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River logjams cause frequent large-scale forest die-off events in Southwestern Amazonia.

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Abstract. This paper investigates the dynamics of logjam-induced floods and alluvium deposition in the Bolivian Amazon and the effects these have on forest disturbance/recovery cycles. It expands on previous work by Gullison et al (1996) who reported a case of catastrophic floods triggered by logjams in the Chimane Forest on the Bolivian Amazon. No further studies have followed up on this observation and no research has been published on the effects of large wood in tropical lowland rivers. The study is based on the analysis of a time series of Landsat imagery (1984 – 2016) and field evidence. Results show that logjam-induced floods are a major driver of forest disturbance along the Andean piedmont in the Bolivian Amazon. Logjams form on an almost yearly basis and migrate upriver until an avulsion takes place. Logjam-induced floods are here characterized by a sudden deposition of a thick sand layer and the death of forest in a V-shaped area. The Bolivian Amazon offers a unique opportunity to further research on how large wood affects river behavior in lowland tropical settings and how large and frequent forest disturbance events resulting from river logjams affect forest biodiversity and community successions.

1 Introduction

Understanding the spatial and temporal frequency of disturbance events is of great relevance to forest ecologists, due to the importance of disturbance in shaping forest ecological processes (Asner, 2013). Forest disturbance and recovery cycles affect forest tree species distribution, community composition, ecosystem processes, biodiversity patterns, nutrient cycles and the carbon balance (Chambers et al., 2013; Lewis et al., 2004; Phillips et al., 2004; White and Jentsch, 2001). Disturbance events are commonly classified along a continuum that goes from small scale/frequent events, such as a tree fall that creates an open space, to large scale/more rare events, such as large fires (White and Jentsch, 2001). The study of the geography of forest disturbance is particularly important in Amazonia, as it is home to about 10% of world's biodiversity (Lewinsohn and Prado, 2005) and among the most important terrestrial carbon sinks (Pan et al., 2011).

In Amazonia, where large forest fires are uncommon and there are no hurricanes, large scale disturbance (>30 Ha) is mostly caused by blowdowns (Nelson et al., 1994) that result from convective cloud downdrafts (Garstang et al., 1998). However, at least in Western Amazonia, studies have shown that river activity can also be an important driver of forest disturbance and landscape reshaping via lateral erosion, overbank deposition, crevasse formation and avulsions (Aalto et al., 2002; Kalliola et al., 1992; Lombardo, 2016; Salo et al., 1986).

Earth System Dynamics
Discussions

In 1996, Gullison et al. (1996) observed that 48000 hectares of forest in the Bolivian Amazon died-off and were replaced by savannah due to scouring, flooding and the deposition of alluvial sediments. These processes were caused by the overbank flow of the Cuberene River triggered by a logjam. Here, the term logjam refers to a partial or complete obstruction of a river channel caused by large wood (LW). Logjams can affect rivers and floodplains in several ways. They can decrease stream flow to an extent that it leads to bank erosion and overbank flow, influencing channel-floodplain interactions and shaping the evolution of floodplain topography (Montgomery and Abbe, 2006; Sear et al., 2010; Wohl, 2013). Logjams are also an important component of river ecosystems, as they influence the transfer of solutes, mineral sediment and organic material within the river channel system and between river and floodplain (Coe et al., 2009; Gurnell et al., 2002; Jochner et al., 2015; Wohl and Beckman, 2014). Despite the fact that logjams can have a dramatic impact on fluvial dynamics and fluvial-floodplain exchanges, their systematic study is relatively recent and has mostly been carried out in temperate zones (Dixon, 2016; Ruiz-Villanueva et al., 2016; Wohl, 2017, 2013). Very few studies have looked at the wood-river interactions in the neotropics and these have mostly focused on headwater rivers (Cadol and Wohl, 2011, 2010; Iroumé et al., 2015; Wohl et al., 2012). Wohl (2017) reports that no field-based studies of LW in Amazonian rivers has ever been published in the English-language literature. Nevertheless, the observations of Gullison et al. (1996) do suggest that logjams are an important factor driving forest disturbance and biodiversity patterns in the Bolivian Amazon. For example, it has been shown that the increase in light that follows forest die-off events caused by logjams creates optimal conditions for the regeneration of Mahogany *(Swietenia macrophylla* King), influencing its population dynamics (Gullison et al., 2003; Snook, 1996). Gullison et al. (1996) also reported the transformation of large areas of forest into savannahs after being flooded. Despite these indications of the importance of logjams in shaping Bolivian forests, no further studies have followed up on Gullison et al. (1996). As of today, very little is known about the spatial extent and recurrence of these logjam-induced floods.

In this paper, I use a time series of Landsat imagery and field evidence to study logjam-induced floods and alluvium deposition in the Bolivian Amazon and map their extent and recurrence. I discuss why logjams form in these rivers and how they affect modern forest disturbance/recovery cycles and pre-Columbian landuse in the past.

The Bolivian Amazon is largely covered by a seasonally flooded savannah known as the Llanos de Moxos. The area focus of this study is located between the flat Llanos and the Bolivian Andes, where lowland forests grow on relatively well drained fluvial sediments. This area of lowland forests is approximately 60 km wide and 400 km long and runs parallel to the Bolivian Andes (Fig. 1).

2 Methods

The phenomena described by Gullison et al. (1996) - formation of logjam, forest die-off and transformation of forest into savannah - can be studied through the visual analysis of remote sensing Imagery (Gullison et al., 2003). In this paper, rivers affected by logjam-induced floods have been identified by analyzing the changes in river path and vegetation cover visible on the Timelapse application of Google Earth Engine (https://earthengine.google.com/timelapse/). In the study area, the forested lowland bordering the Bolivian Andes piedmont, there are a total of 22 rivers that experience logjam-induced flooding (Fig. 1). These include all the small rivers between the River Secure and the Beni and all but three of the rivers north of the Beni River. A subset of eight of these rivers has been selected and their evolution analyzed throughout the period for which cloud-free landsat images are available: from 1984 to 2016. These have been chosen in order to cover the whole area where the logjam-induced floods take place and in order to have a representation of rivers of different size. These eight rivers are: the Tequeje, the Tacuaral, the Colorado and the Cuberene and other four rivers, here referred to as Y, Z, W and Q, for which the toponyms could not be found (Fig. 1). The location of the logjams (shown in Fig. 5) has been measured as the distance between the logjam and an arbitrary line parallel to the Andean piedmont. The Landsat coverage of these eight rivers during the period 1984-2016 has been downloaded through the USGS Landsat look viewer (https://landsatlook.usgs.gov/). Field work was carried out during the dry season of 2016. A survey was conducted along the Tacuaral and Colorado rivers (Fig.1), because of their easier access and the availability of local guides in these areas.

3 Results

Fig. 2 shows a few examples of forest die-off due to logjam-induced floods. Reddish plumes diverging from the river channel show dead forest. Here trees have lost their leaves and the soil has been covered with alluvium or eroded. As it can be seen in Fig. 2 and Fig. 3, logjams induce a total collapse of the river, as the totality of the river flow is diverted towards the forested floodplain and the river channel downstream of the logjam dries up. The areas where the forest has died off are also visible on the SRTM DEM as depressions of several meters (Fig. 4).

The analysis of Google Earth Engine Timelapse identified twenty-two rivers in this area of the Bolivian Amazon that are affected by logjam-induced floods. The river logjams occur within a 400 km long belt along the eastern Andean piedmont, from Lat -15.9 to Lat -13.5. All but two, of the 22 rivers affected by logjam-induced floods, have their headwaters on the eastern side of two small pre-Andean mountain chains (Fig. 1). The northern one, between the Beni River and the Maniqui River, has a maximum elevation of about 1100 m. a. s. l.; the southern mountain chain, between the Maniqui River and the Secure River, has a maximum elevation of 650 m. a. s. l. (Fig. 1B). Rivers originating in the southern part of the study area cross the Chimane Forest, where forest die-offs induced by logjams were first reported by Gullison et al. in the floodplain of the Cuberene River (Fig. 2A and Fig. 3). These small pre-Andean mountain chains act as a water divide between the basin of large rivers on the west (i.e. Maniqui and Secure Rivers in Fig. 1B) and smaller rivers to the east.

In the 8 rivers analyzed in greater detail, from 1984 to 2016, 174 logjams causing river collapse and forest die-off have been identified and mapped (Fig. 5). The eight rivers show a similar pattern: a new logjam forms upriver from the previous one almost every year, unless an avulsion takes place and the sequence restarts at a greater distance from the Andes (i.e. rivers Colorado, Cuberene, Tacuaral, Tequeje in Fig. 5). The average distance between successive logjams ranges from 1170 meters, in the case of the Cuberene, to 224 meters, in the case of the Colorado.

The river Tequeje, a left hand tributary of the Beni River, is the second largest among the 8 studied. During the period 1987-2016, there were 22 logjams forming along its course and the river underwent 2 avulsions (Fig. 5 and Fig. 6). This river shows all the features which characterize the main traits of the

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Earth System Dynamics
Discussions

behavior of the other rivers affected by logjam-induced floods in the study area. In 1987 (inset A in Fig 6.) a logjam-induced flood killed 173 hectares of forest in a characteristic V shape. The V shape is probably due to two reasons: 1) the fact that the forest in the inner part of the V had already been killed by the floods and sediment deposition of previous years and in 1987 it was covered with pioneer, fast growing vegetation (i.e. *Tessaria integrifolia* Ruiz & Pav.), and 2) the topographic high of sedimentary lobes left by previous floods, which favour the diversion of the water on both sides of the channel. In 1990, a new area was flooded, following the river avulsion of 1989 (inset B in Fig. 6). Here the dead forest has an oval shape, as this is the beginning of a new series of upstream logjam formations and no previous alluvium is diverting the overbank water. The area of savannah visible in 1987 is reduced by 1990 and not visible anymore in 2000 (inset C in Fig. 6). After the avulsion in 1996, logjams occur to the east of the area shown in Fig. 2, with the location moving upriver every year. By 2016, most of the area where the forest died off in 1987 is forested again. In 2016, the logjam is closer to the Andes than at any other moment during the 29 years studied. The sediments deposited between 2014 and 2016 have dammed two small tributaries that have been transformed into small lakes (inset E Fig. 2). Two small areas, which were forested in 1987, have been transformed into savannah after being constantly flooded between 2011 and 2016 (insets A, D, and E in Fig. 6). A total of about 8900 hectares of land have been flooded at least once by the Tequeje River during the 29 years analyzed. Of these, in 1987, 7100 hectares were forested and 1800 hectares were savannah (Table 1). Tequeje's channel shows a meandering pattern from the point at which it enters the alluvial plains till about 4 km upriver from the 2016 logjam (Fig 7). From this point onwards, it has an immature channel. The point where the Tequeje loses the meandering pattern probably indicates the location of the past, most upriver logjam; downriver from this point the avulsive pattern begins. In the 2016 imagery, it can be seen that a new course is about to be established (Fig. 7). The Cuberene River causes the most spectacular transformation of the landscape, with logjams migrating along the main river course and then continuing the upriver migration along the tributaries (Fig. 8). Large areas that were forested in 1995 are transformed into savannah by 2016 because of the repeated flooding. Field work was conducted during the dry season, in August 2016, along the rivers Tacuaral and Colorado. A few tens of meters upriver from the 2016 logjam in the river Colorado (Fig. 9 and 10) sand was deposited by overbank flow and the area immediately colonized by Parajobobo (*Tessaria integrifolia* Ruiz & Pav.). Parajobobo is a pioneer, fast growing species that tends to colonize sand deposits along fluvial channels by forming monospecific stands of the same age (Neiff, 2004). Fig. 10 shows a two meter thick sand layer, which has been deposited overnight at the end of January 2016 (Macario Huanca Quispe, community of Inka Agropecuaria, personal communication). The Parajobobo trees behind the hut in Fig. 10 are seven months old. The plant communities that colonize the clearance that follow the forest die-off (Fig. 11) are the same as the communities that colonize fluvial deposits along the Mamoré River. Besides Parajobobo, abundance of *Echinochloa polystachya*, *Cecropia* sp. (Ambaibo), *Heliconia* sp. (Patucú) and *Gynerium sagittatum* (Maldonado and Beck, 2004). After the sand is deposited, the water moves across the forested areas eroding the topsoil and exposing tree roots. Scouring forms many small channels (Fig. 12). The survey along the Colorado River revealed a paleosol associated to pre-Columbian pottery. The paleosol, located about 4 meters below the top of the river bank, has been radiocarbon dated 1390 ± 43 cal yrs BP. Pre-Columbian raised fields, ancient elevated platforms that were used for

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agriculture (Lombardo et al., 2011; Rodrigues et al., 2016), are visible in Google Earth imagery a few kms downriver from the areas affected by the logjam-induced floods of the Cuberene River (Fig. 13). Fig. 13 shows that pre-Columbian earthworks (raised fields and causeways) are found within the area crossed by paleochannels of the Cuberene River and other small rivers to the south.

4 Discussion

Logjam-induced floods have been largely overlooked as important agents of forest disturbance in Amazonia. The analysis of time series of Landsat imagery shows that, in a vast area of lowland forest (approx 60 km x 400 km) that runs parallel to the eastern Andean piedmont in Bolivia, logjam-induced floods are a major driver of forest disturbance. Logjam-induced floods drive a characteristic form of forest disturbance, as they affect hundreds of hectares of forest recurrently, in most cases on a yearly basis. This is a type of large scale disturbance that can be classified as intense and frequent (Turner et al., 1998).

In the Chimane forest and its surroundings, Paneque-Gálvez et al. (2013) have estimated that, during the period 1986 to 2009, a total of 26000 hectares of old-growth forest was lost due to human activities. During the same period, the Cuberene's logjam induced floods affected 18500 hectares. The rate of forest disturbance caused by rivers here is, therefore, comparable to the current rates of deforestation driven by the expansion of the agricultural frontier.

Forest ecological processes, and in particular tropical forest carbon sinks, are assessed by monitoring relatively small plots of forest during relatively long periods of time (~ 30 yrs) (Lewis et al., 2004; Phillips et al., 2004). However, to what extent the long-term monitoring of small plots can take into account large scale events is controversial (Chambers et al., 2009; Espírito-Santo et al., 2014). This study shows an example of an area where the monitoring of small plots can lead to critically skewed results if logjam-induced forest disturbance is not taken into account. The high rate of logjam-induced forest disturbance could be the reason for the yet unexplained low tree biodiversity observed in the Chimane Forest (Gullison et al., 1996); and can also explain why current models are unable to capture a large part of the floristic variation here (Guèze et al., 2013).

It is known that two of the most important factors controlling the formation of logjams are the recruitment of LW and the relation between the size of the LW and the width of the river channel (Gurnell et al., 2002; Wohl, 2013). The rivers studied here have very high meander migration rates (see Fig. 7) and hence can recruit a large amount of wood because of the lateral erosion of forested areas. They have very small mountain catchments; hence they enter the alluvial plains when they are still not very wide. Moreover, due also to uplift events that have occurred north of the study area (Lombardo, 2014), the study area is extremely flat and rivers have a relatively low transport capacity and a propensity to river channel siltation (Lombardo, 2016). All these conditions contribute to the formation of channel spanning logjams. Although the collapsing of the river on an almost yearly basis is restricted to the small rivers here analyzed, channel spanning logjams causing river avulsions have been reported in larger Bolivian rivers such as the Maniqui and the Secure too (Lombardo, 2016).

To my knowledge, there are no other studies of logjam formation in lowland tropical rivers, therefore it is difficult to assess to what extent the processes that take place in this part of the Bolivian Amazon are specific to this area, due to its hydrological context, or are typical of other small tropical meandering rivers.

The presence of pre-Columbian earthworks in an area crossed by the Cuberene River paleochannels (Fig. 13) suggests, on the one hand, that the preferential location for logjam formation and deposition of alluvium has moved westward, at least since the construction of the earthworks, otherwise these would have been destroyed or, more likely, never built in an area under such a high risk of catastrophic floods in the first place. On the other hand, the presence of Cuberene paleochannels in the very same area as the pre-Columbian earthworks suggests that, prior to the construction of the raised fields, logjams were less frequent or happened further to the east than their modern location. Raised fields were built to mitigate the risk posed by extreme floods (Lombardo et al., 2011) and their geometry, size and location responded to the local hydrology (Rodrigues et al., 2015; Rodrigues et al., 2016). The fact that raised fields in the Cuberene area were built along the whole slope that goes from the former levees of the Cuberene river to the former backswamps (Fig. 13) suggests that the local hydrology was highly variable in pre-Columbian times, as it can be expected in an area subject to frequent river avulsions occurring just a few kilometers upriver. The paleosol in the riverbank of the Colorado River containing pre-Columbian pottery dated 1390 ± 43 cal yrs BP is buried under a 4 meter layer of sediment. This shows the high depositional rate of these rivers, leading to the burial of many archaeological sites in the region. This example highlights the importance of taking into account river dynamics when analyzing the spatial patterns of pre-Columbian settlements in the region. In recent years, the Andean piedmont has been increasingly occupied by small communities of *campesinos* from the Andean region that clear the forest to practice agriculture (Paneque-Gálvez et al., 2013). The agricultural frontier is now expanding eastward from the road that links the towns of Yucumo and Rurenabaque, running along the part of the Andean piedmont north of the Maniqui River (Fig. 1). This is the area where LW is recruited by lateral erosion of forested river banks; therefore, the modern land-use practices here will probably reduce forest recruitment and cause the reduction and eastward migration of the logjam formations in the near future. Most of the studies on logjams have been carried out in rivers of temperate regions, where fluvial dynamics have been impacted by human activity throughout history and logjam dynamics differ from tropical regions (Wohl, 2013). The almost pristine environmental conditions of the Bolivian Amazon and the recent change in land-use here offer an excellent natural laboratory to study the dynamics of wood in lowland tropical rivers, the process of forest disturbance and community successions and how changes in LW recruitment affect both river dynamics and tree communities.

5 Conclusions

This paper analyses the dynamics of logjam formation in tropical meandering rivers in Southwestern Amazonia. The study focuses on rivers that cause logjam-induced floods in an area (approx. 60 x 400 km) of lowland forest that stretches parallel to the Andean piedmont in Bolivia. The analysis of remote sensing imagery shows the existence of 22 such rivers, representing practically the totality of the smaller rivers in the area. These rivers are characterized by i) being relatively small when they enter the alluvial plains, hence their width is similar to the height of the trees they transport; ii) having a high meandering rate that causes lateral erosion of forested areas and a high recruitment rate of LW; and iii) they flow across a very gentle slope, which reduces their capacity to transport LW. The study shows that logjam-induced floods are a major driver of forest disturbance in the Bolivian Amazon. Large logjam-induced floods follow a pattern that is consistent in all the rivers studied: channel spanning logjams form on an almost yearly basis and migrate upriver until an avulsion takes place and the upriver migration of the logjam re-starts in a new location within the alluvial plains, at a greater distance from the Andes. Each logjam-induced flood is characterized by i) a sudden deposition of a thick sand layer a few tens of meters upriver from the logjam and ii) a V shaped area where forest dies off and is replaced by pioneer plants or transformed into a savannah grassland if repeatedly flooded. This study shows that large and frequent floods triggered by logjams have a major impact on forest disturbance/recovery cycles and can potentially explain local floristic variations. This case study offers a unique opportunity to further research on how LW affects river behavior in lowland tropical settings and how large and frequent forest disturbance events resulting from logjams affect forest biodiversity and community successions.

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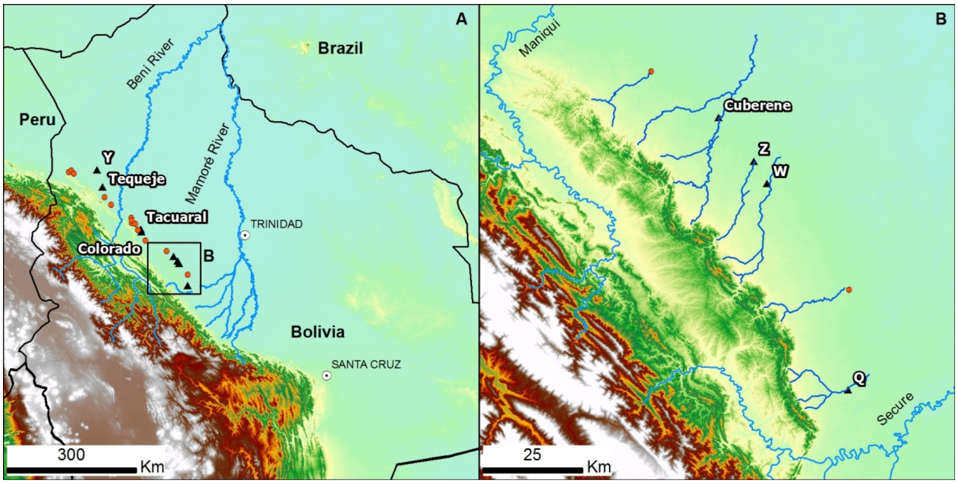
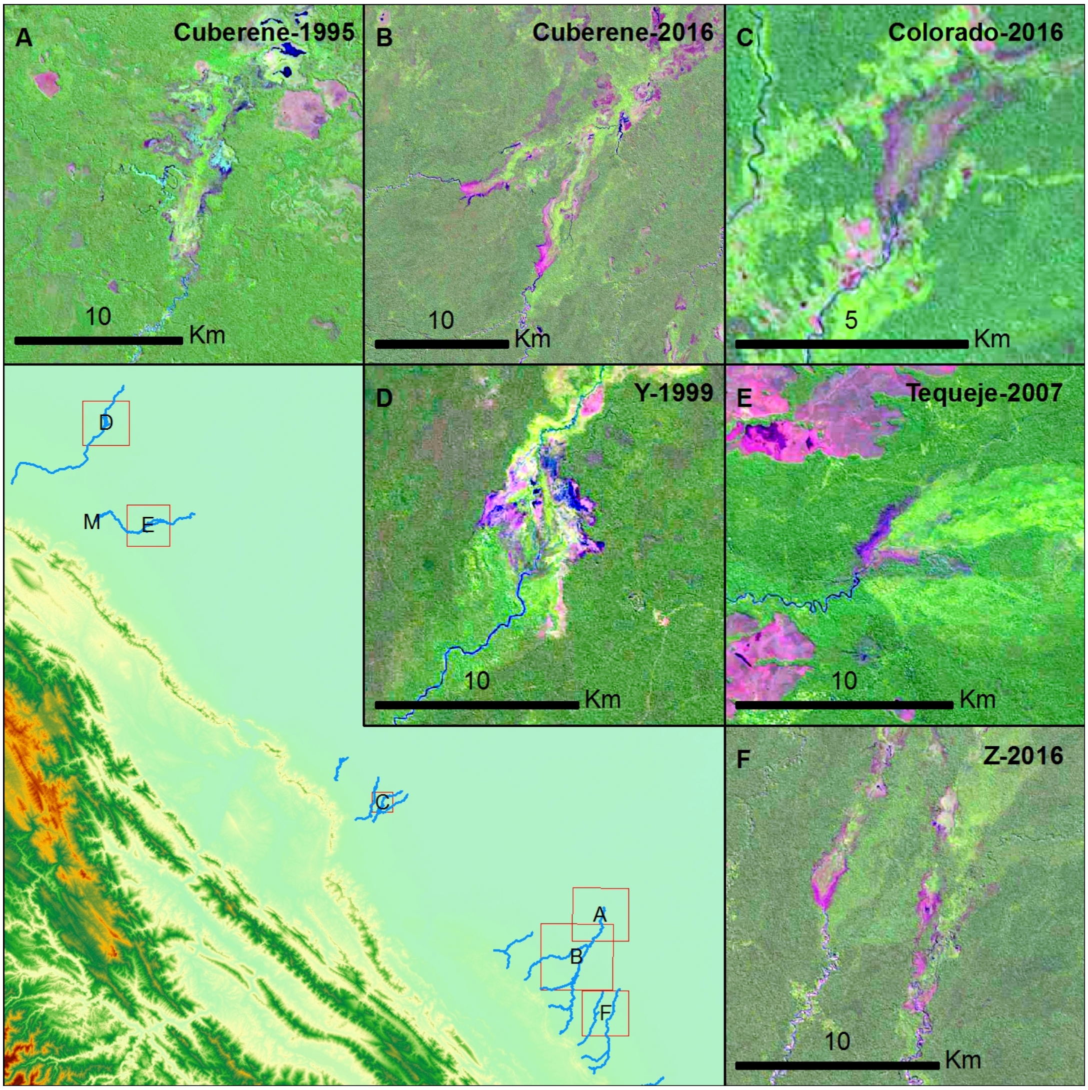


365 **Figure 1: Study area and location of the rivers studied. The study area covers a strip of lowland forest that runs parallel to the Bolivian Andes (aprox. 60 km wide x 400 km long). Black triangles identify the eight rivers analysed here; the orange dots show the location of other rivers that experience logjam-induced floods but that have not been included in the analysis.**

Earth Syst. Dynam. Discuss., doi:10.5194/esd-2017-19, 2017
Manuscript under review for journal Earth Syst. Dynam.
Discussion started: 24 March 2017

Earth System Dynamics
Discussions
Open Access



370 **Figure 2: Examples of forest die-off events as the one described in Gullison et al. (1996). Reddish plumes diverging from the river channel indicate dead forest. Here, trees have lost their leaves and this causes a fall in near infrared reflectance, which is shown in green in the RGB composition of the Landsat imagery (insets A-F), and an increase in mid-infrared reflectance (shown in red) which is mostly due to sediments. Non forested, light green areas are covered by pioneer species; forested, light green areas are young secondary forests which have re-grown after disturbance; forested, dark green areas are old-growth forests. Non-forested, reddish areas are savannah. Blue/black areas are water.**

Earth System Dynamics
Open Access
Discussions

Figure 3: High resolution image of forest die-off caused by a logjam in 2009 along the Cuberene River in the Chimane Forest. Greyish areas show dead forest and land that has been covered with sediments. Note how the totality of the water is diverted towards the forest. Image from Google Earth ®.

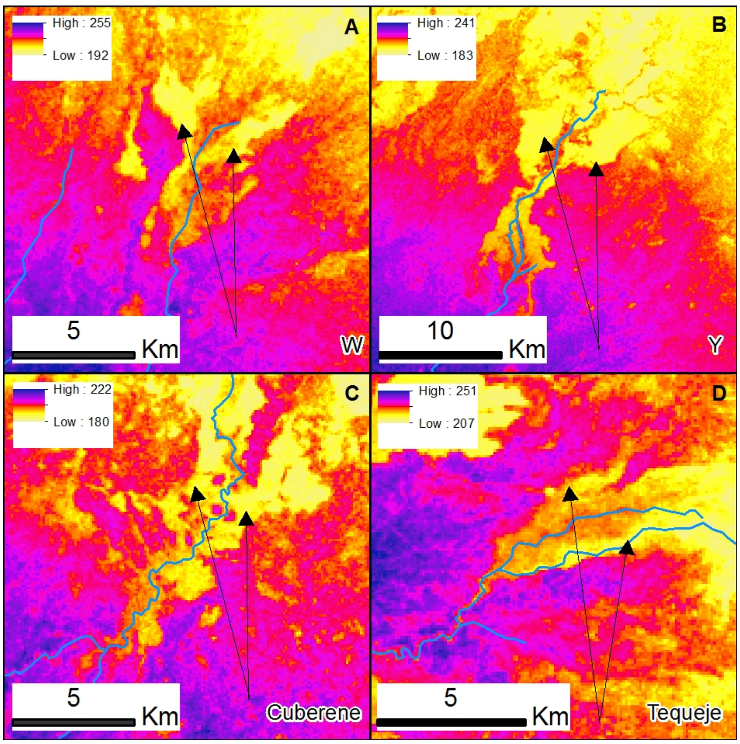


Figure 4: SRTM image of four areas where logjam-induced floods have killed the forest. SRTM imagery shows the situation, in the year 2000, of the rivers Cuberene, Tequeje, W and Y. At any given point, the SRTM digital elevation model gives the elevation of the canopy, not the elevation of the soil, therefore, deforested patches are visible as depressions (here rendered as yellow areas surrounded by red). Arrows indicate the areas where forest has been replaced by herbaceous vegetation.

Earth Syst. Dynam. Discuss., doi:10.5194/esd-2017-19, 2017
Manuscript under review for journal Earth Syst. Dynam.
Discussion started: 24 March 2017

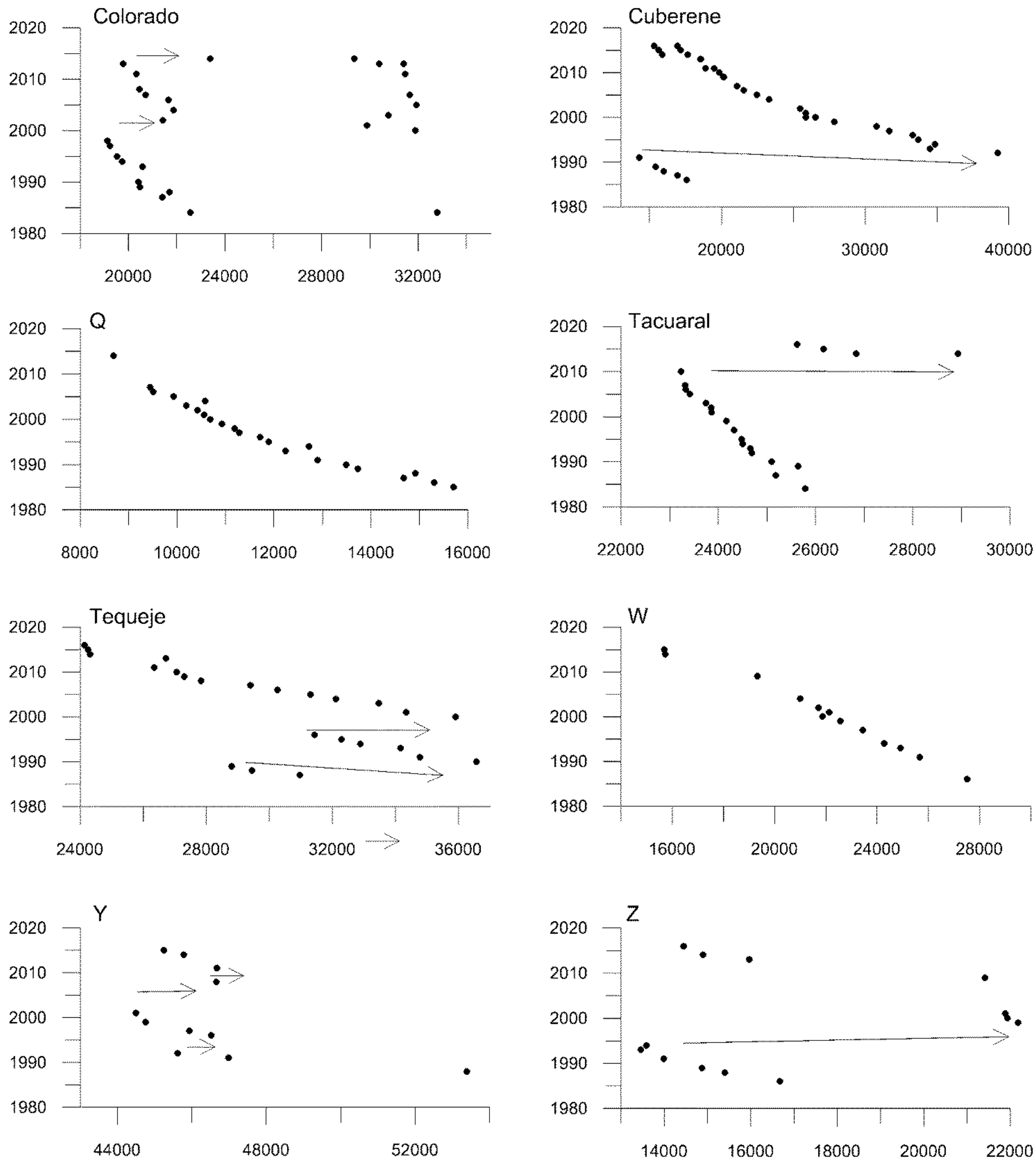


Figure 5: Locations of logjams of the eight rivers here analysed. Year of logjam formation (Y axis) is plotted against the logjam's distance from Andean piedmont in meters (X axis). Arrows indicate river avulsions.

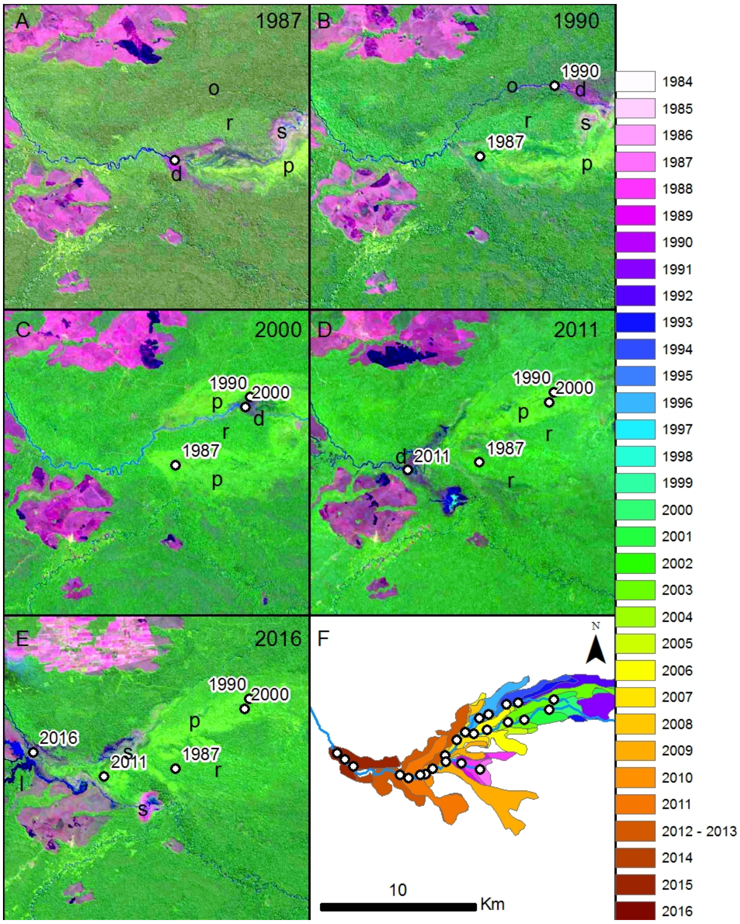
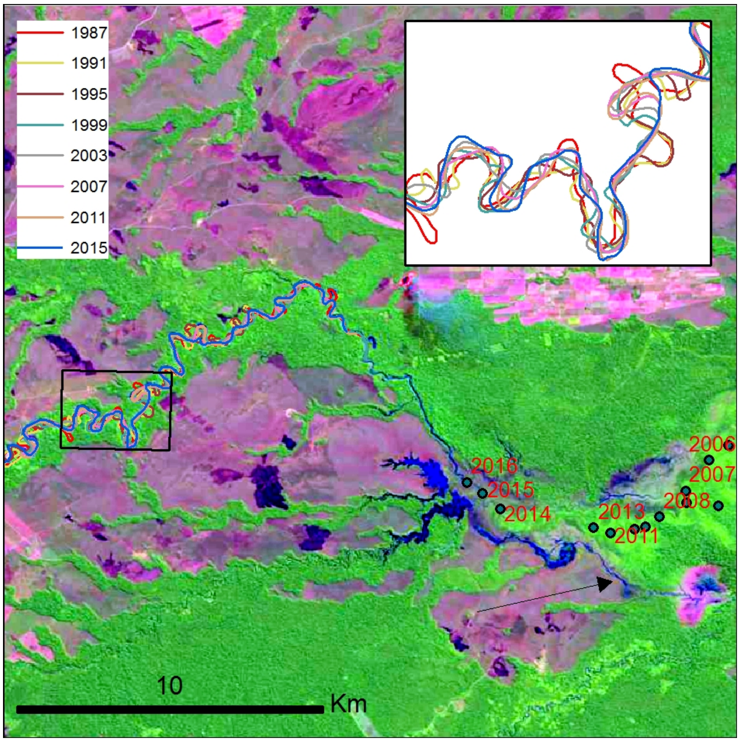
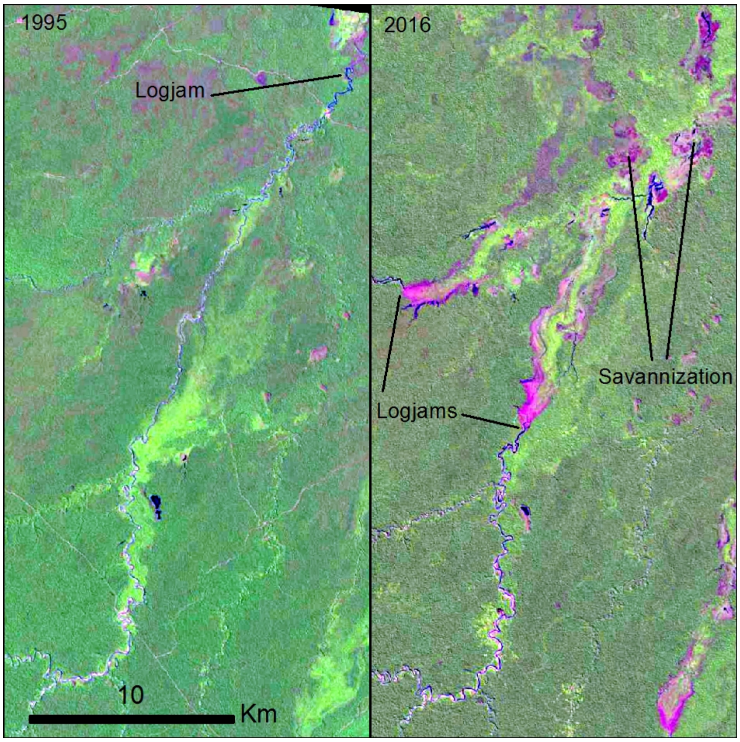


Figure 6: Evolution of the Tequeje River from 1987 to 2016. Inset A shows the situation in 1987, when the coverage of cloud-free Landsat imagery began. Lower case letters indicate landcover: "o" for old growth forest; "p" for pioneer plants; "r" for recently re-grown forest; "d" for recently dead forest; "s" for savannah; and "l" for lakes. Inset E shows the most recent image available with the location of the logjam in 2016. Inset F shows the location of the logjams on a yearly basis from 1987 to 2015 and the extension of dead forest as a result of the flooding. Logjams formed from 1996 to 1999 and flooded regions are located to the east of the area shown here.



400 **Figure 7: Landsat image of the Tequeje River in 2016. Green dots with red labels indicate location and year of past logjams. Inset shows the evolution of the river channel from 1987 to 2015 at 4 years intervals.**



405 **Figure 8: Evolution of the Cuberene River. From 1995 to 2016, the location of the logjams has migrated upriver along the two rivers that form the Cuberene. By 2016, large areas that were forested in 1995 have been transformed into savannah. A east-west road crossing the Cuberene in 1995 is completely obliterated in the 2016 image. Also notice how light green areas in early stages of the successional process in 1995 are already forested by 2016.**

Figure 9: Logjam formed in 2016 in the Colorado River. The logjam spans the entire channel and has low porosity.

Figure 10: Sand layer deposited overnight in 2016 by the Colorado River in the community of Inka Agropecuaria. The posts of the hut were originally 3 meters above the surface, after the deposition only the topmost meter remained above the sand. The house is about 100 meters from the Colorado River and about 1 km upriver from the point where the 2016 logjam formed (Fig. 3). Trees behind and on the right of the house are 7 month old Parajobobos.

Earth Syst. Dynam. Discuss., doi:10.5194/esd-2017-19, 2017
Manuscript under review for journal Earth Syst. Dynam.
Discussion started: 24 March 2017

Earth System Dynamics
Discussions
Open Access

Figure 11: Forest killed by the 2016 flood of the Colorado River rapidly being replaced by *Echinochloa polystachya* and *Tessaria integrifolia*.

Earth Syst. Dynam. Discuss., doi:10.5194/esd-2017-19, 2017
Manuscript under review for journal Earth Syst. Dynam.
Discussion started: 24 March 2017

420 **Figure 12: Scouring channels downriver from the logjam in the Tacuaral River in 2016.**

Earth Syst. Dynam. Discuss., doi:10.5194/esd-2017-19, 2017
Manuscript under review for journal Earth Syst. Dynam.
Discussion started: 24 March 2017

Earth System Dynamics
Discussions
Open Access

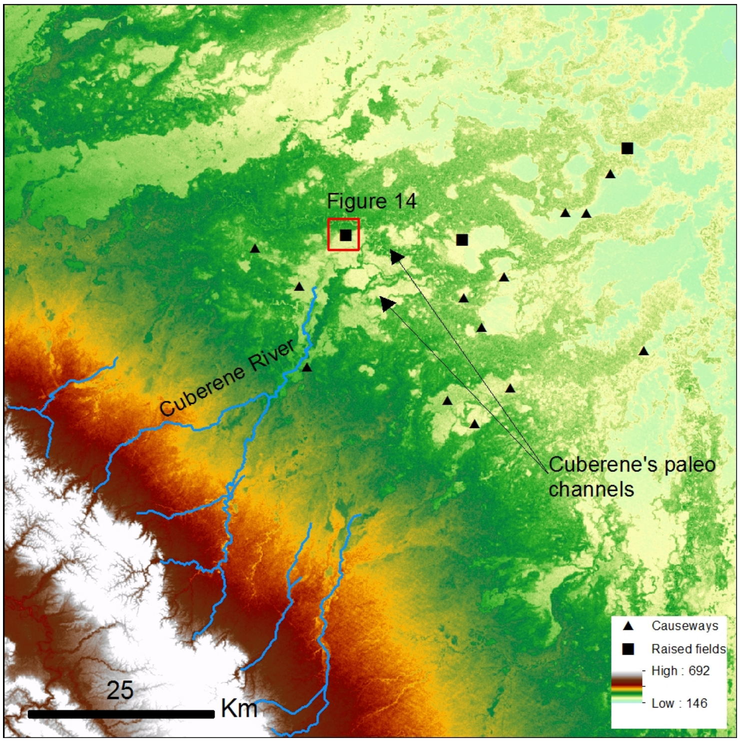


Figure 13: Location of pre-Columbian earthworks in the Chimane Forest and location of Fig. 14. Triangles indicate location of pre-Columbian causeways; squares show location of raised fields, pre-Columbian structures built to allow agriculture in otherwise flooded areas.

Figure 14: Location of raised fields in the proximity of a Cuberene River paleochannel (for location see red box in Fig. 12). In a) raised fields built in the forested upland that grows over the fluvial levee; in b) raised fields built across the current forest-savannah ecotone; in c) fields built in the seasonally flooded savannah.

Table 1: Overview of the dynamics of the logjams and their effect on the forest. "Yrs covered" is the number of years for which cloud-free Landsat imagery was available; "Starting" is the year of the oldest cloud-free Landsat image available; "Width" in the width of the river in meters; "AFA" stands for "average flooded area" and is the average number of hectares that are flooded when there is a logjam induced flood in a given river. TFA stands for "total flooded area" and is the number of hectares that have been flooded in total during the period 1984-2016. TFA is smaller than the sum of the AFA for all the years because large extents of land are often repeatedly flooded, so that there is a significant overlap between areas flooded in different years. "% Savannah" and "%Forest" indicate the type of vegetation cover in 1984 (percentage of the TFA).

River	Yrs covered	Starting	Width	N Logjams	AFA	TFA	% Savannah	%Forest
Tequeje	29	1987	56	22	901	8921	20,4	79,6

Earth Syst. Dynam. Discuss., doi:10.5194/esd-2017-19, 2017
Manuscript under review for journal Earth Syst. Dynam.
Discussion started: 24 March 2017

Earth System Dynamics
Discussions
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Y	27	1984	93	11	1819	6977	22,6	77,4
Taquaral	30	1984	22	21	505	3004	37	63
Colorado	30	1984	13	28	255	3646	2,9	97,1
Z	26	1986	13	13	221	1731	0	100
W	26	1986	18	13	491	4348	0	100
Q	29	1985	19	23	217	1568	0	100
Cuverene	27	1986	41	34	3007	21300	22,4	77,6