The distribution of the Brazil nut (*Bertholletia excelsa*) through time: from range contraction in glacial refugia, over human-mediated expansion, to anthropogenic climate change

Distribuição da castanha-do-brasil (*Bertholletia excelsa*) através do tempo: desde a contração no refúgio glacial, sua expansão mediada pelos humanos, até a mudança climática antropogênica

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Abstract: Brazil nut (*Bertholletia excelsa*) is one of the most important non-timber forest producing tree species in the Amazon. One aspect related to the sustainability of Brazil nut that has so far received very limited attention in literature is how the species' distribution has changed through time and will continue to do so in light of anthropogenic climate change. We modeled the potential distribution of Brazil nut during different past climates as well as during several future time periods. Of the past time periods, the Last Glacial Maximum (~21,000 BP) had the biggest impact on the present distribution of Brazil nut. The distribution of suitable habitat may have been restricted primarily to several potential refugia across southern Amazonia. On the other hand, the oldest Brazil nut remains found at the Pedra Pintada cave (~11,000 BP) were probably harvested by early humans from trees that reached the area after natural range expansion from one or more smaller refugia which may have been located close to the Amazon River delta. Future climate projections predict a positive future for Brazil nut. We conclude with a number of recommendations to improve the species' conservation, use and management, both within and outside its current distribution area.

Keywords: Brazil nut. Species distribution models. Anthropogenic climate change. Last glacial maximum. Amazonia. Ensemble modeling.

Resumo: A castanheira-do-brasil (*Bertholletia excelsa*) é uma das espécies arbóreas não madeireiras mais importantes da Amazônia. Um aspecto relacionado à sustentabilidade da castanheira-do-brasil que tem recebido até agora atenção muito limitada na literatura é o modo como a distribuição da espécie tem mudado ao longo do tempo, o que continuará ocorrendo em virtude das mudanças climáticas causadas por fatores antropogênicos. Modelamos a distribuição potencial da castanheira-do-brasil em diferentes períodos climáticos passados, assim como durante vários períodos futuros. Dentre os períodos pretéritos, o Último Máximo Glacial (~21.000 BP) teve o maior impacto sobre a atual distribuição da castanheira-do-brasil. Nesse período, a distribuição dos *habitats* favoráveis ficou restrita a refúgios potenciais no sul da Amazônia. Por outro lado, os mais antigos restos de castanha-do-Brasil, encontrados na caverna da Pedra Pintada (~11.000 anos de idade), provavelmente foram colhidos por ancestrais humanos de árvores que alcançaram a área por expansão natural, a partir de um ou mais refúgios menores, provavelmente localizados nas proximidades do delta do rio Amazonas. Projeções do potencial de distribuição para diferentes cenários climáticos vindouros predizem um futuro positivo para a castanheira-do-brasil. Concluímos com algumas recomendações para melhorar a conservação, uso e manejo das espécies, tanto dentro quanto fora da sua área de distribuição natural.

Palavras-chave: Castanha-do-brasil. Modelos de distribuição de espécies. Mudança climática antropogênica. Última máxima glacial. Amazônia. Modelagem conjunta.

INTRODUCTION

Brazil nut (*Bertholletia excelsa* Bonpl.) is probably the most widely distributed Lecythidaceae species in the Neotropics and definitely the socio-economically most important non-timber product producing tree whose fruits are predominantly harvested from natural forests. It is found on terra firme forest soils in lowland Amazonia and the Guianas (Mori & Prance, 1990). Brazil nut is an emergent (heights up to 50 m), long-lived pioneer tree that depends on forest clearings for growth and natural regeneration (Mori & Prance, 1990; Salomão, 1991; Zuidema, 2003). De Camargo *et al*. (1994) have estimated the age of a Brazil nut tree with DBH (Diamether at Breast Height) > 500 cm, at around 800-1000 years, while Pires (1984) estimated similar-sized trees (446-509 cm DBH) to be over 1,600 years old (Peres & Baider, 1997). The oldest Brazil nut tree measured thus far using tree rings was 427 years old and had a diameter of 180 cm (Brienen & Zuidema, 2006). The tree grows in areas from sea level to approximately 400 meters above sea level with an annual mean temperature of 23.5 to 27.6 °C, and annual rainfall from 1,445 to 3,399 mm (our calculation based on data presented in this paper). It is typically found on nutrient-poor, well-drained oxisol and ultisol soils (Peres & Baider, 1997).

Brazil nut has allogamous flowers which are pollinated by large bees (mainly *Bombus*, *Centris*, *Xylocopa*, *Epicharis* and *Eulaema*) capable of flying long distances (> 20 km), thus ensuring extensive gene flow between distant Brazil nut trees and populations (Janzen, 1971; Moritz, 1984; Maués & Oliveira, 1996; Santos & Absy, 2010). In a study on the genetic variability of Brazil nut across most of the species' distribution range in the Peruvian department of Madre Dios, Reátegui-Zirena *et al*. (2009) observed that all trees they studied (maximum pairwise distance 108 km) formed part of a large panmictic population which they attributed in part to a combination of the longevity of the tree, its allogamous reproductive system, the long-distance bee pollinators and the absence of topographic barriers for the tree's main animal disperser agent, the agouti (*Dasyprocta* spp.). As the tree is predominantly outcrossing (O'Malley *et al*., 1988),

long-distance gene flow is important to ensure that isolated trees or small tree populations (e.g. established after long-distance dispersal events) are able to produce viable seeds, as well as to reduce potential negative consequences from 'founder effects', the loss of genetic variation that occurs when a new population is established by a very small number of individuals from a larger population.

After successful pollination, fruit maturation takes between 14-15 months, resulting in hard 10-16 cm globose woody capsules (called pyxidia). Therefore it is frequent to find fruits in different development stages on one tree throughout the year (Mori & Prance, 1990). Brazil nut fruits are unique within the Lecythidaceae family being both the hardest in the family and functionally indehiscent. In the absence of humans, dispersal is mainly carried out by scatterhoarding agoutis and acouchis (*Dasyprocta* spp. and *Myoprocta* spp.), and occasionally squirrels and several species of monkeys who are able to open the fruits by gnawing and smashing them against hard surfaces, respectively (Peres & Baider, 1997; Tuck Haugaasen *et al*., 2010). Seeds require 12-18 months of storage under moist conditions for germination, compared with almost instantaneous germination for most other species in the Lecythidaceae family (Mori & Prance, 1990). The establishment of seedlings does not seem to be influenced by light availability as they are typically found in the understory in deep shade (Myers *et al*., 2000; Scoles & Gribel, 2012). However, light is important for juvenile development and growth (Zuidema & Boot, 2002).

In many parts of its distribution range, Brazil nut stands occur in an aggregated pattern, whereby clusters of trees, commonly referred to as 'manchales', 'castanhais' or 'bolas', are interspersed with vast areas of forest with very few or no trees (Mori & Prance, 1990; Peres & Baider, 1997; Salomão, 2009; Baider, 2000; Zuidema, 2003; Scoles & Gribel, 2011). However, there are large differences in the scale at which these patterns occur, or at least in the ways they are being interpreted by different scholars. Most frequently, 'castanhal' refers to local stands of 50 to several hundred Brazil nut trees occurring in areas of a few to

tens of hectares (Mori & Prance, 1990), but in the view of others they can be much larger, stretching out over many thousands of hectares (*e.g.* Shepard Jr. & Ramirez, 2011).

At the local scale (hundreds of meters to kilometers), the patchy distribution of Brazil nut trees can largely be explained by the scatterhoarding activities of the agouti (Peres & Baider, 1997). This large rodent is known to move fruits and seeds over distances up to 60 meters from its original position, although most seeds are buried within 10 m (Tuck Haugaasen *et al.*, 2010, 2012). Distribution patterns at the regional and continental scale (tens to thousands of kilometers), have most likely been profoundly influenced by humans as dispersal agents (Shepard Jr. & Ramirez, 2011; Scoles & Gribel, 2011, 2012), ever since their arrival to the Amazon basin, 12,000-20,000 years ago (Schmidt Dias, 2004; Lahaye *et al.*, 2013). The association between castanhais and archaeological and other evidence of historical human activities such as dark earth soils suggests that humans were responsible for introducing the Brazil nut to new areas and increasing the species' density as a side effect of human activities such as swidden agriculture which seems to promote the natural regeneration of this gap species (Cotta *et al.*, 2008; Scoles & Gribel, 2011; Scoles *et al.*, 2011; Shepard Jr. & Ramirez, 2011).

On a longer time scale, now extinct dispersal agents may have been important. According to Guimarães Jr. *et al.* (2008), the currently known Pleistocene megafauna probably did not play a role in Brazil nut dispersion, as they would have fed primarily on fruits with fleshy pulp. However, it seems insufficiently convincing that a tree would invest so much energy to ensure its dispersion and reproduction through an almost exclusive mutualism with a relatively ineffective long-distance disperser like the agouti (Scoles, 2011), to already abandon the quest for revealing the identity of potential "ghost(s) of past Brazil nut mutualisms" (Barlow, 2001).

The objective of this paper is to gain insight into how the distribution of Brazil nut in the Neotropics has changed in the past and will continue to do so in light of anthropogenic climate change. Human influence on the current geographical distribution of Brazil nut is fairly recent in the species' overall biogeography, and it is very likely that its distribution in the Neotropics still bears the footprint of past climatic change, most notably the last period of glaciation (22,000-13,000 BP) as is the case for other neotropical species like cacao (Thomas *et al.*, 2012). There has long been agreement among palynologists that a significant cooling in temperature (4-5 °C) during the late Pleistocene governed the reassortment of plant associations in the Amazon basin (van der Hammen & Hooghiemstra, 2000; D'Apolito *et al.*, 2013). However, there has been considerable debate about whether a cooler and wet climate or a cooler and dry climate prevailed. Most scholars have defended a drying of the climate (*e.g.* van der Hammen & Hooghiemstra, 2000; Mayle *et al.*, 2004; Pennington *et al.*, 2004; Bonaccorso *et al.*, 2006; Beerling & Mayle, 2006; Rossetti *et al.*, 2004). Recent evidence presented by D'Apolito *et al.* (2013) suggests that the smaller group of scientists (Colinvaux *et al.*, 1996; Colinvaux & De Oliveira, 2001; Bush *et al.*, 2004) who have long stood firm on their conviction of a wet glacial period may have based their arguments on inaccurate interpretations of sedimentary records from the Hill of Six Lakes in northwestern Brazil. D'Apolito *et al.* (2013) examined one of the three parallel cores (originally collected under supervision of P. Colinvaux) that were used as the main proof for a wet Last Glacial Maximum (LGM ~21,000 BP) and concluded that the sedimentary and pollen records are supportive of the dry hypothesis.

Glacial aridity in the Amazon basin has been deduced from a number of other pollen sites like Caquetá river, Colombia; Rondônia and Serra dos Carajás, Brazil; as well as from sites in southcentral, central and southeastern Brazil (van der Hammen *et al.*, 1992; van der Hammen & Absy, 1994; Behling & Lichte, 1997; van der Hammen & Hooghiemstra, 2000; Sifeddine *et al.*, 2001; Rossetti *et al.*, 2004). The drop in precipitation during the LGM may have varied between 500 and 1,500 mm, depending on the exact location in the basin (van der Hammen & Hooghiemstra, 2000). As a consequence of temperature cooling, combined with a reduction in precipitation, and water stress in plants due to lowered atmospheric CO_2 concentrations (Mayle *et al.*, 2004)

non-rainforest vegetation, such as more open dry forest, and in some areas even savannah encroached, constraining wet forest vegetation to isolated refugia (Haffer & Prance, 2001; Bonaccorso *et al*., 2006; Beerling & Mayle, 2006; Pennington *et al*., 2004). For Brazil nut, lower precipitation at the LGM probably meant restriction of populations to areas where conditions remained wet enough to support the species' survival. During the glacial-Holocene transition, evergreen rainforest distribution, and hence probably also Brazil nut, is likely to have gradually increased again owing to ameliorating climatic and CO_2 conditions (Mayle *et al*., 2004; Rossetti *et al*., 2004; D'Apolito *et al*., 2013). The Holocene shows two phases with a climate that was probably more seasonal and drier during the Early-Mid-Holocene causing seasonal widespread, frequent fires in southern Amazonia (Mayle *et al*., 2004), and with hyper humid conditions since approximately 6,000-4,500 BP (Rossetti *et al*., 2004; D'Apolito *et al*., 2013).

Significant research has been devoted to investigating the factors that either promote or undermine the sustainability of Brazil nut stands, particularly those from which Brazil nuts are harvested commercially, to inform the development of appropriate management decisions and silvicultural interventions. Studies have examined patterns in the demography and natural regeneration of Brazil nut at different sites across the Amazon basin (*e.g.* Zuidema & Boot, 2002; Zuidema, 2003; Peres *et al*., 2003; Wadt *et al*., 2005, 2008), variation in fruit production (Kainer *et al*., 2006, 2007); the influence of (human) disturbance on Brazil nut stand dynamics (*e.g.* Cotta *et al*., 2008; Scoles & Gribel, 2011; Paiva *et al*., 2011), optimal conditions for enrichment planting (Kainer *et al*., 1998; Peña-Claros *et al*., 2002), and the compatibility between logging and Brazil nut harvesting (Guariguata *et al*., 2009; Soriano *et al*., 2012), among others. One important factor that has so far received very limited attention in studies on the sustainability of Brazil nut stands is climate change. In this paper we will assess spatial distribution patterns of Brazil nut through time to better understand how (1) past climate conditions may have

contributed to shaping Brazil nut current's distribution and (2) anthropogenic climate change may redefine the tree's distribution. We conclude the paper with a discussion on Brazil nut's future which we believe might be a positive one.

METHODS

We characterized the spatial distribution of favorable habitat conditions of Brazil nut under current, past, and future climatic conditions by means of suitability mapping based on ensembles of modelling algorithms, implemented in R package BiodiversityR (Kindt & Coe, 2005; ensemble.test and ensemble.raster functions available in version 2.3-6 of the package). The working assumption of ensemble modeling is that a combination of algorithms will have higher predictive performance than the constituent algorithms whose individual performance may differ from one case to the next. Modeling algorithms considered were maximum entropy (MAXENT), boosted regression trees (BRT, including a stepwise implementation), random forests (RF), generalized linear models (GLM, including stepwise selection of explanatory variables), generalized additive models (GAM; including stepwise selection of explanatory variables), multivariate adaptive regression splines (MARS), regression trees (RT), artificial neural networks (ANN), flexible discriminant analysis (FDA), support vector machines (SVM), and the BIOCLIM algorithm.

We constructed a dataset containing 936 presence points which provides a fair representation of Brazil nut's current realized niche, according to relevant literature sources (Mori & Prance, 1990; Shepard Jr. & Ramirez, 2011) (Figure 1). One area that may be underrepresented in our dataset is part of southeastern Amazonia. Homma (2000) reported on the existence of dense Brazil nut stands along the Tocantins River and in southeastern Pará, but these were destroyed long before major botanical explorations took place. Presence points were collected from a variety of sources, notably Sylvain Desmouliere for Brazilian RADAM data, members of the Latin American Forest Genetic Resources Network (LAFORGEN),
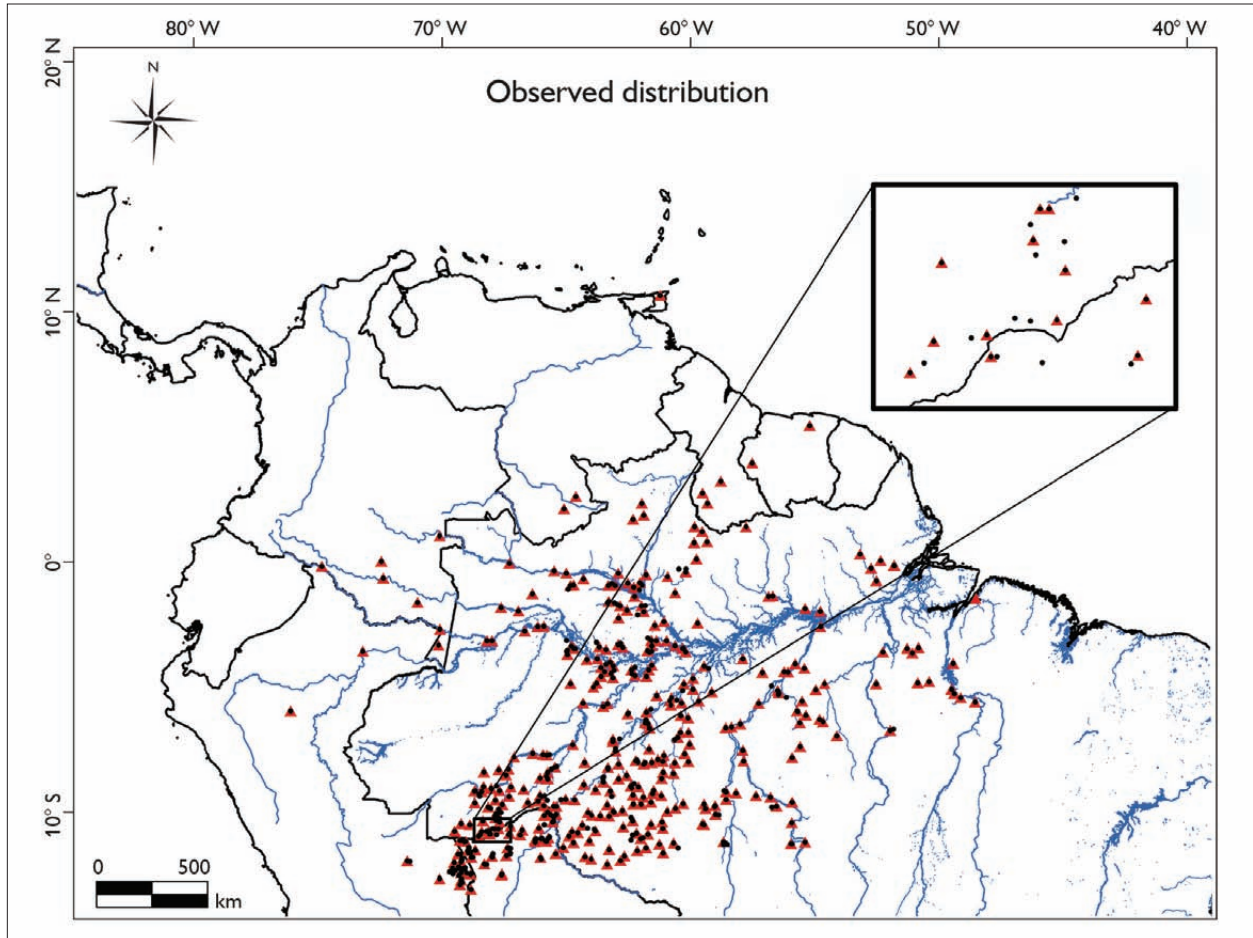
Figure 1. Distribution of Brazil nut observation points. The complete dataset (489 points) and the resampled subset (340 points) are visualized by black dots and red triangles, respectively. The rectangular area amplifies part of the border area between Acre, Brazil, and Pando, Bolivia, and illustrates how the resampled subset (red triangles) reduces sample bias in the complete dataset (black dots).

Scott Mori, GBIF (s. d.), and Reátegui-Zirena et al. (2009). It has been suggested that Brazil nut requires at least two dry months (monthly precipitation < 60 mm) for development and growth (Müller, 1981). This seems to be the case for most of the areas where the species has been observed, but interestingly one third of the 936 tree observations considered here received more than 60 mm of precipitation in their driest month, while 13% received more than 100 mm.

To improve model performance (Acevedo et al., 2012), background points (an overall maximum of 20,000 and maximum one per grid cell) were randomly selected from the area enclosed by a convex hull polygon constructed around all presence points and extended with a buffer corresponding to 10% of the polygon's largest axis. Modeling was performed at 2.5' spatial resolution and we retained only one presence point per grid cell, which reduced the number of presence cells to 489. Models were calibrated based on current climate data obtained from the Worldclim database (i.e. averages from 1960-1990; Worldclim, s. d.). For projection to future climate scenarios we added the following layers to the bioclim variables: ecoregions (FAO, 2001), soil types (FAO/IIASA/ISRIC/ISS-CAS/JRC, 2012), aspect, slope, terrain roughness index, and the direction of water flow.

The latter four raster layers were developed in raster package for R programing language (Hijmans, 2013). The reason for using a more extensive set of environmental variables in the model calibration for posterior projection to future climate scenarios is that we do not expect the additional variables to change so drastically in the coming 60 years to justify their exclusion. The ecoregion layer is composed of very broad geographical units. For example, most of Brazil nut's current distribution is limited to one ecoregion: the tropical pluvial forest which includes the Amazon Basin the Colombian Chocó region and parts of tropical pluvial forest in Mesoamerica. Although we recognize that soil types (at least the top soil) can change relatively rapidly, it is likely that at least the categorical division between soil types will largely be maintained in the absence of profound human disturbance. Aspect, slope, terrain roughness and water flow are likewise unlikely to experience significant changes in the future projections here considered. By contrast, it is clear that these variables have changed substantially over the past millennia, making necessary their exclusion from model calibration for projection to past climates.

Collinear environmental layers were removed based on iterative calculations of variance inflation factors (VIF), retaining only variables with VIFs smaller than 5. The retained variables used in the model calibration for posterior projection to past climate conditions were bio3, bio4, bio7, bio10, bio15, and bio16, and for projection to future climate bio2, bio3, bio4, bio5, bio7, bio13, bio15, bio18, bio19, slope, aspect, direction of water flow, terrain roughness index, soil types and ecoregions.

Spatial autocorrelation among species presence points is an important concern in environmental niche modeling and can strongly influence the quality of potential distribution maps, and bias model evaluations based on cross-validation (Hijmans, 2012). We evaluated the ability of all individual modeling algorithms to cope with spatial autocorrelation for both calibration scenarios (for posterior projections to past and future climates, respectively) by calculating calibrated Area Under Curve (cAUC) values and comparing these with a geographical null model (see Hijmans, 2012). To this end, we (i) randomly partitioned both presence and background points in five groups, (ii) carried out five rounds of calibrating and testing all models (including the geographical null model) each time using four partitions for model calibration, and one partition for model testing from which spatial sorting bias was removed following the procedure explained in Hijmans (2012). We repeated this process twice and compared the ten resulting cAUCs of each of the distribution models with the ten cAUCs of the geographical null model by means of Mann-Whitney tests. Only models that gave cAUC values that were significantly higher than the null model were retained in the ensemble model used for projections. Removal of spatial sorting bias in testing data for different model calibrations yielded AUC values for the null model between 0.499 and 0.501 which is equivalent to a random draw (Hijmans, 2012), and cAUCs values of the different individual modeling algorithms between 0.542 to 0.69 (significantly different from null model; Mann-Whithney tests, $p < 0.05$ in all cases). In a next step, we calculated both the calibrated (following the procedure described above) and non-calibrated AUC values for all possible ensemble combinations of the retained models. Each ensemble combination was constructed as the weighted average of its individual composing models, using the cAUC values as weights. The ensemble that yielded the highest sum of calibrated and non-calibrated AUC values was considered to be the most appropriate scenario for projecting to past and future climate conditions, respectively.

During initial model calibration and evaluation using the overall dataset, we noticed that the different ensemble combinations tended to overfit data when projected to current climate layers. Models and ensembles consistently identified suitable habitat conditions in the broad area from southwestern to central Amazonia, *i.e.* the area with the highest density in species observations. However, along the western, northern, eastern and southern margins of Brazil nut's realized niche, most models and ensemble combinations generally performed very well in predicting

habitat suitability at the exact locations (grid cells) of known Brazil nut observations, but showed very limited predictive power to estimate habitat suitability in areas surrounding presence cells. Hence, along the margins the models were particularly successful to predict the observed rather than the potential distribution of the species. This overfitting of models was believed to be largely due to spatial sample bias in the dataset, with an overrepresentation of presence points in the Brazilian Amazon, compared to other areas. Therefore, we repeated model calibrations based on a subset of the presence points from which bias was at least partly removed. To reduce sample bias, we projected all presence points from the overall dataset (489 points) on a 10'grid and randomly selected one presence point per grid cell, which resulted in a subset of 340 presence points (Figure 1). The selected points were then used for model calibration at 2.5'spatial resolution. For models calibrated based on the subset of presence points, we carried out model evaluation with (1) the overall set of presence points (489 points); (2) the set of presence points not included in model calibration (149); and (3) a combination of (2) and a selection of points from the margins of Brazil nut's realized niche (276 points). The third testing dataset was created because most points in (2) were located in the area with the highest density in presence points, with almost no inclusion of points from the margins of Brazil nut's realized niche.

For model projections to past climate conditions we used the (1) a model of the Last Inter-glacial Period (LIG; ~120,000-140,000 yr BP; Otto-Bliesner *et al.*, 2006); (2) two models (MIROC and CCSM) of the Last Glacial Maximum (LGM; ~21,000 yr BP; Braconnot *et al.*, 2007); and (3) a model of the mid-Holocene (~6,000 yr BP; DKRZ, 1992). For characterizing future climate conditions, we used 19 downscaled climate models for the periods 2020-2049, 2040-2069 and 2060-2089 based on the A2 scenario of greenhouse gas emissions (CCAFS, s. d.). Suitability scores of individual projections theoretically range from 0 to 1,000. However, we restricted the modeled distributions visualized on maps to

the maximum training sensitivity plus specificity threshold obtained from model calibration under current climate conditions. To obtain summarizing maps for the different LGM (2) and future (19) climate models we averaged the different threshold-limited suitability maps constructed for all individual climate scenarios. For future projections, we additionally restricted the so-obtained average suitability maps to values above the calibration threshold value and constructed complementary maps showing the number of climate models (out a total of 19) per grid cell for which suitability scores are higher than the threshold value. The latter maps can be considered two-tier ensemble suitability maps, as they are constructed based on combinations of (1) different distribution modeling algorithms and (2) different climate models.

RESULTS

MODEL CALIBRATION AND PROJECTION TO CURRENT CLIMATE

Calibrations based on a subset of the presence data from which the spatial bias was at least partly removed, led to more realistic, yet still fairly conservative, distribution maps compared to calibrations based on the complete dataset. Therefore in what follows we focus on the modeling results obtained with the latter (small) dataset, and where relevant complement these with results obtained with the complete (big) dataset.

Table 1 provides an overview of the best ensemble combinations obtained for model calibrations based on both datasets. It shows that AUC and cAUC values were consistently higher for models calibrated with the big rather than the small dataset. However, in spite of high AUC values, the modeled distribution obtained for the big dataset (calibration for projection to future climate conditions) contained 'only' 92% of all 489 cells with species presence points, which is lower than for the small dataset which covered 98% of presence cells (Figure 2). Hence it seems that the higher AUC values are at least partly related to the

Table 1. Details about modeling calibration and evaluation under current environmental conditions for projections to past and future climate conditions. For projection purposes we used the lowest threshold values obtained with the different sets of testing data, for each of the respective calibrations.

		Model calibration for projection to past		Model calibration for projection to future	
		Complete dataset (489)	Resampled subset (340)	Complete dataset (489)	Resampled subset (340)
Best ensemble		RF & ANN	MAXENT & GLM & GAM & FDA & GLMSTEP & BIOCLIM & RF	RF & SVM	RF & BRT
AUC	All presence points (489)	1	0.92	1	0.99
	Non-calibration presence points (149)	-	0.88	-	0.97
	Extended non-calibration presence points (276)	-	0.87	-	0.98
Calibrated AUC	All presence points (489)	0.98	0.77	0.99	0.95
	Non-calibration presence points (149)	-	0.64	-	0.85
	Extended non-calibration presence points (276)	-	0.70	-	0.87
Maximum training sensitivity plus specificity threshold	All presence points (489)	171	121	85	36
	Non-calibration presence points (149)	-	112	-	33
	Extended non-calibration presence points (276)	-	113	-	33

model's higher ability to assign lower suitability scores to cells containing background points compared to the model obtained from the small dataset. The fact that cAUC values obtained for the big dataset was much higher than for the small dataset, suggests that cAUC is not a silver bullet solution either to select model scenarios which perform best in spite of the existence of spatial autocorrelation in presence data. Taken together, these observations underline the clear limitations of using AUC and cAUC statistics for evaluating the quality of distribution models, which is important to bear in mind at the time of interpreting model outcomes.

For the small dataset, lower cAUC values were obtained with random partitions of testing data not included in model calibration, compared to random partitions of the complete set of presence points (Table 1). This could indicate that also ensembles based on the small dataset have limited power to predict suitability in areas (grid cells) without species observations, but nonetheless favorable habitat conditions. Model calibrations performed for posterior projection to past climates yielded less satisfactory results compared to model calibration for posterior projection to future climate conditions, as is confirmed by lower AUC and cAUC readings. Only 90% of all 489 presence cells were included in the current modeled distribution obtained after projection to current climate conditions, compared to the 98% for model calibration intended for projection to future climates. This could suggest that climate variables alone are not sufficient to explain the current distribution
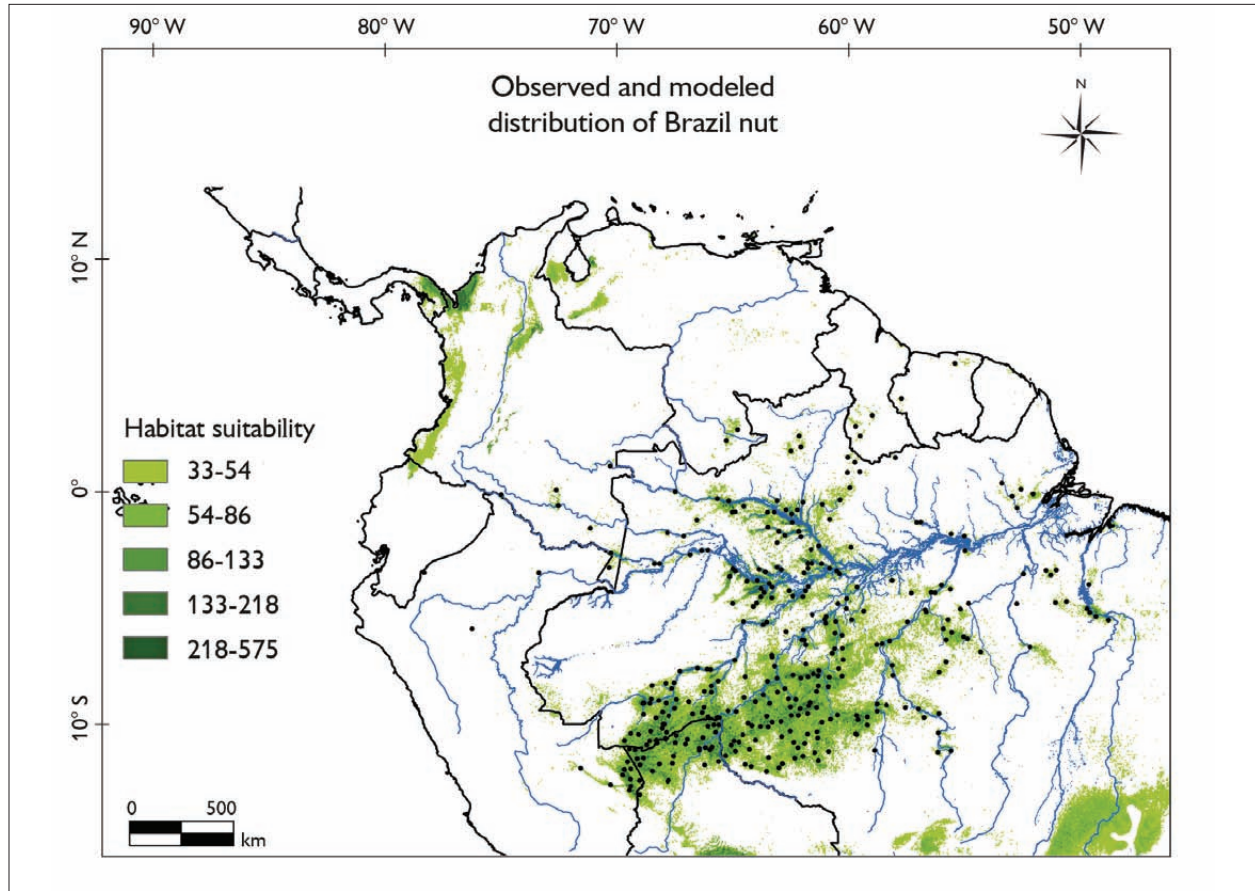
Figure 2. Distribution of suitable habitat of Brazil nut, compared with the locations of presence points (black dots). The same calibration model was used for projections to future climate scenarios.

of Brazil nut and that the additional variables considered here have complementary explanatory power to predict Brazil nut presence and absence.
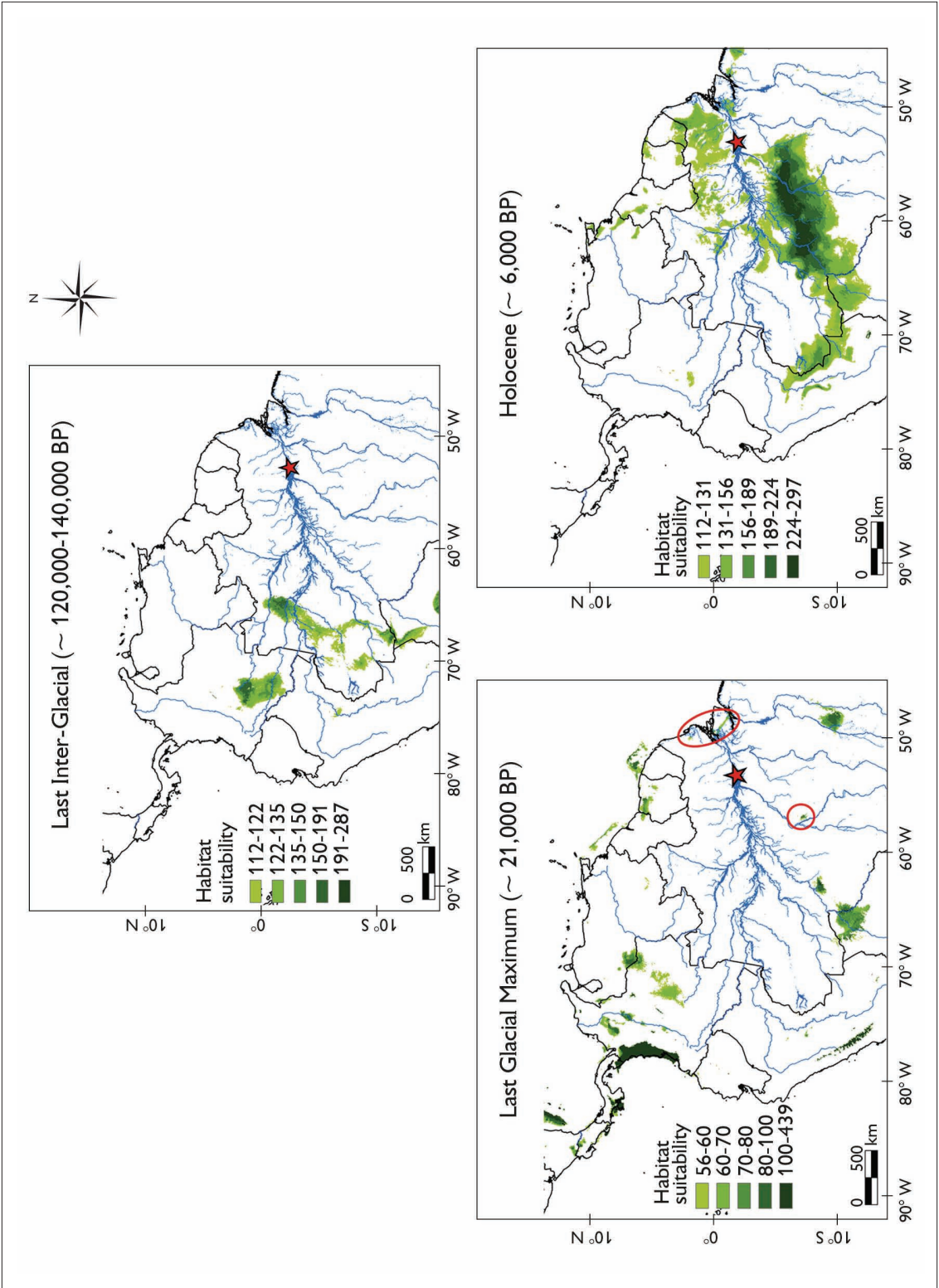
Figure 2 shows that the highest habitat suitability scores of Brazil nut under current climate conditions are found in southwestern and central Amazon. The map suggests that, albeit that Brazil nut does not currently grow there, also the Atlantic and Pacific coastal areas of Colombia and Panama, as well as central Bolivia and southeastern Brazil may hold suitable habitat.

PAST DISTRIBUTION

We constructed habitat suitability maps for three different past time periods: the Last Interglacial period (LIG:

~140,000-120,000 BP), the Last Glacial Maximum (LGM: 21,000 BP), and the Mid-Holocene (~6,000 BP). The only region showing more or less stable suitable habitat conditions for Brazil nut through time is the southwestern Amazon, although there are clear shifts in the distribution of potential areas with suitable habitat within this region between different time periods (Figure 3).

During the LIG suitable habitat conditions may have been located predominantly in western to central Amazonia. As a consequence of temperature cooling and strongly decreased precipitation, suitable habitat conditions were likely to have been seriously reduced during the LGM. Although the models predict favorable conditions in Colombia, Venezuela, the Guyana shield

Figure 3. Potential distribution of suitable habitat conditions for Brazil nut through time. The red circles indicate the location of small areas where favorable habitat conditions may have prevailed during the LGM. The red star indicates the location of the Pedra Pintada cave where the oldest Brazil nut remains have been found, dated to > 11,000 BP (Roosevelt *et al.*, 1996). The lower threshold value of LGM is only half of that of LIG and the Holocene due to the fact that the maps represent average suitability values of maps obtained from projection to two LGM climate scenarios, each of which was limited by the calibration threshold.

and Central America, based on the currently available species distribution data and paleobotanical evidence, it seems unlikely that Brazil nut occurred or survived there during the LGM. The distribution of Brazil nut during the LGM could have been restricted mainly to southern Amazonia. However it is noteworthy that both LGM modeling scenarios also identified suitable habitat conditions north and south of the Amazon River delta. For the Mid-Holocene, the modeling ensemble predicted an expansion of favorable habitat conditions which is already very comparable to current distribution patterns. Generally, highly similar potential distributions under past climate conditions were obtained from models calibrated based on the big dataset.

FUTURE DISTRIBUTION

Projections to future climate scenarios consistently predicted a net increase in areas with suitable habitat for Brazil nut (+233 to +309% on average for different time periods), although there was great variation between climate models (range = +118 to +449% for different time periods; Figure 4), which is related to differences in the severity of changes in climate predicted by different models. The reason for the predicted net increase is that the models predicted greater areas currently not identified as suitable for Brazil nut to become so in the future (+249 to +323% on average for different time periods), compared to currently suitable areas in which climatic conditions may change so drastically that Brazil nut growth might become impossible (-12 to -16% on average for different time periods). It is important to note that this modeling exercise only identifies areas where climate conditions are theoretically favorable to support Brazil nut growth. It does not tell us anything about the actual presence of the species in those sites. The role of humans to introduce Brazil nut in areas that make become suitable in the future will be fundamental to take advantage of the suitability gains predicted under future climate.

Figure 5 summarizes the modeling results geographically. For the maps showing average habitat
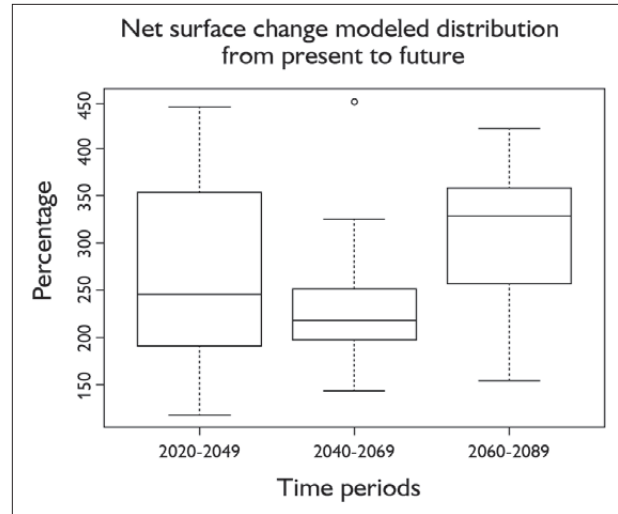

Figure 4. Summary of predicted changes in the future surface of suitable areas for Brazil nut according to different climate models. Each boxplot represents the distribution modeling results for 19 different climate models.

suitability (light to dark green) we applied the same threshold value as for the distribution map under current climate conditions (Figure 2). This is a conservative approach since the modeled distributions of all individual climate models had already been restricted to areas with suitability scores higher than the threshold values, and hence identifies areas with a relatively high probability that Brazil nut will be able to survive there under changing climatic conditions. The maps showing the number of different climate models for which the ensemble of niche modeling algorithms predict presence (yellow to brown) demonstrate how the high variability in climate models is reflected in a highly variable suitability response by the modeling ensemble. In these maps we have only visualized areas where the ensemble predicted habitat suitability for at least ten different climate models. At lower thresholds, nearly all non-Andean areas of northern South America would be included. A closer look at the grid cell-based relation between ensemble suitability scores and the number of climate models for which species presence is predicted, reveals a disproportionally increasing correlation between both.
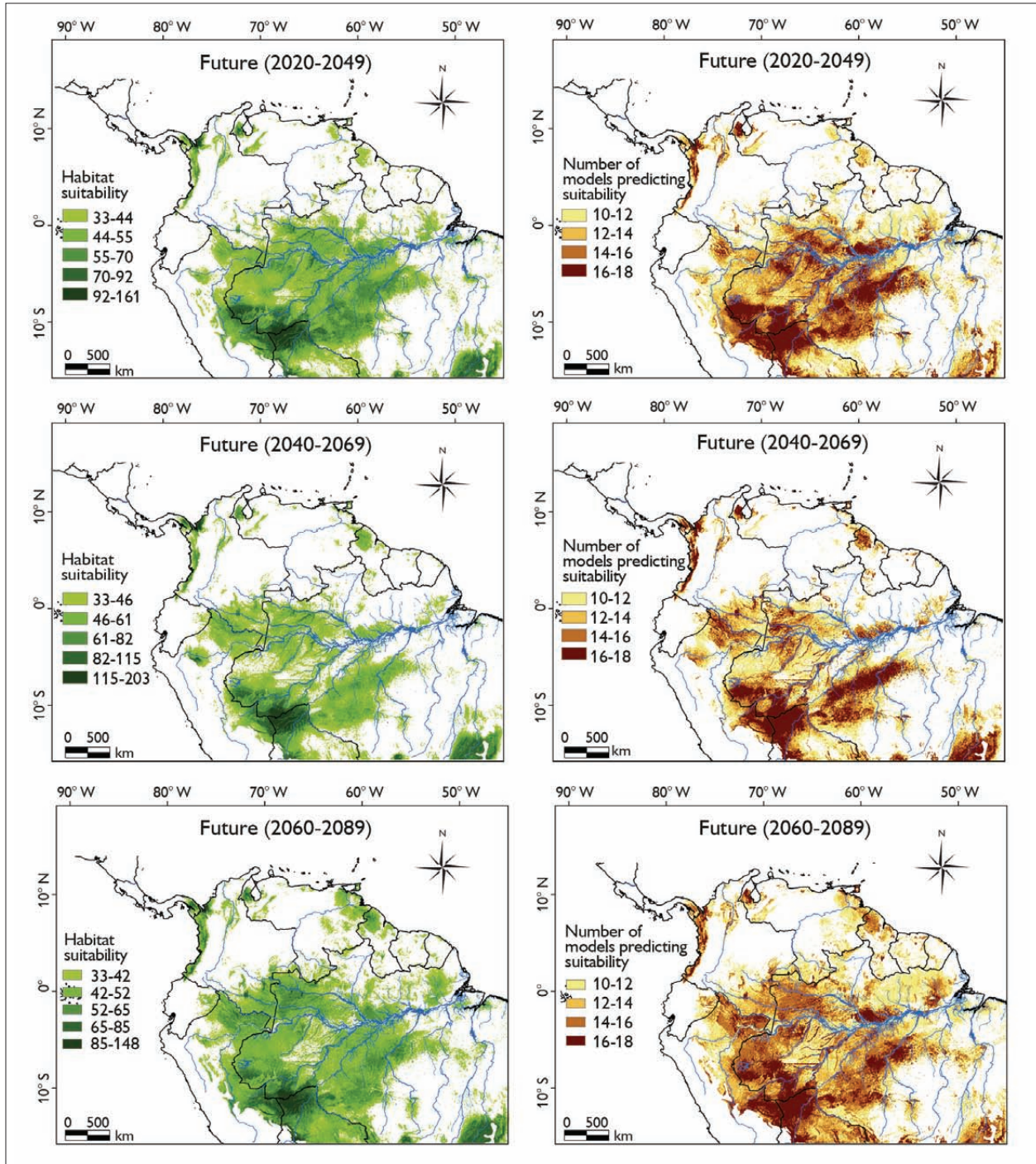
Figure 5. Modeled distribution maps of Brazil nut for future climate periods, constructed through a two-tier ensemble modeling approach. Habitat suitability maps (pale to dark green; left hand side) were constructed by averaging the potential distribution maps obtained for 19 different climate models through application of an ensemble of distribution algorithms. The other maps (yellow to brown; right hand side) show the number of different climate models for which the ensemble of distribution algorithms predicts species presence. Only grid cells for which suitability was predicted for at least ten climate models are shown.

Figure 6 depicts this relation for the period from 2040 to 2069, but highly similar results were obtained for the other time periods. It shows an increasing variability in suitability scores with increasing numbers of models for which the ensemble predicts species presence. Hence, the higher the number of climate models for which the ensemble predicts species presence, the more variable is the suitability score for individual climate models. Figure 6 also shows that the suitability threshold of 33 applied in Figure 5 corresponds to a threshold of approximately ten climate models for which the ensemble predicts species presence, which explains why the different maps for similar time periods in Figure 5 highlight highly similar suitable areas for Brazil nut. Figure 7 shows potential changes in habitat
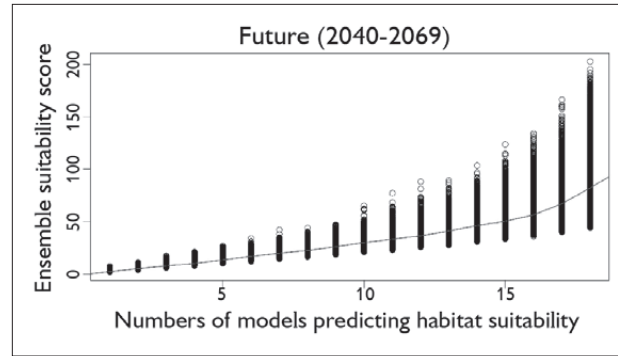

Figure 6. Relation between the number of climate models for which the ensemble of distribution modeling algorithms predict species presence and average habitat suitability in a given raster cell for the time period 2040-2069. Highly similar relations were observed for the other two time periods. A generalized additive model smoother was added to highlight the general trend in data, given that the point data represent more than 370,000 raster cells.
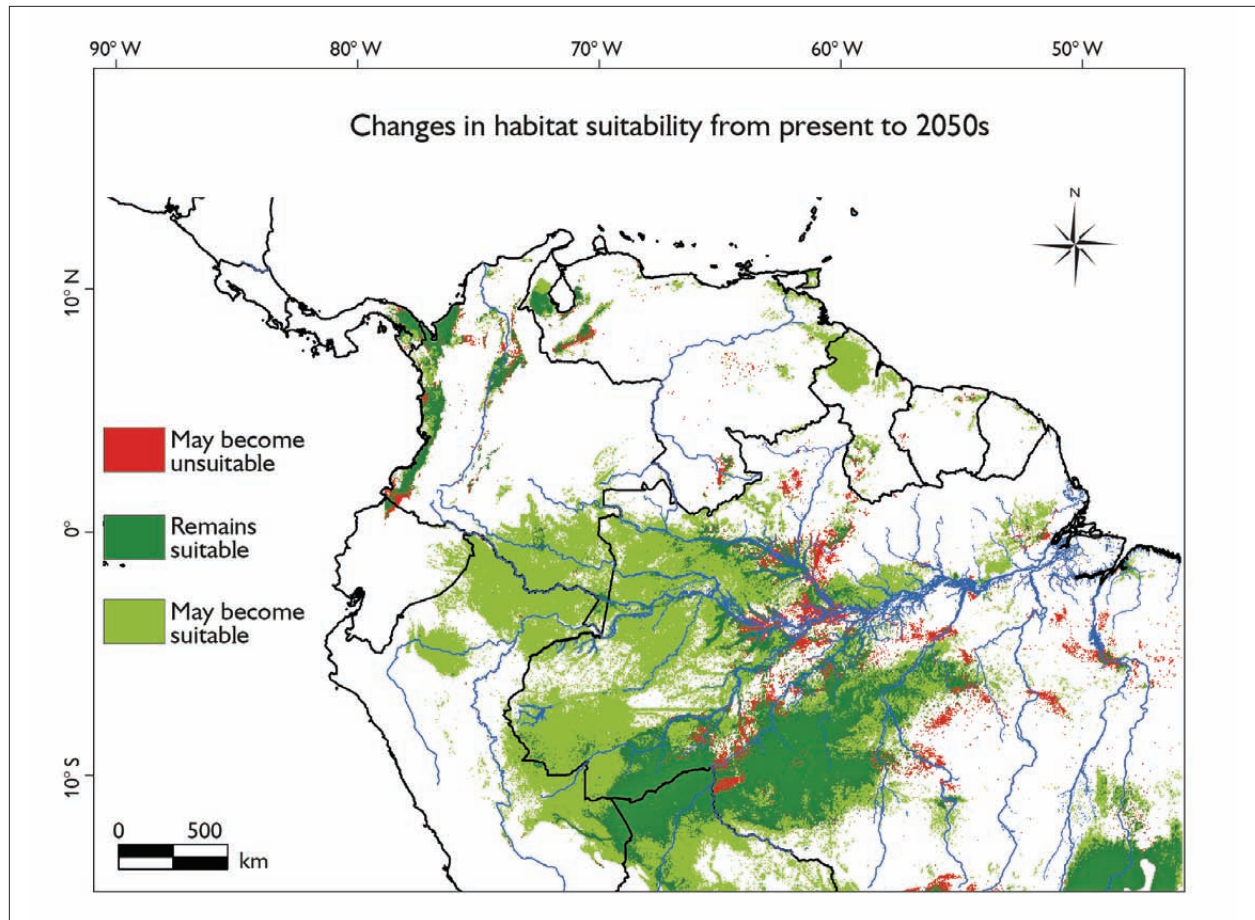

Figure 7. Potential changes in Brazil nut habitat suitability from present to the period from 2040-2069.

suitability for the period from 2040 to 2069 which could be the least favorable of all future time periods for Brazil nut here considered (*cf*. Figure 4). It was obtained through a combination of Figures 2 and 5, and suggests that the areas most negatively impacted by climate change may be located in central and southeastern Amazonia.

Table 2 summarizes the surface areas of the two-tier ensemble suitability maps (green maps in Figure 5) for different time periods, as well as the degree of change in predicted future surface areas compared to modeled distributions under current climate conditions. It confirms our earlier observation for individual climate scenarios (Figure 4) that the future of Brazil nut is likely to be an optimistic one.

DISCUSSION

CURRENT DISTRIBUTION
The distribution of species with longstanding human use and management like Brazil nut is often difficult to model. Apart from constraints and limitations that are inherent to the distribution modeling algorithms and climate models themselves, there are several additional conditions that complicate the construction of the ecological niche of Brazil nut from the different sets of presence points, and hence elaboration of accurate potential distribution maps. Through habitat manipulation and plant management, humans are able to manipulate the densities of plant species at places where they are naturally very scarce or simply would not occur. Furthermore, (historical)

human dispersal and management of plant species do not generally follow regular patterns, and are often the outcome of a series of arbitrary events. These conditions result in sets of species presence points and corresponding values of environmental variables that are a mix of natural and human-influenced plant-environment relations, whereby the human-influenced distribution patterns are more likely to show more irregularities compared to distribution patterns that are entirely due to natural ecological processes. The difficulty is that it is often impossible to distinguish naturally established trees from trees whose occurrence was at least partly influenced by human interference.

Humans have played an important role in the distribution and management of Brazil nut through the Amazon basin. Especially in central, northern and eastern Amazonia Brazil nut distribution has been associated with human activities dating back to pre-Colombian times (Shepard Jr. & Ramirez, 2011). Historical evidence has suggested that the indigenous Amazonian population was not evenly distributed at the time of contact in 1492 (Meggers, 1992; Denevan, 1992, 2003; Clement, 1999). High population densities (as compared to other parts of Amazonia) have been reported for the Amazonian floodplains and varzeas. This is basically because the limits of agriculture using indigenous technology were lower in nutrient-poor interfluves (*i.e.* terra firme soils) than in fertile floodplains (Balée, 1994). McMichael *et al*. (2012) have recently suggested that human disturbance may have been stronger in riverine than in interfluvial forests,

Table 2. Surface areas and proportional changes compared to current modeled distribution areas of sets of modeled distributions obtained through projection to the 19 different climate models for three future time periods. The first number (between brackets) refers to the threshold-limited suitability maps shown in Figure 5 (conservative scenario), while the second number refers to the area where habitat suitability is predicted according to at least one climate model (most optimistic scenario).

Time period	Approximate distribution area (10^6 km^2)	Percent change compared to present
Present	1.30	-
Future (2020-2049)	3.57-7.88	+274 to +606
Future (2040-2069)	2.97-7.79	+228 to +599
Future (2060-2089)	4.14-7.91	+319 to +608

even in the central Amazon where intensive landscape modifications were much more common than in the western Amazon. The current observed distribution of Brazil nuts seems to follow this trend to some extent, particularly in central, and eastern Amazonia (Figure 1), with more trees typically found closer to rivers and less frequently further away from rivers (Levis *et al.*, 2012). At the same time, there are vast areas in the Amazon where Brazil nut does not occur or is extremely scarce, although the habitat is probably suitable. This may be explained by failure of human introduction of the species to those areas (Mori & Prance, 1990; Clement *et al.*, 2010). It is clear that the irregular dispersion of Brazil nut by humans introduces a bias in the environmental niche constructed by the modeling algorithms whereby the overrepresentation of Brazil nut trees that were established at least partly as a consequence of human interference may be interpreted by the distribution models as indicative of greater niche suitability, possibly leading to skewed modeled distributions. It is likely that our original dataset contains a high number of Brazil nut observations that are biased towards places with historical human occupation. Possibly, the tendency of different tested ensemble combinations based on the big dataset to overfit the Brazil nut potential distribution certain areas of its actual realized niche (particularly the margins) is related to this bias.

Part of the problem is also related to the limitations of the AUC statistic for evaluating model performance. Smith (2013) has advocated that the use of presence data that disproportionately represent suitable habitat across the landscape may artificially inflate AUC values. In addition, AUC values calculated on the basis of randomly selected background points as we have done here are known to penalize predictions of high favorability in unoccupied areas, thereby favoring models that predict the actual *vs*. potential distribution of a species (Jiménez-Valverde, 2012). Although calculated on the basis of background and presence testing data from which spatial sorting bias is removed (Hijmans, 2012), the calibrated AUC values seemed to suffer from the same problems as the AUC described above, given that higher cAUC values (0.98-0.99) were obtained for the big dataset (the overfitted distribution) than for the small dataset (cAUC = 0.77-0.95). Interestingly, this suggests that it is not necessarily the quantity of presence points that matters to improve model performance, but rather how proportionate their density is to the representation of suitable habitat across the landscape. In this case "less was clearly more".

We believe our map of Brazil nut's potential distribution strikes a good balance between predicting (1) the trees' observed distribution (evidenced by the fact that 98% of all 489 presence cells are included in the modeled distribution area), and (2) habitat suitability in areas without observation points but with a high likelihood to harbor Brazil nut (evidenced by the fact that the 95% of the 149 presence cells not included in the model calibration are located in the modeled distribution area). It is likely that our map is a conservative representation of the species' true potential distribution and should be updated as more data become available. However, the fact that our distribution map confirms several field observations reinforces its usefulness. For example, according to Homma (2000) there used to be enormous Brazil nut stands along the Tocantins River. Although we do not have any observation point from this area, the ensemble did predict vast areas with suitable habitat. Another example is that in central, eastern and northern Amazonia the modeled distribution is very discontinuous and diffuse which corresponds with field observations that Brazil nut typically occurs at high densities in certain locations but is absent in vast areas of forest surrounding those locations, which in itself has been attributed to past human influences (Mori & Prance, 1990; Peres & Baider, 1997; Salomão, 2009; Baider, 2000; Scoles & Gribel, 2011). Also the typically clustered occurrence of Brazil nut around rivers in central, eastern and northern Amazonia described in literature (*e.g*. Levis *et al.*, 2012) is confirmed by our potential distribution map.

There is growing evidence that more accurate potential distributions are generally obtained on the basis of higher rather than lower resolution layers (Seo *et al*., 2009; Gillingham *et al*., 2012), hence probably more accurate distribution maps can be developed for Brazil nut at higher resolution than the 2.5 minutes we have used here. At the same time, the elaboration of such high resolution distribution maps is probably better done at a smaller geographical scale, inter alia, because the adaptive potential of Brazil nut populations may be different from one area to the next, and because more detailed data to characterize the tree's habitat preferences are often available at smaller scales. At (sub-)country level, generally more extensive and spatially proportional presence/absence data, as well as more detailed thematic maps (soils, topography, vegetation etc.) are available which can greatly improve model performance. At a continental scale, the availability of presence/absence data is often much more clumped, with some areas being overrepresented and others underrepresented in the overall dataset, resulting in sub-optimal modeling outcomes.

PAST DISTRIBUTION

Of the three past time periods here considered, the LGM most likely had the greatest impact on the current distribution of vegetation and flora in the Amazon basin (van der Hammen & Hooghiemstra, 2000). The potential distribution of Brazil during the LGM seems to have been much more restricted than today, with most of the suitable areas being located across southern Amazonia. These areas may have acted as refugia in which climate conditions remained favorable during the most likely generally dry and cold LGM. Of these, the southwestern Amazon region appears to have been the only continuous area to provide suitable habitat to Brazil nut since the LIG, or at least since the LGM (Figure 3). This is also the same area where Brazil nut is a characteristic element of the vegetation and from where the vast majority of

commercial Brazil nut has been harvested in recent history (Stoian, 2004; Wadt *et al*., 2008).

Shepard Jr. & Ramirez (2011) have presented the hypothesis of a central Amazon origin of Brazil nut. We believe this hypothesis is very difficult to prove considering that the species very likely occurred in the region for at least several hundreds of thousands if not millons of years. The evidence available today only permits us to make allusions about the most recent part of the lengthy natural history of the tree. It is likely that Brazil nut used to have a broader distribution before the last glaciation, at least during certain time periods. During the Miocene (23-5.3 Ma BP), the generic composition of the flora in South America was already very similar to present and the diversity was probably higher than at present (van der Hammen & Hooghiemstra, 2000). Since then there have been frequent environmental changes in Amazonia, some more stressful than others, with the last most stressful event being the LGM. Hence it is likely that the distribution of Brazil nut through time has been characterized by a series of periods of range contraction and range expansion, which may, or may not, have left clues which would allow tracing back the species' true origin. One aspect of Brazil nut's reproductive system that supports the hypothesis of a wide pre-LGM distribution is the highly specialized nature of its fruits, which suggests a long-term co-evolution with a now extinct effective dispersal agent that could have been more effective in dispersing the tree over the Amazon basin compared to the agouti rodents. Indeed, as indicated in the introduction it seems difficult to believe that a tree would invest so much energy in such specialized fruits and seeds for the sake of the relatively inefficient dispersal carried out by agoutis (Scoles, 2011). Although the possibility of a known but now extinct Pleistocene megafauna dispersal agent has recently been ruled out for Brazil nut (Guimarães Jr. *et al*., 2008), it is still possible that either the remains of such a disperser are yet to be found, or that the dispersal agent which co-evolved with Brazil nut predates the late Pleistocene period.

The locations of the different putative refugia identified by our modeling ensemble (Figure 3), partially coincide with potential LGM refugia identified in the literature based on climatic conditions and levels of endemism in different groups of organisms (Haffer & Prance, 2001; Haberle & Maslin, 1999; van der Hammen & Hooghiemstra, 2000; van der Hammen & Absy, 1994). It is probable that during the LGM, wet forest refugia were surrounded by drier vegetation types, which acted as effective dispersal barriers. Rossetti *et al*. (2004) have presented compelling evidence, drawing on an integrated approach using paleontology, sedimentology and radiocarbon and isotope data, that the dominant vegetation in central Amazonia corresponded to arboreal savanna between 15,000-11,000 BP (and probably even longer), a habitat which was clearly not suitable for Brazil nut. During the Holocene, Brazil nut populations probably expanded again from the different (micro-)refugia areas where they survived during glaciations, owing to increasing temperature and precipitation. According to our modeling exercise, favorable conditions for Brazil nut may have appeared in most of its current growing areas as early as 6,000 BP.

It is noteworthy that the ensemble predicted small potential LGM refugia for Brazil around the Amazon River delta (Figure 3). This area has also been identified by other authors as a potential glacial refugium (van der Hammen & Hooghiemstra, 2000). If our hypothesis that Brazil nut probably had a wider distribution prior to the last glacial period is correct, it is likely that one or more populations were able to survive there during glaciations. In any case, these potential refugia are located closer to the Pedra Pintada cave site that was occupied some 11,000 years ago by ancient hunter-gatherers and where the oldest remains of carbonized Brazil nuts were found (Roosevelt *et al*., 1996), than the potential central Amazon refugium located at the mouth of the Teles Pires and Tapajos rivers (Figure 3). Given that agoutis normally do not disperse seeds further than 100 m away from the mother tree (Tuck Haugaasen *et al*., 2010, 2012), and that under natural forest conditions, Brazil nut trees need at least 20 years to reach reproductive age, a reasonable expansion rate would be 1 km every 20 years, even when considering the possible occurrence of occasional longer distance dispersal events mediated by other animals like monkeys. Based on this, bridging the 400-500 km distance from the coastal or river delta refugia shown in Figure 3 would require at least 8,000-10,000 years, while for the Teles Pires-Tapajos refugium it would take at least 12,000-14,000 years and for the southeastern and southwestern Amazon refugia more than 18,000 and 20,000 years, respectively. The southeastern and southwestern refugia are clearly much too far for Brazil nut to already have reached the Pedra Pintada site through natural processes at the time of its human inhabitance. Range expansion from either the coastal or central Amazon refugia is more likely. Theoretically this is a realistic possibility for the coastal refugia, considering the time gap of ~10,000 years between the LGM and the age of the Brazil nut remains found at Pedra Pintada. Additionally, the Pedra Pintada site is located at the northern side of the Amazon river. As transport of Brazil nut fruits or seeds over water by the species' presently known animal dispersal agents is very unlikely, it seems more probable that Brazil nut reached the Pedra Pintada site from one or more LGM refugia located north of the Amazon River, rather than from a potential refugium on one of the islands of the Amazon River delta. As shown in Figure 3, suitable habitat conditions did prevail in coastal areas north of the Amazon delta.

More clarity about range contraction in Pleistocene refugia and posterior expansion patterns could possibly be obtained from genetic studies. Genetic studies in Brazil nut so far have demonstrated very limited genetic differentiation among Brazil nut stands separated by large distances (up to 2,800 km; Kanashiro *et al*., 1997; Gribel *et al*., 2007). This could point to three things. First, that all the sampled populations are derived from parent populations with

a common ancestry in one Pleistocene refugium, else one would expect to see stronger genetic differentiation between populations, as is for example the case for cacao, for which human management can be assumed to have been more intense than for Brazil nut (Thomas *et al*., 2012). Second, it could suggest a fairly recent irradiation across the Amazon basin whereby humans acted as the principal long-distance dispersal agents (Gribel *et al*., 2007). A third possibility is that the signals of genetic differentiation in Pleistocene refugia have been obscured by more recent introductions of germplasm by humans. The effective long distance pollination by the bee pollinators would have favored fast introgression of newly introduced genes in resident populations and vice versa. It is clear that more genetic studies covering Brazil nut's overall distribution range are necessary to obtain clarity about the locations of the potential source populations that led to Brazil nut's current distribution, and the existence or not of different genetic groups in the species. Particular attention should be paid here to include Brazil nut populations that are located in or nearby the putative refugia we have identified here.

FUTURE DISTRIBUTION

Projection of the distribution modeling ensemble to future climate conditions returned relatively consistent indications of a positive future for Brazil nut, provided that land use allows this, and that there are no restrictions to dispersal (*e.g.* mediated by humans). Although the present climate change impact assessment can be informative for identifying expected large scale trends in the potential distribution of Brazil nut, the elaboration of concrete conservation and management strategies should best be based on similar assessments carried out at higher resolution for specific target areas. As mentioned before, more accurate potential distributions are generally obtained based on higher rather than on lower resolution layers, particularly when making projections to future climate scenarios (Seo *et al*., 2009; Gillingham *et al*., 2012; Moudrý & Šímová, 2012). Additionally, distribution of modeling of Brazil

nut at smaller geographical scales are likely to allow for more robust decision making. We performed a similar modeling exercise as presented in this paper for Brazil nut in the Peruvian department of Madre de Dios, but at a resolution of approximately 250 m and on the basis of many thousands of presence points, which not only resulted in a very accurate map of Brazil nut's current distribution in the region, but also displayed very similar trends as those described here, but with a greater level of detail (Evert Thomas *et al*., unpublished data). Similar to the present analysis, habitat expansion was suggested for all 19 different climate models, although average suitability scores for projections to future climates were lower than for present climate conditions.

The usefulness of species distribution modeling for guiding conservation and management decisions is increasingly being recognized (Guisan *et al*., 2013). However, caution is important when using modeled distributions in the decision making process. Most importantly, one should bear in mind that most species distribution models, including the ones we have used here, have been designed for predicting habitat suitability only. Although positive correlations between suitability scores and population density have been reported before, and we have been able to confirm this pattern for Brazil nut populations from the Peruvian Amazon (Evert Thomas *et al*., unpublished data), it is much less clear how suitability scores relate to population stability and persistence under rapid environmental change (Oliver *et al*., 2012; Guisan *et al*., 2013). Hence, one should not blindly trust modeled distribution maps under future climate scenarios to guide climate change adaptation decisions. Rather, these maps need to be interpreted in combination with as many other relevant data sources as possible. For example, landscape metrics that take into account habitat heterogeneity or configuration and data from monitoring schemes can provide important additional insights (Oliver *et al*., 2012). Also, a better understanding of past, present and expected future human impacts is important for the

development of effective conservation and management strategies. Anthropogenic disturbance, for example, comes in many forms and may affect the sustainability of Brazil nut stands in different ways, as illustrated by MAPFORGEN (s. d.) which presents a habitat-based assessment of different anthropogenic threats on Brazil nut in South-America, such as fire and the conversion of wild habitats to agricultural land.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

The generally optimistic future for Brazil nut predicted by our modeling exercise is in line with general trends emerging from the growing knowledge about the tree's ecology, regeneration and management. The current distribution of Brazil nut across the south-American continent has largely been influenced by humans ever since their arrival to the Amazon basin (Shepard Jr. & Ramirez, 2011), and there is no reason why this would need to change in the future. In fact, increasing evidence suggests that Brazil nut establishment and growth may be promoted by small scale human disturbance such as swidden agriculture (Kainer et al., 1998; Paiva et al., 2011; Scoles et al., 2011). The necessary protocols and technology for propagation and establishment and management of plantations are available (Mori & Prance, 1990). Vegetative propagation through grafting holds great potential, as trees are smaller, which may facilitate harvesting, and grafted trees may start producing as early as 3.5-4 years after grafting (Müller, 1981; Mori & Prance, 1990). The success rate of propagation through cuttings is still very low (less than 1%), but research is underway to overcome this limitation (Ronald Corvera, personal communication). Extensive areas of Brazil nut plantations have been established in Brazil since the 1950s with promising results (Mori & Prance, 1990). In general the tree seems to perform well in plantations, even on soils degraded by mining, suggesting its potential role in restoration activities (Salomão et al., 2006).

Future climate projections predict either stable or increased habitat suitability in many different areas where Brazil nut currently does not grow, such as the Colombian Pacific and Atlantic coast areas, the Guianas, central Bolivia and southeastern Brazil. This offers opportunities to start establishing Brazil nut in these areas now, not only with the prospect of increasing the future conservation status of the species, but probably more importantly, to create additional sources of income for local communities. Different approaches are possible in these new areas; from monospecific plantations over establishment of Brazil nut in agroforestry systems, to enrichment planting in existing forests (Müller, 1981; Costa et al., 2009). In addition to the nuts, also exploitation of the wood of the tree from plantations holds great potential. Not only do young Brazil nut trees grow very fast, they also resprout after cutting. Experiments in Brazil have shown that monospecific plantations established at high initial planting densities (~1,000 trees/ha) allowed for cutting cycles of only four years. Owing to vigorous resprouting of the young trees, several cutting cycles appear to be possible. The wood harvested from such plantations can be commercialized in niche markets, such as in the parquet industry. If future seed trees are identified and protected from the onset, in the longer term these short-rotation plantations can become stands for fruit production (Ronald Corvera, personal communication). Commercialization of Brazil nut wood should, however, not interfere with the legal ban on logging of the tree from natural forests in Bolivia, Brazil and Peru. Different approaches can be used to control illegal harvesting of Brazil nut timber. One measure could be to allow only small diameter logs to be commercialized. Such logs originating from short-rotation plantations would probably much cheaper than similar logs harvested from natural stands, which would take away the economic incentive for illegal harvesting. A probably more waterproof control mechanism would be through the combined use of genetic and isotope markers, a methodology currently being tested by the global timber tracking network (GTTN, s. d.).

For the establishment of Brazil nut in any area where it currently does not occur, it will be very important to use diverse germplasm from sources that have the highest potential to survive in the target sites and establish self-sustaining populations (Thomas *et al*., 2014). Diverse seeds are also important for fruit production. Moritz (1984) has shown that fruit production as the result of pollination between trees of the same clone is low, emphasizing the importance of using reproductive material from trees that are not only most productive, but also represent a broad genetic base. Genetic improvement in Brazil nut was initiated with the work of Moritz (1984) and recent research (Camargo *et al*., 2010) has demonstrated the good potential to improve fruit characteristics and productivity though selection and breeding. Ideally, well-designed continental-scale provenance trials in a variety of habitats, including sites where Brazil nut currently does not occur yet but where environmental conditions are similar to those expected to become more prevalent under climate change, could be established to generate knowledge on the adaptive potential of different provenances (*cf*. Thomas *et al*., 2014). However, much useful information could also be obtained from already established plantations, clonal gardens and smaller provenance trials, as long as detailed and trustworthy information is available about the origin of the source material. Also, observations from natural and anthropogenic Brazil nut stands can be highly informative. For example, Picanço (2010) reported higher densities in transition areas between Cerrado (tropical savanna vegetation) and Amazon forest (11.3 trees/ha) than in terra firme forest (6.7 trees/ha), Brazil nut's naturally preferred habitat (Mori & Prance, 1990), which could suggest that the species has a certain level of plasticity and that some provenances may show higher drought tolerance than others. If Brazil nut has been able to survive past periods of cooling and warming, and drying and wetting, it must surely be able to persist under future climate change particularly when the right conditions for establishment and growth are created.

Although not unique, the legal ban on logging of Brazil nut in Bolivia, Brazil and Peru is quite exceptional in the world of nature conservation. This measure may not be very effective in preserving Brazil nut trees that are left behind after the conversion of forest to other types of land uses (Viana *et al*., 1998), but it does prevent or reduce the logging of trees in forest environments. A significant proportion of the currently most productive Brazil nut forests already enjoy a certain protection status; in Brazil through the extractive reserves system, in Peru through Brazil nut concessions and in Bolivia through community ownership over Brazil nut forests. Also these types of protection are not absolute, but at least they reduce the fragmentation and isolation of populations and promote gene flow. Large population sizes and extensive gene flow are important for the long-term persistence of tree species because they promote the generation of new gene combinations and allow natural selection to shift fitness-related traits so that populations can adapt to changing environmental conditions (Thompson *et al*., 2010). Brazil nut's pollinator bees are clearly very effective in ensuring long-distance gene flow (Janzen, 1971; Maués, 2002), another pro on the trees' list of beneficial mechanisms promoting climate change adaptation. However, the bees themselves are also likely to be affected by climate change, and ensuring sustainability of Brazil nut stands might require more research in this domain as well.

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