

Uncovering spatial patterns in the natural and human history of Brazil nut (*Bertholletia excelsa*) across the Amazon Basin

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ABSTRACT

Aim Our goal was to test the hypothesis that ancient humans substantially contributed to shaping the current distribution of Brazil nut (*Bertholletia excelsa*), an Amazonian tree species that has been important for human livelihoods since pre-Columbian times. We scrutinized the putative association between Brazil nut and Amazonian Dark Earth soils (ADE) and geometric earthworks called geoglyphs, and examined the existence of continental patterns in human footprints on Brazil nut stands.

Location Amazon Basin.

Methods We carried out a spatially explicit meta-analysis of the variation of Brazil nut stand metrics across the Amazon Basin based on 87,617 density estimates and 488 average stand diameter assessments, and related these to previously published datasets and suitability maps of Brazil nut, ADE and geoglyphs.

Results We found consistently higher Brazil nut suitability scores, stand densities and average stand diameters in the vicinities of ADE than at larger distances, regardless of their position along a gradient from south-western to north-eastern Amazonia. For geoglyph sites such a pattern was only found for Brazil nut habitat suitability scores. The available data further revealed an accumulation of Brazil nut stands with increasing densities and average diameters from south-western to central and eastern Amazonia.

Main conclusions Our findings suggest that the chance of encountering Brazil nut stands bearing the marks of past human influences increases from south-western to central and eastern Amazonia. In south-western Amazonia, the regeneration of Brazil nut seems to have been controlled predominantly by natural processes, whereas in central and eastern Amazonia, anthropogenic disturbance has been more important since pre-Columbian times. However, it remains challenging to disentangle human influences on the distribution and abundance of Brazil nut from existing environmental gradients across the Amazon Basin. In general, the results of this meta-analysis bode well for the future coexistence of Brazil nut with different forms of contemporary human land use.

Keywords

Amazonian Dark Earth soils, Brazil nut, disturbance, genetic diversity, geoglyphs, historical ecology, megafauna, palaeodistribution, seed dispersal anachronism, *terra preta*.

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INTRODUCTION

Brazil nut (*Bertholletia excelsa* Bonpl., Lecythidaceae) has been important for human livelihoods since the peopling of the Amazon Basin. The first documented evidence of human use of Brazil nut seeds dates back more than 11,000 years (Roosevelt *et al.*, 1996), and today it is the only internationally traded nut species predominantly harvested from natural populations (Wadt *et al.*, 2008). As a consequence of the longstanding human interest in Brazil nut, its current distribution and patterns therein are most likely to be a reflection of a complex intertwining of ecological and human-influenced processes. Despite recent assessments of the influence of existing environmental gradients across the Amazon Basin on the distribution and demography of tree communities (Gentry, 1988; Phillips *et al.*, 2004; ter Steege *et al.*, 2006, 2013; Quesada *et al.*, 2012), relatively few studies have been conducted at the species level, and to date surprisingly little is known about how such gradients may have contributed to shaping distribution patterns in Brazil nut. Similarly, there is growing evidence from different disciplines, such as forest ecology, palaeoecology, population genetics, anthropology, ethnobotany, linguistics and archaeology, that humans contributed substantially to shaping the current distribution of Brazil nut across the Amazon (Kanashiro *et al.*, 1997; Scoles & Gribel, 2011, 2012; Shepard & Ramirez, 2011; Balée, 2013; Ribeiro *et al.*, 2014; Thomas *et al.*, 2014a). Our main purpose here was to assess the spatial distribution and intensity of human influences on Brazil nut that may have been superimposed on past and ongoing natural processes ever since the arrival of humans to Amazonia. More specifically, we investigated spatial patterns in the clues of anthropogenic influences on Brazil nut commonly identified in the literature.

Shepard & Ramirez (2011) presented numerous examples of associations between pre-Columbian human land-use activities and present-day occurrence of Brazil nut. It has, for example, been hypothesized that the probability of encountering Brazil nut in the vicinities of *terra preta* or Amazonian Dark Earth soils (ADE), and geoglyphs would be higher than predicted by chance (e.g. Balée, 1989, 2013; Clement & Junqueira, 2010; Levis *et al.*, 2012). Created 3000–500 years ago (Neves *et al.*, 2004), ADE are fertile anthropogenic soils rich in charcoal, and organic and inorganic human waste (Glaser & Birk, 2012). They are a legacy of the emergence of sedentary life-styles in Amazonia that were initiated some 4000–3000 years ago, when food production systems became the major sources of subsistence (Piperno & Pearsall, 1998). Based on currently available survey data, ADE are quite common in the Brazilian Amazon but much less so in western and especially in south-western Amazonia, where geoglyphs appear to be the dominant vestiges of ancient human occupation (Schaan *et al.*, 2012; McMichael *et al.*, 2014a). Geoglyphs are geometrically shaped earthworks consisting of a flat centre and surrounding ditch, ranging from 0.1 to 10 ha in area (Saunaluoma & Schaan, 2012). If it is true that the

occurrence of anthropogenic Brazil nut stands is correlated with prehistoric human activities, then the currently observable human influences on the distribution and demography of Brazil nut stands should be more pronounced in the vicinities of these sites.

Other indications of the possibility of human influences on the distribution patterns of Brazil nut are believed to be apparent in demographic profiles observed at different sites across the Amazon Basin. In central and eastern Amazonia, it is common to find relatively clustered Brazil nut groves with densities ranging from 10 to 20 trees (≥ 10 cm d.b.h.) per hectare, interspersed with vast areas of forest (literally up to thousands of hectares) with little to no Brazil nut trees (Mori & Prance, 1990; Peres & Baidier, 1997; Salomão, 2009; Scoles & Gribel, 2011; Shepard & Ramirez, 2011; Guedes *et al.*, 2014). In south-western Amazonia such a clustered spatial pattern seems to be largely absent (Wadt *et al.*, 2005), or at least has a much reduced salience. Instead, Brazil nut has a more continuous distribution there, and the maxima of tree densities are lower (Zuidema & Boot, 2002; Zuidema, 2003; Wadt *et al.*, 2005; Licona Vasquez *et al.*, 2010). We speculate that a more even distribution at the landscape level is associated more with natural dispersal processes, while the clumped distribution described above is related more to human-influenced dispersal.

The diameter distribution of Brazil nut stands has also been thought to contain information about past human influences. Most demographic studies of Brazil nut populations across the Amazon Basin have reported a preponderance of trees in intermediate size classes (80 cm < d.b.h. < 160 cm; e.g. Viana *et al.*, 1998; Zuidema & Boot, 2002; Peres *et al.*, 2003; Zuidema, 2003; Wadt *et al.*, 2005, 2008; Salomão, 2009; Licona Vasquez *et al.*, 2010; Scoles & Gribel, 2011, 2012). Both natural and human factors have been proposed to explain this hump-shaped distribution. First, experimental research has shown that diameter growth in Brazil nut peaks in the smaller diameter classes (30–60 cm d.b.h.) and then exponentially decreases for larger size classes (Zuidema & Boot, 2002; Zuidema, 2003). The latter authors argued that the fact that trees grow faster through the smaller diameter classes could result in an accumulation of trees in intermediate size classes, while the lower abundance of very large trees would be due to a higher degree of mortality. Second, it has been argued that effective seedling recruitment and regeneration in mature forest may depend on less frequent storm-induced events causing large-scale canopy disturbance that would lead to even-aged cohorts of trees (Peres & Baidier, 1997). A third explanation relates the high abundance of intermediate size classes to gap creation activities by humans, whereby regeneration of Brazil nut in fallows would lead to more or less even-aged tree stands (Mori & Prance, 1990; Paiva *et al.*, 2011; Scoles & Gribel, 2011). Given that trees with a d.b.h. of 100–150 cm are roughly between 300 and 500 (≥ 650) years old (Vieira *et al.*, 2005; Scoles & Gribel, 2011), it is likely that many of the trees in intermediate size categories in Brazil nut stands

across the Amazon Basin were established in the period from just before until the first centuries after the beginning of European colonization of Amazonia (Salomão, 2009; Scoles, 2011). During the first two centuries after contact, native Amazonian populations were reduced by 90–95%, principally as a result of devastating European diseases to which indigenous people lacked tolerance (Dobyns, 1966). The collapse of the indigenous population coincides with a decline in indigenous fires in the Neotropics after 1492, which is apparent in soil charcoal profiles (Dull *et al.*, 2010). The void observed in smaller diameter classes could thus be the consequence of the decimation of native Amazonian societies and the concomitant drop in anthropogenic forest clearing, and hence human-influenced Brazil nut regeneration (Scoles & Gribel, 2011).

To assess the validity of the abovementioned hypotheses regarding human influences on the contemporary distribution patterns of Brazil nut, here we aim to answer the following research questions.

1. Is the probability of encountering Brazil nut in the vicinity of ADE and geoglyph sites higher than at random sites in the overall species range?
2. Are the observed maxima of Brazil nut densities and average Brazil nut stand diameters in the vicinities of ADE and geoglyph sites higher than at random sites in the overall species range?
3. Can any geospatial pattern be detected in observations of the above parameters?

MATERIALS AND METHODS

Datasets

We used a rescaled version of a Brazil nut suitability map developed by Thomas *et al.* (2014a) at a resolution of 2.5 arc minutes (Fig. 1) as a proxy for the probability of encountering the species at any given site in the Amazon Basin. This suitability map was based on an ensemble of two distribution

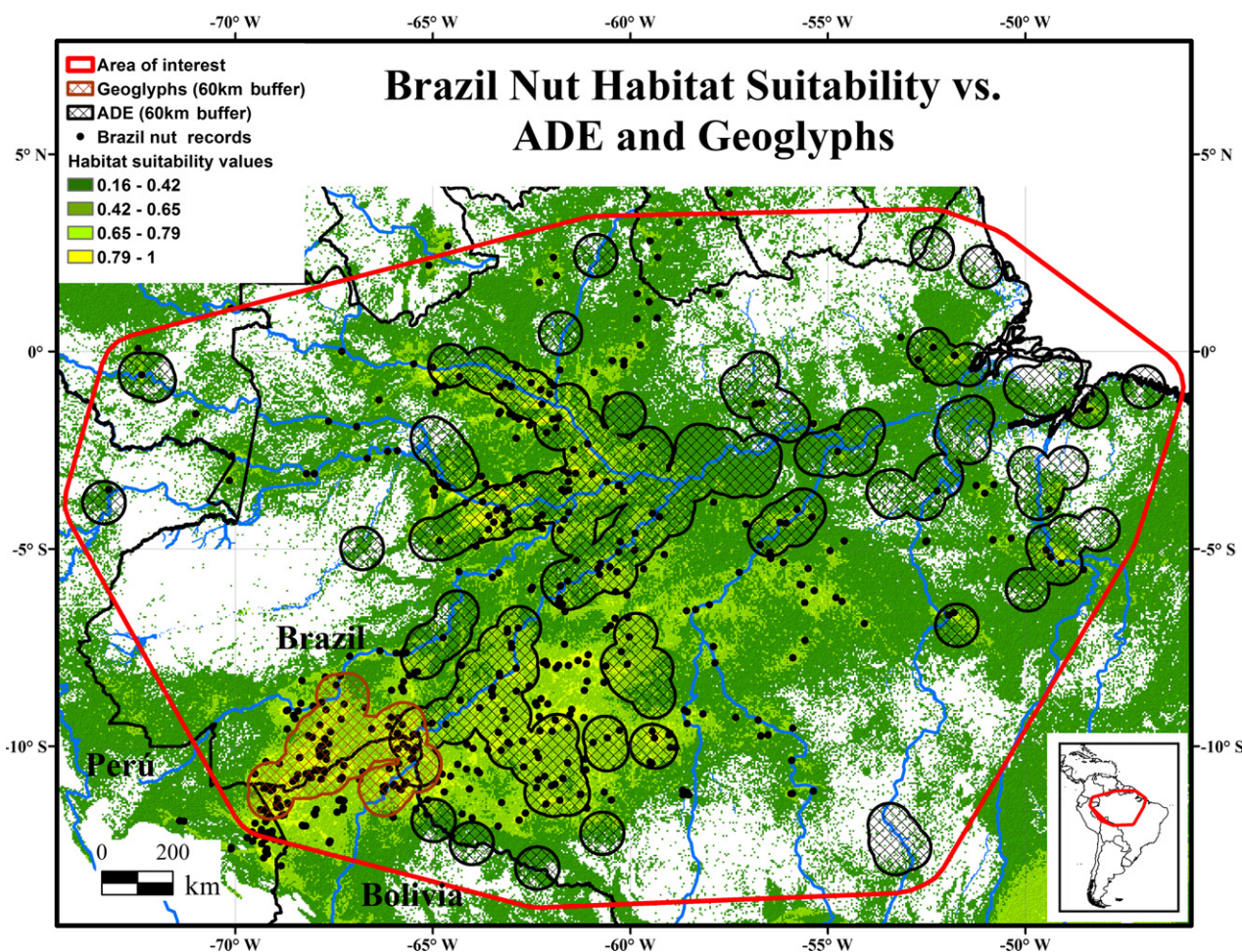


Figure 1 Habitat suitability of Brazil nut, compared with the locations of presence points (based on Thomas *et al.*, 2014a). The 0.16 threshold corresponds to the highest possible suitability score that ensures inclusion of all presence points in the modelled distribution area; the maximum training sensitivity plus specificity threshold corresponds with 0.42. The hatched areas represent buffer areas of 60-km radius around known Amazonian Dark Earth (ADE; black) and geoglyph (brown) sites, respectively. The red polygon represents a convex hull constructed around all ADE and geoglyph sites and extended with 1 arc degree.

modelling algorithms (boosted regression trees and random forests), generated from 936 Brazil nut observations from across the species' distribution range and a number of different environmental variables related to climate, soil, vegetation and physical landscape characteristics (see Appendix S1 in Supporting Information). We log-transformed and standardized the suitability scores to obtain a more even distribution of scores between 0 and 1. The lower threshold of the map shown in Fig. 1 was selected to include all Brazil nut presence points in the modelled distribution area, but for suitability comparisons we considered all possible suitability values between 0 and 1 (i.e. all the cells within the red polygon in Fig. 1).

Density and diameter (d.b.h. ≥ 10 cm) distribution data from Brazil nut stands across Amazonia were collected from a number of sources (see Appendix S2). A first source was published literature ($n = 154$ and 43 for density and diameter samples, respectively). To reduce issues of comparability related to disparities in sample sizes, sampling strategies and experimental designs (Zuidema, 2003; Scoles & Gribel, 2011), we aimed to include as many individual hectare-based density observations as possible. However, many publications only provide density values averaged over several (tens of) hectares, and occasionally report maximum density values observed. When available, we gave preference to density maxima over averages, based on the hypothesis that the upper limits of stand density are most representative of human influences. This hypothesis is supported by empirical evidence that Brazil nut regenerates much more effectively in swiddens and fallows than under natural forest conditions (higher survival rates, stronger growth and higher densities; Kainer *et al.*, 1998; Cotta *et al.*, 2008; Paiva *et al.*, 2011; Scoles *et al.*, 2011; Guedes *et al.*, 2014). For example, Paiva *et al.* (2011) measured the impact of repeated forest clearing for subsistence agriculture on Brazil nut regeneration in Amapá, eastern Amazonia, and found that densities increased from 9 to 14 and 27 trees ha^{-1} after one, two and three or more shifting cultivation cycles, respectively. In the absence of humans, Brazil nut's main animal dispersal agents – scatter-hoarding agouti (*Dasyprocta* spp.) and acouchi (*Myoprocta* spp.) rodents – are also likely to create an aggregated distribution pattern (Peres & Baider, 1997), but it is probable that under these conditions stand densities will fall short of the human-influenced maxima. Agoutis appear to direct seed dispersal towards areas with low conspecific tree density (Gálvez *et al.*, 2009; Hirsch *et al.*, 2012), whereas at sites with high conspecific tree density, recruitment does not seem to be influenced by dispersing activities of these rodents (Jansen *et al.*, 2014). Taken together, these findings suggest that the dispersal activities of scatter-hoarding rodents would not necessarily contribute to the formation of high-density stands, but rather promote a more even (low-density) distribution of the tree species whose seeds they disperse. Furthermore, as agoutis and acouchis occur throughout the distribution range of Brazil nut, continental patterns in the species' density distribution are likely to be attributable to

other factors, notably anthropogenic ones. We used average density only in cases where it was the only metric reported. As averages generally underestimate maximal stand densities, their inclusion can only dilute, rather than strengthen or overemphasize, potential patterns.

Similar reasoning applies for using average stand diameters. Senescing Brazil nut stands are expected to have higher average diameters compared with actively regenerating stands (either naturally or through ongoing human disturbance). On the assumption that a demographic shift towards higher diameter classes is associated with the decline of the indigenous population that followed the European colonization of the Amazon, higher average stand diameters are likely to be indicative of prehistoric human influence on Brazil nut stands (Scoles & Gribel, 2011). We only considered diameter estimates based on at least 20 tree individuals with d.b.h. ≥ 10 cm. Studies that explicitly related the regeneration of Brazil nut to either ongoing human forest disturbance or recent large-scale natural disturbance events (Appendix S2) were omitted from diameter comparisons as these would undesirably dilute the signal of historic human influence.

We complemented literature data with an extensive dataset from Madre de Dios, Peru. This dataset is composed of 135,715 georeferenced trees (115,162 with diameter data) from Brazil nut concessions and the data were originally collected by various institutions (Asociación para la Conservación de la Cuenca Amazónica (ACCA), Fondo de Promoción del Desarrollo Forestal, AIDER, Pro Naturaleza, Programa Regional de Manejo de Recursos Forestales y Fauna Silvestre, and Forestal Rio Piedras SAC) in response to the Peruvian Forest law no. 27308 of 2001. Projecting all trees on a map with approximately one hectare grid cells resulted in 87,436 density estimates of at least one tree per hectare. Estimates of average stand diameters were obtained in a similar manner by projecting tree occurrences onto a 1 arc-minute grid (approximately 400 ha at the equator) and retaining only cells containing at least 100 trees, which resulted in 452 data points.

To broaden the geographical scope of data, we also included RADAM data from Brazil in the density comparisons. These collections utilized a higher sampling threshold (d.b.h. ≥ 31.8 cm), and hence are underestimates of the d.b.h. ≥ 10 cm data. In principle their inclusion can only dilute potential patterns in a similar fashion as average densities; however, to reduce potential undesirable noise we only considered sites with more than five Brazil nut trees per hectare ($n = 27$, out of a total of 287 RADAM density estimates), in line with our argument above that the maxima of stand density are most representative of human influences.

Locations of ADE sites were obtained from WinklerPrins & Aldrich (2010), Levis *et al.* (2012) and McMichael *et al.* (2014a). Although the large majority of currently known ADE sites are located in central and eastern Amazonia, it cannot be ruled out that their under-representation in south-western Amazonia actually reflects lower survey

intensity when compared with central and eastern Amazonia. To partially account for this sampling bias, additionally we used the ADE modelled distribution developed by McMichael *et al.* (2014a), which predicts the probability of encountering ADE soils in areas not yet explored, based on the habitat characteristics of known ADE sites. However, as for any model, this map is likely to be influenced by the higher number of ADE sites from central and eastern Amazonia than from other regions, and hence may underestimate ADE suitability in areas where ADE sites have not been mapped. In spite of these limitations, both the georeferenced locations of ADE sites, and the modelled ADE distribution are the best proxies currently available for the true distribution of ADE across the Amazon Basin (see Fig. S1 in Appendix S3). Locations of geoglyph sites are based on Parssinen *et al.* (2009), Saunaluoma (2010, 2012), Schaan *et al.* (2012), McMichael *et al.* (2014b) and Geoglifos (<http://www.geoglifos.com.br/>). Additionally, we used a suitability map developed by McMichael *et al.* (2014b) to estimate the potential distribution of geoglyphs (see Fig. S2 in Appendix S3).

To visualize the spatial distribution of density and diameter data, we created maps at spatial resolution of 30 arc minutes (approximately 55 km at the equator) of the maxima per grid cell of observed Brazil nut stand density (Fig. 2) and average stem diameter (see Fig. S3 in Appendix S3). For the Madre de Dios area, more detailed maps were constructed at 2.5 arc-minutes resolution (approximately 4.6 km at the equator).

Data analysis

While soil signatures, such as potsherds, charcoal, ADE or crop phytoliths, provide unmistakable evidence of past human occupation, (pre)historic human alterations of the composition and density of useful species in the vegetation are known to persist many centuries after abandonment, for example relict vegetation of the Romans in France (Dambérine *et al.*, 2007), indigenous societies in eastern North America (Munoz *et al.*, 2014) and the Mayas in Belize (Ross, 2011). In eastern North America, indigenous silvicultural

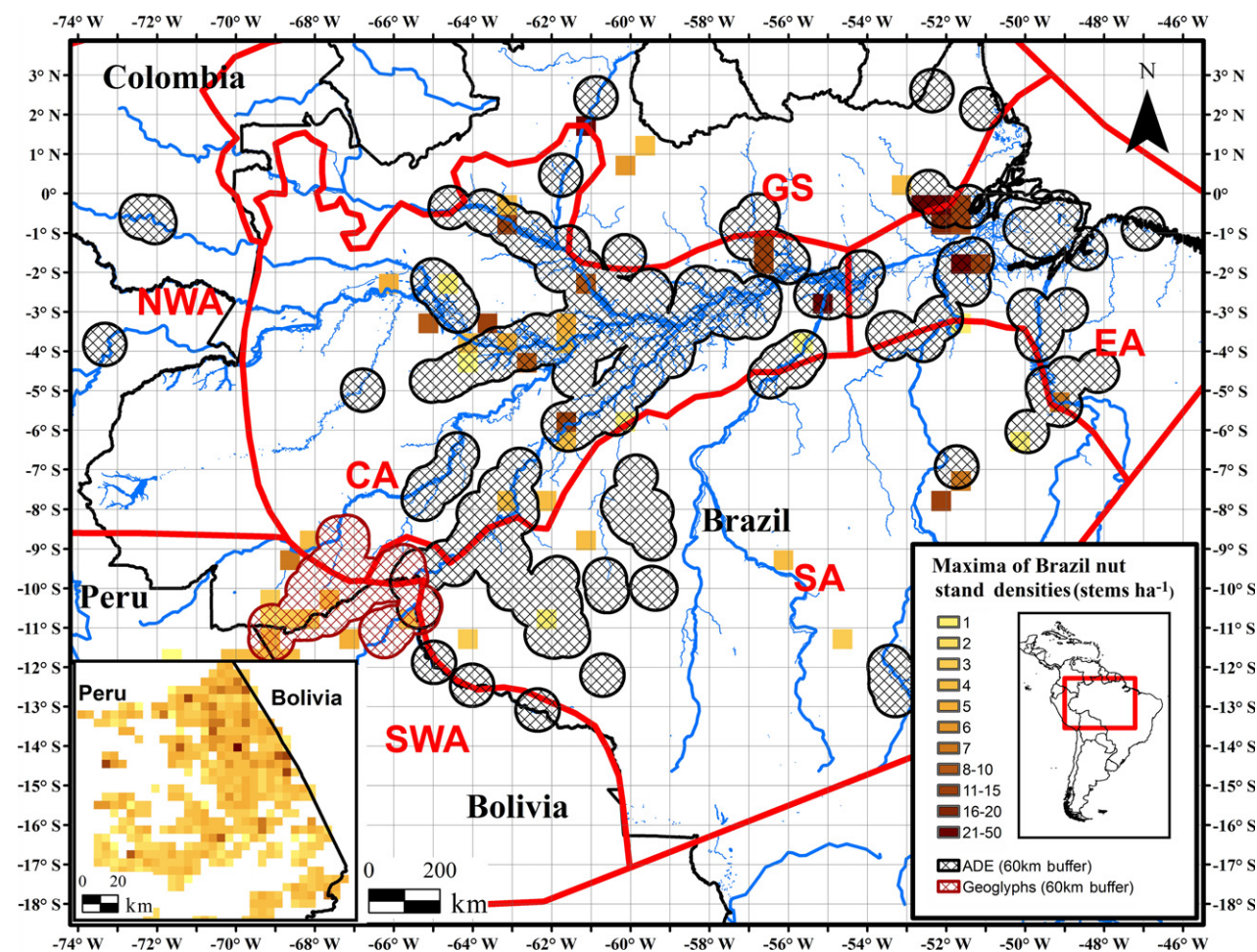


Figure 2 Maxima of Brazil nut stand densities (stems ≥ 10 cm d.b.h.) at a resolution of 30 and 2.5 arc minutes for the Amazon Basin and Madre de Dios, respectively, to improve visual representation. The hatched areas represent buffer areas of 60-km radius around known Amazonian Dark Earth (ADE; black) and geoglyph (brown) sites, respectively. The red polygons represent different regions in Amazonia (NWA: north-western Amazonia; SWA: south-western Amazonia; CA: central Amazonia; SA: southern Amazonia; EA: eastern Amazonia; GS: Guiana shield; after ter Steege *et al.*, 2013)

practices extended kilometres to tens of kilometres around Native American settlements and travel corridors (Munoz *et al.*, 2014). In the Amazon anthropogenic influences on the vegetation may extend beyond 30 km from known occupation sites (Levis *et al.*, 2012). In line with this, we used two distance intervals around known ADE and geoglyphs sites (30 and 60 km). These intervals were chosen for two reasons. First, we are only beginning to understand the full distribution of ADE in the Amazon (Levis *et al.*, 2012; McMichael *et al.*, 2014a), and it is likely that more sites will be found in the vicinities of existing ones. Second, the density and stem diameter data used here were obtained from studies that were not originally designed for investigating the co-occurrence of ADE and Brazil nut. Hence, many observations were made at distances > 30 km from known ADE sites. An additional usefulness of the buffer approach is that it covers the entire distribution range of Brazil nut, whereas the ADE modelled distribution of McMichael *et al.* (2014a) does not include important Brazil nut areas such as Amapá, strengthening their complementary value (Fig. S1).

To assess whether habitat suitability scores of Brazil nut are higher in the vicinities of ADE and geoglyph sites compared with random sites in the Brazil nut distribution range, we generated 1000 bootstrapped pairs of subsets of data cells. These pairs were composed of cells located in (1) ADE or geoglyph buffer areas, and (2) the remaining area enclosed by a convex hull constructed around all ADE and geoglyph sites and extended with 1 arc degree, respectively (see 'area of interest' in Fig. 1). Subset size was set equal to the size of the smallest of both groups. We compared each pair of subset samples by means of Wilcoxon tests and calculated average values that were in turn used to calculate standard errors and overall averages. Additionally we carried out grid cell-based Spearman correlations between suitability scores of Brazil nut (Thomas *et al.*, 2014a) and ADE and geoglyphs (McMichael *et al.*, 2014a,b). For ADE, we repeated the Wilcoxon comparisons and Spearman correlations for subsections of the overall study area created by stepwise increases of the southernmost parallel and westernmost meridian, to examine the potential existence of south-western to north-eastern trends.

For Brazil nut densities and diameters we compared proportions of individual georeferenced stands above different density (5, 8, 10 and 15 trees ha⁻¹) and diameter (125, 130, 135 and 140 cm) thresholds located within and outside ADE and geoglyph buffers by means of bootstrap tests (1000 repetitions, based on equal-sized samples, corresponding to the size of the smallest of both groups). Furthermore, we compared ADE and geoglyph suitability scores from McMichael *et al.* (2014a,b) of sites with Brazil nut densities and average stand diameters above and below these different thresholds. As fairly similar results were obtained for different density and diameter thresholds, here we will report on the most illustrative thresholds of 5 and 8 trees ha⁻¹ and 130 cm d.b.h., respectively. Standard errors of the mean were calculated based on 1000 bootstrap samples. All analyses were carried out in R version 2.14 (R Development Core Team,

2011) and associated packages RASTER (Hijmans, 2013), MAPTOOLS (Bivand & Lewin-Koh, 2013), RGEOS (Bivand & Rundel, 2013), and dependencies.

RESULTS

Average Brazil nut suitability scores in the 30 and 60 km buffer areas around the locations of known geoglyph sites (Fig. 1) were significantly higher than suitability scores inside ADE buffers and outside buffer areas (see Fig. S4 in Appendix S3). Grid cell-based Brazil nut suitability scores correlated positively with geoglyph suitability scores (McMichael *et al.*, 2014b; Spearman's $\rho = 0.20$; $P < 0.001$). However, proportions of high-density stands (≥ 5 trees ha⁻¹) inside geoglyph buffers were similar to outside, but significantly lower than in ADE buffers (Fig. S4). No convincing differences could be detected with respect to the proportion of stands with average diameters ≥ 130 cm between ADE and geoglyph buffers, or outside of buffers.

We found consistently higher habitat suitability scores in ADE buffer areas than outside for all south-west to north-east area comparisons (Fig. 3a). While average suitability values inside and outside ADE buffers decreased from south-west to north-east, increasing values of Spearman's ρ were obtained for correlations between ADE and Brazil nut suitability scores, suggesting that Brazil nut suitability is increasingly associated with ADE when moving towards central and eastern Amazonia (Fig. 3b). Also, proportions of stands with high densities and average stem diameter were consistently higher in ADE buffer areas than outside, although not all south-west to north-east area comparisons were significant (Fig. 4). On average, high-density stands were consistently located at sites with higher ADE suitability scores than stands with lower densities (see Fig. S5 in Appendix S3). No significant differences were observed for comparisons based on stand diameters.

The data considered here reveal an accumulation of Brazil nut stands with increasing densities and average diameters from south-western to central and eastern Amazonia (Fig. 5). These trends persist after carrying out a sample bias correction using bootstrap estimates based on minimum sample sizes (see Figs S6 & S7 in Appendix S3). Some indications of past human influences on Brazil nut populations do exist in the south-westernmost region of Madre de Dios, but they are much more sporadic than in central and eastern Amazonia. For example in Madre de Dios only 5 out of 87,436 (0.006%) one-hectare density estimates had more than 10 trees ha⁻¹, while outside of this area there were 25 such observations out of a total of 145 (17%; Fig. 2). The latter number is an underestimate as most publications disclosed stand diameters averaged over multiple hectares.

DISCUSSION

In what follows, we provide a discussion on how past and ongoing natural and human processes have contributed to

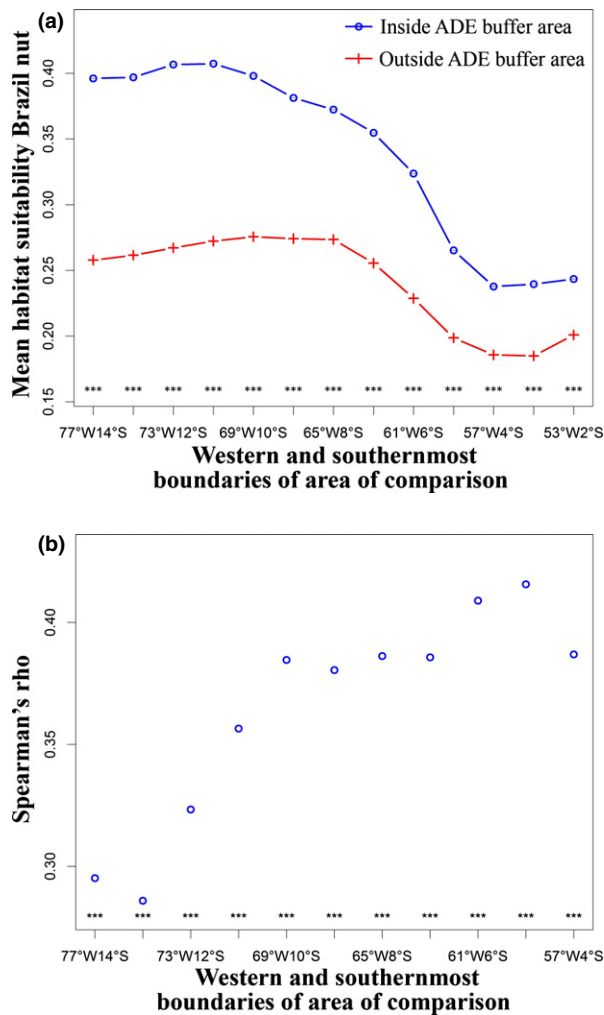


Figure 3 (a) Mean of habitat suitability scores of Brazil nut inside and outside of 30 km Amazonian Dark Earth (ADE) buffer areas along a gradient from south-western to north-eastern Amazonia ($***P < 0.001$; Wilcoxon tests). Error bars, representing standard errors of the mean, are too short to be visible (evaluations are based on 21,013–1571 cell pairs). (b) Spearman's rho of correlations along a gradient from south-western to north-eastern Amazonia between ADE and Brazil nut suitability scores, based on McMichael *et al.* (2014a) and Thomas *et al.* (2014a), respectively ($***P < 0.001$).

the trends observed in the distribution and demography of Brazil nut across Amazonia. We argue that among the natural processes, now extinct megafauna and past climate change are likely to have been elemental in shaping the distribution of Brazil nut trees encountered by the first humans arriving to the Amazon Basin. Furthermore, increasingly studied biotic and abiotic continental-scale gradients appear to have conditioned the natural history of the species since times remote. Our results strongly suggest that human influences were superimposed on the naturally created continental patterns in the distribution and demography of Brazil nut, mostly through range expansion, and as a side effect of swidden cultivation activities. Human footprints on Brazil nut

seem closely related to the distribution of ADE across the Amazon Basin, the creation of which is increasingly linked to pre-Columbian human occupation and livelihood strategies based on swidden agriculture.

The natural history of Brazil nut

The seeming contradiction between the highly specialized nature of Brazil nut fruits (manifested by a large indehiscent lignified capsule and lignified testae protecting individual seeds), and its present-day relatively inefficient dispersal agents, which hardly ever disperse seeds further than 100 m (Haugaasen *et al.*, 2010), points to the likelihood of a seed dispersal anachronism. Considering the nutty character of Brazil nut fruits, potential extinct dispersers are likely to have been rodents as well (Guimarães *et al.*, 2008). There is growing evidence that Amazon tree species are of Neogene origin, with ages ranging between 1 and 8 Ma (Hoorn *et al.*, 2010; Dick *et al.*, 2013). If this is correct, it seems reasonable to assume that the origin of Brazil nut as a species may also be placed in this time period. Rodent diversity during the Neogene up to the early Pleistocene was much higher than today, and included large species with body masses of up to a tonne, and incisor teeth of over 30 cm (Sánchez-Villagra *et al.*, 2003; Rinderknecht & Blanco, 2008). Co-evolution with massive rodents seems a more plausible explanation for Brazil nut's investment in an energy-expensive double protection layer for its seeds than with the current scatterhoarding rodents. Such a disperser is likely to have been more effective in long-distance dispersal, perhaps even swallowing entire testa-protected seeds, which once passed through the digestive tract would have been ready for germination in the nutrient-rich excrement. Long-distance dispersal over several thousands to millions of years may at one point have resulted in a continent-wide distribution of Brazil nut, both north and south of the Amazon River.

However, with repeated changes in climate during the (hundreds of) thousands of years between the disappearance of a putative megarodent disperser and the arrival of humans (cf. Hoorn *et al.*, 2010), Brazil nut may have experienced a series of range contractions and expansions. The latest period when this may have happened is the last glacial period (22–13 ka; see Thomas *et al.* (2014a) for a discussion). Based on palaeoclimate modelling, Thomas *et al.* (2014a) suggested that suitable habitat conditions for Brazil nut during the Last Glacial Maximum (LGM; c. 21 ka) may have been limited to several isolated refugia across southern Amazonia, as well as to a set of smaller putative refugia around the Amazon River Delta. They argued that Brazil nut may have reached the Pedra Pintada cave area (located north of the Amazon River, Fig. 6), where the oldest seed remains have been found, from one or more smaller refugia north of the delta (Amapá, Brazil), at the latest during the time of its human occupation more than 11,000 years ago (Roosevelt *et al.*, 1996).

The potential existence of glacial refugia in south-western Amazonia and the Amapá region is corroborated by genetic

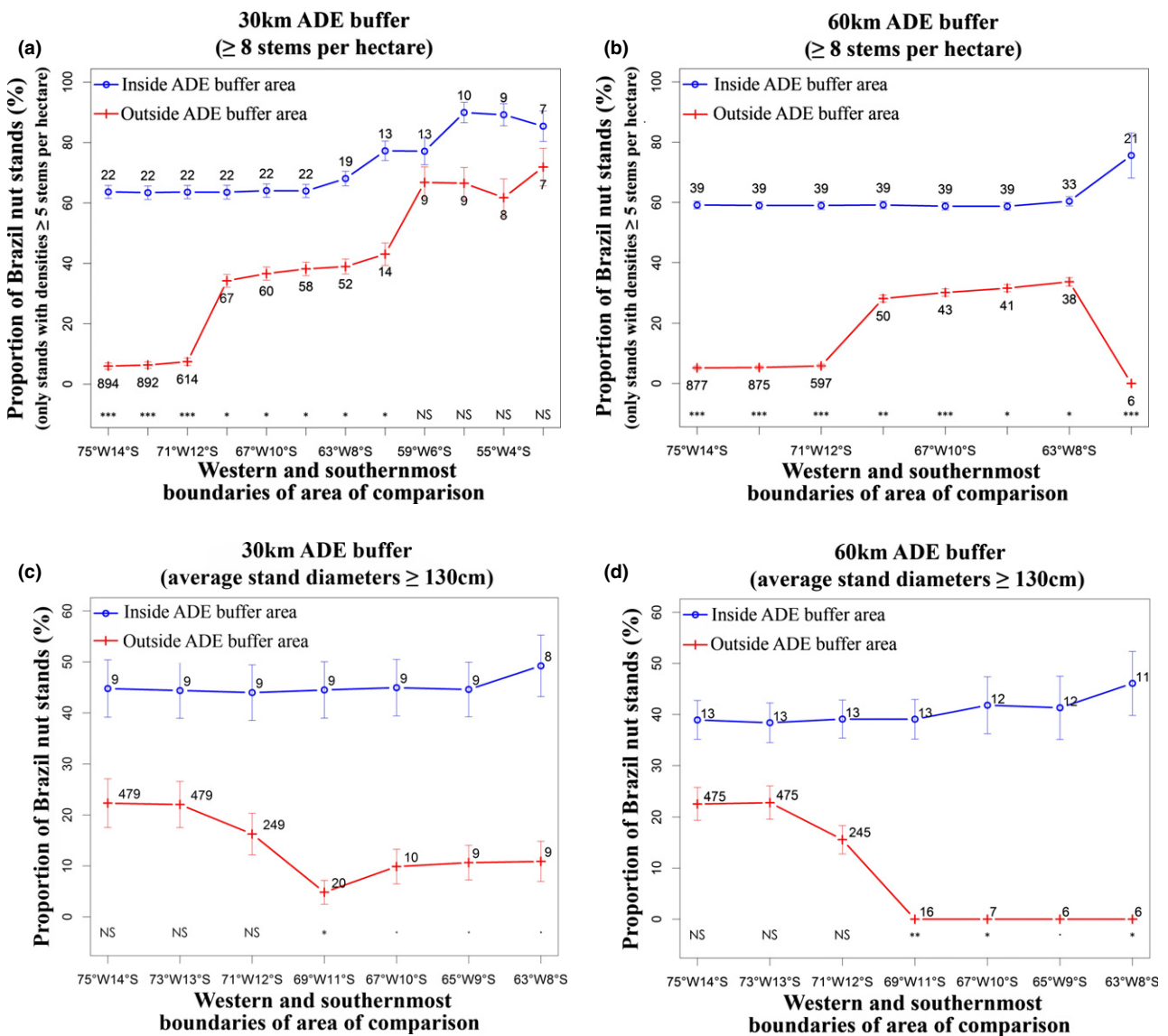


Figure 4 Proportions of Brazil nut stands with densities of 8 trees ha^{-1} or higher (only stands with ≥ 5 trees ha^{-1}) (a and b) and average diameters of 130 cm or higher (c and d) inside and outside of 30 and 60 km Amazonian Dark Earth (ADE) buffer areas, respectively, along a gradient from south-western to north-eastern Amazonia. Numbers associated with points are sample sizes. Significance levels are given above the x-axis (NS, not significant; $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; bootstrap comparisons). Error bars represent standard error the mean.

characterization data of Brazil nut compiled by Sujii *et al.* (2015) (Fig. 6). Key genetic parameters (allelic richness, private alleles and expected heterozygosity) all reach their maximum values in the vicinities of the putative south-western Amazonia and Amapá refugia and show patterns of decreasing diversity – characteristic for range expansion – in E–W and SW–NE directions, north and south of the Amazon River, respectively (Fig. 6). This, together with the spatial distribution of the genetic clusters identified by Sujii *et al.* (2015) suggests genetic differentiation of Brazil nut populations in refugia in south-western Amazonia and Amapá, in a similar fashion as described for cacao (Thomas *et al.*, 2012). If the LGM refugia scenario is correct, it is likely that Brazil

nut had not yet attained its current distribution range when the first humans arrived in the Amazon Basin, owing to the relatively inefficient dispersal capacity of the agoutis and acouchis (see discussion in Thomas *et al.*, 2014a), even when considering recent evidence that dispersal distances by agoutis can occasionally be over 300 m (Jansen *et al.*, 2012).

Some of the patterns observed in the demography of Brazil nut stands across the Amazon Basin are probably due in part to prevailing continental biotic and abiotic gradients. A notable difference between western Amazonia and central and eastern Amazonia is that natural disturbance regimes and forest turnover are higher in western Amazonia (Nelson *et al.*, 1994; Espírito-Santo *et al.*, 2010, 2014). Natural

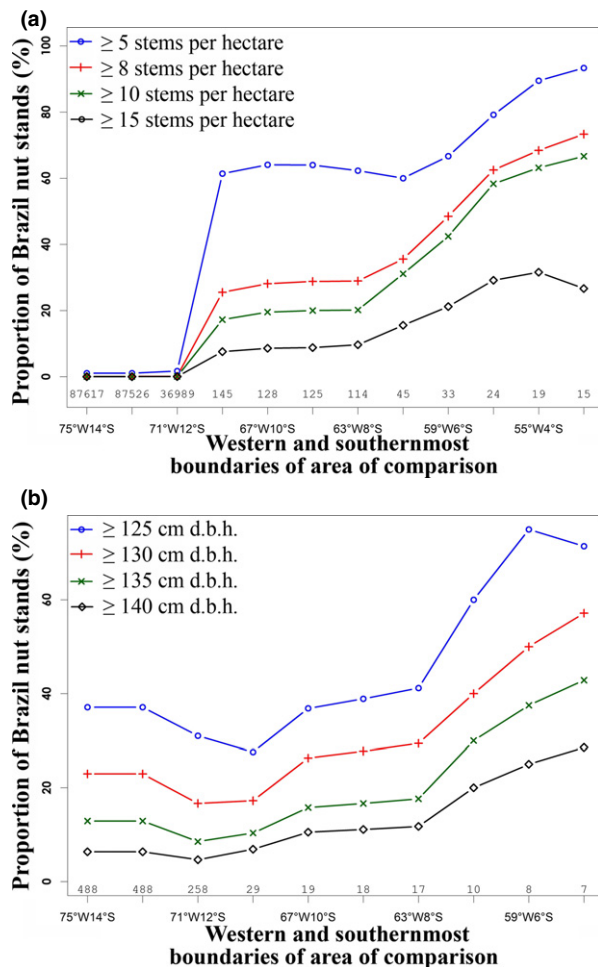


Figure 5 Proportions of Brazil nut stands with (a) densities and (b) average diameters above different thresholds along a gradient from south-western to north-eastern Amazonia. Sample sizes for different subsections of the overall study area created by stepwise increases of the southernmost parallel and westernmost meridian are given above the x-axis.

disturbance can lead to the creation of humps in intermediate size classes of Amazonian tree species (Pitman *et al.*, 2005). For Brazil nut, more frequent natural creation of forest gaps in south-western than central and eastern Amazonia could translate into more effective natural regeneration, as suggested by ecological sampling. Studies carried out in the south-western Amazon have consistently reported healthy population structures, evidenced by reverse J-shaped curve, with a larger number of individuals in the smaller d.b.h. (< 10 cm) categories (Viana *et al.*, 1998; Zuidema & Boot, 2002; Cotta *et al.*, 2008; Wadt *et al.*, 2008). Conversely, in central and eastern Amazonia there have been contrasting observations. Most studies from these regions report on population structures that are deficient in seedlings, saplings and juveniles (Peres *et al.*, 2003; Salomão, 2009; Scoles & Gribel, 2011, 2012). In the cases where healthy natural regeneration patterns were observed, recent or ongoing anthropogenic or natural forest disturbance regimes have been

identified among the principal drivers (Scoles, 2011; Scoles & Gribel, 2011, 2012; Shepard & Ramirez, 2011; Guedes *et al.*, 2014; Ribeiro *et al.*, 2014).

In addition to differences in disturbance regimes, other abiotic conditions, such as climate and chemical and physical soil characteristics, are known to structure diversity gradients across the basin (Gentry, 1988; ter Steege *et al.*, 2006; Thomas, 2009; Hoorn *et al.*, 2010). These gradients have also been related to the faster growth but generally smaller size and shorter life span of trees in western than in central and eastern Amazonia (Phillips *et al.*, 2004; Davidson *et al.*, 2012; Quesada *et al.*, 2012). This could partly explain the increasing maxima of average stand diameters from south-western to north-eastern Amazonia observed in our dataset. Also, variation in the spatial distribution of precipitation over the year may have an influence. For example, most of the sites in our dataset holding the highest densities are located in parts of central and eastern Amazonia receiving elevated levels of rainfall during the coldest quarter of the year (see Fig S8 in Appendix S3). However, the consistently higher stand densities and mean tree diameters of Brazil nut populations inside than outside ADE buffers throughout the basin (Fig. 4) suggest additional human influences superimposed on existing environmental gradients.

The human history of Brazil nut

Although there is no strong evidence of widespread planting of Brazil nut by native Amazonian societies, it is likely that early humans actively distributed germplasm, for example when colonizing new areas and through indigenous trade networks. Seeds may have been planted in home gardens or swiddens, whereas in other cases seeds carried for food during long-distance (riverine) travel or hunting trips and inadvertently dropped, may have established continuously expanding founder populations, in line with contemporary observations among the Brazilian Kayapó (Ribeiro *et al.*, 2014). Inter-ethnic exchange and trade of Brazil nut germplasm may have sped up or intensified the species' dispersal.

Shepard & Ramirez (2011) argued in favour of a human-influenced Brazil nut dispersal pattern from central to south-western Amazonia. However, based on our data and as suggested by others, an opposite dispersal direction seems more likely. Clement *et al.* (2009) contended that *Bactris gasipaes*, the most important Neotropical domesticated palm, was dispersed across the Amazon Basin from a potential origin in south-western Amazonia, which may have been catalysed by migrations of Arawak language speakers. Drawing on an extensive linguistic analysis, Walker & Ribeiro (2011) similarly suggested that the Arawak expansion may have started from an origin in western Amazonia. If correct, the putative Brazil nut refugium in south-western Amazonia (Fig. 6) could have represented a major source from where germplasm was dispersed by indigenous groups during their expansion towards central Amazonia. In line with this, Balée (2013) argued that Brazil nut was present in the homeland

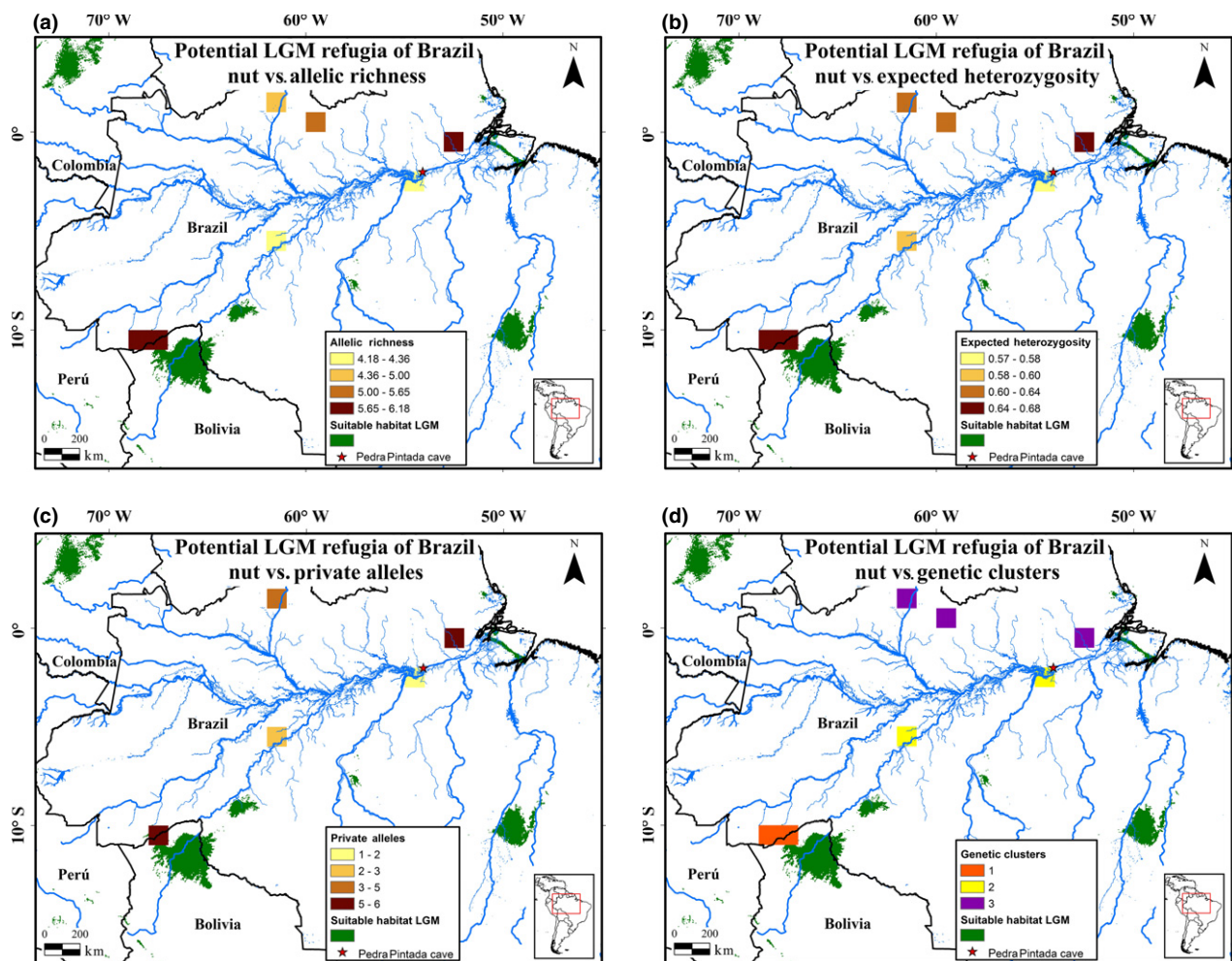


Figure 6 Overlay of habitat suitability of Brazil nut during the Last Glacial Maximum (c. 21 ka) (based on Thomas *et al.*, 2014a) and different genetic parameters (based on Sujii *et al.*, 2015): (a) allelic richness; (b) expected heterozygosity; (c) richness of private alleles; and (d) genetic clusters. The red star indicates the location of the Pedra Pintada cave where the oldest Brazil nut remains have been found, dated to > 11 ka (Roosevelt *et al.*, 1996). Please note the small areas with suitable habitat around and just north of the Amazon River Delta.

of the Proto-Tupí-Guaraní people, which is likely to have been in the south-west. Furthermore, human dispersal of Brazil nut from a south-western stock to central Amazonia (south of the Amazon River) could explain why some studies (Kanashiro *et al.*, 1997; Gribel *et al.*, 2007) have found very limited genetic differentiation between Brazil nut populations in this region.

Humans not only contributed to the distribution of Brazil nut, but also influenced its abundance, especially through the creation of high-density stands called ‘manchales’, ‘castanhais’ or ‘bolas’ (Mori & Prance, 1990; Peres & Baider, 1997; Salomão, 2009; Scoles & Gribel, 2011). Contemporary evidence has shown that certain traditional activities of indigenous groups, both consciously and unconsciously, augment the density of Brazil nut trees (Shepard & Ramirez, 2011; Ribeiro *et al.*, 2014). However, a growing body of knowledge suggests that the positive human influence on Brazil nut stand density may have been predominantly unintentional

(Cotta *et al.*, 2008; Paiva *et al.*, 2011; Scoles *et al.*, 2011; Guedes *et al.*, 2014). Brazil nut is a gap-dependent, long-lived pioneer species, implying that its natural regeneration is strongly favoured by the availability of light through gap creation (Mori & Prance, 1990; Myers *et al.*, 2000; Cotta *et al.*, 2008). The swiddens and fallows created by humans provide ideal forest gaps for Brazil nut regeneration. More effective regeneration of Brazil nut in swiddens and fallows as compared with high forest (see also Materials and Methods) have been attributed to a combination of the preferential dispersion activities of agoutis, the more favourable growth conditions in cultivated fields and the species’ capacity to re-sprout after cutting (Kainer *et al.*, 1998; Cotta *et al.*, 2008; Paiva *et al.*, 2011; Scoles *et al.*, 2011; Guedes *et al.*, 2014). Seedling recruitment is likely to be additionally favoured by hunting of agoutis, thus freeing more abandoned scatter hoards for germination (Shepard & Ramirez, 2011; Ribeiro *et al.*, 2014).

Every slash-and-burn cycle is a drastic intervention that eliminates most biotic life and above-ground biomass (except from deliberately spared species), while liberating scarce nutrients through fire ash. Sprouters, like Brazil nut, are favoured over seeders when disturbance regimes are frequent and severe (Bond & Midgley, 2001). Because of cyclical disturbances, swidden cultivation creates gaps at a much higher frequency than do natural tree falls in the forest, and hence is more likely to result in higher Brazil nut densities (Paiva *et al.*, 2011). Denevan (2001) argued that in contrast to contemporary slash and burn plots, which are generally small and only cultivated for a few years and then left to fallow, pre-Columbian swiddens were larger and more continuously cultivated with more use of low-intensity fires and shorter fallow periods. Slash-and-burn shifting cultivation as we know it today would have become common only after the introduction of steel axes. If this is correct, the time periods for Brazil nut recruitment in pre-Columbian swiddens would have been longer than at present, additionally promoting the formation of approximately even-aged high-density stands. Similar types of more permanent instead of shifting cultivation seem to have been common among prehistoric indigenous societies of eastern North America as well (Doolittle, 2004). Analysis of historical land surveys in the latter region has shown that after abandonment of crop fields, more or less even-aged stands of pine trees (on the order of square kilometres) established through processes of secondary succession (Munoz *et al.*, 2014).

Our results suggest that the presently observable human impact on Brazil nut occurrence and abundance is more pronounced in the vicinities of known ADE sites. As most of the currently known ADE sites are located in central and eastern Amazonia (Fig. 1), factors underlying ADE distribution patterns may thus also explain the gradient of increasing human footprints on Brazil nut stands from south-western to central and eastern Amazonia. This is exemplified by the typically clustered co-occurrence of Brazil nut and ADE around the main rivers and their tributaries in central and eastern Amazonia (Levis *et al.*, 2012; Fig. 1), where pre-Columbian population densities were much higher than the interior *terra firma* forests (Denevan, 2011).

Among the potential causal factors of differential ADE distribution patterns between south-western and central and eastern Amazonia are differences in extent and intensity of human occupation, differences in livelihood strategies, or both. In many areas of western Amazonia, pre-Columbian human population densities are thought to have been low and highly localized. In contrast, in central and eastern Amazonia dense and complex human settlements with associated areas of widespread, extensive agriculture seem to have been more common, hence the under-representation of ADE in the former region and abundance in the latter (Arroyo-Kalin, 2012; McMichael *et al.*, 2012, 2014a). This difference in occupation may itself be related to the different livelihood strategies associated with sweet and bitter manioc cultivation. According to Arroyo-Kalin (2012), small-scale maize- and

sweet manioc-dependent strategies may have prevailed in western Amazonia, which had a much more limited impact on the landscape as compared with the resilient livelihoods based on bitter manioc cultivation, which may have predominated in central and eastern Amazonia. Burning associated with the latter strategy probably had a much more pronounced impact on the landscape, and has been associated with the creation of ADE (Fraser & Clement, 2008; Shepard & Ramirez, 2011; Arroyo-Kalin, 2012). The higher prevalence of swidden cultivation in central and eastern than in south-western Amazonia, together with the observation that repeated swidden cycles are known to accumulate Brazil nut trees (Paiva *et al.*, 2011; Guedes *et al.*, 2014), may contribute to explaining the higher probability of finding higher stand densities in central and eastern Amazonia.

However, not all of south-western Amazonia was characterized by sparse human occupation. Areas in Brazilian Acre and Bolivian Pando may at one time have sustained high population densities, as suggested by the high abundance of earthworks and geoglyphs. The main use of geoglyph sites seems to have been seasonal, short-term or sporadic, and mainly for ceremonial and ritual purposes, rather than for permanent residence or crop cultivation (Saunaluoma, 2012; Saunaluoma & Schaan, 2012). However, it is likely that people in the broader regions where geoglyphs are located were numerous. ADE are absent in geoglyph areas, which could mean that pre-Columbian societies in these areas used less fire-intensive techniques for food production. Carson *et al.* (2014) have recently provided evidence for the possibility that the Pando and Acre region was covered by an open savanna landscape up until some 2000 years ago when climatically driven rain forest expansion began. If correct, it is possible that the geoglyph builders relied on similar livelihood strategies as those reported from the nearby savannas of Moxos, Bolivia, such as fish weirs and agriculture on raised fields (Erickson, 2000; McMichael *et al.*, 2014a). Livelihood strategies that depended less on fire may not have fostered the creation of ADE to the same extent as swidden cultivation (Walker, 2011), and hence may have had a more reduced impact on Brazil nut stand characteristics.

Aside from differences in livelihood strategies, the low prevalence of high density Brazil nut stands in south-western Amazonia may also have an ecological origin. Studies that compared the performance of Brazil nut seedlings and saplings planted in open field (swidden) with those in understorey conditions (secondary forest, and Brazil nut plantations) seem to suggest that open field seedlings and saplings grow much faster in central (Scoles *et al.*, 2011) than in south-western Amazonia (Kainer *et al.*, 1998; Peña-Claros *et al.*, 2002). Although differences in germplasm and site preparations may have influenced these experiments, it is possible that the lower growth rates of Brazil nut seedlings observed in studies from south-western Amazon sites may be partly caused by similar underlying (a)biotic factors that could be responsible for the constrained development of high density stands in this region. In other words, it is possible that a

swidden cultivation plot in south-western Amazonia with the same characteristics and cleared in the same way as a similar plot in central or eastern Amazonia, would accumulate less Brazil nut individuals, owing to differences in ecological factors such as incidence of pests and diseases (e.g. increased fungal attack, cf. Shepard & Ramirez, 2011), plant competition, soil characteristics etc. One way to test this hypothesis would be to carry out a similar study as Paiva *et al.* (2011) in south-western Amazonia.

The patterns in the diameter distribution of Brazil nut stands we detected were less pronounced than patterns in density distributions, which may in part be because of the fewer diameter data points. Also a better understanding of past human occupation and use of each of the Brazil nut stands considered could help to distinguish stands untouched by humans since the colonization period from stands bearing the marks of more recent human disturbance. In spite of these limitations, we did detect a signal in the diameter dataset suggesting increasing human influences from south-western to north-eastern Amazonia and inside ADE buffer areas compared with outside (Figs 4c,d & 5b, Fig. S7). One explanation for the frequent observation of senescing Brazil nut stands in central and eastern Amazonia (Peres *et al.*, 2003), may be that in the absence of anthropogenic forest disturbance, natural gap creation in these areas occurs at an insufficient scale and intensity to maintain healthy regeneration patterns. Despite some specific sites where strong natural disturbance regimes exist (cf. Shepard & Ramirez, 2011), human gap creation seems to have been crucial in central and eastern Amazonia for Brazil nut regeneration, as opposed to south-western Amazonia where natural disturbance is much more intense. In central and eastern Amazonian, the decline of Amazonian societies took place soon after the initiation of the colonization of the Amazon, while in (south-)western Amazonia, this occurred much later towards the end of the 18th and during the 19th century (Charles Clement, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil, pers. comm.), which could additionally explain the proportionally fewer Brazil nut stands there with high average diameters.

CONCLUSIONS

Based on the results presented here, the answer to all research questions presented in the introduction is affirmative. Our finding that densities and average diameters of Brazil nut stands are higher in the surroundings of ADE sites, regardless of their position along a south-western to north-eastern gradient, suggests that human influences on Brazil nut stands have been superimposed on environmental gradients in nearly all Amazon regions. Although the footprints of human influences seem to increase from south-western to central and eastern Amazonia this gradient is not necessarily representative for the principal direction of human-mediated dispersal of Brazil nut. It is most likely to be a reflection of the interplay between human and natural factors. It remains,

however, challenging to disentangle human influences on the distribution and abundance of Brazil nut from existing biotic and abiotic gradients across the Amazon Basin. Factors such as natural disturbance regimes, climate variations, soil profiles, or natural vegetation structure (e.g. open forests across southern Amazonia and dense forests in the central basin) all may be adapted to in variable degrees by different Brazil nut populations.

Further completion of the different datasets we used here (ADE, geoglyphs and Brazil nut stand metrics) would be useful to improve their geographical coverage and representativeness, and to confirm or refute the continental patterns of human influences on Brazil nut stands we have discussed here. More extensive and exhaustive genetic sampling would further improve our understanding of historical fronts of Brazil nut dispersal. Ideally, future genetic sampling should include Brazil nut populations that are located in the vicinities of putative Pleistocene refugia, along with a set of representative populations across the overall distribution range of Brazil nut, both inside and outside ADE and geoglyph buffer zones. A better understanding of the distribution of genetic diversity of Brazil nut would additionally allow to better guide conservation and restoration activities (Thomas *et al.*, 2014b).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Methodological details of the distribution modelling.

Appendix S2 Brazil nut stand metrics: (a) density and (b) diameters.

Appendix S3 Supporting maps and figures.

BIOSKETCH

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Author contributions: E.T. conceived the ideas; E.T. and C.A.C. collected the data; E.T. analysed the data; and E.T., C.A.C., C.M., R.C. and J.L. wrote the paper.

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