

# Impacts of incentives to reduce emissions from deforestation on global species extinctions

Bernardo B. N. Strassburg<sup>1,2\*</sup>†, Ana S. L. Rodrigues<sup>3†</sup>, Mykola Gusti<sup>4,5</sup>, Andrew Balmford<sup>6</sup>, Steffen Fritz<sup>4</sup>, Michael Obersteiner<sup>4</sup>, R. Kerry Turner<sup>2</sup> and Thomas M. Brooks<sup>7,8,9</sup>

**Deforestation is a major source of anthropogenic greenhouse gas emissions<sup>1</sup>, and the greatest single driver of species extinctions<sup>2</sup>. The reduction of emissions from deforestation and forest degradation (REDD) has been formally recognized as a climate change mitigation option. REDD might have important co-benefits for biodiversity conservation<sup>3–10</sup>, yet the extent of these benefits will depend on as-yet untested associations between fine-scale spatial patterns of deforestation, species distributions and carbon stocks. Here we combine a global land-use model<sup>11</sup> and spatial data on species distributions<sup>12–14</sup> to explore scenarios of future deforestation within REDD-eligible countries, to quantify and map the potential impacts on species extinctions as increased by forest loss and decreased by carbon conservation. We found that the continuation of historical deforestation rates is likely to result in large numbers of species extinctions, but that an adequately funded REDD programme could substantially reduce these losses. Under our deforestation scenarios, the projected benefits of REDD were remarkably consistent across the four methods used to estimate extinctions, but spatially variable, and highly dependent on the level of carbon payments. Our results indicate that, if well designed, adequately funded and broadly implemented, carbon-based forest conservation could play a major role in biodiversity conservation as well as climate change mitigation.**

Emissions from deforestation are the second largest source of human-induced climate change<sup>1</sup>, accounting for 17% of anthropogenic greenhouse-gas emissions, while the associated loss of habitat is the principal cause of species extinctions<sup>2</sup>. In response, the international community has pledged both to avoid dangerous climate change and to conserve biological diversity. Despite its substantial mitigation potential<sup>4,15</sup>, the reduction of emissions from land-use change in developing countries was not included as a mitigation activity in the Kyoto Protocol, which established binding targets for the reduction of greenhouse gas emissions under the United Nations Framework Convention on Climate Change (UNFCCC). Now, however, the Cancún Agreements have confirmed that a scheme of positive incentives to reduce emissions from deforestation and forest degradation (REDD) will be part of the next climate agreement, and urged prompt support for early-action activities. They also noted that REDD actions should be used to promote the conservation

of biological diversity. At the same time the Convention on Biological Diversity (CBD) has established an ambitious new strategic plan to tackle biodiversity loss until 2020. The magnitude of REDD and the scale of the incentives involved, however, are still to be decided.

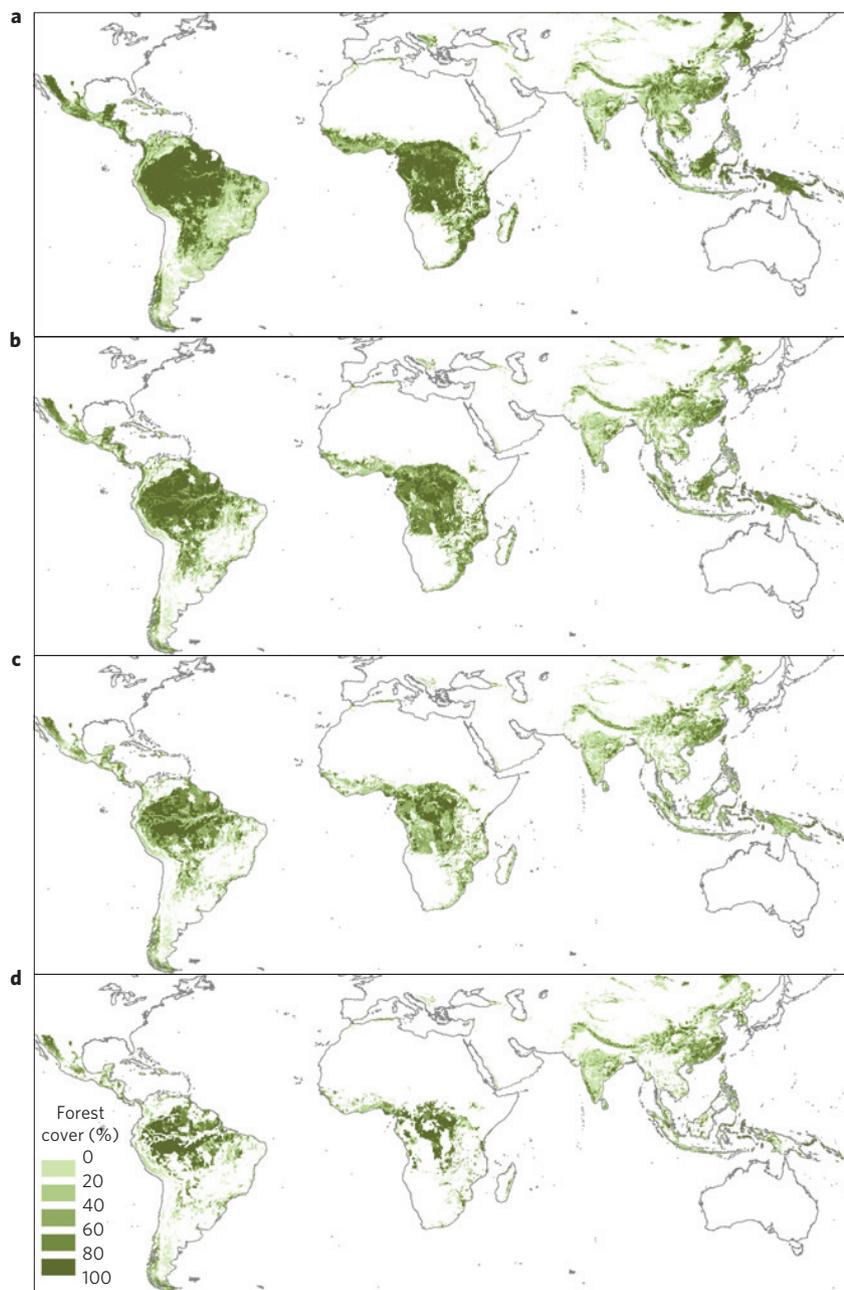
The potential co-benefits of REDD for biodiversity conservation have not gone unnoticed by the scientific community<sup>3–10</sup>. Avoiding deforestation to lower carbon emissions could play a major role in the long-term conservation of biodiversity-rich forests such as those in the Amazon<sup>8</sup> and Indonesia<sup>7</sup>, while incorporating biodiversity values into carbon payments could increase the biodiversity benefits of REDD still further<sup>5</sup>. However, biodiversity and carbon are unevenly distributed across the world's forests<sup>3,4</sup> and therefore the magnitude of the co-benefits of REDD to global biodiversity will depend critically on fine-scale spatial relationships between deforestation, carbon stocks and species distribution. Previous studies have provided useful overarching insights into the implications of REDD for biodiversity. However, all such contributions to date have either been restricted in spatial scale (for example to the national level<sup>5,9</sup>) or geographic extent (for example to individual countries such as Indonesia<sup>7,10</sup>). Here, we provide the first global, high-resolution quantification of the potential impacts of carbon-based conservation on species extinctions through the twenty-first Century.

We used a spatially explicit land-use model (Global Forest Model (G4M), a refined version of Dynamic Integrated Model of Forestry and Alternative Land Use (DIMA); ref. 11) to simulate scenarios of deforestation under different levels of carbon price (0–25 US\$/tonne of CO<sub>2</sub>), with a zero price corresponding to business-as-usual (that is, no REDD; Fig. 1). In this business-as-usual scenario global deforestation rates follow historical levels (1990–2005) through to 2100, but country-level rates vary. Positive values for carbon increase the returns of standing forests, thus leading to lower deforestation rates. We then used four different approaches to investigate how many forest-dependent mammal and amphibian species would be likely to become extinct given the total extent and the spatial patterns of deforestation in each scenario.

## Results and discussion

Under the projections in our business-as-usual deforestation scenario, we estimate there will be substantial losses in global

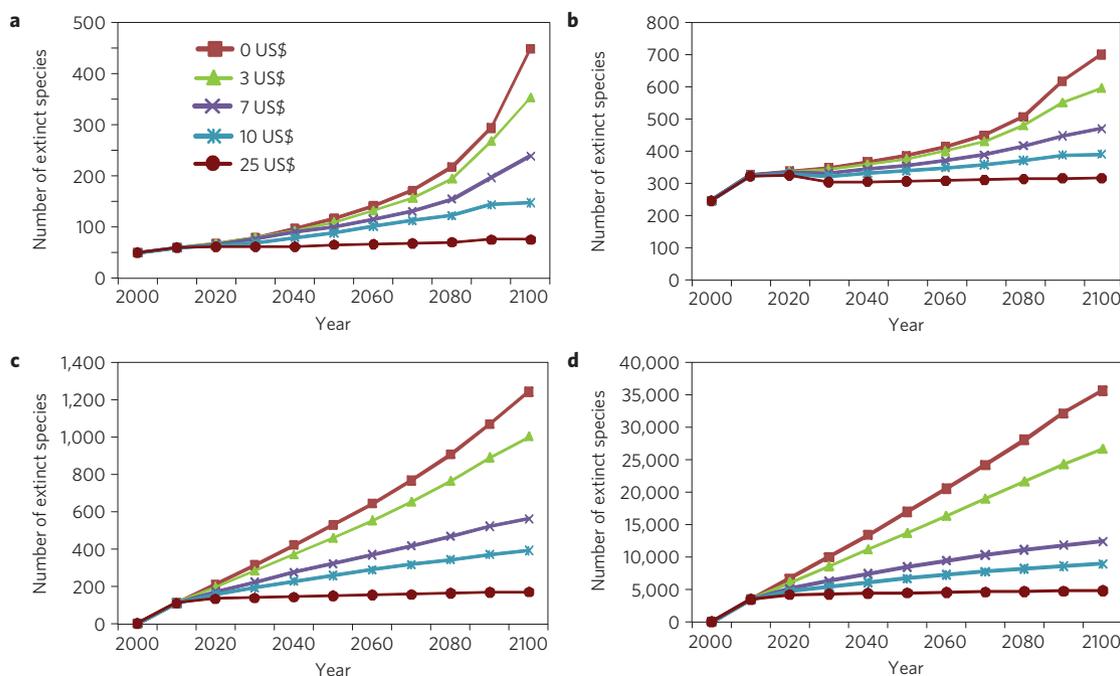
<sup>1</sup>International Institute for Sustainability (IIS), Rio de Janeiro, RJ, 22450-130, Brazil, <sup>2</sup>Centre for Social and Economic Research on the Global Environment (CSERGE), School of Environmental Sciences, University of East Anglia, Norwich, Norfolk NR4 7TJ, UK, <sup>3</sup>UMR5175 Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919 Route de Mende, 34293 Montpellier cedex 5, France, <sup>4</sup>International Institute of Applied Systems Analysis, A-2361 Laxenburg, Austria, <sup>5</sup>Department of International Information, Lviv Polytechnic National University, 12 St. Bandera St., 79013 Lviv, Ukraine, <sup>6</sup>Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK, <sup>7</sup>NatureServe, 4600 N. Fairfax Drive, 7th Floor, Arlington, Virginia 22203, USA, <sup>8</sup>World Agroforestry Center (ICRAF), University of the Philippines Los Baños, Laguna 4031, Philippines, <sup>9</sup>School of Geography and Environmental Studies, University of Tasmania, Hobart, Tasmania 7001, Australia. †These authors contributed equally to this work. \*e-mail: b.strassburg@iis-rio.org.



**Figure 1** | Changes in forest cover over the twenty-first century, within presumed REDD-eligible regions. **a**, As observed in 2000. **b–d**, As projected under our business-as-usual scenario for 2040 (**b**), 2070 (**c**) and 2100 (**d**).

species richness, independent of which approach we adopt for calculating extinctions (Fig. 2). Three methods based on individual species distribution data, all conservative but to different levels, project that out of 4,514 forest-dependent species (Supplementary Fig. S1), habitat loss due to deforestation alone would commit between 399 (9%) and 1,241 (27%) mammal and amphibian species to extinction by 2100. This is three to eleven times the total number of species (117) known to have become extinct globally amongst these taxa since 1500 (ref. 12), and 350 to 10,800 times background extinction rates<sup>16</sup>. Under our fourth approach for quantifying species extinctions, based on aggregated data on endemic species within highly diverse, forest-dominated, biogeographic regions, the business-as-usual deforestation scenario would result in the extinction of 22% of their endemic plants and vertebrates, or >36,000 species (Supplementary Table S1).

Despite the variation in the methods and biodiversity data they use, the four approaches show remarkable agreement in their estimates of how REDD could reduce extinctions across a range of carbon prices (Fig. 3). For example, given a carbon price scenario of 7 US\$/tonne CO<sub>2</sub>, our different methods estimate that REDD would prevent between 51% and 55% of the global extinctions projected under business-as-usual, whereas a price of 25 US\$/tonne CO<sub>2</sub> could reduce them by 84%–93% (for context, the average price of carbon traded worldwide in 2007–2008 was 34 US\$/tonne CO<sub>2</sub>; ref. 17). At the price of 25 US\$/tonne CO<sub>2</sub>, we found that REDD would mitigate up to 4.3 Gt CO<sub>2</sub> (ST3). This would be equivalent to 22% of OECD countries emissions in 2020 (A2 scenario)<sup>18</sup>. This confirms that REDD could be a very powerful mitigation tool, but it also highlights that Annex 1 countries should be prepared to dedicate a substantial fraction of their mitigation efforts to support REDD.

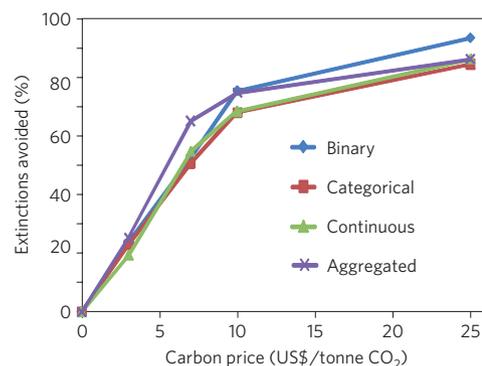


**Figure 2 | Number of estimated species extinctions under each scenario of carbon price, over time.** **a–c**, Panels correspond to each of the methods used to estimate extinctions from deforestation: binary (**a**), categorical (**b**) and continuous (**c**) models of species extinction risk. **d**, Aggregated estimate across biogeographic regions. Carbon prices are in US\$/tonne CO<sub>2</sub>. In **a–c**, species correspond to forest-dependent mammals and amphibians restricted to the study area; in **d** they correspond to plants and terrestrial vertebrates endemic to the nineteen hotspots and four high-biodiversity wilderness areas analysed. In all cases, the values for 2000 and 2010 are the same across scenarios, because the land-use model assumes that REDD starts in 2012.

The relationship between the level of REDD incentives and their relative benefits for conservation also holds across a deforestation scenario involving lower levels of overall forest loss. In this case, lower business-as-usual deforestation leads to disproportionately fewer extinctions (given the exponential relationship between habitat loss and species extinction) but the relative impact of REDD on extinctions is similar (Supplementary Fig. S3). For instance, in this scenario payments of 25 US\$/tonne would avoid 87% of business-as-usual extinctions (compared with 93% in our main scenario). The same is true under an alternative spatial pattern of deforestation based on the assumption that protected areas would suffer no deforestation, where payments of 25 US\$/tonne would avoid 92% of business-as-usual extinctions (Supplementary Fig. S4).

Deforestation as projected in our scenarios is not uniformly distributed across the world (Fig. 1) and, accordingly, neither is its impact on biodiversity. One way of investigating detailed spatial variation in how biodiversity would be affected under each scenario is to map projected local extinctions, calculated as the difference between the original (year 2000) species richness and that expected under each scenario (Fig. 4). Such local-scale extinctions are relevant given their possible negative consequences for local ecosystem functioning, resilience and provision of services<sup>19</sup>, and the fact that all global extinctions are the result of cumulative local losses.

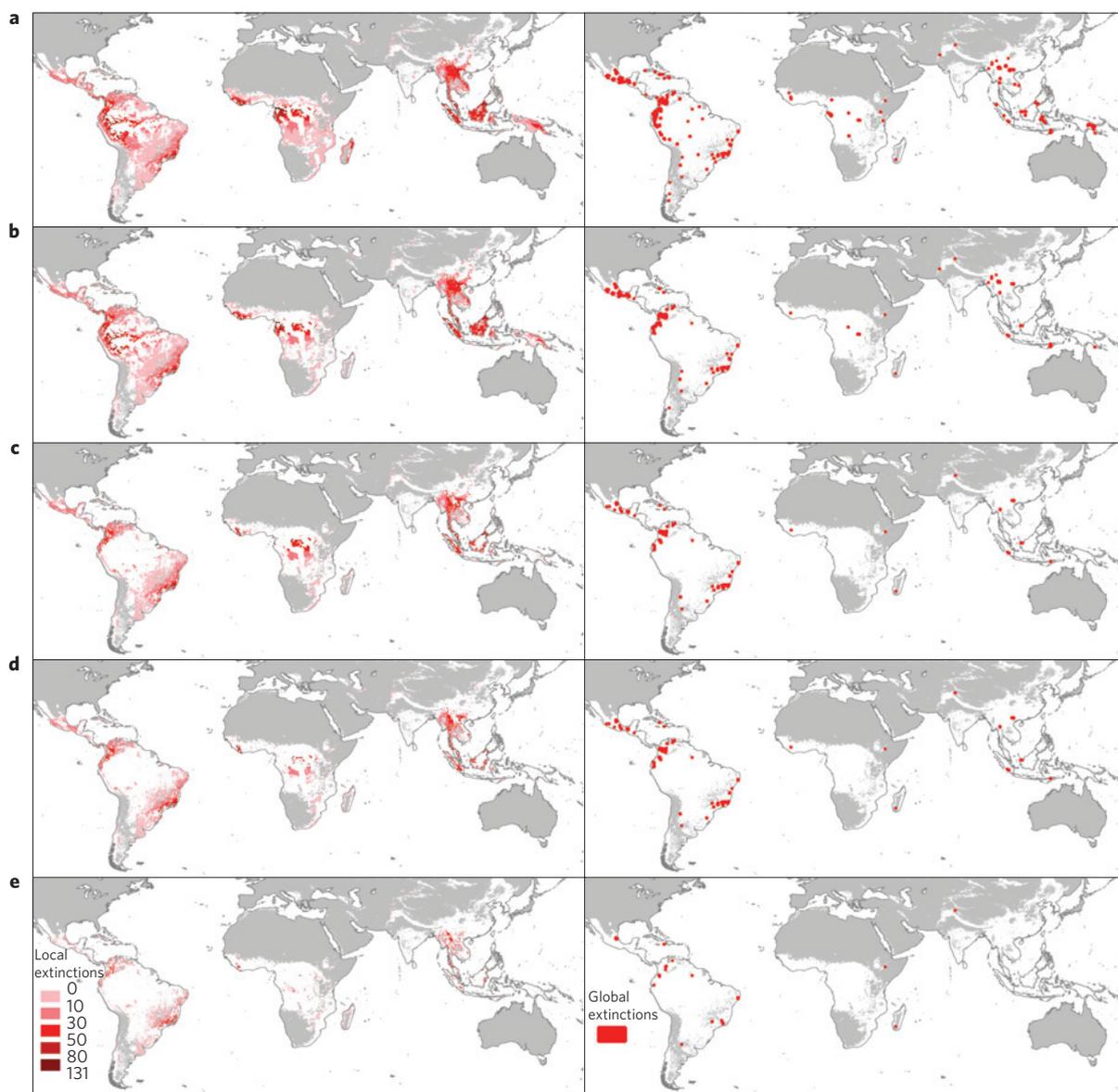
Unsurprisingly, local extinctions will be most severe when deforestation hits regions with high species richness, such as western Amazon, the Congo basin, Southeast Asia and the Atlantic Forest of South America (Supplementary Fig. S1). Under our business-as-usual scenario, these regions would undergo very extensive deforestation by 2100, and therefore suffer dramatic local extinctions. As expected, the higher the level of investment in REDD, the fewer the expected extinctions. For carbon prices of 10 US\$/tonne or higher, our land-use model indicates that deforestation and subsequent local species extinctions



**Figure 3 | Relationship between carbon price and the estimated effects of REDD in avoiding extinctions.** Effects are in relation to a business-as-usual scenario, by 2100, for each of the methods employed to estimate numbers of species' extinctions: binary, categorical and continuous estimates of individual species' extinction risk, and aggregated estimates across species endemic to biogeographic regions.

could be averted in most of the Amazon and Congo. They would however remain substantial (even though much lower than under business-as-usual) in parts of the Atlantic Forest and Southeast Asia (where forest conversion would remain highly profitable owing to the high population and economic pressure) and in other regions important for biodiversity, such as the tropical Andes.

Whereas local species extinctions would be most dramatic in regions of high species richness, future global extinctions are likely to be concentrated in regions of high endemism (Fig. 4; Supplementary Fig. S2), because of concentrations of species whose narrow distribution makes them especially vulnerable to habitat loss<sup>20</sup>. However, deforestation beyond 2000 is estimated to be unequally distributed among centres of endemism (Supplementary



**Figure 4 | Spatial patterns of estimated species extinctions under different scenarios. a–e.** Local (left) and global (right) species extinctions, in year 2100, under a business-as-usual scenario (a) and under REDD scenarios with carbon prices of 3 (b), 7 (c), 10 (d) and 25 (e) US\$/tonne of CO<sub>2</sub>. Local extinctions are the difference between the estimated species richness in 2000 and 2100, based on categorical probabilities of extinction. Global extinctions are calculated using the binary method of estimating species extinctions (whereby a species was considered extinct if all the forest cover within its range disappeared; the cells corresponding to the ranges of extinct species are represented with a thick outline to improve visibility). Cells in grey were not analysed (either because they are outside the study area or because they had zero forest in 2000).

Table S1), with higher levels in some regions than in others (for example, by 2100 under business-as-usual, New Guinea would lose 82% of its forest cover in the year 2000, Madagascar 77%, Atlantic Forest 74%, Tropical Andes 74%; compared with mountains of Southwest China 25%, Himalaya 28%, Philippines 28%). These differences in projected forest loss interact with spatial variation in economic conditions and agricultural suitability so that the sensitivity of conservation benefits to the level of REDD investment is likely to vary among regions. For example, whereas our results indicate that New Guinea could greatly benefit from REDD payments of 10 US\$/tonne CO<sub>2</sub> (avoiding 90% of the deforestation and 93% of its global extinctions estimated by 2100 under business-as-usual), in the Atlantic Forest and Indo-Burma a similar reduction of forest loss and global extinctions would require payments above 25 US\$/tonne CO<sub>2</sub> (Supplementary Table S1).

The scenarios explored in this analysis are clearly simplistic representations of the links between carbon conservation policies, deforestation and biodiversity loss. First, we only considered extinctions due to direct habitat loss, not other threats or potential synergies between them. For example, climate change is forecast to become a major threat to biodiversity<sup>21</sup> and will probably have synergistic effects with habitat loss<sup>22</sup>, indicating our assessment of the benefits of REDD may be very conservative. Second, we did not account for natural regeneration that could restore the habitats of some species (although it is unclear if these would provide a safe haven against extinctions for many species<sup>23</sup>), nor for the possibility that forest-dependent species might survive for a limited time in deforested lands. We did, however, consider permanent forestry lands as equivalent to undisturbed forests for species persistence.

An important issue raised by our results is that in the absence of complementary initiatives to reduce demand for additional

land (for example, by increasing agricultural yields), extinctions would remain significant in areas of high population or economic pressure, such as the Atlantic Rainforest and Southeast Asia. Furthermore, without such efforts REDD might plausibly lead to reduced agricultural output and increased commodity prices, thereby making it more expensive to avoid deforestation as REDD progresses. However, a recent analysis of the likely costs of such further measures<sup>24</sup> indicates that the intermediate and higher carbon prices we are modelling should be sufficient to cover the implementation costs of projects that increase productivity of existing agricultural lands.

We implicitly assumed a globally uniform REDD mechanism driven by carbon price. In practice, there are likely to be complex and variable mechanisms of REDD implementation across and within national boundaries, with varied implications for biodiversity<sup>25</sup>. This may reduce the global efficiency of REDD, for example through leakage of deforestation from countries with stronger to those with weaker REDD mechanisms. On the other hand, a strategic differential allocation of investment across countries creates opportunities for maximizing the biodiversity benefits of REDD (ref. 5).

It is important to consider that second order effects of REDD might result in an increased threat to biodiversity<sup>26</sup>. For instance, we restricted our analysis to forests, therefore not capturing potential harmful side-effects of a forest-focused REDD for other, carbon-poorer biomes<sup>4</sup>. Furthermore, incentives to forest management from a purely carbon perspective may have unforeseen harmful side-effects for biodiversity, such as through the expansion of species-poor tree plantations or some biomass carbon-enhancement activities<sup>27</sup>.

Our results clearly demonstrate that a continuation of historical levels of deforestation is likely to result in very high levels of species extinction. Such losses are incompatible with global commitments to reduce rates of biodiversity decline<sup>28</sup>. However, our analyses also indicate that an adequately funded and widely implemented REDD mechanism could prevent very many of these extinctions, even without considering its indirect support to biodiversity through mitigating climate change<sup>21</sup>. The direct effect of REDD would vary and be more limited in regions of high population and economic pressure, pointing to the need for complementary measures to reduce demand for land conversion. But, evidently, by implementing a global mechanism of financial incentives for avoiding emissions from deforestation and forest degradation the parties to the United Nations Framework Convention on Climate Change can make substantial progress in simultaneously addressing two of the biggest crises humanity has ever faced.

## Methods

Our analysis covers those countries not in Annex I of the UNFCCC (mostly developing countries with no binding targets for reducing emissions under the Kyoto Protocol); we assume that these non-Annex I countries are likely candidates for REDD incentives, and that their forest corresponds approximately to the area that may become eligible to receive REDD payments. A spatially explicit land use model<sup>11</sup> was used to generate scenarios of forest-cover change between years 2000 and 2100. For each cell ( $0.125^\circ \times 0.125^\circ$ ) and period in time, the model allocates the fraction converted to agriculture and the fraction dedicated to sustainable use of the forest. The choice is based on the highest returns, which are functions of biophysical and socioeconomic conditions. Carbon payments increase the relative competitiveness of standing forests vis-à-vis other land uses in net present value terms, thus leading to lower deforestation. A detailed description of the land-use model is available in the Supplementary Information.

We chose a model calibration to define a reference scenario of continued deforestation throughout 2100 equivalent to the total global deforestation rate from the period 1990–2005 (Fig. 1). Country-level deforestation rates for the base period of 2000–2005 were calibrated to match historical levels. In the projection, country-level deforestation rates were allowed to vary in both relative and absolute terms following changing biophysical and socioeconomic conditions.

REDD policy scenarios were defined in terms of carbon prices: 0, 3, 7, 10 and 25 US\$/tonne of CO<sub>2</sub>. A carbon price of zero corresponds to business-as-usual

(without REDD). Each scenario consists of a time series of the projected forest cover in each year (Fig. 1).

We investigated the effects of REDD on global species extinctions within each given deforestation scenario by overlaying the forest-cover maps projected under the scenario with the distributions of 4,514 forest-dependent mammals<sup>13</sup> and amphibians<sup>14</sup> restricted to REDD-eligible regions (Supplementary Fig. S1). We then estimated changes in forest cover for each species, under each scenario, using four approaches to investigate how individual species would be affected. In a first, conservative approach, a species was considered extinct if all the forest cover within its range disappeared; this approach therefore yielded a binary extinction risk (equal to one if all forest was converted and zero otherwise). The resulting estimate of species extinctions is an underestimate because (among other reasons—see Supplementary Information) even species losing almost all of their habitat are assumed to persist. To address this, we considered two further methods to estimate species extinction risks, one categorical and another continuous. The former estimated extinction risk based on the International Union for Conservation of Nature (IUCN) Red List Categories and Criteria (Supplementary Table S2), whereas the latter applied the species–area relationship to project how the range contraction of individual species would translate into extinction risk<sup>21</sup>. In all cases, the individual extinction risk values across species were summed to obtain an overall number of estimated species extinctions (see Supplementary Information for a detailed description of the methods applied).

As a fourth analysis, we used a separate biodiversity dataset covering biogeographic regions within our study area that hold important numbers of endemic species (and accounting for 67% of the total forest extent). Data on the numbers of terrestrial vertebrate and plant species endemic to each forest-dominated biodiversity hotspot and high-biodiversity wilderness area were combined with forest projections to estimate numbers of extinctions within each region, based on the species–area relationship (Supplementary Table S1), which, contrary to a recent claim<sup>29</sup>, is a robust approach<sup>30</sup>. These were then summed into an aggregated number of extinctions.

As sensitivity tests, we repeated all analyses for a family of scenarios based on lower levels of overall deforestation (Supplementary Fig. S3) and for another set based on the assumption that protected areas are wholly invulnerable to deforestation (Supplementary Fig. S4).

More detailed information on materials and methods is in the online Supplementary Information.

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## References

- IPCC *Climate Change 2007: Mitigation of Climate Change* (eds Metz B., Davidson O., Bosch P., Dave R., Meyer L.) (Cambridge Univ. Press, 2007).
- Baillie, J. *et al.* 2004 IUCN Red List of Threatened Species. A Global Species Assessment (IUCN—The World Conservation Union, 2004).
- Miles, L. & Kapos, V. Reducing greenhouse gas emissions from deforestation and forest degradation: Global land-use implications. *Science* **320**, 1454–1455 (2008).
- Strassburg, B. B. N. *et al.* Global congruence of carbon storage and biodiversity in terrestrial ecosystems. *Conserv. Lett.* **3**, 98–105 (2010).
- Venter, O. *et al.* Harnessing carbon payments to protect biodiversity. *Science* **326**, 1368 (2009).
- Strassburg, B., Turner, R. K., Fisher, B., Schaeffer, R. & Lovett, A. Reducing emissions from deforestation—The ‘combined incentives’ mechanism and empirical simulations. *Glob. Environ. Change* **19**, 265–278 (2009).
- Venter, O. *et al.* Carbon payments as a safeguard for threatened tropical mammals. *Conserv. Lett.* **2**, 123–129 (2009).
- Rodrigues, A. S. L. *et al.* Boom-and-bust development patterns across the Amazon Deforestation Frontier. *Science* **324**, 1435–1437 (2009).
- Busch, J., Godoy, F., Turner, W. R. & Harvey, C. A. Biodiversity co-benefits of reducing emissions from deforestation under alternative reference levels and levels of finance. *Conserv. Lett.* **4**, 101–115 (2010).
- Paoli, G. D. *et al.* Biodiversity conservation in the REDD. *Carbon Balance Manag.* **5**, 7 (2010).
- Kindermann, G. *et al.* Global cost estimates of reducing carbon emissions through avoided deforestation. *Proc. Natl Acad. Sci. USA* **105**, 10302–10307 (2008).
- IUCN 2009 IUCN Red List of Threatened Species (2009); available at <http://www.iucnredlist.org>.
- Schipper, J. *et al.* The status of the world’s land and marine mammals: Diversity, threat, and knowledge. *Science* **322**, 225–230 (2008).
- Stuart, S. N. *et al.* Status and trends of amphibian declines and extinctions worldwide. *Science* **306**, 1783–1786 (2004).
- Gullison, R. *et al.* Tropical forests and climate policy. *Science* **316**, 985–986 (2007).
- Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. The future of biodiversity. *Science* **269**, 347–350 (1995).

17. Capoor, K. & Ambrosi, P. *State and Trends of the Carbon Market 2009* (The World Bank, 2009).
18. Riahi, K. & Nakicenovic, N. (eds) *Greenhouse Gases—Integrated Assessment Technol. Forecasting Soc. Change* 74 (Special Issue) 873–1108 (2007).
19. Isbell, F. *et al.* High plant diversity is needed to maintain ecosystem services. *Nature* 477, 199–202 (2011).
20. Manne, L., Brooks, T. & Pimm, S. Relative risk of extinction of passerine birds on continents and islands. *Nature* 399, 258–261 (1999).
21. Thomas, C. *et al.* Extinction risk from climate change. *Nature* 427, 145–148 (2004).
22. Malhi, Y. *et al.* Climate change, deforestation, and the fate of the Amazon. *Science* 319, 169–172 (2008).
23. Gardner, T., Barlow, J., Parry, L. & Peres, C. Predicting the uncertain future of tropical forest species in a data vacuum. *Biotropica* 39, 25–30 (2007).
24. Fisher, B. *et al.* Implementation and opportunity costs of reducing deforestation and forest degradation in Tanzania. *Nature Clim. Change* 1, 161–164 (2011).
25. Harvey, C. A., Dickson, B. & Kormos, C. Opportunities for achieving biodiversity conservation through REDD. *Conserv. Lett.* 3, 56–61 (2010).
26. Stickler, C. M. *et al.* The potential ecological costs and cobenefits of REDD: A critical review and case study from the Amazon region. *Glob. Change Biol.* 15, 2803–2824 (2009).
27. Putz, F. & Redford, K. Dangers of carbon-based conservation. *Glob. Environ. Change* 19, 400–401 (2009).
28. Balmford, A. *et al.* The convention on biological diversity's 2010 target. *Science* 307, 212–213 (2005).
29. He, F. & Hubbell, S. P. Species–area relationships always overestimate extinction rates from habitat loss. *Nature* 473, 368–371 (2011).
30. Brooks, T. M. *et al.* Extinctions: Consider all species. *Nature* 474, 284 (2011).

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### Author contributions

B.B.N.S. and A.S.L.R. contributed equally to this work. The study was conceived by B.B.N.S.. The initial design was developed by B.B.N.S., A.S.L.R., T.M.B. and M.O., A.S.L.R., M.G. and B.B.N.S. conducted the analyses. All authors contributed technical expertise and interpreted the results. B.B.N.S. and A.S.L.R. wrote the initial draft of the manuscript. All authors commented on subsequent drafts.

### Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on [www.nature.com/natureclimatechange](http://www.nature.com/natureclimatechange). Reprints and permissions information is available online at [www.nature.com/reprints](http://www.nature.com/reprints). Correspondence and requests for materials should be addressed to B.B.N.S.