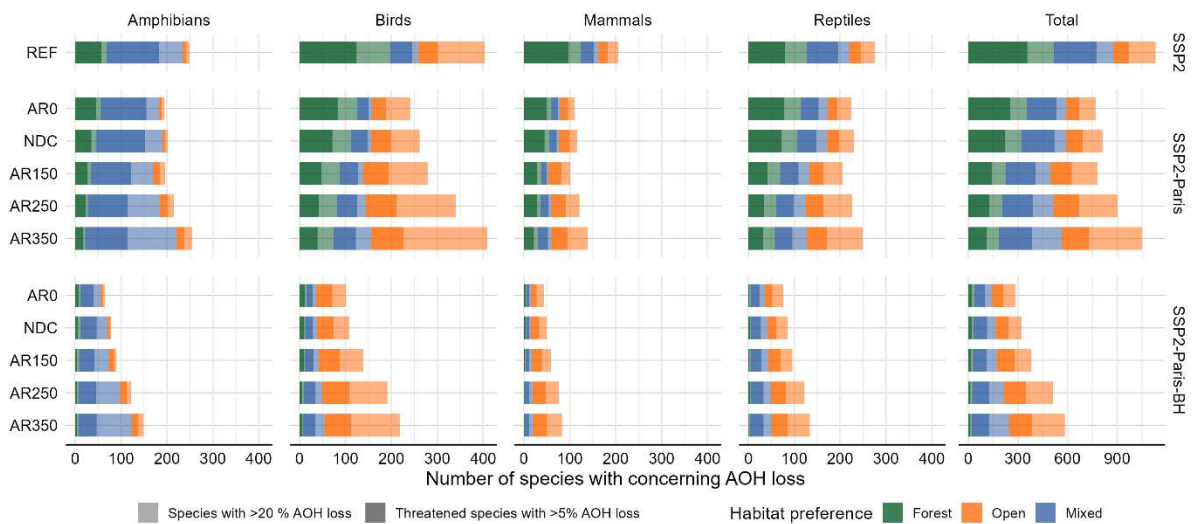
**Fig. 1: CO<sub>2</sub> sequestration and land area used for AR until 2050 across the modelled scenarios.** **a** Modelled time series of CO<sub>2</sub> removal from the atmosphere from AR deployment. Forest growth rates and associated carbon uptake was assumed to be consistent with the succession of native vegetation. **b** Modelled cumulative CO<sub>2</sub> uptake from AR over time. **c** Global land area used for AR. AR was deployed based on expected carbon removal over a 50-year planning horizon, with global area constraints (NDC, AR150, AR250 and AR350) for AR deployment applied after 2020. **d** Estimated total CO<sub>2</sub> sequestration by the biosphere.

Contributions' (NDCs) until 2030 with a global total of 63 Mha of AR and negative emissions of 0.5 GtCO<sub>2</sub> yr<sup>-1</sup> in 2050. The AR0 scenario assumes no additional AR after 2020, reflecting currently implemented AR programmes only. In the AR150, AR250 and AR350 scenarios AR is deployed through a combination between NDC targets and proportional rewards for expected carbon removals based on the carbon price. In addition, AR deployment is restricted to areas where the climatic conditions support forest growth (Supplementary Fig. 2). Forest growth rates are assumed to be consistent with natural succession of native vegetation but exclude disturbance effects such as fire or grazing (see Methods).

We also modelled variants of each scenario (AR0, NDC, AR150, AR250, AR350) that included a stringent land conservation scheme targeting global biodiversity hotspots<sup>37</sup> (BH). These variants aim to provide stylised examples and insights into how conservation planning may interact with AR deployment.

## Results

To evaluate the biodiversity outcomes associated with varying levels of AR deployment, we estimated changes in the area of habitat (AOH) of 27,726 vertebrate species, based on a fine-scale spatial allocation of modelled land-cover dynamics across our scenarios. We thereby link species habitat

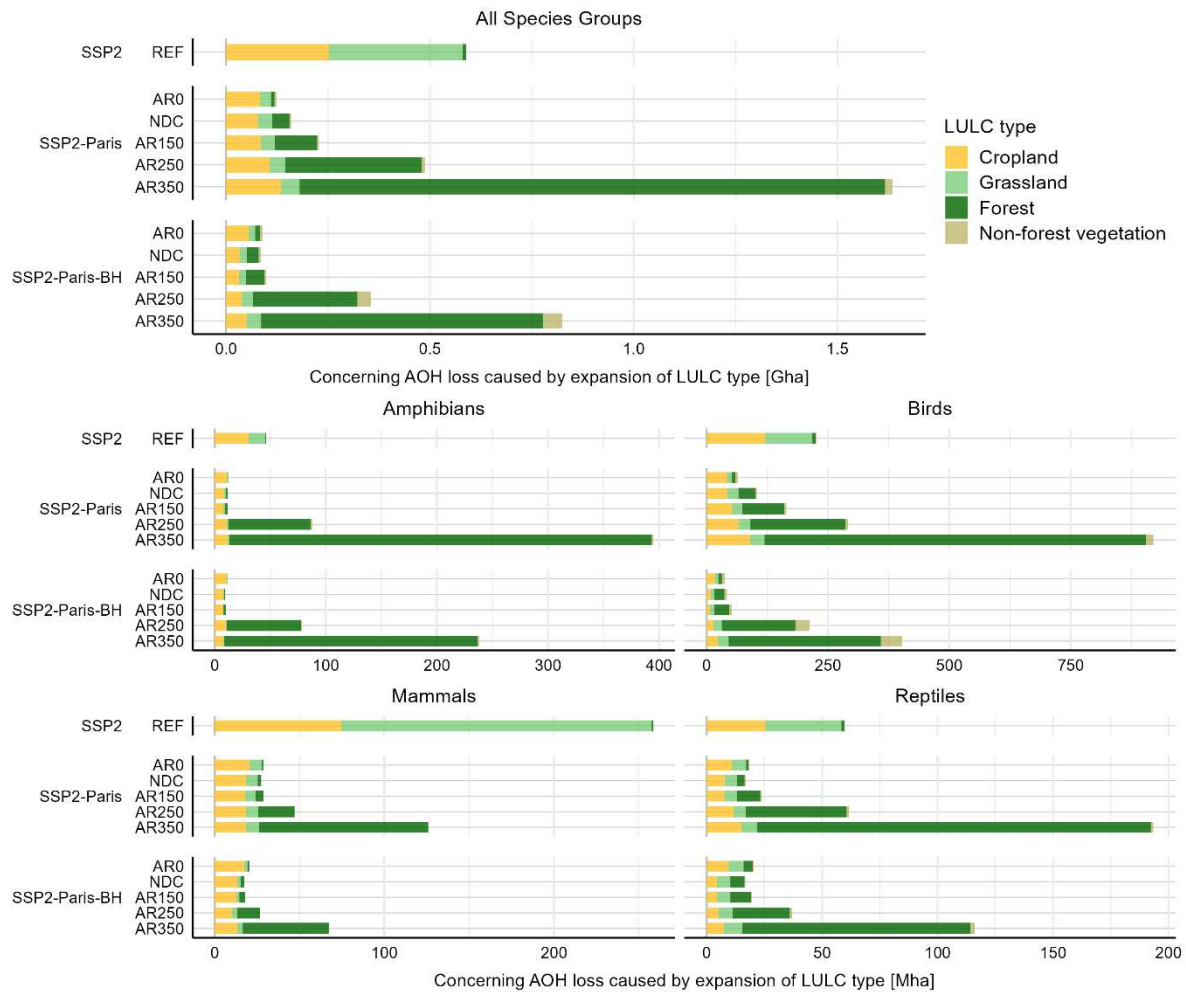


**Fig. 2: Number of species with concerning AOH loss by 2050 and their habitat preference across modelled scenarios.** Concerning AOH encompasses species with more than 20 % of AOH loss or currently threatened species with more than 5 % AOH loss by 2050.

preferences to spatial land cover information via a habitat-land cover model that systematically reduces commission (false presence) errors and achieves high accuracy<sup>38,39</sup>. AOH projections offer valuable insights into potential habitat change and related species extinction risks, making them a useful tool for conservation planning. As such, the AOH has been suggested as a complementary indicator for the IUCN Red List<sup>40,41</sup>. The set of species included in this study covers only about 2.2 % of recorded and ~0.3% of all currently predicted species<sup>42</sup>. However, it encompasses a wide range of taxa, species traits and habitat preferences, which has been shown to reliably capture national, regional and global biodiversity patterns<sup>10,41</sup>. The AOH indicator predominantly reflects a focus on conserving nature's intrinsic value, as conceptualized in the 'Nature for Nature' perspective of the IPBES Nature Futures Framework<sup>43</sup>. Our analysis focuses on concerning AOH loss, here defined as a reduction of more than 5% of suitable habitat for species currently listed as threatened on the IUCN Red List, or more than 20% for currently non-threatened species, by 2050. We also aggregate outcomes according to species' habitat preferences, including forest, open and mixed (forest and open) habitats.

### High AR deployment reshapes scale and patterns of concerning AOH loss

Under a business-as-usual (BAU) scenario without additional land-use interventions, 1132 species could experience concerning AOH loss, mostly affecting species that prefer forest and mixed habitats (Figure 2). This loss was primarily driven by pasture and cropland expansion across Asia, Sub-Saharan Africa and Latin America (Figure 3, Supplementary Figs. 4 & 5). In contrast, the incentive to avoid CO<sub>2</sub> emissions from land conversion in line with the targets of the Paris Agreement alone (AR0) causes a drastic reduction in agricultural land expansion, especially across Asia and Sub-Saharan Africa. This reduces the number of species with concerning AOH loss globally by nearly one third. While AR deployment in line with countries' current NDCs lowers the number of forest species affected by concerning AOH loss (–10%), it leads to a higher total number of affected species due to



**Fig. 3: Sum of concerning habitat loss from 2020 to 2050 caused by the expansion of aggregated land-use/land-cover (LULC) types across different species groups.** The total area of concerning AOH loss exceeds the projected global and regional LULC change. This is because the expansion of a single LULC type can result in AOH loss for multiple species simultaneously. Consequently, this metric reflects the relative importance of different LULC expansions for habitat loss, with a greater weight in areas affecting a larger number of species.

increases among species dependent on open (+21%) and mixed (+15%) habitats, compared to the Paris-aligned scenario without AR (Figure 4).

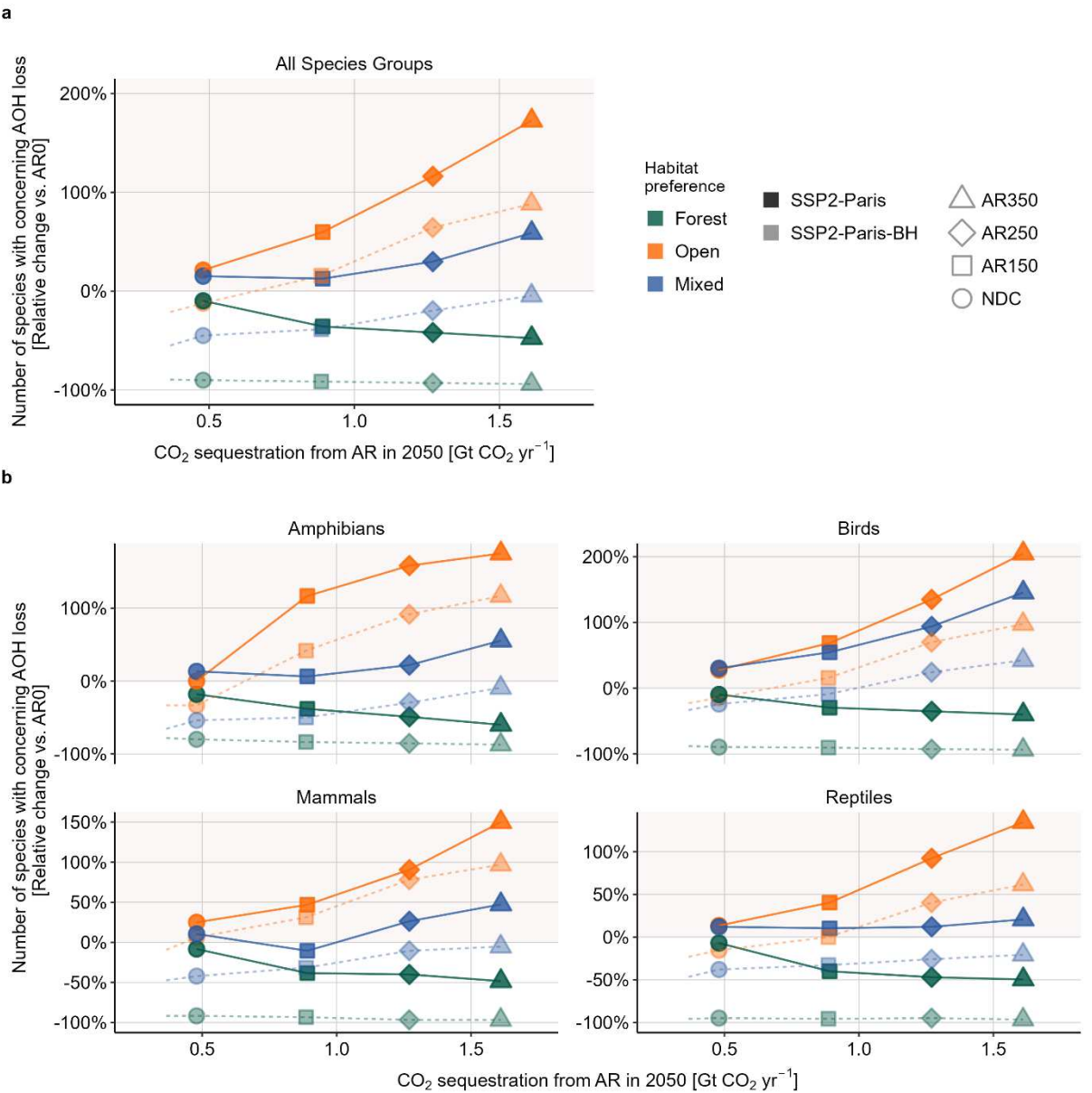
With increasing AR deployment two patterns emerge: (1) a marked decline in forest-dependent species with concerning AOH loss, and (2) a strong and disproportionate increase in open- and mixed-habitat species experiencing concerning AOH losses (Figure 4). In the moderate AR150 scenario, the number of affected forest species declines by 36 %. However, the total number of species with concerning AOH loss (782) remains comparable to that in the AR0 scenario (772) because of the higher impacts across open- and mixed-habitat species. Under high AR deployment, the disproportionate increase in affected open- and mixed-habitat species even results in an increase in the total number of affected species (AR250: +17%; AR350: +36% relative to AR0). Hence, in the AR350 scenario the total number of species with concerning AOH loss is only 7% lower than in the BAU scenario, yet with important differences in the species affected. Concerning AOH losses under high AR deployment are mostly driven by reductions in suitable habitat for open habitat bird and reptile



species as a result of forest expansion, particularly in Latin America (Figure 2; Supplementary Figs. 4, 7 & 9). Under high AR deployment (AR250 and AR350) forest expansion may surpass agricultural land expansion as the main driver of habitat loss (Figure 3). In the AR350 scenario the total area of concerning AOH loss caused by forest expansion alone (1.4 Gha) was more than double the area of concerning AOH loss from all land cover changes in the BAU scenario taken together (0.6 Gha).

### Potential habitat gains from AR are qualitatively different than losses

The decline in the number of species that suffer from concerning AOH losses among forest habitat species with increasing levels of AR deployment is mirrored by substantial potential habitat gains across a broad set of forest-dependent species (Supplementary Fig. 11). Notably, already a moderate AR scenario (AR150) increases the number of forest-dependent species experiencing habitat gains by



**Fig. 4: CO<sub>2</sub>-sequestration and relative change in the number of species with concerning habitat loss across AR scenarios and different species groups.** The response of species with different habitat preference is shown in different colours, while shaded lines show scenario variants with an additional protection of biodiversity hotspots (BH).

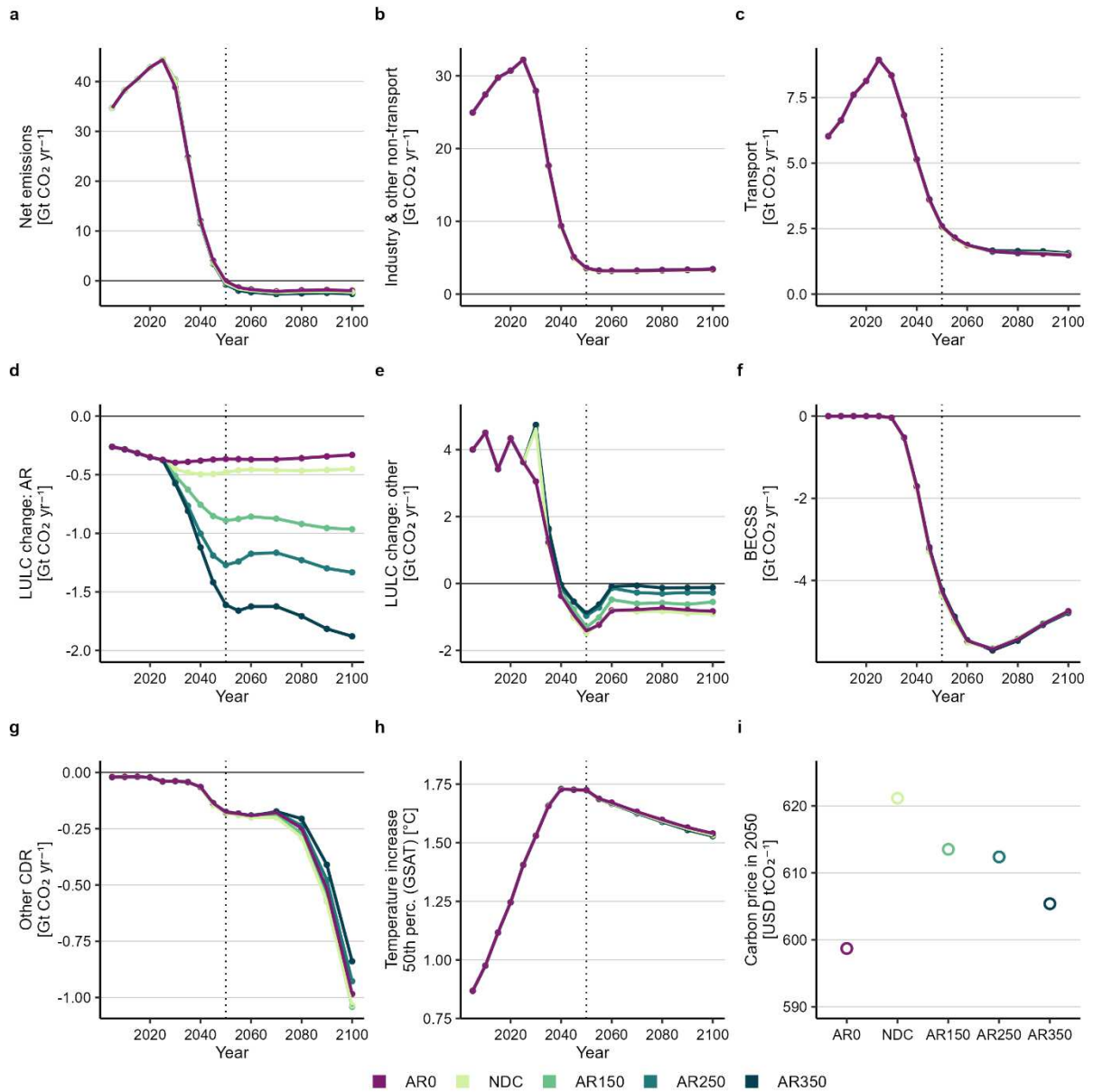
82% relative to AR0, rising to 100% and 131% under the AR250 and AR350 scenarios, respectively. While our results also show that habitat gains would disproportionately benefit species with currently low conservation risk (Supplementary Fig. 12), AR deployment—even at a moderate level (AR150)—would still lead to considerable habitat gains for currently threatened species. However, habitat gains from AR deployment critically depend on the quality of forest restoration and are often only realised with forest maturation over long time scales<sup>44</sup>. A direct comparison between habitat losses and gains presented here would thus be misleading not only due to their marked differences in the species affected, but also because habitat loss from land conversion occurs on a far shorter time scale than habitat restoration<sup>44</sup>. Although forest growth and associated carbon dynamics were included in our modelling approach, important qualitative differences between restored young secondary and mature forest ecosystems could not be captured here.

### **Spatial planning can notably reduce biodiversity side effects of AR**

In our analysis we also aimed to quantify the extent to which improved spatial planning could reduce the biodiversity side effects of ambitious AR deployment. To this end, we assessed a variant of our core scenario set, in which the conservation of global biodiversity hotspots<sup>37</sup> (BH) was prioritised over AR deployment, partially displacing it to other areas. These stylised scenario variants illustrate the significant co-benefits that could be obtained between carbon- and biodiversity-focused land protection and restoration approaches (Figure 4). In the AR350 scenario, the improved spatial planning halved the number of species with concerning AOH loss. As a result, biodiversity side effects in AR350 remained comparable to those in the AR150 scenario (without spatial planning), but with a 78 % higher annual CO<sub>2</sub> sequestration potential (0.9 vs. 1.6 GtCO<sub>2</sub> yr<sup>-1</sup> in 2050). Nonetheless, even with the added land conservation forest-dependent species were disproportionately favoured, while concerning AOH losses of open and mixed habitat species were only partly mitigated, especially under high AR deployment. These findings reflect the challenge of aligning ambitious land-based climate mitigation with strategies that simultaneously balance diverse conservation needs.

### **The scale of AR only has minor impact on emission reductions**

In terms of energy-system adjustments to varying levels of AR, we find that near-term emission reductions are far more important for adhering to a carbon budget consistent with the targets of the Paris Agreement than the scale of AR (Figure 5). Regarding near-term CO<sub>2</sub> emissions up to 2050, the additional cumulative carbon sequestration from AR in AR350 compared to AR0 is only 18.3 GtCO<sub>2</sub>—equivalent to 41% of CO<sub>2</sub> emissions in 2025 alone (44.4 GtCO<sub>2</sub>). This suggests that deploying 350 Mha of AR by 2050 would provide only about five months of delay in near-term emission reductions. The difference in carbon uptake from AR between the AR150 and AR350 scenarios is only 9.3 GtCO<sub>2</sub> by 2050—just 21% of 2025 CO<sub>2</sub> emissions—implying that an additional 200 Mha of AR would only allow a further delay in near-term emission reductions of roughly three months. By 2100, however, AR350 could provide an additional 87.3 GtCO<sub>2</sub> and 50 GtCO<sub>2</sub> of



**Fig. 5: Projected CO<sub>2</sub> emissions across different components, temperature increase and carbon prices.** **a** Projected global net CO<sub>2</sub> for the different scenarios. **b-g** CO<sub>2</sub> emission components including industry and other non-transport (**b**), transport (**c**), land-use/land-cover (LULC) change emissions from AR (**d**), other LULC change emissions (**e**), bioenergy with carbon capture and storage (BECCS) (**f**), and other CDR including direct air carbon capture and storage (DACCS) (**g**). **h** Global mean surface air temperature (GSAT) increase (50<sup>th</sup> percentile). **i** Carbon prices across the land and energy system in 2050. Carbon prices are phased in after 2025 and remain constant after 2050.

cumulative carbon uptake relative to AR0 and AR150, respectively. This suggests that, although CDR from AR has minimal impact on near-term emissions, it may still contribute to stabilising or reducing the global mean surface air temperature (GSAT) after 2050 (Figure 5h).

The minor effect of AR on the near-term energy-system transformation required to meet the Paris Agreement is also reflected in the cropland area devoted to second-generation bioenergy crops, such as short-rotation coppice and bioenergy grasses, and in the corresponding negative emissions from BECCS, which exhibit only small variations across different levels of AR deployment (Figure 5f; Supplementary Fig. 13). Bioenergy crops predominantly replace food and feed crops on existing

cropland, as overall cropland decreases in all AR scenarios (Supplementary Figs. 13–15). Carbon prices in the energy and land systems likewise show only minor changes across different levels of AR deployment (Figure 5i). However, the spatial allocation of AR has a greater impact on modelled carbon prices than the total AR area itself, which became evident in the higher carbon prices observed in the NDC scenario as compared to the AR0 case. This was because in the NDC scenario, AR was exogenously prescribed based on country-level targets, which caused spatial shifts in agricultural production and corresponding initial leakage effects in CO<sub>2</sub> emissions from land-use change (Figure 5e).

## Discussion

Several key insights have emerged from this model analysis. First, our results showed that increasing levels of AR deployment can substantially affect the scale and pattern of habitat loss. While avoided land conversion under stringent climate policy aligned with the Paris Agreement would offer notable co-benefits by reducing habitat loss, these benefits are largely offset at high levels of carbon-focused AR deployment ( $\geq 250$  Mha) due to disproportionate losses of open habitats. Secondly, we find that improved spatial planning would enable higher carbon uptake with fewer biodiversity side effects. However, concerning losses in open habitats remain difficult to mitigate and would require more targeted conservation efforts. Our scenario of expanding land protection across global biodiversity hotspots offers a stylised example of how climate and biodiversity protection could provide important synergies. Yet the marked differences in conservation outcomes across species with divergent habitat preferences suggest that open habitat species are still widely neglected. This highlights the need for balancing conservation objectives in the context of protected area enlargement under the Global Biodiversity Framework (GBF)<sup>45</sup>. Lastly, our integrated analysis of energy and land system interactions showed that AR deployment has only a minor impact on cumulative CO<sub>2</sub> emissions throughout the 21<sup>st</sup> century, and that rapid near-term emission reductions are far more critical than the scale of AR for meeting the targets of the Paris Agreement. Yet it is important to note that the relatively low carbon uptake potential of AR in our analysis largely reflects our assumption that forest growth rates are consistent with successional dynamics of native vegetation. While the use of fast-growing forest plantations—often with non-native species—could result in higher carbon uptake rates<sup>46</sup>, such plantations would likely come with greater biodiversity and other sustainability trade-offs<sup>47</sup>.

These findings suggest that shifting from a dominant focus on large-scale tree planting to broader ecosystem management and restoration approaches in line with global biodiversity goals would not noticeably affect the required energy transition, while substantially reducing potential biodiversity trade-offs. This aligns with evidence from other studies showing that ecosystem-based approaches, targeting both forested and non-forested ecosystems, can simultaneously deliver high carbon removals and support biodiversity conservation<sup>15,48–51</sup>. More diverse land restoration approaches that consider

different conservation perspectives in cultured landscapes<sup>52</sup> may also increase social acceptance and prevent trade-offs with other sustainability goals<sup>53,54</sup>. However, a strong emphasis on interventions that limit further land conversion and protect current forest and non-forest ecosystems is essential. This would not only avoid habitat loss and further CO<sub>2</sub> emissions from land-use change but also preserve the high near-term carbon uptake potential of existing forest vegetation<sup>55</sup>, which also provided a substantial contribution in our analysis. In our analysis, we also assumed that fire or (native) grazing were suppressed in sites of AR deployment. While our findings imply no substantial impact on a Paris-aligned energy transition from a smaller AR area that may result from disturbance events, considerable disturbance losses in existing forest by contrast could have more severe implications for emission reductions<sup>56</sup>.

Our study is subject to several limitations. First, our assessment of AOH changes was solely based on current species distributions and did not account for potential range shifts due to climate change. Our scenario set primarily focused on ambitious mitigation pathways associated with low-end climate change and we thus excluded climate impacts to reduce the overall complexity of our modelling approach. Although low-end climate change has been shown to have limited effects on land-use dynamics<sup>57</sup>, residual climate change is still expected to drive species range shifts<sup>58</sup>. Under higher emission trajectories, such as in our REF scenario, these range shifts could become more pronounced<sup>59</sup>. Yet habitat loss and fragmentation may also impede the ability of species to track temperature gradients<sup>58</sup>. The availability and accessibility of suitable habitat along elevational and latitudinal gradients will shape the extent to which range shifts affect future habitat change<sup>59,60</sup>, and thereby influence AOH outcomes especially for range-restricted species. Conservation measures that support species movement and sustain sufficient and contiguous habitat can markedly reduce climate-driven habitat loss, even under high emission trajectories<sup>61</sup>. Secondly, we did not consider how different growth stages during AR deployment would affect different species groups. Mixed young secondary forests may benefit both forest- and non-forest species, while forest specialists often favour mature forests<sup>62–64</sup>. These successional dynamics could temporarily alleviate some of the projected negative consequences of AR for open habitat species. Thirdly, in our stylised climate change mitigation scenarios AR deployment was incentivised through a universal carbon price. Hence AR was spatially allocated solely based on projected carbon sequestration potentials—an approach commonly used in IAM studies<sup>30,32,65,66</sup>. Incorporating regionally differentiated AR incentives or broader criteria beyond carbon could result in different AR deployment patterns. Lastly, the relatively limited role of AR as a CDR option in our mitigation scenarios also reflects assumptions about bioenergy yields and the cost-effectiveness of BECCS as an alternative. Lower yields from short-rotation coppice or bioenergy grasses would reduce BECCS efficiency and competitiveness and substantially increase its land footprint. Assessing the biodiversity impacts of BECCS was beyond the scope of this study, but evidence indicates notable biodiversity gains in farmed landscapes when annual food and feed crops are replaced with woody or perennial grass bioenergy crops<sup>67</sup>.

## Methods

### Model descriptions

**REMIND-MagPIE.** Our quantitative analysis is based on the coupled integrated land- and energy system modelling framework REMIND-MagPIE. It consists of the multiregional global energy-economy model REMIND<sup>31</sup> (v3.5.1) and the spatially-explicit land-system model MAgPIE<sup>29</sup> (v4.11.0). The framework furthermore draws on consistent biophysical information on crop yields, carbon dynamics, and water availability from the global vegetation, crop and hydrology model LPJmL<sup>68,69</sup>, and integrates the reduced-complexity climate model MAGICC<sup>70,71</sup>.

**REMIND.** The Regional Model of Investments and Development (REMIND) uses a multiregional approach to cover the global economy and energy system<sup>30,31</sup>. The macro-economy of the twelve world regions (Supplementary Fig. 1; Supplementary Tab. 1) which group smaller countries while major economies (China, India, USA) are resolved individually, is modelled following a Ramsey-type growth model that uses a production function with constant elasticity of substitution and capital, labour and energy as the main production factors. The energy demand and associated costs resulting from economic activity are hard-linked to a detailed representation of the energy system that includes all major primary energy carriers, conversion technologies and end-use sectors (transport, industry, and buildings)<sup>31</sup>. In each region intertemporal welfare is first optimised separately, before the global solution is found by iteratively adjusting market prices for primary energy carriers and tradable goods until all market surpluses and deficits are cleared. Existing infrastructure, technology learning curves, and adjustment costs create path dependencies and inertia, which in turn constrain the transformation of the energy system. The model also tracks the emissions of all major greenhouse gases (GHG) from economic activity.

**MAgPIE.** The Model of Agricultural Production and its Impact on the Environment (MAgPIE) is a land-system modelling framework developed to assess global land-use dynamics and their implications for sustainable development throughout the 21<sup>st</sup> century<sup>32,51</sup>. The model uses a dynamic cost-optimisation approach to spatially allocate the production of food, feed, bioenergy and biomass under socioeconomic and biophysical constraints in order to meet global demand. MAgPIE accounts for various cost components including factor requirements (capital, labour, fertiliser), investment into agricultural research & development, as well as transport, land conversion, trade and irrigation costs. It also considers the depreciation of capital stocks over time and costs for new investments into crop production, prioritising historical agricultural locations while restricting production shifts to areas with suitable climate and soil conditions but insufficient infrastructure. Trade flows are modelled as a combination of historical import and export patterns and comparative advantages in agricultural production with a modest trade liberalisation over time along the SSP2 pathway<sup>72</sup>. Socioeconomic constraints, such as trade or investments into agricultural productivity, are formulated at the scale of twelve model regions, which were aligned to the multiregional setup of REMIND. Spatially-explicit

biophysical information on vegetation, litter, and soil carbon stocks as well as water availability based on historical climate data<sup>73</sup> were taken from LPJmL4<sup>68,69</sup> at 0.5 degree spatial resolution. Yield patterns for 19 food, feed and bioenergy crop functional types, grassland yields, as well as crop irrigation water requirements at 0.5 degree were derived from LPJmL5 simulations with unlimited nitrogen supply<sup>74</sup>. All model inputs at the 0.5-degree resolution were clustered to 200 spatial simulation units with similar biophysical properties using a k-means clustering approach<sup>75</sup>. MAgPIE covers all major crop and livestock species, non-food agricultural commodity production, as well as food waste and supply chain losses. CO<sub>2</sub> emissions from land-use change are calculated based on carbon losses and uptake resulting from the conversion of forested and non-forest ecosystems and regrowth on abandoned/restored agricultural land between time steps<sup>76</sup>.

Forest growth in MAgPIE is represented using the approach of Humpenöder et al.<sup>5</sup> with updated parameters for the Chapman-Richards growth function for native vegetation and timber plantations from Braakhekke et al.<sup>46</sup>. For this analysis we used the growth curve for native vegetation to model forest growth in areas of AR deployment (NDC and carbon-price induced AR, see below). Consistently, we assumed that AR had the same carbon density, and thus consisted of the same species, found in the succession of native ecosystems over time<sup>77</sup>. The age class distribution of existing forests was initialised using the Global Forest Age Dataset (GFAD V1.1) by Poulter et al.<sup>78</sup>. Future AR deployment was restricted to areas outside the boreal zone and to locations where climatic conditions support forest growth, excluding forest disturbance factors such as grazing or fire. Eligible areas for AR deployment were identified based on a minimum carbon density threshold of 20 t C ha<sup>-1</sup>, using carbon density estimates for native vegetation derived from LPJmL4 data.

In our integrated land- and energy-system modelling framework, REMIND and MAgPIE were run iteratively in a soft-coupled mode, thereby allowing for a high level of detail in process representation across both the land and energy systems<sup>79</sup>. Information on GHG prices, second-generation lignocellulosic bioenergy demand and land-use related emissions were iteratively balanced and harmonised between the REMIND and MAgPIE models in order to generate consistent land-use and energy transition scenarios based on a single combined optimisation problem<sup>30–32</sup>. Cross-sectoral GHG emissions from REMIND-MAgPIE were then used to estimate corresponding changes in GHG concentrations in the atmosphere, radiative forcing levels and changes in the global mean surface air temperature (GSAT) with the reduced-complexity climate model MAGICC<sup>70,71</sup> based on a probabilistic setup.

**SEALS.** The Spatial Economic Allocation Landscape Simulator (SEALS) was applied to allocate land-use projections from MAgPIE provided at the 0.5-degree level to a spatial scale suitable for assessing habitat change at a high level of detail<sup>34,51,77</sup>. SEALS operates at a spatial resolution of 10 arc-seconds (~300 m at the equator) and allocates projected land-cover changes by ranking grid cells using a composite suitability score. This score includes information on spatial adjacency—capturing how

surrounding land cover influences the likelihood of conversion—as well as physical properties such as soil quality, topography, climate, and accessibility, represented by travel time to the nearest market. Additionally, SEALS accounts for conversion eligibility constraints that restrict agricultural land expansion into urban land, current or future protected areas, and water bodies. The initial land-cover distribution is based on the 2020 ESA-CCI map. The 37 ESA-CCI land-cover classes were reclassified into seven functional land types: cropland, grassland, forest, non-forest vegetation (e.g., shrublands and herbaceous cover), urban, barren land, and water. Adjacency relationships are quantified by analysing both the proximity and the spatial agglomeration of neighbouring land-cover types. Suitability maps based on spatial adjacency, physical suitability and conversion eligibility are used to guide an iterative allocation process, by which projected land-use changes from MAgPIE between 2020 and 2050 are assigned to the most suitable available locations until all coarse land-cover changes are spatially distributed at 10 arc-seconds. Model parameters for spatial adjacency and suitability are empirically calibrated using observed land-cover transitions from ESA-CCI data between 2000 and 2010. The final set of coefficients was selected based on their ability to reproduce observed land-cover changes in withheld validation data from 2011 to 2015<sup>77,80</sup>.

**Area of habitat.** Area of habitat (AOH) refers to the area of a species' geographic range that meets its habitat requirements<sup>40</sup>. We generated AOH maps for 6,374 amphibian, 9,124 bird, 5,351 mammal, and 6,877 reptile species for the year 2020, and used land-cover projections based on REMIND-MAgPIE scenarios and SEALS to assess changes in AOH under different scales of AR deployment<sup>51</sup>. Species range polygons were obtained from the IUCN Red List database<sup>81</sup> and BirdLife International<sup>82</sup>. In our analysis, we retained seasonal range information and assessed AOH changes separately for resident, breeding, non-breeding, and uncertain seasonality ranges. Ranges with unknown presence or no habitat preference information were excluded. Species' habitat preferences were derived from the IUCN Red List database. The twelve major habitat types defined in the IUCN Habitats Classification Scheme<sup>83</sup> were linked to spatial land cover information using the habitat–land cover translation model developed by Lumbierres et al.<sup>38</sup>. The model maps IUCN habitat classes to ESA CCI land cover classes based on varying strengths of association. We used the strongest habitat-land cover association threshold, which in prior studies has been shown to reduce commission errors without affecting validation performance of estimated AOH<sup>39,41</sup>. For artificial degraded forests and plantations, for which no associations exceeded the strongest threshold, we used the second-highest threshold, linking them to ESA CCI classes 12 (cropland, rainfed, tree or shrub cover), 20 (cropland, irrigated or post-flooding), and 190 (urban areas) (see Supplementary Tab. 2). Habitat types classified as marginal or of no major importance in the IUCN Red List Database were excluded. For abandoned agricultural areas and locations of AR deployment we employed the same approach as in the MAgPIE simulations (see above). Consistent with this approach, land that maintained a carbon density  $\leq 20 \text{ t C ha}^{-1}$  in the assessed time step was classified as non-forest vegetation (i.e., native grassland or shrubland), while land exceeding this threshold was considered forest vegetation.



AOH changes were estimated using two-step process approach with a pre-processing and a scenario analysis step<sup>51</sup>. In the pre-processing step, habitat preferences of each species were translated to ESA CCI land cover classes and unsuitable elevation zones were removed based on species-specific elevation limits from the IUCN database using WorldClim 1 km elevation data<sup>84</sup>. Species polygons with no area remaining within the elevation range were omitted from the set of assessed species. During scenario analysis, land-cover projections from REMIND-MagPIE and SEALS were used to subtract unsuitable habitat from the pre-processed ranges to derive final AOH estimates for each scenario. For the baseline year 2020, AOH was derived directly from ESA CCI land-cover data. All spatial analyses were performed in R using the terra<sup>85</sup> package, while data processing was parallelised and executed on a high-performance computing cluster using the foreach<sup>86</sup> and doParallel<sup>87</sup> packages because of the high computational demand.

### **Scenario set-up**

The primary goal of our scenario set was to assess the emerging biodiversity and energy system responses of different levels of AR deployment under a stringent Paris-aligned climate change mitigation pathway. Regarding socioeconomic trends of population and income growth over time, we based our scenarios on the moderate ‘middle-of-the-road’ socioeconomic pathway (SSP2), which also assumes compliance with currently implemented land and energy policies (e.g. no cropland expansion in current protected areas<sup>51</sup>). Food demand projections were derived from population and income trajectories based on anthropometric and econometric approaches that consider body-height, age-cohort, sex and body mass index distributions using elasticities obtained from historical data. Energy demand is modelled using EDGE (‘Energy Demand GEnerator’) models for the transport<sup>88</sup>, industry<sup>31</sup>, and buildings<sup>89</sup> sectors that account for sector-specific energy-demand drivers and trends following the SSP2 pathway, such as infrastructure inertia, consumer lifestyles, or floor space demand. Energy demand in each sector is also sensitive to GHG pricing under climate policy<sup>31</sup>.

**Climate policy.** To limit the global mean temperature increase to ‘well-below’ 2° C throughout the 21<sup>st</sup> century and to meet the 1.5° C target by the end of the century in line with the Paris Agreement, we constrained cumulative CO<sub>2</sub> emissions to a total carbon budget of 750 GtCO<sub>2</sub> from 2020 until 2100 across all scenarios except of the ‘business-as-usual’ (BAU) case. To meet this constraint, we modelled linearly increasing GHG prices for all types of emissions across the land and energy systems. Modelled GHG prices remained sensitive to available CDR options such as AR deployment. In the energy sector, GHG prices incentivised a decarbonisation, a partial substitution of fossil fuels by bioenergy, and the deployment of carbon capture, especially through bioenergy with carbon capture and storage (BECCS). In the land sector, GHG prices strongly discouraged emissions from land-use change, especially from carbon-rich forest and non-forest ecosystems such as peatlands<sup>90</sup>. At the same time, AR deployment was incentivised through GHG pricing by calculating the expected CO<sub>2</sub> uptake over a 50-year planning horizon, multiplying it by the projected GHG price, discounting the result to

present value, and applying an annuity factor to convert it into an average annual reward. We here assumed that rewards for AR deployment were equivalent to the modelled GHG prices to maximise the incentive for AR deployment. However, to explore the implications of different levels of AR deployment, we imposed area-based constraints on AR after 2020 of 150 Mha, 250 Mha and 350 Mha in the AR150, AR250 and AR350 scenarios, respectively. In the AR0 scenario, no AR deployment was allowed after 2020, while in the NDC scenario AR followed country-specific targets submitted under nationally determined contributions (NDCs), which amounted to an area of 63 Mha of AR until 2030. These NDC-based targets for AR were also included in the upper boundary for AR across the AR150, AR250 and AR350 scenarios, so that carbon-priced induced AR accounted for only 87 Mha, 187 Mha and 287 Mha of AR, respectively, across these scenarios. All AR deployment was constrained to areas where climatic conditions support forest growth. These areas were identified using estimated carbon densities of the potential natural vegetation derived from LPJmL. Areas with a potential carbon density  $>20 \text{ tC ha}^{-1}$  were classified as suitable for forest growth, yet without natural disturbances, e.g. through grazing or fire (Supplementary Fig. 2).

For each the stylised AR0, NDC, AR150, AR250 and AR350 climate mitigation scenarios, we also modelled scenario variants that included stringent land conservation in biodiversity hotspots (BHs)<sup>37,91</sup>, in order to quantify interactions between conservation planning and AR deployment. Biodiversity hotspots host nearly 43% of global vertebrate species and over half of all endemic plant species. Yet, they are also characterised by a loss of native habitat of  $>70\%$ . Prominent examples include the Atlantic Forest, the Cerrado, Mesoamerica, the Andes, and Chilean Forests in Latin America, and Madagascar, the Horn of Africa, and the Guinean Forests of West Africa. Land conservation in BHs included the protection of all remaining native vegetation and land restoration of land covers based on pre-industrial (1750) levels<sup>51</sup> as reported in the LUH2v2 dataset<sup>92</sup>, instead of strict AR deployment.

## **Data availability**

The model results presented in this analysis are available via Zenodo at <https://doi.org/10.5281/zenodo.17611595> (ref<sup>93</sup>).

## **Code Availability**

The model code of the MAgPIE model is openly available under GNU Affero General Public License, version 3 (AGPLv3), and is accessible via GitHub at <https://github.com/magpiemodel/magpie>. The release version (MAgPIE 4.11.0) on which this work is based is available via Zenodo at <https://doi.org/10.5281/zenodo.15862748> (ref<sup>94</sup>). MAgPIE 4.11.0 is accompanied by a technical model documentation (<https://rse.pik-potsdam.de/doc/magpie/4.11.0/>), which was compiled using the GAMS code documentation toolkit goxygen (ref<sup>95</sup>). REMIND is also openly available under GNU Affero General Public License, version 3 (AGPLv3) and available on GitHub. The model version used in this

study is 3.5.1, which can be downloaded at <https://github.com/remindmodel/remind/releases/tag/v3.5.1>. SEALS is also accessible via GitHub at [https://github.com/jandrewjohnson/seals\\_dev/releases/tag/v1.0.0](https://github.com/jandrewjohnson/seals_dev/releases/tag/v1.0.0) and documented under [https://justinandrewjohnson.com/earth\\_economy\\_devstack/seals\\_overview.html](https://justinandrewjohnson.com/earth_economy_devstack/seals_overview.html).

## Competing interests

The authors declare no competing interests.

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