

Report

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The Environmental Legacy of Modern Tropical Deforestation

Highlights

- Time lags in historical tropical deforestation ensure an emission debt of 8.6 PgC
- Tropical deforestation resulted in a debt of more than 140 forest-specific vertebrates
- The carbon emissions debt is equivalent to 5–10 years of global deforestation
- The extinction debt would increase 20th-century extinctions in vertebrates by 120%

Authors

Isabel M.D. Rosa, Matthew J. Smith,
Oliver R. Wearn, Drew Purves,
Robert M. Ewers

Correspondence

isabel.rosa@idiv.de

In Brief

Rosa et al. estimate that historical tropical deforestation has indebted the future with 5–10 years of global deforestation's worth of carbon emissions and more extinctions than estimated to have already occurred since 1900. Habitat protection alone will do little to avoid paying these debts that have already accumulated from historical habitat loss.



The Environmental Legacy of Modern Tropical Deforestation

Isabel M.D. Rosa,^{1,4,6,*} Matthew J. Smith,² Oliver R. Wearn,^{1,3} Drew Purves,^{2,5} and Robert M. Ewers¹

¹Imperial College of London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK

²Computational Science Laboratory, Microsoft Research, Cambridge CB1 2FB, UK

³Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK

⁴German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5E, 04103 Leipzig, Germany

⁵Google Deepmind, 5 New Street Square, London EC4A 3TW, UK

⁶Twitter: @isamdr86

*Correspondence: isabel.rosa@idiv.de

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SUMMARY

Tropical deforestation has caused a significant share of carbon emissions and species losses, but historical patterns have rarely been explicitly considered when estimating these impacts [1]. A deforestation event today leads to a time-delayed future release of carbon, from the eventual decay either of forest products or of slash left at the site [2]. Similarly, deforestation often does not result in the immediate loss of species, and communities may exhibit a process of “relaxation” to their new equilibrium over time [3]. We used a spatially explicit land cover change model [4] to reconstruct the annual rates and spatial patterns of tropical deforestation that occurred between 1950 and 2009 in the Amazon, in the Congo Basin, and across Southeast Asia. Using these patterns, we estimated the resulting gross vegetation carbon emissions [2, 5] and species losses over time [6]. Importantly, we accounted for the time lags inherent in both the release of carbon and the extinction of species. We show that even if deforestation had completely halted in 2010, time lags ensured there would still be a carbon emissions debt of at least 8.6 petagrams, equivalent to 5–10 years of global deforestation, and an extinction debt of more than 140 bird, mammal, and amphibian forest-specific species, which if paid, would increase the number of 20th-century extinctions in these groups by 120%. Given the magnitude of these debts, commitments to reduce emissions and biodiversity loss are unlikely to be realized without specific actions that directly address this damaging environmental legacy.

RESULTS

Estimated Tropical Deforestation 1950–2009

The size of the environmental legacy of tropical deforestation is dependent on both the magnitude and timing of past land

cover changes, rather than the snapshot of forest cover that is directly observable today. We used a validated regional data-constrained spatial model of tropical deforestation [4] to back-cast deforestation from 2009 to 1950 in the three main tropical regions (Figure S1): the Amazon, the Congo Basin, and Southeast (SE) Asia, which was further divided into six sub-regional models (see Supplemental Experimental Procedures and Data S1). Our model provided estimates of deforestation rates for the 1980s, 1990s, and 2000s that fell within the ranges reported previously for all three tropical regions (Table S1).

Tropical deforestation resulted in the clearance of 2.27 million km² of forest by 2010. We estimate through our model that rates of tropical deforestation were very low in the 1950s and then accelerated first in the Amazon in the 1970s, then in SE Asia in the 1990s and most recently in the Congo Basin (Figure 1). This pattern is in line with accepted histories for the regions [7, 8], as is the slowdown in deforestation in the Amazon after 2004 that our model also captured [9].

Gross Vegetation Carbon Emissions

Combining potential vegetation carbon maps with our simulated historical deforestation maps, we estimated that the modern era of tropical deforestation resulted in cumulative emissions of 49.93 petagrams (Pg) of vegetation carbon (± 1.99 Pg, 95% confidence interval [CI]) between 1950 and 2009. Annual emissions from gross tropical deforestation rose sharply over the modern period to 2.30 Pg of vegetation carbon per year (± 0.06 Pg, 95% CI) by 2009 (Figure 2A).

Even if deforestation had stopped completely in 2010, the vegetation carbon emissions debt of modern tropical deforestation ensured there was 8.6 PgC (± 2.24 Pg, 95% CI) of committed emissions still to be released, equivalent to roughly 5–10 years of global deforestation [10]. The legacy is highest in the Amazon, where we estimated 3.72 PgC (± 1.10 Pg, 95% CI) was still to be released. In SE Asia and the Congo Basin, we estimated the legacies to be 3.54 PgC (± 1.50 Pg, 95% CI) and 1.34 PgC (± 0.34 Pg, 95% CI), respectively, with the SE Asian legacy [9] concentrated in the present-day deforestation hotspots of Sumatra and southern Borneo (Figure 3).

The Amazon is the largest remaining continuous tropical forest and accounts for 49% of total tropical forest carbon stock, with the remainder shared roughly evenly between SE Asia (26%) and the Congo Basin (25%) [11]. Over time, 28%–66% of the gross



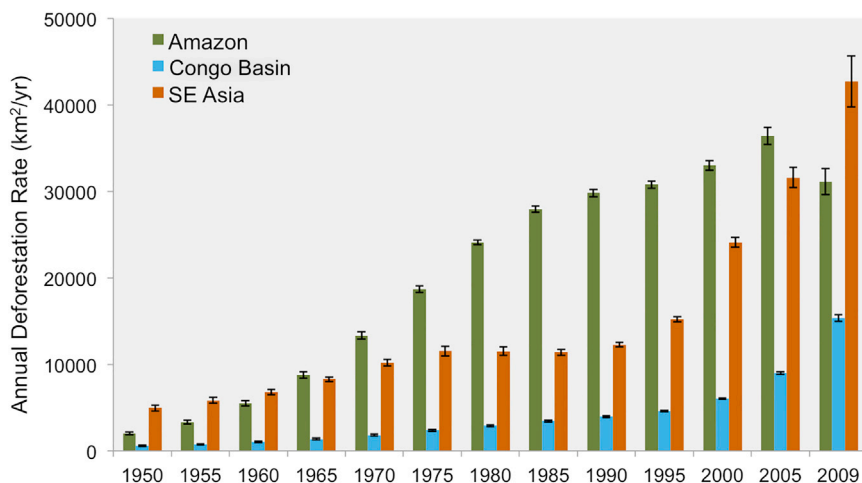


Figure 1. Modeled Annual Deforestation Rates from 1950 to 2009 in Five-Year Intervals

Rates are shown in km²/year. Error bars represent 95% confidence interval estimate from 100 model replicates. See also [Figure S1](#) and [Table S1](#).

emissions came from the Amazon, an estimated 25%–62% from SE Asia, and a much lower share of 9%–14% from the Congo Basin ([Supplemental Experimental Procedures and Figure S2](#)). In each of the three tropical regions, committed gross emissions by 2009 accounted for 60% of the carbon emissions in that year.

Species Losses

We estimated that modern gross deforestation has led to an extinction debt of 144 forest-specific vertebrate species (± 14 , 95% CI) ([Figure 2B](#)), which is a number 20% larger than the total number of extinctions known to have occurred in vertebrate groups since 1900 ($n = 124$ [12]). While SE Asia was responsible for the majority of this debt until the 1980s (50%–70%; [Figure S3](#)), from the 1990s onward this legacy has been dominated by land cover changes that have occurred in the Amazon (>50%). The Congo Basin still represents a low share (~5%) due to the slower rates of deforestation in this region.

Of the 4,125 forest-specific tropical vertebrate species (mammals, birds, and amphibians), 52% were found in the Amazon, 38% in SE Asia, and 10% in the Congo Basin ([Supplemental Experimental Procedures](#)). We estimated that a total of 41 vertebrate species (± 4 , 95% CI) have already been driven irreversibly extinct, with the Amazon being the region with the highest number of species lost by 2009: 28 (± 2 , 95% CI), compared to 15 (± 3 , 95% CI) in SE Asia and only 1 (± 0 , 95% CI) in the Congo Basin. Our model predicted that 1.1% of tropical vertebrate forest-specific species would have gone extinct by 2010, similar to the 1.2% of forest-specific species that are classified as Extinct by the IUCN, indicating our model is accurately recreating the pan-tropical patterns of extinction threat to forest-specific vertebrate species.

Spatial Distribution of Environmental Legacy

We found that within each tropical region, environmental legacies of past deforestation are not evenly distributed across space ([Figure 3](#)). In the Amazon, environmental legacies are broadly concentrated in the heavily deforested regions of the “Arc of Deforestation” along the southeastern rim of the Amazon, whereas in the Congo Basin these are mainly concentrated in the south and eastern parts of the basin, where agricul-

tural activity has been most intense. In SE Asia, there are large differences in the size of both environmental legacies among different island groups. For example, intensive deforestation in mainland Indochina and in the Philippines mostly occurred earlier than elsewhere, meaning that more of the debt has already been paid compared to other areas, such as the islands of Sumatra and Borneo, where much of the deforestation has occurred more recently.

Furthermore, we found that carbon and extinction debts are poorly correlated in all regions ([Figure 4](#)), despite both being created by the same historical patterns of deforestation. This occurs because the time delays in carbon emissions are shorter than those involved in species extinction, meaning that patterns of extinction debt reflect deforestation from earlier periods than the patterns of carbon emissions debt. This same variation in time delays ensures that the proportional magnitude of the deforestation legacy is higher for biodiversity than it is for carbon ([Figure 2](#)).

DISCUSSION

Carbon dioxide emissions from tropical deforestation are already impacting the Earth’s atmosphere and climate and account for 10%–20% of annual anthropogenic emissions [10]. Furthermore, widespread habitat loss has already caused significant species losses globally [13], with important impacts on ecosystems [14]. Here we have shown that the carbon debt is equivalent to almost one-fifth of all historical gross emissions from tropical deforestation over the 60-year period we modeled, and to the emissions of 5–10 years of global deforestation. The extinction debt of vertebrate species, on the other hand, if paid, will increase the number of known extinctions in these groups since 1900 [12] by 120%. In both cases these are substantial, and previously unquantified, debts that must be paid unless specific actions, including habitat restoration and targeted interventions for threatened species, are put in practice. To generate these estimates, we have utilized a model that has been validated on the basis of accurately simulating the time course of deforestation over time in tropical regions. Uncertainty was propagated throughout our study ([Supplemental Experimental Procedures](#)): in the relationship between deforestation and its drivers (allowing parameter values to vary), when estimating carbon emissions (both in the biomass maps and in the carbon bookkeeping parameters), and in the extinction debt estimates (allowing both z and k values to vary). As a result of rigorously validating our model against multiple different datasets and accounting for multiple different sources of uncertainty, we

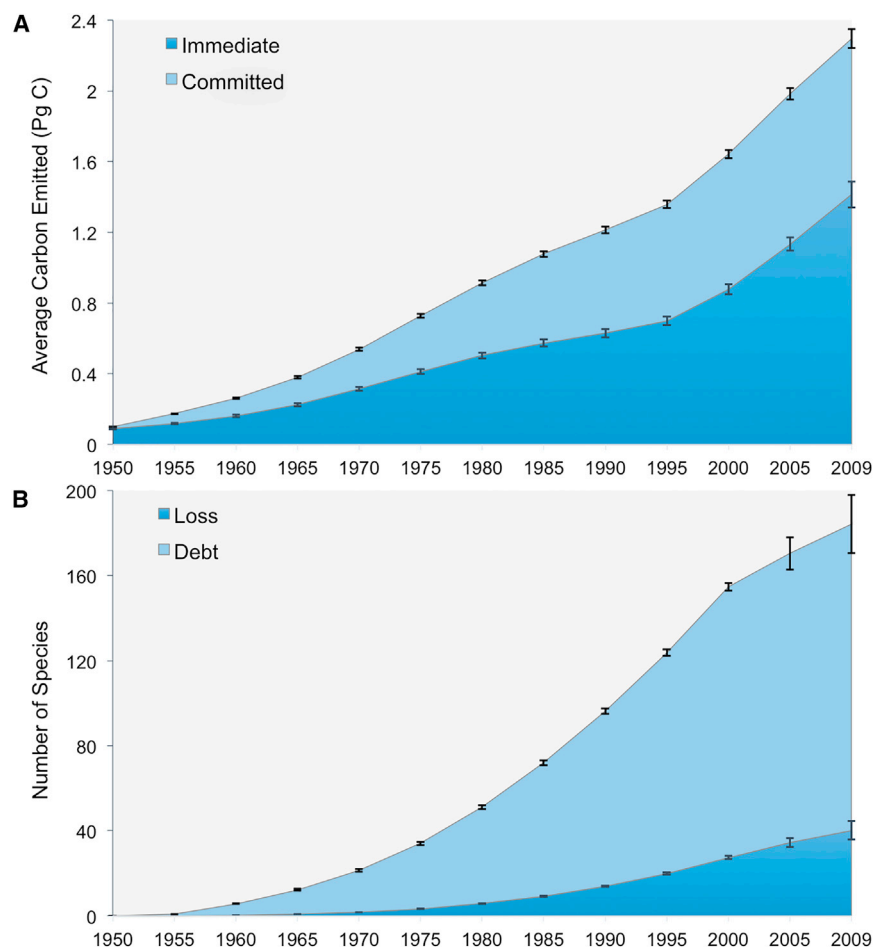


Figure 2. Vegetation Carbon Emissions and Species Losses from the Deforestation of Tropical Forests from 1950 to 2009

(A) Vegetation carbon emissions, separated into those that occurred from deforestation that took place in that year (immediate) versus those that occurred as a result of time lags in the release of carbon from deforestation in previous years (committed).

(B) Species losses, separated into those that have already occurred (loss) and those that will occur as a result of time delays in the extinction of species (debt).

Error bars represent 95% confidence intervals from 100 model replicates. Figures for the Amazon, the Congo Basin, and SE Asia are presented in [Figures S2](#) and [S3](#).

emissions of 43% by 2030. Reducing deforestation is the most immediate method available to meet these stringent targets, which is partially why, at the 2009 Conference of the Parties in Copenhagen, Brazil committed to reduce Amazon deforestation rates by 80% relative to the 1995–2005 baseline. However, our results demonstrate clearly that reductions in actual emissions will lag many years behind reductions in deforestation rate.

We necessarily assumed that the variables found to be driving deforestation in the 2000s also drove deforestation in previous decades (owing to the lack of data for previous decades), but this

believe we have produced the best current estimates of the environmental legacy of modern-day tropical deforestation.

Our results show that reaching national and global emissions targets may, in practice, be more difficult than expected. The carbon debt means that emissions in any one year are a function of deforestation over previous years. For instance, the carbon debt in the Amazon in 2010 is equivalent to the total carbon emissions from 3.5 years of deforestation at the average rate observed in the 2000s. Thus, changes in annual deforestation rates will initially have a smaller than expected effect on annual emission rates. This time lag means, for example, that the 30% reduction in deforestation rates seen in the Brazilian Amazon between 2005 and 2010 has so far resulted in a reduction of just 10% of actual carbon emissions over the same time period.

At the Cancun Conference of the Parties of the United Nations Framework Convention on Climate Change in 2010, several tropical countries, where emissions from land use and land cover change often exceed those from the energy sector [15], voluntarily committed to reduce their carbon emissions: Brazil aims to reduce its total greenhouse gases emissions by 36%–39% from its “business as usual” levels by 2020, and Indonesia aims to reduce its emissions by at least 41% between 2009 and 2020. Recently, at the United Nations Sustainable Development Summit 2015 in New York, Brazilian President Dilma Rousseff committed to a further “intended reduction” of Brazil’s

does not seem to have caused substantial bias in our results. This appears to be because deforestation resulting from different causes (e.g., conversion to agricultural land or fires following timber extraction) tends to generate similar spatial patterns of forest loss (e.g., occurring primarily along road networks). This consistency in the deforestation patterns arising from different root causes, and our explicit approach of modeling the spatial expansion of deforestation directly, means that our simulations about the spatial and temporal patterns of deforestation history are relatively robust to uncertainty about the underlying processes. Deforestation activities evolved over time from small-scale slash-and-burn agriculture to large-scale industrial agriculture, which impacted the fractions of carbon immediately lost versus left to decay over time. However, there are no spatial high-resolution datasets available with the full history of land use change in the tropics to take this into account.

Our gross vegetation carbon emissions estimates are larger than those reported in other studies for all three tropical regions ([Supplemental Experimental Procedures](#)). In part, this can be explained by the fact that we used a potential vegetation carbon map, which included belowground carbon stored in roots, not just aboveground stems and leaves. This map ignores the fact that some of the forests covered in our study could have an initial carbon stock lower than the potential carbon, for example as a result of harvesting or fire events. However, an important reason

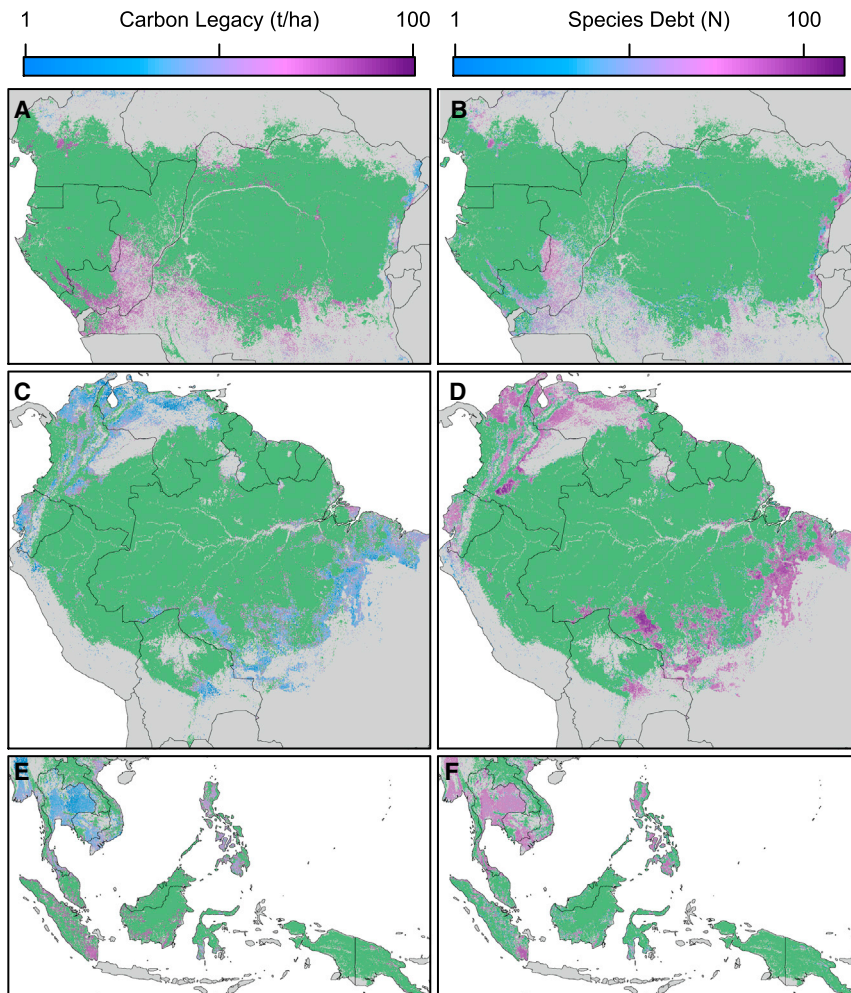


Figure 3. Magnitude of Carbon Emissions and Extinction Debts in the World's Tropical Forests in 2009

(A) and (B) show results for the Congo Basin, (C) and (D) for the Amazon, and (E) and (F) for SE Asia. See also Table S2.

(A, C, and E) Carbon emissions. Maps display the (log-normal transformed) median carbon tons per hectare left to decay after 2009.

(B, D, and F) Extinction debts. Maps show the (log-normal transformed) median number of forest-specific species committed to extinction as of 2009 due to past tropical deforestation.

tion status by 2020. Our results suggest, however, that tropical nations with large extinction debts will be unlikely to succeed in preventing the further loss of species without substantial investment in habitat restoration, as well as targeted conservation interventions for threatened species. Our estimates for species losses and extinction debt in the Amazon are slightly higher than those previously estimated [6], but this is because our analysis encompasses the whole Amazon Basin, not just the Brazilian Amazon. We are not aware of any other previous studies that have estimated extinction debt across all tropical forests with which to compare our results. The total extinction debt, across all taxonomic groups present in these highly biodiverse tropical regions, is likely to be orders of magnitude larger than our estimate, which is based

for the differences between our estimates and other recent regional estimates is that we included the additional time-delayed emissions of carbon, which in recent decades represent a substantial proportion of annual emissions. Initially, in the early years of deforestation (i.e., 1950–1970), our estimates are similar to those in the literature (Supplemental Experimental Procedures). However, as the size of the carbon debt gradually increases through time, an increasing amount of emissions in a given year are contributed by “legacy emissions” (Figure 2). Importantly, our estimates for 2009–2010 (0.51 ± 0.04 PgC/year) are comparable to independent measurements made in the Amazon (0.48 ± 0.18 PgC/year, for 2009–2011) by sampling greenhouse gases in the lower troposphere [16], indicating that our model provides an accurate representation of deforestation-related carbon emissions.

The most commonly employed action to prevent species extinctions is to protect habitat [17], but that approach alone will do little to avoid paying an extinction debt that has already accumulated from historical habitat loss. Under Aichi Target 12 [18] of the Convention on Biodiversity, 78 countries, 9 of which lie within the geographic bounds of this study, have made voluntary agreements at the national level to prevent the extinction of known threatened species and improve their conserva-

tion status by 2020. Our results suggest, however, that tropical nations with large extinction debts will be unlikely to succeed in preventing the further loss of species without substantial investment in habitat restoration, as well as targeted conservation interventions for threatened species. Our estimates for species losses and extinction debt in the Amazon are slightly higher than those previously estimated [6], but this is because our analysis encompasses the whole Amazon Basin, not just the Brazilian Amazon. We are not aware of any other previous studies that have estimated extinction debt across all tropical forests with which to compare our results. The total extinction debt, across all taxonomic groups present in these highly biodiverse tropical regions, is likely to be orders of magnitude larger than our estimate, which is based

solely on three well-studied vertebrate groups. Nonetheless, species movements, adaptation, and mitigation strategies, which we did not consider in our study, would contribute to lower this debt. Previous analyses have demonstrated a poor correlation between stocks of carbon and biodiversity, leading to calls for developing combined carbon-biodiversity conservation strategies, which better resolve trade-offs between the two conservation aims [19, 20]. We have confirmed not only that is true, but also that carbon and extinction debts are poorly correlated in space. However, time delays in carbon emissions and extinctions create a potential window for habitat restoration and conservation actions to alleviate or even avoid having to pay the committed debts [6]. Just as strategies to simultaneously preserve stocks of carbon and biodiversity can be optimized through careful planning [19, 20], the ideal locations for habitat restoration actions to reverse the combined carbon-biodiversity debts will require detailed spatial planning to find cost-effective solutions. Frameworks for making these decisions, including the incorporation of time lags, exist and have demonstrated the counterintuitive result that it can be more cost-effective for conservation strategies to forego a sole focus on habitat protection in favor of restoring degraded areas [21]. These

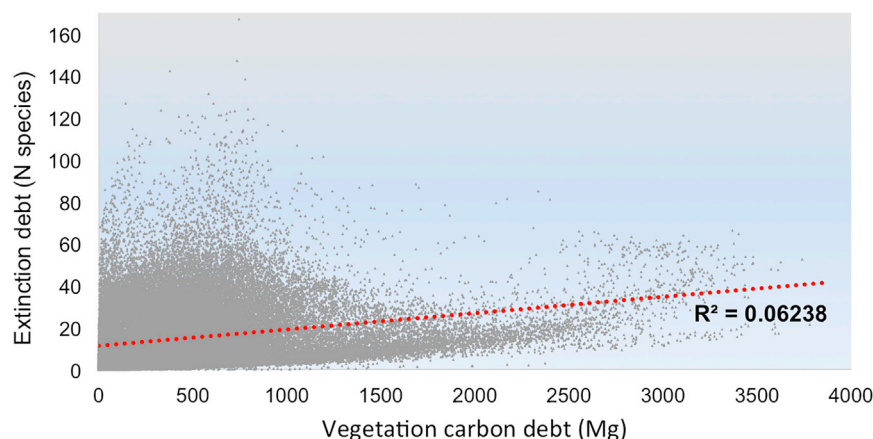


Figure 4. Linear Regression between Carbon and Extinction Debts in the World's Tropical Forests in 2009

Each gray dot represents a 100 km² pixel. The carbon debt was aggregated from its initial 1 km² resolution to match the resolution of the extinction debt. Figures for the Amazon, the Congo Basin, and SE Asia are presented in Figure S4.

decision-making frameworks now need to be applied if we are to avoid paying the full cost of the environmental legacy of tropical deforestation.

EXPERIMENTAL PROCEDURES

We collected data from a variety of freely available sources, including annual global land cover maps from 2001 through 2010 derived from MODIS satellite imagery [22], and variables that could impact deforestation. These included the location of roads, protected areas, and rivers; population density; altitude; and climate. We then used a data-constrained and validated spatial model of tropical deforestation [4] to backcast at 1 km² resolution both the rates and spatial patterns of deforestation from 2009 to 1950 in the three main tropical regions: the Amazon, the Congo Basin, and SE Asia (Supplemental Experimental Procedures).

For each region modeled, we combined our deforestation estimates with spatially explicit maps of potential living vegetation carbon [5] and a modified carbon bookkeeping model [2] to calculate the carbon emissions debt (Supplemental Experimental Procedures; Figures 2A, 3A–3C, and S2). We applied the exponential decay rates provided by Houghton et al. [2] at each annual time step and used bookkeeping to calculate the emissions released in a given year, as well as carried over into the subsequent year. Unlike previous studies, our bookkeeping model allowed for uncertainty in the parameter determining the proportion of emissions release immediately following a deforestation event.

We obtained geographic range data [23, 24] for forest-specific mammal, bird, and amphibian species (Table S2) and combined these with our spatially explicit trajectories of historical forest cover (Figure S1) to estimate species losses and extinction debt in each region (Supplemental Experimental Procedures; Figures 2B, 3D–3F, and S3), following Wearn et al. [6]. The model uses the species-area relationship (SAR) to predict the equilibrium species richness expected under habitat loss but extends the SAR to include a time-delayed community “relaxation” to equilibrium [6]. By explicitly incorporating time, this model allowed for estimation of species loss and extinction debt at any point between 1950 and 2009. Appropriate parameter values for the model were obtained using past studies [19], with uncertainty in these parameters accounted for using Monte Carlo simulations. We applied this model at two scales, regional and local. For the coarser regional-scale analysis, we aggregated all of our input data at the scale of eight broad regions (Amazon, Congo Basin, and the six sub-regions of SE Asia), treating each region as a single cell. We then used the temporal trajectories of forest cover simulated by our deforestation model to determine losses and extinction debt of forest-specific species in each unit. The fine-scale analysis was done within 10 × 10 km cells. We used cell-specific trajectories of past forest loss (Figure S1) to estimate the impact of modern deforestation on the levels of local species loss and extinction debt in each cell (Figures 3D–3F).

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures, two tables, Supplemental Experimental Procedures, and eight datasets and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.06.013>.

AUTHOR CONTRIBUTIONS

I.M.D.R. assisted with formulation of the research question, generated code, conducted all the analyses and interpretation of results, and wrote the manuscript. M.J.S. obtained the potential carbon maps, helped with outputs interpretation, and provided critical manuscript revisions. O.R.W. helped run the extinction debt model and interpret its results, and assisted with valuable reviews of the manuscript. D.P. helped develop the deforestation model and provided important feedback on the manuscript. R.M.E. assisted with formulation of the research question, assisted in results interpretation, and provided critical revision of the manuscript.

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REFERENCES

1. Ramankutty, N., Gibbs, H.K., Achard, F., Defries, R., Foley, J.A., and Houghton, R.A. (2007). Challenges to estimating carbon emissions from tropical deforestation. *Glob. Change Biol.* 13, 51–66.
2. Houghton, R.A., Skole, D.L., Nobre, C.A., Hackler, J.L., Lawrence, K.T., and Chomentowski, W.H. (2000). Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature* 403, 301–304.
3. Diamond, J.M. (1972). Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest pacific islands. *Proc. Natl. Acad. Sci. USA* 69, 3199–3203.
4. Rosa, I.M.D., Purves, D., Souza, C., Jr., and Ewers, R.M. (2013). Predictive modelling of contagious deforestation in the Brazilian Amazon. *PLoS ONE* 8, e77231.

5. Smith, M.J., Vanderwel, M.C., Lyutsarev, V., Emmott, S., and Purves, D. (2013). The climate dependence of the terrestrial carbon cycle; including parameter and structural uncertainties. *Biogeosciences* 10, 583–606.
6. Wearn, O.R., Reuman, D.C., and Ewers, R.M. (2012). Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science* 337, 228–232.
7. Rudel, T.K. (2007). Changing agents of deforestation: From state-initiated to enterprise driven processes, 1970–2000. *Land Use Policy* 24, 35–41.
8. Zhao, S., Peng, C., Jiang, H., Tian, D., Lei, X., and Zhou, X. (2006). Land use change in Asia and the ecological consequences. *Ecol. Res.* 21, 890–896.
9. Nepstad, D., Soares-Filho, B.S., Merry, F., Lima, A., Moutinho, P., Carter, J., Bowman, M., Cattaneo, A., Rodrigues, H., Schwartzman, S., et al. (2009). Environment. The end of deforestation in the Brazilian Amazon. *Science* 326, 1350–1351.
10. Van der Werf, G.R., Morton, D.C., DeFries, R.S., Olivier, J.G., Kasibhatla, P.S., Jackson, R.B., Collatz, G.J., and Randerson, J.T. (2009). CO₂ emissions from forest loss. *Nat. Geosci.* 2, 737–738.
11. Saatchi, S.S., Harris, N.L., Brown, S., Lefsky, M., Mitchard, E.T., Salas, W., Zutta, B.R., Buermann, W., Lewis, S.L., Hagen, S., et al. (2011). Benchmark map of forest carbon stocks in tropical regions across three continents. *Proc. Natl. Acad. Sci. USA* 108, 9899–9904.
12. Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., and Palmer, T.M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci. Adv.* 1, e1400253.
13. Pereira, H.M., Navarro, L.M., and Martins, I.S. (2012). Global biodiversity change: the bad, the good, and the unknown. *Annu. Rev. Environ. Resour.* 37, 25–50.
14. Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., and O'Connor, M.I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105–108.
15. Van Minnen, J.G., Goldewijk, K.K., Stehfest, E., Eickhout, B., van Drecht, G., and Leemans, R. (2009). The importance of three centuries of land-use change for the global and regional terrestrial carbon cycle. *Clim. Change* 97, 123–144.
16. Gatti, L.V., Gloor, M., Miller, J.B., Doughty, C.E., Malhi, Y., Domingues, L.G., Basso, L.S., Martinewski, A., Correia, C.S.C., Borges, V.F., et al. (2014). Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature* 506, 76–80.
17. Becker, C.G., and Loyola, R.D. (2008). Extinction risk assessments at the population and species level: implications for amphibian conservation. *Biodivers. Conserv.* 17, 2297–2304.
18. Convention on Biological Diversity (2010). COP 10 Decision X/2: Strategic Plan for Biodiversity 2011–2020. <https://www.cbd.int/decision/cop/?id=12268>.
19. Venter, O., Laurance, W.F., Iwamura, T., Wilson, K.A., Fuller, R.A., and Possingham, H.P. (2009). Harnessing carbon payments to protect biodiversity. *Science* 326, 1368.
20. Thomas, C.D., Anderson, B.J., Moilanen, A., Eigenbrod, F., Heinemeyer, A., Quaife, T., Roy, D.B., Gillings, S., Armsworth, P.R., and Gaston, K.J. (2013). Reconciling biodiversity and carbon conservation. *Ecol. Lett.* 16 (Suppl 1), 39–47.
21. Possingham, H.P., Bode, M., and Klein, C.J. (2015). Optimal conservation outcomes require both restoration and protection. *PLoS Biol.* 13, e1002052.
22. Friedl, M.A., McIver, D.K., Hodges, J.C.F., Zhang, X.Y., Muchoney, D., Strahler, A.H., Woodcock, C.E., Gopal, S., Schneider, A., Cooper, A., et al. (2002). Global land cover mapping from MODIS: algorithms and early results. *Remote Sens. Environ.* 83, 287–302.
23. International Union for Conservation of Nature (2014). The IUCN Red List of Threatened Species, Version 2014.1. <http://www.iucnredlist.org>.
24. Ridgely, R.S., Allnutt, T.F., Brooks, T., McNicol, D.K., Mehlman, D.W., Young, B.E., and Zook, J.R. (2007). Digital Distribution Maps of the Birds of the Western Hemisphere, Version 3.0 <http://www.natureserve.org/conservation-tools/digital-distribution-maps-birds-western-hemisphere>.