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Predicting aboveground forest biomass with topographic variables in human-impacted tropical dry forest landscapes

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Abstract. Topographic variables such as slope and elevation partially explain spatial variations in aboveground biomass (AGB) within landscapes. Human activities that impact vegetation, such as cattle grazing and shifting cultivation, often follow topographic features and also play a key role in determining AGB patterns, although these effects may be moderated by accessibility. In this study, we evaluated the potential to predict AGB in a rural landscape, using a set of topographical variables in combination with indicators of accessibility. We modeled linear and non-linear relationships between AGB, topographic variables within the territorial boundaries of six rural communities, and distance to roads. Linear models showed that elevation, slope, topographic wetness index, and tangential curvature could explain up to 21% of AGB. Non-linear models found threshold values for the relationship between AGB and diffuse insolation, topographic position index at 19 × 19 pixels scale and differentiated between groups of communities, improving AGB predictions to 33%. We also found a continuous and positive effect on AGB with increased distance from roads, but also a piecewise relationship that improves the understanding of intensity of human activities. These findings could enable AGB baselines to be constructed at landscape level using freely available data from topographic maps. Such baselines may be of use in national programs under the international policy Reducing Emissions from Deforestation and Forest Degradation.

Key words: aboveground biomass; landscape approach; Reducing Emissions from Deforestation and Forest Degradation (REDD+); rural communities; topographic variables.

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Introduction

Aboveground biomass (AGB) patterns, and hence carbon stocks, are unevenly distributed in the space, even within the same forest ecotype (Houghton 2005). These uneven patterns are determined by multiple biophysical factors, such as elevation, slope, and insolation, but also by human factors (Galicia et al. 1999, Jaramillo et al. 2003, Lovett et al. 2006, Alves et al. 2010, Marshall et al. 2012, Toledo-Garibaldi and Williams-Linera 2014). Often referred to as perturbations, the effects of human uses on forest which remains forest include changes in the overall amount of standing stock (AGB) and changes in structure, through selective removal of certain species, while others find the opportunity to regenerate. The changes may be small, but they may also be considerable, to the point where the ecosystem may be considered secondary forest (although this term is often also used to refer to regrowth of forest following clearance). The magnitude and the impact of human uses on forest structure depend primarily on the particular type of use: Grazing, shifting cultivation, and harvesting for firewood or for charcoal will all leave distinctly different footprints on the forest (Chazdon et al. 2016).

Human factors may, however, be partially dependent on the biophysical determinants (Méndez-Toribio et al. 2016), or independent of them, as in the case of accessibility from roads or human settlements (Mon et al. 2012). While the influence of human factors on AGB may be fluid, varying over time and space as a result of different human activities (Lovett et al. 2006, Alves et al. 2010, Toledo-Garibaldi and Williams-Linera 2014), biophysical factors such as water availability are strongly influenced by relatively permanent topographic variables such as elevation, slope, and aspect (Laurance et al. 1999, Lovett et al. 2006, Marshall et al. 2012). The aim of this paper was to explore the possibilities of modeling the impacts of topographic and human variables on vegetation structure and particularly on carbon stocks. One purpose of such modeling may be to provide technical support to governments in their planning for Reductions in Emissions from Deforestation and forest Degradation (REDD+), which involves reducing losses of biomass and enhancing forest carbon stocks while ensuring biodiversity conservation and sustainable development. If biomass and carbon stocks can be predicted using a set of topographical variables in combination with indicators of accessibility, locally realistic targets for improvement in carbon stock can be constructed.

Environmental factors that influence forest biomass

Many studies have related variation in forest structure and density to topographic variables, which are used as proxies for the factors that are believed to cause the variation. Water availability is one of the main such factors in seasonally dry tropical forest (SDTF; Galicia et al. 1999, Brienen et al. 2010, Jaramillo et al. 2011, Maass and Burgos 2011). For example, strong differences in biomass associated with relative position and water availability have been reported in deciduous upland and the semi-deciduous floodplain forests in Chamela (Jaramillo et al. 2003). Since water availability is strongly affected by elevation above sea level, aspect, slope angle, and terrain convexity, these variables are often used as indirect measures (Pachepsky et al. 2001), usually in combination, since water availability may be substantially modified over short distances in response to the interplay of such topographical factors (Leij et al. 2004).

Elevation and slope are the most commonly considered topographic variables in relation to forest structure (Appendix S1: Table S1). Elevation or factors related to it such as air temperature and solar radiation affect forest biomass through evapotranspiration rates (Homeier et al. 2010, Sundqvist et al. 2013). Forest biomass may relate to elevation to it both in a monotonic (Lieberman et al. 1996) and in a hump-shaped (Marshall et al. 2012) pattern. While the former trend suggests that temperature decreases and stress increases with elevation, the latter suggests that there exist constraints that co-vary with elevation. Slope angle has also been reported as an explanatory variable of forest structure, particularly of biomass and canopy height (Laurance et al. 1999, Yanagisawa and Fujita 1999, Sawada et al. 2015; Appendix S1: Table S1).

The effect of aspect on forest structure has been well recognized, but in tropical areas this does not usually play a key role in structuring vegetation (Gallardo-Cruz et al. 2009). However, results from some studies performed in the Northern Hemisphere have shown northern-facing slopes having higher biomass levels (Kariuki et al. 2006) than southern-facing ones. This is probably linked to a number of other environmental factors that lessen or mask the effect of aspect (Kirkpatrick et al. 1988). Solar radiation, that is, the amount of radiant energy received at a certain location, varies not only with the amount of sunshine but with slopes, aspect, and adjacent relief (Wilson and Gallant 2000).

Human factors that affect forest biomass

It is important to note, however, that almost all studies that evaluate topographic variables as determinants of forest biomass and forest structure have been carried out in preserved forests (Appendix S1: Table S1), that is, in forests that are hardly affected by human factors. In many tropical forests, natural forest cover is being reduced and forests are being modified by human uses (FAO 2016), and it is precisely in these forests that the potential for REDD+ is greatest. Clearly, the addition of anthropogenic factors complicates the relationships between environmental variables and biomass and makes prediction of biomass levels over space even more challenging. However, while human intervention is an extra factor modifying carbon stocks, these effects may not be random. They may well follow a topographic template, since human uses of forest such as shifting cultivation and grazing tend to occur at specific elevations and on specific types of slopes and may therefore have relatively predictable effects (Vázquez and Givnish 1998, Morales-Barquero et al. 2015, Méndez-Toribio et al. 2016). For example, common uses of SDTF in Mexico include temporary clearing of patches of trees for shifting cultivation on the lower slopes and on the shoulders of hilly terrain (Borrego and Skutsch 2014, Morales-Barquero et al. 2015), which is followed by regrowth, resulting in a spatial mosaic of varying biomass densities across these zones. Wet season grazing by small farmers, which takes place largely on the steeper slopes between these two zones, has the effect of lowering biomass stocks slightly across these areas (Jardel et al. 2012, Morales-Barquero et al. 2015). However, where pressure is greater as a result of accessibility to roads and human settlements, there is obviously more likelihood of direct or indirect impact on natural vegetation (Cincotta et al. 2000, Luoga et al. 2002, Mon et al. 2012, Malhi et al. 2014, Morales-Barquero et al. 2015). The effects of firewood gathering also depend on the intensity of this activity and may be very limited if much of it dead wood. It is therefore to be expected that there will be a response in forest structure due to human activities, and that this may be partly related to topography but to the gradient of intensity, which may be expressed in terms of accessibility (Luoga et al. 2002, Mon et al. 2012).

Policy context and setting of the study

This study has been carried out in the context of Reducing Emissions from Deforestation and forest Degradation in developing countries (REDD+) and recent calls for this to follow a “landscape” approach. Reducing Emissions from Deforestation and Forest Degradation is a policy framework under the United Nations Framework Convention on Climate Change (UNFCCC). It proposes a performance-based payment mechanism to reduce the emissions of greenhouse gases from tropical forest sources (Pelletier et al. 2016). Although popularly considered a mechanism to slow down the rate of deforestation, REDD+ also aims to reduce forest degradation and promote forest enhancement, and in this context, it is logical to target secondary forests. Strategies to promote natural regeneration by removing the human factors that cause degradation may in some countries result in greater carbon savings than reductions in deforestation, given the fact that so much of the forest is degraded (e.g., Trejo and Dirzo [2000] estimate that 80% of SDTF in Mexico is degraded, while the rate of deforestation of SDTF was <0.4% per annum from 2002 to 2007, and has since been decreased even further) (CONAFOR 2010). The rate of uptake of carbon when secondary forest is allowed to recover naturally may be substantial. For example, Pan et al. (2011) explored the differences in sink activity between intact and regrowth forests and found that the absorption rates in anthropogenically and naturally modified (i.e., degraded but regenerating) forests are more than three times higher than those in intact forests across the tropics. Poorter et al. (2016) have provided evidence of carbon uptake rates in secondary forests across the Neotropics, which are up to 11 times higher than those in intact forests, at around 3 t C per ha per year. Chazdon et al. (2016) have estimated that secondary growth forests in Latin America and the Caribbean have the potential over the next 40 yr to absorb carbon equivalent to that emitted by the region from all fossil fuel and industrial sources between 1993 and 2014.

To deal effectively with the potential of secondary forests under REDD+, it is necessary to better understand the drivers which cause degradation and stand in the way of enhancement. For this reason, a “landscape approach” has been proposed with the idea that improved forest management will depend on managing entire rural production systems in more sustainable ways (GLF 2013*a*, *b*, Minang et al. 2015). Particularly in Mexico, REDD+ policy is moving toward a landscape approach in which territorial plans at the community level will be the basis for financial support for management activities (Madrid and Deschamps 2014, Rantala et al. 2014, CONAFOR 2016).

Our study focused on SDTF, which is widely distributed throughout Mexico (Trejo and Dirzo

2000) in areas with strongly marked seasonal rainfall (Murphy and Lugo 1986, Bullock et al. 1995, Dirzo et al. 2011). Aboveground biomass in this forest type ranges from 45 to 390 Mg/ha and belowground biomass from 26 to 66 Mg/ha (Jaramillo et al. 2011). Seasonally dry tropical forest is generally water, rather than nutrient, limited (Murphy and Lugo 1986), so biomass in sites with high soil water storage capacity may be high (Jaramillo et al. 2003). This is thought to be the primary explanation for the wide range of AGB figures that have been observed within Mexico (Jaramillo et al. 2011).

Almost all SDTF in Mexico has been affected by anthropogenic activity. About half of the original area covered by this vegetation type was cleared in the 20th century and the majority of the remaining part is used by rural populations for shifting cultivation, grazing, and collection of a variety of forest products including firewood and fencing posts (Maass et al. 2005). Aboveground biomass in the majority of Mexican SDTF is well below that in the intact forest (Morales-Barquero et al. 2015), which offers opportunities for reversal under programs such as REDD+.

The paper explores the possibilities of modeling the impacts of topographic and human variables on AGB. Standing forest biomass levels will be related to variables that describe the physical form of landscape, such as elevation, slope, curvature, based on empirical evidence gathered in a case study site in a SDTF zone. If forest biomass levels can be statistically explained by combinations of such factors, this could be used to estimate the carbon potential of a given landscape and assist in the identification of areas where levels are well below this, pointing to areas most appropriate for REDD+ interventions at the local level and thus filling an important role for the implementation of this policy at the local level. These relationships would be expected to differ under different topographic landscape configurations, due more to regional topographic controls on forest structure than local ones.

Methods

Study area

The study was conducted in the central part of the basin of the Rio Ayuquila, in Jalisco, a state in west-central Mexico (Fig. 1), within an area which falls under the Inter-municipal Association of the Ayuquila River Basin (JIRA). This is a group of 10 municipalities, which aims to coordinate environmental management and has been selected as an Early Action Area for REDD+. The area is surrounded by uplands such as Sierra de Manantlan, Sierra de la Amula, Sierra de Cacoma y, and Sierra de Tapalpa and includes three distinct plains areas: Autlán, El Grullo, and el Llano en Llamas.

The study area is dominated by undulating hills grading to steep slopes and narrow river valleys with elevations ranging from 515 to 1711 m above sea level. The slopes range from 0 to 87%. Elevation and slope generate a gradient in micro-climatic conditions, particularly with regard to humidity and temperature. Mean rainfall is between 400 and 1600 mm (Vidal-Zepeda 1990), with a dry season from mid-November through May; summer rains occur between June and September (Jardel et al. 2012). Temperature range is between 20° and 24°C (García 1998). The eastern section of study area is warmer and drier than the western.

Several forest types are found in the study area (Jardel et al. 2012), but this study focused on SDTF. In the study area, this type of vegetation is used for a number of productive activities, including extensive cattle ranching (Jardel et al. 2012) and shifting cultivation, which is locally called *coamil* (Borrego and Skutsch 2014, Salinas-Melgoza et al. 2017).

Six rural communities (*ejidos*) were included: Agua Hedionda, Ayutita, Chiquihuitlán, El Temazcal, Tonaya, and Zenzontla (Fig. 1). These communities show a wide range of topographical characteristics within the SDTF zone, enabling relationships between forest structure and topographical variables tested in this study (Table 1).

Vegetation in the study area has been modified by humans at least since Mexico's colonial era for productive purposes such as cattle, sugar cane (Louette et al. 2001, Gerritsen and van der Ploeg 2006). Clear evidence of human disturbances has been reported close to human settlements (Vázquez and Givnish 1998, Morales-Barquero et al. 2015). The agrarian communities in the study area were set up between 1920 and 1950 in a land reform process, which allocated land to

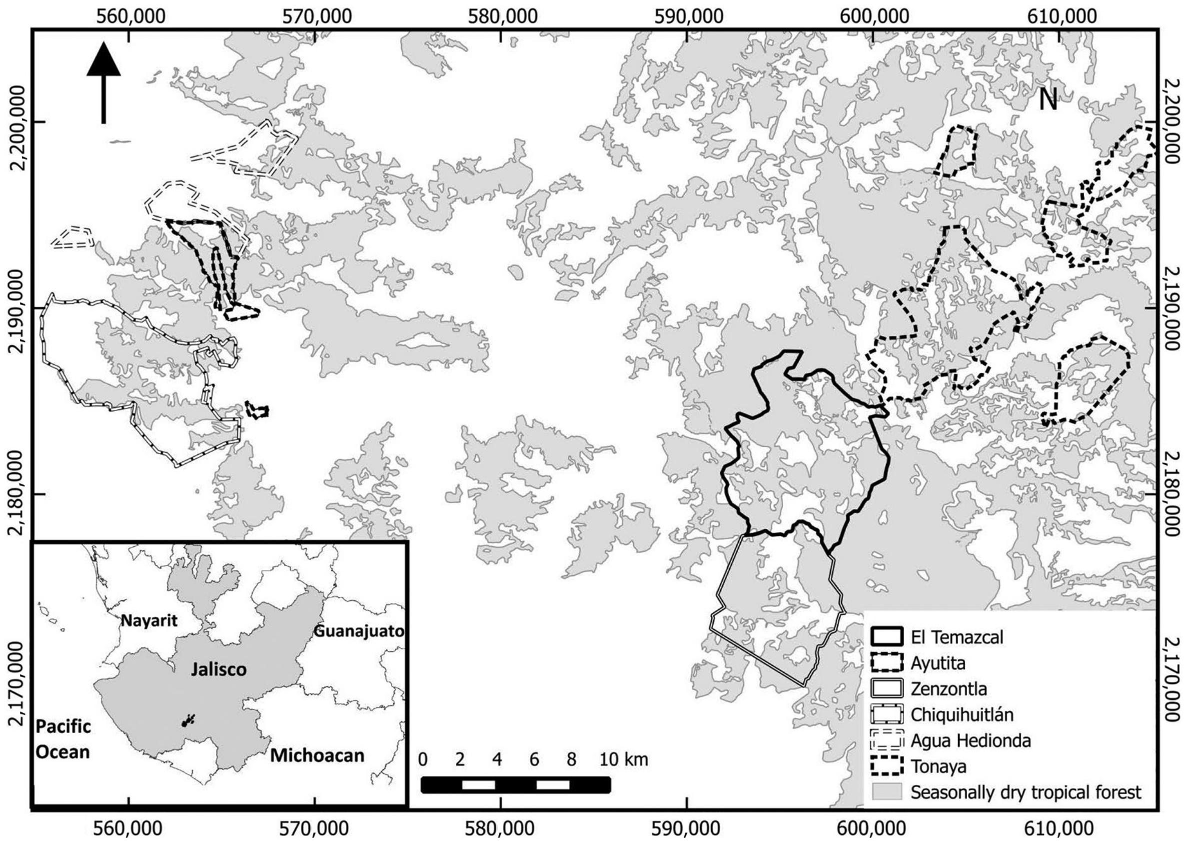

Fig. 1. Geographical distribution of seasonally dry tropical forest (data: Jardel et al. 2012) and location of agrarian communities in study area in Jalisco state, western Mexico (EPSG projection: 32613-wgs84/utm zone 13N). Note that some communities are made up of several polygons.

Table 1. Characteristics of forest inventory datasets used in the study.

Parcel characteristics	1st dataset†	2nd dataset‡	3rd dataset§
Number of sites	34	106	23
Shape plot	Circular	Circular	Circular
Plots per site	4	1	1
Nested designee (radius)	Yes (11.28 m and 3 m)	Yes (12.62 m and 4 m)	No
Plot size	400 m^2	500 m^2	400 m^2
Minimum dbh included	2.5	2.5	2.5
Range of elevation (m a.s.l.)	515–1144	899–1711	778–1048
Range of slope angle (°)	8–76	8–87	1–33

† Salinas-Melgoza et al. *unpublished data*.
‡ Jardel et al. (2012).
§ Salinas-Melgoza et al. (2017). dbh, diameter at breast height.

groups of landless people on a communal basis. After land rights were decreed, forest was cleared for farming in communities, but agriculture cannot be practiced on steep areas; such areas were therefore allocated to forest-based uses. Generally, the flatter areas are used for permanent agricultural systems (*yuntas*), some of which are irrigated; crops grown in these systems include maize, sorghum, and agave. The lower slope areas are used for small plots of shifting agriculture. These areas, like the *yuntas*, are considered to belong to individual farmers. In addition, there are common areas in many communities that may be used by all members as unplanned silvopastoral systems, where livestock graze freely. These common forest areas are also the source of building materials, poles for fences, and fuel wood (Morales-Barquero et al. 2015).

Data sources

Two different sources of information were used in this study. A forest survey was used to obtain AGB levels, while data on physical conditions of the sites were obtained by physical measurements in the sampling sites and from digital elevation models (DEM), that is, from existing topographic maps.

Forest inventory data from 144 sampling sites were obtained from three different datasets from different sources; sites in these datasets cover a wide range of topographical conditions. The combination of these three datasets increased the size of the sample used in analyses. Although some of the communities are duplicated in different datasets, plots are unique by community and by dataset. All plots are circular. Plots in two of the datasets used two concentric circles. Diameter at breast height from each tree registered in each dataset was used to infer dry AGB (Table 1).

Different allometric equations give different results (Návar 2010), and it is difficult to know which one is most reliable. In order to improve the accuracy of biomass estimates, Chave et al. (2014) suggest using locally developed equations. No allometry specific to our sites was available, but we used an equation that had been developed using destructive tree sampling in a SDTF site characterized, like our area, by having a large number of small stems; this site was only about 60 km from our study area (Martínez-Yrízar et al. 1992) (see Eq. 1). Biomass of multi-stemmed trees was calculated separately for each stem and summed. Identification of individual trees was done at the species, genera, or morphospecies level. Aboveground biomass and total basal area measurements are not independent, because both are calculated from stem diameters (Brown 1996).

$$\log_{10} B = -0.5352 + 0.9996 \log \mathrm{BA}, \qquad (1)$$

where B is aboveground dry biomass in kg and BA is basal area (cm^2).

Information by site includes basal area, which was measured using diameter tapes, biomass (calculated using Eq. 1), and total number of stems. Slope was measured using a clinometer, elevation estimates were taken using an altimeter, and aspect was obtained with a compass; geographic location was obtained with a handheld Global Positioning System (GPS).

Data analysis

It is often difficult to obtain a strong signal from complex non-linear relationships and the methods of data analysis were designed to explore a wide range of possible interactions before focusing on those with the most influence. An initial selection of 19 topographic explanatory variables was made, based on current knowledge of determinants of AGB (topographic variables related to ecological processes). An analysis of multi-collinearity reduced these to a set of 11 variables to analyze overall patterns (further details in Appendix S2). Two variables that relate to potential human impact on vegetation were added to the topographical variables: distance to roads and distance to human settlements (Appendix S1: Table S2). Details of selection and calculation of all variables are in Appendix S2.

The use of different scales for the topographic position index (TPI) calculation is to provide a measurement of plot-level topographic exposure to shade, due to nearby hills. As TPI is determined by the neighborhood scale used in the analysis, TPI with significant change (see Appendices S1 and S2) with regard to change in scale of analysis would indicate more favorably sheltered areas for tree development (Fig. 2).

Data analysis strategy

The data analysis strategy to relate biomass to the topographic variables encompassed two approaches (Fig. 3). Firstly, in order to investigate overall patterns, a number of linear models were constructed using generalized linear model (GLM) and generalized linear mixed model (GLMM). Non-linear relationships were evaluated with multivariate adaptive regression splines analysis (MARS) and classification and regression tree analyses (CART). Secondly, non-linear relationships were used to identify breakpoint or threshold values where patterns change dramatically between subgroups of data of AGB; to this end, CART and piecewise-generalized linear model (PGLM) were used. Furthermore, GLM and PGLM were used to investigate overall linear and non-linear relationships between human factors and AGB.

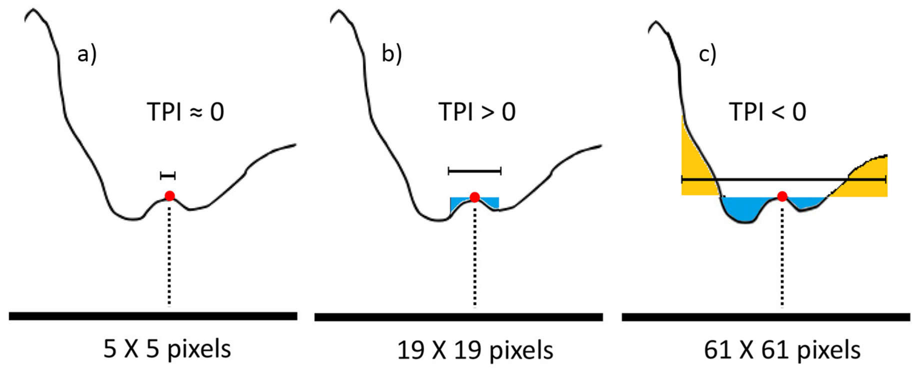

Fig. 2. Representation of topographic position index (TPI) for the same point (red point) at three different scales (horizontal line above red point). (a) TPI is around zero because point elevation is about the same as the whole analysis region, (b) TPI higher than zero means that point elevation is above analysis region mean elevation, and (c) TPI lower than zero means that point elevation is above analysis region mean elevation.

GLM, PGLM, and GLMM analysis

In order to evaluate linear and non-linear relationships between AGB and the independent variables, several linear models were estimated using GLM, GLMM, and PGLM. The independent variables used in these analyses were the topographic and human factors. We obtained a full model that included the 11 selected variables. Then, we obtained optimal GLM and GLMM that statistically explain the relationship between independent topographic variables and AGB using a simplification procedure suggested by Crawley (2013). Generalized linear model and GLMM for AGB were fitted for the entire dataset. Furthermore, GLM and PGLM were used to evaluate the effect of distance to roads and settlements on AGB.

Generalized linear mixed model random intercepts and random slope models were constructed to investigate whether differences in any of the significant explanatory topographic variables within the territory of communities explain AGB. This analysis identifies at the same time a nested hierarchy of sites within communities (Bates et al. 2014). This type of model allows fitting a regression model to the individual communities, while accounting for systematic unexplained variation among the six communities with regard to topographic variables. In the model, topographic variables were used as fixed

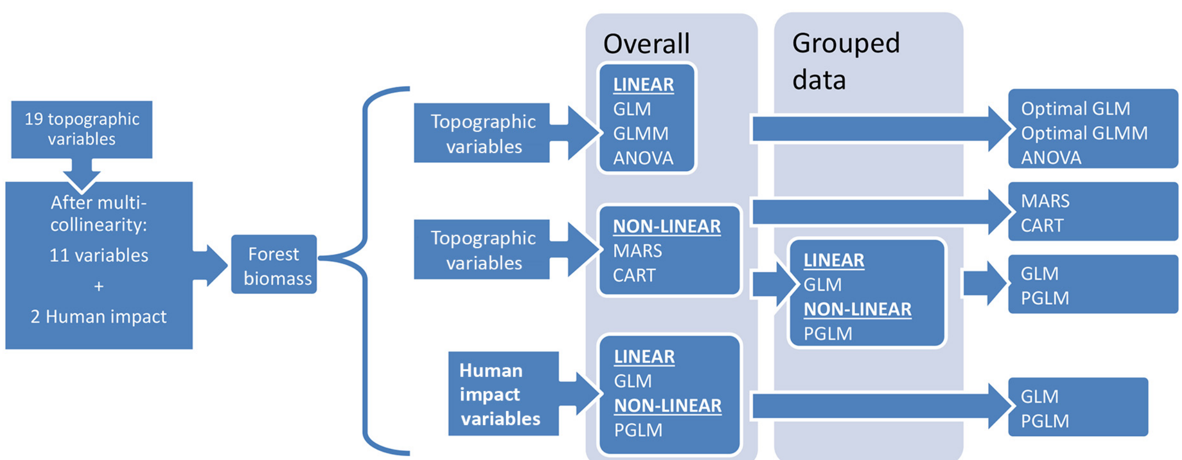

Fig. 3. Schematic representation of the analysis steps used in the study.

factors, and two random structures were used, one with communities as the grouping variable (random intercept variable) and another with topographic variables as the random slope variables. The former allows the intercept to deviate from the mean intercept for each community, while the latter allows slope of the linear regression to vary for each community. In this way, the consistencies of resulting effects were tested across both communities and topographic variables. The significance of the random intercept was evaluated at the 95% confidence interval. Statistical differences would imply that variation in biomass patterns comes from more than one source, in this case, the character of the different rural communities (Bates et al. 2014, Faraway 2016).

Two different proportions of variance generated by the GLMM were calculated using the method explained in Nakagawa and Schielzeth (2017): the proportion of variance explained by the model as a whole and the proportion of variance explained by topographic variables (fixed factor). Following the procedure developed by these authors, the proportion of variance explained by communities (as grouping factor) was quantified, obtaining the intra-class correlation coefficient. The best model was selected on the basis of the proportion of variance explained (pseudo-R^2).

Further, GLM was used to investigate the relationship between topographic variables and a subgroup of data on AGB obtained from a CART, as explained in more detail below.

In order to specify the appropriate error distribution to be used and the associated link in performing GLM, PGLM, and GLMM for AGB, several potential distributions were considered, and eventually, a gamma error distribution with log link was selected (Faraway 2016). For GLMM, all numerical predictors were standardized (so that they have a mean equal to zero and variance equal to one) by centering them and dividing by two standard deviations (Faraway 2016). This procedure alleviates computational challenges of numerical stability of the GLMM algorithm (Faraway 2016). Relative importance (%) of each variable in the optimal GLM and GLMM was obtained through a randomization approach. These values then were normalized to 100; the stronger the influence on the response variable, the higher the value.

Piecewise-generalized linear model evaluates thresholds iteratively along the extent of variation in the independent variables, but a starting threshold must be provided. In order to provide this, changes in the slope of the GLM were performed using the Davies test. This test chooses a number of fixed thresholds along the x-axis and looks for statistically significant differences in regression slopes on each side of the threshold. Piecewise models are statistically significant when threshold estimates do not overlap the 95% confidence intervals (Muggeo 2008, further details in Appendix S2).

MARS

Multivariate adaptive regression splines analysis was conducted to evaluate whether AGB follows more complex non-linear functions of topographic predictable variables, and was used to unravel high-dimensional data patterns. This is a nonparametric analysis that produces simpler and easier-to-interpret piecewise models. They are fitted by several piecewise linear basis functions (BFs) using a threshold value called a knot (Friedman 1991). This technique allows for the use of multiple variables that may not have common effects across the sample (Faraway 2016, further details in Appendix S2).

CART

Classification and regression tree analyses is a nonparametric approach for constructing classification and regression tree models based on rules (Faraway 2016). Classification and regression tree analyses was used as an exploratory procedure to find subgroups in the data, which were then used to perform further parametric linear regression models, as mentioned above. This type of procedure uses a partitioning approach on single variables to perform a binary split in a recursive manner that continues until a terminal node and a constant estimate of y is obtained (Faraway 2016; see Appendices S1 and S2). Classification and regression tree analyses first splits the dataset into homogeneous subsets based on relationships between the dependent and predictor variables, identifying breakpoint or threshold values on the splitting variable to form a tree structure (Faraway 2016). It then looks for the relative importance of each of the variables within different parts of the tree (Faraway 2016).

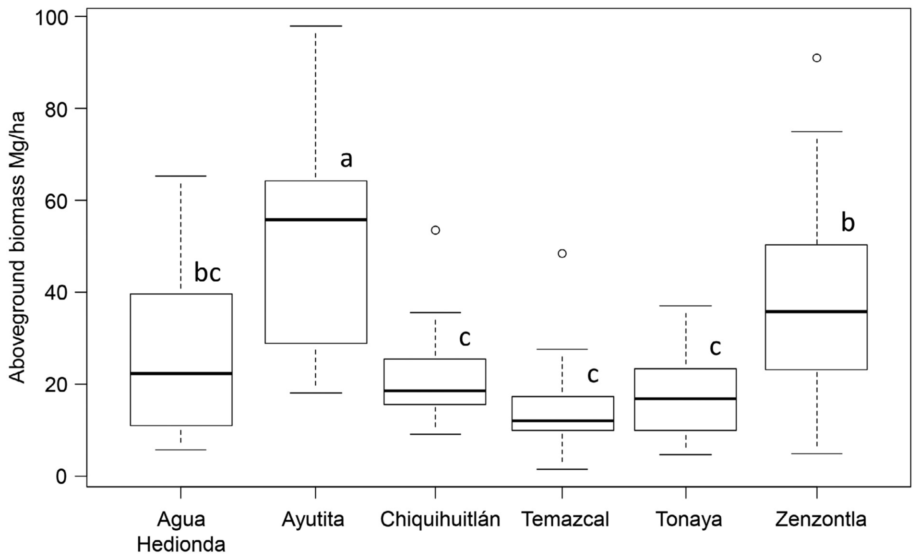

Fig. 4. Aboveground biomass variation by community. Boxes show the 25th and 75th percentiles. The whiskers of each plot extend to ±1.5 of the interquartile range to detect very extreme outlying data points, which are represented by dots. Letters above the whiskers indicate the communities, which are significantly different from each other according to Tukey's HSD test.

As we will show, this analysis first divided the data into two distinct groups, four of the communities making up group A and two communities making up group B (further details in Appendix S2).

ANOVA

A one-way analysis of variance (ANOVA) was also run to evaluate whether mean biomass was equal across all the communities. Aboveground biomass values were log-transformed to meet ANOVA assumptions regarding homogeneity of error variances and distribution of residuals. Aboveground biomass was considered the dependent variable, and rural community as the independent variable. Tukey's HSD tests were used to identify differences between communities (Faraway 2016).

All the analyses were carried out in R 3.3.2 (R Core Team 2016) using different packages for specific analysis. Generalized linear mixed model was performed with lme4 (Bates et al. 2014). Piecewise-generalized linear model was obtained with Segmented package (Muggeo 2008). Multivariate adaptive regression splines analysis was performed using earth package (Milborrow 2017), while CART was conducted using the rpart package (Therneau et al. 2015). The potential distribution and associated link for AGB was checked with fitdistrplus package (Delignette-Muller and Dutang 2015). To graph GLMM, the sjPlot package was used (Lüdecke 2017). The relative variable importance was calculated with the function varImpBiomod (Thuiller et al. 2009).

Results

Aboveground biomass variation within communities

Analysis of variance indicates that there is a significant variation within groups of communities ($F_{5,\ 138} = 15.08$, $P < 0.0005$). Tukey's post hoc tests showed that pairwise comparisons were significantly different at $P < 0.05$ for the group of communities that included Chiquihuitlán, Temazcal, and Tonaya and the group that included Ayutita and Zenzontla. It was also found that the former group has lower mean biomass than the latter. Agua Hedionda does not differ significantly from the other communities ($P > 0.05$; Fig. 4).

Linear effects of topographic factors on biomass

The optimal GLM and GLMM for the entire dataset showed evidence for the effect of

Table 2. Results of different models for topographic factors.

Model	GLM	GLMM
(Intercept)	7.711** (1.766)	3.216*** (0.006)
Elevation	1.001*** (0.0003) [73%]	0.138*** (0.006) [33%]
Slope	1.001** (0.0038) [27%]	0.135*** (0.006) [25%]
TWI	NA	0.112*** (0.006) [13%]
ctan	NA	0.135*** (0.006) [29%]
Pseudo-R^2	$R^2_{N1} = 0.19$	$R^2_{N2(m)} = 0.10$ $R^2_{N2(c)} = 0.21$ $ICC_{N2(Community)} = 0.13$
AIC	1199	1170.84
ΔAIC	22.3	50.5
Log-likelihood	−595.51 (df = 4)	−578.42 (df = 7)
RD	56.83	41.48

Notes: Values in each cell indicate the estimate. GLM, generalized linear model; GLMM, generalized linear mixed model. R^2_N, pseudo-R^2, indicates the proportion of the variation explained: R^2_{N1}, using Nagelkerke (1991); $R^2_{N2(m)}$, by topographic variables (fixed factor); $R^2_{N2(c)}$, for model as a whole; $ICC_{N2(Community)}$, intra-class correlation coefficient community (grouping factor), using Nakagawa and Schielzeth (2017). RD, residual deviance; ΔAIC, change in AIC; ctan, tangential curvature; TWI, topographic wetness index; NA, not applicable. In parentheses, standard error. In square brackets, relative importance (%) of variables in models.

$^{**}P < 0.01$ $^{***}P < 0.001$.

elevation on AGB (Table 2). Optimal GLM was positively statistically significant ($F = 6.40$, df = 141, $P < 0.05$), explaining 19% of the variation in biomass (Table 2, column 1). For this GLM optimal model, elevation above sea level was the variable with the highest relative importance, followed by slope (Table 2, column 1; Fig. 5). The piecewise form of this model (Table 3) was statistically significant and slightly improved the proportion of biomass variation explained by the GLM (Table 2).

Four variables were significant (elevation, tangential curvature, slope, and topographic wetness index) in the optimal GLMM, which accounted for the random effect of rural communities while testing for the fixed effect of topographic variables ($X^2 = 4.14$, df = 1, $P < 0.05$, Table 2). There is a positive effect on predicted AGB of each of the four significant variables, after adjusting for the other three variables. That is, AGB will be higher at sites with the steeper terrain, with convergent flow of water (higher values of tangential curvature), with relatively more runoff (higher values of topographic wetness index), and at higher elevations (Fig. 6). These positive linear trends did not differ among communities. The predicted random intercept effect (±95% confidence intervals) for this GLMM was statistically significant for Ayutita = 0.36 (0.12–0.59), Temazcal = −0.24 (−0.46 to −0.03), and Zenzontla = 0.37 (0.23–0.51), while it was not significant for Agua Hedionda = −0.11 (−0.34 to 0.11), Chiquihuitlán = −0.13 (−0.34 to 0.06), and Tonaya = −0.16 (−0.34 to 0.01). This means that AGB follows two similar trends (Fig. 6). Overall, elevation above sea level, tangential curvature, slope, and topographic wetness index accounted for most AGB variability. This model has the lowest residual deviance, better performance (the best log-likelihood and Akaike Information Criteria [AIC] scores), and the highest proportion of the explained variation (Table 2, column 2). Elevation has the highest relative importance in this GLMM optimal model, followed by tangential curvature. The proportion of variation explained by community was higher than the proportion explained by topographic variables (Table 2, column 2).

Non-linear effects of topographic factors on biomass

The MARS interactions model performed for the entire dataset showed more complex non-linear relationships that best fit AGB. This model is composed of three basis functions and interactions that were found statistically significant (BF1, BF2, and BF3; Table 4). These basis functions combine diffuse insolation and two rural communities, plus one function that relates to knot threshold values. Function BF1 decreases overall AGB (Table 4); this means that in general, sites with diffuse insolation lower than 320 kWh/m^2 have lower biomass. Functions BF2 and BF3 increase overall AGB, that is to say, biomass at sites in Ayutita with diffuse insolation of <320 kWh/m^2 would be higher but not as high as in sites in Zenzontla. Basis function BF1 is used in basis function BF2 to express the interactions between Ayutita community and diffuse insolation (Table 4). The performance of this model was 33%.

The CART for the entire dataset that includes the relationships between AGB and each of the 11 topographic variables together found six of

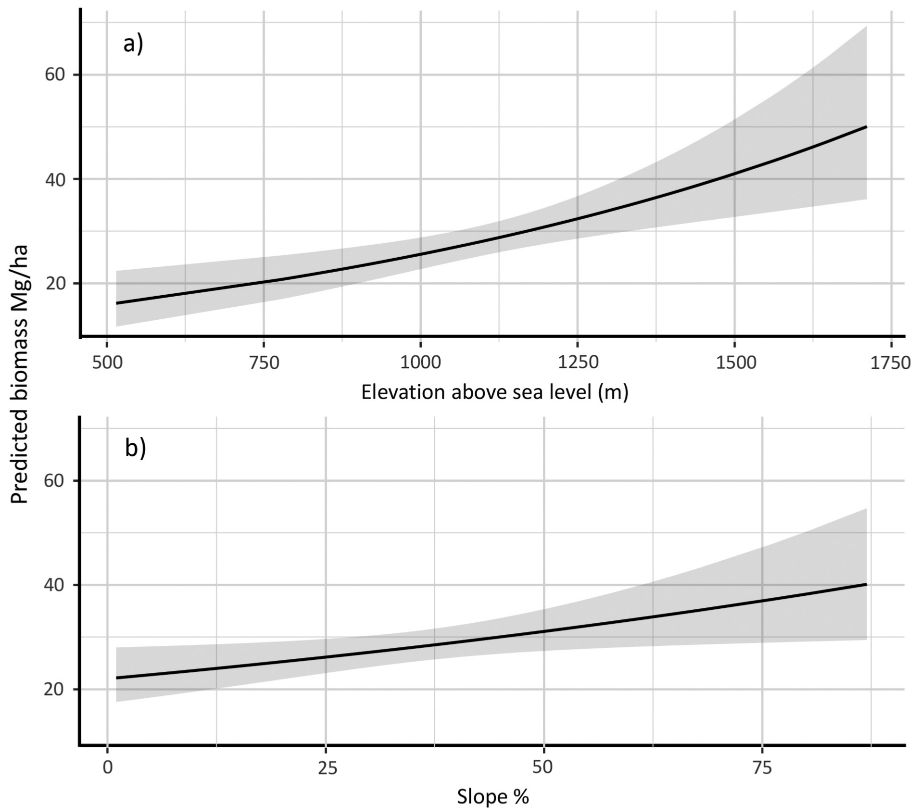

Fig. 5. Mean predicted aboveground biomass variation over the observed range of each of the topographic variables: (a) elevation above sea level and (b) slope, for communities together. The fitted lines are generalized linear model estimates. Gray area around the black line shows confidence region.

these variables to be significantly non-linearly related to biomass (Appendix S1: Table S3, column 2). The most important variable explaining variation in biomass was community, since biomass levels varied more between individual rural communities than with any of the biophysical variables individually. This analysis created two groups of communities, as suggested by the GLMM, group A (four communities) and group B (two communities). Using just this as the breakpoint, more than 30% of the variation in AGB of the root node error is explained. This CART then split the A and B branches on the basis of variables relative importance (Appendix S1: Table S3, columns 3 and 4), resulting in a tree with two terminal nodes each group (Fig. 7).

The tree for group A accounts for about 28% of the variance in overall biomass, and the breakpoint variable in this branch of the tree was tpi19 at 17.41 (Fig. 7). This variable together with topographic wetness index contributed with 60% of the explanatory value within this branch

Table 3. Results of PGLM model for elevation and slope.

Parameter	PGLM model	
Breakpoints	Elevation = 1400 (1078–1722)	Slope = 47.28 (35.02–59.55)
$\beta0_a$	1.79	1.791
$\beta0_b$	4.35	0.43
$\beta1_a$	0.0013 (0.0005–0.0021)	−0.0009 (−0.0104–0.0085)
$\beta1_b$	−0.0004 (−0.0037–0.0028)	0.0276 (0.0068–0.0483)

Notes: Breakpoints refer to sudden and sharp change in directionality of the linear relationships. $\beta0_a$, estimate of the intercept for first piece; $\beta0_b$, intercept for second piece; $\beta1_a$, estimate of the slopes for first piece; $\beta1_b$, estimate of the slopes for second piece. The 95% confidence intervals are shown in parentheses for breakpoints and slope. Pseudo-R^2 = 24, (indicates the proportion of the variation explained using Nagelkerke (1991)); AIC = 1198.7; Log-Likelihood = −591.35; Residual deviance = 53.82.

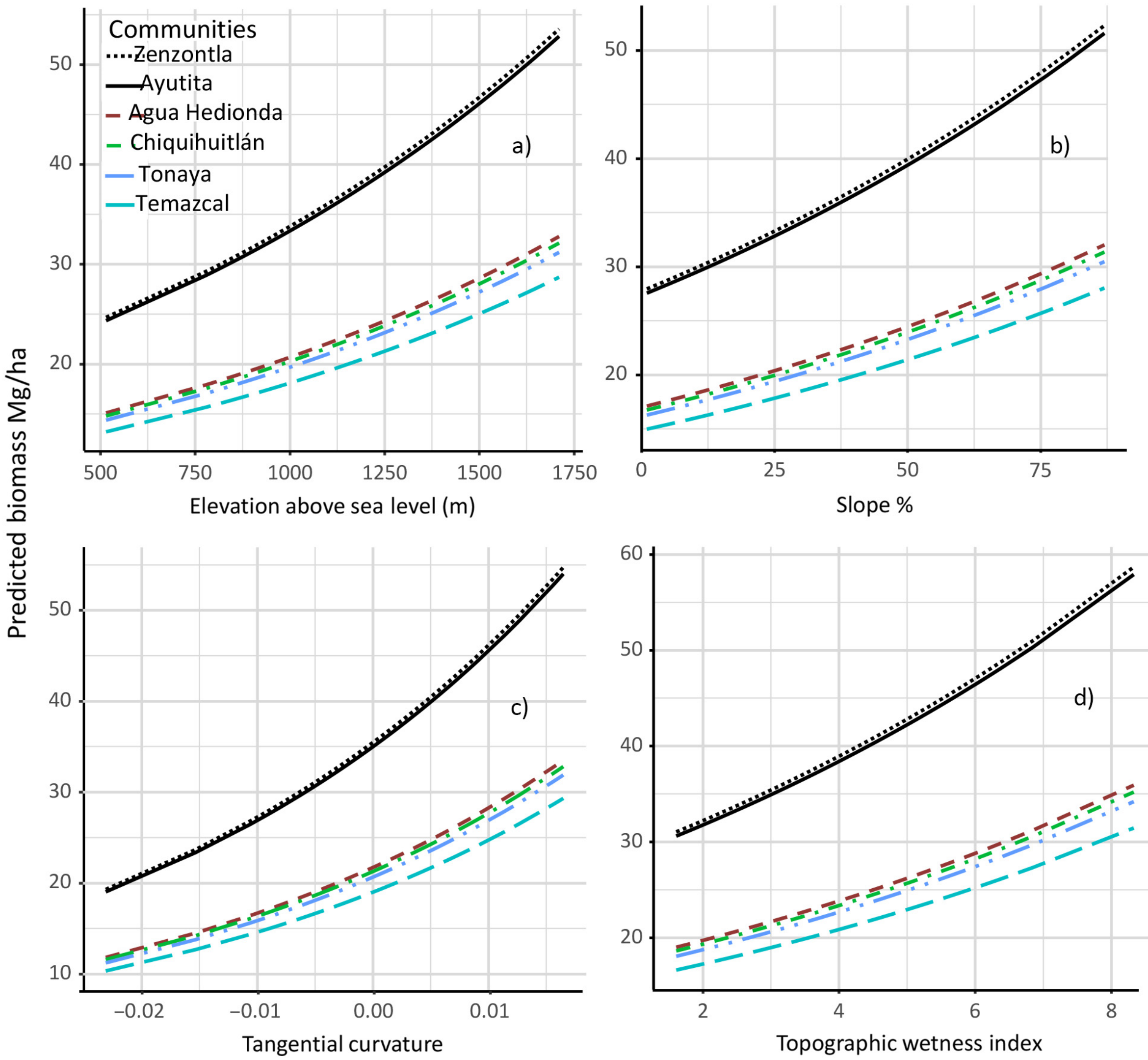

Fig. 6. Relationships between mean predicted aboveground biomass and each topographic variable within the rural community's territory: (a) elevation above sea level, (b) slope, (c) tangential curvature, and (d) topographic wetness index. The fitted lines are generalized linear mixed model estimates for each community.

(Appendix S1: Table S3, column 3). The tree for group B accounts for about 17% of the overall biomass variance. The breakpoint variable for group B was elevation, with a threshold at 1248 m a.s.l. (Fig. 7). Together with two other variables (diffuse insolation and planar curvature), this accounts for 82% of the explanatory value within this branch.

After identifying the complex non-linear relationships for the entire dataset, rather than binary splitting, the two splitting explanatory variables identified as having most influence within each of the groups (tpi19 and elevation) were assessed to determine their relative linear and non-linear influence on biomass by means of a GLM and a PGLM.

For group A of communities, both linear ($F_{1,78} = 9.58$, $P < 0.005$) and non-linear (Davies test $P = 0.003$) relationships were found between biomass and tpi19 (Fig. 8). Piecewise-generalized linear model found a significant negative trend at values of tpi19 lower than 11.8, and positive

Table 4. Basis functions (BF) of the multivariate adaptive regression splines analysis for aboveground biomass, including their knot threshold value (h) and their corresponding magnitude of effect of the basis function.

Id	Basis function	Estimate	SE	T
Int	(Intercept)***	3.28	0.087	37.52
BF1	h(difinsol-320.62)***	−0.01	0.004	−3.80
BF2	Ayutita × h(320.62-difinsol)***	0.07	0.021	3.75
BF3	Zenzontla***	0.52	0.104	5.06

Notes: SE, standard error; t, t value; difinsol, diffuse insolation. Null deviance = 67.40, df = 143. Residual deviance = 46.37, df = 140. R-squared of the mode = 0.33.
***<0.0005.

above this breakpoint (Table 5, Fig. 8). This indicates that biomass decreases slowly at sites which are lower than the average elevations within the immediate neighborhood; above this threshold, biomass increases rapidly. The PGLM analysis explains 27% of the variation in biomass, while GLM explained only 12% (Table 5). This result matches the AIC values, which indicates that PGLM using tpi19 has the best trade-off between the goodness of fit and the complexity of the model (Table 5).

For the communities in group B, there is also a statistically significant linear relationship between AGB and elevation ($F_{1,62} = 9.93$, $P > 0.005$), explaining around 14% of the variation of AGB in this group of communities (Appendix S1: Fig. S1). The slope of the non-linear relationship was not statistically significantly different from zero (Davies test $P > 0.05$).

In short, five models were constructed and their results compared to determine which topographic factors best explain the variation in AGB. The overall optimal linear model was the GLMM which allowed the individual weighting of variables to be applied in the different communities; this performed better than the other linear models including GLM, in which such weighting was not applied. Generalized linear mixed model also performed better than the non-linear models (PGLM, CART, MARS) in this sense. However, the MARS model achieved higher levels of explanation (33%) but only under particular conditions, for example, in specific sites in specific communities, which experience higher levels of diffuse insolation.

Effect of accessibility on biomass

No statistically significant linear ($F_{1,\ 142} = 0.40$, $P > 0.05$) nor non-linear (Davies test P-value = 0.19) relationship between biomass and distance from settlements was found. There is a statistically significant linear ($F_{1,\ 142} = 18.92$, $P < 0.0005$) and non-linear (Davies test P-value = 0.023) relationship between biomass and distance from roads. The slope of this non-linear relationship was statistically significant: positive at low distances from road and negative after breakpoint (2273 m; Fig. 9, Table 6). The threshold also provides an empirical means of separating signals of human impact into two pieces. That is, between 0 and 2273 m, there is great human impact; this means that sites closer to roads have less AGB. The second part of the line shows higher biomass figures at distance to roads greater than 2273, which subsequently steeply decreases (Fig. 9). We also found that PGLM has a better fit than GLM; it attributed 20% of variation in biomass to road accessibility, compared to 13% in the GLM (Table 6).

Discussion

This study differs from others in that it focuses on the explanators of biomass variation in human-modified SDTF landscapes rather than in natural, undisturbed SDTF. This is highly relevant in the context of REDD+ policy. Overall, the results suggest that in these modified landscapes, AGB is correlated not only with a number of regional and local topographic variables including elevation, slope, topographic wetness index, tangential curvature, diffuse insolation, and the topographic position on the slope, but also with human factors. While GLM places primary importance on regional topographic variables such as elevation, mixed GLM, CART, and MARS models show that elevation and the details of microtopography in different communities may have important effects in explaining differences in biomass density. This was shown in particular by the MARS model for the sites with scattered sun radiation, at the highest elevations. This was also revealed by piecewise regression where AGB of communities at lower elevations was shown to be affected by shading from

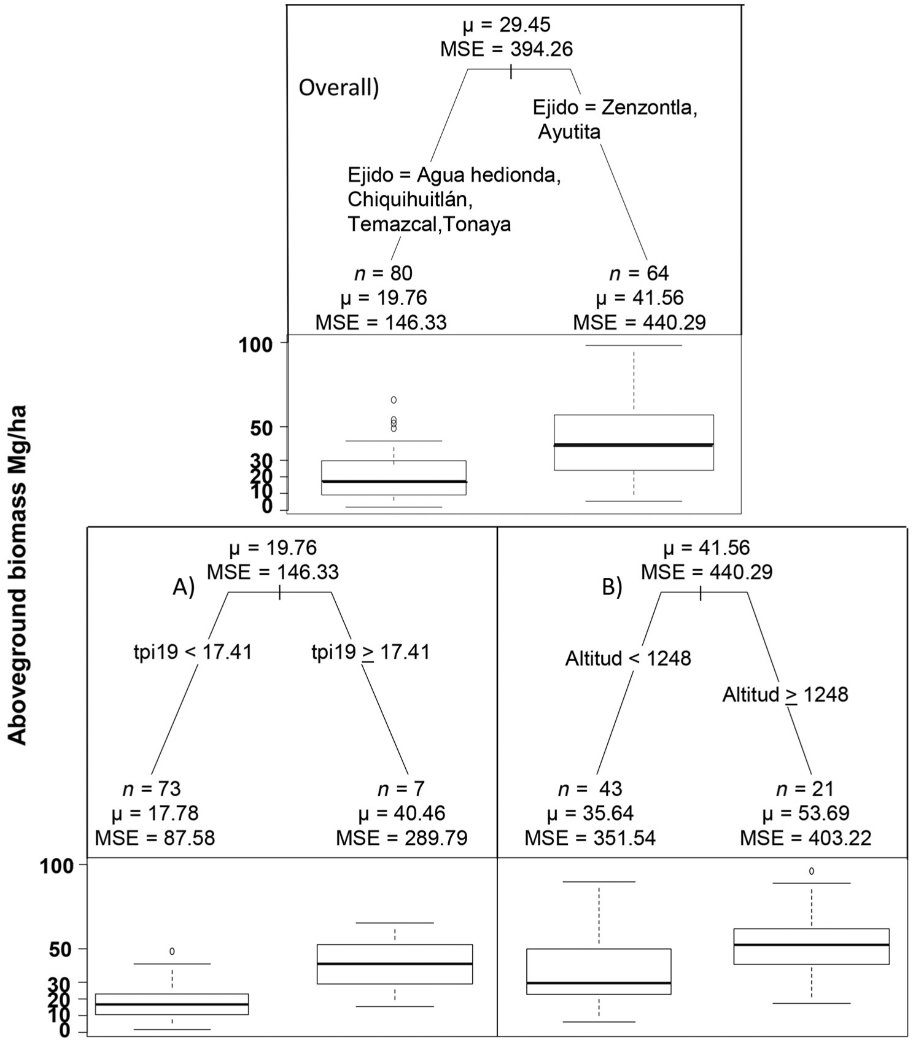

Fig. 7. Regression tree for biomass for total dataset and for community groups A and B. MSE, mean squared error; μ, mean aboveground biomass (Mg/ha); *n*, number of plots in that particular terminal node. The boxplots at bottom section show the biomass variability in each of the terminal nodes. Boxes show the 25th and 75th percentiles. The whiskers of each plot extend to ±1.5 of the interquartile range to detect very extreme outlying data point, which are represented by dots.

nearby hills. We expected that human factors in the landscape would impact biomass levels, and analysis performed in this study supports this. We found that AGB increases not just in a linear monotonic relation with increasing distance to roads, but also in a non-linear way. The monotonically increasing density of biomass with elevation may also in part be explained in terms of human uses such as shifting cultivation, grazing, and poles extraction, which are themselves highly selective as regards elevation.

Effects of specific indicators on biomass

In this study, four topographic variables were shown to be potential predictors of AGB when combined: elevation, slope, topographic wetness index, and tangential curvature. On the one hand, the first two variables together using a GLM approach enabled the inference of biomass over the entire study area. On the other hand, our best model that includes all the four variables together in a GLMM enabled the inference within each community individually. Elevation had the

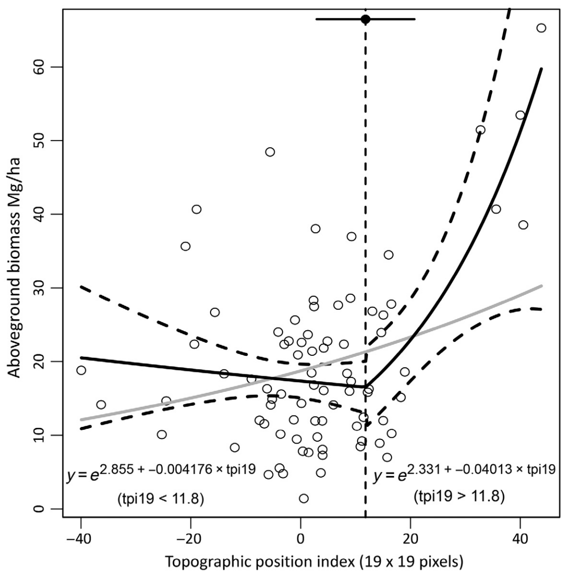

Fig. 8. Generalized linear model (GLM) and piecewise-generalized linear model (PGLM) for biomass in Group A as a function of tpi19. GLM, gray solid line; PGLM, solid black lines. Vertical dashed line shows threshold for PGLM. Continuous dashed line, PGLM confidence intervals for tpi19 at 95%. Equations shown in the graph for each segment in base of the threshold from PGLM.

greatest relative importance in both models, while tangential curvature was indicated as a second major explanator in the GLMM. It was possible to obtain 21% predictive power using GLMM to improve our understanding of how environmental and human-based variables affect standing carbon. Generalized linear mixed model was also able to show that different AGB/topography patterns exist in lower-lying communities compared to communities at higher elevations.

No differences in slope of the regression equation but marked differences in the interceptor (*y*-axis) between two groups of communities were found, so that the monotonic positive trend of biomass with elevation for each community is similar. A possible reason for the difference in interceptors is that terrains Ayutita, Zenzontla, and Temazcal have a distinctly different topographic form from those Agua Hedionda, Chiquihuitlán, and Tonaya with regard to elevation, terrain curvature, and the amount of diffuse insolation received, as indicated by CART. As noted in the results section already, the MARS model enables us to explain 33% of the AGB level variation relating to diffuse insolation values in sites above average elevations and particularly at the highest elevations.

This finding suggests that diffuse insolation may modify the effect of topography on soil water availability (corroborating Galicia et al. 1999), which impacts positively on AGB. Moreover, in Ayutita and Zenzontla, the plot-level topographic exposure to shade from nearby hills would be more favorable to biomass growth (see Appendix S1: Table S3). The average AGB for the four remaining communities (Agua Hedionda, Chiquihuitlán, Tonaya, and Temazcal) is lower, with water availability related simply to elevation. The findings reported here support general trends concerning the link between soil water availability and AGB (Bullock et al. 1995, Jaramillo et al. 2003, 2011, D'Odorico and Porporato 2006), and concur with those of studies from within the same region of Mexico (Maass 1995, Maass and Burgos 2011), which indicates the importance of inter- and intra-annual rainfall distribution on biomass.

Our findings are in complete contrast, however, to many studies that show a unimodal decrease in biomass with elevation in tropical forests (Raich et al. 1997, Marshall et al. 2012, Sundqvist et al. 2013). This negative relationship is usually

Table 5. Results of GLM and Piecewise GLM models for the relationship between tpi19 and aboveground biomass GLM for group A of communities.

Parameter	PGLM model	GLM model
Breakpoints	tpi19 = 11.81 (2.88–20.74)	NA
Intercept	NA	2.931318***
$\beta 0_a$	2.855	NA
$\beta 0_b$	2.331	NA
Slope	NA	0.010921*
$\beta 1_a$	−0.004 (−0.016–0.007)	NA
$\beta 1_b$	0.045 (0.012–0.063)	NA
R^2_N	27	12
AIC	588.01	597.31
LL	−289.00	−295.65
RD	22.75	26.65

Notes: Breakpoints refer to sudden and sharp change in directionality of the linear relationships. $\beta 0_a$, estimate of the intercept for first piece; $\beta 0_b$, intercept for second piece; $\beta 1_a$, estimate of the slopes for first piece; $\beta 1_b$, estimate of the slopes for second piece. The 95% confidence intervals are shown in parentheses for breakpoints and slope. R^2_N, Pseudo-R^2, that is, the proportion of the variation explained using Nagelkerke (1991); AIC, Akaike Information Criteria; LL, Log-Likelihood; RD, residual deviance. NA, not applicable.
*<0.05; ***<0.0005.

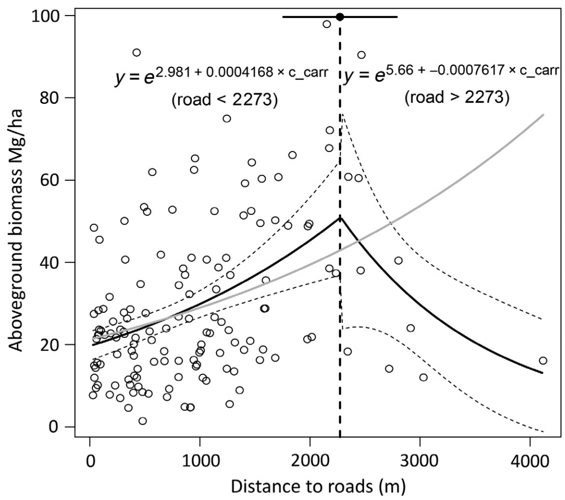

Fig. 9. Linear and non-linear relationship for aboveground biomass as function of distance from roads. GLM, gray solid line; PGLM, solid black lines. Vertical dashed line shows threshold for piecewise-generalized linear model (PGLM). Continuous dashed line shows PGLM confidence intervals for tpi19 at 95%. Equations shown in the graph for each segment on basis of the threshold derived from the PGLM.

explained in terms of limited soil nutrient/slower litter decomposition and lower water availability at higher elevations (Galicia et al. 1999, Brienen et al. 2010, Jaramillo et al. 2011, Maass and Burgos 2011). However, these studies have almost all been carried out on undisturbed forests (Aiba and Kitayama 1999, Leuschner et al. 2007, Homeier et al. 2010), where there are no human factors at play. Human perturbation is markedly stronger in low-lying areas (Lovett et al. 2006, Alves et al. 2010, Toledo-Garibaldi and Williams-Linera 2014). These areas have the best production potential (Maass 1995) and are where the majority of the human productive activities take place (Maass et al. 2005). Large-scale human disturbance (deforestation) characterizes these areas, where the forest coverage may be almost completely removed. Extractive practices that have less impact, as well as cyclical shifting cultivation, are normally performed on slopes with less fertile soils (Morales-Barquero et al. 2015, Salinas-Melgoza et al. 2017). Human disturbance in these areas is mainly on a small scale with continuous removal of a small fraction of AGB for, for example, posts and firewood (Morales-Barquero et al. 2015), and vegetation changes may also be caused by grazing cattle in the forests (Vázquez and Givnish 1998, Méndez-Toribio et al. 2016).

As expected, human activities have a continuous and negative effect on AGB, which increased with distance from roads. This finding is in agreement with Mon et al. (2012) and Luoga et al. (2002). This trend can be explained in part by the human tendency to utilize the more accessible areas in preference to those that are more difficult to reach, as the remaining patches of SDTF are in remote places (Trejo and Dirzo 2000). One unanticipated finding was the threshold at which the negative effect reverses. A possible explanation for this might be a dual relation between the extractive activities and the distance to roads; some activities are carried out between the road and the threshold of 2273 m, but beyond that, other activities may be implicated. It is possible, for example, that illegal activities such as charcoal production might be deliberately hidden from view. More studies are needed to address and understand this interesting pattern.

These findings add another dimension to the so-called REDD+ landscape approach to emission reduction (GLF 2013*a*, *b*, Minang et al. 2015). The method we present could enable the identification of areas which are well below their potential biomass levels, for targeting REDD+ activities

Table 6. Results of GLM and Piecewise GLM for the relationship between distance to roads and AGB.

Parameter	PGLM model	GLM model
Breakpoints	2273 (1758–2787)	NA
Intercept	NA	21.29 (1.7940)***
$\beta 0_a$	2.98	NA
$\beta 0_b$	5.66	NA
Slope	NA	1.0003 (0.0001)***
$\beta 1_a$	0.0004 (0.0002–0.0005)	NA
$\beta 1_b$	−0.0007 (−0.0015–0.000002)	NA
R^2_N	0.20	0.13
AIC	1199.49	1205.17
LL	−594.74	−599.58
RD	56.26	59.92

Breakpoints, refers to sudden and sharp change in directionality of the linear relationships. $\beta 0_a$, estimate of the intercept for first piece; $\beta 0_b$, intercept for second piece; $\beta 1_a$, estimate of the slopes for first piece; $\beta 1_b$, estimate of the slopes for second piece. The 95% confidence intervals are shown in parentheses for breakpoints and slope. R^2_N, Pseudo-R^2, that is, the proportion of the variation explained using Nagelkerke (1991); AIC, Akaike Information Criteria; LL, Log-Likelihood; RD, residual deviance. NA, not applicable.
*** <0.0005.

designed to halt further degradation and promote forest enhancement through natural regrowth, increasing overall carbon stocks. This could be done across the entire landscape of communities using only data from DEM (i.e., from existing topographic maps that are freely available from the national statistical institute of Mexico, INEGI [2017]), without the need for extensive ground forest surveys or for high-resolution remote sensing images, which are costly. The differential forest biomass response along environmental gradients will be a critical information input for the design of locally appropriate REDD+ interventions. Although the models presented in this study explain only part (19–33%) of the variation in AGB, their level of accuracy is similar to that of other exercises based on expensive remote sensing inputs (Solórzano et al. 2017). For this reason, this approach could be an attractive and cost-effective alternative.

Conclusions

The main goal of the current study was to determine causal relationships between the geometry of the landscape and standing AGB in order to model AGB based on a quantitative description of the form of the land surface, which can be derived simply from topographical maps. As explained in the discussion, we find that the GLMM is the most effective overall in explaining variations in AGB and that four topographical variables (elevation, tangential curvature, slope, and topographic wetness index) together explain 21% of the variation. One of the more significant findings to emerge is that elevation was the most important variable among these, and that in SDTFs that are subject to human disturbance, this relationship is positive (higher biomass levels at higher elevations), which is contrary to patterns found in undisturbed forests. The second major finding was that topographic configuration (i.e., all four variables) of rural communities as a whole defined average AGB, in such a way that Ayutita and Zenzontla have more biomass than Agua Hedionda, Chiquihuitlán, Temazcal, and Tonaya, although elevation still plays the greatest role. It was also shown that human activities affect AGB and that the intensity of human activities is related to distance from roads in a non-linear way.

The study has implications in terms of REDD+. It indicates the possibility of estimating AGB levels in similar areas of SDTF without the need for a forest survey or high-resolution remote sensing, using just quantitative land surface information, derived cheaply from topographic maps. This may be particularly useful in the context of the so-called landscape approach to REDD+, which aims at treating emission reductions not merely in full forest areas but across landscapes in which agricultural and other human activities are integrated within forests, where they form dynamic mosaic patterns and shifting locations of carbon stocks. Reducing Emissions from Deforestation and Forest Degradation policy in Mexico is moving toward a landscape approach in which territorial plans at the community level will be the basis for financial support for landscape management activities which will hopefully result in reduced emissions and increased sequestration (CONAFOR 2016). In this context, our study provides a feasible tool by which it is possible to predict from 19% to 34% of current biomass levels in rural communities with SDTF landscapes within the study area, just from the DEM data. This information could be used to set targets for potential carbon stocks in different parts of the landscape, that is, to suggest where in the landscape REDD+ activities should best be targeted. While the calibration of these models is specific to this region and vegetation type, the method itself could be extended for use in other areas and other types of forest.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2063/full