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Holocene Dynamics of Temperate Rainforests in West-Central Patagonia

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Analyses of long-term ecosystem dynamics offer insights into the conditions that have led to stability vs. rapid change in the past and the importance of disturbance in regulating community composition. In this study, we (1) used lithology, pollen, and charcoal data from Mallín Casanova (47°S) to reconstruct the wetland, vegetation, and fire history of west-central Patagonia; and (2) compared the records with independent paleoenvironmental and archeological information to assess the effects of past climate and human activity on ecosystem dynamics. Pollen data indicate that *Nothofagus-Pilgerodendron* forests were established by 9,000 cal yr BP. Although the biodiversity of the understory increased between 8,480 and 5,630 cal yr BP, forests remained relatively unchanged from 9,000 to 2,000 cal yr BP. The charcoal record registers high fire-episode frequency in the early Holocene followed by low biomass burning between 6,500 and 2,000 cal yr BP. Covarying trends in charcoal, bog development, and Neoglacial advances suggest that climate was the primary driver of these changes. After 2,000 cal yr BP, the proxy data indicate (a) increased fire-episode frequency; (b) centennial-scale shifts in bog and forest composition; (c) the emergence of vegetation-fire linkages not recorded in previous times; and (d) paludification in the last 500 years possibly associated with forest loss. Our results therefore suggest that *Nothofagus-Pilgerodendron* dominance was maintained through much of the Holocene despite long-term changes in climate and fire. Unparalleled fluctuations in local ecosystems during the last two millennia were governed by disturbance-vegetation-hydrology feedbacks likely triggered by greater climate variability and deforestation.

Keywords: anthropogenic impact, charcoal, climate, pollen, stability, vegetation, Holocene, forest

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INTRODUCTION

Instrumental and tree-ring records from the southern Andes show a strong warming trend during the last 50 years coupled with a decline in precipitation (Villalba et al., 2003). With rising temperatures, glaciers in the North and South Patagonian icefields are receding up to 100 times faster than at any time since the Little Ice Age (Glasser et al., 2011). These trends are projected to continue in the coming decades and lead to increased moisture deficits, further ice recession, tree mortality, and greater risk of fires (Cabré et al., 2016).

Paleoenvironmental data from Patagonia suggest that past changes in climate and land use have profoundly influenced not only the water balances and disturbance regimes, but also the composition and distribution of vegetation (e.g., Huber et al., 2004; Markgraf et al., 2013). Prior to ca. 18,000 cal yr BP, cold, dry and windy conditions were associated with extensive glaciation in western Patagonia and led to the extirpation of several plant species over much of their former range (Barreda et al., 2007). Open steppe/heath prevailed in unglaciated areas, and trees either migrated to northern latitudes or survived in local refugia (Pastorino and Gallo, 2002). Higher temperatures and a shift in dominance from year-round Antarctic air during glacial times to more humid Pacific winds in the Holocene (Heusser, 2003) promoted the reorganization of vegetation (e.g., Iglesias et al., 2014). In particular, *Nothofagus*-dominated forests expanded throughout the western Andes. This increase in woody fuel allowed a progressive rise in regional fire activity that peaked between 10,000 and 7,000 cal yr BP (Whitlock et al., 2006). The Late Holocene was characterized by fluctuations in moisture availability that resulted in spatial and temporal variability in vegetation composition and probability of fire (Fletcher and Moreno, 2012). In recent centuries, deforestation has affected forest diversity and soil structure, and these changes threaten ecosystem services, including carbon storage, forage production, and water supply (Veblen et al., 2011). In this study, we reconstruct the Holocene vegetation and fire history in west-central Patagonia (Mallín Casanova 47°38′36.86″S; 72°58′30.81″W; 126 m elev), and assess the impact of climate, fire, and volcanic eruptions on vegetation and wetland dynamics. By analyzing the long-term history of this site, we offer insights into the conditions that have driven change in terrestrial and wetland communities in the past.

STUDY AREA

Lake Casanova and the surrounding ombrotrophic *Sphagnum* bog (Mallín Casanova) are situated in the Baker River watershed, between the North and South Patagonian icefields (**Figure 1**). The rugged topography of the area results from Pleistocene glaciation and postglacial alluvial and slope activity (Niemeyer et al., 1984; Sernageomin, 2002). Precipitation is associated with frontal storm systems that migrate eastwards along the path of the Southern Westerlies (Garreaud et al., 2013). Uplift of low-level winds over the Andes produces year-round orographic precipitation on the west side of the mountains (e.g., 4,300 mm yr^{-1} on San Pedro island; Dirección Meteorológica de Chile, 2017). Conversely, forced subsidence on the leeward slopes causes adiabatic warming of the air masses, resulting in increasingly drier conditions toward the east (e.g., 800 mm yr^{-1} in Cochrane; Dirección Meteorológica de Chile, 2017).

The present-day west-to-east precipitation gradient leads to a transition from evergreen cool rainforests of *Nothofagus nitida-N. betuloides-Pilgerodendron* in the lowland (precipitation => 1,500 mm yr^{-1}) to deciduous forests of *Nothofagus pumilio* (precipitation = 1,500–400 mm yr^{-1}) at higher elevations to steppe characterized by a matrix of tussock grasses, herbs, and cushion shrubs (precipitation < 500 mm yr^{-1}). M. Casanova is surrounded by *N. betuloides-Pilgerodendron* forest with open shrub/grassland and *Sphagnum* peatland (precipitation = 3,000 mm yr^{-1}). The presence of burned trees on the bog and homogeneous stand structure attest to the effects of recent fires (Holz et al., 2012), which burned both tree crowns and surface fuels. These mixed-severity fires are associated with interannual moisture variability (Holz and Veblen, 2009, 2012). Since ca. 1930 AD, the wetland has been surrounded by *Estancia* Casanova, a small family farm (Holz and Veblen, 2011).

METHODS

A 1-m-long, 80-mm-diameter piston sampler was used to collect a 350-cm-long sediment core from Mallín Casanova at the southeastern margin of the lake. The record provides evidence of environmental change from the beginning of sediment deposition at the wetland to present day. Core segments were transported to the Australian National University, Canberra, where they were split into working and archival halves and subsampled. Description of the sedimentary structures and biological components was performed visually following Schnurrenberger et al. (2001). Magnetic susceptibility (SI) was measured at 1-cm contiguous intervals to assess changes in inorganic sediment input to the wetland (Gedye et al., 2000).

Eight charcoal samples were submitted for AMS radiocarbon dating to the W. M. Keck Carbon Cycle AMS facility (University of California, Irvine) and calibrated with the ShCal13 calibration curve (Hogg et al., 2013; **Table 1**). Chronologies were developed by modeling depth as a function of the explicitly combined probability distribution of each calibrated date and prior expectations about temporal variability in sediment accumulation rates (Blaauw and Christen, 2011). Specifically, the prior distribution for sediment accumulation rates had a mean of 0.05 cm yr^{-1} and a shape equal to 1.5. Depths were adjusted by removing volcanic ashes >1 cm in thickness on the assumption that these layers were deposited in a negligible span of time.

Past vegetation dynamics were inferred from changes in pollen abundance through time. Standard techniques were employed to extract pollen residues from 0.5 cm^{-3} sediment samples at 2–5 cm intervals (Faegri and Iversen, 1989). Pollen identification was based on published atlases (Heusser, 1971; Markgraf and D'Antoni, 1978) and a modern reference collection, and performed at 250 and 400x magnification. Pollen percentages (both terrestrial and aquatic) were calculated as a function of the sum of terrestrial pollen types, which in all cases exceeded 250 grains per sample to ensure replicability (Iglesias et al., 2016b).

Empetrum and Caryophyllaceae were excluded from the terrestrial pollen sum. Modern pollen-vegetation studies suggest that, due to the very limited pollen dispersal capabilities of these taxa, they are depicted in the pollen rain only when locally present in the landscape (Fletcher and Thomas, 2007; Iglesias et al., 2016b). This high fidelity is likely to be reinforced in peat deposits, where local vegetation is overrepresented in the pollen spectrum (Janssen, 1973). For these reasons, we assumed that variations in the pollen abundance of *Empetrum*

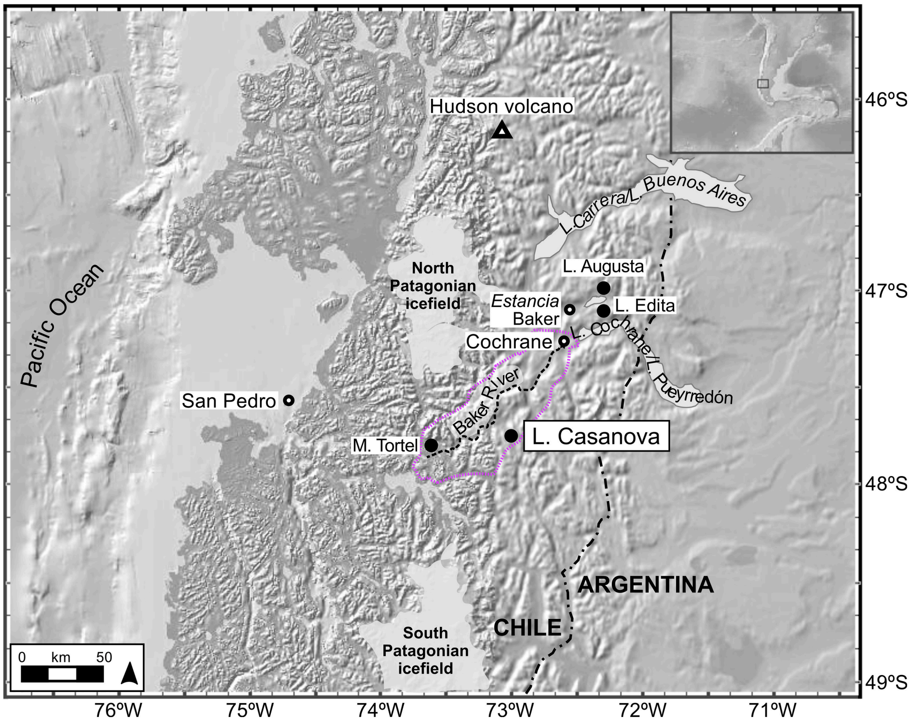

FIGURE 1 | Study area and location of L. Casanova and other sites mentioned in the manuscript. M. Casanova is the ombrotrophic *Sphagnum* bog surrounding the lake. The coring site is located southeast of L. Casanova. The approximate boundaries of the Baker River watershed are shown in color.

TABLE 1 | Radiocarbon and calibrated dates from M. Casanova.

Depth (cm)	Lab. no.	Radiocarbon age (^{14}C yr BP)	Age error (yr)	Calibrated age (cal yr BP; 1 sigma range)[a]
0	NA	Inferred	NA	−57 to (−47)
10	83174	−525	15	Invalid age for calibration curve[b]
37	83175	745	30	574 to 674
62	83176	1,410	40	1,194 to 1,311
93	83177	1,785	40	1,607 to 1,705
143	83178	3,685	30	3,897 to 4,065
242	83179	6,370	40	7,178 to 7,310
312	83180	7,165	50	7,874 to 8,001
333	83181	8,720	40	9,553 to 9,664

[a] *Relative area under probability distribution = 1.000 (Hogg et al., 2013).*
[b] *Not included in the chronology.*
^{13}C values were not measured.

and Caryophyllaceae probably reflected changes in wetland composition rather than changes in terrestrial vegetation at the watershed-scale (Huber et al., 2004), although we recognize that both taxa have wider ecological distributions.

For this study, pollen types exceeding 3% of the terrestrial pollen sum are discussed in detail, while poorly represented taxa were grouped according to their ecological affinities. *Nothofagus dombeyi*-type includes *N. pumilio*, *N. dombeyi, N. nitida, N. betuloides,* and *N. antarctica*. Currently, only *N. betuloides* and *N. antarctica* grow in the study area. Cupressaceae pollen is attributed to *Pilgerodendron uviferum*, although *Fitzroya cupressoides* and, less likely, *Austrocedrus chilensis* may have been long-distance contributors. Pollen from *Hydrangea, Eucryphia/Caldcluvia*-type, Myrtaceae, *Weinmannia*, *Coriaria*, *Drimys*, *Pseudopanax,* and *Saxegothaea* are grouped into "Other rainforest taxa." "Other shrubs" includes *Schinus*, *Embothrium*, *Escallonia*, Verbenaceae, Rhamnaceae, and *Berberis*. "Other grassland taxa" corresponds to pollen from xerophytic shrubs and herbs, such as *Acaena*, *Phacelia,* and *Mulinum*. Selected pollen percentages were plotted as a function of time. The resulting pollen diagram was zoned by visual inspection to aid in the description of the stratigraphic changes.

In order to obtain a local high-resolution fire reconstruction, macroscopic charcoal (i.e., particles $>125\,\mu$m in diameter) was extracted from contiguous 1-cm thick samples and quantified under a binocular dissecting microscope (Whitlock and Larsen, 2001). Changes in sediment accumulation rates and sampling variability were accounted for by converting charcoal concentrations to charcoal accumulation rates (CHAR; particles cm^{-2} yr^{-1}) and interpolating the data to the median time resolution.

A locally weighted scatterplot smoother was used to isolate the high-frequency component of the charcoal time series (i.e., positive residuals of the model) from the long-term trends in CHAR (i.e., "background charcoal"). Comparison of the charcoal data and fire scars in tree rings of *P. uviferum* shows high correlation coefficients and suggests that the CHAR times series constitutes a record of biomass burning within 10 km of the bog (Holz et al., 2012). Large CHAR values (i.e., positive residuals of the model that exceeded the 95th percentile of a locally fit Gaussian distribution; "charcoal peaks") were tested for significance with a Poisson distribution and interpreted as local fire episodes (i.e., fire events occurring within the time span of the charcoal peak; Higuera et al., 2009). Local fire episodes were summarized as fire-episode frequency (i.e., fire episodes 1,000 years^{-1}).

To explore the relationship between variations in fire and climate, we calculated the probability of fire episodes occurring at times of regional glacier advance or retreat as:

$$(1) \quad \Pr(\mathrm{fire_{gl}}) = \mathrm{Sum(Fire\ episodes_{gl})} * \mathrm{Total\ samples_{gl}^{-1}}\ \text{and}$$

$$(2) \quad \Pr(\mathrm{fire_{non\text{-}gl}}) = \mathrm{Sum(Fire\ episodes_{non\text{-}gl})} * \mathrm{Total\ samples_{non\text{-}gl}^{-1}},\ \text{respectively,}$$

with Pr(fire$_{gl}$): probability of fire at times of glacier advances; Sum(Fire episodes$_{gl}$): total number of fire episodes at times of glacier advances; Total samples$_{gl}$: number of sample at times of glacier advances; Pr(fire$_{non\text{-}gl}$): probability of fire at times of glacier retreat; Sum(Fire episodes$_{gl}$): total number of fire episodes at times of glacier retreat and Total samples$_{non\text{-}gl}$: number of sample at times of glacier retreat. Times of glacier advances and retreat were obtained from Aniya (2013). A Chi-squared test for proportions was used to assess if the probabilities of fire at times of glacier advances and retreat were statistically different at the 0.05 alpha-level (**Table 2**).

Long-term changes in community composition were inferred from a dissimilarity matrix produced for the terrestrial taxa tallied in the pollen samples. Specifically, we calculated the squared chord distance (SCD) between every sample and the first sample of the record (i.e., 344 cm depth; 9,840 cal yr BP) as an assessment of their dissimilarity from the oldest pollen assemblages. We interpreted this time series as a measure of long-term trends in the stability of the vegetation. Under the premise that stable ecosystems remain mostly unchanged over time or fluctuate around an equilibrium point, our null hypothesis was that SCDs would be equal to the median Holocene SCD. SCDs larger than the median would provide evidence of statistically significant change in vegetation composition. In order to account for change in sampling effort, rates of change between pairs of consecutive samples were also estimated. Rates of change were defined as:

$$(3) \quad \text{Rate of change}_{(t)} = \mathrm{abs}[(\mathrm{SCD}_{(t)} - \mathrm{SCD}_{(t-1)}) / (\mathrm{Age}_{(t)} - \mathrm{Age}_{(t-1)})]$$

TABLE 2 | Probability of fire episodes at times of glacier advances or glacial retreat.

	Glacier advance	Glacier retreat
9,950 cal yr BP—present	0.02	0.05
Before 2,000 cal yr BP	0.01	0.04
After 2,000 cal yr BP	0.03	0.09

Rates of change of zero would result from the comparison of identical samples (i.e., no temporal changes in composition = stable plant communities), while non-zero values would be indicative of changes in vegetation composition or unstable communities between times *t* and *t*–1. Because we acknowledge the possibility of sampling errors, we bootstrapped confidence intervals for the median Holocene SCD and for rates of change equal to zero. SCDs and rates of change were visually compared with charcoal data, climate variability inferred from independent proxies, and the archeological and historical record. The same procedure was applied to aquatic taxa and interpreted as a proxy of wetland dynamics.

Spectral analysis was conducted on the terrestrial SCD time series to detect possible changes in the periodicity of oscillations in vegetation composition. Specifically, a dynamic Lomb-Scargle periodogram was used to identify periodic signals in the unevenly spaced time series (Press and Rybicki, 1989). All analyses and figures were performed with R (R Core Team, 2015).

RESULTS

Chronology

Seven AMS radiocarbon dates and the inferred age of the top sample were used in the construction of a calibrated age-depth model (**Table 1**). The radiocarbon age corresponding to the sample extracted at 10-cm depth (−525 ± 15 ^{14}C yr BP) was judged to be anomalously young and not included in age model development. The estimated age-depth relationship was relatively linear, suggesting quite stable sediment accumulation rates (0.01–0.07 cm yr^{-1}; **Figure 2**).

Lithology

Two lithological units were visually identified in the core from M. Casanova (**Figure 2**). The basal unit (Unit 1: 350–275 cm depth; 9,950–7,840 cal yr BP) was composed of fine clay. With the exception of two peaks at 326 and 310 cm depth (9,220 and 8,520 cal yr BP; 0.19 and 39.62 SI, respectively), magnetic susceptibility was always negative (median = −0.18 SI), suggesting that the sediment was mainly composed of diamagnetic minerals, such as quartz, calcite, and/or organic matter. A large peak in magnetic susceptibility at 310 cm depth corresponds with a 4-cm-thick tephra, possibly derived from the H4 eruption of the Hudson volcano. H4 tephra deposits are widespread in Patagonia. AMS radiocarbon dates place the mean age of this tephra at 8,440 cal yr BP in lake cores and 7,891 cal yr BP in outcrops, bog, and soil samples (Stern et al., 2016). Due to this systematic difference between radiocarbon dates, which has been attributed to the percolation of humic acids in soils and bogs (Bertrand et al., 2012) as well as to ^{14}C reservoir effects in lakes (Stern et al., 2016), the age of this tephra was not employed in the development of the core chronology.

The uppermost unit (Unit 2: 275–0 cm depth; 7,840 cal yr BP-present) was characterized by brown fibrous peat, low magnetic susceptibility (median = 0.20 SI), and overall low sedimentation rates (median = 0.03 cm yr^{-1}). Gray-brown fine material was observed at 258 and 251 cm depth (7,510 and 7,320 cal yr BP, respectively). Weakly positive magnetic susceptibility values at

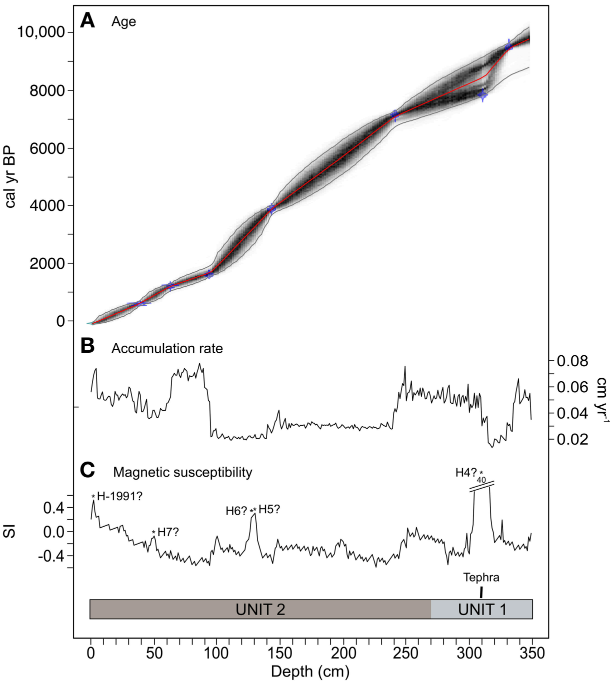

FIGURE 2 | (A) Age-depth model (The red curve shows the weighted mean age for each depth. Dark and light gray lines depict the more likely age-depth models and 95% confidence intervals, respectively. Blue areas represent the probability distributions of the calibrated dates), **(B)** sediment accumulation rates and **(C)** magnetic susceptibility for M. Casanova. Lithology and tephra –probably derived from eruptions of the Hudson volcano (H)- are shown. Depths are given in true core measurements, not the adjusted depths used in the development of the chronology.

those depths, as well as in the 136–131 and 27–0 cm depth segments (3,630–3,400 and 450 cal yr BP-present, respectively) indicate the presence of paramagnetic minerals (e.g., iron oxides, iron carbonates, and/or iron silicates). Although no lithological changes were visually identified in this unit, it is possible that magnetic enrichment of these three segments resulted from the deposition of basaltic to andesitic tephra produced during the H5 (pooled mean age = 3,840 cal yr BP), H6 (pooled mean age = 2,740 cal yr BP) and 1991 AD eruptions of the Hudson volcano (Haberle and Lumley, 1998).

Pollen and Charcoal Records

The pollen record from M. Casanova was visually divided in five pollen zones to aid in the description of vegetation and fire history reconstructions (**Figures 3**, **4**). Pollen data are publicly available at Neotoma Paleoecology Database (www.neotomadb.org), and charcoal data have been deposited in the Global Charcoal Database (www.gpwg.org).

Zone MC-1 (350–308 cm depth; 9,950–8,480 cal yr BP) was dominated by *N. dombeyi*-type (72–86%), Poaceae (<11%) and Cupressaceae (<11%). Other rainforest taxa, Other shrubs, and Other grassland taxa, including Asteraceae and Amaranthaceae, were poorly represented in the pollen assemblage (1<% in all cases). The vegetation probably resembled present-day *Nothofagus/Pilgerodendron* forest, and was relative stable (rates of change <0.003% yr^{-1}; Haberle and Bennett, 2001). Aquatic and wetland pollen and spores were virtually absent (<0.7 %; rates of change <0.005% yr^{-1}), suggesting that the wetland was poorly developed at the time, or that the modern lake extended to the coring site. CHAR levels oscillated between 0 and 0.49 particles cm^{-2} yr^{-1}, and local fire-episode frequency steadily declined from 4.8 episodes 1,000 yr^{-1} at 9,950 cal yr BP to 1.7 episodes 1,000 yr^{-1} at the top of the zone.

Zone MC-2 (308–195 cm depth; 8,480–5,630 cal yr BP) continued to be dominated by *N. dombeyi*-type (65–88%) and Cupressaceae (15–19%), but pollen from *Misodendron* (<12.3%), *Maytenus* (<3%), Other shrubs (<3%), and Other grassland taxa (<2%) was higher than before. This increase in palynological richness implies diversification of the understory and/or opening of the *Nothofagus/Pilgerodendron* forest. High rates of change in terrestrial SCDs point to fast changes in vegetation composition at the 8,320–8,150 and 7,660–7,510 cal yr BP periods. These fluctuations are evidenced by pronounced variability in *N. dombeyi*-type pollen percentages. *Empetrum*, *Myriophyllum,* and Cyperaceae rose up to 4%, but the aquatic rates of change remained low (<0.01% yr^{-1}). CHAR was lower than before (<0.15 particles cm^{-2} yr^{-1}), and fire-episode frequency declined to 0.1 after reaching a local maximum of 3.5 fire episodes 1,000 yr^{-1} at 7,100 cal yr BP.

Zone MC-3 (195–101 cm depth; 5,630–2,000 cal yr BP). *N. dombeyi*-type increased to 85.4% at expense of *Misodendron* (<3%), Cupressaceae (<12%), Other rainforest taxa (<2.5%), *Maytenus* (<0.6%), and Other shrubs (<1.5%). Vegetation-pollen calibrations indicate that the vegetation was dominated by closed *Nothofagus/Pilgerodendron* forest (rates of change<0.003% yr^{-1}; Haberle and Bennett, 2001). *Empetrum* pollen and *Sphagnum* spores rose and reached peaks of 112 and 23% of the total terrestrial sum, respectively, suggesting the establishment of the modern *Sphagnum* bog at the beginning of this zone. Although *Sphagnum* values were erratic, modern studies suggest that the presence of spores in the sediment is indicative of moss accumulation (Halsey et al., 2000). Terrestrial rates of change remained stable throughout the zone while aquatic SCDs began to slowly rise at ca. 5,000 cal yr BP. CHAR declined to <0.08 particles cm^2 yr^{-1}, and so did local fire-episode frequency, which ranged between 0 and 2 fire episodes 1,000 yr^{-1}.

Zone MC-4 (101–31 cm depth; 2,000–530 cal yr BP). *N. dombeyi*-type (<77%), *Misodendron* (>1.6%), and Other rainforest taxa (<2%) declined, and *Podocarpus* and Cupressaceae pollen percentages were higher than before (<47.4 and <27.3%, respectively). CHAR and fire-episode frequency increased to 0.19 particles cm^2 yr^{-1} and 4.8 fire episodes 1000 yr^{-1}, respectively, suggesting that the forest supported more frequent and possibly more severe fires than before. Terrestrial and aquatic SCDs greater than the Holocene median and high rates of change imply large and rapid variations in terrestrial and bog vegetation throughout the period. Dynamic spectral analysis of terrestrial SCDs shows high power at 300- and 700-year periods during the last 2000 years (**Figure 5**).

Zone MC-5 (31–0 cm depth; 530 cal yr BP-present) was characterized by rapid fluctuations in pollen percentages of

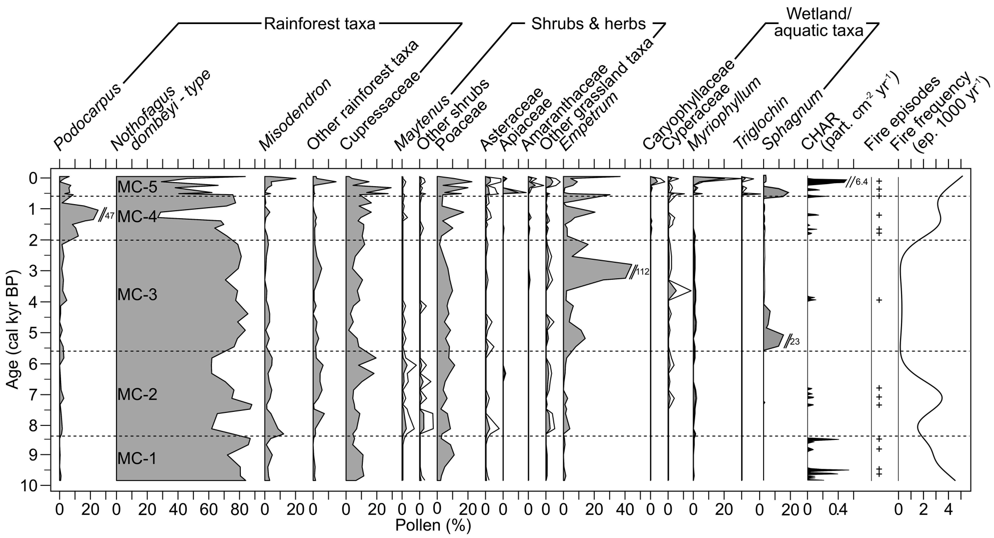

FIGURE 3 | Pollen percentages of selected taxa and macroscopic charcoal data from M. Casanova. Exaggeration curves depict 3*taxa percentages.

most taxa (terrestrial rates of change >0.003% yr^{-1}). Overall, *Podocarpus and N. dombeyi*-type declined to >3.4% and >26.8%, respectively, while Cupressaceae (<29.3%), Poaceae (<22.6%), Apiaceae (<9.8%), and Other grassland taxa (<7%) increased. This pollen assemblage compares well with modern samples from the forest/grassland ecotone found in the wet Chonos archipelago in westernmost Patagonia (44–47°S; Haberle and Bennett, 2001). CHAR (0–6.4 particles cm^2 yr^{-2}), pollen of Caryophyllaceae (<5%), Cyperaceae (<3%), *Myriophyllum* (<21%), and *Triglochin* (<3%), terrestrial rates of change, and aquatic SCDs reached their highest Holocene values. Fire-episode frequency increased to Zone 1 levels (4.8 fire episodes 1,000 yr^{-1}).

DISCUSSION AND CONCLUSIONS

Vegetation and Fire History of West-Central Patagonia

During the Last Glacial Maximum (LGM; 23,000–19,000 cal yr BP), sea-surface temperatures off the coast of Chile were ~6°C lower than at present (Lamy et al., 2004; Kaiser et al., 2007). Reconstructions of glacier extent suggest that the North and South Patagonian icefields along with their outlet glaciers coalesced to form a >1200-m-thick ice sheet (Caldenius, 1932; Glasser et al., 2008; ~38–56°). Rapid thinning of the ice sheet at 17,500 cal yr BP was associated with changes in atmospheric circulation and regional warming, and resulted in ice-free conditions in the study area by 15,000 cal yr BP (Hulton et al., 2002; Boex et al., 2013).

As the glaciers retreated, deep glacially-carved valleys filled with a system of lakes. Present-day Lake General Carrera/Lake Buenos Aires and Lake Cochrane/Lake Pueyrredón (**Figure 1**) are the remnants of a glacial lake that extended between 46 and 48°S. Dammed in the west by the icefields and mountains, the glacial lakes drained into the Atlantic Ocean (Clapperton, 1993). Between 12,800 and 8,000 cal yr BP, the water breached the ice dam resulting in a regional drainage reversal toward the west. The watershed of the Baker River, where M. Casanova is located, adopted its modern configuration at this time (Turner et al., 2005; Bell, 2008).

In late-glacial times (17,500–10,000 cal yr BP), rising winter and annual insolation coupled with changes in atmospheric circulation led to increasingly higher temperatures in Antarctica (**Figure 4A**) and southern South America, forcing a poleward shift of the Southern Westerlies to a position south of the study region (Rojas et al., 2009). This trend toward warmer conditions and longer growing seasons peaked in the early Holocene and favored the expansion of tree populations throughout western Patagonia (Moreno, 2004; Iglesias et al., 2016a). Initial tree expansion was time transgressive, occurring as early as 16,500 cal yr BP at 41°S (Whitlock et al., 2006), at 15,000 at 44–45°S (Haberle and Bennett, 2004; Massaferro et al., 2005), at 12,500 at 46°S (Lumley and Switsur, 1993), and not until 7,000 cal yr BP at 52°S (Markgraf and Huber, 2010). This north-to-south pattern represents a response to changes in effective moisture associated with warming and a southward shift of the westerly storm tracks (Iglesias et al., 2016a). It is possible that poorly developed soils and the presence of ice in high-elevation valleys (Aniya, 2013) were contributing factors to the late colonization of areas adjacent to the Patagonian icefields.

Pollen data from Lake Augusta (Villa-Martínez et al., 2012) and Lake Edita (Henríquez et al., 2016) located on the eastern flanks of the Andes at 47°S (**Figure 1**) indicate that expansion of *Nothofagus* began with ice recession and continued until 9,000 cal yr BP. At M. Casanova, *Nothofagus* (possibly *N. betuloides*) and Cupressaceae (likely *Pilgerodendron*) dominated mountain slopes before 8,480 cal yr BP (**Figure 3**). Deposition of fine clay and low percentages of aquatic pollen and spore percentages (<0.7%) suggest the presence of open water.

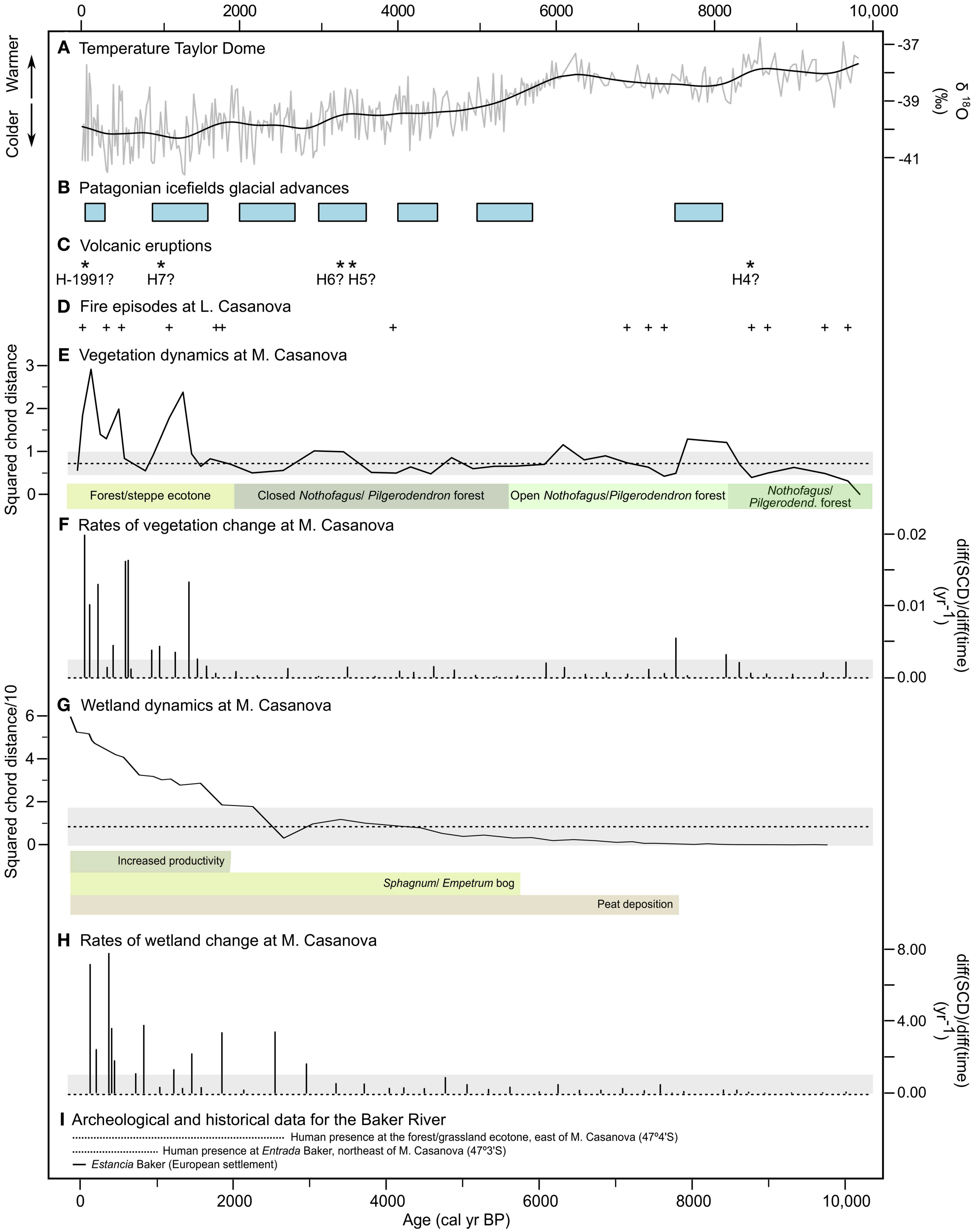

FIGURE 4 | (A) δ^{18}O record from Taylor Dome (Grootes et al., 1993). **(B)** Holocene glacial advances of the Patagonian icefields (Aniya, 2013). **(C)** Possible events of tephra deposition associated with known eruptions of the Hudson volcano. **(D)** Reconstructed fire episodes from M. Casanova charcoal data. Long-term dynamics in **(E)** vegetation and **(G)** wetland composition as inferred from the squared chord distance (SCD) between every pollen sample and the first sample of the record. The median Holocene SCDs (dashed line) and their confidence intervals (gray shading) are shown. Pollen zones and wetland characteristics (as interpreted from changes in lithology, sedimentation rates, magnetic susceptibility, and the presence/absence of *Sphagnum* spores) are indicated. Estimated rates of change in **(F)** vegetation and **(H)** wetland composition inferred from pollen data. Confidence intervals for 0 yr^{-1} (i.e., no change) are depicted in gray. **(I)** Archeological and historical information for the study area (Martinic, 1977; Mena and Jackson, 1991; Fuentes-Mucherl et al., 2012).

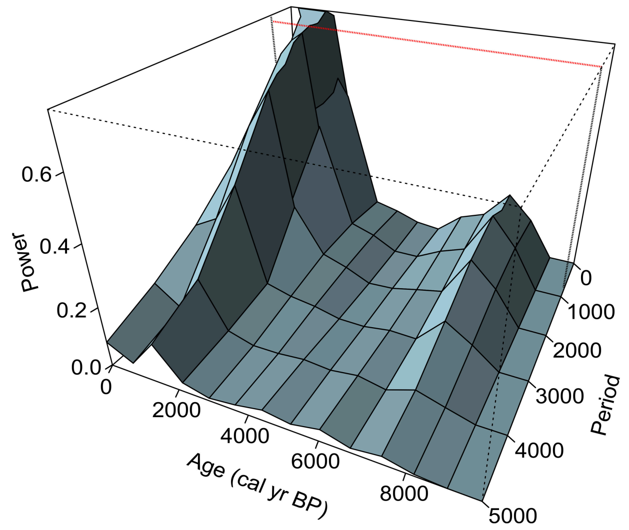

FIGURE 5 | Dynamic Lomb-Scargle periodogram for the SCD time series. Note the increase in power at 700- and 300-year periods during the last 2,000 years. Power values larger than 0.78 are statistically significant ($p = 0.05$; depicted with a red line).

Fire frequencies declined from 4.8 episodes 1,000 yr^{-1} at 9,840 cal yr BP to 1.7 episodes 1,000 yr^{-1} at 8,500 cal yr BP (**Figure 3**). Frequent fires prior to 9,000 cal yr BP are consistent with charcoal records throughout western Patagonia. Frequent burning at the time is attributed to increasing fuel loads coupled with an early onset of the fire season and higher probability of lightning (Haberle and Bennett, 2004; Moreno, 2004; Whitlock et al., 2007; de Porras et al., 2012; Villa-Martínez et al., 2012; Markgraf et al., 2013; Iglesias and Whitlock, 2014). Although it is possible that anthropogenic ignitions were an additional cause of fire, these early-Holocene fire episodes pre-date archeological evidence of humans in the study area.

Between 8,480 and 5,630 cal yr BP, vegetation continued to be dominated by *Nothofagus* forest. Higher-than-before pollen percentages of *Maytenus* and other shrubs and herbs, however, point to a more diverse understory and/or forest openings (**Figure 3**). CHAR was lower than before (<0.15 particles cm^{-2} yr^{-1}), and fire-episode frequency declined to 0.1 fire episodes 1,000 yr^{-1} after reaching a maximum of 3.5 fire episodes 1,000 yr^{-1} at 7,100 cal yr BP. Forest expansion and reduced fire activity have been inferred at sites on both sides of the Andes (e.g., Haberle and Bennett, 2004; Moreno, 2004; Markgraf et al., 2007; Abarzúa and Moreno, 2008; Wille and Schäbitz, 2009; de Porras et al., 2012; Iglesias et al., 2016a) in association with the onset of effectively wetter conditions during the mid-Holocene (Berger and Loutre, 1991; Liu et al., 2003).

Increasingly cooler/wetter conditions during the late Holocene (5,800 cal yr BP-present) supported advances of outlet glaciers from the Patagonian icefields (Aniya, 2013; **Figure 4**) and aquifer recharge in southern Patagonia (51°S; Larson et al., 2008). At 5,630 cal yr BP, closed forest prevailed in the M. Casanova watershed, and fire activity declined sharply and remained very low until 2,000 cal yr BP (CHAR < 0.08 particles cm^2 yr^{-1}). Similar trends toward closed forest and reduced fires are observed south of the study site (e.g., Villa-Martínez and Moreno, 2007; Mancini, 2009; Moreno et al., 2009; Wille and Schäbitz, 2009; Echeverría et al., 2014). These conditions contrast with steppe expansion at 44°S (de Porras et al., 2012, 2014) and may be explained by a southward shift and/or weakening of the northern margin of the Southern Westerlies, which would have prevented storm tracks—and therefore precipitation and lightning—from reaching northern Patagonia (Lamy et al., 2010).

Peat accumulation started at the coring site at 7,840 cal yr BP (**Figure 2**). A rapid increase of *Empetrum* pollen and *Sphagnum* spores at 5,800 cal yr BP, nonetheless, suggests that maximum development of the ombrotrophic bog did not occur until the onset of effectively more humid conditions between 5,800 and 2,000 cal yr BP (**Figure 3**). The rise of *Empetrum* pollen to its Holocene maximum at 3,500–2,700 cal yr BP is associated with peaks in magnetic susceptibility possibly derived from the H5 and H6 eruptions. This association suggests that *Empetrum* populations resisted the effects of tephra deposition on soil permeability and geochemistry. Low CHAR at times of *Empetrum-Sphagnum* bog expansion has also been reported in Fuego-Patagonia (50°S) during the Holocene (Huber and Markgraf, 2003). Huber et al. (2004) interpret the relationship between low fire occurrence and *Sphagnum* growth as evidence of infrequent burning of forest and bog during periods of higher effective moisture conducive to peat accumulation.

Between 2,000 and 530 cal yr BP, rising lake levels and forest expansion south of 44°S have been recorded east and west of the Andes and are attributed to higher effective moisture (Mancini, 2009; de Porras et al., 2014; Echeverría et al., 2014; Iglesias et al., 2016a). At M. Casanova, faster peat accumulation and lower-than-before magnetic susceptibility (**Figure 2**) suggest increased bog productivity (**Figure 4**). Higher effective moisture may also explain the expansion of *Podocarpus* on poorly drained fluvio-glacial deposits west of the lake or at higher elevations in the study area between 2,000 and 1,000 cal yr BP (Pérez et al., 2016; **Figure 3**). Rising CHAR at M. Casanova (**Figure 3**) is consistent with fire-history reconstructions throughout Patagonia that suggest increased biomass burning during this period (Szeicz et al., 2003; Haberle and Bennett, 2004; Villa-Martínez and Moreno, 2007; de Porras et al., 2014; Iglesias and Whitlock, 2014).

The last 530 years are characterized by changes in bog hydrology at M. Casanova, including the establishment of Caryophyllaceae, *Triglochin*, and other wetland plants, and rapid deposition of peaty sediments (**Figures 2–4**). The presence of submersed aquatic taxa, such as *Myriophyllum*, indicates that areas of the bog were flooded at times. High percentages of Asteraceae, Apiaceae, Amaranthaceae, and other herbaceous taxa and a decline in arboreal pollen suggest a loss of forest cover in recent centuries (**Figure 3**). Frequent fires (up to 5 fire episodes 1,000 yr^{-1}; **Figure 3**) would have favored the expansion of disturbance-adapted taxa (e.g., Amaranthaceae and herbs) at expense of less-tolerant trees. A decline of arboreal taxa in the last 500 years has also been reported north (44°S; Haberle and Bennett, 2004; de Porras et al., 2014) and south of the study area (50–55°S; Huber et al., 2004; Mancini, 2009). Deforestation through burning and, more recently, logging probably reduced evapotranspiration and facilitated paludification (Holz and Veblen, 2011).

Effects of Climate, Disturbance, and Human Impact on Ecosystem Stability

Paleoenvironmental data from L. Augusta (47°S) suggest that *Nothofagus* forests prevailed relatively unchanged in the watershed from the time of their establishment at ca. 9,800 cal yr BP to European arrival in the area in the twentieth century. Villa-Martínez et al. (2012) attribute this stability to the high tolerance of *N. pumilio*, the dominant tree, to changes in precipitation. The pollen record from M. Casanova shows that *Nothofagus-Pilgerodendron* forests have existed in the study area for about 9,000 years despite long-term changes in climate and fire (**Figure 3**). Rates of change statistically equal to zero indicate that terrestrial pollen percentages did not vary significantly over the period from 9,000 to 1,400 cal yr BP (**Figure 4**). The temporal and taxonomic resolution of the pollen time series, however, does not allow examining whether this stability resulted from *Nothofagus*' resistance to environmental change, its rapid recovery after disturbance (i.e., resilience), or trade-offs in the *Nothofagus* species [i.e., deciduous, fire-adapted *N. antarctica* vs. deciduous, obligate-seeder, fire-sensitive *N. pumilio* vs. evergreen, obligate-seeder, fire-sensitive *N. betuloides* and *N. nitida* (Correa, 1984), all of which grow at this latitude and whose pollen cannot be differentiated].

Two periods of rapid change before 1,400 cal yr BP were identified in the terrestrial SCD series. One occurred between 8,320 and 8,150 cal yr BP, when shrub taxa, Asteroideae, herbs, and grasses expanded at the expense of *Nothofagus*. The other one took place from 7,660 to 7,510 cal yr BP as a result of a pronounced increase in *Nothofagus*, and was coeval with the start of peat accumulation in the wetland (**Figure 4**). A reorganization of the ecosystem toward more open vegetation occurred between these two periods of rapid change (8,150–7,660 cal yr BP) and coincided with renewed glaciation in the Patagonian icefields (Aniya, 2013; Bourgois et al., 2016), suggesting that low temperatures probably limited seedling survival. Additionally, tephra from the H4 eruption of the Hudson volcano (**Figures 2**, **4**) may have promoted the acidification of the soils and precluded tree establishment in the study area. It is possible, however, that the change in pollen composition registered from 7,660 to 7,510 cal yr BP did not reflect changes in terrestrial vegetation but rather a shift in depositional environments (i.e., shift from fine clay to peat; **Figure 2**).

Charcoal times series from the Baker River watershed (i.e., Mallín Tortel [47°48′S, 73°28′W] and M. Casanova; Holz et al., 2012) show synchronous changes in fire activity in the last 7,000 years, including a pronounced rise in biomass burning at 2,000 cal yr BP. Comparison of reconstructed fire episodes at M. Casanova and the glacial record from the Patagonian icefields indicates that the probability of fire was significantly lower during times of ice advance (**Table 2**; **Figure 4**). Increased effective moisture and/or lower temperatures are likely to have favored ice expansion and bog productivity and suppressed fire activity (**Figure 4**).

During the last 2,000 years, fire-episode frequency was as high as that of the early Holocene (>3 fire episodes 1,000 yr^{-1}), despite wetter and/or cooler conditions (**Table 2**; **Figure 4**). The large SCDs indicate that, in contrast with the early- and mid-Holocene wetland and vegetation history, the bog has been highly variable since ca. 1,800 cal yr BP, while *Nothofagus-Pilgerodendron* forests have experienced pronounced and rapid departures from the long-term median composition after ca. 1,400 cal yr BP (**Figure 4**). The frequency spectrum of terrestrial squared chord distances reveals statistically significant power at centennial-scales during the last 2,000 years (300-year cycles; **Figure 5**), indicating that changes in vegetation occurred in a quasi-periodic manner. This periodicity matches that reconstructed for late-Holocene fire episodes (**Figure 3**), pointing to fire-induced forest loss followed by forest recovery/fuel accumulation and renewed fire activity in ca. 300-year cycles. These shifts in local ecosystem dynamics could have been an abrupt response to human impact and/or resulted from nonlinear climate-vegetation-fire linkages.

Humans arrived in Patagonia ca. 18,500 years ago (Dillehay et al., 2015) and lived throughout the region as small, dispersed groups until 7,000 cal yr BP, when population densities increased (Pérez et al., 2016). Resource availability in highly variable ecosystems would have been unpredictable, and when combined with the greater demands from growing human populations (Pérez et al., 2016), would have motivated the use of the Baker River watershed. The increasing presence of people in the area in the last two millennia may have therefore been an adaptation strategy in response to reduced resources per capita. Higher human population densities, in turn, possibly reinforced climate-disturbance-vegetation feedbacks operating at the local scale.

Comparison of reconstructed patterns of human occupation and environmental records from the central Patagonian Andes in Chile (44°S) suggests that hunter-gatherers likely increased the probability of fire, particularly in the last 3,000 years (Méndez et al., 2016). For example, Holz and Veblen (2011) reported burning of *Pilgerodendron* stands primarily by the Kawésqar canoeing group to secure dry firewood and canoe-building material. Similarly, fires set by aboriginal peoples to hunt guanacos (*Lama guanicoe*) and rheas (*Rhea* spp.) in northern Patagonia (∼41–43°S) were described by early European explorers and missionaries (Musters, 1871; Cox, 1963).

The shift in vegetation, fire activity and hydrology observed at M. Casanova after ca. 2,000 cal yr BP may therefore be partly anthropogenic. Faunal and lithic analyses from a small rock shelter in the Chacabuco Valley to the east (47°4′48″S, 72°16′20″; ca. 40 km from the study site) suggest use of the forest/grassland ecotone as early as 2,800 cal yr BP (Fuentes-Mucherl et al., 2012). Conversely, archeological evidence from the Baker River watershed shows human presence only after 1,000 cal yr BP (Mena and Jackson, 1991), and permanent settlement is not recorded until the establishment of the *Estancia* Baker by European ranchers in 1902 AD (ca. 35 km from the study site; Martinic, 1977). The late settlement record in this watershed, however, may reflect a lack of older archeological data, rather than an absence of people before Europeans.

The possibility of human ignitions at M. Casanova does not rule out climate as a driving force of change in local ecosystem dynamics reconstructed for the last 2,000 years that include (a) high fire activity; (b) unprecedented variability in bog composition; (c) emergence of regular fluctuations in the relative abundance of trees and shrubs that seem related to post-fire regeneration; and (d) paludification in association with forest loss. Decadal- and centennial-scale climate variability in the mid- and high latitudes of Patagonia has been ascribed to the Southern Annular Mode (Moreno et al., 2014), El Niño-Southern Oscillation (Whitlock et al., 2006), and to changes in solar irradiance associated with the Vries/Suess solar cycle (Lüdecke et al., 2015). Heightened moisture variability probably favored fires, and well-drained, acidic, tephra-rich soils may have slowed the post-fire regeneration of sensitive taxa. Fire, whether natural or anthropogenic in origin, led to forest loss in the last 500 years, which, in turn, contributed to paludification. Thus, the long-term trend toward cooler, effectively wetter conditions, combined with extreme wet and dry events and more frequent disturbance created a unique set of conditions that led to unprecedented change at M. Casanova starting at ca. 2,000 cal yr BP.

AUTHOR CONTRIBUTIONS

VI and SH: Designed research; SH and CW: Contributed reagents; VI: Counted pollen samples and analyzed data; VI, SH, AH, and CW: Interpreted results; VI: Wrote the paper; SH, AH, and CW: Edited the manuscript.

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