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Potential distributions of pre-Columbian people in Tropical Andean landscapes

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Much has yet to be learned of the spatial patterning of pre-Columbian people across the Tropical Andes. Using compiled archaeological data and a suite of environmental variables, we generate an ensemble species distribution model (SDM) that incorporates general additive models, random forest models and Maxent models to reconstruct spatial patterns of pre-Columbian people that inhabited the Tropical Andes east of the continental divide, within the modern countries of Bolivia, Peru and Ecuador. Within this region, here referred to as the eastern Andean flank, elevation, mean annual cloud frequency, distance to rivers and precipitation of the driest quarter are the environmental variables most closely related to human occupancy. Our model indicates that 11.04% of our study area (65 368 km^2) was likely occupied by pre-Columbian people. Our model shows that 30 of 351 forest inventory plots, which are used to generate ecological understanding of Andean ecosystems, were likely occupied in the pre-Columbian period. In previously occupied sites, successional trajectories may still be shaping forest dynamics, and those forests may still be recovering from the ecological legacy of pre-Columbian impacts. Our ensemble SDM links palaeo- and neo-ecology and can also be used to guide both future archaeological and ecological studies.

This article is part of the theme issue 'Tropical forests in the deep human past'.

1. Introduction

That environmental gradients structure vegetation patterns was one of the earliest biogeographical observations [1]. Nowhere is this effect more conspicuous than on mountains, where species turnover occurs over very short vertical distances [2]. The Tropical Andes (*ca* 6° N–23° S) are perhaps the most spectacular example of such close-packed biogeographical niches in the world. With many species having very small distributions [3], the Tropical Andes are a biodiversity hotspot, containing an estimated 1567 endemic species, with *ca* 6.7% of the global endemic plant species and *ca* 5.7% of the global endemic vertebrate species [4].

The Tropical Andes contain many unique ecosystems, but the mid-elevation humid montane forests, typically extending from *ca* 1400 to 3400 m above sea level (hereafter m a.s.l.) from Colombia through Bolivia on the eastern cordillera (hereafter humid montane forests), contain some of the greatest biodiversity in the world. Often shrouded in low-lying, persistent cloud cover, these epiphyte-laden humid montane forests provide a unique habitat for many species and support a higher density of endemic species than the adjacent highlands or Amazonian lowlands [5–7]. High topographic complexity within the forest creates strong climatic contrasts between dry ridges and mesic valley bottoms that contribute to vicariance and speciation [8]. Although these characteristics shape the overall patterns of diversity and endemism, little is known of the local history of past disturbances, and how that has shaped our perception of naturalness in these humid montane forests.

Long histories of human occupation have shaped the distributions of species and ecosystems in the high Andes and the Amazonian lowlands [9,10], but the possibility that such human-influenced landscapes also exist in humid montane forests has received less attention. Archaeological evidence documents human occupation as early as 12.8 thousand years before present in the Andean highlands [11] and 13 thousand years in the Amazonian lowlands [12]. Populations across South America probably grew exponentially beginning 5000 years ago [13], coincident with the onset of cultivation and domestication in the Andes and Amazonia [14,15]. Across the Andes and Amazonia, evidence of human occupation becomes more frequent in the last several thousand years [16,17]. In the centuries before European arrival, major cultures such as the Tiwanaku (*ca* 550–1000 Common Era (CE), [18]), Wari (*ca* 650–1000 CE, [18]), Chachapoya (*ca* 1000–1470 CE, [19]) and Inca (*ca* 1000–1572 CE, [20]) extended across portions of the Tropical Andes. Many of these cultures had their centres in the highlands, i.e. above *ca* 3400 m elevation, but distributions that reached down into the humid montane forest (3400–1401 m a.s.l.; electronic supplementary material, figure S1). Meanwhile, lowland cultures exerted their influence upslope into the humid montane forests [21]. Disease-induced mortality, enslavement and mistreatment caused a massive population collapse throughout South America between *ca* 1550 and 1650 CE [22]. Land abandoned during that population collapse allowed forests to regrow. Thus, some modern humid montane forests could have been completely cleared or modified as recently as 500–350 years ago. As such, the legacy of past forest disturbance expressed in successional change may still be influencing forest structure and composition, species abundances and carbon sequestration [23–25].

Conditions in these humid montane forests, such as light limitation [26], frequent cloud immersion and continuous high humidity [26], steep terrain [27] and poor soils [28], are seemingly hostile for human occupation [29]. Indeed, many areas show no obvious palaeoecological signs of human occupation [30], but the humid montane forests contain some areas of high settlement density, i.e. the mound settlements of the Upano valley, Ecuador [31,32]. In fact, some of the most iconic monumental sites of South America, i.e. Machu Picchu [33] and Kuelap [34] in Peru, lie within humid montane forests. Despite these harsh environments, the humid montane forests were important pre-Columbian cultural crossroads, and it is therefore likely that areas within the major valleys connecting the lowlands and highlands may have been occupational centres for millennia [21,35].

Adaptive strategies in humid systems were manifested as engineering and behavioural responses [36]. Deforestation would have led to soil erosion and altered hydrologies. An engineering response was to build terracing that retained soil and regulated waterflow [37,38]. Particularly in the lowlands, mound building lifted homes and cultivation fields out of marshy conditions [39]. Behavioural adaptations also included opportunism in which people moved in (during dry periods) or out (during wet periods) of humid montane forests in response to climate change [40].

Much of our knowledge of human technological and behavioural adaptation to adverse environments comes from archaeological sites. Archaeological databases, however, reflect incomplete sampling, and the distribution and impact of pre-Columbian people on humid montane forests is probably much larger than currently documented. Species distribution models (SDMs) are used to predict the distributions of species across regions when sampling is incomplete in ecological and biogeographical studies [41,42], and the approach has also been used to predict the distributions of past people across landscapes [16,43,44]. Here, we generate an ensemble of SDMs [45] using archaeological datasets and a suite of environmental parameters to predict the potential distribution of pre-Columbian people in the Tropical Andes. Specifically, we ask: (i) which regions are most likely to harbour undocumented archaeological sites?, (ii) were areas frequently immersed in cloud largely avoided? and (iii) which regions would provide both disturbed and undisturbed histories to assess patterns of species composition and forest dynamics in ecological surveys?

2. Methods

(a) Study region

Our study region includes Andean areas that are between 700 and 6200 m a.s.l.), on the east side of the continental divide (the eastern Andean flank), and located in the modern countries of Bolivia, Peru and Ecuador (figure 1). Andean montane forests included in this study typically receive *ca* 2000–6000 mm of annual precipitation ([46,47], https://chelsa-climate.org/). Even in the driest quarter of the year, precipitation can reach up to *ca* 1180 mm. Many areas experience a mean annual cloud frequency greater than 90%, creating the distinctive, cloud-soaked forest ([48]; electronic supplementary material, figure S2). Humid montane forests sit on topographically heterogeneous landscapes, often on slopes up to 60° ([46,47], https://chelsa-climate.org/; electronic supplementary material, figure S2). However, the topographic complexity of the Andes creates much variability in rainfall and mean annual cloud frequency, and some valleys, typically in rain shadows, receive little precipitation and cloud cover. The mean annual temperature ranges from *ca* −6°C to 26°C and is strongly related to elevation ([46,47], https://chelsa-climate.org/).

(b) Archaeological data

We compiled the locations of 21 199 pre-Columbian archaeological sites within the study region from published literature (see electronic supplementary material for full list), from the Radiocarbon Database for Central Andes (https://andesc14.pl/en/, accessed July 2016) and from the Sistema de Información Geográfica de Arqueología database (http://sigda.cultura.gob.pe/index.php, accessed May 2020). Archaeological sites were designated as pre-Columbian if they were used by humans in any capacity prior to European contact (*ca* 1588 CE). The dataset includes archaeological sites that dated before European contact but were still occupied by pre-Columbian humans during European conquest. Archaeological sites that had not been radiocarbon dated but were published as being used by humans prior to European contact were also

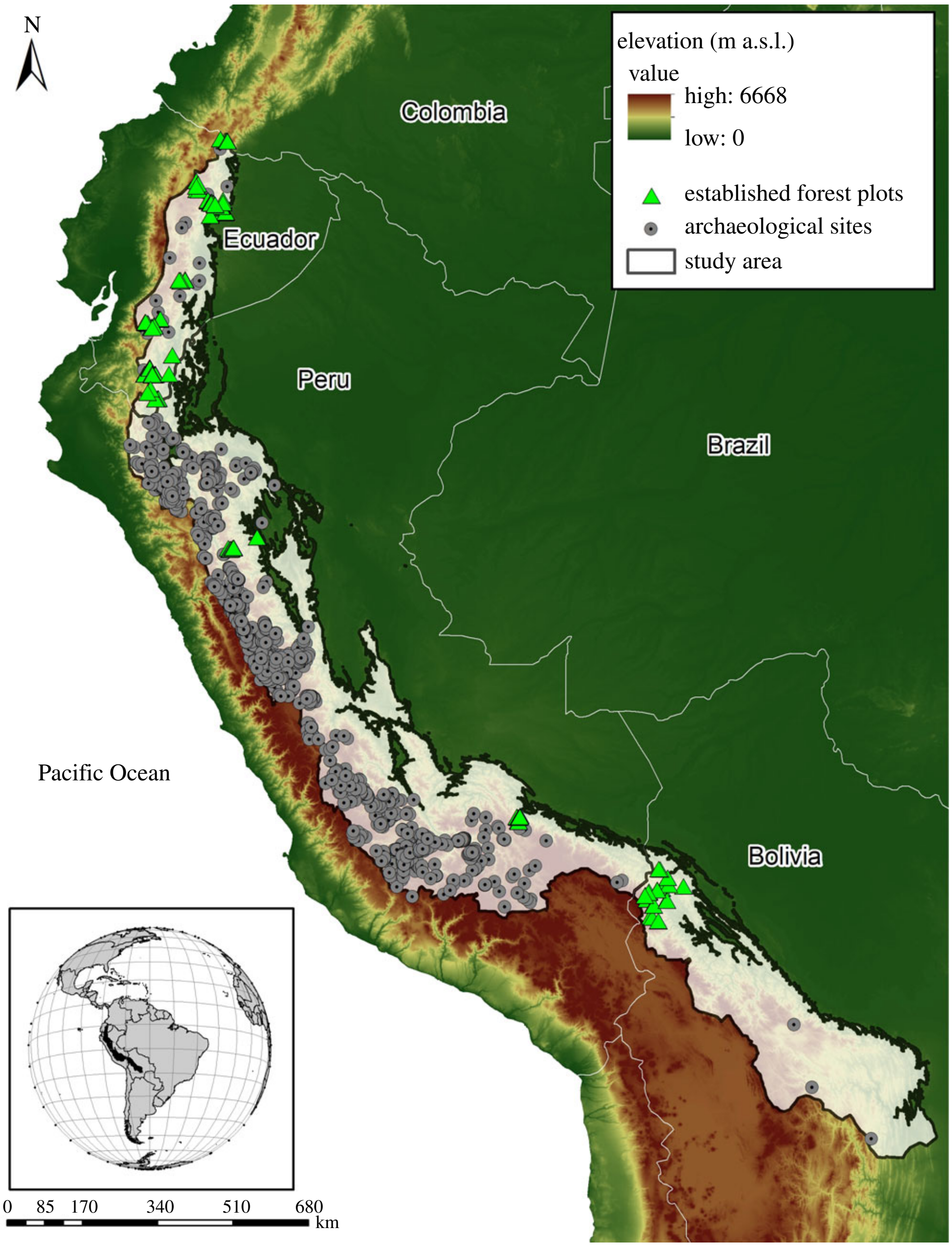

Figure 1. Study region of the Tropical Andes, outlined in black and coloured white. The circles are known archaeological sites used to create the ensemble SDM ($N = 1965$). Established Andean forest plots ($N = 351$) are shown by triangles. (Online version in colour.)

included as pre-Columbian sites. To reduce the effect of spatially collinear occurrence points, the archaeological site locations were geographically filtered at 1 km resolution, so that only one point fell within any 1 km^2 grid cell within the study region. A 1 km^2 cell size was chosen because all the environmental variables were compiled at that resolution (see below). Additionally, any error associated with the coordinates of the archaeological sites should be within 1 km. After geographical filtering, 1965 occurrence points were retained and used in the ensemble SDM (electronic supplementary material, table S1).

(c) Environmental variables

We compiled a total of 27 environmental variables for the Tropical Andes for consideration in the SDMs (electronic supplementary material, figure S2 and table S2). For the environmental variables, we used 1 km^2 resolution because that is the highest resolution available for the climatic datasets. All environmental variables had to be resampled accordingly. A cross-correlation analysis was used to identify and eliminate correlated variables (electronic supplementary material, table S3, [49]). The cross-correlation extracted the value of every environmental variable in every grid cell and ran a Pearson's correlation using these values ($N = 5\,210\,024$, i.e. the number of cells in each raster). When variable pairs had a Pearson's correlation coefficient greater than 0.75, one of the variables was eliminated from the analysis. We retained the variables that we hypothesized would have had the greatest impact on occupation patterns based on previous literature and analyses of Amazonian systems [16,43,50]. Seven environmental variables were included in the SDM: elevation, mean annual cloud frequency, precipitation of the driest quarter, slope, aspect, topographic position index (TPI) and distance to river (table 1). Mean annual cloud frequency, slope, aspect and TPI have not been used in previous studies but were included because of their importance in determining suitable crop cultivation areas, which are linked to light availability and humidity.

(d) Ensemble species distribution models

We generated an ensemble of SDMs on our archaeological and environmental datasets using several algorithms: general additive models (GAMs), random forest (RF) models and Maxent models (Maxent) [41,54,55]. Sufficient true absence data, or sampled locations where archaeological sites were not

Table 1. Environmental variables used in the final ensemble species distribution model for modelling the likelihood of pre-Columbian human occupancy on the eastern Andean flank.

environmental variable	definition	unit	resolution	source
elevation	location in metres above sea level	metres (m)	1 km	digital elevation model (DEM) derived from: NASA/NGA shuttle radar topography mission (http://srtm.csi.cgiar.org/)
aspect	the direction an area faces; calculated using the Horn [51] setting in the *raster* package [52]	degrees (°)	1 km	calculated from the DEM
slope	the steepness of an area; calculated using the Horn [51] setting in the *raster* package [52]	degrees (°)	1 km	calculated from the DEM
topographic position index (TPI)	the difference of the elevation of a cell and the mean elevation of the eight surrounding cells [53]	metres (m)	1 km	calculated from the DEM
precipitation of the driest quarter (bio17)	three consecutive driest months of the year based on monthly mean precipitation amounts (AD 1970–2013)	millimetres per quarter (mm per quarter)	1 km	CHELSA [46,47] (https://chelsa-climate.org/)
distance to river	distance to the nearest river (upstream drainage area >16.2 km^2 or 2000 upcell value) calculated using Euclidean distance	metres (m)	1 km	hydrosheds 'rivers' dataset (https://www.hydrosheds.org/)
mean annual cloud frequency	per cent of a year that a 1 km area is covered in clouds, calculated from 2000 to 2014	mean annual per cent (%)	1 km	MODIS data (http://www.earthenv.org/cloud)

found, are lacking because archaeologists rarely report when a location did not yield an archaeological finding. Given the lack of true absence data, we generated 1965 pseudo-absence points, a number equal to observed datapoints, from within our study area [56,57]. The SDMs were run five times using five-fold cross-validation techniques for each algorithm. We assessed the performance of each model using area under the receiver operating characteristic curve (AUC) scores [48,58]. Individual SDMs were retained as an input for the ensemble model only if the AUC value exceeded 0.65 [16]. Each individual SDM was run five times, and the AUC value was used to weight the individual algorithms within the ensemble distribution model. The output of the ensemble model was based on the weighted averages of the weighted individual SDM algorithms, and outputs were generated on a probability scale of 0 to 1. Probabilities were converted to binary predictions using a threshold value that maximized sensitivity (true positive rates) and specificity (true negative rates, [59]). The ensemble model also produced uncertainty values, which showed the differences between individual models within the ensemble model across the study region. The importance of the environmental predictors used in the model was also evaluated. All analyses and visual outputs were created in R (v. 4.0.3, [60]).

From the results of our final ensemble SDM, we extracted the likelihood of pre-Columbian human occupation at all of the existing Andean forest plots in our study region ($N = 351$, electronic supplementary material, figure S3) from the Andes Biodiversity and Ecosystems Research Group (ABERG, http://www.andesconservation.org/), the Consortium for the Sustainable Development of the Andean Ecoregion (CONDESAN, [61]) and the Amazon Forest Inventory Network (RAINFOR, [62]). Forest plots were binned by likelihoods of 0.05, and a histogram was created of the likelihoods of pre-Columbian human occupancy in the forest plots.

3. Results

All three algorithms (GAM, RF model, Maxent) used to model the potential distribution of past people in our study region generated robust models with AUC scores exceeding 0.75 (table 2) and were included in the ensemble SDM (figure 2*a*). The proportion of sites correctly classified based on the five-fold cross-validation ranged from 0.78 to 0.82 for the GAM, RF and Maxent models (table 2). The ensemble model had an AUC of 0.798, and the five-fold cross-validation indicated that the ensemble model predicted 79.8% of the sites correctly (table 2). The ensemble model indicated that 11.04% of the total study region likely contained pre-Columbian human occupation (figure 2*b* and table 2) when the threshold that maximized the per cent correctly classified (0.546) was applied to the modelled probabilities (figure 2*a*). Because all three of the individual SDMs were highly correlated with each other (table 2), the uncertainty of the

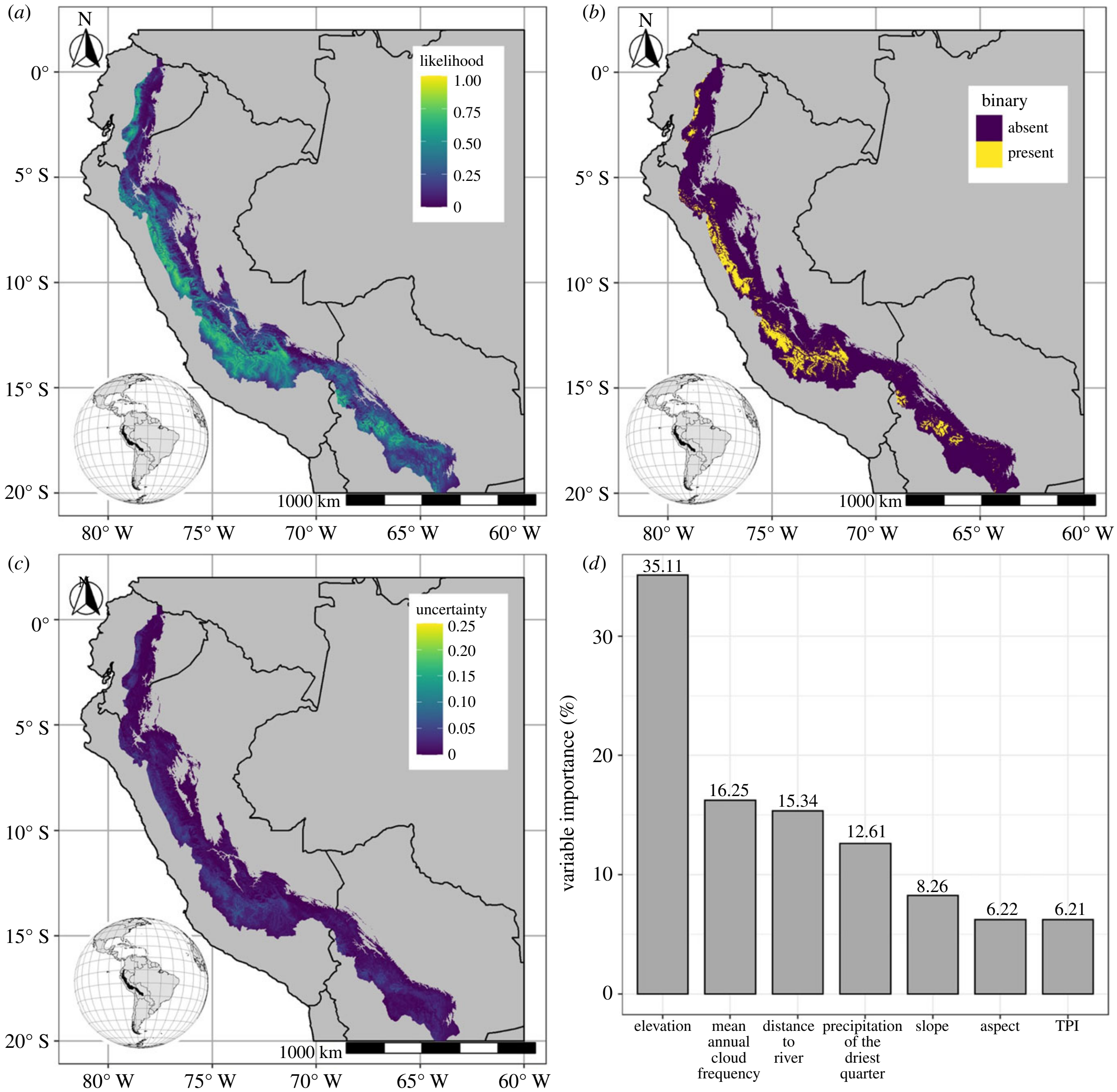

Figure 2. (*a*) Ensemble species distribution model predicting the likelihood of pre-Columbian human occupation. (*b*) Binary output of the ensemble species distribution model after applying the maximum sensitivity plus specificity threshold of the ensemble model (0.546). (*c*) Uncertainty of the ensemble species distribution model. (*d*) Importance of the variables in the ensemble species distribution model as defined through Pearson's correlation. (Online version in colour.)

Table 2. Various assessments of individual species distribution models and the ensemble species distribution model.

model	AUC	threshold for binary	area of potential distribution (km^2)	proportion correctly predicted	correlation with GAM	correlation with RF	correlation with Maxent
generalized additive model (GAM)	0.783	0.554	65 368 (10.43%)	0.783	1	0.849	0.909
random forest (RF)	0.823	0.526	79 658 (12.71%)	0.823	0.849	1	0.886
Maxent	0.787	0.559	62 861 (10.03%)	0.787	0.909	0.886	1
ensemble	0.798	0.546	69 174 (11.04%)	0.798	n.a.	n.a.	n.a.

ensemble model never exceeded 0.23, with the highest uncertainty of the ensemble model occurring in central Peru (figure 2*c*).

The importance of each environmental variable to the ensemble SDM was evaluated using a Pearson's correlation. Elevation and mean annual cloud frequency were the most

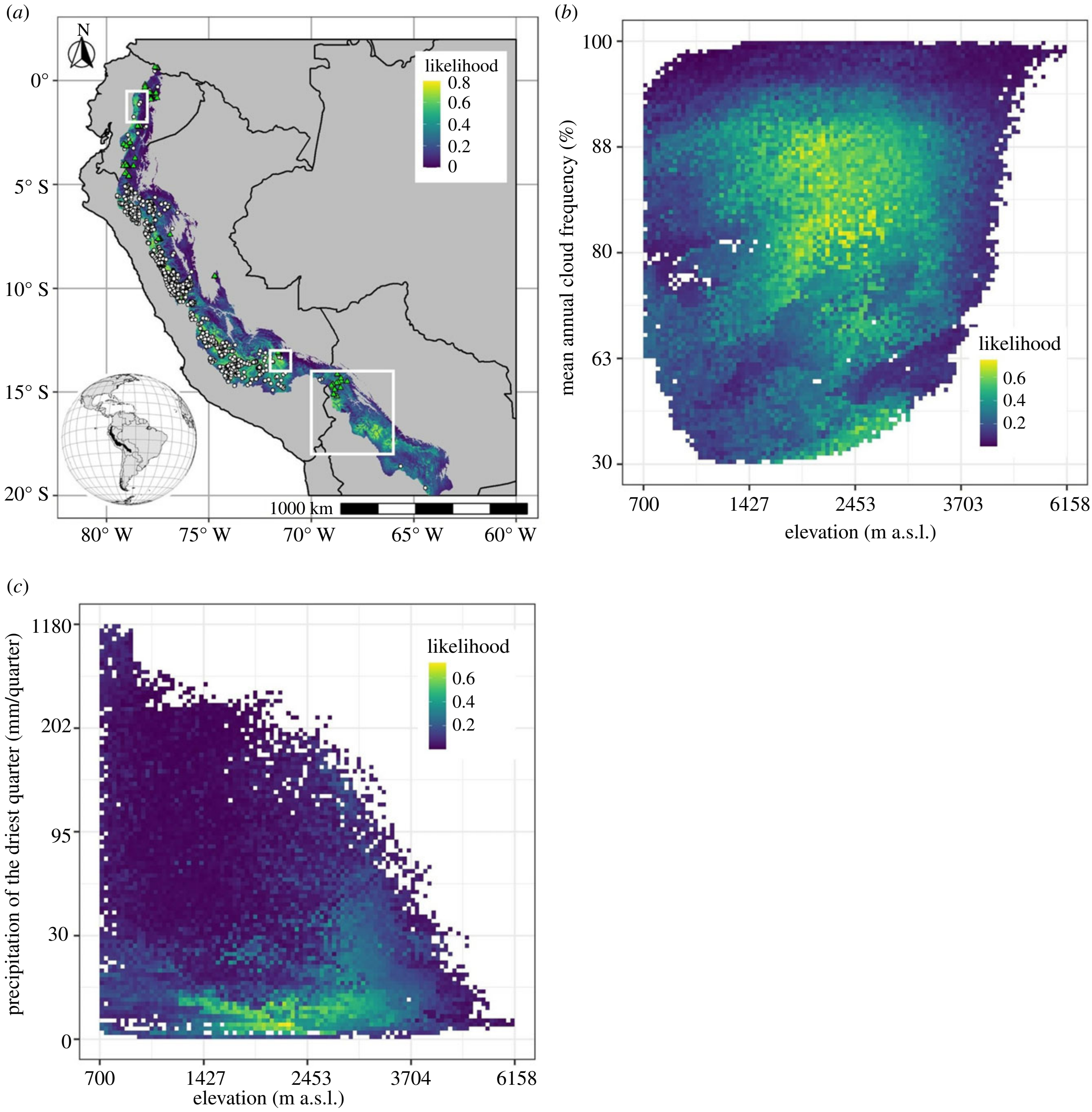

Figure 3. (*a*) Possible areas for new archaeological and palaeoecological studies are shown in the white-outlined box. The circles show known archaeological sites used to create the ensemble distribution model. Established Andean forest plots are shown by triangles. (*b*) Likelihood of pre-Columbian human occupation across elevation and mean annual cloud frequency. (*c*) Likelihood of pre-Columbian human occupation across elevation and precipitation of the driest quarter.

significant predictor variables in the ensemble SDM, with a permutation importance of 35.11 and 16.25%, respectively (figure 2*d*). Hereafter, we will be referring to the results only of the ensemble SDM instead of the individual algorithms used to create it. The likelihood of occupation generally increased as elevation increased until *ca* 4000 m a.s.l. (figure 3*b*; electronic supplementary material, figure S4). Areas with a mean annual cloud frequency greater than 90% had a lower likelihood of occupation than areas with a mean annual cloud frequency less than 90% (electronic supplementary material, figure S4). Distance to river and precipitation of the driest quarter also had permutation importance values exceeding 10% (figure 2*d*). The likelihood of human occupation decreased as the distance to major river and precipitation of the driest quarter increased (figure 3*a*; electronic supplementary material, figure S4). Slope, aspect and TPI had permutation importance values less than 9%. Likelihoods of pre-Columbian human occupation at the forest plots ranged from 0.007 to 0.58. Based on the ensemble SDM binary threshold of 0.546, only one of the 351 forest plots was highly likely to have been occupied by pre-Columbian humans before European arrival (table 2).

4. Discussion

(a) Spatial heterogeneity of pre-Columbian people on the eastern Andean flank

The ensemble SDM (AUC = 0.798) indicated that environmental variables hold (statistically) significant predictive power over pre-Columbian human occupation of the eastern flank of the Tropical Andes (figure 2 and table 1). Elevation was shown to be the most important predictor of where humans chose to live (figure 2*d*). The optimum likelihood of occupation between 2300 and 3500 m a.s.l. (figure 3*b*) may reflect that people wanted to live near the boundary between humid montane forest and high elevation grasslands. This elevation range would provide access to both sets of resources, such as vicuña, alpaca, white-tailed deer and taruca in the highlands [63]. Areas between 2300 and 3500 m a.s.l. also probably offered benefits of lower disease and parasite probability than low and mid-elevations, higher light availability than mid-elevations and favourable conditions for growing crops such as quinoa, manioc, rice and potato compared with both lower and higher regions of the Tropical Andes [14,64].

Mean annual cloud frequency and precipitation of the driest quarter were factors that influence the formation of low-lying, characteristic clouds of the Andean humid montane forests [65,66]. People likely preferred settings that, although moist, had a pronounced reduction in precipitation during the dry season and were as cloud-free as possible (electronic supplementary material, figure S4; figure 3*b*,*c*). Our model suggests that areas just outside the humid montane forest, in sunnier areas of the Andes, were more likely to be occupied than areas within the forests (figures 2*a*, 3*b*). Locations near the upper limit of the forest, which may have become drier during past decadal droughts, may have been more likely to be occupied than locations far from forest limits, which would likely have been too moist for human occupation even during decadal droughts. Even slightly seasonally drier areas would increase the amount and variety of crops, as supported by the domestication of roots and tubers, which occurred in seasonally dry areas of the Andes [64].

There have been changes in moisture, however, during the Holocene, which would have impacted the position of the low-lying cloud in Andean humid montane forests [67,68]. Our model shows that mean annual cloud frequency influenced pre-Columbian human distributions, and so understanding changes in mean annual cloud frequency is critical (figure 2*d*). Some shift in the base of the low-lying cloud is expected to have occurred throughout the Holocene. For example, fossil pollen data from Lake Palotoa suggest a downslope movement of lower montane forest taxa at *ca* 200 calibrated years before present (hereafter cal yr BP), meaning that the upper limit of the cloud probably moved upslope about 100–200 m [30]. Fossil pollen data from Lake Condores suggest an upslope shift in the cloud base at *ca* 850 cal yr BP [40]. Neither lake shows an absence of cloud though, and the shifts in the cloud base are within the margin of error of our environmental data (i.e. ±1 km, or the resolution of our environmental variables). Although changes in mean annual cloud frequency are undoubtably important for pre-Columbian human occupation [40,69], current mean annual cloud frequency and precipitation data are the best modelled and highest-resolution estimates we have for detecting the presence of the Andean low-lying cloud. Future studies should work to improve our understanding of how the mean annual cloud frequency and precipitation in the Andes has changed throughout the Holocene.

Distance to river is another important variable in the ensemble model (figure 2*d*). For pre-Columbian people, it would have been advantageous to settle close to a river. In the Tropical Andes, distance to river serves as a proxy for proximity to a valley because Andean valleys are formed by rivers. The rivers themselves are probably less important than their valleys and adjacent ridges, which formed important trade routes [70,71]. The idea of rivers as corridors for easy transportation and communication has been suggested in Amazonia [72] and shown to be significant in predicting anthropogenic soils [43]. In the Andes, valleys are known to have been important trade routes for fish, salt, feathers, shells and obsidian [38,70] that connected the lowlands to the highlands. Occupancy of these valleys may also have benefitted from fertile alluvial soils deposited by the rivers [73].

Our model highlights the spatial heterogeneity of the potential distribution of pre-Columbian people in the eastern flank of the Tropical Andes (figure 2*a*) and the environmental characteristics most responsible for shaping those patterns (figure 3*a*,*b*). The interrelationships of these environmental characteristics and the probability of human occupation may be useful to target areas for future archaeological surveys and site conservation in currently unsampled or undersampled areas (figure 3*c*). Our analysis shows that large unsampled areas of northern Bolivia (figure 3*c*) have a likelihood of pre-Columbian occupation greater than 75%, particularly in the areas between 2300 and 3500 m a.s.l., where cloud immersion lasts just 30–45% of the year (figure 3*b*). Other potential areas for study are in southern Peru and central Ecuador (figure 3*c*), with characteristics of 2300 and 3500 m a.s.l., where cloud immersion is between 80 and 88% of the year, but the sites exhibit strong dry seasons (figure 3*a*,*b*). Finding new archaeological sites over such a vast area is demanding, especially over forested land and steep terrain such as the eastern Andean flank. Technological advances such as light detection and ranging (LIDAR) and drone photography have helped locate pre-Columbian archaeological sites in Amazonia [74], but these methods can be costly depending on the terrain and area surveyed and are difficult in some mountainous terrain [75]. Most LIDAR surveys also encompass relatively small geographical areas because LIDAR requires an airborne platform with a laser attached to be flown over the area of interest, whereas our model can be used over larger geographical scales and could refine search areas for the more expensive methodologies.

(b) Potential ecological legacies in biodiversity hotspots

The humid montane forests, typically located from 1400 to 3400 m a.s.l. in the Tropical Andes, are some of the most unique and biodiverse forests in the world [4,76]. Humboldt and other early explorers considered much of these humid montane forests to be a vast wilderness, largely untouched by humans [2], but subsequent archaeological surveys and palaeoecological analyses have shown otherwise (e.g. [69,77,78]). Several palaeoecological records show that human activities, including the use of fire in non-adapted wet forests, likely played a strong role in the extinction of the Pleistocene megafauna in Andean systems [79,80]. If megafauna were important to ecosystem structure and function, their extinction probably initiated ecological cascades (legacy effects) that persist until modern times [81,82].

In terms of the strength of legacy effects on modern forests, the intensity, duration and recentness of disturbances will influence residual effects. The loss of a seed disperser is probably less likely to exert a profound influence than repeated burning of a non-fire-adapted system [83]. Similarly, disturbances that lasted for millennia, only ending as Europeans occupied the landscape, are more likely to shape

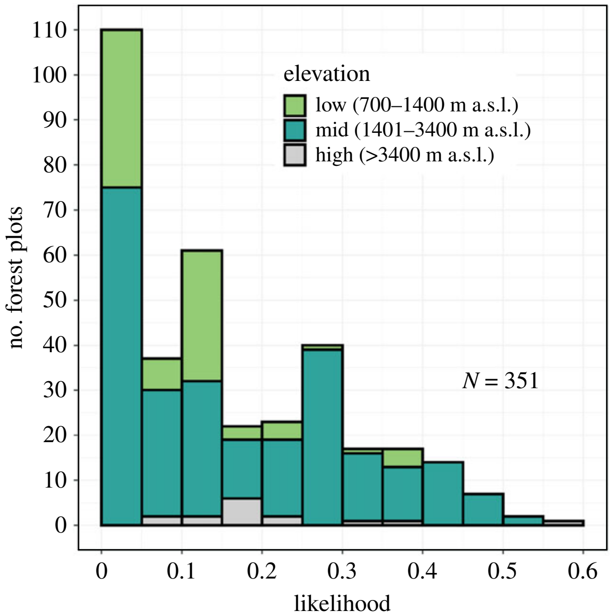

Figure 4. Likelihood of pre-Columbian occupation in existing forest plots ($N = 351$) in the Andes. (Online version in colour.)

modern ecologies than the ephemeral use of a location in the distant past [84]. Our ensemble SDM does not contain a time parameter (see electronic supplementary material for more detail), but the identification of favourable sites is likely to also predict overlap of occupation from one time to another [16]. Thus, sites that we identify as having high probabilities of human occupation are also likely to have long, although not necessarily continuous, histories of use. Likewise, areas with lower probability of human occupation are also likely to have less intense, or more ephemeral, pre-Columbian human impacts. Despite not having a time parameter, our ensemble SDM performed well (table 2), and we suggest that it be used to inform future studies.

Most ecological knowledge of Andean forests are obtained from forest inventory networks, such as ABERG, CONDESAN and RAINFOR. Our analyses suggest that 30 of 351 (8.5%) of these forest plots are in ideal settings according to our model; that is, they are between 2300 and 3500 m a.s.l. and have a mean annual cloud frequency between 80–88% (figure 4; electronic supplementary material, figure S5). If only the subset of forest plots that lie between 2300 and 3500 m a.s.l. is considered, the proportion of forest plots with a mean annual cloud frequency between 80 and 88% and are thus likely to have been occupied by pre-Columbian people, increases to 25% (figures 3 and 4; electronic supplementary material, figure S5). The binary output of our ensemble SDM indicates that only one forest plot was likely occupied by pre-Columbian people (PN Río Abiseo from CONDESAN), indicating that this one forest plot was likely intensely occupied for a long period of time, while other forest plots likely had less pre-Columbian human influence or were used intermittently.

Our model does not predict a uniform probability of legacy effects being evident in the eastern Andean flank, and at this stage, we do not advocate that the Andean flank should be discussed as a manufactured landscape, that is, a landscape transformed by human disturbance (*sensu* [85]), which has been suggested for the high Andean grasslands [85] and the Amazonian lowlands [86,87]. Rather, particularly dry and seasonal habitat types, especially near the modern upper forest line, are more likely to have legacy effects, and ecological studies in such regions should carefully assess the forest for signs of past use, i.e. soil charcoal, fallen structures, or ceramics (figure 4). Equally, although nowhere can be categorically predicted as 'not used', areas between 700 and 1400 m a.s.l. on steep slopes with frequent cloud immersion are the least likely to have been altered by human actions (figures 2*a* and 3). Future studies should focus on determining how changes in human cultural practices shaped forest dynamics through time, which our ensemble SDM does not address. For example, mobile foragers and cultivators would have had a much different impact on humid montane forests compared with agriculturalists.

5. Conclusion

We built an ensemble SDM showing that environmental variables hold significant predictive power over the spatial distribution of pre-Columbian people in the Tropical Andean landscape. Our model showed that elevation, mean annual cloud frequency and distance to river are all highly related to pre-Columbian settlements and that people tended to avoid cloud-soaked environments. Our potential distribution of pre-Columbian humans extended beyond known archaeological sites, demonstrating that ecological legacies in Tropical Andean landscapes could be significant in more locations than currently documented. Around 25% of forest plots established at 2300–3500 m a.s.l. are likely still recovering from pre-Columbian human impacts because of their ideal environmental conditions, and their legacies may be impacting our understanding of modern Andean ecology. Nevertheless, many areas of the eastern Andean flank are unlikely to support former occupation, and we do not support an all-encompassing assessment of the eastern Andean flank as a manufactured landscape. Lower mid-elevation slopes in wet areas away from major valley systems are most likely to have not been impacted by human activity. Our model is intended as a tool that archaeologists may choose to use while investigating Tropical Andean landscapes and for ecologists in assessing the likelihood that they will encounter ecological legacies in their study areas.

Data accessibility. R code for generating the ensemble SDM and the associated data are available on Zenodo: https://doi.org/10.5281/zenodo.5784334.

Authors' contributions. R.K.S. combined the archaeological data, collected and edited the environmental data, ran all the analyses, created all the figures, and wrote and edited the text. M.B.B. and C.N.H.M. contributed ideas, suggested figure edits, and wrote and edited the text. C.N.H.M. advised on analyses. S.G.A.F., K.H., J.R.Z., C.G.-A. and W.B.C. contributed archaeological data, advised on ideas, and wrote and edited the text.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

Competing interests. We declare we have no competing interests.

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