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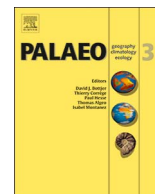
Landscape-scale drivers of glacial ecosystem change in the montane forests of the eastern Andean flank, Ecuador

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ABSTRACT

Understanding the impact of landscape-scale disturbance events during the last glacial period is vital in accurately reconstructing the ecosystem dynamics of montane environments. Here, a sedimentary succession from the tropical montane cloud forest of the eastern Andean flank of Ecuador provides evidence of the role of non-climate drivers of vegetation change (volcanic events, fire regime and herbivory) during the late-Pleistocene. Multiproxy analysis (pollen, non-pollen palynomorphs, charcoal, geochemistry and carbon content) of the sediments, radiocarbon dated to ca. 45–42 ka, provide a snap shot of the depositional environment, vegetation community and non-climate drivers of ecosystem dynamics. The geomorphology of the Vinillos study area, along with the organic-carbon content, and aquatic remains suggest deposition took place near a valley floor in a swamp or shallow water environment. The pollen assemblage initially composed primarily of herbaceous types (Poaceae-Asteraceae-Solanaceae) is replaced by assemblages characterised by Andean forest taxa, (first Melastomataceae-*Weinmannia*-*Ilex*, and later, *Alnus*-*Hedyosmum*-*Myrica*). The pollen assemblages have no modern analogues in the tropical montane cloud forest of Ecuador. High micro-charcoal and rare macro-charcoal abundances co-occur with volcanic tephra deposits suggesting transportation from extra-local regions and that volcanic eruptions were an important source of ignition in the wider glacial landscape. The presence of the coprophilous fungi *Sporormiella* reveals the occurrence of herbivores in the glacial montane forest landscape. Pollen analysis indicates a stable regional vegetation community, with changes in vegetation population co-varying with large volcanic tephra deposits suggesting that the structure of glacial vegetation at Vinillos was driven by volcanic activity.

1. Introduction

Mid-elevation tropical forests have been identified as some of the most biodiverse yet at risk terrestrial ecosystems in the world due to their high degree of endemism, sensitivity to climate change and anthropogenic impact (Bruijnzeel et al., 2011; Churchill et al., 1995; Hamilton et al., 1995). However, questions remain regarding their ecosystem processes and the role of environmental drivers as mechanisms of ecosystem change.

Tropical montane cloud forests (TMCF) are distinguished from other types of tropical forest by their association with montane environments immersed in frequent ground level cloud (Grubb, 1971, 1977). TMCF on the eastern Andean flank of northern Ecuador occur between ca.

1200–3600 m above sea level (m asl) and inhabit a dynamic and heterogeneous landscape (Harling, 1979; Sierra, 1999). Steep topographical changes produce environmental gradients that change abruptly with variation in precipitation, temperature and solar radiation (Sarmiento, 1986). Changes in climate associated with cloud cover play an important role in natural cloud forest structure and composition (Churchill et al., 1995; Fahey et al., 2016; Hamilton et al., 1995). However, modern anthropogenic pressures (e.g. land-use change, land-cover modification, pollution) arguably exceeded climate as the dominant control on vegetation structure through much of the TMCF of the eastern Andean flank (Sarmiento, 1995).

Non-climate drivers of ecosystem change in TMCF play a key role in increasing landscape and vegetation heterogeneity (Crausbay and
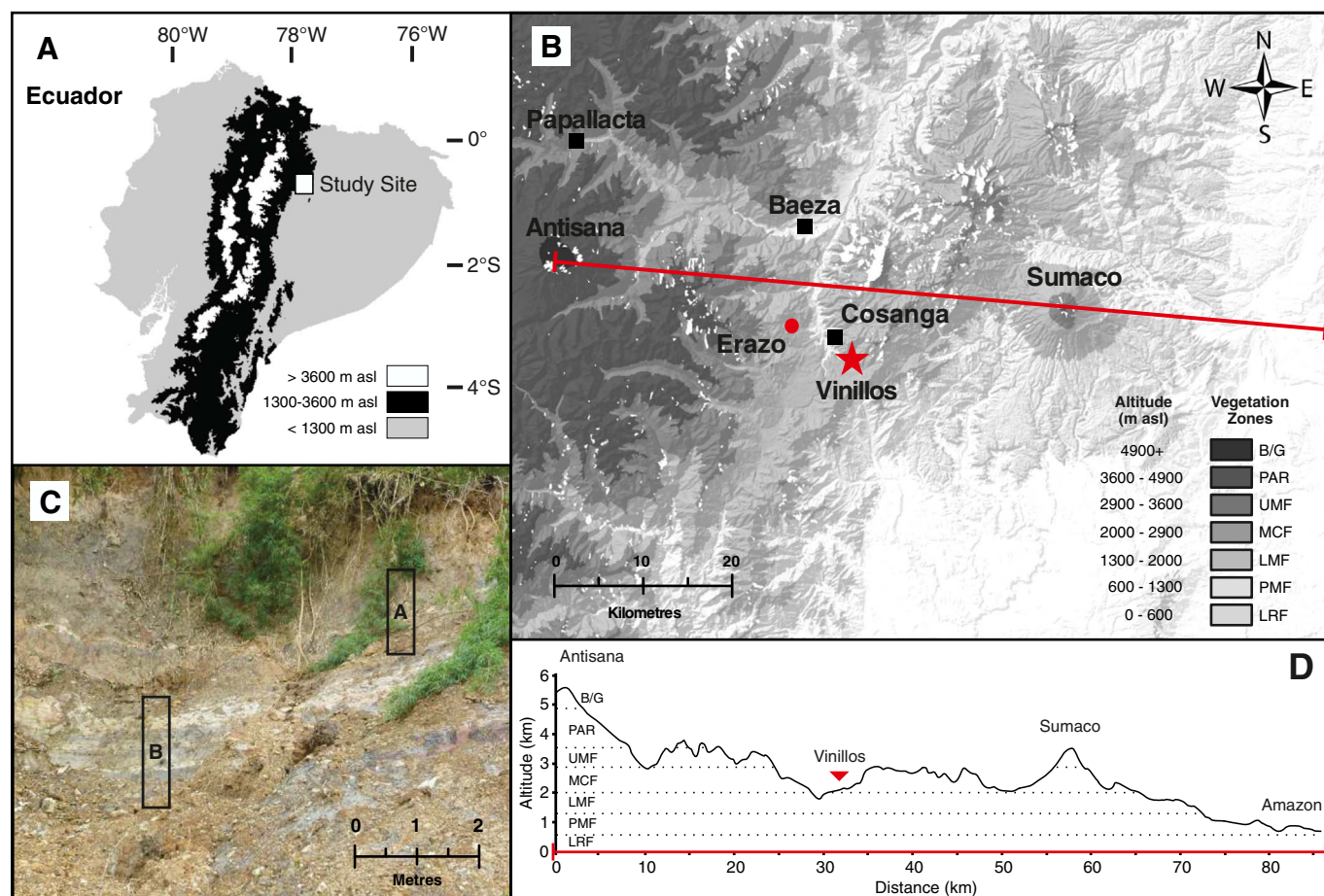
Fig. 1. Study sites. A. Location of study site in Ecuador, within montane forest vegetation zone (1300–3600 m asl), B. Topographic map of study region with generalized vegetation zone from Sierra (1999). LRF-lowland rainforest; PMF-pre-montane forest; LMF-lower montane forest; MCF-montane cloud forest; UMF-upper montane forest; PAR-páramo; B/G-barren/glaciers. Black squares indicate towns, red circle is Erazo section (Cárdenas et al., 2011), and red star is the location of the Vinillos exposure. Red line represents cross-section as seen in 'D', C. Photograph of Vinillos exposure prior to sampling and position of Section A and B, D. Cross-section across eastern Andean flank through Antisana and Sumaco volcanos, with generalized vegetation zones and position of Vinillos. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Martin, 2016). Modern natural (non-human) drivers of ecosystem change include abiotic processes such as volcanic eruptions, earthquakes, landslides and fire, while biotic processes such as plant-animal interactions, disease, forest die-back and a variety of edaphic factors, e.g. nutrient limitation, are all associated with landscape-scale modification of the environment. The stochastic nature of these abiotic and biotic drivers, coupled with high landscape heterogeneity can alter vegetation at a local to regional scale, over geologically short periods of time. In order to better understand ecosystem function in montane environments the role of non-climate drivers of vegetation change during different climate regimes (e.g. glacial periods), and in the absence of modern anthropogenic impact, needs to be ascertained.

Long sedimentary records from large lakes indicate climate is the primary driver of vegetation change over millennial scale time frames within the Andes (Hanselman et al., 2011; van der Hammen and Hooghiemstra, 2003). The only lake records from within the TMCF habitat of the eastern Andean flank that extend from prior to the last glacial maximum occur at Lake Consuelo in southern Peru (Bush et al., 2004; Urrego et al., 2005, 2010) and at Funza and Fúquene in central Colombia (Bogotá-A et al., 2011; Hooghiemstra, 1984; van der Hammen and Hooghiemstra, 2003). Analysis of past vegetation change in the TMCF of the eastern Andean flank of Ecuador is limited due to the paucity of suitably preserved sediments. Palynological analysis of discontinuous sediments from cliff sections at the Mera, Erazo and San Juan de Bosco sites indicate changing forest assemblages through the Quaternary are driven by long-term changes in climate (Bush et al.,

1990; Cárdenas et al., 2011, 2014; Colinvaux et al., 1997; Keen, 2015; Liu and Colinvaux, 1985). However, the role of short-term non-climate drivers of vegetation change has yet to be investigated in this setting.

Here we use a multi-proxy approach (pollen, non-pollen palynomorphs, wood macro-remains, charcoal, geochemistry and carbon content) to reconstruct a snap shot of a glacial montane forest vegetation community. We assess the role of volcanic activity (volcanic tephra layers), fire regime (charcoal) and herbivory (*Sporormiella*) as ecosystem drivers of vegetation change in a glacial montane forest and discuss the importance of incorporating non-climate drivers of vegetation change into palaeoecological reconstructions of TMCF.

2. Study site

A new section was located at Vinillos (0°36′2.8″S, 77°50′48.8″W), near the town of Cosanga in the Napo Province, Ecuador. The Vinillos site is situated at 2090 m asl between the Cordillera Real and Napo Uplift on the eastern Andean flank of northern Ecuador (Fig. 1). The exposure is located on the eastern side of the Cosanga Valley, and was uncovered during construction of the Troncal Amazónica (E45); the highway adjacent to the Río Cosanga.

Modern climate data from the study region is sparse, however, 15 years of data from the nearby town of Baeza (Fig. 1) indicates an average of 2320 mm of precipitation per annum (Valencia et al., 1999). High levels of orographic rainfall and semi-permanent ground level cloud lead to persistent moist conditions (Harling, 1979). Mean annual
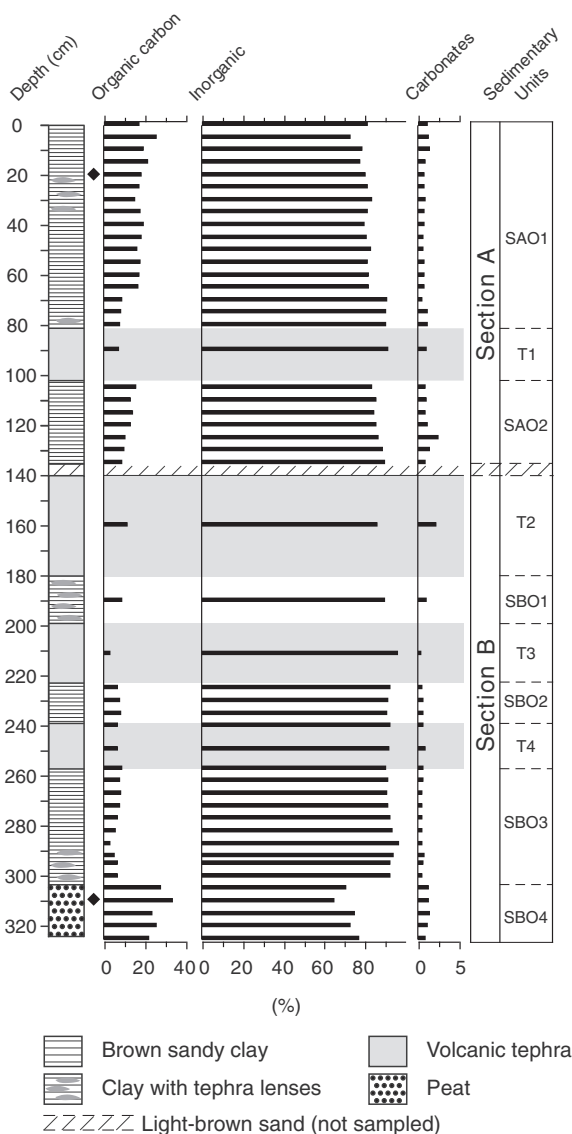
Fig. 2. Sediment description. Loss-on-ignition results of 48 samples indicating the percent weight loss of organic material, carbonate material and remaining inorganic material. Sedimentary units as used in the text.

(Fig. 1) does provide a representation of the human impacted pollen signal showing an over representation of the disturbance indicator *Cecropia* (Cárdenas et al., 2014). Studies of pollen-vegetation relationships from montane forests elsewhere in the Andes indicate that the modern pollen rain of tropical montane cloud forests is comprised of a combination of Andean and lowland forest taxa (Rull, 2006; Weng et al., 2004b).

3. Methods

3.1. Sediment sampling

The Vinillos section is composed of 325 cm of interbedded organic layers (identified with the prefix O) and volcanic tephra deposits (identified with the prefix T) (Fig. 2). Forty-four sediment samples were collected in 2012 through the six organic layers at approximately 5 cm intervals. A further four samples were collected, one from each of the four volcanic tephra layers. The exposure was cleared of surface sediment and vegetation prior to sampling, which commenced in the uppermost dark-brown organic layer below the weathered surface soils. A knife was used to extract 1 cm wedges of sediment from the section, which were placed in zip locked bags, labelled and kept cool prior to transport to The Open University (UK) where they were stored in a cold store (3–5 °C). Descriptions of the sediments were recorded during sampling.

3.2. Radiocarbon dating

Accelerator mass spectrometry (AMS) radiocarbon (^{14}C) dating of two palynomorph residues from the top and base of the Vinillos section was undertaken to constrain the age of the sediments. Palynomorph residues were used as they have been shown to produce more reliable ages than bulk samples in regions of high rainfall (Newnham et al., 2007; Vandergoes and Prior, 2003). Guidelines, based on standard palynological protocols (Faegri and Iversen, 1989) were provided by the Natural Environment Research Council (NERC) Radiocarbon Facility-East Kilbride (NRCF). Preparation included the mechanical sieving of the sediment at 100 μm and the use of HCL, KOH and HF to concentrate palynomorphs from the bulk sediment.

3.3. Loss-on-ignition

Forty-eight 2 cm^3 subsamples of sediment were extracted for loss-on-ignition (LOI) analysis. A standard LOI protocol was undertaken (Heiri et al., 2001). Samples were dried at 40 °C for up to 5 days to remove moisture, followed by with controlled burns at 550 °C for 4 h to remove organics, and 950 °C for 2 h to remove carbonates, with the remaining material classified as siliciclastics. Weighing of samples took place after each phase and the weight loss converted to a percentage of the dry weight.

3.4. X-ray fluorescence

Major element analysis using X-ray fluorescence (XRF) was undertaken on the four tephra layers and two internal standards using standard protocols (Enzweiler and Webb, 1996; Thomas and Haukka, 1978). Glass disks were produced and analysed using an ARL 8420 + dual goniometer wavelength dispersive XRF spectrometer at The Open University to determine the major element composition (SiO_2, TiO_2, Al_2O_3, Fe_2O_3, MnO, MgO, Cao, Na_2O, K_2O, P_2O_5) of the tephra material.

3.5. Charcoal analysis

Twenty-nine samples from the organic sediments were examined for microscopic charcoal (5–100 μm) in the slides mounted for palynomorphs analysis. Fifty random fields of view from each palynomorph

temperatures range from 16 to 20 °C throughout the year due to stable levels of solar radiation and low seasonality (Galeas and Guevara, 2012; Harling, 1979), however, diurnal changes in temperature of up to 20 °C can occur at higher elevations, acting as a much more significant control on vegetation distribution than seasonal changes in temperature (Neill and Jørgensen, 1999).

Today the Vinillos section is situated within tropical montane cloud forest vegetation (Fig. 1) (Neill, 1999; Sierra, 1999; Webster, 1995). The modern vegetation at Vinillos is composed primarily of Andean forest elements such as Arecaceae, Betulaceae (*Alnus*), Chloranthaceae (*Hedyosmum*), Cunoniaceae (*Weinmannia*), Ericaceae, Fabaceae, Lauraceae, Melastomataceae, Moraceae, Rubiaceae and Urticaceae (*Cecropia*) with abundant epiphytic mosses, lichens, ferns, Bromeliaceae, Araceae and Orchidaceae (Cárdenas et al., 2014; Grubb et al., 1963; Valencia et al., 1998).

Anthropogenic disturbance and deforestation in the region means that the modern vegetation is a mosaic of arable land, pastures and secondary forest. Modern pollen-vegetation relationships have not been studied extensively in the region of Vinillos, however, a modern pollen altitudinal transect (1895 m–2220 m asl) from the nearby Erazo site

slide were recorded for microscopic charcoal remains and exotic *Lycopodium* at $200\times$ magnification (Clark and Patterson, 1997; Whitlock and Larsen, 2001). Micro-charcoal values were then converted to concentration per cm^3. Fifty 1 cm^3 subsamples of material were also processed and analysed for macroscopic charcoal particles ($> 100\,\mu m$). Sediment was deflocculated in 15 ml of a 10% solution of KOH at 80 °C for 20 min and then washed through a sieve at 100 μm (Whitlock and Larsen, 2001). The remaining residue was then analysed under a low power ($20\times$) microscope in a bogorov tray and all charcoal particles recorded. Particles were identified by their angular form, brittle nature and high reflectivity (Clark and Royall, 1995).

3.6. Palynomorph analysis

Twenty-six discrete sediment samples were chosen for the examination of palynomorphs at approximately 10 cm intervals through the organic layers and in all of the volcanic tephra layers. Organic samples of 1 cm^3 were processed using standard laboratory procedures (Faegri and Iversen, 1989). Volcanic tephra samples of 6 cm^3 were processed using density separation (Bromoform; 2 mol), due to the highly siliciclastic nature of the sediments and low palynomorph concentration (Moore et al., 1991). Samples using these two methods of palynomorph recovery have been shown to be directly comparable (Campbell et al., 2016). The addition of an exotic marker; here *Lycopodium* batch #124961: averaging 12,542 ± 931 spores per tablet, was added in order to determine palynomorph concentrations (Stockmarr, 1971). Samples were mounted in glycerol on glass slides and counted at $400\times$ and $1000\times$ magnification using a Nikon Eclipse 50i microscope. Counting of all palynomorphs (pollen, algae, fungal and zoological remains) was undertaken until a minimum of 300 terrestrial pollen grains (305–474) were recorded per sample, corresponding to between 0–113 algal remains, 0–2620 fungal NPPs and 0–12 zoological remains. Reference material at The Open University, an open access online pollen database (Bush and Weng, 2007) and published pollen atlases (Colinvaux et al., 1999; Hooghiemstra, 1984; Roubik and Moreno, 1991), were used to identify pollen grains. Non-pollen palynomorph (NPP) identification was undertaken using the available literature (Bakker and Van Smeerdijk, 1982; Cugny et al., 2010; Gelorini et al., 2011; Hooghiemstra, 1984; López-Vila et al., 2014; Montoya et al., 2010, 2012; Rull et al., 2008; Rull and Vegas-Vilarrúbia, 1998, 1999; van Geel, 1978; van Geel et al., 1981, 1983, 1989, 2003, 2011; van Geel and Aptroot, 2006; van Smeerdijk, 1989). New NPP morphotypes (assigned with the prefix OU) were recorded and are described in Loughlin et al. (2017).

3.7. Zonation of palynomorphs

Statistically significant zones were established for pollen assemblages in the program PSIMPOLL (Bennett, 2008). Data were filtered to include only terrestrial pollen taxa that occurred in > 1 sample and at an abundance of $> 2\%$ in at least a single sample. Aquatic elements, spores and NPPs were excluded. Zonation was performed by optimal splitting by information content, using the broken stick method to

determine the significant number of zones (Bennett, 1996). The pollen assemblages were then applied to the palynomorph diagrams which were plotted in the program C2 (Juggins, 2007).

4. Results

4.1. Chronology

Radiocarbon dating from the upper and lower portion of the Vinillos section (20 cm and 309 cm) returned dates whose one standard deviation error overlap. Calibration of reported dates was undertaken in OxCal 4.2.4 (Bronk Ramsey et al., 2013) using the IntCal13 atmospheric curve (Reimer et al., 2013). Uncertainties in the dates indicate it is not possible to construct a robust chronology or establish the rate of sedimentation. However, the radiocarbon dates do indicate deposition of the Vinillos sediments took place during the late Pleistocene ca. 45–42 ka (Table 1).

4.2. Sediments

The Vinillos section is composed of dark-brown to black organic layers with occasional pale grey lenses of volcanic ash interbedded with pale grey to beige volcanic tephra deposits. The sedimentary succession is composed of two offset portions, starting from the base of the exposure, Section B (SB) occurs from 325 cm to 140 cm and Section A (SA) from 135 cm to 0 cm, separated by a 5 cm sand layer that was not sampled, giving an overall thickness of 325 cm in length (Fig. 2). LOI of the basal 20 cm of the Vinillos section (a black organic-rich clay) indicates an organic carbon content of 22–34 wt%. Organic carbon is reduced to 3–9 wt% for the remainder of SB following the first occurrences of lenses of volcanic ash occurring at ca. 300 cm. Units SAO2 and SAO1 which make up the organic units of SA show a gradual increase in organic carbon through the beds after each tephra layer from 9 to 16 wt% and 8–20 wt% respectively. Carbonate content is low throughout the Vinillos section ranging from 0.5–2.5 wt%, with a mean of 0.9 wt%. Two unidentified large (> 30 cm in length and > 10 cm in diameter) wood macro-fossils were recovered from the outcrop, one within organic bed SBO1 and the other in SBO2 where it meets tephra layer T4 (Fig. 4).

4.3. Volcanic tephra layers

Four discrete volcanic tephra layers of different thicknesses were identified at Vinillos, T1 (18 cm), T2 (25 cm), T3 (40 cm) and T4 (23 cm). Geochemical analysis of the volcanic tephra layers using XRF indicate chemical compositions that can be characterised as an andesite (T1), basaltic andesite (T2), trachy-andesite (T3) and dacite (T4) (Fig. 3). Combustion of samples using LOI prior to XRF indicate that volcanic tephra samples contain between 3 and 12% organic carbon and are therefore not purely inorganic volcanic deposits (Fig. 2). Pollen was detected and identified within each tephra layer. Fungal NPPs were identified within T3 and T4, but no discernible NPP remains were identified from T1 and T2.

Table 1
Accelerator mass spectrometry (AMS) radiocarbon (^{14}C) dating of palynomorph residues.

Publication code	Sample depth (cm)	$\delta^{13}C_{VPDB}$[a] (‰)	Radiocarbon age[b] (yr B.P. ± 1σ)	Calibrated* radiocarbon age (yr B.P. ± 1σ)	Calibrated* radiocarbon age (median probability)
SUERC-58952	20	− 27.4	38,503 ± 968	41,885–43,325	42,670
SUERC-58953	309	− 27.1	40,524 ± 1245	43,091–45,218	44,300

[a] $\delta^{13}C_{VPDB}$ (‰) values were determined from using an aliquot of sample CO_2 and were measured on a dual inlet stable isotope mass spectrometer (Thermo Scientific Delta V Plus) and are representative of $\delta^{13}C$ in the pre-treated sample material.

[b] Conventional radiocarbon years B.P. (relative to 1950 CE), expressed at the ± 1σ level for overall analytical confidence. Calculated from 14/13 ratios analysed by AMS which were subsequently corrected to $\delta^{13}C_{VPDB} = -25‰$ using the $\delta^{13}C$ values listed in this table and corrected for background contamination using the NERC Quartz tube combustion background of + 0.17 ± 0.1% modern carbon.
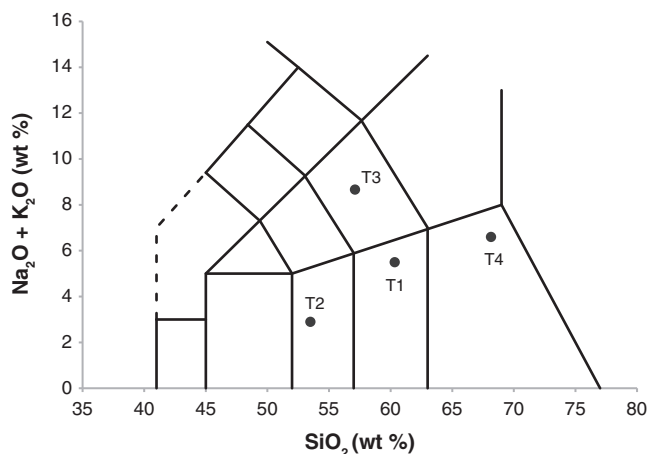
Fig. 3. TAS diagram of X-ray fluorescence data. T1-andesite; T2-basaltic andesite; T3-trachy-andesite; T4-dacite.

4.4. Macro- and micro-charcoal

Macro-charcoal was recovered from eleven of the forty-eight samples examined (Fig. 4). The charcoal occurred at a concentration of
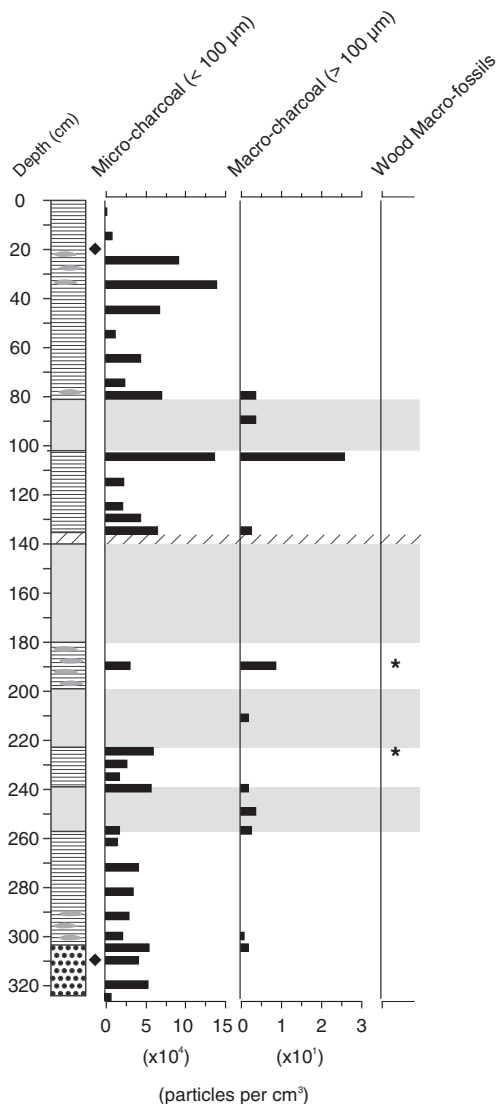

Fig. 4. Micro- and macro-charcoal concentrations and wood macrofossils. Micro-charcoal (< 100 μm) and macro-charcoal (> 100 μm) are displayed as fragments per cm³. Asterisk (*) mark position of individual wood macro-fossil remains.

1–26 fragments per cm³. Nine of the eleven samples which contained macro-charcoal occur in the volcanic tephra layers or directly adjacent to them, the two other samples were from near the base of SBO3, concomitant with the first organic sediments to contain volcanic ash lenses. Micro-charcoal is present in each of the 29 samples analysed. The abundance of micro-charcoal ranged from 2500 to 140,000 fragments per cm³, with a mean of 44,500 fragments per cm³. Maximum micro-charcoal concentrations correlate with the maximum macro-charcoal concentration, occurring directly below T1 and in the samples collected at a height of 35–25 cm (SAO1) where the youngest organic samples occur with volcanic ash lenses.

4.5. Palynomorphs

Zonation of pollen yielded three statistically significant stratigraphic zones, VIN 1 to VIN 3. (Figs. 5, 6 and 7).

4.5.1. Pollen zone VIN 1

VIN 1 (13 samples, 320–140 cm) corresponds to SB and is characterised by abundant Poaceae (4–30%) and fern spores (22–36%). *Alnus* has a low abundance (2–9%) at the base of the zone increasing after T4 to 7–21%, while Solanaceae occurs at 1–9% at the base of the zone and decreases after T4 to 0.3–1.4%. Asteraceae (3–17%), Melastomataceae (2–13%), *Hedyosmum* (3–10%), Ericaceae (1–9%) and Clusiaceae (4–10%) are consistently present but in low abundance. Pollen concentrations occur at 60,000–270,000 grains per cm³ at the base of the zone decreasing to 17,000–84,000 grains per cm³ after T4. The most abundant fungal NPP morphotypes in VIN 1 include HdV.123 (1–24%), HdV.495 (1–19%) and IBB.259 (1–14%). The obligate coprophilous fungal spore *Sporormiella* is present in two samples in low abundance (< 3%). *Coniochaeta* cf. *ligniaria* occurs in low abundances below T4 (0–6%) increasing to 7–17% in the beds containing wood macro-fossils. The semi-aquatic Cyperaceae fluctuate between 1 and 13%. The lower part of the zone aquatic remains include *Isoëtes* (< 3%), *Spyrogyra* (< 3%), *Concentricystis* (< 8%) and *Mougeotia* (< 5%) and along with the sole aquatic zoological remains of HdV.179 (< 4%). Above the lowest volcanic tephra layer aquatic remains are reduced with only *Spirogyra* (< 4%) occurring in a single sample (Fig. 7).

4.5.2. Pollen zone VIN 2

VIN 2 (6 samples, 140–75 cm) corresponds to SAO2, T1 and the lower most sample in SAO1 and is characterised by an abrupt decrease in the percentage of Poaceae (2–5%), fern spores (12–17%), *Alnus* (3–7%) and Asteraceae (3–5%). Melastomataceae (15–27%), *Weinmannia* (6–27%) and *Ilex* (1–8%) increase along with a sharp increase in pollen concentration to 300,000–950,000 grains per cm³, with Melastomataceae and *Weinmannia* peaking at 251,000 and 282,000 grains per cm³ respectively in sample 115 cm, before dropping to < 110,000 per cm³ immediately at T1. Fungal NPP concentration is at its lowest point in VIN 2 (< 20,000 per cm³) and is effectively barren (< 10,000 per cm³) for 4 of the 6 samples within the zone. Semi-aquatic Cyperaceae are reduced occurring at 1–2%, with aquatic elements *Isoëtes* (< 1%) and *Spirogyra* (< 2%) only present in single samples.

4.5.3. Pollen zone VIN 3

VIN 3 (7 samples, 75–0 cm) corresponds to SAO1 except for the lowermost sample and is characterised by an increase in *Alnus* (20–28%), Myricaceae (3–9%) and fern spores (18–41%) in conjunction with a moderate increase in *Hedyosmum* (8–13%), Asteraceae (4–11%) and Poaceae (7–8%). Melastomataceae (5–11%), *Weinmannia* (< 5%) and *Ilex* (< 1%) all decrease. The pollen concentration is reduced again to that of VIN 1 (30,000–210,000 grains per cm³). Fungal NPP remains OU-108 (9–75%), HdV.123 (9–690%), HdV.495 (6–16%) and IBB.259 (5–18%) are the primary morphotypes with OU-108 dominant and
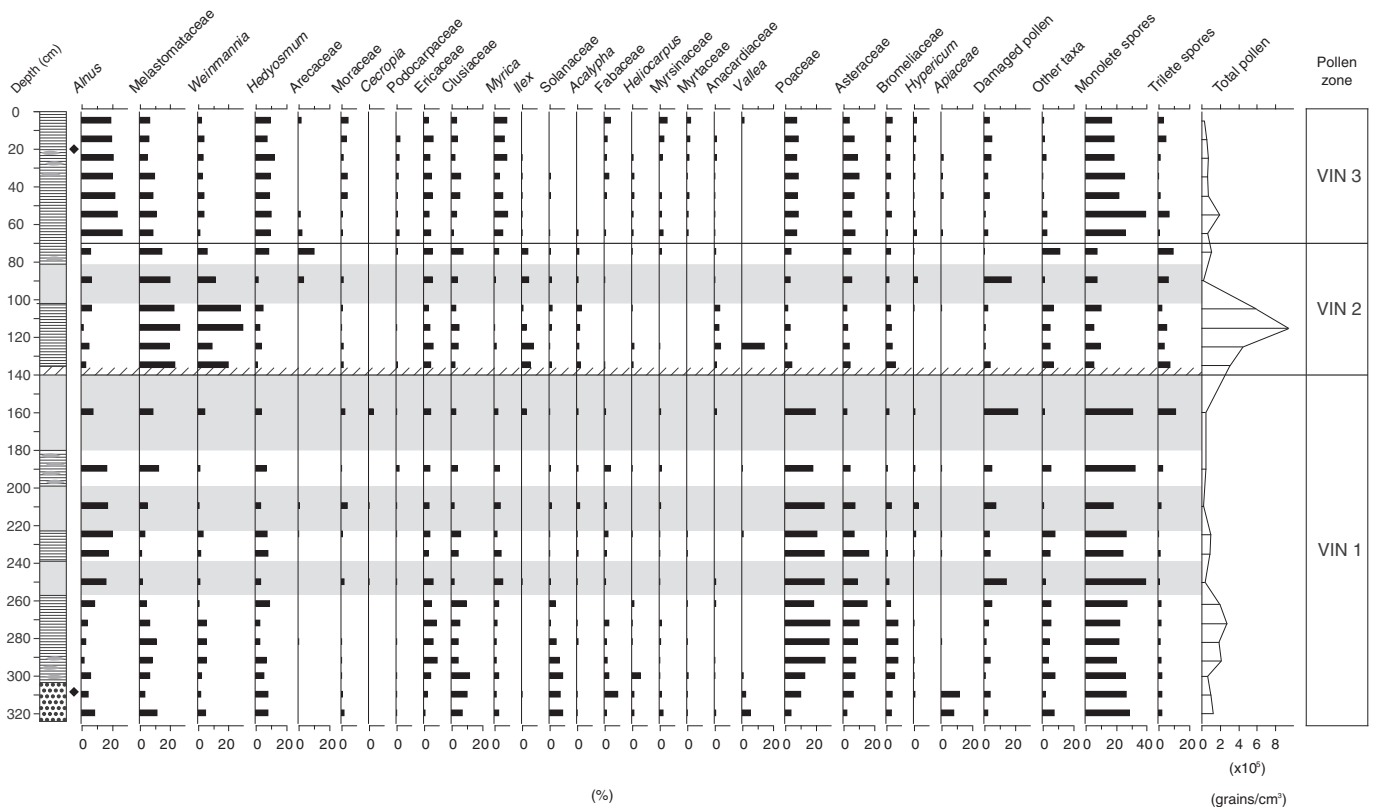
Fig. 5. Fossil pollen percentage diagram from Vinillos. Taxa include types that occur at > 2% abundance in at least one sample. Black diamonds indicate position of radiocarbon dates (Table 1).

HdV.123 hyper-dominant in the samples from 15 cm and 5 cm respectively. NPP concentration is highly variable in VIN 3 (ca. 40,000–250,000 per cm³) and reaches peak abundance in sample 55 cm. The obligate coprophilous fungi *Sporormiella* (0–3%) returns in low abundance in VIN 3 appearing in a more continuous fashion. Semi-aquatic Cyperaceae increase (4–8%) along with the return of more persistent aquatics elements *Isoëtes* (1–14%), *Spirogyra* (0–33%), *Concentricystis* (0–3%) and *Mougeotia* (0–3%).

5. Interpretation and discussion

Calibrated radiocarbon dates from the top and bottom of the Vinillos section indicate that the sediments were deposited over a period of approximately 2000 years between 44.3 and 42.7 ka (Table 1). Deposition of the sediments occurred between intervals of increased precipitation during Heinrich events HE 4 (38.3–40.2 ka) and HE 5 (47.0–50.0 ka) (Mosblech et al., 2012; Sanchez Goñi and Harrison, 2010), within a period characterised by an oscillating climate corresponding to Dansgaard-Oeschger interstadials 11–9 (Blunier and Brook, 2001; Mosblech et al., 2012). Long sedimentary records from Andean lakes have shown vegetation responding to these climate fluctuations (Hanselman et al., 2011; van der Hammen and Hooghiemstra, 2003). These changes in climate likely contributed to vegetation change within the sedimentary snap shot at Vinillos, however, here we show that the often neglected non-climate drivers of vegetation change are vital in interpreting past ecosystem dynamics driving landscape-scale change in the glacial montane forest of the eastern Andean flank.

5.1. Depositional environment

The position of the Vinillos section near the base of an Andean valley suggests that deposition of the sediments took place in aquatic conditions on or near the valley floor. Fungal NPPs characteristic of

swamp or bog conditions (HdV-123, HdV-16A) and the modern cloud forests (IBB.259) suggest deposition in a shallow water environment (Loughlin et al., 2017). Preservation of the sediments occurred as incision of a tributary of the Río Cosanga, now ca. 29 m below the Vinillos section exposed the Vinillos sediments within the valley wall. Down cutting of the river is therefore calculated to occur at a rate of 6.9 mm per year between present day and the deposition of the youngest Vinillos sediments ca. 42 ka. This rate is at the upper end of predicted rates of denudation for eastern Andean montane rivers and is likely to reflect the high levels of precipitation that occur in the region (Aalto et al., 2006). No evidence of fluvial channel sediments have been identified in the Vinillos section sediments. The multiple volcanic tephra layers interbedded with the organic beds may have acted as a protective cap, preserving palynomorphs and wood macro-fossil remains from oxidisation (Keen, 2015).

Aquatic pollen, algae and zoological remains preserved in the section signify the aquatic depositional environment of VIN 1 and VIN 3 (Fig. 7), with the highest proportion of aquatic remains occurring prior to the oldest volcanic tephra layer (T4) and subsequent to the youngest volcanic tephra layer (T1). This increase in the aquatic components may correspond to periods of reduced moisture availability during Dansgaard-Oeschger interstadials 11–9, as observed in Lake Consuelo (Urrego et al., 2010). Aquatic remains become rare or absent during deposition of the four volcanic tephra layers, within VIN 2 and where lenses of volcanic ash occur within the organic sediments. This suggests that volcanic ash deposition may have led to inhospitable aquatic conditions during and immediately after its deposition, driving the change in aquatic remains.

5.2. Glacial vegetation on the eastern Andean flank

The Vinillos section contains pollen taxa which are present within the modern pollen spectra of the eastern Andean flank, however, the
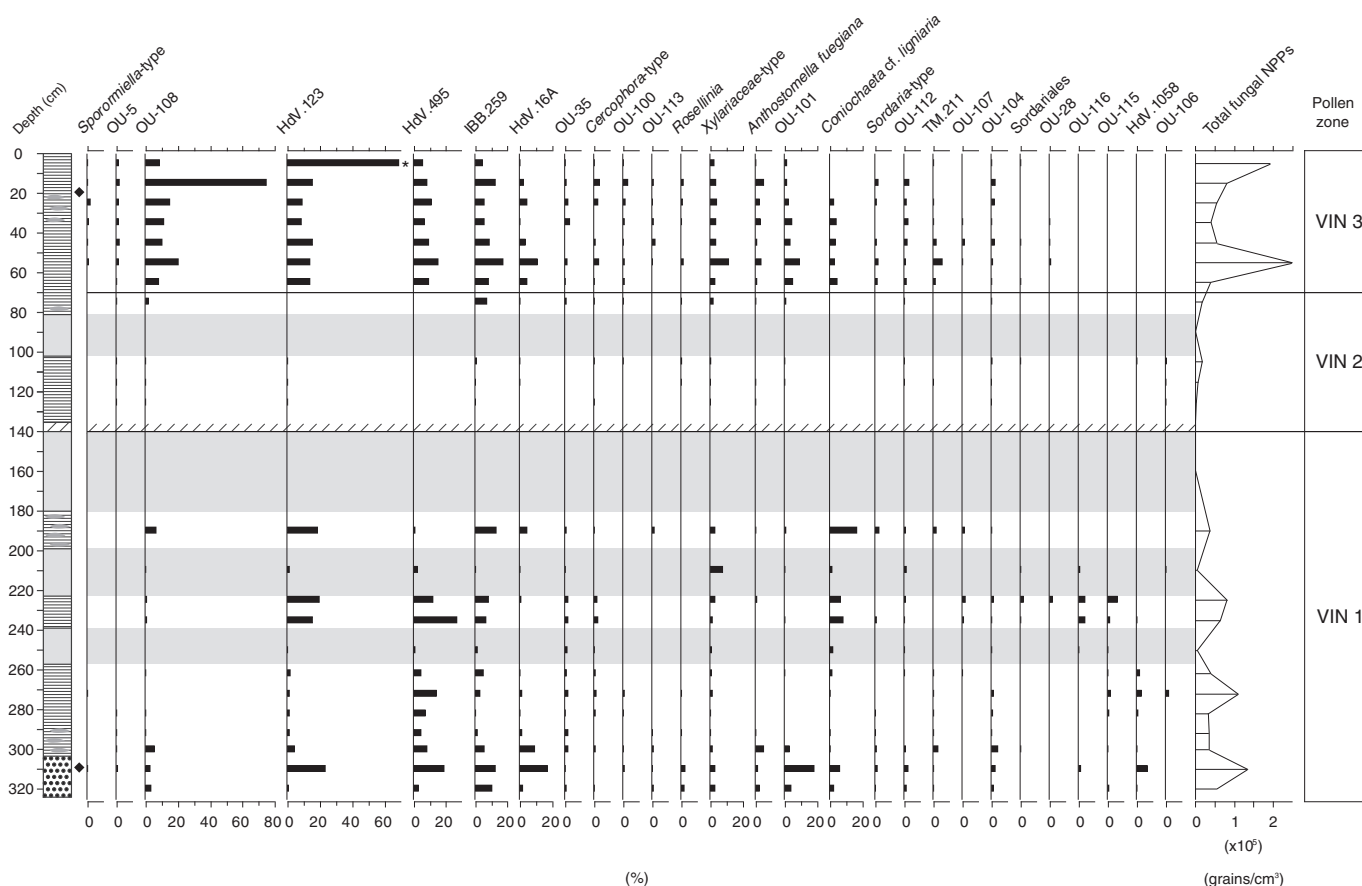
Fig. 6. Fossil non-pollen palynomorph diagram from Vinillos based on pollen percentage. NPP morphotypes represent types that occur at > 2% abundance of the pollen sum in at least one sample. Asterisk (*) indicates count for morphotype HdV-123 in sample at 5 cm has been divided by 10 (687% of pollen sum). Black diamonds indicate position of radiocarbon dates (Table 1).

fossil pollen assemblages are compositionally unlike any comparable modern pollen assemblage from the region (Cárdenas et al., 2014; Marchant et al., 2001; Rull, 2006; Weng et al., 2004b). This no-analogue pollen assemblage (sensu Williams and Jackson, 2007), indicates that a novel vegetation community existed at Vinillos during the late Pleistocene. The high abundance and association of typical Andean arboreal pollen taxa (e.g. *Alnus*, *Weinmannia*, *Hedyosmum*), presence of large wood macro-fossils and low levels of Poaceae throughout the section (mean 13.5%) are used to suggest a montane forest community was present during the deposition of the Vinillos sediments. Three pollen zones provide evidence for dynamic changes to the glacial forest pollen assemblage characterised by the dominance of Poaceae-Asteraceae-Solanaceae in VIN 1, Melastomataceae-*Weinmannia-Ilex* in VIN 2, and *Alnus-Hedyosmum-Myrica* in VIN 3. These changes in pollen assemblage through the Vinillos section are due to shifts in the abundance of particular pollen taxa and not the wholescale replacement of particular species, indeed every taxon except Myrtaceae and *Cecropia* can be found in each of the three pollen zones (Fig. 5). This change in pollen abundance between assemblages within a closed canopy moist tropical forests can indicate distinct changes in vegetation structure (Gosling et al., 2005, 2009). Pollen analysis from glacial Neotropical sedimentary archives have previously been used to conclude that millennial scale changes in temperature and moisture balance have driven vegetation change through the Quaternary (Baker et al., 2001; Bogotá-A et al., 2011; Bush et al., 2004; Colinvaux et al., 2000; Gosling et al., 2008; Groot et al., 2011; Mourguiart and Ledru, 2003; Urrego et al., 2005, 2010, 2016). However, the cumulative effect of climate change on landscape-scale drivers such as increased precipitation leading to more frequent landslides is rarely discussed (Stern, 1995; Bussmann

et al., 2008). Incorporating landscape-scale drivers into past and future projections of vegetation change is essential in understanding how montane forest respond to environmental change. The three pollen assemblage shifts at Vinillos occurring over approximately 2 ka (44.3–42.6 ka) and in conjunction with volcanic tephra deposits suggest that non-climate factors can be the primary driver of short-term change in glacial montane forest communities. This pattern of population change is analogous to modern montane forest communities, where landscape heterogeneity, environmental variability and stochastic disturbance events lead to local variation in vegetation population within an identifiable vegetation zone.

5.3. Landscape-scale drivers of vegetation change

5.3.1. Herbivory

Remains of Pleistocene megaherbivores such as giant ground sloths (Megatheriidae), armadillos (Chlamyphoridae) and Proboscideans (Gomphotheridae) have been found in the inter-Andean plain and lowland Amazonian rainforest of Ecuador (Coltorti et al., 1998; Marshall et al., 1983), but little evidence exists of herbivory within the steep slopes of the intermediate montane forest region. The Vinillos record contains low abundances (< 3%) of the ascospore *Sporormiella* (Fig. 6), an obligate coprophilous fungi which requires ingestion by herbivorous before being deposited in dung to complete its life cycle (Krug et al., 2004). *Sporormiella* has been used to determine changes in herbivore population and collapse during the late-Quaternary extinction (Davis, 1987; Gill et al., 2009), when large Pleistocene herbivores were likely important drivers of ecosystem change within the tropics (Corlett, 2013). The presence of *Sporormiella* at Vinillos suggests the
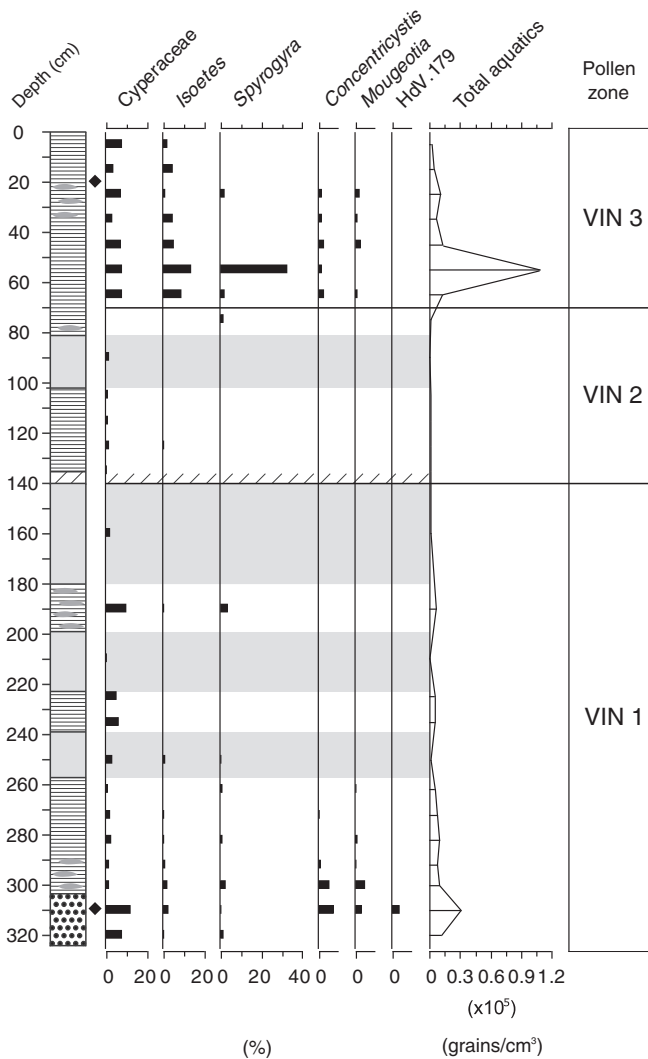
Fig. 7. Fossil aquatic remains diagram from Vinillos based on pollen percentage. Remains include vegetative and zoological remains indicative of semi to fully aquatic conditions. Black diamonds indicate position of radiocarbon dates (Table 1).

local presence of herbivores along the valley floor within the glacial montane forest environment, but cannot provide further information on the type of herbivore or their abundance. The presence of small and large fauna may have contributed to seed dispersal, vegetation openness and hence fire reduction within the glacial montane forest environment.

5.3.2. Fire regime

Fire is an important a driver of vegetation change in the Neotropics (Bond and Keeley, 2005; van der Werf et al., 2008). However, high levels of year-round precipitation and ground level cloud within modern TMCF mean that they rarely burn naturally (Crausbay and Martin, 2016). The global fire regime has been shown to be diminished during glacial periods (Daniau et al., 2010), with Neotropical charcoal records containing reduced concentrations during the last glacial period (Hanselman et al., 2011; Mayle et al., 2009). Regional fires are indicated by the presence of micro-charcoal (< 100 μm) throughout the Vinillos sediments, however the rare and limited concentrations (< 27 fragments per cm^3) of macro-charcoal (> 100 μm) (Fig. 4), which are indicative of local fires, suggests local burning was unlikely to have occurred (Whitlock and Larsen, 2001). The prevalence of burning in fire prone high elevation Páramo environments may indicate that charcoal fragments deposited at Vinillos were transported from this more

combustible habitat (Coblentz and Keating, 2008; Hanselman et al., 2011). Vinillos is located between two active volcanos, Antisana (5704 m asl) and Sumaco (3990 m asl) (Fig. 1) (Hall et al., 2017). The co-occurrence of charcoal and tephra material throughout the Vinillos sediments suggests that volcanic eruptions were the likely ignition source of regional fires and that charcoal was transported to Vinillos during volcanic eruption events. The minimal macro-charcoal remains indicate that fires were not a major driver of vegetation disturbance within glacial montane forest environments.

5.3.3. Volcanic activity

The response of an ecosystem to volcanic activity is linked closely to the type and quantity of volcanic material deposited. The volcanic tephra layers deposited at Vinillos are considered to be air fall deposits due to their fine-grained nature, however, some of the deposits may also have their origin in fine-grained material winnowed from pyroclastic flows. Each of the tephra layers contains low concentrations of pollen (15,000–48,000 grains per cm^3) and NPPs (< 3400 grains per cm^3) similar in composition to their adjacent organic layers (Figs. 5 and 6) suggesting the period of deposition was long enough to incorporate a representative palynomorph signal or that the palynomorphs were transported within the tephra material.

The presence of three tephra layers within one pollen zone (VIN 1) indicates that the vegetation assemblage changed little after the deposition of T4 and T3. An increase in the proportion of *Alnus* pollen, a typical pioneer species in the Andes (Grau and Veblen, 2000; Weng et al., 2004a) within and adjacent to T4 and T3 indicates some disturbance of the forest community took place, but that no overall change in vegetation composition occurred. Pollen zone VIN 2 occurs immediately after the largest volcanic tephra layer (T2, 40 cm) and contains a change in the palynomorph assemblage to one characterised by high concentrations of *Weinmannia*, Melastomataceae and *Ilex* pollen, but an absence of fungal NPPs (Fig. 8). This shift in pollen assemblage and loss of fungal NPPs is interpreted to indicate that the amount of volcanic ash deposited by T1, T2 and T3 caused the population dynamics and edaphic factors of the local area to change. Deposition of the youngest tephra layer (T1) coincides with a return to an assemblage comparable to that of VIN 1 with an increase in *Alnus*, *Hedyosmum* and *Myrica* (Fig. 5). Changes in the pollen zones through the Vinillos section broadly correspond to changes in sediment associated with the introduction of volcanic tephra material, indicating that volcanic activity is likely to have been an important driver of landscape-scale ecosystem dynamics in glacial montane forest on the eastern Andean flank.

The occurrence of these non-climatic landscape-scale drivers (volcanic events, fires and herbivores) in conjunction with disturbance events which occur in modern montane environments, e.g. landslides, forest die-back, tree fall events, and presumably occurred in the glacial landscape allowed for stochastic local disturbances in the vegetation assemblages to occur (Fig. 8). These dynamic landscape-scale processes led to local ephemeral vegetation assemblages occurring within the wider montane forest ecosystem. The persistent local level vegetation instability occurring through glacial climate regimes may have allowed for individual species to react quicker to climate driven vegetation change during the transition to an inter-glacial climate regime and potentially to cope with continued anthropogenic landscape degradation and future changes in climate.

6. Conclusions

The composition of the palynological assemblages through the Vinillos section indicates a stable regional vegetation community occurred on the eastern Andean flank of northern Ecuador during the last glacial period ca. 45–42 ka, despite landscape-scale processes driving local changes in forest structure. Deposition of volcanic ash was found to be the primary non-climate driver of landscape-scale changes in vegetation populations. Local vegetation population dynamics were
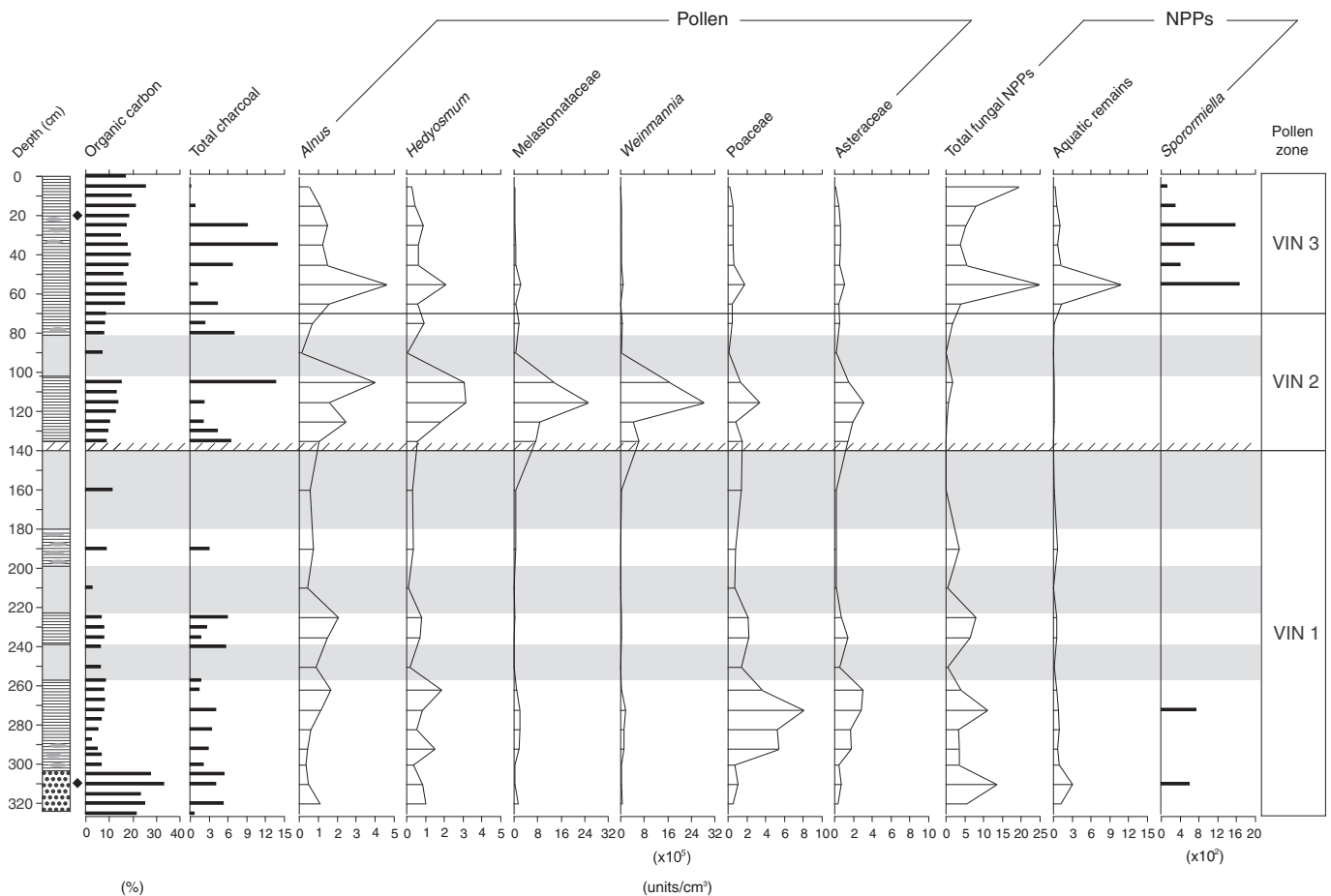
Fig. 8. Synthetic diagram of proxies used in reconstructing the Vinillos section. Selected pollen taxa (*Alnus*, *Hedyosmum*, Melastomataceae, *Weinmannia*, Asteraceae and Poaceae), NPPs and combined charcoal are plotted as concentration per cm³. Organic carbon is plotted as a percentage. Black diamonds indicate position of radiocarbon dates (Table 1).

driven primarily by these stochastic disturbance events, maintaining local vegetation heterogeneity during the last glacial period. No-analogue pollen assemblages from Vinillos indicate the presence of glacial forest communities that differ compositionally to the tropical montane cloud forest vegetation that occurs today, with higher abundances of characteristic montane taxa i.e. *Podocarpus*, *Alnus*, *Hedyosmum* and *Weinmannina* indicating cooler conditions. The presence of obligate coprophilous fungi e.g. *Sporormiella*, provides evidence for the existence of herbivores within the glacial forest, however, low concentrations suggest they would have had a negligible impact on vegetation dynamics. The association between volcanic sediments and charcoal suggests that volcanic eruptions were the principle source of ignition in the Andes prior to the arrival of humans. Micro-charcoal observed in the record was likely transported from extra-local regions which were more susceptible to burning, e.g. Páramo, or entrained within ash falls. The paucity of macro-charcoal indicates that local fires were absent, or rare, within glacial montane forests.

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