




Major shifts in Amazon wildlife populations from recent intensification of floods and drought

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Abstract: *In the western Amazon Basin, recent intensification of river-level cycles has increased flooding during the wet seasons and decreased precipitation during the dry season. Greater than normal floods occurred in 2009 and in all years from 2011 to 2015 during high-water seasons, and a drought occurred during the 2010 low-water season. During these years, we surveyed populations of terrestrial, arboreal, and aquatic wildlife in a seasonally flooded Amazonian forest in the Loreto region of Peru (99,780 km²) to study the effects of intensification of natural climatic fluctuations on wildlife populations and in turn effects on resource use by local people. Shifts in fish and terrestrial mammal populations occurred during consecutive years of high floods and the drought of 2010. As floods intensified, terrestrial mammal populations decreased by 95%. Fish, waterfowl, and otter (*Pteronura brasiliensis*) abundances increased during years of intensive floods, whereas river dolphin and caiman populations had stable abundances. Arboreal species, including macaws, game birds, primates, felids, and other arboreal mammals had stable populations and were not affected directly by high floods. The drought of 2010 had the opposite effect: fish, waterfowl, and dolphin populations decreased, and populations of terrestrial and arboreal species remained stable. Ungulates and large rodents are important sources of food and income for local people, and large declines in these animals has shifted resource use of people living in the flooded forests away from hunting to a greater reliance on fish.*

Keywords: climate change, fishing, floods, hunting, indigenous people, Peru

Grandes Cambios en las Poblaciones Silvestres del Amazonas a partir de la Intensificación Reciente de Inundaciones y Sequías

Resumen: *En la cuenca occidental del Amazonas la reciente intensificación de los ciclos de niveles en los ríos ha incrementado las inundaciones durante la temporada de lluvias y ha disminuido la precipitación durante la temporada seca. En 2009 y en todos los años de 2011 a 2015 hubo inundaciones mayores a lo normal durante la temporada de creciente, y en 2010 hubo una sequía durante la temporada de niveles bajos. Durante estos años, censamos las poblaciones de fauna terrestre, arbórea y acuática en un bosque amazónico de anegación temporal en la región de Loreto en Perú (99,780 km²) para estudiar los efectos de la intensificación de las fluctuaciones climáticas sobre las poblaciones de fauna silvestre, y a la vez los efectos sobre el uso de recursos por parte de la gente local. Ocurrieron cambios en las poblaciones de peces*

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y mamíferos terrestres durante los años consecutivos de las inundaciones y la sequía de 2010. Conforme las inundaciones se intensificaron, las poblaciones de mamíferos terrestres disminuyeron en un 95%. La abundancia de peces, aves acuáticas y nutrias (*Pteronura brasiliensis*) incrementó durante los años de las inundaciones intensas, mientras que las poblaciones de delfines de río y caimanes tuvieron una abundancia estable. Las especies arbóreas, incluyendo a las guacamayas, aves de caza, primates, felinos, y otros mamíferos arbóreos tuvieron poblaciones estables y no fueron afectadas directamente por las inundaciones. La sequía de 2010 tuvo el efecto contrario: las poblaciones de peces, aves acuáticas y delfines de río disminuyeron, y las poblaciones de especies terrestres y arbóreas permanecieron estables. Los ungulados y los grandes roedores son fuentes importantes de alimento y de ingresos para la gente local, y las grandes declinaciones de estos animales ha cambiado el uso de recursos de las personas que habitan en los bosques inundados de la caza a una mayor dependencia de la pesca.

Palabras Clave: cambio climático, caza, inundaciones, Perú, pesca, poblaciones indígenas

摘要: 近期西亚马逊盆地的河流水位周期性加剧增加了雨季的洪涝发生, 并减少了旱季的降雨量。在2009及2011-2015年的高水位季节, 洪涝的发生要高于正常水平;而在2010年的低水位季节, 却发生了干旱。2009-2015年, 我们在秘鲁洛雷托 (Loreto) 一块发生季节性洪涝的亚马逊林区 (99,780 km²), 对陆生、树栖以及水生野生动物种群进行了调查, 以研究气候自然波动的加剧对野生动物种群的影响及随之产生的对当地人资源利用的影响。在持续的高洪涝年份和2010年的干旱年份, 鱼类和陆生哺乳动物种群发生了变化。因洪涝加剧, 陆生哺乳动物种群减少了95%。在洪涝加剧的年份, 鱼类、水鸟以及水獭 (*Pteronura brasiliensis*) 的丰度增加了, 而淡水豚和凯门鳄种群丰度保持稳定。树栖物种, 包括金刚鹦鹉、猎鸟、灵长类、猫科动物以及其它树栖的哺乳动物, 其种群保持稳定, 未直接受到高洪涝的影响。2010年的干旱则有相反的影响: 鱼类、水鸟和淡水豚种群下降, 而陆生和树栖物种种群保持稳定。有蹄类和大型啮齿类动物是当地人重要的食物和收入来源, 这些动物种群的下降改变了在洪涝林区生活的人们对资源的利用模式, 从狩猎转为更加依赖渔捞。

关键词: 秘鲁, 气候变化, 洪涝, 土著人, 狩猎, 渔捞

翻译: 单磊

审校: 胡义波

Introduction

Human-induced emissions of greenhouse gases, including CO₂, have increased global temperatures, and the International Panel on Climate Change predict climate will continually change at a relatively rapid rate during this century (Qin et al. 2013). For the western Amazon Basin, recent models predict an intensification of the hydrological cycles: increased intensity and duration of flooding during wet seasons (Cook et al. 2012; Langerwisch et al. 2012; Gloor et al. 2015) and lower water levels and less precipitation during the dry season (Phillips et al. 2009; Espinoza et al. 2011; Boisier et al. 2015). The observed consequences of these climatic fluctuations include increased tree mortality (Doughty et al. 2015), decreased carbon sinks (Brienen et al. 2015), deforestation and forest dieback (Malhi et al. 2008), and probable changes that will affect livelihoods of local people.

The Amazon forest, with an area of 6.7 million km², is the world's largest expanse of intact tropical rainforest, and one of the most prominent reservoirs of cultural and biological diversity (Pimm et al. 2014). Most Amazonian indigenous societies identified as vulnerable to climate change still maintain traditional socioeconomic livelihoods based on subsistence use of natural resources (Nyong et al. 2007), and hunting and subsistence fishing are key to daily animal protein intake of traditional Ama-

zonian people (Townsend 2004). Populations of major resource species, such as fish, ungulates, and large rodents, depend on the hydrological cycles of river water during dry and wet seasons that characterize the Amazon floodplain (Junk et al. 1989; Goulding et al. 2003). Thus, indigenous communities living along the Amazon floodplain have developed divergent livelihood strategies to cope with annual fluctuations in water levels (Kvist et al. 2001; Endoa et al. 2016). However, greater multiyear fluctuations in water levels such as intensive floods and droughts may cause shifts in wildlife populations in floodplain forests that are greater in intensity and are likely driving both wildlife populations and human resource use.

The ecology of wildlife in flooded forests revolves around the aquatic and terrestrial cycles, and populations are sensitive to intensification of seasonal patterns of flooding and drought (Bodmer 1990; Henderson et al. 1998). Consequently, fish and terrestrial mammals are most affected by this intensification, and local people will need to change their hunting and fishing patterns to adapt to these climatic-induced changes.

We examined the impact of 5 years of consecutive intensive flooding on terrestrial, arboreal, and aquatic wildlife in flooded forests of the Peruvian Amazon in a case study in the Samiria River basin of the Pacaya-Samiria National Reserve. We sought to provide a current picture of the impact these hydrological changes are having on this tropical rainforest.

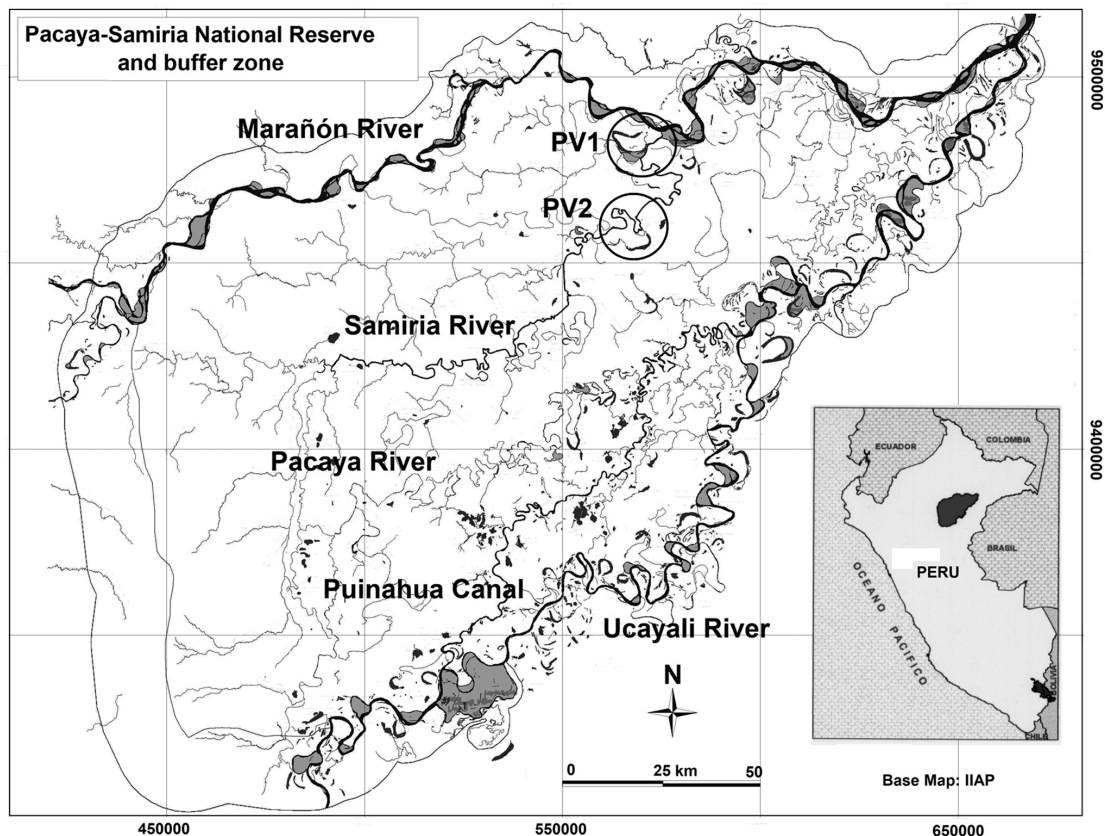


Figure 1. Pacaya-Samiria National Reserve showing the study areas (PV1 and PV2) (IAP, Instituto de Investigaciones de la Amazonía Peruana).

Methods

Study Area

The Samiria River basin in the Pacaya-Samiria National Reserve is in the Marañón-Ucayali subsidence area of the Ucayali depression (Zulkafli et al. 2016). The Pacaya-Samiria National Reserve is the largest block of várzea flooded forests in the western Amazon and extends over 2,080,000 ha in the Department of Loreto, Peru. The study sites included the mouth of the Samiria River (PV1) (UTM E 575967, N 9483245) and the lower midsection (PV2) (UTM E 571310, N 9460666); each had an area of approximately 200 km² (Fig. 1). The study sites had land formations with varying levels of annual flooding that we divided into 6 broad categories: riverine forests, open understory flooded forests, levee forests, liana forests, tree-fall gaps, and aguaje palm (*Mauritia flexuosa*) swamps. Aquatic formations included the Samiria River, oxbow lakes, and channels.

The Pacaya-Samiria National Reserve was decreed in 1982 and is managed by the Peruvian Protected Area Service (SERNANP - Servicio Nacional de Áreas Naturales Protegidas) and the Cocama (Kukama) indigenous people through community-based management groups. Sustainable resource use and traditional activities are permit-

ted within the reserve, including subsistence fishing and hunting. The Cocama people rely on small-scale agriculture and fishing as their primary activities and hunting to a lesser extent. They adapt their hunting and fishing activities according to the seasonal water level and the availability of fish and wild-meat resources. They focus on fishing during the low-water seasons and increase hunting during the high-water seasons (Bodmer et al. 2008).

Water Level and Climate

The climate in the region is typically equatorial; annual temperatures range from 22 to 36 °C, relative humidity is 80–100%, and annual rainfall is 1500–3000 mm. We used water-level data from the limnometric station of Iquitos collected by the Servicio de Hidrografía y Navegación de la Amazonía. Data were logged near the study area and were complete daily records from 1978 to 2015 and partial records from 1968 to 1977 (Servicio de Hidrografía 2015). Water levels from the Servicio de Hidrografía agreed with trends and pulses used in previous studies that came from different data sets (Espinoza et al. 2011, 2013; Zulkafli et al. 2016). Duration of intensive floods included consecutive days when water level exceeded 117.65 m asl.

The Pacaya-Samiria National Reserve and surrounding areas have a predictable annual water-level cycle: high-water season from February-May, transitional period to low water from June-July, low-water season from August-October, and transitional period to high water in November-January. The percentage of dry land remaining during peak flood pulse was determined using the height of water marks of trees in 20, 20 × 20 m vegetation plots.

Wildlife Surveys

We surveyed wildlife to estimate the effect of intensive floods on different wildlife communities, according to landscape categories (aquatic, terrestrial, and arboreal) and species categories (indicator species and human-resource species). Indicator species are not harvested by local people, whereas resource-use species are harvested. We used a matrix of 6 combinations of landscape and species categories to determine wildlife groups surveyed that included: aquatic indicator species (river dolphins, otter [*Pteronura brasiliensis*], and waterfowl), aquatic resource-use species (fish and caimans), terrestrial indicator species (edentates and felids), terrestrial resource-use species (ungulates and rodents), arboreal indicator species (small-bodied primates and macaws [*Ara* spp.]), and arboreal resource-use species (game birds, large-bodied primates, and rodents). The matrix is provided in Supporting Information.

To determine population trends of species and species groups over time we conducted surveys. The research design was based on multiyear population analyses of species groups, and the protocol was the same for all years from 2009 to 2015. To improve precision, we surveyed similar transects over years to maintain continuity and spatiotemporal relationships and did not make subjective judgments or use previous knowledge of animal abundance for placement of surveys (Buckland et al. 2001). Species groups were surveyed independently, and surveys were conducted in all years during flooded, low-water, and transition seasons. The annual average was 188 (SD 16) survey days per year (120 [SD 12] at PV2 and 60 [SD 5] at PV1).

Survey teams included one Cocama field assistant, one Peruvian biologist fully trained in the methods, and an average of 3 volunteers or students (range 1–8). The team composition was held constant throughout the study to ensure consistent data collection, similar detection probability, and constant methods.

We surveyed terrestrial mammals (ungulates and rodents), arboreal mammals (primates and other mammals), and game birds along transects. Twenty trails (12 in PV2 and 8 in PV1) 2.6 km long on average were cut prior to the surveys, and each was walked multiple times at approximately 1 km/hour. An average of 1098 (704–1826) km were surveyed annually. We used the distance-

sampling method, and observers walked transects from 0700 to 1200 and from 1400 to 1800. When a group of animals was encountered, the number of individuals was recorded, and the perpendicular distance from the trail to the first individual sighted was measured. Clusters, such as primate troops, were considered independent units, and cluster size was used to determine density of individuals (Buckland et al. 2001). The data were analyzed with Distance software (version 6.0). Population densities were calculated as number of individuals per square kilometer.

We also surveyed terrestrial mammals and felids with infrared and motion camera traps set over areas of approximately 200 km² at PV2 and distributed across habitats in 2009, 2011, 2013, 2014, and 2015. The annual average number of camera days was 1200 (range 833–2214). Independent events had a minimum gap of 30 minutes for captures of the same species. Camera traps were checked weekly to determine battery levels and functioning of the units. Capture rates per species were calculated as independent events as number of individuals/1000 camera days (mcd).

We surveyed macaws with 15-minute point counts set in sampling units separated by 500 m along the shoreline of rivers, lakes, and channels. Surveys had between 6 and 9 points. There were 8 shoreline areas at PV2 and 10 at PV1. Censuses were done in the morning (530–900) and afternoon (1600–1830), when movement is usually unidirectional from roosting to feeding sites and vice versa, respectively. A mean of 1046 (968–1753) points were surveyed annually. We determined species through visual and auditory identification, and recorded the number of individuals in a flock and minute of observation. The number of individuals per point was used to measure population trends.

We caught fish with nylon gill nets 30 m long and 3 m deep with a mesh size of 9 cm set for 1 hour in rivers, lakes, channels, and flooded forest with weak currents. Mean number of annual survey hours was 372 (range 182–494), and survey hours were divided equally between morning (700–1100) and afternoon (1400–1800). Species, subject's weight and standard length (total length minus the tail fin), and geographic coordinates were recorded. Catch per unit effort (CPUE) was calculated as individuals per net hour and biomass per net hour. The majority of fish were released back into the water, and the method resulted in only 5% mortality of fish, which was in accordance with the protocol of SER-NANP (Servicio Nacional de Áreas Naturales Protegidas por el Estado, Perú).

We surveyed waterfowl along shoreline transects in the morning (530–900) and afternoon (1600–1830), when flocks are generally perched, thus decreasing the chances of double counting. At approximately 2 km/hour in an aluminum skiff powered by a 25 hp engine, 8 shoreline transects at PV2 and 8 at PV1 of 5.0 km were surveyed

along rivers, lakes, and channels. An average of 404 (281–969) km was surveyed annually. All perched or flying waterfowl were recorded. Population abundance of species was calculated as number of individuals per kilometer.

We surveyed dolphins diurnally along 5-km aquatic transects in rivers, lakes, and channels at a velocity of approximately 2 km/hour (6 transects at PV2 and 5 at PV1). A mean of 1013 (922–1958) km were surveyed annually during morning (700–1200) and afternoon (1400–1600). Dolphins were recorded visually when breaching the water surface, and the number of dolphins was determined by visual tracking. A 12-m covered launch powered by a 25 hp inboard engine was used for dolphin surveys. Population abundance of species was calculated as number of individuals per kilometer.

We surveyed caimans through visual counts at night (2000–2400). We traveled along 5.0-km transects at approximately 2 km/hour on a single side of the river, lake, or large channel (>40 m wide) or simultaneously on both sides in smaller channels (<40 m wide). A mean of 833 (range 605–1109) km were surveyed annually (6 transects at PV1 and 6 at PV2). We located caimans by their eye reflections in a spotlight and approached to a distance where observations could be made. Survey speed was approximately 2 km/hour, and we stopped when caimans were sighted. An aluminum skiff with a 25 hp outboard engine was used for caiman surveys. Population abundance per species was calculated as number of individuals per kilometer.

Harvest Registers

In 2009, 2012, and 2015, we conducted semi structured household interviews with locals living in the Samiria River basin to collect information on the harvesting of fish and wild meat. We used information on resource use of families to calculate the percentage of families involved in fishing and hunting activities. In 2015, we interviewed families in 6 villages (mean 45 families, range 20–60) to determine annual harvests of wildlife and fish. We used open-ended questions to heads of households to discuss the frequency, duration, and approximate catch during hunting and fishing events and estimated monthly returns. We followed the ethics protocol of the School of Anthropology and Conservation, University of Kent, United Kingdom.

Analyses

Population trends of species assemblages were correlated with water-level data, and we categorized annual water-level as normal, intensive flood, historic flood, or extreme drought.

We used the Shapiro–Wilks test to assess data normality. Time series regressions were done on annual data sets of species and species groups. We combined PV1

and PV2 data on fish, dolphins, waterfowl, terrestrial and arboreal mammals, felids, macaws, and game birds. For primate and caiman, we used only PV2 data.

Results

Intensification of flooding was seen from 2011 to 2015 during high-water seasons of February–May. When water level exceeded 117.65 m asl, 75% of the PV2 study site flooded, leaving only 25% dry levee forests. We defined this water level as intensive floods. The years of 2011–2015 was the only period in the 40-year data set of the Servicio de Hidrografía that had 5 consecutive years of intensive floods; other consecutive periods had only 2 years (1986–1987, 1993–1994, 1999–2000).

Intensification of floods was also seen in the relationship between peak flood pulses and the duration of intensive flood levels. Throughout 2011–2015, water levels were significantly higher and duration of inundation above 117.65 m asl was significantly longer than in previous years ($F_{1,36} = 6.95$, $p = 0.01$, and $F_{1,36} = 10.31$, $p = 0.002$, respectively) (Fig. 2). The 2 highest water levels also had the longest duration and occurred during the consecutive floods of 2011–2015. The highest flood pulse occurred in 2012 at 118.97 m asl and lasted 66 days, and in 2015 the second highest water level was observed at 118.67 m asl and lasted 99 days. At 118.37 m asl all surveyed plots in the study site were flooded, including the elevated levee forests. Very few dry patches of levee forest remained in the Samiria River basin, and we defined these years as historic flood levels.

There was also an intensification of low water during the dry seasons of August–October. The 40-year data set of the Servicio de Hidrografía showed a slight negative regression in the trough of low-water seasons ($r^2 = 10.0$, $p = 0.02$). The lowest troughs in water level occurred during the dry seasons of 2010 (105.43 m asl) and 2005 (106.09 m asl). The average trough for all years was 108.19 m asl (SD 1.08) m asl, and the annual variation of water level was 9.17 m (SD 1.19) between peaks of high water and troughs of low water.

Terrestrial mammal populations decreased by over 95% during 2009–2015, coinciding with the recent consecutive years of high water levels ($r^2 = 0.73$, $p = 0.013$). In 2009, density was 5.18 ind/ km² (SD 0.60) and in 2014 it was 0.02 ind/ km² (SD 0.01). No terrestrial mammals were sighted in 2015. White-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), red brocket deer (*Mazama americana*), black agouti (*Dasyprocta fuliginosa*), paca (*Cuniculus paca*), giant anteaters (*Myrmecophaga trydactyla*), and nine-banded armadillo (*Dasybus novemcinctus*) numbers declined on transects and in camera-trap surveys during consecutive years of high flood levels. Results from transect surveys concurred with camera-trap surveys ($r^2 = 97.5$,

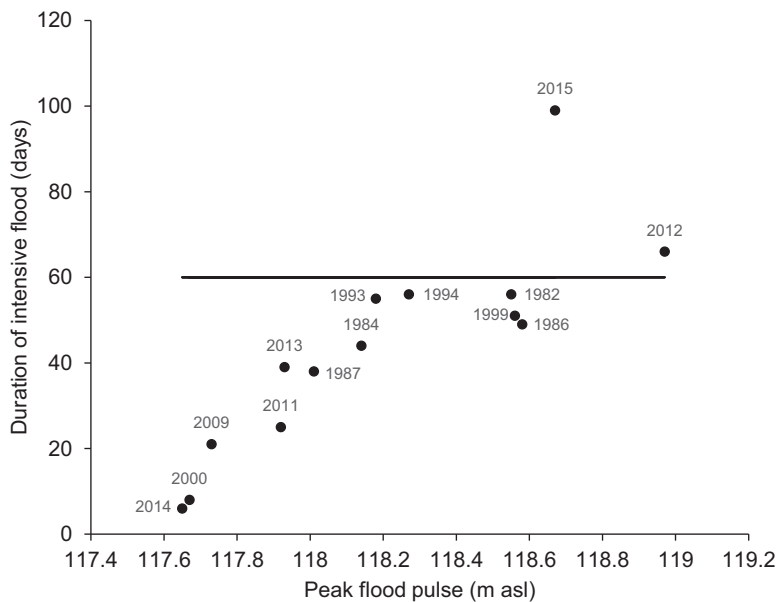


Figure 2. Relationship between peak flood pulse and duration of flooding in intensively flooded years. Data are from the Servicio de Hidrografía (2015).

$p = 0.001$). The annual number of terrestrial mammals captured on camera traps prior to the historic flood of 2012 was 625 ind/1000 camera days (hereafter mcd) (range 402–848), whereas the yearly capture rate after 2012 was 67 ind/mcd (range 58–72). The lowland tapir (*Tapirus terrestris*) was the only terrestrial ungulate to have stable numbers. Jaguar (*Panthera onca*), puma (*Puma concolor*), and ocelot (*Leopardus pardalis*) populations numbers fluctuated during the consecutive years of high floods and did not have significant time series regressions (Table 1).

Populations of arboreal species, including macaws, game birds, primates, and other arboreal mammals remained stable during consecutive years of high floods. Total macaw numbers were stable from 2009 to 2015 (9.82 ind/point [SD 3.89]; $r^2 = 0.01$, $p = 0.781$). However, there was a negative interspecific relationship between Red-bellied Macaw (*Orthopsitaca manilata*) and Chestnut-fronted Macaw (*Ara severus*) during years of consecutive high floods; Red-bellied increased during years of intensive floods and Chestnut-fronted decreased ($r^2 = 0.55$, $p = 0.054$). Total densities of game birds, including Tinamous (*Tinamus* spp.), Spix's Guan (*Penelope jacquacu*), Piping Guan (*Pipile cumanensis*), and Razor-billed Curassows (*Mitu tuberosum*) were stable from 2009 to 2015 (3.41 ind/km² [SD 1.84]; $r^2 = 0.43$, $p = 0.105$). Tinamous, the most terrestrial of the assemblage, was the only game birds that declined during this period (Table 2).

The total densities of primates were stable during consecutive years of high floods (145.50 ind/km² [SD 32.66]; $r^2 = 0.35$, $p = 0.155$), as were densities of primate species, including woolly monkey (*Lagothrix poeppigii*), howler monkey (*Alouatta seniculus*), brown capuchin (*Cebus apella*), saki monkey (*Pithecia monachus*),

squirrel monkey (*Saimiri boliviensis*), and saddled-back tamarin (*Saguinus fuscicollis*). Likewise, other arboreal mammal densities were stable (7.34 ind/km² [SD 0.00]; $r^2 = 0.15$, $p = 0.374$), as were individual species, including Amazon squirrel (*Sciurus spadiceus*), brown-throated sloth (*Bradypus variegatus*), common opossum (*Didelphis marsupialis*), coati (*Nasua nasua*), and tyra (*Eira barbara*) (Table 3).

Populations of aquatic species made up of fish, dolphins, waterfowl, caimans, and otters generally increased or remained stable during consecutive years of high water levels from 2010 to 2015. After the drought of 2010, fish stocks in the Samiria River basin benefitted from consecutive years of intensive floods and increased year on year to 2015 in number and biomass (Table 4). The most common species were tiger wolf fish (*Hoplias malabaricus*), gold wolf fish (*Hoplerhytrinus unitaeniatus*), white piranha (*Serrasalmus humeralis*), black piranha (*Serrasalmus rhombeus*), red piranha (*Pygocentrus nattereri*), black prochilodus (*Prochilodus nigricans*), common armoured catfish (*Liposarcus pardalis*), and oscar (*Astronotus ocellatus*).

Total waterfowl numbers increased during consecutive years of high flood levels (302.99–783.75 ind/km; $r^2 = 0.77$, $p = 0.020$) and were associated with increased fish stocks ($r^2 = 58.3$, $p = 0.045$); Neotropical Cormorants (*Phalacrocorax brasilianus*) increased the most (Table 4).

Populations of both pink river dolphin (*Inia geoffrensis*) and grey river dolphin (*Sotalia fluviatilis*) maintained stable populations during consecutive years of high flood levels (4.48 ind/km [SD 1.56]; $r^2 = 0.26$, $p = 0.29$). Giant river otter (*Pteronura brasiliensis*) populations increased in consecutive years of intensive floods year on year from 2010 to 2015 (Table 4).

Table 1. Time-series regressions of terrestrial mammal species in the Samiria River basin showing significant population trends as ranges and nonsignificant time series as means (SD) from 2009 to 2015, beginning with the first intensive flood pulse of 2009.

Species	Survey type ^a	Range (2009–2015) or mean (SD) ^b	trend ^c	r ²	p
<i>Tayassu pecari</i> white-lipped peccary	T	5.46–0	neg	0.59	0.043
<i>Pecari tajacu</i> collared peccary	C	9.86–0.45	neg	0.89	0.015
<i>Mazama americana</i> red brocket deer	T	0.19–0	neg	0.57	0.048
<i>Tapirus terrestris</i> lowland tapir	C	29.02–2.71	neg	0.87	0.019
	T	0.21–0	neg	0.76	0.010
	C	36.36–2.25	neg	0.92	0.009
	C	22.73 (7.93)	ns	0.03	0.775
<i>Dasyprocta fuliginosa</i> black agouti	T	1.25–0.02	neg	0.92	<0.001
<i>Cuniculus paca</i> Paca	C	445.45–27.10	neg	0.87	0.018
	C	113.64–13.55	neg	0.86	0.021
<i>Myrmecophaga trydactyla</i> giant anteater	C	22.72–3.16	neg	0.81	0.034
<i>Dasypus novemcinctus</i> nine-banded armadillo	C	127.27–3.61	neg	0.79	0.043
<i>Panthera onca</i> Jaguar	C	10.22 (3.18)	ns	0.33	0.304
<i>Puma concolor</i> Puma	C	9.02 (4.84)	ns	0.06	0.672
<i>Leopardus pardalis</i> Ocelot	C	18.06 (18.89)	ns	0.03	0.758

^aSurvey types: T, terrestrial transect (individuals per square kilometer); C, camera traps (individuals per 1000 camera days).

^bRange $p < 0.05$, mean $p > 0.05$.

^cAbbreviations: neg, negative; ns, not significant.

The spectacled caiman (*Caiman crocodilus*) populations showed a long-term decrease that began before the intensification of river levels. Their mean density from 2004 to 2008 was 1.1 ind/km (SD 0.3), whereas it was 0.5 ind/km (SD 0.2) from 2009 to 2015. The spectacled caiman continued to decrease during years of consecutive flooding. Black caiman (*Melanosuchus niger*) had stable populations during consecutive years of high flood levels (Table 4).

The drought of 2010 had the opposite effect on wildlife as the years of consecutive floods. During and following the drought in the dry season of 2010, populations of aquatic fauna decreased. Fish stocks decreased from an annual biomass of 10.45 kg/net hour (SD 1.35) in 2009 to a biomass of 9.23 kg/net hour (SD 1.29) in 2010. Similar decreasing trends were observed in the populations of the pink river dolphin, which fell from 3.30 ind/km (SD 1.81) in 2009 to 1.83 ind/km (SD 1.28) after the drought. Waterfowl also decreased from 287.7 ind/km (SD 34.1) prior to the drought to 112.5 ind/km (SD 33.6) afterward. After 2 consecutive years of high floods (2011–2012), populations of all these species groups were back to predrought levels.

Terrestrial and arboreal species did not show any obvious declines during the drought of 2010. The terrestrial mammals had an initial decrease after the intensive flood of 2009 from 5.2 ind/km² (SD 3.1) to 2.0 ind/km² (SD 1.2) in 2010. During the drought, terrestrial mammals maintained their populations with a 2011 density of 1.5 ind/km² (SD 1.0). Then, after the historic flood of 2012 the terrestrial mammals crashed to a density of 0.3 ind/km² (SD 0.3). Trends in species populations from 2009 to 2015 are provided in Supporting Information.

Household surveys showed how Cocama indigenous people in the Samiria River basin have increased fishing and decreased hunting as a result of shifts in wildlife populations. In 2009, 84% of Cocama families fished, whereas 67% hunted. In 2012, 100% of families fished and 57% hunted, and in 2015, 100% of families fished and only 33% continued to hunt. In 2015, fish was the most important animal protein consumed by households; an average extended family caught 4251 kg (SD 2329) of fish annually, whereas the average annual wild meat they hunted was 135 kg (SD 267).

Table 2. Time-series regressions of avian species in the Samiria River basin showing significant population trends as ranges and nonsignificant time series as means (SD) from 2009 to 2015, beginning with the first intensive flood pulse of 2009.

Species	Survey type ^a	Range (2009–2015) or mean (SD) ^b	trend ^c	r ²	p
Macaws					
<i>Orthopsitaca manilata</i> Red-bellied Macaw	P	0.42–15.44	pos	0.66	0.024
<i>Ara severus</i> Chestnut-fronted Macaw	P	9.65–0.11	neg	0.65	0.027
<i>Ara ararauna</i> Blue & Yellow Macaw	P	2.20 (1.46)	ns	0.11	0.449
Game birds					
<i>Tinamus</i> spp Tinamous	T	6.95–0.84	neg	0.75	0.011
<i>Mitu tuberosum</i> Razor-billed Curassow	T	0.19 (0.32)	ns	0.04	0.659
<i>Penelope jacquacu</i> Spix's Guan	T	0.37 (0.16)	ns	0.17	0.346
<i>Pipile cumanensis</i> Piping Guan	T	0.66 (0.41)	ns	0.11	0.454

^aSurvey types: T, terrestrial transect (individuals per square kilometer); P, point counts (individuals per 15-minute point).

^bRange $p < 0.05$; mean $p > 0.05$.

^cAbbreviations: neg, negative; ns, not significant; pos, positive.

Discussion

Climate models for the western Amazon Basin predict an intensification of the hydrological cycles with increased height and duration of flooding during wet seasons (Cook et al. 2012; Gloor et al. 2015; Zulkafli et al. 2016) and lower water levels and less precipitation during the dry season (Phillips et al. 2009; Espinoza et al. 2011; Boisier et al. 2015). From 2009 to 2015, the Loreto region of the Peruvian Amazon experienced 5 consecutive years of above normal flooding (2011–2015) preceded by 1 year of intense drought (2010). This 5-year period was the longest consecutive period of high flood pulses since 1973–1977, which coincided with La Niña events (Espinoza et al. 2013) and began with the intensive flood of 2009 (Davidson et al. 2012). There has been an overall decrease in the trough of low-water seasons since the early 1980s (Espinoza et al. 2011). Conservation scientists, in the context of these climate changes, will need to understand how physical changes, in this case hydrological intensification, result in biological changes in wildlife and how these cause changes in resource use, sustainability, and management by local people in the Loreto region of the Peruvian Amazon.

Terrestrial mammal populations showed a dramatic dieback in flooded forests of the Samiria River basin from

consecutive years of intensive floods. When water levels increase, terrestrial mammals take refuge on dry levee forests. These are long, thin stretches of slightly raised land formed by changes in river channels that are typically 1–2 km long and 200 m wide. Years with high flood pulses have less dry forests, which forces terrestrial mammals onto smaller areas resulting in greater competition and increased predation (Bodmer 1990). The lack of dry land at the study site during record high floods of 2012 and 2015 also caused drowning in terrestrial mammals. Lowland tapir was the only terrestrial mammal that maintained stable populations during consecutive years of intensive floods, possibly because of their folivorous diet and aquatic habits, which allow them to live on flooded levees (Brooks et al. 1997).

Wildlife that ascend trees or have arboreal habits can escape physical effects of floods and are less vulnerable to high pulses than ground-dwelling mammals. All of the felids are scansorial, and their populations did not show negative regressions during years of intensive floods. However, their prey base of ungulates and large rodents crashed, and it appears they adapted by changing prey types. Shells from turtles eaten by felids have been found (R.B., M.A., P.P., & K.C., personal observation), and when the agouti populations crashed ocelots may have changed to tinamous, which may explain why

Table 3. Time-series regressions of arboreal mammals showing nonsignificant time series as means (SD) from 2009 to 2015, beginning with the first intensive flood pulse of 2009.

Species	Survey type ^a	Mean (SD) ^b	trend ^c	r ²	p
Primates					
<i>Lagothrix poeppigii</i> woolly monkey	T	3.22 (1.91)	ns	0.22	0.504
<i>Alouatta seniculus</i> howler monkey	T	11.19 (2.42)	ns	0.44	0.102
<i>Cebus apella</i> brown capuchin	T	15.23 (4.18)	ns	0.01	0.830
<i>Pithecia monachus</i> saki monkey	T	2.96 (0.94)	ns	0.17	0.344
<i>Saimiri boliviensis</i> squirrel monkey	T	69.21 (25.49)	ns	0.47	0.088
<i>Saguinus fuscicollis</i> saddled-back tamarin	T	15.00 (4.66)	ns	<0.01	0.999
Other arboreal mammals					
<i>Sciurus spadiceus</i> Amazon squirrel	T	3.83 (2.41)	ns	0.32	0.756
<i>Bradypus variegatus</i> brown-throated sloth	T	0.13 (0.51)	ns	0.01	0.728
<i>Didelphis marsupialis</i> common opossum	C	113.27 (55.65)	ns	0.52	0.165
<i>Nasua nasua</i> Coati	T	1.74 (2.06)	ns	0.36	0.152
<i>Eira Barbara</i> Tyra	T	0.53 (0.33)	ns	0.25	0.251

^aSurvey types: T, terrestrial transect (individuals per square kilometer); C, camera traps (individuals per 1000 camera days).

^bMean $p > 0.05$.

^cAbbreviation: ns, not significant.

their population decreased. Arboreal species may exhibit population shifts as changes in forest structure and food resources occur that are associated with decreased seed dispersal and seed predation functions of ungulates and large rodents (Beck 2006).

Fish stocks benefited from consecutive years of high water levels. The Pacaya-Samiria National Reserve is the largest flooded forest in the Peruvian Amazon and in turn is the area with the most productive fisheries. During the high-water season fish enter the flooded forest and access abundant food resources, and during intensive floods fish stay longer in the high nutrient várzea waters, extending breeding seasons that result in larger stocks (Henderson et al. 1998; Goulding et al. 2003). When water recedes in the dry season large numbers of fish migrate out of the Samiria River basin into the larger Marañón River, and during this period flocks of Neotropical cormorants and great egrets and pods of pink and grey dolphins congregate along the middle and lower sections of the Samiria River to feed on the abundant fish stocks.

Droughts have been less common than intensive floods, and our surveys covered only the 2010 occurrence. The drought affected aquatic wildlife as a result of reduced water levels, and fish mortality was high. It took 2 years of intensive flooding for fish, dolphin, and waterfowl populations to recover to pre-drought levels. In contrast, terrestrial and arboreal wildlife maintained their populations during the drought.

Traditionally, people of Amazonian várzea use subsistence resources of fish and wild meat according to an annual cycle (Endoa et al. 2016). Hunting is more frequent during the flooded season when terrestrial mammals are concentrated on levees (Bodmer et al. 2008). In contrast, fishers are more successful during low water, when fish stocks are concentrated in lakes, rivers, and channels (Endoa et al. 2016).

Artiodactyls and large rodents are important wild meat species (Silvius et al. 2004), and their recent decline has resulted in lower hunting success and diminished sustainability. Similar to other tropical forest people (Rowcliffe

Table 4. Time-series regressions of aquatic species in the Samiria River basin showing significant population trends as ranges and nonsignificant time series as means (SD) from 2010 to 2015, beginning with the historic drought of 2010.

Species	Survey type ^a	Range (2010–2015) or Mean (SD) ^b	trend ^c	r ²	p
Fish					
Individuals	N	9.23–13.42	pos	0.82	0.012
Biomass	N	1.17–3.08	pos	0.76	0.022
Waterfowl					
<i>Phalacrocorax brasilianus</i>	ST	270.60–761.29	pos	0.77	0.020
Neotropical Cormorant					
<i>Ardea alba</i>	ST	19.81 (14.02)	ns	0.15	0.435
Great Egret					
Aquatic mammals					
<i>Inia geoffrensis</i>	AT	3.05 (0.85)	ns	0.21	0.357
pink river dolphin					
<i>Sotalia fluviatilis</i>	AT	1.16 (0.85)	ns	0.23	0.329
grey river dolphin					
<i>Pteronura brasiliensis</i>	T	0.77–10.03	pos	0.78	0.018
giant river otter					
Caimans					
<i>Caiman crocodilus</i>	ST	0.95–0.32	neg	0.75	0.011
spectacled caiman					
<i>Melanosuchus niger</i>	ST	0.48 (0.20)	ns	0.38	0.708
black caiman					

^aSurvey types: N, gill net survey of individuals (individuals per net hour); N, gill net survey of biomass (kilograms per net hour); T, terrestrial transect (individuals per square kilometer); ST, shore-line transect (individuals per kilometer).

^bRange $p < 0.05$; mean $p > 0.05$.

^cAbbreviations: neg, negative; ns, not significant; pos, positive.

et al. 2005), the Cocama are adapting to recent years of intensive floods because fish stocks have remained large and can compensate for decreases in wild meat.

The recent intensification of the hydrological cycles in western Amazonia allows us to predict consequences for wildlife and subsistence resource use if future climate change occurs as forecast (Davidson et al. 2012). Wetter conditions in the western Amazon will result in dieback of terrestrial mammals and increases in aquatic species in flooded forests. Wild meat for local people will become scarce, but fishing will increase. Occasional drought years will result in declines of fish stocks and other aquatic species, but they will recover in years of high flooding. Terrestrial mammals will not have sufficient time to recover during occasional droughts because of their low reproductive rate compared with fish. Consecutive years of drought conditions will result in more severe dieback in aquatic fauna and low fish stocks, and species used for wild meat will begin to recover. The worst conditions for wildlife and local people will be in years of consecutive high floods followed by consecutive droughts. In this situation, first terrestrial mammals will decrease and then fish stocks will decrease. Fish mortality will happen

more quickly than recovery of wild meat species, which will reduce food security of local people. In turn, a cascade of events may lead to higher levels of unsustainable hunting and fishing that would progressively exacerbate the process.

Many Amazonian indigenous people, including Cocama, are conserving their traditional lands to help ensure food security (Constantino 2016). Large expanses of flooded forests in Loreto are protected areas managed with indigenous communities (Pacaya-Samiria National Reserve) or on indigenous lands (Pastaza Ramsar) (Blackman et al. 2017). Adaptation strategies by local people to the forecasted climate changes in the western Amazon will need to include maintenance of habitats and wildlife populations, sustainable use of food resources, and avoidance of forest overuse and deforestation.

People have adapted to their environment over time, thus long-time residence in a region that has multiyear climatic cycles is centrally important (Brondizio & Moran 2008). Knowledge acquired through daily observation of the environment generally overrides descriptive knowledge gained through the uptake of scientific information (Myers et al. 2013; Zaval et al. 2014). Although most

responses to global environmental change are focused on the diversification of production strategies (Pyhälä et al. 2016), in the Samiria basin, the Cocama people have intensified fishing. In this case, people's adaptations are reflecting the shifts in animal populations, which ultimately helps maintain food and income benefits and sustainable use. This adaptive strategy to climate change is surely not new, and past climatic cycles have likely occurred that have influenced people's ability to change and adapt (Brondizio & Moran 2008). This shows the importance of understanding how multiyear climate fluctuations result in shifts in wildlife populations and in turn how conservation and local people will need to adapt.

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Supporting Information

The matrix of landscape and species categories, and species trends from 2009–2015 (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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