Title: Ecological consequences of post-Columbian depopulation in the Andean-Amazonian corridor

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Abstract

European colonization of South America instigated a continental scale depopulation of its indigenous peoples, the extent of whose impact on the tropical forests of South America prior to AD 1492 varied across the continent. The role that indigenous peoples have played in transforming the biodiverse tropical forests of the Andean-Amazonian corridor through time remains unknown. Here we reconstruct the last 1000 years of changing human impact on the cloud forest of Ecuador at a key trade route, which connected the Inkan Empire to the peoples of Amazonia. We compare this historical landscape to the pre-human arrival (c. 44-42 kya) and modern environment, demonstrating that intensive land-use within the cloud forest prior to European arrival deforested the landscape to a greater extent than modern (post-AD 1950) cattle farming. This intensive land-use ended abruptly c. AD 1588 following the catastrophic decline of the indigenous peoples. Forest succession then took c. 130 years to establish a structurally intact forest, one comparable to that which occurred prior to the arrival of the first human to the continent. We show that 19th century descriptions of the Andean-Amazonian corridor as a pristine wilderness record a shifted ecological baseline, one that less than 250 years earlier had consisted of a heavily managed and cultivated landscape.

Main

The cultural collision that followed the arrival of Europeans to the Americas in AD 1492 (all dates hereafter in years AD) triggered conflict, disease and enforced labour that resulted in the deaths of estimated 80 million indigenous people [1]. Uncertainty remains over the ecological consequences which followed this depopulation and the influence that indigenous peoples exerted on the landscape prior to European arrival [2,3]. In South America historical and ecological evidence points to disparities in the timing, spatial distribution and magnitude to which tropical forests have been modified by pre- and post-European contact peoples [4–11] . Here we examine how the tropical montane cloud forests of the eastern Andes (2000-2900 meters above sea level (m asl)), today one of the most biodiverse, carbon rich and threatened habitats on Earth [12], were transformed over the last 1000 years of changing human impact.

Prior to European arrival in the Americas indigenous peoples inhabited the Quijos Valley on the eastern Andean flank of northern Ecuador [13–15] (Fig.1). Evidence from archaeological [16,17], anthropological [13,14] and historical records [18] indicate that this Andean-Amazonian corridor formed the eastern frontier of the Inkan Empire (1400-1532) [14,19]. The Inka undertook expeditions into the Quijos region during their expansion subjugating the native population, however, they established no infrastructure or permanent presence [14,19]. The people of the Quijos Valley remained a distinct group that facilitated exchange between the Inka and the peoples of the Amazon [13,15]. Following European arrival Gonzalo Díaz de Pineda (1538) and Gonzalo Pizarro (1541) led the first excursions by Spanish conquistadors into the Ecuadorian Amazon [14]. Leaving from the capital city of Quito they travelled east over the Andes, through the Quijos Valley and into the Amazonian lowlands in search of gold and cinnamon [13,14]. By 1559 the Spanish town of Baeza had been founded in the Quijos Valley, near the indigenous settlement of

Hatunquijos (Fig.1). Contemporary Spanish accounts indicate that at contact the indigenous population dispersed throughout the wider Quijos region numbered c. 35,000, and that by 1577 a population of c.11,400 indigenous people were concentrated around the town of Baeza [14]. However, brutal treatment of the indigenous peoples, disease, the establishment of '*encomienda*' (forced labour and tribute) [20] and numerous indigenous uprisings (1560-1578) [13] led to a 75% decline in the native population by 1600 [14]. Depopulation continued and the region was virtually abandoned for the next 250 years, so that by the middle of the 19th century the former town of Baeza consisted solely of three small huts [21,22].

Results

Lake Huila (00° 25.39' S, 78° 01.06' W; 2608 m asl) is 30 metres in diameter, and located on an isolated lava terrace within the Quijos Valley, underlain by volcanic rocks derived from the nearby Antisana Volcano [23] (Fig.1, Supplementary Figure 1 and Supplementary Figure 2). A mosaic of open cattle pastures and secondary forest fragments occupy the valley floor along the Río Quijos, a tributary of the Río Coca and Río Napo (Fig.1). Montane cloud forest scarred by landslides and deforestation cover the steeper slopes of the valley. In 2013 two parallel sediment cores of 209 cm were recovered from the centre of Huila using a Livingstone piston corer [24]. A multiproxy palaeoecological approach was used to reconstruct past environmental change from the top 50 cm of the core (Fig.2 and Supplementary Figure 3) representing approximately the last 700 years (Supplementary Figure 4). Pollen analysis provided evidence of past local (< 100 m) to regional (< 30 km) vegetation change [25], while macro- (> 100 µm) and micro-charcoal (< 100 µm) provided evidence of local to regional burning [26]. Microfossils of aquatic elements were used to interpret shifts in lake conditions and fungal non-pollen palynomorphs (NPPs) changes in local ecosystem dynamics, with characteristic morphotypes used to determine changes in lake edge vegetation (HdV.201), local burning (*Neurospora*), erosion (*Glomus*) and herbivory (coprophilous fungi *Sporormiella* and *Podospora*) [27]. To contextualise the Huila record proxy data were compared to modern local surface samples and the closest pre-human arrival sedimentary record (Vinillos) [28] (Supplementary Figure 1 and Supplementary Table 1).

Proxy data from Huila revealed four distinct past vegetation communities (Fig. 2). The oldest zone HUI-1, covers the pre-European period and up to 1588. The zone is characterised by a pollen assemblage indicative of open conditions (Caryophyllaceae, Amaranthaceae, *Thalictrum* sp. (12-28%) and Poaceae (30-53%)), the cultivation of maize (*Zea mays*) (< 3%), high concentrations of charcoal, the presence of the charcoal-loving fungal spore *Neurospora*, and pottery sherds (Fig. 2). The shift to HUI-2 (1588-1718) occurs at a spike in macro-charcoal concentration, followed by an increasing abundance of aquatic indicators, grasses (Poaceae), pollen of the disturbance indicator *Cecropia* sp. and early successional *Hedyosmum* sp. and Moraceae (Fig. 2). HUI-3 (1718-1819) sees increases in forest pollen from characteristic cloud forest taxa (Melastomataceae, *Weinmannia* sp., Fabaceae and Solanaceae) [29]. This is followed by HUI-4 (post-1819) where pollen indicative of open conditions return during the period of Ecuadorian independence. Here forest pollen declines in association with increasing coprophilous fungal spores (*Sporormiella* and *Podospora*) characterising the early stages of modern population expansion, deforestation and cattle farming that occurred in the region during the late 19th century.

Detrended correspondence analysis (DCA) of pollen (Fig.3a) and fungal NPP (Fig.3b) data from Huila, the modern samples and the pre-human arrival sediments is used to characterise the relationship between the vegetation assemblages through time. This ordination technique identifies the similarity between individual samples based on composition. Pollen data from the pre-human arrival samples (Vinillos) is most similar to that of the montane cloud forest that occurred at Huila between 1718-1819 (HUI-3) both characterised by the pollen of Melastomataceae and *Weinmannia* sp. The signal from the modern mosaic landscape (HUI-4 and modern samples) is most similar to that of the period following indigenous depopulation (HUI-2; 1588-1718) both characterised by the pollen of Poaceae, Moraceae and *Hedyosmum* sp. While the pollen from the pre-European contact cultivated landscape occurs in its own distinct cluster (Fig.3a). Fungal NPP data shows that along DCA axis-1 assemblage's from all post-European contact settings, i.e. modern samples, HUI-2, HUI-3 and HUI-4, are all more similar to that of the intact pre-human arrival forest seen at Vinillos, than to the pre-European cultivated landscape seen in HUI-1 (prior to 1588) (Fig.3b). Both pollen and fungal NPP data therefore reveal that the indigenous peoples transformed the landscape into a novel vegetation assemblage prior to the arrival of Europeans, one more different from the pre-human arrival forest at Vinillos than that of the modern mosaic landscape seen today.

Discussion

Zea mays is known to have been cultivated in the adjacent Amazonian lowlands from c. 6000 years ago [30] and has been found at the Huila site for at least the last 1000 years (Supplementary Figure 4), consistent with the earliest reliable pottery dates from Baeza c.1045 [16]. Macro-charcoal particles and the presence of the charcoal-loving fungal spore *Neurospora* prior to 1588 indicates local burning occurred in an environment where intact montane cloud forest rarely burns naturally [31]. Evidence of cultivation and the presence of pottery sherds at

Huila suggests that humans were present and likely the primary source of ignition of local fires. The prevailing wind direction moving up the Andean flank from the indigenous settlement of Hatunquijos (< 10 km east of Huila) is the likely source of micro-charcoal within the wider Quijos Valley (Fig.1). The high proportion of pollen indicative of open conditions, maize, the fungal spore HdV.201, in conjunction with abundant charcoal indicates that the landscape around Huila was an open environment, cultivated and managed by an indigenous population for at least 500 years prior to the arrival of the first Europeans.

An abrupt change in the palaeoecological proxies at the transition from HUI-1 to HUI-2 (c.1588) occurs shortly after the height of indigenous uprising against Spanish rule (1560-1578) [13]. A massive intensification in local burning around Huila is revealed by increased macro-charcoal fragments (up by two orders of magnitude). This spike in charcoal is coincident with historical records of open warfare in which Baeza was attacked and the settlements of Archidona and Avila destroyed [14] (Fig.1). The disappearance of pollen from cultivated species, coinciding with a sharp rise in grasses, pioneer species (*Cecropia* sp.) and aquatic elements signifies the abandonment of intensively cultivated fields around Huila shortly after the largest uprising in 1578. The palaeoecological signatures of conflict and abandonment found at Huila suggest that warfare in this period was widespread across the landscape impacting indigenous peoples places of food production as well as centres of population (Baeza, Archidona and Avila; Supplementary Figure 1).

The transition from an open managed landscape to that of a secondary forest colonized by pioneer species occurs soon after the height of regional conflict. A rapid increase in grass pollen (623% of the pollen sum) and the presence of disturbance indicators such as *Cecropia* sp. characterise early secondary succession. An increasing percentage of forest pollen taxa through

HUI-2 to the more established montane cloud forest environment of HUI-3 occurs over approximately 130 years, during a period where little evidence of human impact is observed in the Huila record or recorded historically [14]. The proximity of the samples from the period of montane cloud forest recovery (HUI-3) to those of pre-human arrival in the DCA (Fig.3a) demonstrate forest recovery dynamics of a human impacted site converge with that of an intact Andean montane forest, supporting an equilibrium model of tropical forest recovery [32]. Transformation from an intensely managed cultivated landscape (HUI-1) to that of a montane cloud forest (HUI-3) therefore alludes to the ability of an Andean montane cloud forest to recover to a structurally intact state over a period of c. 130 years (1588-1718).

Written accounts of the Quijos Valley from 1857 [21] and 1867 [22] describe "a dense forest, impenetrable save by trails" in a region that "has remained unpeopled by the human race". However, evidence of renewed human impact on the vegetation is already seen to occur by c. 1820 (HUI-4). An increasing proportion of openness indicators and the first occurrence of coprophilous fungal spores signify a more open landscape grazed by herbivores, indicating that even the impact of low human populations drive changes in cloud forest vegetation composition and structure. The apparent wilderness described during the 19th century represented a shifted ecological baseline [33], one structurally and compositionally distinct from the mature montane cloud forest present between 1718-1819 (HUI-3), itself having undergone 130 years of vegetation recovery following the more than 500 years of intensive land management and cultivation prior to European contact. Reforestation of the Quijos Valley after 1588 corresponds to indigenous depopulation following the arrival of Europeans in 1492. Despite likely landscape-scale variations [9,34] our findings indicate that for some areas the intensity of pre-European indigenous people's impact on tropical ecosystems may be severely underestimated.

Methods

Sampling of Lake Huila was undertaken using a modified Livingstone corer [24] from a floating platform located in the centre of the lake. Parallel offset cores were recovered to a total depth of 209 cm. Modern surface sediments (soil and moss) were collected and stored in double zip-lock bags. Details of the pre-human Vinillos section can be found in reference [28]. All materials were stored at 3-6 °C until required. Pollen, non-pollen palynomorphs (NPPs) and micro-charcoal was processed from 26 samples in the Huila record using standard palynological protocols [25], including the addition of *Lycopodium* as an exotic marker (University of Lund batch #124961, 12,542 ± 931 spores per tablet). Palynomorph residues for radiocarbon dating were processed in the same manner, excluding acetolysis and the marker. Macro-charcoal was processed using standard protocols [26]. Pollen was counted at 400× and 1000× magnification to a minimum of 300 terrestrial pollen grains per sample. Grass pollen was excluded from the pollen sum due to its dominance in several samples and an inability to accurately separate aquatic and terrestrial taxa. Fungal NPPs and aquatic remains were counted in conjunction with the pollen. Micro-charcoal was recorded using 50 random slide views at 200× magnification along with *Lycopodium*, estimates of microcharcoal were made based on *Lycopodium* added per cm^3 of sediment. A chronology of the Huila core was established based on eleven accelerator mass spectrometry radiocarbon dates using the Bayesian statistical package Bacon [35] in "R" [36] (Supporting Information). Statistically significant palynomorph zones in Fig. 2 were established using optimal splitting by information content, and the broken stick method in the program PSIMPOLL [37]. Detrended correspondence analysis, using the statistical package Vegan [38] in "R"

[36] was used to explore the variance in the pollen and fungal NPP data. Counts were normalized using a square root transformation.

Data Availability

The datasets generated during the current study are available from the corresponding author and the Natural Environment Research Council (NERC) Environmental Information Data Centre.

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Supplementary Information:

Supplementary information is available in the online version of the paper.

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Author Contributions:

NJDL, EM and WDG determined the research objectives. PM located the sample site and secured permissions. Lake sampling was undertaken by NJDL, EM and WDG. Sediment processing, data collection and analysis was performed by NJDL. The manuscript was written by NJDL, EM and WDG with input from PM. All authors have read and approved the manuscript for submission.

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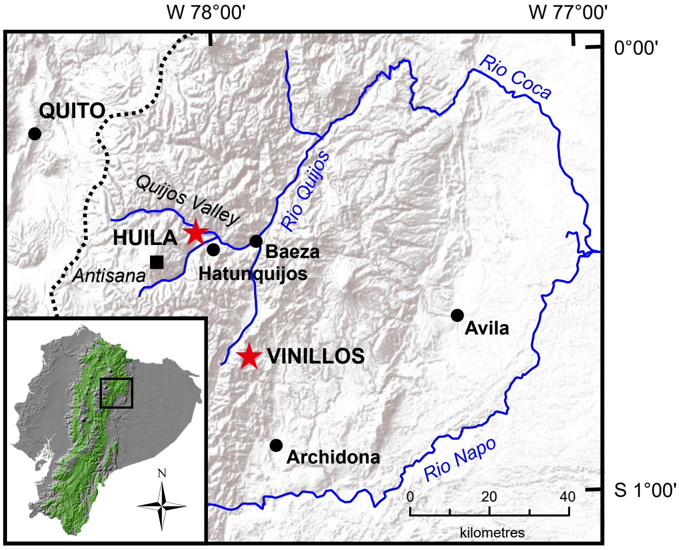
Figure captions:

Fig.1. Region of the Andean-Amazonian corridor inhabited by the indigenous Quijos peoples. The dashed line represents the boundary between the Inkan Empire and the peoples of the Quijos region. Black circles indicate present and past population centres. Red stars indicate the location of the principle study site (Huila) and the nearby pre-human arrival site (Vinillos); the location of all modern surface samples are shown in Supplementary Figure 1. Black square represent the peak of the nearby Antisana volcano. Inset panel shows Ecuador with elevations corresponding to montane forest (1,300-3,600 m asl) shaded in green. Altitudinal classification of montane forest vegetation zones, including cloud forest, is shown in Supplementary Figure 1.

Fig.2. Summary palaeoecological proxy diagram from Lake Huila plotted against age. Sediment age was derived using radiocarbon dating (Supplementary Figure 3). Silhouettes represent, from left to right, the period of cultivation by indigenous peoples (pre-1588), the principal indigenous uprising represented by a monument in the town of Tena to the 'Great Cacique Jumandi' (1578), 19th Century descriptions of the region (1857) and the beginning of cattle farming (c.1950). Pollen percentages are calculated relative to all terrestrial taxa excluding Poaceae (the pollen sum). Aquatic elements, fungal NPPs and Poaceae are calculated as percentages of the pollen sum.

Fig.3. Detrended correspondence analysis of (A) pollen and (B) fungal NPP data. Blue through green colour ramp correspond to the pollen zones at Huila (Fig.2). Grey circles are pre-human samples and grey crosses modern surface samples.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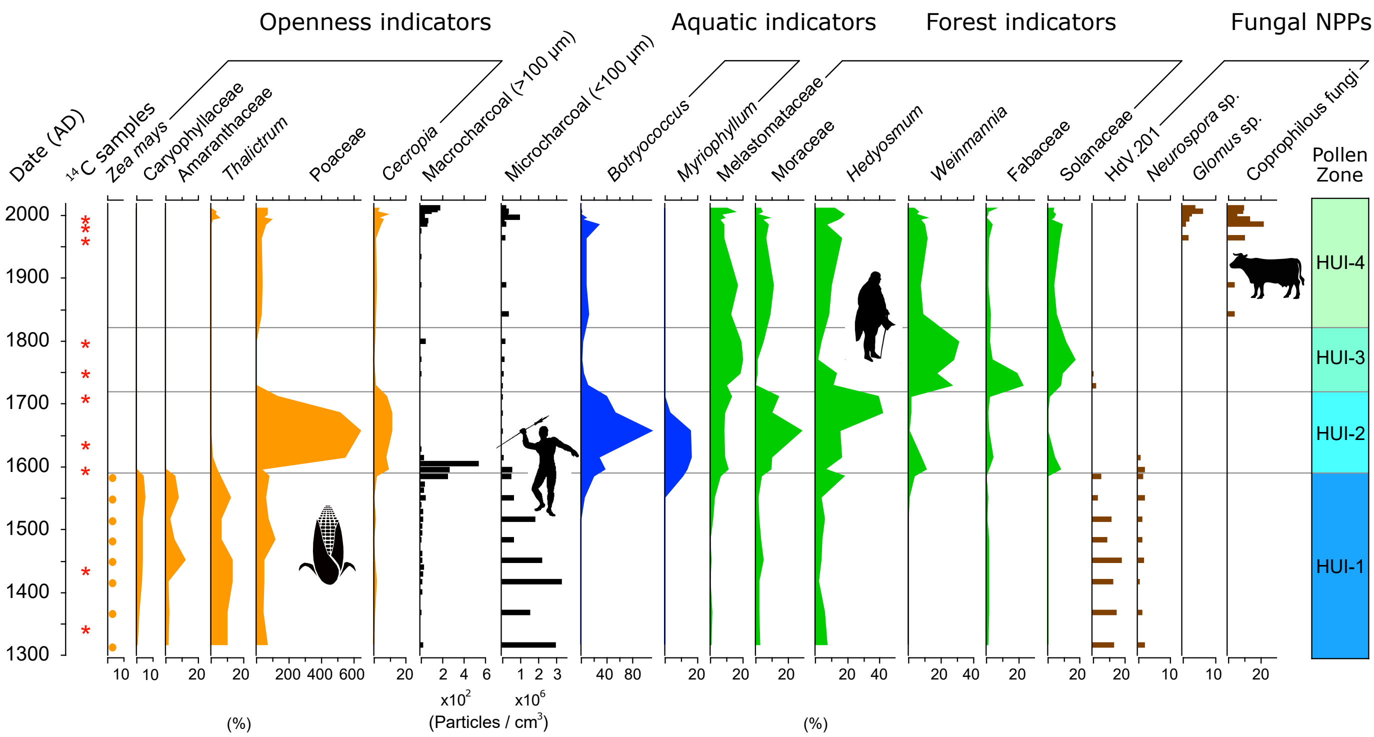
Openness indicators
Aquatic indicators
Forest indicators
Fungal NPPs
Date (AD)
¹⁴C samples
Zea mays
Caryophyllaceae
Amaranthaceae
Thalictrum
Poaceae
Cecropia
Macrocharcoal (>100 μm)
Microcharcoal (<100 μm)
Botryococcus
Myriophyllum
Melastomataceae
Moraceae
Hedyosmum
Weinmannia
Fabaceae
Solanaceae
HdV.201
Neurospora sp.
Glomus sp.
Coprophilous fungi
Pollen Zone
HUI-4
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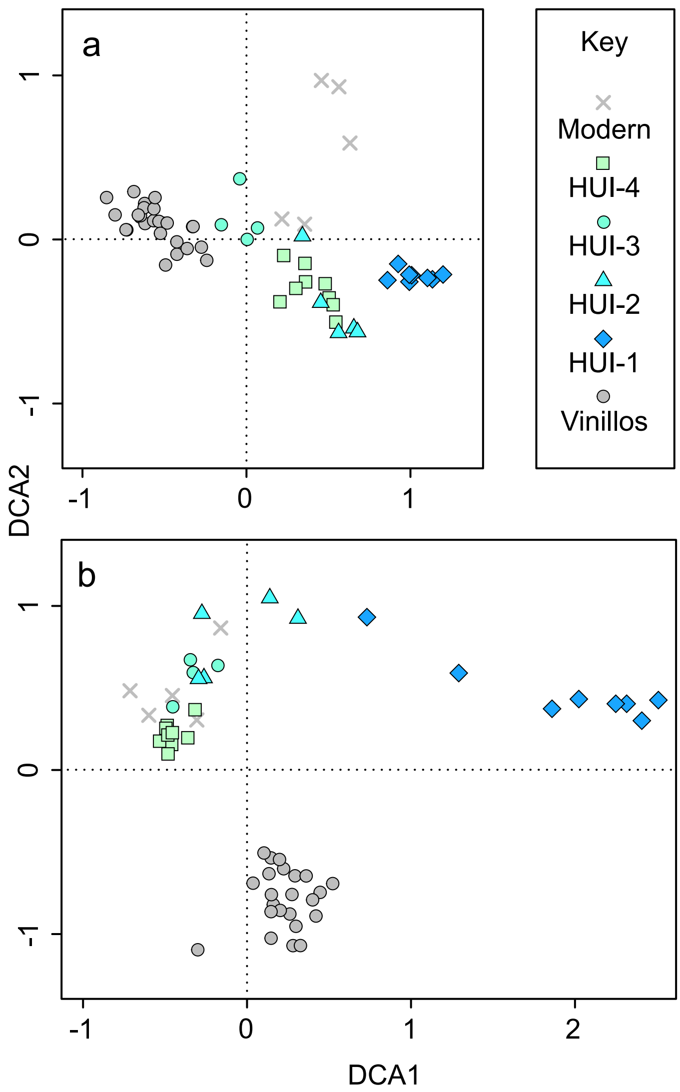
a
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Key
Modern
HUI-4
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