Floodplains as an Achilles' heel of Amazonian forest resilience

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Edited by Gregory P. Asner, Carnegie Institution for Science, Stanford, CA, and approved March 14, 2017 (received for review October 29, 2016)

The massive forests of central Amazonia are often considered relatively resilient against climatic variation, but this view is challenged by the wildfires invoked by recent droughts. The impact of such fires that spread from pervasive sources of ignition may reveal where forests are less likely to persist in a drier future. Here we combine field observations with remotely sensed information for the whole Amazon to show that the annually inundated lowland forests that run through the heart of the system may be trapped relatively easily into a fire-dominated savanna state. This lower forest resilience on floodplains is suggested by patterns of tree cover distribution across the basin, and supported by our field and remote sensing studies showing that floodplain fires have a stronger and longer-lasting impact on forest structure as well as soil fertility. Although floodplains cover only 14% of the Amazon basin, their fires can have substantial cascading effects because forests and peatlands may release large amounts of carbon, and wildfires can spread to adjacent uplands. Floodplains are thus an Achilles' heel of the Amazon system when it comes to the risk of large-scale climate-driven transitions.

climate change | tropical forest | tropical savanna | fire | drought

The sensitivity of the Amazon rainforest to climate change is a central issue in global change research (1, 2). In particular, there are concerns that a drier climate may promote a shift from forest to savanna (3, 4). All studies so far suggest that this is most likely at the southern and eastern peripheral regions where precipitation is relatively low and seasonal (2–5) and the risk of wildfires is higher (4, 6–11). Although rainfall is a dominant factor explaining forest resilience, other environmental factors obviously play a role (12–14). Arguably, the most striking variation in the nature of forests in the wet Amazonian system is related to seasonal inundations. Approximately one-seventh of the Amazon is inundated a substantial part of the year (15), causing these ecosystems to differ in many ways from the dominant upland terra firme forests (*SI Brief Ecology of Floodplain and Upland Ecosystems*). Here we ask whether these differences related to seasonal inundation affect forest resilience and the risk of shifting into a fire-dominated savanna state. We used two approaches to contrast the resilience of floodplain and upland forests across the Amazon (Fig. 1 *A* and *B*). First, we estimated the long-term relative resilience of forest and savanna in both ecosystems from the density distributions of tree cover (3, 16) using MODIS vegetation continuous field (VCF) data at 250 m resolution (*SI Methods*). Second, we studied postfire recovery of both forest types using field and remote sensing data (Fig. S1). Using annual MODIS VCF data, we measured the recovery of over 250 sites that burned during the severe droughts of 1997 and 2005 (Fig. S1; Table S1; and Dataset S1). Using field data on tree basal area and soil variables from multiple burned forests in the central Amazon region, we validated the basin-wide analyses of postfire recovery (Fig. S1 and *SI Methods*).

The rationale behind studying the density distributions of tree cover is that under homogeneous environmental conditions (14), density distributions may reveal alternative attractors in the vegetation and their relative resiliencies (3, 16, 17). Comparative studies across the global tropics (3, 4) reveal that tree cover tends to be either high or low, with intermediate (~50%) cover being remarkably rare. The interpretation is that closed forest and savanna are attractors, and the intermediate state is an intrinsically unstable repellor. In fact, one may reconstruct the well-known potential (ball-in-cup) landscapes directly from the data. The mathematical underpinning is somewhat technical (17), but the idea is intuitively straightforward. Thinking of long time-spans, one can imagine that stochastic events occasionally push the system over the boundary between the basins of attraction of alternative attractors. Sampling such a system long enough, one thus expects it to be sometimes close to one of the attractors (e.g., forest), sometimes close to the alternative attractor (e.g., savanna), and more rarely somewhere in between (16). Importantly, in places where forest is relatively more resilient, the system will spend more time in the state with high tree cover, whereas in places where savanna is relatively more resilient, the system will spend more time in the state with low tree cover. Thus, the ratio of the number of observations in the forested state vs. the number of observations in the savanna state tells us something about the relative resiliencies of the two alternative states. We do not have long time-series, but if information for sufficient sites of

Significance

Climate change may alter the distribution of biomes in tropical regions with implications for biodiversity and ecosystem services. Here we reveal that if the Amazon region becomes drier as predicted, forests may collapse first on seasonally inundated areas due to their vulnerability to wildfires. The widespread distribution of floodplain forests at the western and central regions implies that fire-prone savannas may expand deep into this massive forest biome, threatening the resilience of the entire system. Our findings suggest the need for a strategic fire management plan to strengthen Amazonian forest resilience in the face of climate change.

Author contributions: B.M.F., M.H., and M.S. designed research; B.M.F., M.H., C.X., C.C.J., and M.S. performed research; B.M.F., C.X., C.C.J., and R.C.G.M. contributed new reagents/analytic tools; B.M.F., M.H., C.X., E.H.v.N., and M.S. analyzed data; and B.M.F., M.H., and M.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1617988114/-/DCSupplemental.

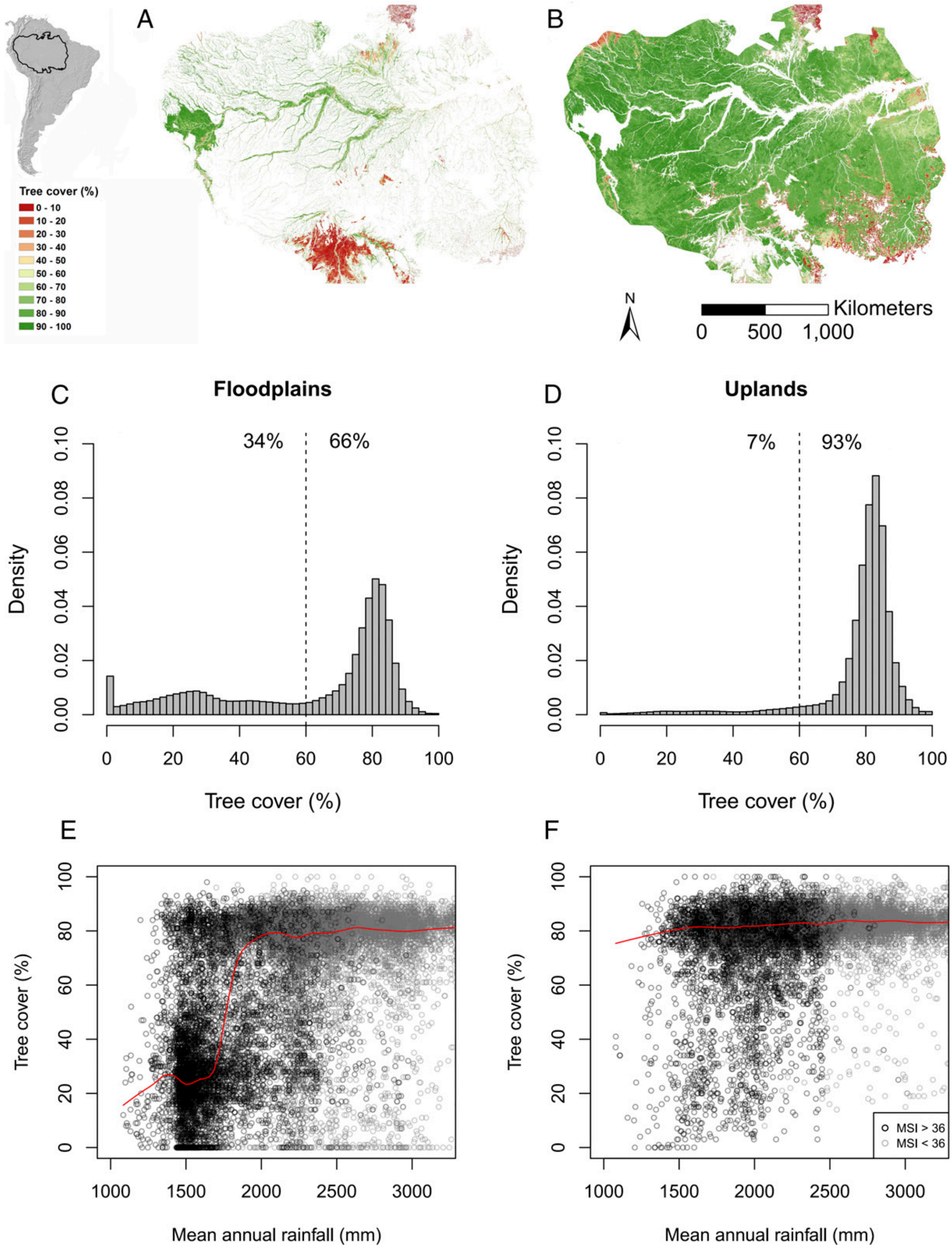

Fig. 1. Distribution of tree cover across the Amazon basin. (*A*) Floodplains and (*B*) uplands separated by the wetlands' mask (15). Deforested areas were excluded (*SI Methods*). Density distributions of tree cover for (*C*) floodplains and (*D*) uplands. A cutoff at 60% tree cover (dashed lines) separates forest from savanna (3), and percentage values are the proportion in each state. Relation between mean annual rainfall and tree cover for (*E*) floodplains and (*F*) uplands. Markham seasonality index values >36 (black circles) and <36 (gray circles) are shown. Red lines are fitted locally weighted scatterplot smoothing (LOWESS). Circles are 15,000 data points randomly sampled for each case.

comparable conditions is available, one may interpret snapshots of the states on all sites in the same way as one would interpret samples from a single, long time-series. Such a space-for-time substitution has been used before to show how resilience of tropical forest and savanna varies with mean annual precipitation (3). We now use the same approach to infer how resilience of

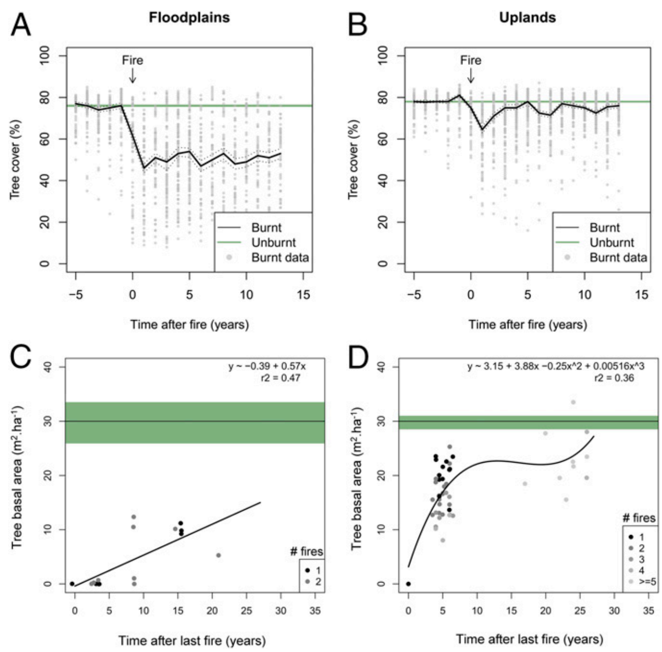

Fig. 2. Compared sensitivity of floodplain and upland forests to fire. Time series of annual tree cover (median ± SE) showing changes after a fire in (*A*) floodplains and (*B*) uplands. After fire (time = 0), tree cover median persists below 50% in floodplains, yet recovers in uplands. Field data on tree basal area recovery after the last fire in (*C*) floodplains and (*D*) uplands of the central Amazon. For all plots, green shaded area is SE intervals for unburned forests. In *D*, unburned reference was obtained from ref. 40 (see *SI Methods* for details).

forest and savanna varies between floodplains and uplands of the Amazon.

Results and Discussion

In Amazonian uplands, the density distribution of tree cover has a single mode around 84%, reflecting dense forest, with sparse tree cover being rare (Fig. 1*D* and Fig. S2*B*). In contrast, floodplains have an additional mode around 34% tree cover, reflecting the presence of a savanna state (Fig. 1*C* and Fig. S2*A*). As explained previously, assuming our density distributions (Fig. 1 *C* and *D*) reflect long-term dynamics of a stochastically perturbed system, the ratio of the number of observations falling in the two modes reflects their relative resiliencies (3, 16). Forest/savanna ratios we found suggest that forests are much less resilient in floodplains than in uplands (ratios of 66/34 vs. 93/7; Fig. 1 *C* and *D* and Table S2). The difference is especially pronounced in parts of the Amazon where rainfall is relatively lower, more seasonal, and interannually variable (Fig. 1 *E* and *F* and Fig. S3). From the relation between tree cover and rainfall, we computed potential landscapes (Fig. S4 and *SI Methods*), which revealed that a savanna basin of attraction appears around 1,500 mm of mean annual rainfall in floodplains. In uplands, a hint of the savanna basin of attraction only becomes apparent around 1,000 mm of annual rainfall.

Thinking of our tree cover density distributions as the long-term balance between shifts from forest to savanna and vice versa, the forest/savanna ratio should approximately reflect the average time that the system spends in each state (16). Long-term tree cover time-series are lacking, making it difficult to check this inference systematically. An alternative is to analyze the response of the system to stochastic perturbations. Wildfires have been the dominant historical mechanism driving shifts from forest to savanna in times when climate was drier and seasonal (4, 18). The megadroughts of 1997 and 2005 invoked a large number of wildfires in Amazonian upland and floodplain forests (6–9), allowing us to compare their resilience. Our remotely sensed information from over 250 burned forest sites reveals that fires had a strong and long-lasting impact on tree cover in the floodplains, whereas in the uplands, effects of fire were typically small and ephemeral (Fig. 2 *A* and *B* and Fig. S5). This broad-scale pattern was confirmed by field measurements in burned forests of the central Amazon region, showing a systematically lower recovery rate of tree basal area in the floodplains (Fig. 2 *C* and *D*). We also found a marked decrease in soil nutrients and fine clay particles in floodplain forests upon fire that was absent in the uplands (Fig. 3).

In summary, the observed difference in density distributions of tree cover indicates that floodplain forests are relatively less resilient and therefore less likely to persist in the long run, which does not imply that upland forests are resilient, but rather that their resilience depends on overall environmental conditions. In fact, our results suggest that at ∼1,000 mm of mean annual rainfall, upland forests reach a tipping point in which they may collapse into a savanna state (Fig. S4). As climatic conditions change, however, such tipping points will likely be reached first by forests on seasonally inundated areas. Our detailed field and remote sensing measurements of the response to fire confirm this pattern and suggest an explanation. Both the slow forest regrowth and the quick loss of soil fertility plausibly make these floodable forests more likely to be trapped by repeated fires in an open vegetation state. Indeed, studies in other forest systems reveal that canopy openness upon the first fire enhances the risk of subsequent fires (19) and the spread of herbaceous vegetation (7, 10, 11). The loss of tree cover to fire allows the intensification of hydrological processes that lead to soil erosion and nutrient leaching (20), creating limiting conditions for forest regrowth that may instead favor savanna-adapted plant species (21). Another reason that makes floodplain forests more vulnerable is their

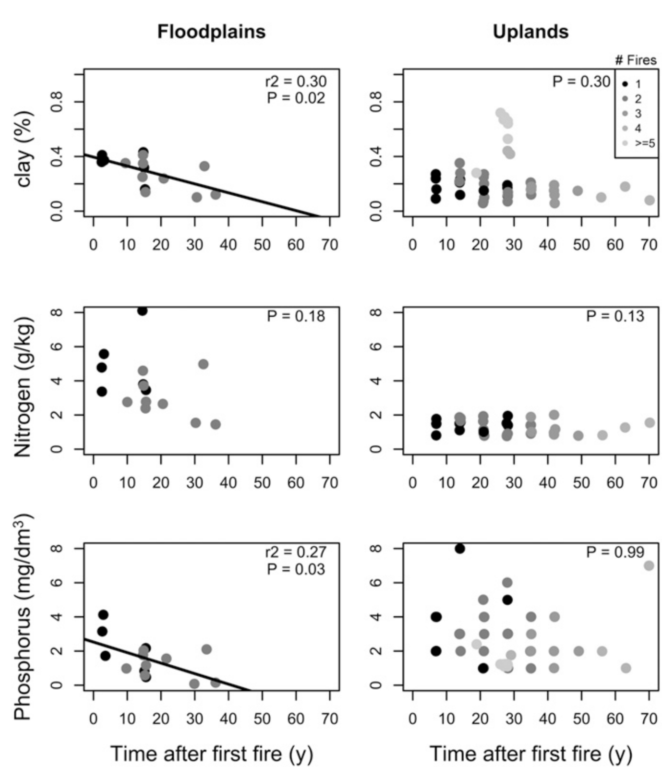

Fig. 3. Changes in soil texture and fertility that initiate with a forest fire. (*Left*) Floodplains. (*Right*) Uplands.

naturally higher flammability compared with upland forests. In addition to having a slightly more open structure (22, 23), upon the annual retreat of the waters, floodplain forests typically have large masses of exposed root mats (24) that burn easily and may spread fire effectively in drier years (6, 7) (Fig. S6). The combustion of this organic material by fire may plausibly facilitate subsequent floods to wash away nutrients and fine sediments, leaving behind relatively poor sandy soils. Overall, forest recovery upon fire in the floodplains may be hindered by a combination of recruitment limitations partly caused by lost soil fertility (Fig. 3) with seasonal inundation that restricts the time in which trees can grow (25).

Independent of the precise mechanisms slowing down forest recovery, patterns we revealed imply strong evidence that Amazonian forests on floodable terrains have a lower resilience when it comes to the risk of transition into a fire-prone vegetation state. Although these ecosystems cover 14% of the basin, there are two reasons why their vulnerability may have substantial cascading effects. First, floodplains in the western and central Amazon include peatlands that store enormous amounts of carbon (estimates of ~3.14 Pg C, available only for western peatlands) (26, 27), which could potentially be released to the atmosphere by fire. Second, our results imply that if the climate becomes drier, fire-prone savannas might expand through floodable areas toward the core of the Amazon forest and become sources of fires that may spread to large parts of that region. Indeed, the spread of fires from floodplains to adjacent uplands has been shown in Africa (28) and central Amazon (22) with negative impacts on vegetation structure (22) and biodiversity (29). In conclusion, our results suggest that seasonally inundated forests throughout the Amazon represent an Achilles' heel when it comes to resilience of this massive system. Considering the projected increase in dryness (30) and expected effects of climatic variability intensification on tropical vegetation (31), it follows that maintaining a safe operating space for the Amazon forest (32) may require special protection not only of the driest parts of the Amazon forest, but also of the floodable heart of the system.

Methods

To contrast the resilience of Amazonian floodplain and upland forests, we first analyzed density distributions of tree cover for the entire basin using MODIS VCF data at 250 m spatial resolution (*SI Methods*). We also analyzed postfire recovery rates as a measure of resilience for over 250 sites in both forest types using annual tree cover data from MODIS VCF at 250 m (*SI Methods*). To identify forest fires, we selected eight Landsat scenes with extensive areas of floodplain and upland to allow equal probability of observing forest fires. These scenes are distributed across the Amazon basin and cover most of the annual rainfall gradient (1,500–3,000 mm; Fig. S1). In each scene we identified forest sites that were burned during the droughts of 1997 and 2005 using a systematic visual method (33). This method allows distinguishing fire from other disturbances because signs from fire typically have rounded borders and fade away quickly. It has proven to be effective for floodplain forests (6, 7), and we found it to be even more effective on uplands where signs of fire disappear within 3 y (Fig. S5). In each scene we identified multiple sites to accommodate MODIS pixels (250 m), spreading their locations within the burned and unburned areas, maintaining at least 1 km distance between two pixels and from perennial water bodies (see all sites in Dataset S1).

To ground-truth our basin-wide remote sensing analysis of tree cover recovery after wildfires, we analyzed tree basal area and soil data from field sites at the central Amazon region (Fig. S1). In both floodplain and upland areas, we selected a series of forest sites with different "times since the last fire" to produce chronosequences (space-for-time) and measure recovery rates of tree basal area [>1 cm in diameter at breast height (DBH)]. Using these same sites, we produced chronosequences of "time since the first fire" (when mature forests were burned for the first time) to analyze changes that may have occurred in the superficial soil fertility (0–20 cm depth) while repeated fires maintained the vegetation vulnerable to soil erosion (20).

In this study we considered forest and savanna as alternative vegetation states with contrasting structure and plant composition, maintained by positive feedbacks among plants, fire, and soil (34). Different lines of evidence support the use of tree cover data from MODIS VCF to assess forest and savanna distribution and resilience. VCF has been validated in the field with a relationship of 95% with crown cover (35) and 56% with forest biomass (36); more recently it was shown to have a good correlation with field tree cover across the whole tropics (37). Spatial patterns of VCF correlate well with tree canopy height, distinguishing degraded forests from savannas as well as closed savannas from forests (38). Because closed canopies are known to suppress fire percolation, forests that recover faster also recover their capacity to suppress recurrent fires (39); therefore, VCF also indicates spatial variation in flammability. In addition, VCF provides us massive data on forest tree cover at global scales.

Most data sets used in this study are openly available and have been used in other publications. The location of all wildfires studied from remote sensing can be found in Dataset S1. For access to field data from burned upland forests, contact C.C.J. for the Tefé area and R.C.G.M. for the Manaus area. Field data from burned floodplain forests at Barcelos are available from a previous publication (7).

ACKNOWLEDGMENTS. We thank G. G. Mazzochini for assistance with R scripts for remote sensing analyses, and J. L. Attayde, M. C. X. Flores, C. R. Fonseca, C. Levis, P. Massoca, A. Staal, and E. Venticinque for helpful comments. Support for this work was provided by National Council for the Improvement of Higher Education, Brazil, and the Sandwich Fellowship Program from Wageningen University (to B.M.F.); National Natural Science Foundation of China Grant 41271197 (to C.X.); and an European Research Council Advanced Grant (to M.S. and E.H.v.N.). This work was partially carried out under the program of the Netherlands Earth System Science Centre.

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