Mid-elevation ecosystems of Panama: future uncertainties in light of past global climatic variability

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ABSTRACT: Modern changes in regional climates will result in high ecosystem turnover and substantial biodiversity rearrangements. Understanding these changes requires palaeoecological studies at temporal resolutions comparable to the time window at which modern climate change is occurring. Here we present a multi-proxy, high-resolution record of forest and lake ecosystem change that occurred during the last 1100 years at middle elevations in Panama. From ~900 to 1400 CE, regional forest and lake ecosystems were characterized by high seasonality, probably associated with both high El Niño activity and higher global temperatures. At ~1400 CE, an abrupt transition marked the decoupling of forest and lake responses, with forest responding mostly to local patterns of human occupation, and lake trophic status being controlled mostly by the regional precipitation–evaporation balance, possibly associated with solar irradiance. Factors that played important roles in shaping regional ecosystems during the last 1100 years will probably again play critical roles within the coming decades, i.e. higher precipitation seasonality and higher temperatures. Past responses of the system, together with pervasive human activities, suggest that future conditions will simplify mid-elevation forests. Given the importance of these geographical locations as hotspots of biological diversity, substantial losses of global biodiversity are foreseen. Copyright © 2016 John Wiley & Sons, Ltd.

KEYWORDS: biodiversity; climate change; Little Ice Age; Medieval Climate Anomaly; precipitation seasonality.

Introduction

Multi-annual climate variability plays a fundamental role in shaping vegetation assemblages and influencing aquatic ecosystems. Indeed, modern displacement of climate space occurring at decadal time scales will probably result in high ecosystem turnover and substantial biodiversity rearrangements (Loarie et al., 2009). In past times, the amount of extraterrestrial energy received by Earth has exerted strong control on climate and ecosystems at millennial to sub-millennial time scales (Bush and Colinvaux, 1999; Hodell et al., 2001). Over shorter time scales, regional patterns of climate variability, and therefore the evolution of ecosystems, are mostly modulated by the planet’s intrinsic dynamics, e.g. the El Niño-Southern Oscillation (Moy et al., 2002; Conroy et al., 2008; Toth et al., 2015). Thus, palaeoclimatic and palaeoecological studies are useful to understand the effects of modern climate changes on ecosystem structure and function in the future. Such is the case of abrupt climate change, defined by the IPCC Fifth Assessment Report as a large-scale change in the climate system that takes place over a few decades or less and persists long enough to cause disruptions in human and natural systems (IPCC, 2013). However, understanding this requires decadal-to-subcentennial temporal-scale records that allow the evaluation of biotic systems’ sensitivity to global changes similar to those taking place today.

The geological and climatic histories of Panama have favoured the development of exceptionally rich biodiversity. Whereas the closure of the Panama Isthmus facilitated the convergence of elements from the Nearctic and Neotropical floras and faunas (Graham, 2010), Quaternary climatic variability has modulated the resultant biodiversity at different time scales (e.g. Bush and Colinvaux, 1999; Bush et al., 1992). High diversity has been maintained through time by migration, adaptation and the existence of microrefugia (Bush, 2002; Correa-Metrio et al., 2014). These ecological features are of particular interest in the middle elevations of the tropical mountain ranges (premontane and lower montane altitudinal belts of Holdridge et al., 1964), regions that have been poorly studied in terms of their environmental history. These areas are characterized by broad environmental gradients over relatively short distances, and high topographic diversity that makes highly likely the existence of microhabitats that could be used as refugia during times of environmental hardship (Bush, 2002). Thus, palaeoecological studies from these regions would contribute to understanding the role of the middle elevations at sheltering diversity through time.

Here we present a 20-year resolution environmental reconstruction that spans the last ~1100 years. It is based on multiple proxies from a sediment core collected from Lake San Carlos, an 8.3-m-deep water body that occupies 3 ha at 783 m a.s.l. in central Panama (Fig. 1). We analysed pollen, charcoal, diatoms and organic carbon isotopes to infer vegetation and lake dynamics through time. Given the lake’s geographical location, the time span covered by the sediment core, and the temporal resolution we used for our analyses, the record offers a unique opportunity to study the interplay between local and global environmental drivers at different time scales. In fact, we provide hints on the confluence of global temperature
changes that occurred during the Medieval Climate Anomaly warming (MCA) and the Little Ice Age cooling (LIA) (Mann et al., 2009), and regional and local factors such as El Niño frequency (Moy et al., 2002; Conroy et al., 2008), and human occupation that has been documented for the area throughout the Holocene (e.g. Cooke, 2005; Piperno, 2006).

Study area
Lake San Carlos is a small (~3.3 ha), shallow ($z_{\text{max}} = \sim 8.3$ m), hydrologically closed water body located in central Panama (8°37'32.44"N, 80°03'4.24"W, 783 m a.s.l.). The lake lies on a volcanic substrate on the Pacific flank of the Central Cordillera of Panama (Fig. 1). At an elevation of ~780 m a.s.l., the northern and eastern shores of the lake abut cliffs that reach up to 1000 m a.s.l. (Supporting Information, Appendix S1). In contrast, the western and southern shores give way to slopes that descend towards the Gulf of Panama coastline, about 18 km away. With a mean annual precipitation of 2700 mm, 190 mm falling during the driest quarter, the regional vegetation of San Carlos represents the transition between wet and seasonal moist forest (Graham, 2010; Leigh et al., 2014). Most of the precipitation of the Pacific flank of the Central Cordillera comes from the Pacific Ocean that leads to a seasonal pattern in its intra-annual distribution.

Because of the elevation, moisture deficit through the dry quarter is ameliorated by lower evaporation and orographic precipitation. Additionally, the areas of the Central Cordillera that are near the mountain ridge that divides the Pacific and Caribbean flanks probably receive moisture subsidies from the Caribbean Sea. Thus, the Lake San Carlos basin would be highly sensitive to climate changes at sub-centennial time scales (e.g. changes in the atmospheric convective activity over the ocean and seasonal distribution of temperature).

Methods
In 2012, a 276-cm-long sediment core was retrieved from Lake San Carlos, central Panama, using a Livingstone piston corer (Colinvaux et al., 1999). Chronological control for the record was established using five radiocarbon dates at different depths (Appendix S2). These radiocarbon dates were calibrated using the IntCal13 curve (Reimer et al., 2013) and used to construct a Bayesian depth–age model using Bacon (Blaauw and Christen, 2011).

The core was sampled every 5 cm for diatoms, pollen and charcoal analyses, which were undertaken using standard techniques. For diatom analyses, 0.2 g of dry sediment from each depth was digested in 30 mL H$_2$O$_2$ for 48 h, and two 0.3-mL aliquots were mounted on microscope slides...
(Battarbee et al., 2001). Diatoms in each sample were counted until at least 400 diatom frustules were enumerated. For pollen analysis, 0.5 cm² of sediment from each depth was deflocculated and prepared using standard protocols (Faegri and Iversen, 1989), which included acetylation and gravimetric separation. Pollen grains in each sample were counted until a sum of 300 pollen grains was reached, excluding spores and aquatic plants. For charcoal analysis, 0.5-cm² samples of wet sediment were deflocculated using sodium pyrophosphate, and charcoal particles were manually separated under a stereomicroscope (Clark, 1988). Photographs of all particles were taken to estimate their area and calculate charcoal concentration (mm² cm⁻³). Relative abundances of pollen and diatoms are expressed as percentages of the total sum in each sample, and charcoal is expressed as area per volume (mm² cm⁻³).

The core was sampled every 2 cm for organic carbon isotopic analyses. Sediment samples were freeze-dried and crushed with a mortar and pestle. Approximately 3–15 μg of carbonate-free bulk sediment was loaded into tin sample capsules placed in a 50-position automated carousel on a Carlo Erba NA 1500 elemental analyser. After combustion in a quartz tube at 1020 °C in an oxygen-rich atmosphere, the sample gas was transported in an He carrier stream and passed through a hot reduction column (650 °C) consisting of elemental copper to remove oxygen. The effluent stream then passed through a chemical (magnesium perchlorate) trap to remove water followed by a 0.8-m GC column at 115 °C to separate N₂ from CO₂. The sample gas next passed into a Conflo II preparation system and into the inlet of a Thermo Electron Delta V Advantage isotope ratio mass spectrometer running in continuous flow mode where the sample gas was measured relative to laboratory reference N₂ and CO₂ gases. The isotopic analyses included 26 measurements of USG40 standard that yielded a standard deviation of 0.03‰ for carbon isotopes. Organic carbon isotopes are expressed in standard delta notation relative to VPDB (δ¹³Corg hereafter).

All data were plotted in stratigraphic diagrams using C2 (Juggins, 2007). A principal-component analysis (PCA) was performed using all data to identify and summarize environmental variability through time. Whereas isotopic data were used untransformed, pollen, diatom and charcoal data were log transformed to meet the multi-normality assumption of the analysis. Organic carbon isotopes were standardized to take them to common units, and vectors associated with diatoms aligned with PCA Axis 2, whereas vectors associated with pollen taxa mostly aligned with PCA Axis 1. All statistical analyses were performed using R (R Core Team, 2015).

Results

The sedimentary sequence from Lake San Carlos was mostly composed of organic clay and peat with a layer characterized by clay/peat fine laminae between ~145 and 63 cm below lake floor (Fig. 2). With a basal age of ~10800 cal BP (870 CE) at a depth of 276 cm below lake floor, the average sedimentation rate over the whole core was ~0.24 cm a⁻¹. Although all dates were in stratigraphic order, the upper three dates were statistically undifferentiable (Fig. 2; Appendix S2). These three dates could be representing a layer of sediments produced by a rapid or even instantaneous deposition event. However, the three dates came from layers of sediment of distinctive nature (Fig. 2), suggesting they were deposited at different times. Their lack of statistical difference might be the result of recurrent ¹⁴C ages during the most recent centuries in the IntCal13 calibration curve (Appendix S2, Reimer et al., 2013). The probability distribution of calibrated ages for each of these three ¹⁴C dates coincided around three time points (~1790, 1650 and 1540 CE, Appendix S2), and we selected the highest probability peak from each of them to produce the most parsimonious age model (Fig. 2; Appendix S2).

Our results show a highly dynamic pattern of environmental changes (Figs. 3 and 4; Appendices S3 and S4). The most important change in regional vegetation occurred around 1400 CE, when the dominance of Asteraceae, Areaceae, Bursera and Poaceae was replaced by Anacardiaceae, Cordia and Moraceae, Spondias and Zanthoxylum, among others (Fig. 3). Also, an important change took place at ~1150 CE, when pollen taxa such as Begonia, Eugenia, Cespediaz, Melastomataceae and Trichilia became abundant and persisted up to the present (Fig. 3). Zea mays (maize) was represented from ~1550 CE to the present, accompanied by a slight increasing trend in Cecropia, Cellis, Poaceae and Asteraceae, and decreases in Moraceae. Stable carbon isotopes on organic matter followed the trend shown by Poaceae and Asteraceae (Fig. 4). High values of δ¹³Corg characterized the sediments from the bottom of the record to ~1400 CE (average ~25.25‰, Fig. 4). At ~1400 CE, δ¹³Corg reached an absolute minimum (~31.19%), followed by an increasing trend that reached relatively stable values between 1830 CE and the present (~24.73‰, Fig. 4). Similarly, high charcoal concentrations characterized the period between the bottom of the record and 1400 CE, when a decreasing trend started and reached values near zero from ~1700 to the present (Fig. 4).

The diatom record was heavily dominated by Fragilaria crotonensis, although peaks in other species differentiated three main assemblages. From the bottom of the record up to ~1150 CE, F. crotonensis showed relatively low percentages and was mostly accompanied by Aulacoseira granulata var. angustissima, Diadesmis contenta, Eunotia formica, N. radiosa and N. angustissima (Fig. 3). From ~1150 to ~1700 CE, the diatom assemblages were almost entirely dominated by F. crotonensis with occasional peaks of other species. From ~1700 CE to the present, there was a decreasing trend in the abundance of F. crotonensis, and relatively high percentages of Achnanthes minutissimus, A. exiguum, Discostella stelligera, E. silesiacum and Nitzschia amphibia (Fig. 3).

The first two axes of the PCA explained 84.7% of the total variance contained in the dataset (Axis 1, 81.8%; Axis 2, 2.9%). However, when variables were standardized before the analysis, the percentage of explained variance went down to 21% (Axis 1, 12.16%; Axis 2, 8.74%), with axes above the 5th dimension associated with <5% of the variance. Vectors associated with pollen taxa mostly aligned with PCA Axis 1, and vectors associated with diatoms aligned with PCA Axis 2 (Fig. 5). PCAAxis 1 sample scores were high from the bottom of the record to ~1350 CE, showing a transition to low values, which in turn prevailed from ~1400 to ~1650 CE. From ~1700 CE to the present, sample scores were intermediate (Fig. 6). In contrast, PCA Axis 2 sample scores were low and variable from the bottom of the record to 1700 CE, but trended towards higher values thereafter.
According to our data, this is a more likely scenario for our study area, which was probably occupied by a highly seasonal tropical forest with recurrent fires (high charcoal concentrations) maintaining relatively open vegetation throughout this period (Fig. 4). It is likely that human occupation, which has been documented archaeologically in the region from the middle to late Holocene (Cooke, 2005; Piperno, 2006), also played a role in maintaining the low-stature forest. In fact, the connection between more seasonal climates and human occupation is evident in multiple records from Central and South America (Piperno et al., 2015). The Z. mays record in the San Carlos core, however, indicates that the most intense human activities occurred from 1500 CE to the present (Fig. 4), i.e. after European arrival, and during a period of less precipitation seasonality. High abundances of diatom taxa such as "Achnanthidium" spp., "Aulacoseira" spp., D. contenta, E. formica, E. silesiacum and "Navicula" spp.

Discussion

Environments of middle-elevation central Panama through the last millennium

Pollen, diatom, charcoal and stable isotope data show a dynamic pattern of vegetation and lake trophic state changes in middle-elevation central Panama over the last ~1100 years. The raw data and PCA ordination scores (Figs. 3, 4 and 6) indicate at least five different environmental settings through the last millennium. This discretization is not meant to create a formal biostratigraphy, but rather to facilitate the description and interpretation of the regional environmental history.

From ~950 to ~1150 CE, the vegetation was dominated by weeds (Asteraceae) and grasses (Poaceae), which together with high abundances of Bursera and palms (Areceae) suggest dominance of low-stature vegetation (Figs. 3 and 4). Through the studied period, δ¹³Corg mostly remained within the range that has been reported for C3 plants (between ~−32 and −24‰, Meyers, 2003), indicating there has not been a significant change in the main primary productivity sources. Nevertheless, from the bottom of the record to ~1400 CE, the dominance of grass pollen might have been the cause of the relatively high δ¹³Corg values. In the middle and low elevations of Panama and Costa Rica, the only modern pollen spectra with similar percentages of open vegetation elements come from savannas (Rodgers and Horn, 1996; Bush, 2000). However, the isotopic evidence does not support the interpretation of this vegetation type dominating the landscape. Pollen spectra that characterized this period have also been observed in modern samples from seasonal forests on the Yucatán Peninsula (Correa-Metrio et al., 2011). According to our data, this is a more likely scenario for our study area, which was probably occupied by a highly seasonal tropical forest with recurrent fires (high charcoal concentrations) maintaining relatively open vegetation throughout this period (Fig. 4). It is likely that human occupation, which has been documented archaeologically in the region from the middle to late Holocene (Cooke, 2005; Piperno, 2006), also played a role in maintaining the low-stature forest. In fact, the connection between more seasonal climates and human occupation is evident in multiple records from Central and South America (Piperno et al., 2015). The Z. mays record in the San Carlos core, however, indicates that the most intense human activities occurred from 1500 CE to the present (Fig. 4), i.e. after European arrival, and during a period of less precipitation seasonality. High abundances of diatom taxa such as "Achnanthidium" spp., "Aulacoseira" spp., D. contenta, E. formica, E. silesiacum and "Navicula" spp.

Figure 2. Basic stratigraphy and age–depth model of the sedimentary deposit of Lake San Carlos. The right rectangles show the depth intervals for the Medieval Climate Anomaly and the Little Ice Age under the constructed age model (solid lines) and an alternative model that considers the upper radiocarbon dates as equal (dashed lines).

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near the lake. Subsequently, from 1550 to 1700 CE, there was an increase of $\sim$10% in lower montane forest (LMF) taxa, mainly Melastomataceae and *Quercus*, whereas the abundance of TRF taxa remained relatively stable. This vegetation mixture suggests that whereas minimum temperature remained unchanged, maximum temperature, which represents the limiting factor for montane vegetation, decreased. Mean annual temperature decreases with altitude at an average rate of $6^\circ\text{C} \cdot \text{km}^{-1}$, a temperature gradient known as lapse rate (Graham, 2010). Modern LMF in Panama has it lower altitudinal boundary at $\sim$1100 m a.s.l. (Bruijnzeel, 2001), implying that under the mentioned lapse rate, the highest temperature of the year at Lake San Carlos ($\sim$780 m a.s.l.) during the LIA was $\sim$1.8$^\circ$C lower than today. The increase in LMF taxa coincided with increased ice accumulation on the Quelccaya ice cap in Peru (Thompson et al., 2013) (Fig. 3), indicating that the cooling revealed by our record was probably associated with the first half of the LIA, the coldest period of the last several millennia (Mann et al., 2009). The LIA has been reported as a dry period for several locations in the Neotropics (e.g. Haug et al., 2003; Hodell et al., 2005; Novello et al., 2012); the San Carlos record shows no sign of drier conditions at that time. Relatively high charcoal concentrations were probably the result of local human activities, revealed by the presence of maize pollen (Fig. 4).

Moist aseasonal conditions between 1530 and 1670 CE were probably the result of lower temperatures, which resulted in less evaporation. Also, the persistence of orographic precipitation on the flanks of the mountains, as has been reported for other locations (Lozano-Garcia et al., 2007), could have offset any regional precipitation decrease. These two factors probably maintained a low soil moisture deficit, so there was no substantial change in vegetation structure. A change in composition is nevertheless evident, with local flora relatively enriched by downslope migration of LMF taxa, a pattern that probably occurred regionally. Our

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**Figure 3.** Selected diatom and pollen records from Lake San Carlos sediment core.

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<th>Age (CE)</th>
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<th>DIATOMS</th>
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<td>Aulacoseria granulata v. angustissima</td>
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<td>Aulacoseria ambigua</td>
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<td>Eunotia formica</td>
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<td>Fragilariopsis crotonensis</td>
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<td>Navicula lanceolata</td>
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<td>Navicula leptiostrata</td>
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<td>Encyonema silesiacum</td>
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<td>Achnanthidium exiguum</td>
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<td>Diadesmis contenta</td>
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<td>Navicula radiosa</td>
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<td>Achnanthidium minutissimum</td>
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<td>Nitzschia amphibia</td>
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The last 350 years have been marked by a progressive decrease in TRF and increases in relative abundance of grasses and $^{13}$C values. The presence of maize through this period indicates human disturbance, although charcoal concentrations at this time are the lowest of the record. It is possible that when human settlements became permanent, people suppressed fire after adopting more advanced agricultural technologies (Ellis et al., 2013). From 2003 to 2014 CE, the maximum number of annual fires within a radius of 30 km around Lake San Carlos occurred in 2003 (24 events, Fig. 1). The area covers ~2.6 km$^2$ around the lake and has an intermediate level of human occupation. Although the area represents 3.4% of the Panamanian territory, it accounts only for 2% of all fire events in Panama, indicating a possible anthropogenic suppression of fire activity. One additional element that suggests the changes of the last 350 years have been strongly associated with human disturbance is the sudden increase and persistence of *Nitzschia amphibia* and *Achnanthidium* spp. in the diatom assemblage since ~1900 CE (Fig. 3), both genera commonly associated with cultural eutrophication characterized by high concentrations of phosphorus (Lange Bertalot, 2000; Bellinger et al., 2006).

Main drivers of environmental change: abrupt and gradual changes

Although using standardized variables produced a less explicative ordination, we preferred it to the non-standardized ordination for two main reasons (Legendre and Legendre, 1998): (i) standardization takes all variables to the same units making comparable proxies with different scales of measurement (e.g., charcoal concentration, species relative abundance and $^{13}$C$_{org}$); and (ii) standardization confers all variables the same ecological importance, an assumption more reasonable than considering relative abundance as a direct indication of the individual role in the ecosystem. The PCA ordination on standardized proxies clearly separated terrestrial from aquatic components of the record; whereas...
pollen taxa mostly aligned with PCA Axis 1, diatoms aligned with PCA Axis 2 (Fig. 5). Thus, the aquatic and terrestrial ecosystems, although probably driven by similar exogenic factors, showed independent responses. Such independence probably reflects the different temporal scales at which environmental drivers act upon terrestrial and aquatic ecosystems.

According to ecological preferences, Axis 1 had a clear direct relationship with soil moisture deficit. TRF taxa aligned on the negative side of Axis 1, whereas grasses and palm trees, usually associated with dry and/or seasonal conditions (Bush, 2000; Correa-Metrio et al., 2011), displayed positive scores along this axis. Contrastingly, Axis 2 scores were directly associated with lake trophic status, with the separation of F. crotonensis from the other taxa suggesting slight variations in nutrient and light availability via this axis (Bradbury, 1988; St-Jacques et al., 2009). Negative Axis 2 scores were associated with a low-light, slightly stratified mesotrophic lake, and positive scores were associated with a poorly mixed eutrophic lake. Thus, we interpret PCA Axis 1 as representative of vegetation variability (regional climate), and Axis 2 as representative of variability in the aquatic system (local conditions).

From the bottom of the record to ~1400 CE, high PCA Axis 1 scores support our initial interpretation of a climate system more seasonal than modern (Fig. 6). High erosion probably caused by precipitation has been reported for the Ecuadorian Andes (Moy et al., 2002) and Galapagos Islands (Conroy et al., 2008). Together with the San Carlos record, these lines of evidence suggest an invigorated activity of El Niño through this period. Nevertheless, evidence from corals that lie within the epicentre of El Niño–Southern Oscillation (ENSO) activity do not support this interpretation (Gobb et al., 2013). Tree-ring reconstructions and climate models show pervasive droughts in western North America during the MCA (e.g. Cook et al., 2010; Woodhouse et al., 2010), conditions that have been linked to higher temperatures through this period (Woodhouse et al., 2010). It is possible that the warmer global climate caused El Niño-like conditions expressed through high precipitation seasonality in Panama, intense rains in the Ecuadorian Andes and Galapagos Islands, and droughts in North America.

Moving probability density functions applied to the PCA scores were consistent with our initial interpretation. A first abrupt change in both regional and local conditions (PCA axes 1 and 2) took place at ~1150 CE and was characterized by a substantial seasonality decrease, which caused increases in TRF taxa and a substantial turnover of diatom species (Figs. 4 and 6). This abrupt change was characterized by increasing variance and multimodal behaviour of the system (Fig. 6), suggesting the existence of a tipping point (sense Lenton, 2011), which could have been the result of passing a critical threshold associated with the decreasing sea surface temperatures reported for the Panamanian Pacific (Toth et al., 2015).

A second abrupt change in regional conditions (PCA Axis 1) occurred at ~1350 CE (Figs. 4 and 6), marking the transition towards an even less seasonal distribution of precipitation throughout the year and the establishment of a TRF, and coinciding with decreasing erosion in the Andes and Galapagos Islands (Moy et al., 2002; Conroy et al., 2008).

From 1600 CE to the present, changes were rather gradual, although increases of variance in both PCA axes suggest larger environmental variability (Fig. 6). After the abrupt change of Axis 1 at ~1350 CE, the signal of PCA Axis 2 shows a substantial variance increase, and the average signal is closely associated with total solar irradiance (Moy et al., 2002). High (low) solar irradiance is associated with high (intermediate) lake trophic state conditions. Similar to the Yucatán Peninsula (Hodell et al., 2001), high solar irradiance may be associated with relatively dry episodes, which would result in greater evaporation and consequent lake eutrophication. It is likely that the insolation signal was always present in the lake component, but until ~1600 CE was overridden by the more powerful effects of the high seasonality that characterized the region.

Overall, the most obvious changes in the terrestrial and aquatic ecosystems were very probably associated with seasonality changes, with the date ~1350 CE marking a clear transition towards a less seasonal climate. High abundances of small charcoal particles reveal the persistence of intense and frequent regional fires from ~950 to 1350 CE (Fig. 6). The modern association of fire frequency with El Niño events (Fig. 1) and high charcoal concentrations through the MCA offer evidence of an El Niño-like seasonality pattern through this period. Nevertheless, there were two stages within this high-seasonality time interval. From ~950 to ~1175 CE, the region was characterized by higher sea surface temperatures and the highest seasonality of the last millennium. This...
climate system abruptly transitioned to a second phase of less seasonality (from ~1150 to 1350 CE). From 1350 CE to the present, the system has been characterized by a relatively aseasonal precipitation regime, and the lake trophic state has been strongly influenced by insolation, possibly as an indirect result of changes in total annual precipitation.

The instability of the lake system during the last 600 years has probably been associated with local dynamics. Indeed, since 1550 CE, the presence of Z. mays in the San Carlos record is evidence for human occupation as an important local driver of the system. Additionally, a temperature decline (~1.8°C) between ~1500 and ~1700 CE, which was not detected by the PCA, was identified from a substantial increase in montane taxa. This increase was coincident with maximum ice accumulation in the Andes (Thompson et al., 2013), which probably resulted from wetter and relatively colder conditions in the Neotropics.

Conclusions

Our results show that during the last ~1100 years, aquatic and terrestrial ecosystem dynamics at middle elevations in Panama were driven mostly by global climate variability. The dominance of highly seasonal forests in the region coincided with El Niño-like conditions reported for other regions (Moy et al., 2002; Conroy et al., 2008) and a warmer planet during the MCA (Mann et al., 2009). Although predictions for ENSO behaviour in the coming century are poorly constrained, the IPCC foresees that ENSO-related precipitation variability will probably intensify within the next few decades (IPCC, 2013). Intensified precipitation variability, together with higher temperatures, will probably push the system towards conditions similar to those during the MCA. This will result in a change from TRF, which dominates the region today, to more open, deciduous vegetation. This scenario has important consequences in terms of biodiversity loss and release of carbon stored in soils and live biomass. Whereas the warmer conditions of the MCA were associated with a highly dynamic system and abrupt changes, cooling during the LIA was not associated with substantial changes in the vegetation or the lake. This highlights the fact that ecosystem responses to climate change are not linear, and that dramatic vegetation turnovers are probably associated with warming and changing seasonality.
The sediment record from Lake San Carlos illustrates that the terrestrial and aquatic ecosystems have been subject to high climate variability during the late Holocene, and as a consequence have been occupied by different biotic communities. Thus, environmental stability does not explain the high diversity in tropical piedmonts and middle elevations, as has been hypothesized (Sandel et al., 2011). The record also shows that ecosystems are more dynamic and adaptable than commonly thought. The global temperature rise that is predicted for the next few centuries evidently does not represent a dire threat for biodiversity at middle elevations in the tropics. Indeed, populations in the region have adapted to abrupt changes in the past through equally abrupt responses (Correa-Metrio et al., 2014). Such fast responses of communities have probably been facilitated by landscape heterogeneity, which enables disjunct populations to persist through times of environmental hardship (Bush, 2002). Thus, the most dangerous threat to biodiversity will come from climate change in the context of human-driven homogenization of the landscape and habitat fragmentation.

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Supplementary Information
Appendix S1. Photographs of lake San Carlos.
Appendix S2. Chronological control.
Appendix S3. Pollen diagram.
Appendix S4. Diatom diagram.

Abbreviations. ENSO, El Niño–Southern Oscillation; LIA, Little Ice Age; LMF, lower montane forest; MCA, Medieval Climate Anomaly; PCA, principal components analysis; TRF, tropical rainforest.

References