Hydrobiologia
DOI 10.1007/s10750-017-3384-z

PRIMARY RESEARCH PAPER

Twenty-three-year timeline of ecological stable states and regime shifts in upper Amazon oxbow lakes

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Received: 6 March 2017 / Revised: 16 September 2017 / Accepted: 18 September 2017

Abstract Regime shifts in shallow lakes are often associated with anthropogenic impacts, such as land-use change, non-point source nutrient loading, and overfishing. These shifts have mostly been examined in lakes in temperate and boreal regions and within anthropogenically disturbed basins. Here, it is demonstrated that tropical floodplain lakes in a region of virtually no human disturbance naturally undergo frequent regime shifts. We demonstrate this using satellite imagery to provide a 23-year time series of 22-oxbow lakes or "cochas" along 300 km of the Manu River in SE Perú. In any year, a majority of these lakes is in a macrophyte-free, phytoplankton-dominated state. However, over the 23 years covered by images, roughly a third of the lakes experienced abrupt shifts to a floating macrophyte state. Macrophyte cover persisted for ≤ 3 year. Analysis of water level fluctuations sampled on a subset of the lakes for 1 year suggests that lake isolation from streams and the main river facilitates regime shifts. Multiple forcing factors, both internal and external to the lakes themselves, could drive the observed regime shifts, but insufficient data exist from this remote region to identify the key processes.

Keywords Amazon · Floodplain lakes · Perú · Lake hydrology · Regime shifts · Remote sensing

Introduction

Since catastrophe theory was first introduced in the 1970s (Zeeman, 1977), equilibria and bifurcation analysis has permeated numerous ecological fields. Regime shifts in shallow lakes provide an important application of this theory and have been a topic of growing interest in recent decades (Richey et al., 1989; Izaguirre et al., 2004; Scheffer, 2004; Scheffer & Jeppesen, 2007; Scheffer et al., 2012). Here we shall be concerned with shifts between phytoplankton and

Electronic supplementary material The online version of this article (doi:10.1007/s10750-017-3384-z) contains supplementary material, which is available to authorized users.

Handling editor: Mariana Meerhoff

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Published online: 18 October 2017

macrophyte-dominated states in a series of tropical floodplain lakes. Such lakes normally reside in a steady state stabilized by positive feedback mechanisms that maintain the system within a given range of conditions (Ludwig et al., 1978; Scheffer & van Ness, 2007). Shifts from phytoplankton to macrophytes or vice versa can occur as a response to a subtle drift in endogenous conditions, such as the accumulation or loss of nutrients, or to abrupt exogenous events such as floods (Hilt et al., 2011; de Tezanos Pinto & O'Farrell, 2014). Many types of perturbations have been confirmed or suspected as triggers of regime shifts (Scheffer et al., 2001), including changes in trophic structure (Carpenter, 2003), nutrient pulses from exogenous sources (Camargo and Esteves, 1995), fluctuations in water level (Loverde-Oliveira et al., 2009; O'Farrell et al., 2011), fish migrations (Brönmark et al., 2010; Mormul et al., 2012), internal heterogeneity (Meerhoff et al., 2007), and grazing by zooplankton (Lacerot et al., 2013) or arthropods (Marshall & Junor, 1981). Interactions between drivers can, in certain circumstances, produce highly complex dynamics (Schooler et al., 2011).

Regime shifts are prototypical to anthropogenically impacted basins in temperate and boreal regions, where rapid decreases in water clarity (eutrophication), have been observed in association with land-use change, increased nutrient loading, and manipulation of trophic structure (Carpenter, 2003). Despite the extensive literature on regime shifts in shallow lakes, few studies have documented natural regime shifts in shallow lakes, largely because lakes free of human influences are rare (Scheffer & Jeppesen, 2007). Here we report on the occurrence of spontaneous regime shifts in a set of floodplain (oxbow) lakes along the Manu River in a protected and largely unpopulated watershed at the base of the Andes in Perú.

The Manu River is a white-water, upper tributary of the Amazon River and has its headwaters on the Eastern Slope of the Andes. The Manu River watershed is entirely contained within the 1.9 M hectare Manu National Park (Fig. 1) and encompasses an elevational range from 300 m in the lowlands to > 4,000 m in the Andes. Fewer than 2,000 indigenous inhabitants live in the watershed, or about 0.1 per km^2. There are no roads within the lowland sector of the park, the only access being by boat.

The Manu River basin contains approximately 33 lakes within a floodplain that ranges from 2 to more than 8 km wide (Fig. 1). One of these lakes, Cocha Cashu, has been the site of a research station since 1969 and thus provides a long-term perspective on the stability of lake states. Cocha Cashu is 2.5 km long and up to 150 m wide with a mean depth of about 1.4 m and a maximum depth of 2.1 m in the dry season (June to October). From 1973 until 2003, the water body was open and supported a high concentration of phytoplankton. In January 2003, the most extreme flood in 40 years passed down the Manu River, inundating the entire floodplain for several days. A strong current scoured Cocha Cashu and replaced the entire water body with floodwater, essentially runoff from a torrential rain. There then ensued a series of slow-motion transformations of lake state, from 2003 to 2008, beginning with a period of dominance by submerged aquatic vegetation (SAV), followed by 2 years in which more than half of the lake surface was covered by floating macrophytes, at first *Pistia stratiotes* L., and later *Oxycaryum cubense* Poeppig & Kunth (Lye). The lake did not return to a phytoplankton state until late 2008. During the years following the flood, 2003–2008, Cocha Cashu thus assumed 3 distinct states dominated, respectively, by SAV (*Najas* spp.), floating macrophytes, and phytoplankton (Dent et al., 2002). It was the first-hand experience of observing these transformations after 30 years of stability that inspired us to undertake the present research.

We designed the research to address the following questions: Do all the lakes of the Manu basin exhibit distinct ecological states and abrupt shifts between them? How often do these shifts occur? Are regime shifts floodplain-wide phenomena? Can the tendency to undergo regime changes be associated with a lake's physical features (area, depth and location in the watershed and connectivity to the river)? We endeavored to answer these questions by analyzing a 23-year time series of Landsat images covering 22 Manu River floodplain lakes and visiting 27 lakes in 2012 to document their physical state and vegetation.

Methods

Identification of regime shifts via remote sensing

Much of the Manu National Park lies within a single Landsat scene (Row 4, Path 68; Landsat 5 and 7). We

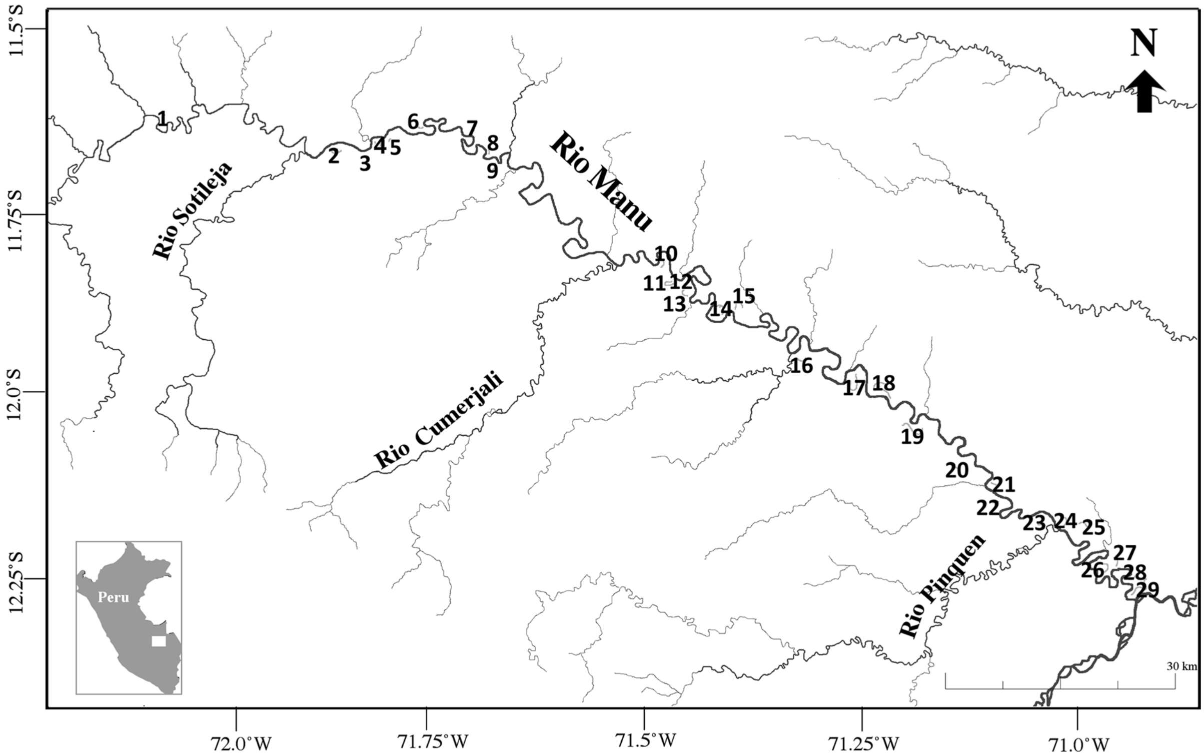

Fig. 1 Map of the Manu River basin in Perú showing the locations of the 29 lakes listed in Table 1

selected 22 lakes for analysis, beginning with the lake farthest upstream and ending with the last lake above the confluence of the Rio Pinquén, a major tributary of the lower Manu. Several of the lakes farthest upstream are remote and have not been named. The remaining lakes are labeled by name as well as number, the number referring to the lake's position in the watershed (Table 1; Fig. 1). Only 4 of the lakes are regularly fished by indigenous people (#'s 4, 9, 13, 29). The remaining lakes are unfished and support naturally regulated populations of piscivores, including giant otters, caimans, and birds.

As described above, Manu floodplain lakes can assume 3 distinct states with respect to primary producers: phytoplankton, submerged aquatic vegetation (SAV), and floating macrophytes. These states are readily distinguished by eye (Fig. 2). Lakes in the phytoplankton state have low transparency and may or may not carry narrow fringes of floating vegetation on the shallow side, but contain little SAV. The transparency of lakes containing SAV is characteristically much greater than that of phytoplankton-dominated lakes. Floating macrophyte cover is conspicuous, both to a ground observer and from space, and by shading the water column, suppresses phytoplankton or SAV development (Peñuelas et al., 1993). Senescent lakes become gradually shallower through time as river-borne sediment accumulates, eventually becoming carpeted by floating vegetation containing a diversity of plants, including *Azolla* sp., *Salvinia* sp., grasses, sedges, *Polygonum* sp., *Ludwigia* spp., ferns, orchids, etc.

To evaluate lake states, we collected all available images with less than 50% cloud cover over the floodplain from archives of the United States Geological Survey (USGS) and the Brazilian National Institute for Space Research (INPE). This resulted in a collection of 27 Landsat-5 images spanning 23 years from 1986 to 2008. All images were radiometrically and atmospherically corrected using the revised calibration procedures of Chander et al. (2009) and Dark Object Subtraction (Song et al., 2001). To detect lake surface vegetation, Bands 3 (Red), and 4 (Near Infrared (NIR)) of the corrected images were then used to create a Normalized Difference Vegetation Index (NDVI) image, (NIR-Red)/(NIR + Red)

Table 1 Locations and features of 29 floodplain lakes in the Manu River basin, Madre de Dios, Perú

Lake number and rank in watershed	Lake name	Latitude/longitude	Area (ha)	Connectivity	Shortest distance to river	Mean depth (m)	Max depth (m)	NVDI 2012	No. observed state changes	Vegetation observed August–September, 2012
1	Cocha 1	11°36′27″S 72°4′16″W	9.8	I	120	NM	NM	NM	0	NM
2	Cocha 2	11°39′33″S 71°51′48″W	5.7	Ft	480	1.5	2.7	0.330	0	FV (fringing)
3	Cocha 3	11°39′23″S 71°49′1″W	0.4	I	200	1.3	1.5	0.505	9	FV (scattered)
4	Cocha Sophuapa	11°39′30″S 71°48′9″W	10.1	I/Ft	350	1.7	4.8	0.080	NM	Phytoplankton
5	Cocha 5	11°38′55″S 71°47′42″W	0.7	I	425	0.8	0.8	0.475	2	FV (scattered)
6	Cocha 6	11°38′30″S 71°45′30″W	5.2	I	400	0.8	1.2	0.347	0	FV (Pistia)
7	Cocha Piraña	11°38′52″S 71°41′34″W	6.2	ND	600	NM	NM	0.239	3	FV (covering)
8	Cocha Vieja	11°40′32″S 71°40′37″W	4.2	I/Ft	275	1.6	2.0	0.113	0	FV (scattered)
9	Cocha Nueva Felipe	11°41′41″S 71°40′46″W	20.2	I/Ft	350	0.9	2.0	0.090	NM	Phytoplankton
10	Cocha Gamarota	11°49′21″S 71°28′31″W	15.4	I	500	1.3	1.5	0.592	3	FV (covering)
11	Cocha Maizal	11°51′5″S 71°28′12″W	27.1	I	200	1.3	3.0	Clouds	0	Phytoplankton
12	Cocha Secreta	11°51′14″S 71°27′5″W	1.5	I	550	0.4	0.4	Clouds	1	FV (water lilies)
13	Cocha Nueva	11°51′35″S 71°27′14″W	13.5	I/Ft	320	0.9	2.0	Clouds	0	Phytoplankton
14	Cocha Cashu	11°53′5″S 71°24′31″W	23.0	I	450	1.4	2.1	0.135	2	Phytoplankton
15	Cocha Totora	11°52′38″S 71°23′21″W	3.5	I/Ft	1300	0.5	0.8	0.190	2	FV (scattered)
16	Cocha Gallareta	11°57′22″S 71°18′60″W	15.2	I	1050	1.0	2.0	0.177	0	SAV
17	Cocha Salvadorcillo	11°59′37″S 71°15′37″W	16.7	Ft	475	1.4	2.4	0.150	0	FV (fringing)
18	Cocha Salvador	11°59′45″S 71°13′57″W	77.8	I	200	2.5	5.6	0.117	0	Phytoplankton
19	Cocha Otorongo	12°2′40″S 71°11′27″W	43.7	Ft	225	1.7	3.3	0.160	0	FV (fringing)
20	Cocha Sacarita	12°5′34″S 71°8′33″W	16.8	I	1500	1.4	2.4	Clouds	5	FV (scattered)
21	Cocha Juarez	12°7′5″S 71°5′5.00″W	26.9	I	450	1.1	2.2	0.034	0	Phytoplankton
22	Cocha Garza	12°8′29″S 71°5′40.00″W	10.5	ND	575	1.5	2.7	0.184	4	FV (scattered)
23	Cocha Largarto	12°9′54″S 71°2′19″W	19.2	I	475	1.0	2.1	0.010	0	Phytoplankton
24	Cocha Brasco	12°10′3″S 71°0′30″W	15.6	I	800	1.6	3.7	0.054	0	Phytoplankton
25	Cocha Tipisca	12°10′41″S 70°59′13″W	14.4	I	1625	2.3	2.5	0.126	NM	Phytoplankton
26	Cocha Romero	12°13′50″S 70°57′43″W	34.2	I	650	NA	NA	NM	NM	FV (covering)
27	Cocha Limonal	12°13′18″S 70°57′9″W	3.9	ND	250	1.1	2.4	NM	NM	Phytoplankton
28	Cocha Paña	12°14′51″S 70°56′7″W	5.8	I	260	NM	NM	NM	NM	NM
29	Cocha de los Valles	12°15′38″S 70°54′59″W	36.0	Ft	100	1.6	3.2	Clouds	NM	FV (fringing)

I isolated lake, *Ft* flow-through lake, *I/Ft* isolated arm of a dual lake (see text), *ND* status not determined, *NM* not measured, *FV* floating vegetation

Fig. 2 Photos taken in 2012 of Manu River lakes in different ecological states: **a** phytoplankton-dominated state (Cocha Cashu, #14), **b** submerged aquatic vegetation (SAV, C. Gallereta, #16), **c** floating macrophyte state (Cocha #6, note colonizing shoots of *Oxycaryum cubense*), **d** senescent state (C. Gamarrota, #10)

(Rouse et al., 1973). We did not succeed in distinguishing SAV from phytoplankton lakes in the images because the spatial resolution of the imagery proved to be too coarse and the signal of subsurface vegetation too weak to confidently differentiate between them. Therefore, transitions between these states could not be detected.

For estimates of lake area and NDVI, we used the largest body of open water in a given lake, avoiding vegetation, whether floating or fringing, unless the lake was in a macrophyte-dominated state, in which case, the NDVI measurement was taken from the floating vegetation. In the case of dual lakes possessing flow-through and isolated arms (see below for explanation), measurements of area and NDVI were taken of the arm with the largest area of open water, in all cases, the dead (isolated) arm. Within each lake, 300 random points were sampled within the area of open water and averaged to calculate a mean NDVI and standard deviation for each date. In the smaller lakes, individual pixels were sampled multiple times, but this should not have affected the estimated mean NDVI.

Regime Shifts

We based our initial detection of regime shifts on the known historical record for Cocha Cashu (1973–2014) compared with NDVI values calculated from the Landsat imagery (Fig. 3). A regime shift from phytoplankton-dominated open water to cover by floating macrophytes was determined to have occurred if the NDVI value for the lake was ≥ 0.3. This value represents approximately the mid-point between the highest values of NDVI (ca 0.15) observed for Cocha Cashu in the phytoplankton state and the highest value observed in the floating macrophyte state (0.53). We chose the criterion realizing that threshold values greater than 0.3 would risk underestimating transitions to the floating macrophyte state and lower values would risk overestimating them. The criterion of ≥ 0.3 is high enough to reduce potential error caused by inadvertent inclusion of fringing vegetation along lake margins. To allow for hysteresis, we employed separate criteria for forward (NDVI ≥ 0.3) and backward (NDVI ≤ 0.15) transitions between phytoplankton and floating macrophyte states in the chronoseries of images. Had we used a single criterion for both forward and backward transitions, for example, NDVI $= 0.3$, this would have led to serious

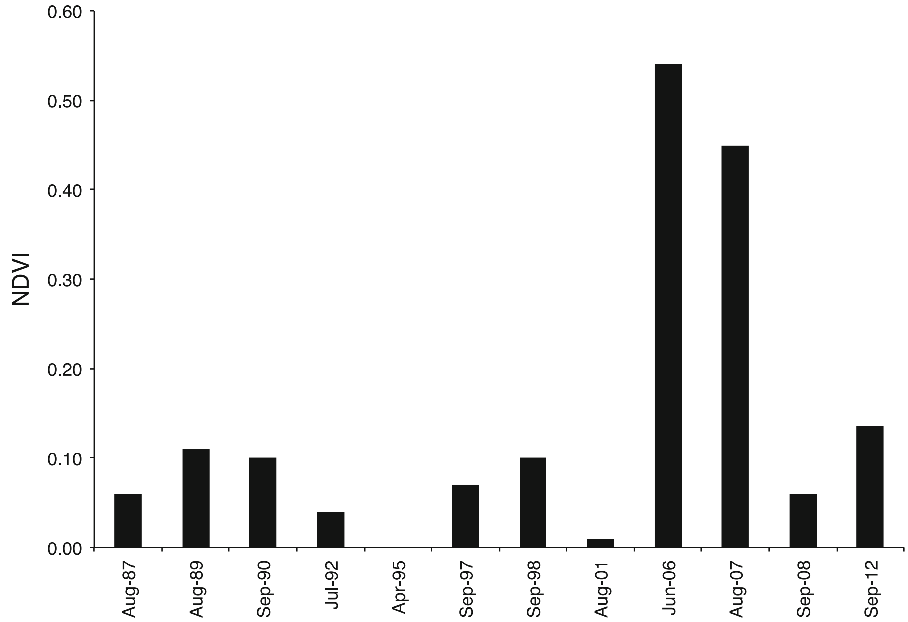

Fig. 3 NDVI values extracted from Landsat images of Cocha Cashu (Lake #14) covering the period 1987 to 2012. The lake was observed to be in a phytoplankton state except in 2006 to 2008 when it was covered by floating macrophytes. By September, 2008, it had returned to the phytoplankton state

overcounting of transitions in lakes where NDVI values fluctuated around 0.3 in successive images.

Ground truth

Landsat imagery is capable of distinguishing vegetation from open water but lacks sufficient resolution to identify the diversity of macrophyte-dominated vegetation types occurring in these lake ecosystems. To assess lake states by visual inspection, we mounted an expedition between July 16 and September 12, 2012 to visit Manu River lakes. In all, we evaluated 27 lakes, including 21 of the 22 lakes used in the image analysis. The remaining lake (#1) was far upriver in an area occupied by uncontacted tribes, so was not assessed. At each lake visited, we took a series of photographs, wrote a verbal account of its vegetation and general setting, conducted a series of physical, chemical and biological measurements (not reported here), and identified the principal floating and submerged macrophytes.

To evaluate the interpretation of the 1986–2008 Landsat images, we also analyzed Landsat 7 images from August and September, 2012, which coincided in time with the ground truth survey. Landsat 7 images after 2003 (SLC-off) are banded so that the information for roughly a quarter of each scene is missing. Nevertheless, some portion of most Río Manu lakes was included in resolved sections of the image, allowing evaluation of NDVI for 20 lakes. These images (from USGS) were corrected and processed in the same manner as the historical dataset.

Analysis

To investigate whether the tendency of a lake to undergo state changes could be related to any of the measured variables listed in Table 1 (lake area, distance to river, connectedness (isolated or flow-through), mean depth, maximum depth, and NDVI in August, 2012), we conducted a series of exploratory univariate and multivariate analyses using linear regression or ANOVA, as appropriate, with the number of observed state changes for each lake as the response variable ($N = 22$ lakes in most cases).

Hydrology of isolated versus flow-through lakes

Lakes that are entered by a stream are referred to here as “flow-through” lakes to distinguish them from “isolated” lakes that are decoupled from the river by its fringing levee except during occasional and brief periods of high water (Tejerina-Garro et al., 1998). The constantly exiting flow creates a permanent connection between flow-through lakes and the river. Sediment-laden main-stem river water frequently backs up into flow-through lakes but only infrequently intrudes into isolated lakes (Davenport, 2008; Osorio et al., 2011). The stream entering a flow-through lake rapidly forms a plug of sediment at the point of entry. The plug then often creates a dual lake by deflecting the stream toward one end while leaving the other arm in an isolated condition. We used satellite imagery (Google Earth) and on the ground assessments (verification of incoming streams) to distinguish isolated from flow-through lakes or lake arms.

To document the differences in annual flooding regimes in isolated versus flow-through lakes, we placed 6 Onset Hobo U20 Water Level loggers in 3 isolated lakes (Cashu, Gallareta and Salvador, #s14, 16 and 18, respectively) and 3 flow-through lakes (Nueva, Otorongo, and Valles, #s 13, 19 and 29). Loggers were deployed at depths between 0.5 and 1.0 m in September 2009 (dry season) by attaching them to stakes driven deep into the lake bottom. Loggers recorded hourly the height of water over the sensor via static pressure measurements. An additional U20 datalogger was placed under forest cover at Cocha Cashu Biological station to maintain a record of changes in air pressure throughout the year. Data were retrieved after 1 y at the end of the 2010 dry season. Water level estimates were corrected using the Barometric Pressure Compensation assistant of Hoboware Pro software (v. 3.7.2) for the period September 4, 2009 through November 7, 2010.

We analyzed the depth data to assess whether lake-level fluctuations differed between isolated and flow-through lakes. Because the lakes differed in size and contributing sources of floodwater (affecting the absolute size of excursions), the behavior of positive excursions (or the probability density function positive 'tail,' denoted as δH) was explored for the normalized water level (i.e., normalized to zero long-term mean and unit variance for each lake). Normalization standardizes the mean squared amplitude water level excursions among lakes. Differences in hydrologic regimes manifest themselves as differences in the probability density function or autocorrelation function of the δH time series. Exceedance probability (Exc) refers to the frequency of occurrence of values exceeding a reference value. The choice of analyzing pdf and Exc of δH instead of raw water level changes is to minimize the effects of differences in rainfall pattern, contributing area, and lake size.

Results

NDVI versus on-site observations in 2012

Table 1 lists Río Manu oxbow lakes in order of their locations within the watershed along with depths, NDVI values in 2012 from images of 20 cloud-free lakes, and an on-site assessment of lake vegetation in 2012. Open water NDVI values of 14 phytoplankton- or SAV-dominated lakes in 2012 fell in the range of 0.01–0.20. Several lakes with relatively low open water NDVI values supported extensive floating meadows, either in the shallows at the ends and/or along the margins (e.g., #s 2, 8, 17, 19, 22). One lake (#7) yielded an open water NDVI value ≥ 0.20, < 0.30 and was heavily blanketed with floating vegetation of various sorts, affirming the conservative nature of our criterion of NDVI ≥ 0.3 for regime changes. Five lakes (#s 2, 3, 5, 6, 10) yielded NDVI values ≥ 0.3 in 2012. One of these is a flow-through lake with broad fringing mats of floating vegetation (#2), two are small, isolated lakes that were observed to be partially covered by *Pistia stratiotes* L. and other floating plants in 2012 (#s 3, 5), one was completely covered by *P. stratiotes* (#6, see Fig. 2c) and the fifth was in a senescent state (#10, see Fig. 2d). Senescent lakes (#s 7, 10, 26 appear to be more or less permanently covered by floating meadows that must rise and fall with seasonal fluctuations in water level.

Regime shifts

NDVI values range from -1 to $+1$, but all vegetation produces positive values. Forest cover in the Manu Basin ranged between 0.6 and 0.7 NDVI, whereas the lake surfaces varied between small negative values and $+0.53$. The observed carpeting of Cocha Cashu by floating vegetation in 2006–2007 yielded values as high as 0.53 NDVI, whereas NDVI values from periods of SAV dominance fall within the range yielded by open water (Fig. 3).

Using the conservative NDVI value of ≥ 0.3 as a minimum criterion for the floating macrophyte state and, to allow for hysteresis, a value of ≤ 0.15 for a return to the phytoplankton state, we identified floating vegetation in one or more images in 9 lakes (Fig. 4), which amounts to 41% of all lakes in the sample. Three lakes exhibited NDVI values ≥ 0.3 in 1990, 4 in 2004 and 7 in 2006/2007. Thirteen lakes did not undergo a state change during the 23 years of observation. Three of the lakes that experienced state changes are senescent lakes (#'s 3, 7, and 10) that have been chronically covered by floating vegetation, respectively, since 2006, 2004, and 1992. Three more (#5, 12, 15) are small (0.4–3.5 ha), shallow (0.5–1.5 m maximum depth) lakes that were partially to largely covered by floating vegetation in 2012. The remaining 3 (#14, 20, 22) are larger (10.5–24 ha), deeper (2.1–2.7 m maximum depth) lakes that once or twice in 23 years experienced brief episodes of floating macrophyte dominance.

Four of the 22 lakes (#s 1, 2, 11, 17) exhibited NDVI values of ≥ 0.2 and < 0.3 in one or more images in the chronoseries, but never > 0.3. Two of these were flow-through lakes (#s 2, 17) that supported dense mats of floating vegetation extending from the margins toward the center and partially covering the water body. The other two are phytoplankton lakes for which the NDVI value exceeded 0.2 in only 2–4 out of 27 images. Overall, the record contains a total of 31 regime shifts, 18 in the upper 11 (#s1–13) lakes, and 13 in the lower 11 (#s 14–24).

Univariate and multivariate regression or ANOVA analyses with lake area, distance to river, connectedness (isolated or flow-through), mean depth, maximum depth, and NDVI in August 2012 as explanatory variables and the number of regime shifts as response variable were all statistically negative except for one, the 2012 NDVI value ($P = 0.014, N = 17$). However, it is no surprise that the amount of floating vegetation on a lake, as represented by NDVI, provides a prediction of tendency to change states to the floating macrophyte condition.

A recurrent pattern in the chronosequences was a rapid appearance of floating vegetation, persistence for one to 3 years, followed by a rapid return to the phytoplankton state. NDVI values ≥ 0.3 did not persist for longer, with the exception of senescing

Date	1	2	3	5	6	7	8	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1986 Aug	0.11	0.05	0.00	-0.15	-0.11	0.00	-0.02	0.13	0.00	0.04	-0.08	-0.03	-0.02	0.06	0.00	-0.06	-0.02	-0.06	-0.11	-0.08	-0.05	-0.10
1987 Aug	0.12	0.10	0.35	0.07	-0.04	-0.15	-0.17	0.02	0.13	0.00	-0.09	0.06	-0.18	-0.09	0.18	-0.15	-0.26	-0.14	-0.36	-0.16	-0.03	-0.20
1989 Aug	0.00	-0.01	0.30	0.03	-0.10	-0.21	-0.15	0.35	-0.17	0.15	-0.11	0.11	-0.17	-0.15	0.09	-0.23	-0.26	-0.24	-0.35	-0.35	ND	ND
1989 Oct	0.22	0.08	0.46	0.08	-0.04	-0.28	-0.19	0.22	-0.07	0.16	-0.21	0.03	-0.25	-0.02	0.10	-0.13	-0.18	-0.16	-0.20	-0.21	-0.10	-0.19
1990 May	0.16	0.13	-0.02	-0.12	-0.12	0.51	-0.11	0.39	0.25	0.07	-0.19	-0.03	-0.19	0.02	0.20	-0.03	-0.02	0.44	-0.10	0.19	-0.09	-0.22
1990 Jul	0.03	-0.01	0.27	-0.11	-0.15	0.63	-0.08	0.44	0.02	0.19	-0.11	-0.03	-0.12	-0.16	0.20	-0.09	-0.10	0.42	-0.18	-0.14	ND	ND
1990 Sep	0.06	0.14	0.55	0.21	-0.02	0.58	-0.04	0.42	-0.11	0.29	-0.07	0.10	-0.09	-0.17	0.22	-0.20	-0.20	-0.02	-0.32	-0.25	ND	ND
1991 Jul	0.07	-0.27	-0.16	-0.35	-0.28	0.04	-0.37	0.04	-0.47	-0.27	-0.46	-0.37	0.01	-0.55	-0.25	-0.48	-0.54	0.25	ND	ND	ND	ND
1992 Jul	0.20	0.21	0.24	0.14	-0.02	0.22	0.03	0.36	0.26	0.22	-0.05	0.04	0.04	0.12	0.11	0.02	0.11	0.39	0.04	0.03	0.04	ND
1995 Apr	0.01	0.12	0.02	-0.18	-0.10	0.09	-0.30	0.47	ND	ND	ND	ND	0.00	-0.30	0.01	-0.32	-0.32	0.09	-0.32	0.31	0.05	-0.22
1996 Jun	0.11	0.12	0.23	0.18	-0.03	0.19	-0.02	0.46	-0.07	0.12	-0.12	-0.03	0.16	-0.13	0.18	-0.11	-0.09	-0.16	-0.08	0.31	0.00	ND
1996 Jul	0.11	0.09	0.23	0.09	-0.03	0.22	-0.16	0.48	-0.11	0.23	-0.09	-0.06	0.28	-0.05	0.23	-0.17	-0.11	-0.07	-0.09	0.18	0.02	-0.11
1997 Aug	0.17	0.21	0.39	-0.02	-0.18	0.08	-0.09	0.23	-0.18	0.08	-0.15	-0.05	-0.22	-0.10	0.00	-0.18	-0.10	-0.09	-0.25	-0.05	0.04	-0.22
1997 Sep	0.20	0.21	0.33	0.10	0.04	0.13	0.04	0.25	0.00	0.16	0.03	0.07	0.01	0.06	0.12	0.02	0.04	0.07	-0.01	0.09	0.08	0.00
1998 Jun	0.25	0.21	0.12	0.03	-0.02	0.22	-0.07	0.43	-0.03	0.05	-0.19	-0.07	-0.10	-0.04	0.10	-0.03	-0.10	-0.19	-0.25	0.29	-0.04	-0.32
1998 Aug	0.22	0.08	0.19	0.03	-0.01	0.17	0.01	0.31	-0.01	0.16	-0.05	-0.02	-0.08	0.00	0.10	-0.08	0.05	-0.01	-0.16	0.33	0.03	-0.13
1998 Sep	0.22	0.13	0.32	0.12	0.01	0.19	0.09	0.29	0.06	0.21	0.02	0.10	0.07	0.10	0.17	0.05	0.09	0.08	-0.02	0.26	0.11	0.01
1999 Jul	0.03	0.16	0.22	0.16	-0.03	0.12	-0.07	0.30	-0.14	0.14	-0.14	-0.11	0.10	0.00	0.22	-0.10	-0.23	-0.18	-0.24	-0.04	0.04	-0.12
2000 Sep	-0.15	0.10	0.34	0.22	0.13	0.07	-0.15	0.33	-0.20	0.29	-0.18	-0.19	0.25	-0.23	0.03	-0.39	-0.36	-0.25	-0.38	0.08	ND	ND
2001 Aug	0.06	0.26	0.33	0.20	0.03	0.28	0.06	0.45	-0.03	0.23	-0.01	0.01	0.46	0.10	0.29	-0.08	-0.03	-0.02	-0.01	0.05	ND	ND
2004 Aug	0.17	-0.05	0.24	-0.15	-0.16	0.06	0.09	0.34	-0.12	0.17	-0.16	-0.07	-0.23	0.00	0.07	-0.14	-0.09	-0.14	-0.26	-0.07	-0.17	-0.14
2004 Sep	0.04	0.12	0.44	0.28	0.05	0.33	0.11	0.40	-0.14	0.48	-0.08	-0.17	0.12	-0.04	0.20	-0.26	-0.22	-0.21	-0.28	-0.08	-0.24	-0.18
2005 Jan	-0.29	-0.54	-0.11	-0.25	-0.11	0.16	-0.41	0.29	-0.51	0.37	-0.30	-0.28	0.09	-0.37	-0.13	-0.59	ND	ND	ND	ND	ND	ND
2006 Jun	-0.44	-0.58	0.44	-0.10	-0.29	0.38	-0.24	0.29	-0.58	0.43	-0.39	0.54	0.10	ND	ND	ND	ND	ND	ND	ND	ND	ND
2007 May	-0.02	0.02	0.23	0.31	0.00	0.40	-0.03	0.33	-0.21	0.41	-0.17	0.40	0.09	-0.10	0.21	-0.24	-0.27	0.59	-0.25	-0.07	ND	ND
2007 Aug	-0.03	-0.05	0.25	0.13	-0.08	0.33	-0.03	0.30	-0.10	0.42	-0.09	0.45	0.11	-0.11	0.09	-0.14	-0.17	0.36	-0.26	-0.05	-0.21	-0.16
2008 Sep	0.01	0.06	0.46	0.20	-0.15	0.40	-0.09	0.40	-0.22	0.59	-0.06	0.06	0.23	-0.09	0.13	-0.19	-0.13	0.36	-0.30	-0.07	-0.22	-0.22

NDVI:	Color
0.0 to 0.29	
0.3 to 0.39	
0.4 to 0.49	
≥ 0.5	

Fig. 4 NDVI values for 22 Manu River lakes over a 23-year chronosequence extending from 1986 to 2008. Shading indicates NDVI values ≥ 0.3, the threshold value for distinguishing the floating macrophyte state. ND indicates that the value was not determined because of obscuring clouds. Lake numbers given in top row. The corresponding names are listed in Table 1

Lakes 3 and 10. Transitions were often rapid, raising, or lowering NDVI values between < 0.15 and > 0.3 in less than a year.

Depth fluctuations in isolated and flow-through lakes

We obtained pressure-corrected depth records for 3 flow-through (#'s 13, 19 and 29) and 3 isolated (#'s 14, 16 and 18) lakes to compare their hydrology (Fig. 5). The records reveal large differences between the responses of isolated versus flow-through lakes to rainfall events in the watershed. Distance from the main trunk of the river had a damping effect (e.g., #16), but the occurrence of internal flow appears to dominate lake hydrology, as seen in the comparison of Cocha Nueva (#13) to Cocha Cashu (#14). The 2 lakes are of similar size and depth and only 4 km apart, but Cocha Nueva experienced 16 rises of > 0.5 m whereas Cocha Cashu experienced only 1. Maximum rise in lake level was 4 m at Cocha Nueva but only 0.7 m at Cocha Cashu.

For a more formal analysis of water levels, we compared the probability density function (pdf, Fig. 6) and exceedance probabilities (Exc, Fig. S1) of lake levels normalized to zero-mean and unit variance. When comparing the entire pdfs in Fig. 6 to a zero-mean and unit variance Gaussian distribution, all estimated pdfs for the normalized lake levels deviated significantly from Gaussian when using a Kolmogorov-Smirnoff test at the 95% confidence level. However, it is also evident from the pdfs in Fig. 6 that the positive tails (i.e., large excursions above the mean) are more frequent when compared to a Gaussian in lake #'s 13 (Nueva) and 19 (Otorongo—flow-through lakes). The positive tails in the 3 isolated lakes roughly decay as near Gaussian (Fig. S1). The pdf of the normalized water levels in Cocha de los Valles closely resemble those of isolated lakes despite its status as a flow-through lake. The reason for this will be discussed.

Exceedance comparisons further support this outcome, with δH in Nueva and Otorongo exceeding 2 times the standard deviation, one order of magnitude more than shown by the isolated lakes, though Valles again remains an exception. Flow-through lakes Nueva and Otorongo also displayed a consistent positive skewness in a central moment analysis on the raw water level time series (Table S1), indicating high and persistent positive excursions from the mean

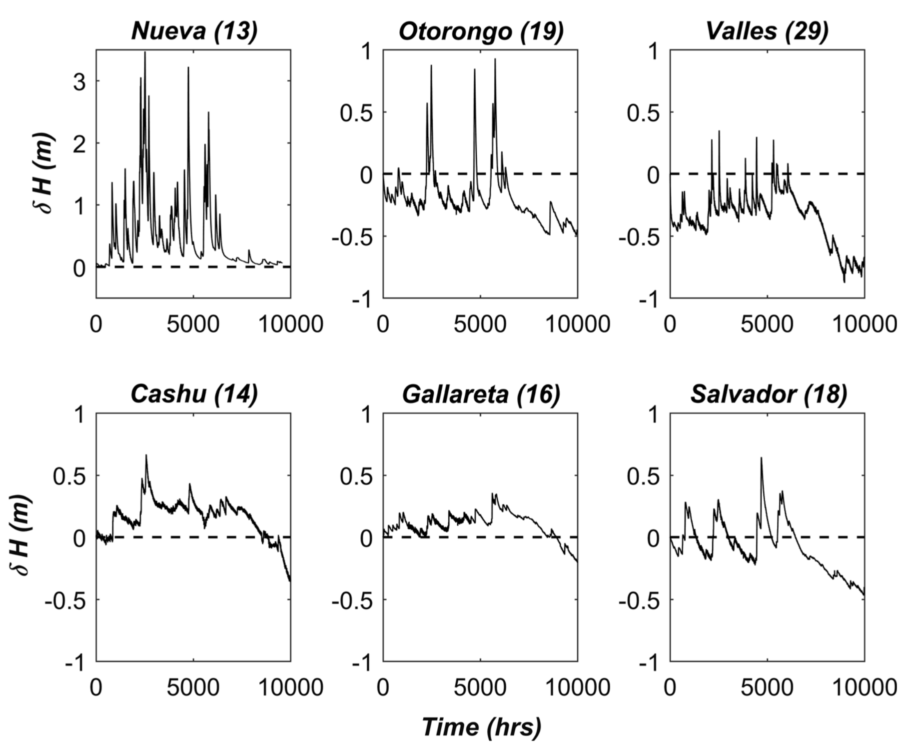

Fig. 5 Depth fluctuations in 6 Manu River lakes, 2009–2010. The trace records depth relative to the initial value (details in text). The 3 frames on the top represent flow-through lakes, those on the bottom represent isolated lakes. The wet season began shortly after the records were initiated and continued to 6000–7000 h

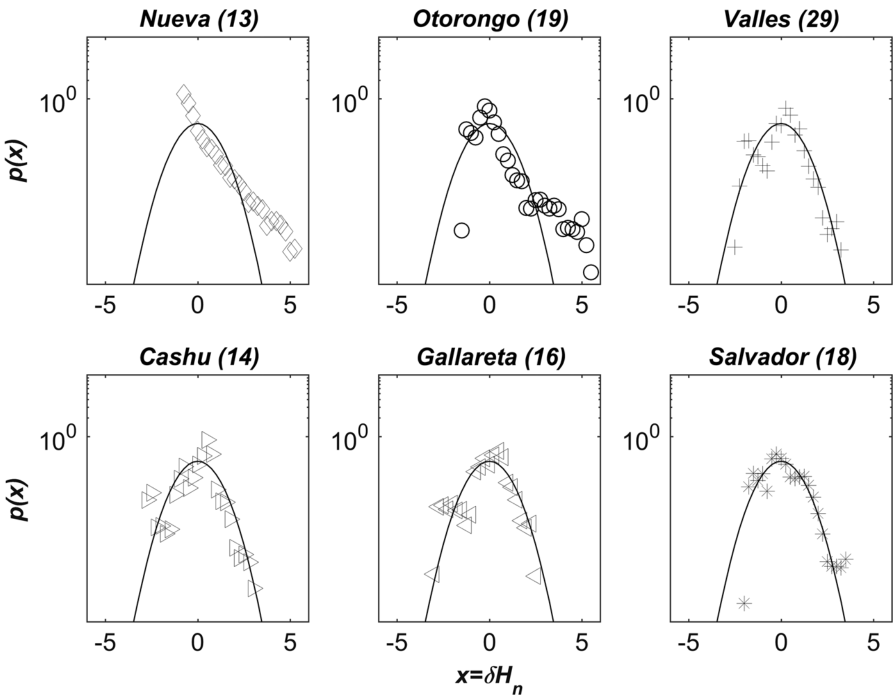

Fig. 6 Probability density functions (pdf) of depth in 3 flow-through (top row) and 3 isolated lakes (lower row) in the Manu River basin, Perú, normalized to zero-mean and unit variance. The positive tails (i.e., large excursions above the mean) are more frequent when compared to a Gaussian in Nueva and Otorongo (flow-through lakes). The positive tails in the 3 isolated lakes roughly decay as near Gaussian. The pdf of the normalized water levels in C. de los Valles closely resemble those of isolated lakes despite its status as a flow-through lake. The reason for this is discussed in the text

state and high flatness factors (i.e., on–off behavior) when compared to isolated lakes, again with the exception of Cocha de los Valles. It is also interesting to note that the raw time series variance was not effective at discriminating isolated and flow-through lakes, suggesting that large positive excursions and on–off pattern in lake level better distinguish the two types of lakes.

Discussion

Ecological regime shifts

The goal of our study was to document the occurrence and frequency of regime shifts between phytoplankton and floating macrophyte states in a series of floodplain lakes in a remote upper Amazon watershed. Landsat images covering the period 1986 through 2008 revealed 31 spontaneous regime shifts in these upper Amazonian lakes, most of which were free of human disturbance, including fishing. We were not able to find cloud-free images for every year between 1986 and 2008, leaving open the possibility that we missed some short-lived state changes, so the number of observed shifts is likely to be an underestimate. We did not attempt to determine the forcing factors that triggered the observed regime shifts, most of which took place long before we initiated the research in lakes few of us had then ever seen.

Low-resolution Landsat images permit only a rough qualitative interpretation of lake states, because several distinct types of floating vegetation occur in Manu River lakes. Macrophyte dominance typically begins with a carpet of *P. stratiotes*. The free-floating plants are driven back-and-forth by the wind from one end of a lake to the other. In two cases we have witnessed, *P. stratiotes* dominance ended under dry season conditions in the absence of flooding when the *P. stratiotes* carpet was colonized by a sedge, *Oxycaryum cubense*, that used the *P. stratiotes* plants as a platform on which to establish (facilitation, Fig. 2b). Points of *O. cubense* establishment then expanded at the expense of the supporting *P. stratiotes*, forming floating islands laced firmly together by intertwined *O. cubense* roots. In Cocha Cashu, the *O. cubense* phase lasted two years (2007–2008) before declining for unknown reasons.

Shifts from phytoplankton to floating vegetation typically occurred at the end of the rainy/beginning of the dry season, with the highest NDVI values recorded between May and July. In the majority of cases, floating vegetation had gone or been greatly reduced by the next year's dry season. However, one or two images a year are not enough to associate shifts with seasonal events, such as major fluctuations in water level (Loverde-Oliveira et al. 2009). Short-term persistence of floating macrophytes raises the question of whether the condition truly represents an alternative state in this system. Two lines of evidence suggest it does. First, the normal positive feedbacks that maintain the condition are operative, in that cover by floating plants casts shade that prevents the development of either phytoplankton or SAV. Second, floating macrophyte dominance sometimes persisted 2 years or more (as at Cocha Cashu 2006–2008), prevailing through successive wet and dry seasons. Floods offer one obvious mechanism to disrupt the floating macrophyte state by washing out the plants and leaving behind open water suitable for phytoplankton development (Wanzten et al., 2008). Floods represent the type of catastrophic pulse event that can overcome hysteresis and reset the system (Scheffer et al., 2001; Guttal & Jayaprakash, 2008; O'Farrell et al., 2011).

In any given year, the majority of lakes in the Manu River basin are in a phytoplankton-dominated state regardless of degree of isolation, with floating vegetation covering less than 12% of the lakes. Floating macrophytes are dependent on high nutrient availability and are therefore favored in shallow lakes where wind-driven turbulence drives sediment suspension (Scheffer et al., 2003). However, the default state of most Manu lakes is the phytoplankton condition in direct contrast to shallow temperate lakes where the default state is one of submerged macrophytes (Scheffer et al., 2001).

Limnological research in Amazonia has been concentrated in the downstream portions of the basin in Brazil where the hydrological regime consists of a high-amplitude (up to 14 m) seasonal rise and fall of river level (Sioli, 1984; Melack & Forsberg, 2001). Most lakes in this region are partially or completely covered with floating vegetation, regardless of season (Tundisi, 1983; Camargo & Esteves, 1995). Oxbow lakes in the lower Parana River, the second largest river in South America, display similar features. Annual flooding lasts for months and lakes are frequently covered with floating vegetation (Camargo & Esteves, 1995; Izaguirre et al., 2004; O'Farrell et al., 2011).

In contrast with the situation in central Amazonia, there is no long-term flooding at the base of the Andes where our research was conducted. Throughout the rainy season, the river is continuously rising or falling in response to rains in the headwaters. The low amplitude, short-duration flood regime apparently favors phytoplankton-dominated systems over floating macrophytes. Complete inundation of the Manu River floodplain has been observed only 3 times since 1973, in 1982, 1999, and 2003. Lakes closer to the river, especially flow-through lakes, experience more of the river's short-term fluctuations than isolated lakes like Cocha Cashu (Osorio et al., 2011). Thus, the level of direct interaction with the river can vary greatly among lakes in a single river basin with likely consequences for susceptibility to regime shifts (Fantin-Cruz et al., 2008).

Statistical analysis of the number of regime shifts observed for each lake over the 23-year chronosequence failed to reveal lake features associated with a tendency to change states. However, as only 9 out of 22 lakes exhibited regime shifts, the analyses lacked statistical power. All recorded instances of regime shift involved isolated lakes or the dead arms of dual lakes. No flow-through lake changed state. Figure 4 reveals many instances (e.g., Lake 3) in which a high NDVI value for a given lake reverted to a low value in the next image, suggesting that ecosystem state is more volatile in isolated than in flow-through lakes (Carpenter & Brock, 2006; Scheffer et al., 2012).

We have drawn a distinction between "isolated" and "flow-though" lakes because they differ in important features (Schneider et al., 2015). The record for flow-through lakes indicates considerable variability through time within a range of low to moderate but not high ($\geq$ 0.3), NDVI values. High NDVI values are precluded by the presence of a central band of flowing open water. The marginal floating meadows of these lakes are tightly laced together by deep intertwined root masses, making the floating vegetation of these lakes less subject to washout than carpets of unanchored floating plants like *P. stratiotes*.

Hydrological records from 6 lakes, 3 isolated, and 3 flow-through, revealed that depth fluctuations in isolated lakes are damped and slow to return to the resting state, implying persistent water levels, whereas flow-through lakes, being directly coupled to the river, undergo frequent and abrupt high-amplitude depth fluctuations. Residence times of water in flow-through lakes are thus short, leaving little time for the development of conditions needed to induce regime shifts (van Geest et al., 2005; Hilt et al., 2011).

The one exception to a consistent hydrological difference between isolated and flow-through lakes was #29 (Cocha de los Valles). This lake occupies what until 1978 was the final section of the Manu River. In that year, the river forged a new mouth, abandoning its former channel and leaving the lake, which drains into the high-gradient Madre de Dios River and is independent of its parent river, the Manu. The Madre de Dios has a braded channel and wide floodplain such that its floods are of relatively low amplitude, accounting for the idiosyncratic hydrology of Cocha de los Valles.

Changes in top-down forcing can trigger regime shifts (Carpenter et al., 1987; Daskalov et al., 2007), but only four Manu lakes experience any fishing (#'s 4, 9, 13, and 29) and none of these experienced regime shifts during the period of observation.

Conclusion

Using Landsat imagery, we constructed a 23-y timeline of NDVI values of 22 oxbow lakes in the Manu River basin of southeastern Perú, documenting 31 spontaneous shifts from low to high or high to low values. Forty years of observing one lake (Cocha Cashu) and first-hand inspection of 27 Manu River lakes in 2012 affirmed that high NDVI values are produced by floating macrophytes. Regime shifts from phytoplankton to macrophyte states occurred only in isolated lakes or lake arms that are decoupled from the main river except during brief interludes of high water. Streams flowing down the length of flow-through lakes wash out plankton and free-floating plants like *P. stratiotes*, permitting the outgrowth of coherent floating meadows from lake margins. Such lakes undergo relatively minor fluctuations in NDVI values.

Although the current understanding of ecological regime shifts in shallow lakes is heavily biased towards anthropogenically impacted ecosystems, our research demonstrates that regime shifts occur frequently and naturally in remote upper Amazonian floodplain lakes. Further research in protected regions with limited anthropogenic impacts, such as the Manu National Park, will be necessary to fully understand the mechanisms behind natural regime shifts in freshwater systems.

Acknowledgements We are grateful to the Matsigenka community of Tayakome for hospitality and assistance, particularly Romulo and Niconor who accompanied the 2012 expedition. Antonio Guerra Rosas, Marcos Maguiña, Ricardo Ricci Bazán and Jessica Espino Ciudad are thanked for essential collaboration in the field. We also thank SERNANP (Peruvian parks agency) for authorizations that allowed us to carry out the research. A National Geographic Society grant (#8672-09) provided partial financial support.

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