Article

How deregulation, drought and increasing fire impact Amazonian biodiversity

https://doi.org/10.1038/s41586-021-03876-7

Received: 22 November 2019

Accepted: 4 August 2021

Published online: 01 September 2021

Check for updates

Xiao Feng[1,23]✉, Cory Merow[2,23], Zhihua Liu[3,23], Daniel S. Park[4,5,23], Patrick R. Roehrdanz[6,23], Brian Maitner[2,23], Erica A. Newman[7,8,23], Brad L. Boyle[7,9], Aaron Lien[8,10], Joseph R. Burger[7,8,11], Mathias M. Pires[12], Paulo M. Brando[13,14,15], Mark B. Bush[16], Crystal N. H. McMichael[17], Danilo M. Neves[18], Efthymios I. Nikolopoulos[19], Scott R. Saleska[7], Lee Hannah[6], David D. Breshears[10], Tom P. Evans[20], José R. Soto[10], Kacey C. Ernst[21] & Brian J. Enquist[7,22,23]

Biodiversity contributes to the ecological and climatic stability of the Amazon Basin[1,2], but is increasingly threatened by deforestation and fire[3,4]. Here we quantify these impacts over the past two decades using remote-sensing estimates of fire and deforestation and comprehensive range estimates of 11,514 plant species and 3,079 vertebrate species in the Amazon. Deforestation has led to large amounts of habitat loss, and fires further exacerbate this already substantial impact on Amazonian biodiversity. Since 2001, 103,079–189,755 km^2 of Amazon rainforest has been impacted by fires, potentially impacting the ranges of 77.3–85.2% of species that are listed as threatened in this region[5]. The impacts of fire on the ranges of species in Amazonia could be as high as 64%, and greater impacts are typically associated with species that have restricted ranges. We find close associations between forest policy, fire-impacted forest area and their potential impacts on biodiversity. In Brazil, forest policies that were initiated in the mid-2000s corresponded to reduced rates of burning. However, relaxed enforcement of these policies in 2019 has seemingly begun to reverse this trend: approximately 4,253–10,343 km^2 of forest has been impacted by fire, leading to some of the most severe potential impacts on biodiversity since 2009. These results highlight the critical role of policy enforcement in the preservation of biodiversity in the Amazon.

The Amazon Basin[6] supports around 40% of the world's remaining tropical forests[7] and has a vital role in regulating the Earth's climate[8]. Amazonia contains 10% of all known species[6] and it has been estimated that 1,000 tree species can be found in a single square kilometre of the forest[9]. Such high biodiversity also enhances ecosystem resilience through functional diversity[10] and influencing rates of secondary forest recovery[11], and has probably enabled Amazonia to remain relatively stable and to buffer ecosystem functioning in the face of climate change[1,2]. However, continued degradation and loss of forest cover and biodiversity therein could undermine ecosystem resilience and hasten an irreversible tipping point[12]. Indeed, a loss of 20–25% of Amazonian forests could precipitate a rapid transition to savannah-like formations[13,14].

Since the 1960s, approximately 20% of Amazonian forest cover has been lost as a result of deforestation and fires[15]. Forest loss is predicted to reach 21–40% by 2050, and such habitat loss will have large impacts on Amazonian biodiversity[16,17]. In conjunction with ongoing habitat loss due to deforestation, increasing fires in the Amazon potentially pose another great threat to biodiversity[4]: because Amazonian species have largely evolved in the absence of fire, they generally lack adaptations to fire-related damage (ref. [18] and references therein). Fires associated with deforestation generally lead to a total loss of forest habitat[3], and the burning of felled vegetation impairs regeneration and facilitates the invasion of exotic grasses[19]. Forest fires also have largely negative impacts on the habitats and long-term fitness of species due to habitat degradation[20–22]. Repeated burning can result in considerable species loss and turnover[23,24]. Burning can also initiate a series of positive feedbacks, including increases in dry fuel loads and midday temperatures, desiccation of biomass and flammability of native forests at the edges of clearings[25].

Fires in the Amazon are collectively influenced by climate, deforestation, forest fragmentation, selective logging and forest policies[26–28].

[1]Department of Geography, Florida State University, Tallahassee, FL, USA. [2]Eversource Energy Center and Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA. [3]CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China. [4]Department of Biological Sciences, Purdue University, West Lafayette, IN, USA. [5]Purdue Center for Plant Biology, Purdue University, West Lafayette, IN, USA. [6]The Moore Center for Science, Conservation International, Arlington, VA, USA. [7]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA. [8]Arizona Institutes for Resilience, University of Arizona, Tucson, AZ, USA. [9]Hardner & Gullison Associates, Amherst, NH, USA. [10]School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA. [11]Department of Biology, University of Kentucky, Lexington, KY, USA. [12]Departamento de Biologia Animal, Universidade Estadual de Campinas, Campinas, Brazil. [13]Department of Earth System Science, University of California, Irvine, Irvine, CA, USA. [14]Woodwell Climate Research Center, Falmouth, MA, USA. [15]Instituto de Pesquisa Ambiental da Amazônia (IPAM), Brasilia, Brazil. [16]Insitute for Global Ecology, Florida Institute of Technology, Melbourne, FL, USA. [17]Department of Ecosystem and Landscape Dynamics, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands. [18]Institute of Biological Sciences, Federal University of Minas Gerais, Belo Horizonte, Brazil. [19]Department of Mechanical and Civil Engineering, Florida Institute of Technology, Melbourne, FL, USA. [20]School of Geography, Development and Environment, University of Arizona, Tucson, AZ, USA. [21]Department of Epidemiology and Biostatistics, College of Public Health, University of Arizona, Tucson, AZ, USA. [22]The Santa Fe Institute, Santa Fe, NM, USA. [23]These authors contributed equally: Xiao Feng, Cory Merow, Zhihua Liu, Daniel S. Park, Patrick R. Roehrdanz, Brian Maitner, Erica A. Newman, Brian J. Enquist. ✉e-mail: fengxiao.sci@gmail.com

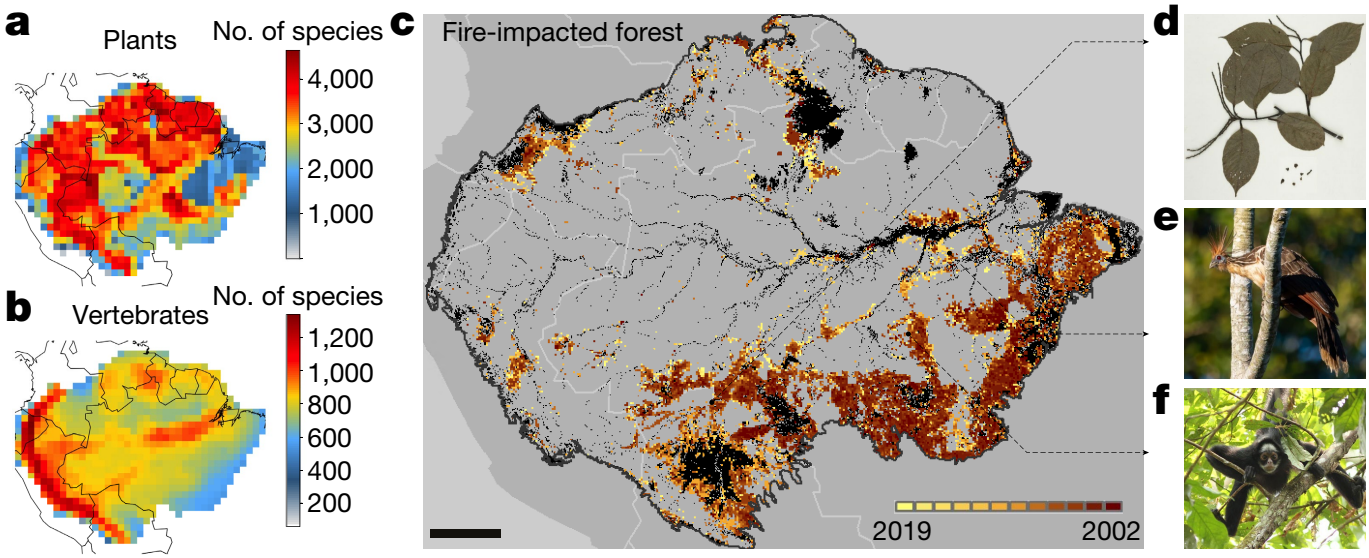


Fig. 1 | Overview of plant and vertebrate species richness and fire-impacted forest in the Amazon Basin. a, **b**, Richness map of plant (**a**) and vertebrate (**b**) species in the Amazon Basin. **c**, MODIS burned area (resampled to 10 km) shows fire-impacted forest, with black representing non-forested areas masked out from this study. Scale bar, 500 km. **d**–**f**, Examples of three species, *Allantoma kuhlmannii* (**d**) (IUCN status: critically endangered), *Opisthocomus hoazin* (hoatzin) (**e**) (IUCN status: least concern) and *Ateles marginatus* (white-cheeked spider monkey) (**f**) (IUCN status: endangered), which are estimated to have 36.7–37.7%, 1.8–2.6% and 4.1–5.9% of their Amazonian forest range impacted, respectively. Photograph credits: **d**, adapted from The New York Botanical Garden Herbarium under a CC BY 4.0 licence (https://creativecommons.org/licenses/by/4.0/); **e**, Mathias M. Pires; **f**, adapted from Rich Hoyer under a CC BY 2.0 licence (https://creativecommons.org/licenses/by/2.0/).

Recent drought events in 2005, 2010 and 2015 have been associated with increases in the detection of active fires[29]. Deforestation provides a major source of ignition and increases the flammability of remaining forests by increasing edge density, raising regional temperatures and reducing rainfall[3]. Logging operations can also increase forest flammability by reducing the coverage of the forest leaf canopy and by altering microclimates[3,28]. Socioeconomic factors, governmental policy and initiatives by non-governmental organizations are increasingly recognized as major factors that influence deforestation rates, and therefore deforestation fires and forest fires in the Amazon[3,30]. Beginning in the mid-2000s and especially after 2008, a series of policies implemented by the Brazilian government and international organizations resulted in a substantial reduction in deforestation rates until 2018. The widely reported increase in satellite-detected fires in 2019 has been attributed to the relaxed enforcement of existing policies aimed at slowing deforestation[31]. As a large portion of the Amazon is located in Brazil, changes in deforestation rates and policies in the nation have disproportionate impacts on the Amazon rainforest.

Although fires in the Amazon have been broadly studied[3], there remains a gap in knowledge regarding how the increase in fires has impacted Amazonian biodiversity. In addition to habitat loss resulting from deforestation, we investigated the cumulative impact of fires on the geographic ranges of species, which are correlated with spatial requirements to maintain populations and biodiversity[32]; similar approaches have been used in other large-scale studies of biodiversity (for example, refs. [17,33,34]). We compiled satellite-detected fires across forested areas in the Amazon (termed 'fire-impacted forest' hereafter) and, to our knowledge, the most comprehensive collection of range maps of Amazonian plant and vertebrate species to date (Fig. 1, Extended Data Fig. 1; Methods). The satellite-detected fires include deforestation fires and fires that spread into standing forests (forest fires)[3]. The impacts of both types of fire on biodiversity are largely negative, due either to direct loss of habitat or to mortality of organisms, as well as damage to or deficits in fitness of organisms in the areas in which the fires occur (refs. [18,20–22] and references therein). We estimated the extent of species' ranges in the Amazonian forest that have been exposed to and impacted by fires (hereafter termed 'range impact') over the past two decades, and assessed how drought conditions and policy changes in Brazil affected the temporal trend of fire-impacted forest in the Amazon.

The impact of fires on biodiversity

We generated Amazonian biodiversity maps from range maps of 14,593 terrestrial plant and vertebrate species (Supplementary Discussion). Range maps of 11,514 plant species were estimated by different algorithms depending on the number of observation records per species (Methods). For species with at least 10 spatially unique records (n = 7,526) we used a Poisson point process model. For species with 3–9 spatially unique records (n = 2,590) we used a range-bagging algorithm. For species with 1–2 spatially unique records (n = 1,398), we included the grid cells in which records were found (at 10-km resolution). Expert range maps of 3,079 vertebrates were refined to reflect the extent of suitable habitat by limiting the ranges of species to known elevational ranges and habitat associations to produce more accurate estimations. These maps provide conservative estimates of the potential distributions of species based on techniques that aim to minimize the underlying uncertainties (Methods).

Using two remote-sensing products we estimate that, since 2001, a total of 103,079–189,755 km^2 (2.2–4.1%) of the Amazon forest was potentially impacted by fire, affecting the ranges of the majority of plant and vertebrate species therein (Figs. 1, 2, Extended Data Fig. 1). Up to 93.3–95.5% of Amazonian plant and vertebrate species (13,608–13,931) might have been impacted by fires, if only to a minor degree (Supplementary Discussion; Extended Data Figs. 2, 3). However, many of these species are known from a small number of records and probably have restricted ranges[35]. Indeed, the Amazon comprises numerous species (610) that are considered threatened by the International Union for Conservation of Nature (IUCN). Since 2001, a large fraction of these threatened species have now experienced impacts of fire within their ranges: 236–264 IUCN-listed plant species, 83–85 bird species, 53–55 mammal species, 5–9 reptile species and 95–107 amphibian species. These values represent

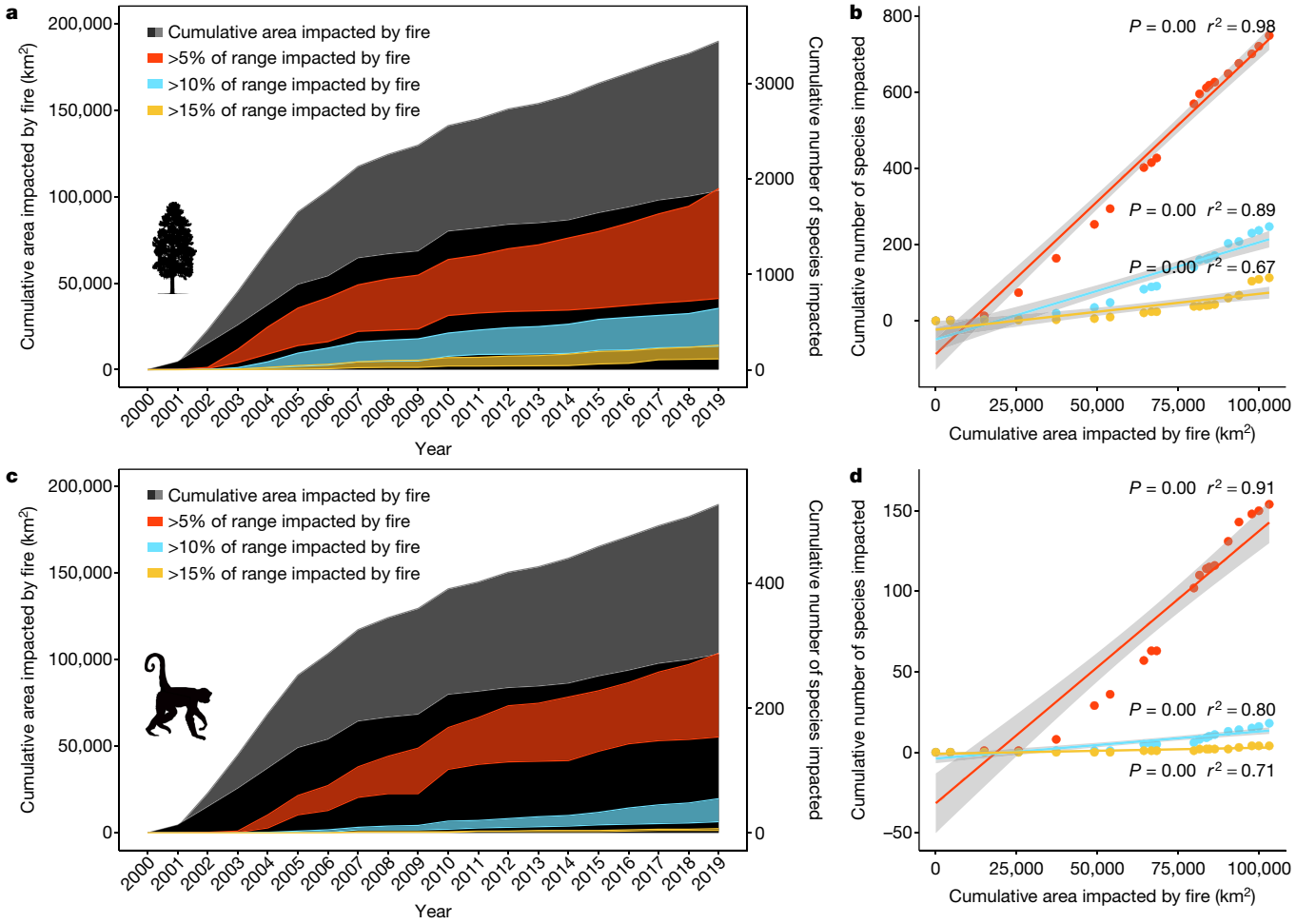


Fig. 2 | Cumulative effects of fire on biodiversity in the Amazon rainforest. **a**, **c**, The black and grey shading represent the cumulative area of forest impacted by fire based on MODIS burned area and MODIS active fire, respectively. Coloured areas represent the lower and upper bounds of cumulative numbers of plant (**a**) and vertebrate (**c**) species ranges impacted by fire since 2001. The silhouette of the tree is from http://phylopic.org/; the silhouette of the monkey is courtesy of Mathias M. Pires. **b**, **d**, The relationships between the cumulative area impacted by fire (based on MODIS burned area) and cumulative number of plant (**b**) and vertebrate (**d**) species. Coloured lines represent predicted values of an ordinary least squares linear regression and grey bands define the two-sided 95% confidence interval (two-sided, *P* values = 0.00).

a range that varies according to the remote-sensing products used to assess the impact of fire (Supplementary Discussion).

The most pronounced species-level impacts are often associated with species that have smaller ranges (Extended Data Fig. 2). For example, fires may have impacted around 60% of the restricted range of *Remijia kuhlmannii* (Rubiaceae) in the southern Brazilian Amazon. Fire-impacted forests over the past two decades have been mainly located in the 'arc of deforestation' that spans the southern edge of the Amazon Basin[36] (Fig. 1, Extended Data Fig. 1). The region that comprises this 'arc' has been recently recognized as containing the widest range of evolutionary lineages of South American trees[37]. This is especially concerning because phylogenetic diversity is positively associated with ecosystem function[38]. Habitat alteration in this region has been pervasive and rapid, and has impacted a considerable number of species (for example, there are 263–700 species for which greater than 10% of their ranges within the Amazon is impacted; Fig. 2, Supplementary Discussion). These numbers are probably underestimates for several reasons: first, knowledge of the spatial distribution of Amazonian biodiversity is limited by a lack of biological collections and observations[39]; second, vertebrate species represent only a small portion of the animal kingdom[40]; third, remote sensing tends to underestimate the number and the extent of forest fires (Methods); and fourth, historical (pre-2001) forest loss and degradation were not considered here. Furthermore, species can become functionally extirpated well before they lose the entirety of their range due to various factors (for example, demographic processes[41]).

Increasing impacts over time

Large areas of habitat loss through deforestation constitutes a major threat to biodiversity in the Amazon, and similar amounts of habitat are further degraded by fire (Fig. 2, Extended Data Figs. 2, 4, 5; see additional discussions in Supplementary Information). Over the past two decades, the area of Amazonian forests that has been impacted by fire has fluctuated, but the potential area of newly impacted forest per year has never decreased below between 889 and 3,127 km^2 (based on moderate resolution imaging spectroradiometer (MODIS) burned area and active fire, respectively) (Fig. 2, Extended Data Table 1). Notably, both the cumulative fire-impacted area and its impacts on species ranges have continued to increase at a steady rate (Fig. 2a, c, Extended Data Fig. 3). The area of fire-impacted forest is tightly correlated with the number of species impacted (Fig. 2). For every 10,000 km^2 of forest that experiences fire, an additional 27–37 plant species and 2–3 vertebrate species that have more than 10% of their ranges within the Amazon will be impacted (Fig. 2b, d).

Both drought and policy affect the area that experiences fire (Supplementary Discussion). The amount of newly fire-impacted forest

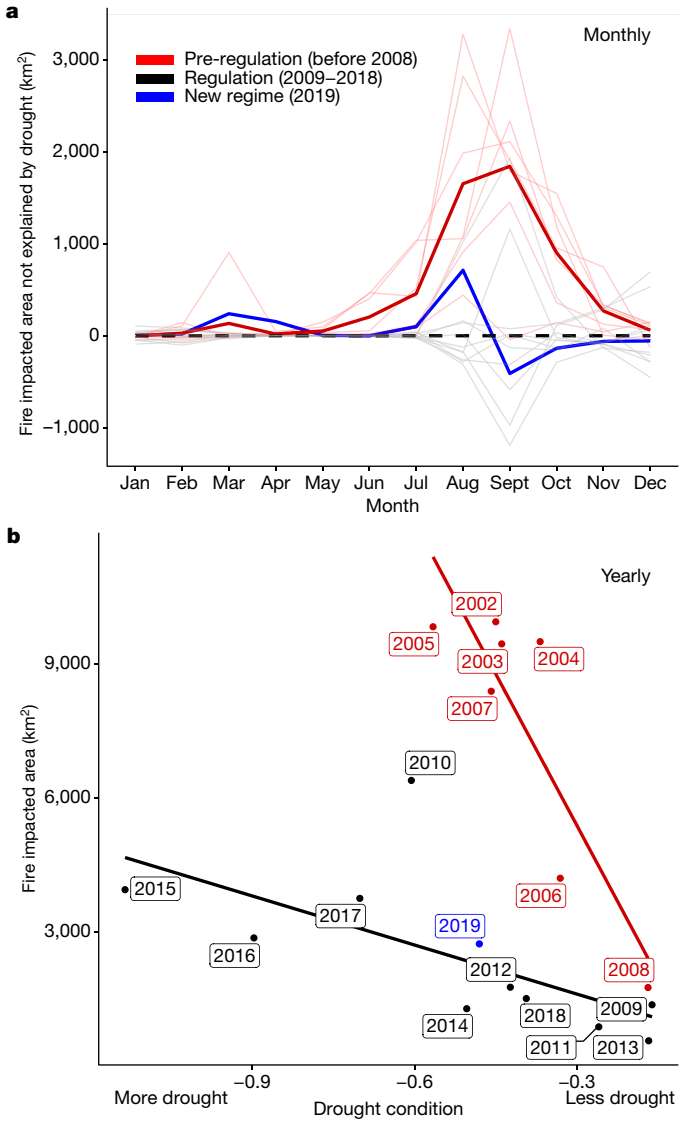


Fig. 3 | Newly fire-impacted forest in Brazil (based on MODIS burned area). **a**, Fire-impacted forest area that is not explained by drought conditions. The colours represent different policy regimes: pre-regulations in light red (mean value in dark red), regulation in grey (mean value in black dashed line) and 2019 in dark blue. The *y* axis represents the difference between actual area and area predicted by drought conditions calibrated by data from regulated years (Methods). A positive value on the *y* axis represents more area than expected, using the regulation years as a baseline. **b**, A scatter plot of newly fire-impacted forest in Brazil and drought conditions (Standardized Precipitation–Evapotranspiration Index (SPEI)); the lines represent the ordinary least squares linear regression between fire-impacted forest and drought conditions for the pre-regulation (red) and regulation (black) periods.

area in Brazil corresponds to three distinct policy regimes: first, the fire-impacted area was larger during the pre-regulation period before 2008[30,42], when forest policies were limited (early in this period) or when the enforcement of new policies had yet to take full effect (later in this period); second, the fire-impacted area was markedly reduced during the regulation period 2009–2018 (with the exception of drought years), when a series of policies aimed at reducing deforestation and forest burning were implemented[30,43]; and third, the fire-impacted area increased in 2019, which coincided with a relaxation of enforcement of those policies[44] by the Brazilian government during the first 8 months of the year. A period of renewed policy enforcement beginning in September 2019[45] (Fig. 3, Extended Data Fig. 6; Methods) saw monthly fire-impacted forest area decrease once more. While drought led to a greater area of fire-impacted forest, enforcement of forest policy lessened the drought effect to 9–16% of that in the pre-regulation period (Fig 3b, Extended Data Fig. 6, Extended Data Table 2). The majority of the newly fire-impacted forest was inside the borders of Brazil (mean = 79%, s.d. = 8–12%) (Extended Data Fig. 7). As a result, policy changes in Brazil have had a large impact on the entire region, and similar drought-related patterns were also observed for the entire Amazon (Extended Data Table 2).

The impact of the 2019 fires

The year 2019 stands out as one of the most extreme years for biodiversity impacts since 2009, when forest regulations were enforced. The area of fire-impacted forest in 2019 shows a shift between the first 8 months and the last 4 months of the year: it is higher than expectations for the former and lower for the latter given drought conditions, compared with the years under regulation (2009–2018) (Fig. 3, Extended Data Fig. 6). This change coincides with the policy shift in Brazil, in which regulations were relaxed during the first 8 months of 2019, after which extra efforts were devoted to control forest fires beginning in September[45]. We estimate a total fire-impacted forest area for 2019 of 4,253–10,343 km^2; this is 463–1,193 km^2 (20–28%) higher than expectations given the drought condition in 2019, reiterating the findings in ref. [3] (Fig. 4, Extended Data Fig. 8). In 2019 alone, we estimate that the ranges of 12,064–12,801 plant and vertebrate species experienced fire. Range impacts in 2019 were 19.6–28.0% higher for plants and 28.6–34.6% higher for vertebrates than expected (Fig. 4, Extended Data Fig. 8). These impacts are 1.42–2.58 times greater for plants and 1.39–2.53 times greater for vertebrates compared with 2014, when the drought conditions were slightly worse. When we exclude the effects of drought, the impact of fire on species' ranges in 2019 is greater than that during most of the regulation period (2009–2018), excluding 2010 (Fig. 4, Extended Data Fig. 8).

In addition to the increased extent of fires that is associated with the 2019 relaxation of forest-protection policies, the high estimated impacts on biodiversity could also be attributed to the locations of fires in 2019 (Fig. 1, Extended Data Fig. 1). Fires have increasingly impacted more interior regions of the Brazilian Amazon, whereas previously they had been mainly confined to the southeast. The spread of fires into the central Amazon is likely to increase the extent of impacts on biodiversity, as these regions are generally more species-rich and contain many species that are not present in southeastern Brazil.

The Amazon and global climate change

Climate change is likely to make drought increasingly common in the Amazon Basin[46]. Our results show that although drought is an important driver of total fire-impacted forest area in the Amazon, drought effects can be significantly mitigated by forest policies (Fig. 3, Extended Data Table 2, Extended Data Fig. 6). We expect that the indirect impacts of fires, exacerbated by the effects of climate change and drought[4], are likely to continue to increase over time through positive feedback. Additionally, deforestation—in combination with climate change—might contribute to increased frequency, intensity and extent of droughts, thereby accelerating reductions in forest cover[47]. It has been estimated that a loss of 20–25% of total forest cover in the Amazon Basin might be enough to trigger a state-change tipping point from tropical forest to savannah-like formations in eastern, southern and central Amazonia[13]. Such a change could have catastrophic impacts on regional biodiversity. Forest cover loss—if sufficiently extensive—can result in changes in local climate that, in turn, can affect the functions of climates and ecosystems across the globe through ecoclimate teleconnections[48].

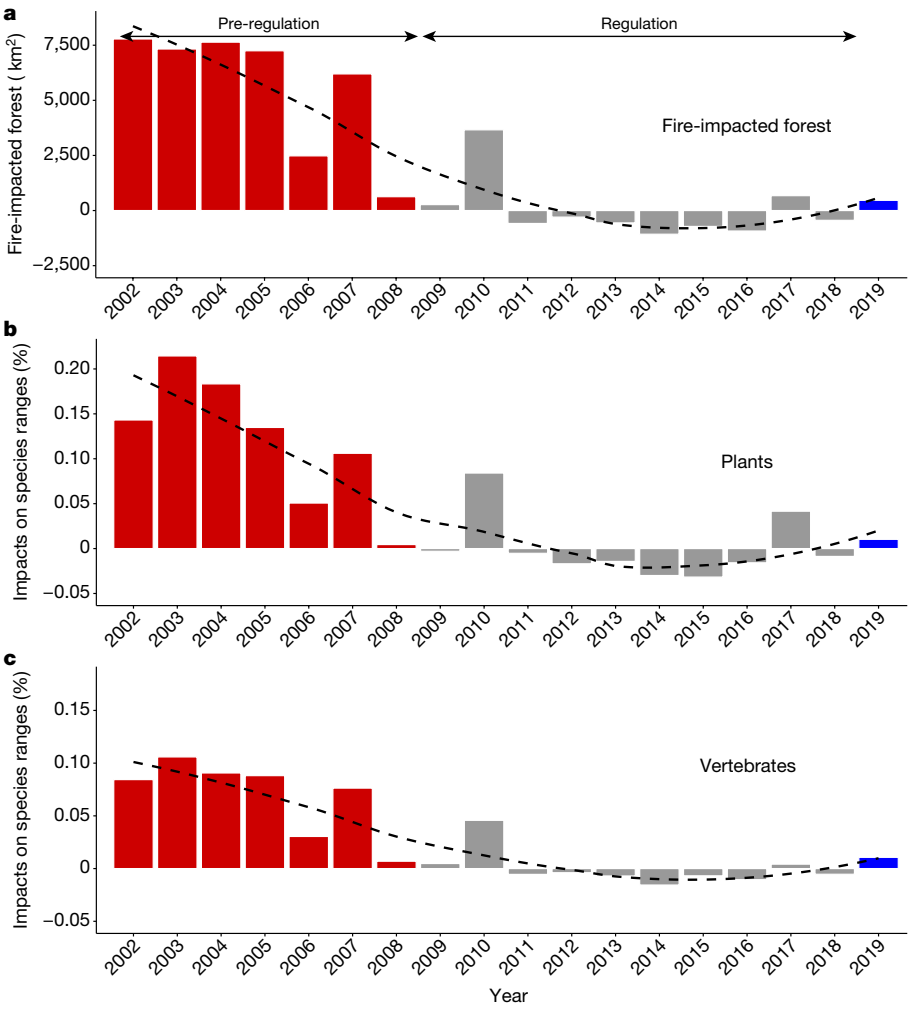


Fig. 4 | Newly fire-impacted forest area and the impacts on plant and vertebrate species in Brazil. a, Residuals of newly impacted forest area from 2002 to 2019. **b**, **c**, Impact of newly fire-impacted forest on plant (**b**) and vertebrate (**c**) species in Brazil. The colours represent three policy regimes: pre-regulation in red, regulation in grey and 2019 in blue. The *y* axis represents the difference between actual values and the values predicted by drought conditions calibrated by data from regulation years (Methods). Positive values on the *y* axes indicate larger-than-expected values compared to those from years under regulation. The dotted lines represent a smooth curve fitted to values based on the loess method.

Implications for future forest policy

Our study highlights a tight connection between policy and forest fires, and shows how these factors can combine to impact biodiversity. In 2019, the relaxation of deforestation policies in Brazil resulted in increased degradation of species ranges and habitats. However, after national and international backlash against the increase in fires between June and August 2019, the Brazilian government again changed course[49], deploying the army to fight fires and once again ramping up the enforcement of existing policy[45]. These findings show that effective policy and its implementation and enforcement are essential[50] to delay or prevent a tipping point[13] being reached in the Amazon that would have potentially catastrophic regional and global consequences.

Conclusions

Habitat loss as a result of deforestation has profound negative impacts on Amazonian biodiversity, and fires can exacerbate these already substantial impacts. There is a tight association between the cumulative amount of forest experiencing fire and the impacts on biodiversity. Over the past two decades, the ranges of the majority of Amazonian species are likely to have been impacted in some way by fires. Many of these impacted species are already considered by the IUCN to be threatened. Although the estimated impact of forest fires on biodiversity has fluctuated over time, the cumulative impact has continued to increase. As fires move closer to the heart of the Amazon Basin—which is characterized by greater levels of diversity (Fig. 1a, b)—the impact of fires on biodiversity will undoubtedly increase, even if the rate of forest burning remains unchanged. Although regulations have been effective in slowing the pace of burning and deforestation, relaxing those regulations—as shown in Brazil in 2019—can quickly erase gains made. Such policy reversals, in combination with more severe droughts, are likely to accelerate the impacts of fire on Amazonian species and destabilize the role of biodiversity in mitigating climate change in the future. Our estimation of the fire-induced impacts on biodiversity provides a scientific basis for future conservation and forest policy in the Amazon Basin.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-021-03876-7.

1. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl Acad. Sci. USA* **96**, 1463–1468 (1999).
2. Oliver, T. H. et al. Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* **30**, 673–684 (2015).
3. Barlow, J., Berenguer, E., Carmenta, R. & França, F. Clarifying Amazonia's burning crisis. *Glob. Change Biol.* **9**, 1 (2019).
4. Brando, P. M. et al. The gathering firestorm in southern Amazonia. *Sci. Adv.* **6**, eaay1632 (2020).
5. IUCN. *IUCN Red List of Threatened Species version 6.2*. https://www.iucnredlist.org/ (2019).
6. Flores, M. et al. *WWF's Living Amazon Initiative* (Grambs Corporación Gráfica, 2010).
7. Hubbell, S. P. et al. How many tree species are there in the Amazon and how many of them will go extinct? *Proc. Natl Acad. Sci. USA* **105 Suppl. 1**, 11498–11504 (2008).
8. Nepstad, D. C., Stickler, C. M., Filho, B. S.- & Merry, F. Interactions among Amazon land use, forests and climate: prospects for a near-term forest tipping point. *Philos. Trans. R. Soc. Lond. B* **363**, 1737–1746 (2008).
9. Rankin-de-Mérona, J. M. et al. Preliminary results of a large-scale tree inventory of upland rain forest in the Central Amazon. *Acta Amazon.* **22**, 493–534 (1992).
10. Sakschewski, B. et al. Resilience of Amazon forests emerges from plant trait diversity. *Nat. Clim. Change* **6**, 1032–1036 (2016).
11. Poorter, L. et al. Biomass resilience of Neotropical secondary forests. *Nature* **530**, 211–214 (2016).
12. Beisner, B. E., Haydon, D. T. & Cuddington, K. Alternative stable states in ecology. *Front. Ecol. Environ.* **1**, 376–382 (2003).
13. Lovejoy, T. E. & Nobre, C. Amazon tipping point. *Sci. Adv.* **4**, eaat2340 (2018).
14. Veldman, J. W. Clarifying the confusion: old-growth savannahs and tropical ecosystem degradation. *Philos. Trans. R. Soc. Lond. B* **371**, (2016).
15. Arruda, D., Candido, H. G. & Fonseca, R. Amazon fires threaten Brazil's agribusiness. *Science* **365**, 1387 (2019).
16. Ter Steege, H. et al. Estimating the global conservation status of more than 15,000 Amazonian tree species. *Sci. Adv.* **1**, e1500936 (2015).
17. Gomes, V. H. F., Vieira, I. C. G., Salomão, R. P. & ter Steege, H. Amazonian tree species threatened by deforestation and climate change. *Nat. Clim. Change* **9**, 547–553 (2019).
18. Brando, P. et al. Amazon wildfires: scenes from a foreseeable disaster. *Flora* **268**, 151609 (2020).
19. Balch, J. K. et al. The susceptibility of southeastern Amazon forests to fire: insights from a large-scale burn experiment. *Bioscience* **65**, 893–905 (2015).
20. Barlow, J. et al. The critical importance of considering fire in REDD+ programs. *Biol. Conserv.* **154**, 1–8 (2012).
21. Cochrane, M. A. & Schulze, M. D. Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition. *Biotropica* **31**, 2–16 (1999).
22. Brando, P. M. et al. Prolonged tropical forest degradation due to compounding disturbances: Implications for CO_2 and H_2O fluxes. *Glob. Change Biol.* **25**, 2855–2868 (2019).
23. Barlow, J. & Peres, C. A. Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philos. Trans. R. Soc. Lond. B* **363**, 1787–1794 (2008).
24. Cochrane, M. *Tropical Fire Ecology: Climate Change, Land Use and Ecosystem Dynamics* (Springer, 2010).
25. Uhl, C. & Kauffman, J. B. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* **71**, 437–449 (1990).
26. Cochrane, M. A. Fire science for rainforests. *Nature* **421**, 913–919 (2003).
27. Cochrane, M. A. & Laurance, W. F. Synergisms among fire, land use, and climate change in the Amazon. *Ambio* **37**, 522–527 (2008).
28. Nepstad, D. C. et al. Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* **398**, 505–508 (1999).
29. Aragão, L. E. O. C. et al. 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nat. Commun.* **9**, 536 (2018).
30. Nepstad, D. et al. Slowing Amazon deforestation through public policy and interventions in beef and soy supply chains. *Science* **344**, 1118–1123 (2014).
31. Hope, M. The Brazilian development agenda driving Amazon devastation. *Lancet Planet. Health* **3**, e409–e411 (2019).
32. Brown, J. H. On the relationship between abundance and distribution of species. *Am. Nat.* **124**, 255–279 (1984).
33. Barnagaud, J.-Y. et al. Ecological traits influence the phylogenetic structure of bird species co-occurrences worldwide. *Ecol. Lett.* **17**, 811–820 (2014).
34. Šímová, I. et al. Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. *J. Biogeogr.* **45**, 895–916 (2018).
35. Enquist, B. J. et al. The commonness of rarity: Global and future distribution of rarity across land plants. *Sci. Adv.* **5**, eaaz0414 (2019).
36. May, P. H., Gebara, M. F., de Barcellos, L. M., Rizek, M. B. & Millikan, B. *The Context of REDD+ in Brazil: Drivers, Agents, and Institutions,* 3rd edition, https://doi.org/10.17528/cifor/006338 (Center for International Forestry Research, 2016).
37. Neves, D. M., Dexter, K. G., Baker, T. R., Coelho de Souza, F. & Oliveira-Filho, A. T. Evolutionary diversity in tropical tree communities peaks at intermediate precipitation. *Sci. Rep.* **10**, 1188 (2020).
38. Cadotte, M. W., Cardinale, B. J. & Oakley, T. H. Evolutionary history and the effect of biodiversity on plant productivity. *Proc. Natl Acad. Sci. USA* **105**, 17012–17017 (2008).
39. Hopkins, M. J. G. Modelling the known and unknown plant biodiversity of the Amazon Basin. *J. Biogeogr.* **34**, 1400–1411 (2007).
40. Wilson, E. O. in *Biodiversity* (eds Wilson E. O. & Peter F. M.) Ch. 1 (National Academies Press, 1988).
41. Brooks, T. M. et al. Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* **16**, 909–923 (2002).
42. Gibbs, H. K. et al. Brazil's soy moratorium. *Science* **347**, 377–378 (2015).
43. Alix-Garcia, J. & Gibbs, H. K. Forest conservation effects of Brazil's zero deforestation cattle agreements undermined by leakage. *Glob. Environ. Change* **47**, 201–217 (2017).
44. Escobar, H. There's no doubt that Brazil's fires are linked to deforestation, scientists say. *Science* https://doi.org/10.1126/science.aaz2689 (2019).
45. Amazon fires: Brazil sends army to help tackle blazes. *BBC News* https://www.bbc.co.uk/news/world-latin-america-49452789 (24 August 2019).
46. Marengo, J. A., Tomasella, J., Soares, W. R., Alves, L. M. & Nobre, C. A. Extreme climatic events in the Amazon basin. *Theor. Appl. Climatol.* **107**, 73–85 (2012).
47. Malhi, Y. et al. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proc. Natl Acad. Sci. USA* **106**, 20610–20615 (2009).
48. Swann, A. L. S. et al. Continental-scale consequences of tree die-offs in North America: identifying where forest loss matters most. *Environ. Res. Lett.* **13**, 055014 (2018).
49. McCoy, T. Amazon fires dropped unexpectedly in September, after summer spike. *Washington Post* https://www.washingtonpost.com/world/the_americas/amazon-fires-dropped-unexpectedly-in-september-after-spiking-over-the-summer/2019/10/02/4ddc0026-e516-11e9-b403-f738899982d2_story.html (2 October 2019).
50. Moutinho, P., Guerra, R. & Azevedo-Ramos, C. Achieving zero deforestation in the Brazilian Amazon: what is missing? *Elementa* **4**, 000125 (2016).

Methods

Fire, remote sensing and land cover

We restricted the study area to the Amazon Basin, using a refined boundary of the Amazon[6] based on terrestrial ecoregions of the world[51], and only considered fires in areas that were forested between 2001–2019. To do this, we overlaid the MODIS-derived fire detections of a focal year with the forest land cover from the previous year. The MODIS products uniquely provide a wide temporal coverage of our study area (around 20 years) at the resolution[52] of 463 m. This enabled us to quantify fire-impacted forest and its consequences on the geographic ranges of species each year.

We used two remote sensing products, MODIS burned area (MCD64A1 v006) and MODIS active fire (MCD14ML v006), to quantify lower and upper bounds on the amount of fire-impacted forest. We obtained monthly burned area layers (MCD64A1 v006; https://lpdaac.usgs.gov/products/mcd64a1v006/) at 463 m (colloquially referred to as 500 m) spatial resolution from January 2002 to December 2019[53]. The MODIS burned area product detects the approximate date of burning by locating the occurrence of rapid changes in daily surface reflectance time series data. We also obtained the monthly active fire location product (MCD14ML) from the University of Maryland (https://modis-fire.umd.edu/). The MODIS active fire product detects land surface thermal anomalies at the time of satellite overpass under relatively cloud-free conditions using a contextual algorithm. We used vegetation fire with high detection confidence (≥80%) to avoid false or minor fire signals, and converted the fire locations into monthly 927-m (or 1-km) raster layers[54]. A fire-impacted cell derived from MODIS active fire indicates at least one fire occurred during the detecting window, and the fire is usually large or hot enough to be detectable by the MODIS sensor[54]. The MODIS burned area and MODIS active fire products could represent different degrees of fire impacts. The MODIS burned area algorithm tends to detect fewer fire events than comparable active fire products due to its more stringent detection criteria (hence our lower bound), whereas the MODIS active fire could represent a broader estimation of fire-impacted area in the Amazon (hence our upper bound). Fire estimation from MODIS active fire was restricted to be conservative using a high detection confidence (80%). We used both products to estimate the possible range of fire-impacted forest in the Amazon Basin. Although we did not directly distinguish between fire-impacted forest derived from the two products, we determined the different fates of the fire-impacted forest based on annual forest loss data (see below). We aggregated the monthly pixel-level fire-impacted forest into annual pixel-level fire-impacted forest (1 = burned, 0 = unburned). We determined the pixels that were newly impacted by fire in a focal year (that is, not impacted in any previous years since 2001), to reflect the frontier of the fires.

We used annual forest fractional cover data of years 2001–2018 to estimate fire-impacted forest. The annual forest fractional cover data were resampled from MODIS Vegetation Continuous Fields (MOD44B v006; https://lpdaac.usgs.gov/products/mod44bv006/) at 232-m (or 250-m) to 463-m resolution using the mean function. We further refined our study area to forest pixels within the Amazon basin that had at least 60% tree cover at any year between 2001–2018. This threshold of 60% was also used in defining forest land cover in MODIS Land Cover Type Product (MCD12Q1 v006; https://lpdaac.usgs.gov/products/mcd12q1v006). The refined study area excluded non-forested areas from the subsequent impact analyses—such as previously deforested area, farmland, shrubland or grassland—as our objective was to quantify the fire-impacted forest, where the trees lack the adaptations needed to resist fire-related damage[18,55,56].

With these layers, we overlapped the newly fire-impacted forest (resampled to 463 m) and annual forest fractional cover, and identified pixels that experienced fire in a focal year that were classified as forest pixels in the previous year. This procedure led to a series of layers of annual newly fire-impacted forest, based on which we quantified the cumulative area of fire-impacted forest across 2001–2019. Instead of summarizing the fire-impacted forest using binary values (for example, forest versus non-forest in land cover data), the tree cover percentages within the refined study area were kept to get a more accurate estimation of the fire-impacted forest. There is potential for multiple types of land cover to coexist in one pixel (mixed pixels), which could introduce errors of omission/commission. This is a recognized issue with remote-sensing analyses, but its effect is minimized in this study by restricting the study area to areas where forest is the dominant land cover in a pixel. We calculated the sum of percentages across the pixels of fire-impacted forest and transformed them into area in km^2 based on the resolution of the raster layers. In addition, we calculated the cumulative and newly fire-impacted forest at monthly scale across 2001–2019, using monthly fire-impacted forest of a focal year and forest land cover in the previous year with a similar procedure.

The fire-impacted forest we compiled here essentially represents satellite-detected fires among forested areas. Compared with the terminology in literature, the fire-impacted forest we examined here could include deforestation fires, as well as fires that spread into standing forests (forest fires) and does not include fires in previously cleared areas[3]. The impacts of both types of fire on biodiversity are largely negative, due to loss of habitat and direct mortality of organisms as well as damages to or deficits of fitness in organisms where the fires occurred. Fires of either type create negative effects that go beyond the immediate location and time at which the fire occurred. Deforestation fires generally lead to a total loss of the forest habitat by converting the original forest to other land-cover types, especially cropland, which is often the goal of deforestation fires. As a result, there has been an increase in cropland along the arc of deforestation[57]. Although fire is usually not the causal factor of the forest loss, the burning of felled vegetation can impair regeneration and facilitate the invasion of exotic grasses, thus impeding forest recovery[19]. The fires that encroach upon and sometimes spread into standing forest can also rapidly damage Amazon forests, the trees of which lack adaptations needed to resist fire-related damage[18,55,56]. For example, even light burns are known to remove more than 70% of the sapling and vine populations[21]. Low to medium severity fires can kill more than 50% of trees[58] and almost all of the larger woody lianas[20,59,60]. Fires could be catastrophic and lead to 90% annualized tree mortality when coupled with drought, as shown in studies with experimental fires[22,61]. The impacts of fires are not only on plants but also on animals. Studies also show that wildfires drive the impoverishment of birds[18,62] and high-intensity fires can cause the extinction of forest specialists[63].

Distinguishing the different types of fire can facilitate the understanding of their impacts on biodiversity, but would need additional data and validations[64] that are beyond the objective of this study. Alternatively, we resorted to using annual forest loss data to infer the fate of forest associated with satellite-detected fires. Specifically, we obtained annual forest loss layers from ref. 52 (http://earthenginepartners.appspot.com/science-2013-global-forest) and resampled them from 30 m to 463 m to obtain the percentage of forest loss per pixel using mean function. By overlapping the annual percentage of forest loss with the fire-impacted forest, we classified forest loss and fire-impacted forest into (a) forest loss without fire, (b) fire-impacted forest with forest loss, and (c) fire-impacted forest without forest loss. Such treatment enables us to partition the total impact as fire-related impacts versus non-fire related impacts (b + c versus a), or forest loss versus fire-induced impacts without forest loss (a + b versus c). The forest loss (a + b) is directly associated with the loss of forest habitat and thus loss of species range. The fire-impacted forest without forest loss (c) represents degraded forest habitat and thus degradation of species range. We used the term 'forest loss' to reflect the observation of forest changes by remote sensing. The class (a) could be interpreted as a subset of deforestation. The class (b) may be associated with deforestation

(for example, slash and burn) or fire-induced forest loss. Our analysis showed that forest loss without fire constituted a major driver for the impact on Amazon forest and biodiversity (Extended Data Figs. 2, 5). The forest loss without fire was estimated to be 8,068–8,181 km^2 yr^{-1}, the magnitude of which was comparable to fire-induced impacts (5,425–9,987 km^2 yr^{-1}) (Extended Data Fig. 4). The difference was that the fire-induced impacts were more variable among years (s.d. = 4,089–6,972 km^2 yr^{-1}) than forest loss without fire (s.d. = 3,280–3,414 km^2 yr^{-1}). We caution the interpretation of the relative proportion of forest loss without fire versus fire-impacted forest. The size of the fire-impacted forest was probably an underestimation for several reasons. MODIS sensors cannot consistently detect small and less intense understory fires in the Amazon[50], whereas the area of these can be twice the area of annual deforestation during severe drought years[65]. The use of tree cover percentages within the refined study area (as opposed to binary forest cover) also led to a more conservative estimation of the fire-impacted forest. Our analysis included a one-year temporal window for a conservative estimation; this would not include delayed tree mortality that could occur after fires[21,66]; otherwise, the proportion of fire-impacted forest with forest loss would be larger. Inference about the fate of forest among the fire-impacted forest showed that a small portion was directly associated with forest loss (Extended Data Fig. 4). This proportion could be larger if a multi-year window were used, as the impact of fire is known to go beyond the year in which it occurs[21,66]. However, we restricted our analysis to the same year to limit potential uncertainties of the inferences. The large amount of forest loss without fire echoes the findings that deforestation is a major threat to Amazonian biodiversity[15,16]. The large amount of fire-impacted forest without forest loss also echoes the recent finding that forest degradation could exceed deforestation in the Amazon[67]. We caution that our estimated areas might not be directly comparable with similar studies using different methodologies, because estimates of impacted area depend on a number of factors, including the specific remote-sensing products and algorithms used[68] and definition of concepts and categories[3].

A caveat of our remote sensing-based approach is that it is difficult to verify whether the MODIS-detected fire-impacted forest is totally burned for the focal spatial range (Amazon Basin) and temporal extent (the past two decades). Notably, the fire-impacted forest as identified by the MODIS sensors[69] was probably underestimated due to frequent cloud cover and optically thick aerosols, as well as detection limitations of the MODIS sensor and the algorithm. The MODIS sensors are more likely to capture larger fires (and thus, larger impacts on biodiversity), and omit small and less intense understory fires in the Amazon[65,70] that would have relatively smaller impacts on biodiversity[71]. Besides excluding fires that occurred in non-forested areas, we also selected a relatively high detection confidence (80%) for the active fire product to minimize false signals.

There is substantial empirical evidence that the impact of fire on the rainforest is not only local, but the impact of fires can also stretch far beyond the immediate time and location at which the fire occurred, suggesting that the impact could be passed to the whole pixel if the pixel is not 100% burned. For example, deforestation and fires can fragment forests and create more edges, which further thin the canopy, reduce the fuel moisture within the forest interior, and subsequently increase the likelihood and intensity of fires[28,72–74]. These positive feedbacks among fire, deforestation and forest fragmentation increases the vulnerability of forest to future fires[18,21,75]. Fires can have prolonged effects on tree lifespan and fitness: when not directly killing trees, the fires can weaken tree trunks and make them vulnerable to breakage by windstorms[22,76]. These analyses were performed within the Google Earth Engine platform (accessed March 2021).

Plant and vertebrate range maps

Plant range maps

Data compilation and cleaning. For plants, we used species distribution models[77] to infer the geographic distributions of species based on species occurrences and climate and soil characteristics. Plant occurrence records used for modelling were from the BIEN database (Botanical Information and Ecology Network; http://bien.nceas.ucsb.edu/bien/about/), which is compiled via a linked workflow that standardizes, integrates, corrects and validates data from disparate data sources and data formats. BIEN data include herbarium collections, ecological plots and surveys[78–87], and trait observations from a large variety of sources. The plant occurrences in the BIEN database are the product of contributions by 1,076 different data contributors, including numerous individual herbaria and data indexers of herbaria. The largest direct data contributors to BIEN include The Global Biodiversity Information Facility (GBIF), the US Forest Inventory and Analysis National Program (FIA)[88], Missouri Botanical Garden, SpeciesLink, Tree flora of the Neotropical Region (NeoTropTree)[89], New York Botanical Garden and VegBank[90]. The distribution records in BIEN were compiled using PostgreSQL (v.10.17).

Taxon names associated with BIEN occurrence records were corrected and standardized using the Taxonomic Name Resolution Service (TNRS)[91] with Tropicos, The Plant List and USDA Plants as taxonomic references, and all other options at their default settings. In addition to correcting misspellings, the TNRS updates synonymous matched names to the current accepted name, according to the taxonomic sources used. When available in the original data, we also included family along with the species name submitted to the TNRS; this additional information enables the TNRS to detect homonyms (identical names referring to different taxa) in different families. The declared political division names of occurrences were standardized using the Geographic Name Resolution Service (GNRS; http://bien.nceas.ucsb.edu/bien/tools/gnrs/), which corrects spelling errors and standardizes names, codes and abbreviations in multiple languages to standard political divisions in the GeoNames gazetteer (https://www.geonames.org). Geographic coordinates of occurrences are flagged as erroneous if they (1) fall outside the coordinate system (for example, longitude >180° or <−180°), (2) contain suspect coordinate values (for example, latitude or longitude exactly zero), (3) fall in the ocean, (4) match a political division centroid or (5) fall outside of a declared political division. Occurrence records that fall outside of a species' native range are identified using the Native Species Resolver (NSR; http://bien.nceas.ucsb.edu/bien/tools/nsr/), which uses published checklists and endemism data to determine if the observed species is native in a given location. Observations are flagged as potentially cultivated and removed from the observation data, on the basis of (1) searching for direct information within the curatorial note fields that the specimen is from a cultivated plant, (2) wildcard searches in the specimen description and locality fields suggesting that the plant is cultivated or growing in a location in which it is likely to be cultivated (that is, keywords such 'farm' or 'plantation' or 'campus' in the locality description, in any of several languages), or (3) any observation occurring within 3 km of a botanical garden or herbarium (the latter are typically in urban areas and associated with botanical gardens) was excluded as potentially cultivated. Full details of the BIEN workflow can be found at http://bien.nceas.ucsb.edu/bien/tools/ and in multiple references[91–95]. The occurrences that coded as specimen, plot, literature or checklist and passed taxonomic validation (http://bien.nceas.ucsb.edu/bien/tools/tnrs/), geovalidation (http://bien.nceas.ucsb.edu/bien/tools/gnrs/) and native/nonnative filters (http://bien.nceas.ucsb.edu/bien/tools/nsr/) were used in the species distribution modelling.

On the basis of these cleaned data, additional steps were undertaken to prepare the data for species distribution modelling. If multiple records were found in a 10-km grid cell, only one was retained. Such thinning is recommended when modelling density of occurrence[96] (in contrast to the density of individuals in which retaining each record is critical[97]). The occurrences were thinned to reduce spatial autocorrelation to ensure that all retained records were at least 20 km from one another using the default thinning algorithm of spthin (v.0.2.0)[98].

We further removed records that could be automatically identified as obvious outliers. Outliers in geographic and environmental space

were determined based on a Grubb's outlier test with[99] $P = 1 \times 10^{-3}$ implemented with the R package outliers (v.0.14)[100]. For each test, we calculated the centroid of all records in geographic or environmental space respectively and then the distance from each point to the centroid. The one-sided Grubb's test then determines whether the single largest distance is an outlier relative to all other points. If it was determined to be an outlier, the point was discarded. The test was repeated on the remaining points until no points were determined outliers.

Environmental data. The geographic distributions of plant species were modelled on six climate and five soil variables (correlation coefficient $|r| < 0.7$) at 10-km resolution: four bioclim variables from WorldClim 2.0 (mean annual temperature, mean diurnal temperature range, annual precipitation, precipitation seasonality)[101], two additional climatic variables that represent seasonality of tropical regions based on expert recommendations. To capture the precipitation peak in the warm and cold period, we calculated the ratio of precipitation in the warmest quarter (BIO18) to sum of precipitation in the warmest quarter and the coldest quarter (BIO18+BIO19), while the calculation of BIO18 and BIO19 follows the method used by WorldClim[102]. The soil variables were resampled from 250 m (raw resolution) to 10 km, by averaging values of the top four horizons of the soil data. To account for the effect of the dry season length and the water deficit experienced by vegetation during dry periods, we calculated an accumulated aridity index. The five soil layers are depth to bedrock, proportion clay, proportion silt in the first four soil horizons, mean bulk density, and mean pH in the first four soil horizons (SoilGrid; http://soilgrids.org), which are expected to be relevant for large-scale biogeography patterns[103].

Species distribution modelling. For plant species with at least 10 spatially unique records, we used Poisson point process models fit with the R package glmnet (v.4.0-2)[104], closely related to the popular Maxent algorithm[105]. For species with 3–9 spatially unique records, we used a range-bagging algorithm[106], which uses an ensemble of statistically generated convex hulls in environmental space. For any species with 1–2 spatially unique records, we used the cells in which records were found (at 10 km resolution) as its range. The selection of the algorithms is based on the philosophy of using a more conservative approach when there are fewer data for model training. The list of plant species was further refined to the checklist in ref. [107] and the species that had at least 10% of their range within the Amazonian forest, which yielded 11,514 plant species (7,526 species with Poisson point process model, 2,590 with range bagging, and 1,398).

Poisson point process models describe the spatially varying intensity of occurrence records as a function of covariates. An inhomogeneous Poisson point process model describes this intensity, λ, as a log-linear function of environmental covariates X_i at location s, with model parameters stored in vector $\beta=(\beta_0, \beta_1,\ldots,\beta_p)$[108,109]

$$log(\lambda(s)) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_p X_p.$$

To fit Poisson point process models, the presence points are contrasted against background points sampled across the modelling domain. For each plant species, we used the ecoregion in which its occurrences fall and the closest ecoregions[110] as the training and projecting domain, from which 20,000 random backgrounds were selected. For the Poisson point process models, different feature classes were used depending on sample size: linear and quadratic features are always selected, and the product features were used for species with 200 or more records. The regularization parameter was determined based on 5-fold cross-validation with each fold, choosing a value one standard deviation below the minimum deviance, which is the standard choice built into the cv.glmnet function[104]. This approach enabled us to find an 'optimal' (in the sense of balancing overfitting with underfitting) regularization parameter based on efficient computation of the entire regularization path[104]. Poisson point process models were fitted using spatially stratified cross-validation[111] using a custom stratification algorithm. This algorithm is designed to (a) remove spatial autocorrelation between records to allow for more accurate performance statistics, (b) avoid extrapolation to the extent possible by maximizing the amount of environmental space spanned within each fold, and (c) enabling species-specific scaling of the appropriate distance between records needed to minimize spatial autocorrelation. Folds were generated by first computing a k-means cluster on the coordinates of records, seeking 25 clusters. These 25 spatial clusters were then randomly assigned to five folds. If a species had fewer than 25 records, a smaller number of groups was used based on sample size, and these were split into five folds. This flexible approach accounts for variation in the spatial scale of aggregation among species by using the cluster analysis. By splitting into 25 groups initially (rather than 5) we obtain better environmental coverage (at least on average) within a fold and hence reduce artefacts from extrapolation[112]. Because this fold assignment was the only stochastic component in the modelling workflow, we set a random seed based on converting each species name to an integer to ensure that all results are exactly reproducible. This resulted in five models per species, which we then combined in an unweighted ensemble. This ensemble prediction can be interpreted as a relative occurrence rate that sums to 1 over the modelling domain[113]. The models were only projected to the training domains, thus avoiding model extrapolation issues[114]. The threshold of 5% training omission rate was used to transform the raw prediction into binary range maps. We evaluated the model performances using three indices: partial area under the curve of the receiver operating characteristic (pAUC), true skill statistics (TSS), and true positive rate (TPR) at the threshold of 5% training omission rate (5% of training presences predicted as absences). We used pAUC instead of traditional AUC to evaluate the model performance at high sensitivity levels (percentage of correctly predicted presences), in our case from 0.8 to 0.95, thus it is more appropriate for cases based on thresholds[115]. We also calculated TSS, which is the sum of sensitivity (true positive rate; proportion of known presences predicted present) and specificity (true negative rate; proportion of known absences predicted absent)[116]. Given that background points instead of absence data were used, omission error (1 − sensitivity) is expected to have higher importance than commission error (1 − specificity), so sensitivity was included as another evaluation index. The evaluation index showed robust performances of the models: 0.70 (s.d. = 0.09) for mean pAUC, 0.33 (s.d. = 0.13) for mean TSS and 0.84 (s.d. = 0.10) for sensitivity.

For species with 3 to 9 unique points on the 10 km grid, we produced species distribution models with the range-bagging algorithm (original version)[106]. Presence data, environmental data preparation and domain selection were based on the methods for Poisson point process models. Range-bagging is an adaptation of machine learning methods that stochastically builds convex hulls in environmental space to produce estimates of relative occurrence probability on a continuous scale[106]. It provides some key advantages: it requires only presence data, sampling bias is important only at range boundaries instead of throughout the range, it can characterize discontinuous ranges in geographic space, and it predicts variation in habitat suitability. The model training randomly takes 33% of occurrences (to capture the variation among samples) and two predictors (to decrease the possible complexity of variable interactions, thus simpler models). This procedure was repeated 100 times and ensembled as 100 voting scores. The models were projected to the same training domains as used for Poisson point process models. The continuous predictions of the range-bagging algorithm were converted to binary maps for our analysis with a threshold (0.165 of votes) that was chosen to ensure that all presences were correctly predicted (true positive rate = 1 for all species). On average, 14.9% (s.d. 13.5%) of background locations in ecoregions in which a species occurs were predicted as occupied, reflecting that spatial extrapolation was minimal for the vast majority of species. Such a low threshold (0.165 of votes) predicts larger range

sizes than would higher thresholds, which leads to more conservative predictions in our analysis about the proportion of range size impacted by fire. In other words, a higher threshold and hence smaller range size estimate would lead to more severe fire impacts estimated, and we chose to be conservative about how these poorly sampled species would influence our analysis. Owing to the small sample sizes (3–9 presences), we used range bagging as a simple first order estimate of species ranges to infer which locations on the landscape are similar to those limited locations in which a species has been observed.

For species with 1–2 spatially unique records (n = 1,398), we used the 10-km resolution cells where records were found as the range. Such maps should be only cautiously interpreted as the species distribution owing to limited available data. Using conservative, if imperfect, estimates of poorly sampled species ranges was preferable to ignoring them entirely, as many of them are probably truly rare[35]. We do not expect the inclusion of species with restricted ranges to bias our results, as their restricted ranges are as likely to overlap with fires as not. Indeed, excluding such species from our analyses reduces both the number of species with their ranges impacted by fire (629–898) and the number of species that have not had their ranges impacted (500–769), in roughly equal proportions. All else equal, underestimating species ranges is as likely to result in an underestimation of fire impacts as it is to result in an overestimation of the proportion of range impacted. Along these lines, excluding species with restricted ranges from our analyses did not influence our central conclusions. It had a minimal effect on the temporal trend in cumulative impacts and the proportion of plant species impacted by fire by 2019, which changed from 6.48–16.52% to 6.36–15.89% based on the 5% threshold, from 2.13–5.60% to 1.67–4.81% for the 10% threshold, and from 0.97–2.23 to 0.50–1.69% for the 15% threshold.

Generally speaking, the workflow of species distribution models constructed conservative estimates of species potential distributions while minimizing the underlying uncertainties. The effort in cleaning the occurrences of species, including cleaning taxonomic name based on TNRS (this avoids erroneous species names and reduces the uncertainties associated with those names), excluding cultivated records (this helps to restrict the prediction to natural areas and reduces the likelihood of overestimations), and excluding spatial and environmental outliers (this helps to avoid extreme broad potential distributions). The workflow incorporated a gradient of complexities based on the amount of data, from the most conservative approach using spatial buffer of species with 1–2 spatially unique records, to limited environmental inferences based on range bagging for species with 3–9 spatially unique records, to more liberal environmental inferences based on Poisson point process models for species with 10 or more spatially unique records, within which group we further distinguished simpler and more complex features for species with more or fewer presences. To minimize the uncertainties, we implemented 5-fold cross-validations and used the ensemble average in the prediction. Last, to minimize the uncertainties during the inference process, we also restricted model predictions to the ecoregions used in model training. The workflow of species distribution modelling has been used in other global biodiversity studies[117,118].

Vertebrate range maps

For vertebrates, we used expert maps provided by the IUCN rather than modelling species distributions, as these have been carefully vetted by taxon specialists and offer comparatively complete coverage of known species. Range polygons coded as 'extant' and 'resident' for all species were obtained from the IUCN spatial data portal[5,119]. IUCN range polygons were modified to reflect the extent of suitable habitat by limiting the species range to the known elevational range and habitat association as it has been shown that this allows for a more accurate representation of species range area for analysis[120].

The dataset we compiled is expected to provide a comprehensive estimation of biodiversity in the Amazon to date. However, we lack data for many of the species that are known to occur in the Amazon, and are undoubtedly missing data for species that have yet to be discovered. Our data did not include 14% (n = 1,949) of the plant species included in a recently published checklist of Amazonian plants[107]. The distribution maps were processed in R (v.3.5.1).

Quantifying the impact of fires on biodiversity

We restricted our study area to the Amazon forest, defined as at least 60% forest cover in MODIS Vegetation Continuous Fields (MOD44Bv006; see section 1) during 2001–2018 within the Amazon Basin[6]. We first identified species that have over 10% of their range within the Amazon forest, so as to exclude species that have large geographic ranges or species that have little of their ranges in the Amazon forest. Within the Amazon forest, we overlapped fire-impacted forest layers (resampled to 10 km using mean function) with species ranges. For each species, we quantified the cumulative impact (percentage of a species' range impacted by fire in Amazon forest) over 2002–2019. We summarized the number of species that had any range impacted, or for which the range being impacted within the Amazon forest reached one or more of three thresholds (5, 10 or 15%). We also examined the relationship between cumulative fire-impacted forest (predictor) and the cumulative number of species affected (response) each year using ordinary least squares linear regression.

Ground-based surveys before and after the fire could give us more accurate knowledge about how fires have impacted biodiversity. But such surveys are only possible for a few case studies, and it is near impossible to assess biodiversity in situ across the entire Amazon Basin. Building upon nearly two decades of remote-sensing data across the Amazon and a large amount of species' range maps, our study provided a basin-wide estimate of the potential impacts of fires on biodiversity. Our estimates should be on the conservative end of the uncertainty spectrum: the MODIS remote-sensing products are more likely to capture larger fires than small fires (including under canopy fires[65,70]), and the size estimations of species range also involves a series of conservative approaches.

Drought, policy and fire-impacted forest in the Amazon

Definition of three periods of policy regimes

We separated our study period into three policy regimes: before 2008, 2009–2018 and 2019. Policy periods were defined through analysis and interpretation of the relevant literature. There are many policy factors that influence deforestation and forest fires in the Amazon, including government policy in Brazil and other countries in the Amazon region and voluntary conservation initiatives spearheaded by non-governmental organizations. Governmental policy varies greatly across different countries in the Amazon region and also within countries depending on how laws and regulations are interpreted and enforced at lower levels of government. Similarly, conservation initiatives advocated by non-governmental organizations and foreign governments are voluntary and rely on market pressures and other tools for implementation. In this paper, our primary concern is the effect of policy on biodiversity and the potential effect of changes in regulatory enforcement in 2019 by Brazil[44], where the majority of Amazon forest and fires are located (Extended Data Fig. 7). As a result, the three policy regime periods selected are consistent with changes in policy regimes in Brazil rather than the entire Amazon region. The pre-regulation period includes years before 2008. During this period, specific policies to prevent deforestation and forest fires were either yet to be implemented or were under development[30,42]. The strict regulation period is 2009 to 2018. During this period, Brazil had strong policies in place and many of the voluntary programs promoted by non-governmental organizations were also fully functional[30,43]. There was then a retraction in the policy regime in Brazil in 2019 as the new president relaxed enforcement of official government policies from January through August[44,121]. From September to the end of the typical burning season, Brazil responded to international pressure and again enforced deforestation and forest burning regulations[45,122]. The first part of this period is a relaxation of

policies rather than a full removal of policies because voluntary programs outside of government control remained in place.

Drought conditions

Drought is a well-known factor that affects fires in the Amazon[61]. We used Standardized Precipitation–Evapotranspiration Index (SPEI) to quantify the drought conditions in the Amazon[123]. The SPEI is a multiscalar drought index based on climatic data and has been used in studying forest dynamics and forest fires[124,125]. The key advantage of SPEI over another commonly used drought index (Standardized Precipitation Index (SPI)) is the indirect incorporation of the effect of temperature, that is by accounting for potential evapotranspiration. The role of heat-induced drought stress is associated with tree mortality and forest fires[66,126]. Another drought index, the maximum climatological water deficit (MCWD), has been used to study the relationship between drought and the Amazon forest[61]. These indices were highly correlated in our study area ($r = 0.77$), thus we did not include MCWD in our analyses.

Monthly SPEI data were downloaded from the SPEI Global Drought Monitor (https://spei.csic.es/map) and spatially and temporally averaged for Brazilian portion of Amazon. We considered monthly SPEI at five temporal scales (1, 3, 6, 9 and 12 months), to account for possible lag effects between drought and fires[67]. The yearly SPEI was calculated as the mean of monthly SPEI based on 1-month SPEI for a focal year, to represent the general drought condition of this year. The drought index was paired with data of fire-impacted forest at monthly or yearly scales in the regression analyses (see below).

Regression between drought, policy and impact on biodiversity

Policy, drought and the fire-impacted forest. We conducted ordinary least squares linear regression using newly fire-impacted forest by year as dependent variable and annual SPEI, policy regime (pre-regulation (2003–2008) or regulation (2009–2018)), and their interaction term as independent variables. The data used for this analysis started in 2002, which is the first year for which the data for newly fire-impacted forests are available. This analysis was implemented for the Brazilian portion of the Amazon and for the whole Amazon. See results in Extended Data Table 1.

Fire-impacted forest and impact on biodiversity in 2019 compared with previous years in the Brazilian Amazon. We assessed the newly fire-impacted forest at both monthly and yearly scales using the regulation period (2009–2018) as a baseline. For the monthly scale analysis, we preselected a 9-month SPEI among the five different scales. Specifically, we constructed linear mixed models using newly fire-impacted forest as the dependent variable, with SPEI and policy regime as fixed effects (pre-regulation or regulation), and using month as a random effect. The model using SPEI based on 9-month SPEI had the lowest Akaike information criterion (AIC) value.

We used the regulation period as the baseline and conducted ordinary least squares linear regressions with data from the regulation period, using monthly or yearly newly fire-impacted forest as dependent variable and using monthly or yearly SPEI as independent variable. We used calibrated models to predict the fire-impacted forest in the pre-regulation period and 2019 given the drought conditions at monthly or yearly scales. We further calculated the difference between the actual fire-impacted forest and predicted fire-impacted forest. For example, the calculated differences could be considered as residuals for the regulation years. See results in Fig. 3a and Extended Data Fig. 6a for results on a monthly scale and Fig. 3b and Extended Data Fig. 6b for the yearly scale. In a similar manner, we compared the mean of species range impacted by fire at a yearly scale. See results in Fig. 4 and Extended Data Fig. 8.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

The plant occurrences from the BIEN database are accessible using the RBIEN package (https://github.com/bmaitner/RBIEN). The climatic data are accessible from http://worldclim.org and the soil data are available from http://soilgrids.org. MODIS active fire and burned area products are available at http://modis-fire.umd.edu. The MODIS Vegetation Continuous Fields data are publicly available from https://lpdaac.usgs.gov/products/mod44bv006/. The annual forest loss layers are available from http://earthenginepartners.appspot.com/science-2013-global-forest. The plant range maps are accessible at https://github.com/shandongfx/paper_Amazon_biodiversity_2021. The vertebrate range maps are available from https://www.iucnredlist.org/resources/spatial-data-download. The SPEI data are available from SPEI Global Drought Monitor (https://spei.csic.es/map).

Code availability

The code to process the remote-sensing data is available at https://github.com/shandongfx/paper_Amazon_biodiversity_2021.

51. Olson, D. M. et al. Terrestrial ecoregions of the world: a new map of life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* **51**, 933–938 (2001).
52. Hansen, M. C. et al. High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013).
53. Giglio, L., Schroeder, W. & Justice, C. O. The collection 6 MODIS active fire detection algorithm and fire products. *Remote Sens. Environ.* **178**, 31–41 (2016).
54. Giglio, L. *MODIS Collection 6 Active Fire Product User's Guide Revision A* (Univ. Maryland, 2015).
55. Barlow, J., Lagan, B. O. & Peres, C. A. Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *J. Trop. Ecol.* **19**, 291–299 (2003).
56. Brando, P. M. et al. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Glob. Change Biol.* **18**, 630–641 (2012).
57. Gibbs, H. K. et al. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proc. Natl Acad. Sci. USA* **107**, 16732–16737 (2010).
58. Barlow, J. & Peres, C. in *Emerging Threats to Tropical Forests* (eds. Laurance, W. F. & Peres, C. A.) 225–240 (Univ. Chicago Press, 2006).
59. Barlow, J. et al. Wildfires in bamboo-dominated Amazonian forest: impacts on above-ground biomass and biodiversity. *PLoS ONE* **7**, e33373 (2012).
60. Gerwing, J. J. Degradation of forests through logging and fire in the eastern Brazilian Amazon. *For. Ecol. Manage.* **157**, 131–141 (2002).
61. Brando, P. M. et al. Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proc. Natl Acad. Sci. USA* **111**, 6347–6352 (2014).
62. Barlow, J. & Peres, C. A. Avifaunal responses to single and recurrent wildfires in Amazonian forests. *Ecol. Appl.* **14**, 1358–1373 (2004).
63. Paolucci, L. N., Schoereder, J. H., Brando, P. M. & Andersen, A. N. Fire-induced forest transition to derived savannas: cascading effects on ant communities. *Biol. Conserv.* **214**, 295–302 (2017).
64. Roy, D. P. & Kumar, S. S. Multi-year MODIS active fire type classification over the Brazilian Tropical Moist Forest Biome. *Int. J. Digital Earth* **10**, 54–84 (2017).
65. Giglio, L., Schroeder, W., Hall, J. V. & Justice, C. O. MODIS Collection 6 Active Fire Product User's Guide Revision B (Univ. Maryland, 2018).
66. Barriopedro, D., Fischer, E. M., Luterbacher, J., Trigo, R. M. & García-Herrera, R. The hot summer of 2010: redrawing the temperature record map of Europe. *Science* **332**, 220–224 (2011).
67. Chen, Y. et al. Forecasting fire season severity in South America using sea surface temperature anomalies. *Science* **334**, 787–791 (2011).
68. Giglio, L. et al. Assessing variability and long-term trends in burned area by merging multiple satellite fire products. *Biogeosciences* **7**, 1171–1186 (2010).
69. Justice, C. O. et al. The MODIS fire products. *Remote Sens. Environ.* **83**, 244–262 (2002).
70. Giglio, L., Boschetti, L., Roy, D. P., Humber, M. L. & Justice, C. O. The Collection 6 MODIS burned area mapping algorithm and product. *Remote Sens. Environ.* **217**, 72–85 (2018).
71. Nóbrega, C. C., Brando, P. M., Silvério, D. V., Maracahipes, L. & de Marco, P. Effects of experimental fires on the phylogenetic and functional diversity of woody species in a neotropical forest. *For. Ecol. Manage.* **450**, 117497 (2019).
72. Alencar, A., Nepstad, D. & Diaz, M. C. V. Forest understory fire in the Brazilian Amazon in ENSO and Non-ENSO years: area burned and committed carbon emissions. *Earth Interact.* **10**, 1–17 (2006).
73. Siegert, F., Ruecker, G., Hinrichs, A. & Hoffmann, A. A. Increased damage from fires in logged forests during droughts caused by El Niño. *Nature* **414**, 437–440 (2001).
74. Cochrane, M. A. & Laurance, W. F. Fire as a large-scale edge effect in Amazonian forests. *J. Trop. Ecol.* **18**, 311–325 (2002).
75. Ray, D., Nepstad, D. & Moutinho, P. Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. *Ecol. Appl.* **15**, 1664–1678 (2005).
76. Silvério, D. V. et al. Fire, fragmentation, and windstorms: a recipe for tropical forest degradation. *J. Ecol.* **107**, 656–667 (2019).
77. Guisan, A. & Zimmermann, N. E. Predictive habitat distribution models in ecology. *Ecol. Modell.* **135**, 147–186 (2000).
78. Fegraus, E. Tropical Ecology Assessment and Monitoring Network (TEAM Network). *Biodivers. Ecol.* **4**, 287–287 (2012).

79. Peet, R. K., Lee, M. T., Jennings, M. D. & Faber-Langendoen, D. VegBank: a permanent, open-access archive for vegetation plot data. *Biodivers. Ecol.* **4**, 233–241 (2012).
80. DeWalt, S. J., Bourdy, G., Chavez de Michel, L. R. & Quenevo, C. Ethnobotany of the Tacana: quantitative inventories of two permanent plots of Northwestern Bolivia. *Econ. Bot.* **53**, 237–260 (1999).
81. USDA Forest Service. *Forest Inventory and Analysis National Program,* http://www.fia.fs.fed.us/ (2013).
82. Wiser, S. K., Bellingham, P. J. & Burrows, L. E. Managing biodiversity information: development of New Zealand's National Vegetation Survey databank. *N. Z. J. Ecol.* **25**, 1–17 (2001).
83. Anderson-Teixeira, K. J. et al. CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Glob. Change Biol.* **21**, 528–549 (2015).
84. Enquist, B. & Boyle, B. SALVIAS – the SALVIAS vegetation inventory database. *Biodivers. Ecol.* **4**, 288 (2012).
85. GBIF.org. *GBIF Occurrence Download* https://doi.org/10.15468/dl.yubndf (2018).
86. Dauby, G. et al. RAINBIO: a mega-database of tropical African vascular plants distributions. *PhytoKeys* **74**, 1–18 (2016).
87. Arellano, G. et al. A standard protocol for woody plant inventories and soil characterisation using temporary 0.1-ha plots in tropical forests. *J. Trop. For. Sci.* **28**, 508–516 (2016).
88. O'Connell, B. M. et al. *The Forest Inventory and Analysis Database: Database Description and User Guide for Phase 2 (version 6.1),* https://doi.org/10.2737/fs-fiadb-p2-6.1 (USDA Forest Service, 2016).
89. Oliveira-Filho, A. T. *NeoTropTree, Flora arbórea da Região Neotropical: Um Banco de Dados Envolvendo Biogeografia, Diversidade e Conservação,* http://www.neotroptree.info (Univ. Federal de Minas Gerais, 2017).
90. Peet, R. K., Lee, M. T., Jennings, M. D. & Faber-Langendoen, D. *VegBank: The Vegetation Plot Archive of the Ecological Society of America*, http://vegbank.org (accessed 2013).
91. Boyle, B. et al. The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinf.* **14**, 16 (2013).
92. Goldsmith, G. R. et al. Plant-O-Matic: a dynamic and mobile guide to all plants of the Americas. *Methods Ecol. Evol.* **7**, 960–965 (2016).
93. McFadden, I. R. et al. Temperature shapes opposing latitudinal gradients of plant taxonomic and phylogenetic β diversity. *Ecol. Lett.* **22**, 1126–1135 (2019).
94. Enquist, B. J., Condit, R., Peet, R. K., Schildhauer, M. & Thiers, B. M. Cyberinfrastructure for an integrated botanical information network to investigate the ecological impacts of global climate change on plant biodiversity. Preprint at https://doi.org/10.7287/peerj.preprints.2615v2 (2016).
95. Maitner, B. S. et al. The BIEN R package: A tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods Ecol. Evol.* **9**, 373–379 (2017).
96. Phillips, S. J. & Dudík, M. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**, 161–175 (2008).
97. Merow, C. & Silander, J. A. A comparison of Maxlike and Maxent for modelling species distributions. *Methods Ecol. Evol.* **5**, 215–225 (2014).
98. Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B. & Anderson, R. P. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* **38**, 541–545 (2015).
99. Grubbs, F. E. Sample criteria for testing outlying observations. *Ann. Math. Statist.* **21**, 27–58 (1950).
100. Komsta, L. outliers: Tests for outliers. R package v.0.14 (2011).
101. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
102. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).
103. Mueller-Dombois, D. & Ellenberg, H. *Aims and Methods of Vegetation Ecology* (Wiley, 1974).
104. Friedman, J., Hastie, T. & Tibshirani, R. glmnet: Lasso and elastic-net regularized generalized linear models. R package v.4.0-2 (2020).
105. Phillips, S. J., Anderson, R. P. & Schapire, R. E. Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**, 231–259 (2006).
106. Drake, J. M. Range bagging: a new method for ecological niche modelling from presence-only data. *J. R. Soc. Interface* **12**, 20150086 (2015).
107. Cardoso, D. et al. Amazon plant diversity revealed by a taxonomically verified species list. *Proc. Natl Acad. Sci. USA* **114**, 10695–10700 (2017).
108. Warton, D. I. & Shepherd, L. C. Poisson point process models solve the "pseudo-absence problem" for presence-only data in ecology. *Ann. Appl. Stat.* **4**, 1383–1402 (2010).
109. Renner, I. W. et al. Point process models for presence-only analysis. *Methods Ecol. Evol.* **6**, 366–379 (2015).
110. Dinerstein, E. et al. An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* **67**, 534–545 (2017).
111. Roberts, D. R. et al. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography* **40**, 913–929 (2016).
112. Phillips, S. J. Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson *et al*. (2007). *Ecography* **31**, 272–278 (2008).
113. Merow, C., Smith, M. J. & Silander, J. A. Jr. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* **36**, 1058–1069 (2013).
114. Qiao, H. et al. An evaluation of transferability of ecological niche models. *Ecography* **42**, 521–534 (2019).
115. Peterson, A. T., Papeş, M. & Soberón, J. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol. Modell.* **213**, 63–72 (2008).
116. Allouche, O., Tsoar, A. & Kadmon, R. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* **43**, 1223–1232 (2006).
117. Jung, M. et al. Areas of global importance for terrestrial biodiversity, carbon, and water. Preprint at https://doi.org/10.1101/2020.04.16.021444 (2020).
118. Carlson, C. J. et al. Climate change will drive novel cross-species viral transmission. Preprint at https://doi.org/10.1101/2020.01.24.918755 (2020).
119. BirdLife International. *IUCN Red List for Birds* http://www.birdlife.org (2019).
120. Brooks, T. M. et al. Measuring terrestrial area of habitat (AOH) and its utility for the IUCN Red List. *Trends Ecol. Evol.* **34**, 977–986 (2019).
121. de Area Leão Pereira, E. J., de Santana Ribeiro, L. C., da Silva Freitas, L. F. & de Barros Pereira, H. B. Brazilian policy and agribusiness damage the Amazon rainforest. *Land Use Policy* **92**, 104491 (2020).
122. Garcia, R. T. After Brazil's summer of fire, the militarization of the Amazon remains. *Foreign Policy* https://foreignpolicy.com/2019/11/19/militarization-amazon-legacy-brazil-forest-fire-bolsonaro/ (19 November 2019).
123. Vicente-Serrano, S. M., Beguería, S. & López-Moreno, J. I. A multiscalar drought index sensitive to global warming: The Standardized Precipitation Evapotranspiration Index. *J. Clim.* **23**, 1696–1718 (2010).
124. Feldpausch, T. R. et al. Amazon forest response to repeated droughts. *Global Biogeochem. Cycles* **30**, 964–982 (2016).
125. Marin, P.-G., Julio, C. J., Arturo, R.-T. D. & Jose, V.-N. D. Drought and spatiotemporal variability of forest fires across Mexico. *Chin. Geogr. Sci.* **28**, 25–37 (2018).
126. Adams, H. D. et al. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proc. Natl Acad. Sci. USA* **106**, 7063–7066 (2009).

Acknowledgements We acknowledge the herbaria that contributed data to this work: HA, FCO, MFU, UNEX, VDB, ASDM, BPI, BRI, CLF, L, LPB, AD, TAES, FEN, FHO, A, ANSM, BCMEX, RB, TRH, AAH, ACOR, AJOU, UI, AK, ALCB, AKPM, EA, AAU, ALU, AMES, AMNH, AMO, ANA, GH, ARAN, ARM, AS, CICY, ASU, BAI, AUT, B, BA, BAA, BAB, BACP, BAF, BAL, COCA, BARC, BBS, BC, BCN, BCRU, BEREA, BG, BH, BIO, BISH, SEV, BLA, BM, MJG, BOL, CVRD, BOLV, BONN, BOUM, BR, BREM, BRLU, BSB, BUT, C, CAMU, CAN, CANB, CAS, CAY, CBG, CBM, CEN, CEPEC, CESJ, CHR, ENCB, CHRB, CIIDIR, CIMI, CLEMS, COA, COAH, COFC, CP, COL, COLO, CONC, CORD, CPAP, CPUN, CR, CRAI, FURB, CU, CRP, CS, CSU, CTES, CTESN, CUZ, DAO, HB, DAV, DLF, DNA, DS, DUKE, DUSS, E, HUA, EAC, ECU, EIF, EIU, GI, GLM, GMNHJ, K, GOET, GUA, EKY, EMMA, HUAZ, ERA, ESA, F, FAA, FAU, UVIC, FI, GZU, H, FLAS, FLOR, HCIB, FR, FTG, FUEL, G, GB, GDA, HPL, GENT, GEO, HUAA, HUJ, CGE, HAL, HAM, IAC, HAMAB, HAS, HAST, IB, HASU, HBG, IBUG, HBR, IEB, HGI, HIP, IBGE, ICEL, ICN, ILL, SF, NWOSU, HO, HRCB, HRP, HSS, HU, HUAL, HUEFS, HUEM, HUSA, HUT, IAA, HYO, IAN, ILLS, IPRN, FCQ, ABH, BAFC, BBB, INPA, IPA, BO, NAS, INB, INEGI, INM, MW, EAN, IZTA, ISKW, ISC, GAT, IBSC, UCSB, ISU, IZAC, JBAG, JE, SD, JUA, JYV, KIEL, ECON, TOYA, MPN, USF, TALL, RELC, CATA, AQP, KMN, KMNH, KOR, KPM, KSTC, LAGU, UESC, GRA, IBK, KTU, KU, PSU, KYO, LA, LOMA, SUU, UNITEC, NAC, IEA, LAE, LAF, GMDRC, LCR, LD, LE, LEB, LI, LIL, LINN, AV, HUCP, MBML, FAUC, CNH, MACF, CATIE, LTB, LISI, LISU, MEXU, LL, LOJA, LP, LPAG, MGC, LPD, LPS, IRVC, MICH, JOTR, LSU, LBG, WOLL, LTR, MNHN, CDBI, LYJB, LISC, MOL, DBG, AWH, NH, HSC, LMS, MELU, NZFRI, M, MA, UU, UBT, CSUSB, MAF, MAK, MB, KUN, MARY, MASS, MBK, MBM, UCSC, UCS, JBGP, OBI, BESA, LSUM, FULD, MCNS, ICESI, MEL, MEN, TUB, MERL, CGMS, FSU, MG, HIB, TRT, BABY, ETH, YAMA, SCFS, SACT, ER, JCT, JROH, SBBG, SAV, PDD, MIN, SJSU, MISS, PAMP, MNHM, SDSU, BOTU, MPU, MSB, MSC, CANU, SFV, RSA, CNS, JEPS, BKF, MSUN, CIB, VIT, MU, MUB, MVFA, SLPM, MVFQ, PGM, MVJB, MVM, MY, PASA, N, HGM, TAM, BOON, MHA, MARS, COI, CMM, NA, NCSC, ND, NU, NE, NHM, NHMC, NHT, UFMA, NLH, UFRJ, UFRN, UFS, ULS, UNL, US, NMNL, USP, NMR, NMSU, XAL, NSW, ZMT, BRIT, MO, NCU, NY, TEX, U, UNCC, NUM, O, OCLA, CHSC, LINC, CHAS, ODU, OKL, OKLA, CDA, OS, OSA, OSC, OSH, OULU, OXF, P, PACA, PAR, UPS, PE, PEL, SGO, PEUFR, PH, PKDC, SI, PMA, POM, PORT, PR, PRC, TRA, PRE, PY, QMEX, QCA, TROM, QCNE, QRS, UH, R, REG, RFA, RIOC, RM, RNG, RYU, S, SALA, SANT, SAPS, SASK, SBT, SEL, SING, SIU, SJRP, SMDB, SNM, SOM, SP, SRFA, SPF, STL, STU, SUVA, SVG, SZU, TAI, TAIF, TAMU, TAN, TEF, TENN, TEPB, TI, TKPM, TNS, TO, TU, TULS, UADY, UAM, UAS, UB, UC, UCR, UEC, UFG, UFMT, UFP, UGDA, UJAT, ULM, UME, UMO, UNA, UNM, UNR, UNSL, UPCB, UPNA, USAS, USJ, USM, USNC, USZ, UT, UTC, UTEP, UV, VAL, VEN, VMSL, VT, W, WAG, WII, WELT, WIS, WMNH, WS, WTU, WU, Z, ZSS, ZT, CUVC, AAS, AFS, BHCB, CHAM, FM, PERTH and SAN. X.F., D.S.P., E.A.N., A.L. and J.R.B. were supported by the University of Arizona Bridging Biodiversity and Conservation Science program. Z.L. was supported by NSFC (41922006) and K. C. Wong Education Foundation. The BIEN working group was supported by the National Center for Ecological Analysis and Synthesis, a centre funded by NSF EF-0553768 at the University of California, Santa Barbara, and the State of California. Additional support for the BIEN working group was provided by iPlant/Cyverse via NSF DBI-0735191. B.J.E., B.M. and C.M. were supported by NSF ABI-1565118. B.J.E. and C.M. were supported by NSF ABI-1565118 and NSF HDR-1934790. B.J.E., L.H. and P.R.R. were supported by the Global Environment Facility SPARC project grant (GEF-5810). D.D.B. was supported in part by NSF DEB-1824796 and NSF DEB-1550686. S.R.S. was supported by NSF DEB-1754803. X.F. and A.L. were partly supported by NSF DEB-1824796. B.J.E. and D.M.N. were supported by NSF DEB-1556651. M.M.P. is supported by the São Paulo Research Foundation (FAPESP), grant 2019/25478-7. D.M.N. was supported by Instituto Serrapilheira/Brazil (Serra-1912-32082). E.I.N. was supported by NSF HDR-1934712. We thank L. López-Hoffman and L. Baldwin for constructive comments.

Author contributions X.F. conceived the idea, which was refined by discussion with D.S.P., C.M., B.M., P.R.R., E.A.N., B.L.B., A.L., J.R.B., D.D.B., J.R.S., K.C.E. and B.J.E.; X.F. and Z.L. processed the remote-sensing data; C.M., X.F., B.M., B.L.B., D.S.P. and B.J.E. conducted the analyses of plant data; P.R.R., C.M., B.M., X.F. and D.S.P. conducted the analyses of vertebrate data; X.F., C.M., S.R.S. and E.A.N. processed the drought data; D.S.P., X.F., C.M., P.R.R. and B.M. designed the illustrations with help from B.J.E., D.D.B., K.C.E. and E.A.N.; E.A.N., X.F., and D.S.P. conducted the statistical analyses with help from B.J.E.; X.F., B.J.E., B.M., A.L., J.R.B., D.S.P., C.M., E.A.N., Z.L. and P.R.R. wrote the original draft; all authors contributed to interpreting the results and the editing of manuscript drafts. B.J.E., C.M., K.C.E. and D.D.B. led to the acquisition of the financial support for the project. X.F., C.M., B.M., D.S.P., P.R.R., Z.L., E.A.N. and B.J.E. contributed equally to data, analyses and writing.

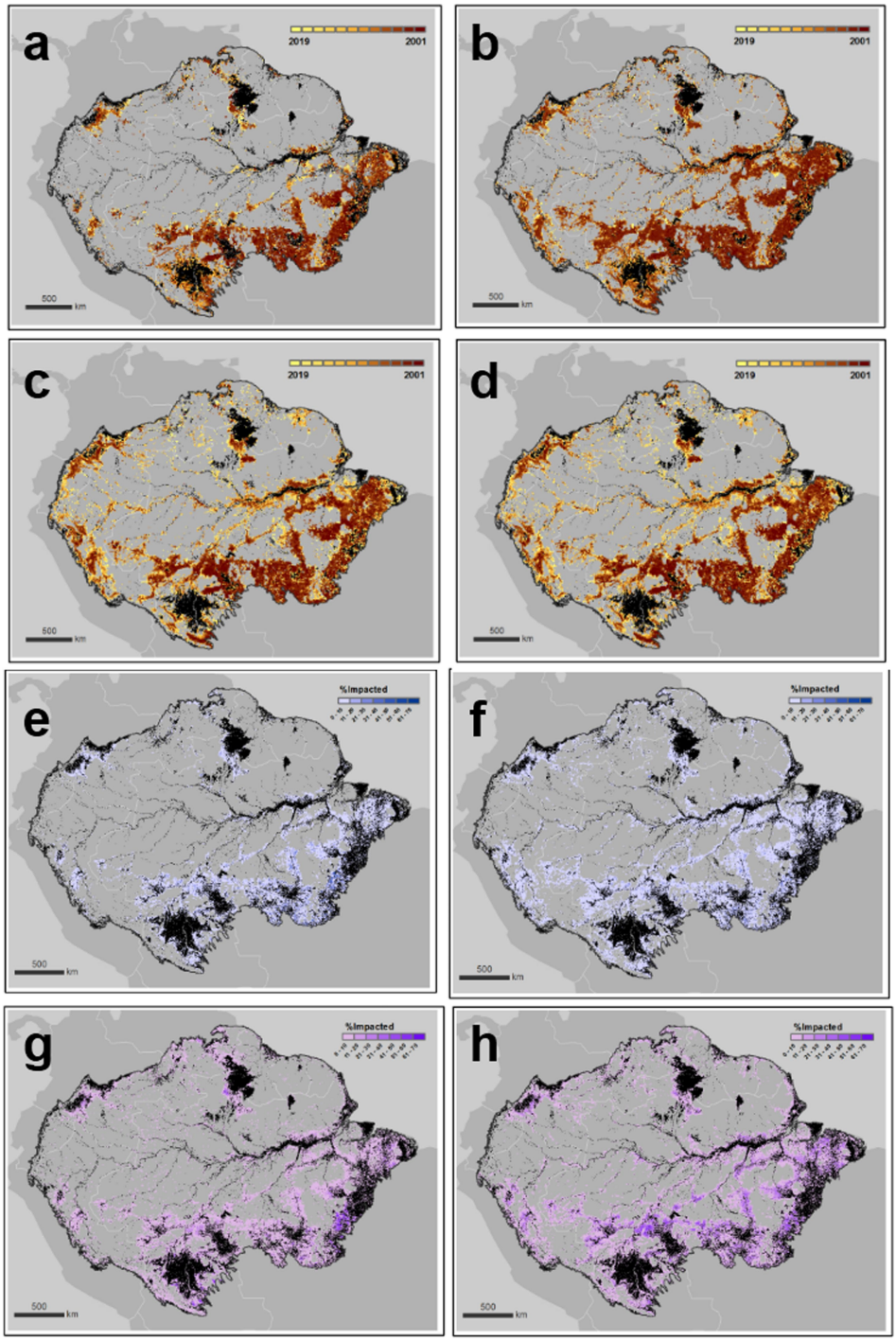
Competing interests The authors declare no competing interests.

Additional information

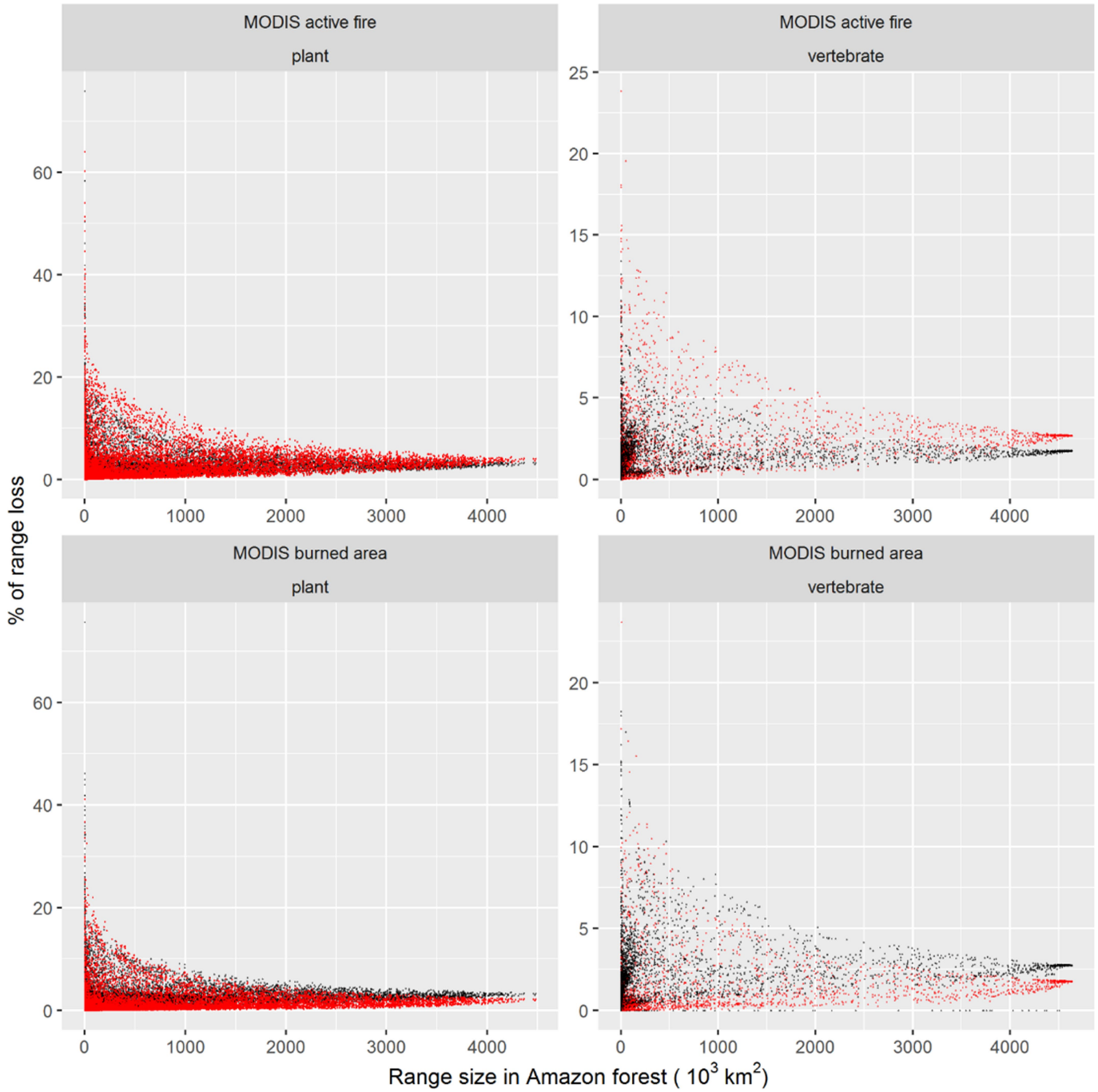
Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41586-021-03876-7.

Correspondence and requests for materials should be addressed to Xiao Feng.

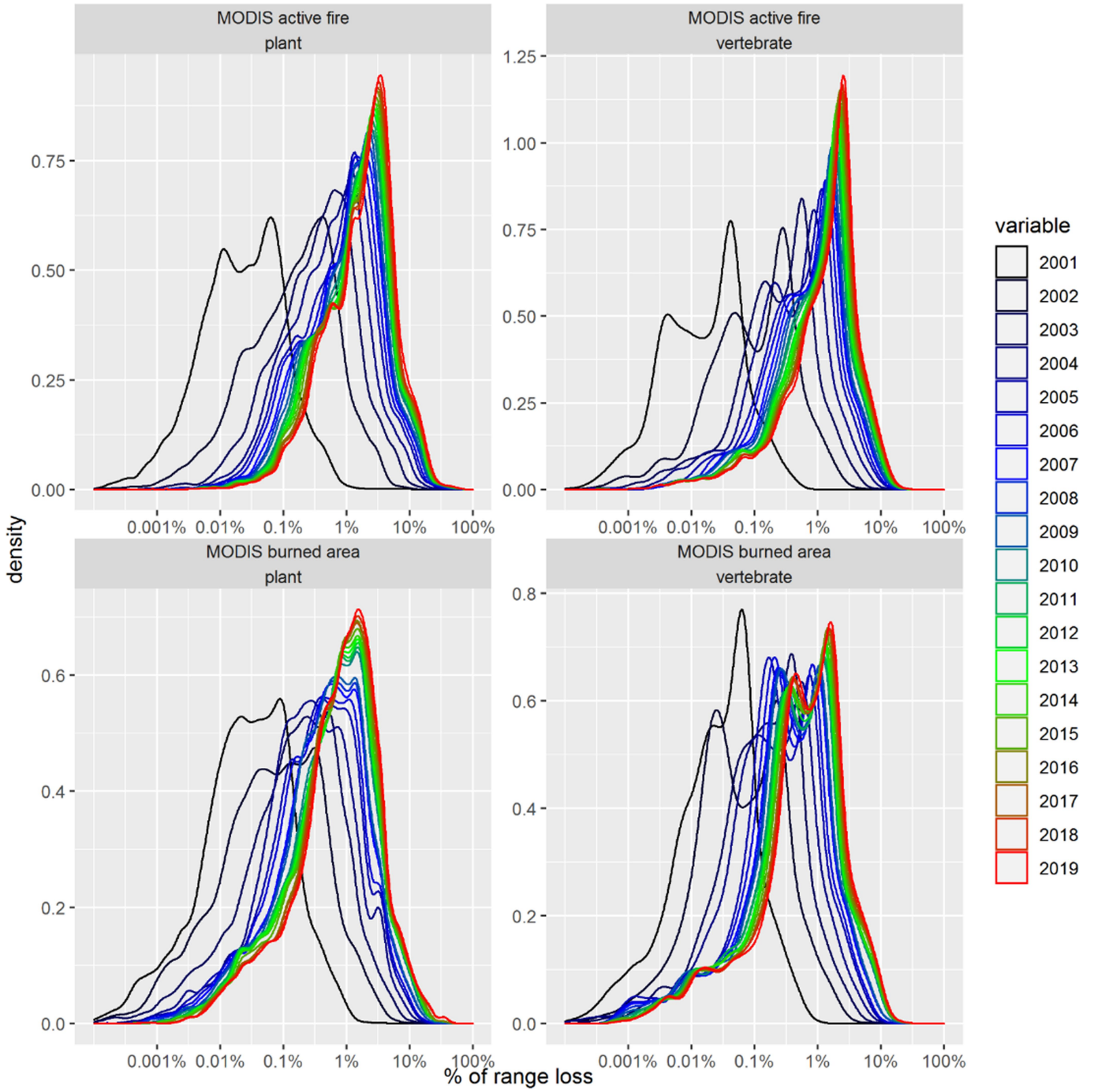
Peer review information *Nature* thanks the anonymous reviewers for their contribution to the peer review of this work.



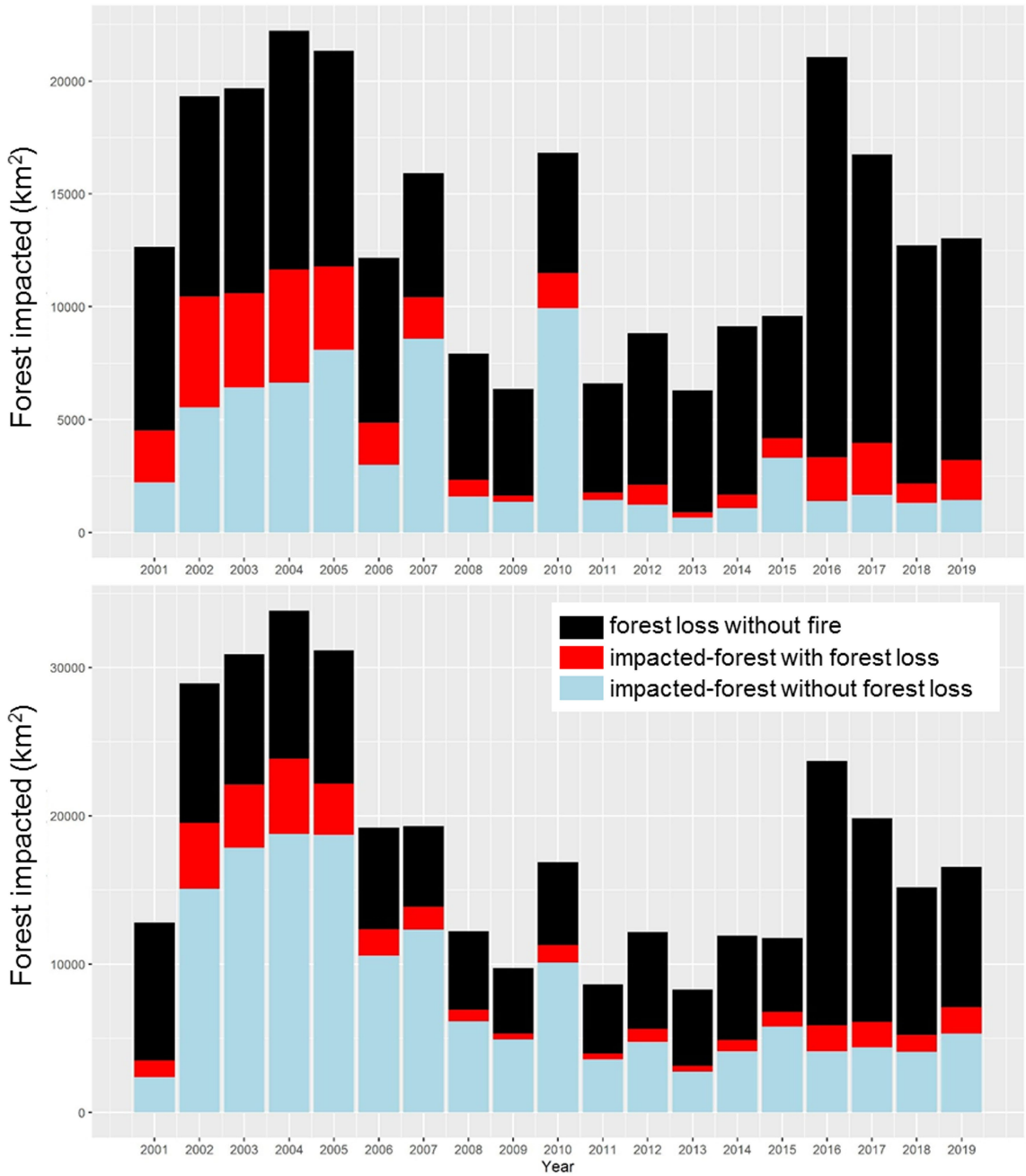
Extended Data Fig. 1 | Fire-impacted forest and forest loss in the Amazon Basin. a–**h**, Visualization of fire-impacted forest (**a**, **b**), forest loss without fire (**c**, **d**), fire-impacted forest with forest loss (**e**, **f**), and fire-impacted forest without forest loss (**g**, **h**) in the Amazon Basin based on MODIS burned area (left panels) and active fire (right panels). Data in **a**–**d** are resampled from the 500m (MODIS burned area) or 1 km (MODIS active fire) to 10 km resolution using mean function and thresholded at 0.01 to illustrate the temporal dynamics. Black represents non-forested areas masked out from this study. The cumulative fire-impacted forest is classified into two categories: fire-impacted forest with forest loss (**e**, **f**) and fire-impacted forest without forest loss (**g**, **h**). Data in **e**–**h** are resampled to 10 km using mean function to illustrate the cumulative percentages of impacts.



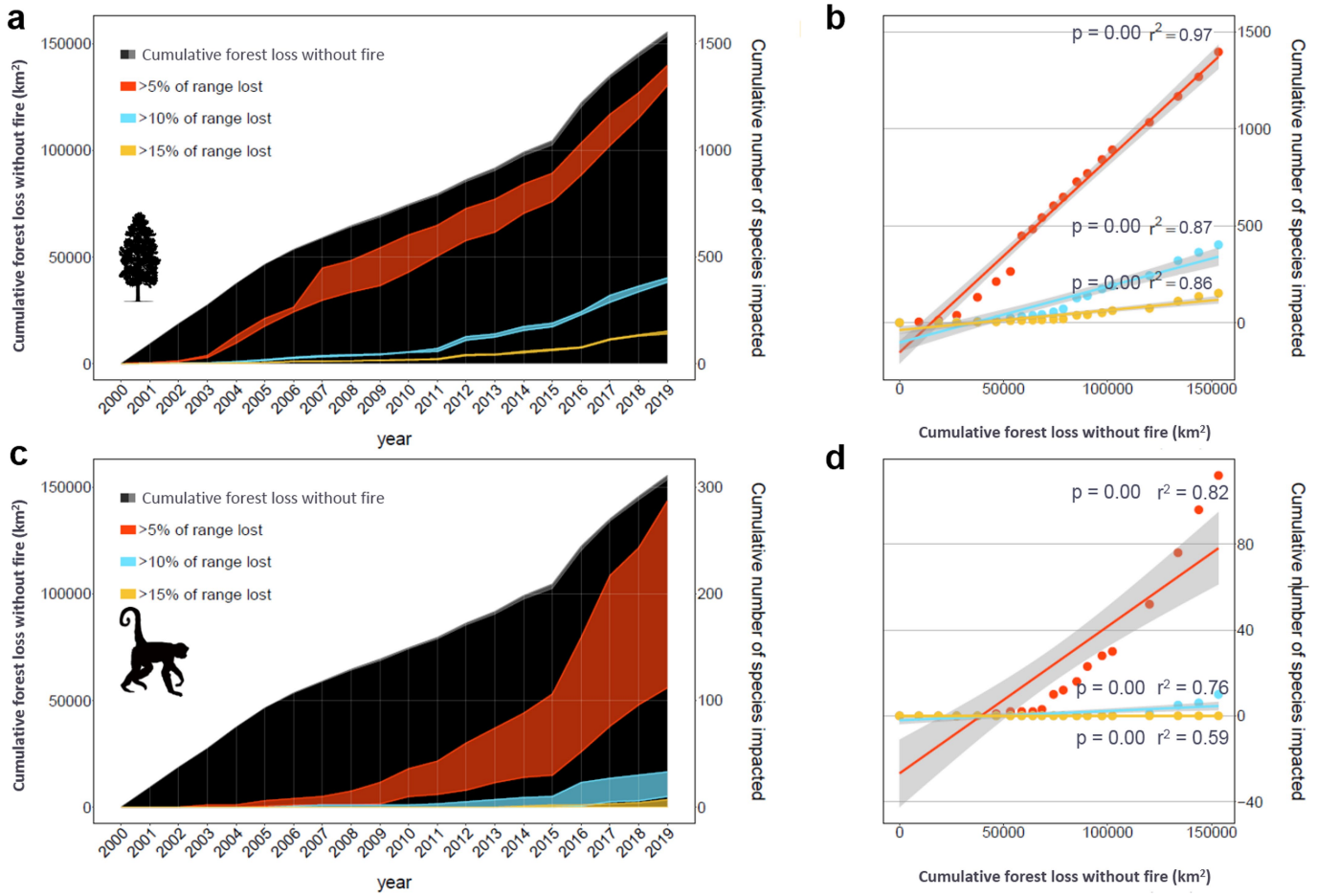
Extended Data Fig. 2 | Scatter plot of species' range impacted by fire. Scatter plot of species' range size in Amazon forest (x-axis) and percentage of total range impacted by fire (red) and forest loss without fire (black) up to 2019 for plants (left panel) and vertebrates (right panel).



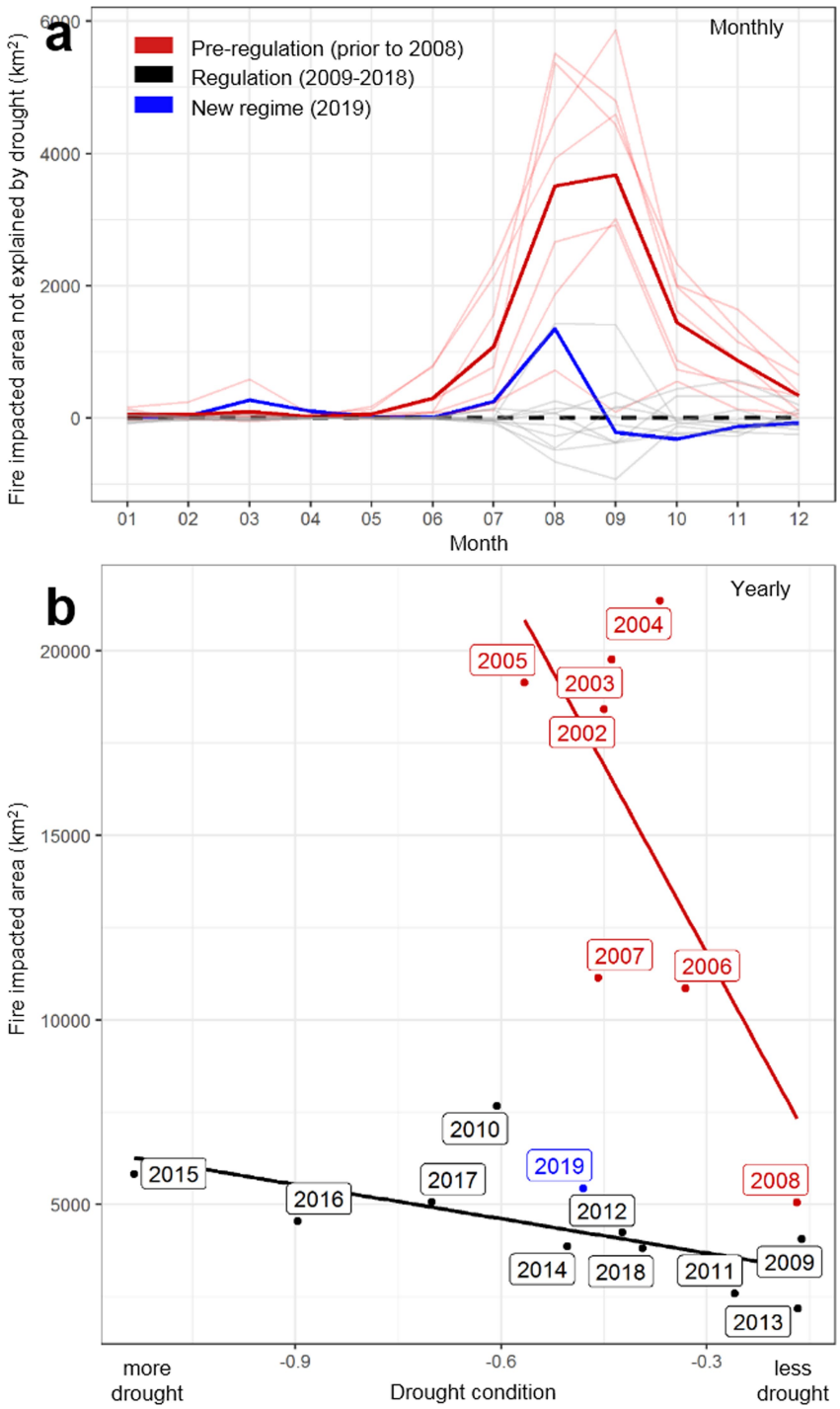
Extended Data Fig. 3 | Density plot of species' cumulative range impacted by fire. Density plot of species' cumulative range impacted by fire. The different colours represent years 2001-2019. The x-axis is log10 transformed.



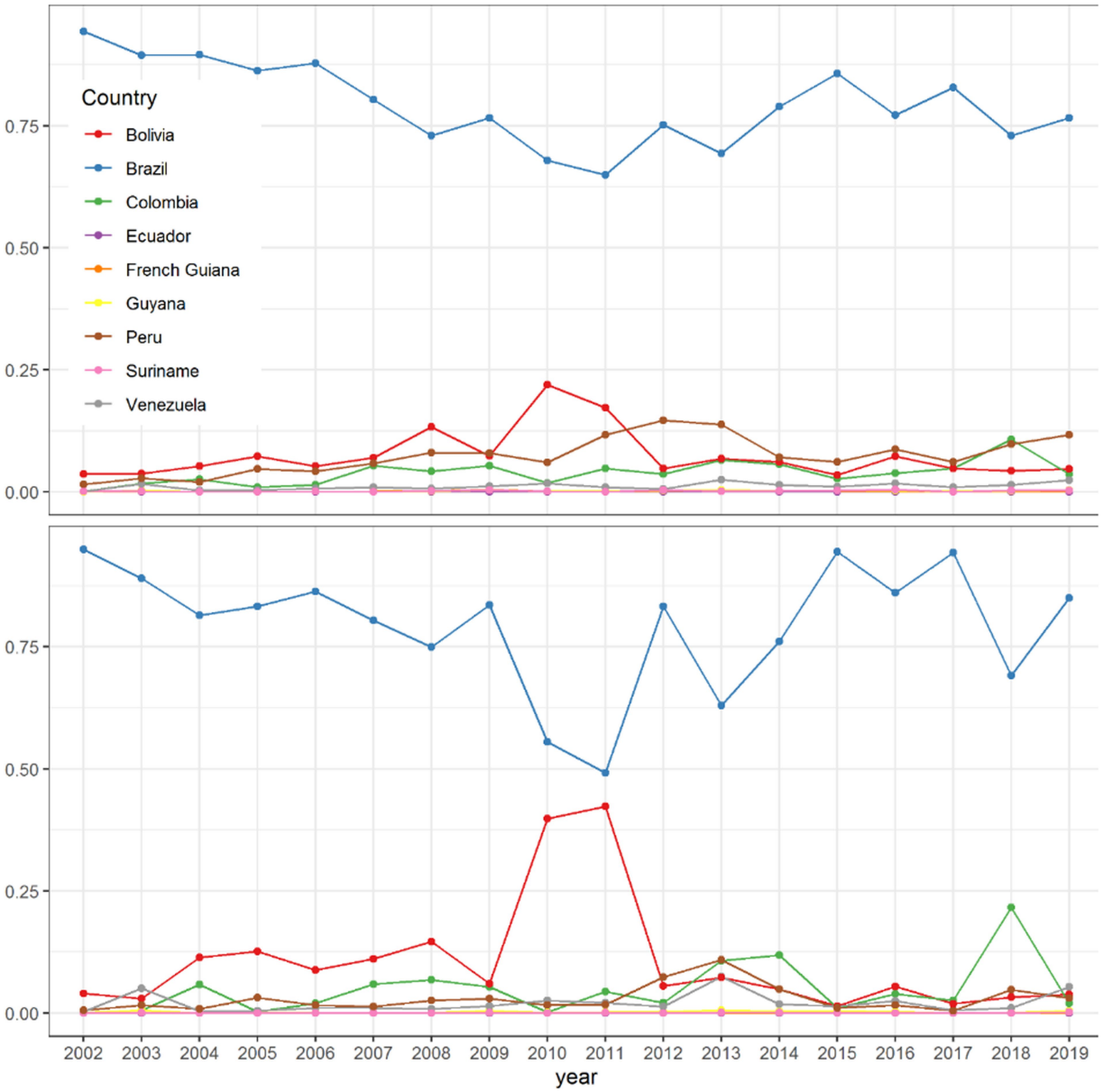
Extended Data Fig. 4 | Summary of forest impacts in the Amazon Basin. Areas of forest impact in the Amazon Basin estimated from MODIS burned area (top) and MODIS active fire (bottom).



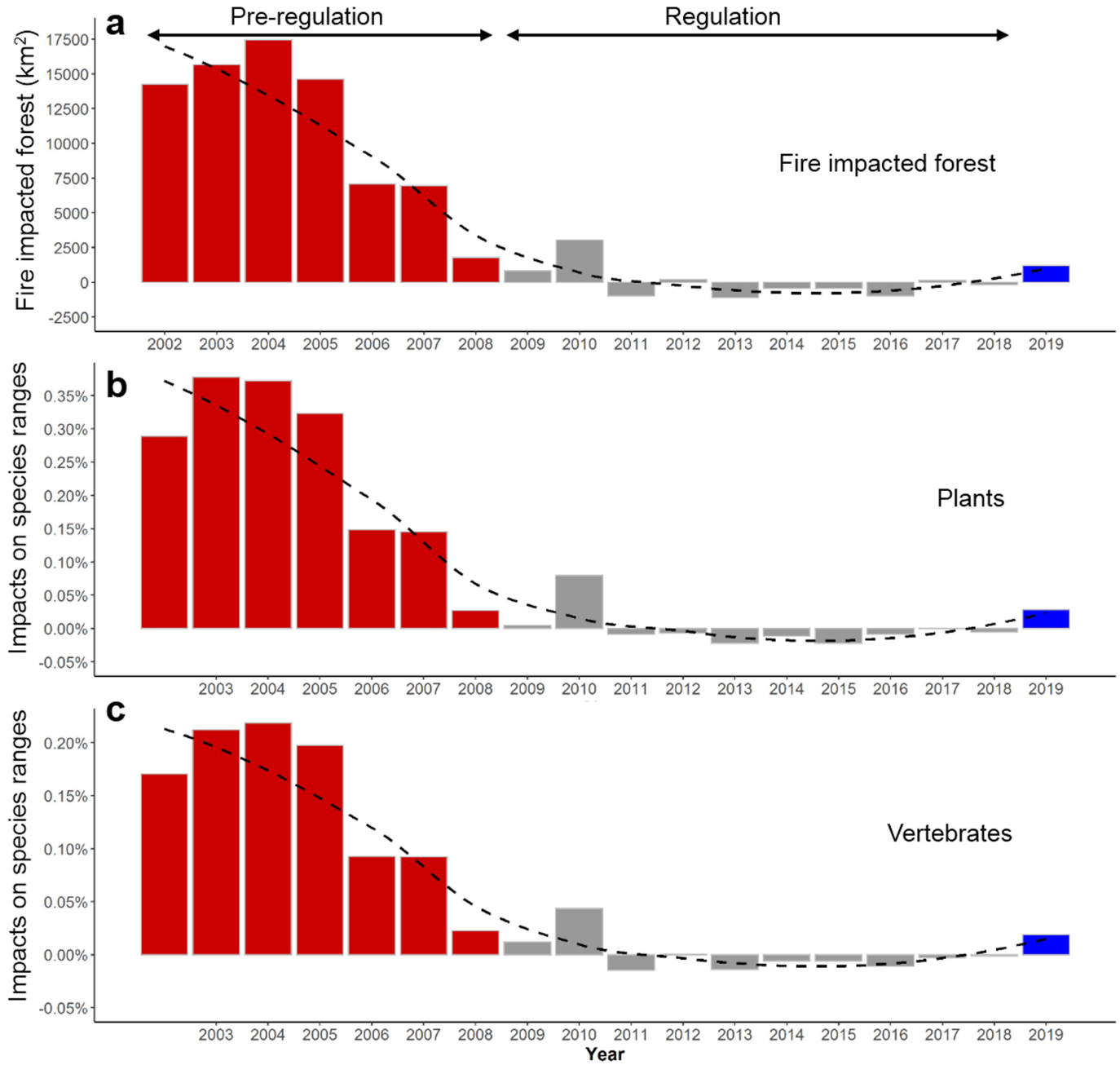
Extended Data Fig. 5 | Cumulative impacts on biodiversity in the Amazon Basin. Cumulative effects of forest loss without fire on biodiversity in the Amazon rainforest. In the left panels, the black and grey shading represent the cumulative forest loss without fire based on MODIS burned area and MODIS active fire, respectively. Coloured areas represent the lower and upper bounds of cumulative numbers of **a**, plant and **c**, vertebrate species' ranges impacted. Right panels depict the relationships between the cumulative forest loss without fire (based on MODIS burned area) and cumulative number of **b**, plant and **d**, vertebrate species. Coloured lines represent predicted values of an ordinary least squares linear regression and grey bands define the two-sided 95% confidence interval (two-sided, *p* values = 0.00). The silhouette of the tree is from http://phylopic.org/; silhouette of the monkey is courtesy of Mathias M. Pires.



Extended Data Fig. 6 | Fire-impacted forest in Brazil. Newly fire-impacted forest in Brazil (based on MODIS active fire). **a** shows the area of fire-impacted forest not explained by drought conditions. Different colours represent years from different policy regimes: pre-regulations in light red (mean value in dark red), regulation in grey (mean value in black dashed line), and 2019 in blue. The y-axis represents the difference between actual area and area predicted by drought conditions calibrated by data from regulation years (Methods). A positive value on the y-axis represents more area than expected, using the regulation years as a baseline. **b** shows a scatter plot of newly fire-impacted forest in Brazil and drought conditions (SPEI); The lines represent the ordinary least squares linear regression between fire-impacted forest and drought conditions for pre-regulation (red) and regulation (black) respectively.



Extended Data Fig. 7 | Fire-impacted forest in different countries. The contribution (0–1) of different countries to the newly fire-impacted forest each year based on MODIS active fire (top) and MODIS burned area (bottom).



Extended Data Figure 8 | Impacts of fire on forest and biodiversity in Brazil. **a**, Newly fire-impacted forest, **b**, new range impact on plants and **c**, new range impacts on vertebrate species in Brazil each year (based on MODIS active fire) that are not predicted by drought conditions. The colours represent three policy regimes: pre-regulation in red, regulation in grey and 2019 in blue. The y-axis represents the difference between actual value (area or range impacted by fire) and the values predicted by drought conditions calibrated by data from regulation years (Methods). A positive value on the y-axis represents more area or range impacted by fire than the expectation using the regulation years as a baseline. The dotted lines represent a smooth curve fitted to the values based on the loess method.

Extended Data Table 1 | Summary of fire-impacted forest

Year	Fire impacted forest				Fire-impacted forest with forest loss				Fire-impacted forest without forest loss			
	MODIS burned area		MODIS active fire		MODIS burned area		MODIS active fire		MODIS burned area		MODIS active fire	
	cumulative	newly	cumulative	newly	cumulative	newly	cumulative	newly	cumulative	newly	cumulative	newly
2001	4,513	4,513	3,505	3,505	2,300	2,300	1,136	1,136	2,213	2,213	2,369	2,369
2002	14,972	10,459	23,033	19,528	7,208	4,908	5,567	4,431	7,764	5,551	17,466	15,096
2003	25,580	10,608	45,139	22,106	11,394	4,186	9,819	4,252	14,186	6,422	35,320	17,854
2004	37,236	11,655	68,990	23,851	16,409	5,015	14,878	5,060	20,827	6,640	54,112	18,792
2005	49,032	11,796	91,165	22,175	20,113	3,704	18,346	3,468	28,919	8,092	72,819	18,707
2006	53,894	4,862	103,527	12,362	21,975	1,863	20,144	1,798	31,918	2,999	83,383	10,564
2007	64,317	10,423	117,409	13,882	23,807	1,832	21,692	1,547	40,510	8,592	95,718	12,335
2008	66,654	2,337	124,341	6,932	24,549	742	22,475	783	42,105	1,595	101,866	6,149
2009	68,288	1,634	129,653	5,312	24,820	271	22,860	385	43,467	1,363	106,793	4,927
2010	79,777	11,490	140,954	11,301	26,376	1,555	24,041	1,181	53,402	9,935	116,914	10,120
2011	81,547	1,770	144,938	3,984	26,701	326	24,439	398	54,846	1,445	120,499	3,586
2012	83,657	2,110	150,582	5,644	27,575	873	25,321	882	56,083	1,237	125,262	4,762
2013	84,546	889	153,729	3,147	27,811	237	25,709	388	56,735	652	128,020	2,759
2014	86,224	1,678	158,627	4,898	28,402	591	26,479	770	57,822	1,087	132,148	4,128
2015	90,395	4,171	165,422	6,795	29,255	853	27,472	992	61,140	3,318	137,951	5,802
2016	93,720	3,325	171,309	5,887	31,187	1,932	29,241	1,769	62,532	1,393	142,069	4,118
2017	97,693	3,974	177,431	6,121	33,500	2,313	30,968	1,727	64,193	1,661	146,463	4,394
2018	99,869	2,176	182,651	5,220	34,375	875	32,082	1,114	65,494	1,301	150,569	4,106
2019	103,079	3,210	189,755	7,105	36,146	1,771	33,874	1,792	66,932	1,439	155,882	5,313

The cumulative and newly fire-impacted forest (km^2) estimated from MODIS products.

Extended Data Table 2 | Summary of regression analyses

	(Intercept)	Drought (SPEI)	Regulation	Regulation * Drought	R^2	N
Newly fire impacted forest based on MODIS active fire (Brazil)	1600.28 (4220.4) (0.71)	-33991.65 (10196.92) (0.01)	1160.96 (4665.54) (0.81)	30897.81 (10713.62) (0.01)	0.82	17
Newly fire impacted forest based on MODIS active fire (Amazon)	1208.89 (3429.19) (0.73)	-52643.52 (10734.83) (0.00)	2501.12 (3940.94) (0.54)	48199.77 (11339.6) (0.00)	0.88	17
Newly fire impacted forest based on MODIS burned area (Brazil)	-1410.11 (2147.74) (0.52)	-22612.66 (5189.15) (0.00)	1916 (2374.27) (0.43)	18952.76 (5452.1) (0.00)	0.84	17
Newly fire impacted forest based on MODIS burned area (Amazon)	-505.36 (3373.64) (0.88)	-30768.31 (10560.94) (0.01)	1273.89 (3877.1) (0.75)	25419.41 (11155.91) (0.04)	0.69	17

Summary of ordinary least squares linear regressions (two-sided) using newly fire-impacted forest by year as dependent variable and annual Standardized Precipitation Evapotranspiration Index (SPEI) and policy regime (pre-regulation or regulation) as independent variables. The estimated coefficients are followed by standard error and *P* value.

nature research

Corresponding author(s): Xiao Feng

Last updated by author(s): Jun 23, 2021

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	The distribution records in BIEN database were compiled using PostgreSQL (version 10.17).
Data analysis	The remote sensing data were processed on Google Earth Engine (accessed March 2021). The R packages spthin (version 0.2.0) and outliers (version 0.14) were used in occurrence data cleaning. The algorithms glmnet (version 4.0-2) and range bagging (original version) were used in modeling plant distributions. The distribution maps were processed in R (version 3.5.1). The code is available from https://github.com/shandongfx/paper_Amazon_biodiversity_2021.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The plant occurrences from the BIEN database are accessible with the RBIEN package (https://github.com/bmaitner/RBIEN). The climatic data are accessible from http://worldclim.org and the soil data are available from http://soilgrids.org. MODIS active fire and burned area products are available at http://modis-fire.umd.edu. The MODIS Vegetation Continuous Fields data are available from https://lpdaac.usgs.gov/products/mod44bv006/. The annual forest loss layers are publicly available from http://earthenginepartners.appspot.com/science-2013-global-forest. The plant range maps are accessible from this repository (https://github.com/shandongfx/paper_Amazon_biodiversity_2021). The vertebrate range maps are available from https://www.iucnredlist.org/resources/spatial-data-download. The

SPEI data are available from SPEI Global Drought Monitor (https://spei.csic.es/map).

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This manuscript studied the impact of forest fires on the distribution of plant and vertebrate species in the Amazon basin.
Research sample	Four sources of remote sensing data were used: MODIS active fire and burned area products are publically available at http://modis-fire.umd.edu. The MODIS Vegetation Continuous Fields data are publicly available from https://lpdaac.usgs.gov/products/mod44bv006/. The annual forest loss layers are publicly available from http://earthenginepartners.appspot.com/science-2013-global-forest. The distribution maps of plant and vertebrate species were from BIEN database (Botanical Information and Ecology Network; http://bien.nceas.ucsb.edu/bien/about/) and IUCN spatial data portal (https://www.iucnredlist.org/resources/spatial-data-download).
Sampling strategy	We restricted the study area to the Amazon Basin, using a refined boundary of Amazon based on terrestrial ecoregions of the world (Olson et al. 2001; Flores et al. 2010). We only included plant species were recorded in a recently published checklist of Amazonian plants (Cardoso et al. 2017) and that had distribution maps available. For vertebrates, we used IUCN-provided expert maps that have been vetted by taxon specialists that offer comparatively complete coverage of known species. Range polygons coded as 'extant' and 'resident' for all species were obtained from the IUCN spatial data portal.
Data collection	The remote sensing data were processed using Google Earth Engine platform, by coauthors Z.L. and X.F. The distribution records in BIEN were compiled from data contributors, led by coauthors B.B. and B.J.E. using PostgreSQL on a linux server. The generation of plant distribution maps were led by coauthors C.M and X.F. in R (version 3.5.1) using a linux server. The vertebrate range maps were download from IUCN website (https://www.iucnredlist.org/resources/spatial-data-download) and processed by coauthor P.R. in R (version 3.5.1) using a desktop computer.
Timing and spatial scale	We obtained monthly active fire and burned area, at 1km and 500m resolution respectively, from January 2001 to December 2019 across the Amazon Basin. We aggregated the monthly pixel-level burned area into annual pixel-level burned area (1-burned, 0-unburned). We also obtained forest land cover data at 250 meter resolution from the MODIS Vegetation Continuous Fields data. We obtained annual forest loss layers at 30 meter resolution. The spatial and temporal resolutions represent the highest resolution available from those products. The temporal range represents the availability of data when this study was carried out.
Data exclusions	We excluded plant species that are not recorded in a recently published checklist of Amazonian plants (Cardoso et al. 2017). We only included species that have over 10% of their range within the Amazon forest, in order to exclude species with large geographic ranges or species with little ranges in the Amazon forest.
Reproducibility	Each step of the workflow has been implemented more than once and checked by two or more coauthors. When necessary, we used a fixed seed for the random number generator. Therefore, the results are reproducible.
Randomization	Our study does not involve assigning samples to different experimental groups, so randomization is not applicable to this study.
Blinding	Our study is not experimental, so blinding is not applicable to this study.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging