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Influence of landscape heterogeneity on spatial patterns of wood productivity, wood specific density and above ground biomass in Amazonia

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Abstract

Long-term studies using the RAINFOR network of forest plots have generated significant insights into the spatial and temporal dynamics of forest carbon cycling in Amazonia. In this work, we map and explore the landscape context of several major RAINFOR plot clusters using Landsat ETM+ satellite data. In particular, we explore how representative the plots are of their landscape context, and test whether bias in plot location within landscapes may be influencing the regional mean values obtained for important forest biophysical parameters. Specifically, we evaluate whether the regional variations in wood productivity, wood specific density and above ground biomass derived from the RAINFOR network could be driven by systematic and unintentional biases in plot location. Remote sensing data covering 45 field plots were aggregated to generate landscape maps to identify the specific physiognomy of the plots. In the Landsat ETM+ data, it was possible to spectrally differentiate three types of *terra firme* forest, three types of alluvial terrain forest, two types of bamboo-dominated forest, palm forest, *Heliconia* monodominant vegetation, swamp forest, disturbed forests and land use areas. Overall, the plots were generally representative of the forest physiognomies in the landscape in which they are located. Furthermore, the analysis supports the observed regional trends in those important forest parameters. This study demonstrates the utility of landscape scale analysis of forest physiognomies for validating and supporting the finds of plot based studies. Moreover, the more precise geolocation of many key RAINFOR plot clusters achieved during this research provides important contextual information for studies employing the RAINFOR database.

1 Introduction

Amazonia is an important part of the global biosphere, playing a major role in influencing climate systems (Andreae et al., 2004; Malhi et al., 2008), and providing vital ecosystem services such as carbon storage and cycling (Houghton et al., 2001; Malhi

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et al., 2004) and water cycling (Betts et al., 2004; Marengo, 2005). It is also a repository for vast stores of biodiversity (Condit et al., 2002; ter Steege et al., 2006). One of the main sources of information about the carbon dynamics and forest ecology of Amazonia has been widely dispersed networks of permanent forest plots such as the RAINFOR network (Malhi et al., 2002; Peacock et al., 2007). Studies of these plots have generated significant insights into the spatial and temporal dynamics of the processes of forest carbon cycling, including biomass (Baker et al., 2004a; Chave et al., 2005; Malhi et al., 2006), wood productivity (Malhi et al., 2004), wood specific density (Baker et al., 2004b), changes in growth (Phillips et al., 2002; Baker et al., 2003; Lewis et al., 2004), turnover (Phillips et al., 1994, 2004), and diversity (Phillips et al., 1994; ter Steege et al., 2000).

The picture gradually emerging from these studies suggests that slow growing forests in central and eastern Amazonia, where soils are poorer, have significantly higher above ground biomass (AGB), higher wood density and larger seeds than stands in northwest and Southwest Amazonia that are situated on more fertile soils (Malhi et al., 2006; ter Steege et al., 2006). However, the opposite pattern is observed in relation to forest productivity and dynamism, which is higher in western Amazonia than in central and eastern forests, possibly driven by higher soil fertility (Phillips et al., 2004; Malhi et al., 2004). Furthermore, it has been shown that maximum tree α-diversity is related to the length of the dry season (ter Steege et al., 2006). In general, taking into consideration the spatial and temporal pattern of sampling, there is good support for the hypothesis that the total biomass of the plots studied has increased over the last two decades (Phillips et al., 1998; Baker et al., 2004a).

These results have significantly influenced the way that scientists think about the interaction between tropical forests and the physical environment. However, many of these findings rest on the assumption that the permanent forest plots are a representative sample of the part of Amazonia in which they are based. In other words, uncertainties still exist as to whether the plots represent a partial sampling of landscapes that are heterogeneous at several scales. Any such systematic sampling error could

challenge some of the findings of previous studies.

The implicit assumption is that a 1 hectare field plot provides a reasonable representation of regional forest structure, species composition and dynamics (Chave et al., 2004). However, to effectively and accurately scale-up these findings it is fundamentally important to consider the landscape mosaic structure, defined by Zonneveld (1989) as the "landscape unit". This sampling unit relies on spatially locating and mapping homogeneous areas in the landscape based on the pertinent available data that drives the vegetation characteristics for a region, and has been used successfully for mapping different vegetation formations in mountain regions (Franklin and Woodcock, 1997), for scaling Photosynthetic Active Radiation (PAR) in heterogeneous ecosystems (Asner and Wessman, 1997), and for identifying the spatial variability of canopy structural characteristics in Amazonia (Aragão et al., 2005).

In relation to the Amazonian RAINFOR sites, the location of study plots may be "landscape biased" because of a range of factors including: 1) access limitations (e.g. proximity to roads, research stations, towns, rivers, etc.); 2) biophysical characteristics of the forest (e.g. slope, understorey, soil moisture, flooding, etc.) and potentially: 3) the underlying scientific reason for setting up a plot, such as different rationale for choosing an area depending on the objective of the specific study, funding availability, etc.

In this study, we evaluate the existence and potential extent of sampling bias in the positioning of forest study plots in the RAINFOR network through the use of remote sensing data to evaluate the heterogeneity of the landscape within which the plot is embedded. Specifically we test whether the regional variations in wood productivity, wood specific density and above ground biomass revealed by the RAINFOR network could be driven by biases in plot location within landscapes. In the process of testing these hypotheses, we aim to achieve the additional goals of describing the landscape characteristics and precisely locating these important plots. As many of these plots have delivered major insights into the dynamics of Amazonian forests, and are likely to continue being monitored over the 21st century, this work also provides a useful background dataset for the future interpretation of RAINFOR plot data.

2 Study sites

We evaluate the landscape and field characteristics of seven sites (45 field plots in total) covering western, central and eastern Amazonia, which have been used in intensive studies (e.g. Laurance et al., 1998; Malhi et al., 2004; Phillips et al., 2004; Lewis et al., 2004; Baker et al., 2004a, b). Western Amazonian sites include: Allpahuayo, Cuzco Amazonico, Jenaro Herrera, Sucusari and Tambopata (all in Peru). Central Amazonia site is represented by Manaus region, and Eastern Amazonia site is represented by the Caxiuanã plots (Table 1). Sites were chosen on the basis of the number and the availability of the field plot data, whether research is still being carried out in these areas, and on the availability of cloud-free remote sensing data (Fig. 1).

The characterization of each field plots, including plot code, central coordinate of the plot, elevation, plot shape, forest type, and Landsat ETM+ path/row and image acquisition dates are depicted in Table 2. Additionally, the description of the forest types is presented in Table 3. All of the field plots are approximately 1 hectare in size, however the shape varies from square plots (100 m×100 m) to rectangular transects of: 40 m×250 m, 20 m×500 m or 10 m×1000 m (see Table 2).

3 Material and methods

3.1 Remote sensing optical data and image processing

Five Landsat 7/ETM+ scenes were used in this study (Table 2). These images were acquired during the dry season (August and September) when cloud free conditions predominate (Table 1). The images were imported into a dataset in the SPRING Geographic Information System (GIS) free software (Câmara et al., 1996) for image processing and spatial data integration. The projection used is geographic and WGS84 datum. The six Landsat/ETM+ spectral bands centred at 479 nm, 561 nm, 661 nm, 834 nm, 1650 nm and 2220 nm (bands 1 to 5 and 7) with 30 m spatial resolution were

geographically rectified using the methodology suggested by Richards (1993). The image-to-image geometric rectification was performed using the NASA GeoCover[1] product, with 14.5 m spatial resolution. The root mean square error (RMSE) was less than two pixels and normally less than one, depending on the number of control points selected in each scene (mainly roads or rivers).

For the Tambopata site, an IKONOS satellite pan-chromatic image with 1 m spatial resolution acquired in 2001 was used as ancillary data to support the interpretation of the classified image, such as the identification of palm tree areas, swamp limits and the bamboo dominated regions which are clearly identified in this image.

3.2 Topographic data processing

The topographic dataset used in this study is the Shuttle Radar Topography Mission (SRTM) version 2[2], which generated a complete high-resolution digital topographic database, with 90 m spatial resolution. These data measure approximately the top of the canopy height and thus do not represent the actual ground elevation value (which will be approximately 30 m below SRTM elevation). To exclude outliers caused by water bodies from the analysis, we replaced them with the mean value of the neighboring pixels. The elevation data were then resampled to 30 m spatial resolution using a nearest neighbor algorithm, for the following step of data aggregation on the Landsat 7 ETM+ images.

3.3 Generating the landscape maps

For this study, a considerable effort was spent precisely locating the field plots. The field plots were firstly located in the images using the Global Position System (GPS) point data acquired during field campaigns by the authors and other investigators. The Tambopata and Caxiuanã plot limits were obtained by walking along the perimeter of

[1] https://zulu.ssc.nasa.gov/mrsid

[2] ftp://e0srp01u.ecs.nasa.gov/srtm/version2

the plots and acquiring several points with the GPS connected to an external antenna placed on a 5 m height structure. The use of the GPS antenna improved the signal reception, providing a relative low spatial error of only 3–5 m. For the other areas, location points were taken at the corners of plots or at some place within the transect and were used in addition to the field information such as distances to other plots, field camps, rivers and roads to demarcate the plot area.

Based on the location of the field plots, a region of 10 km×10 km with the field plots located in the center was established for defining the "landscape" region to be mapped and analyzed. In the two areas where the field plots were located far from each other, larger areas were selected to include all the plots (the Jenaro Herrera landscape is 15 m×10 km and the Manaus landscape is 45 km×30 km).

The image classifications performed in this study were generated by using image segmentation coupled with a region-based algorithm that have previously been successfully applied for mapping purposes (Rodriguez Yi et al., 2000; Almeida Filho and Shimabukuro, 2002). The approach was based on a region-growing technique developed by Kai and Muller (1991) and a non-supervised classification algorithm based on clustering techniques, developed by Bins et al. (1993). When this classification algorithm did not effectively distinguish different forest physiognomies, we used another region-based algorithm that uses a similarity criterion for clustering the differences based on the image histogram (Câmara et al., 1996).

One potential problem associated with automatically classified maps is the production of omission and commission errors due to spectral similarity among targets or algorithm limitations (Shlien and Smith, 1975; Fitzgerald and Lees, 1994; Stehman, 1997; Salovaara et al., 2005). Thus, in order to generate more clearly differentiated results, we performed a manual edit of the maps to correct for class confusion and to adjust the limits of the land cover classes.

The land cover classes defined in this study were based on textural and spectral properties of the satellite images and field data information. According to the literature, Amazonian rain forests have traditionally been divided into two major forest types: in-

undated forests (Alluvial terrain forests) and non-inundated (*Terra Firme*) forests (Salo et al., 1986; Tuomisto et al., 1994, 2003; de Grandi et al., 2000). The Alluvial terrain forests are land cover types located on soils that were deposited by rivers relatively recently (Holocene or Pleistocene) and this feature, unlike inundated forest, is easily recognized in optical remote sensing imagery. The Alluvial terrain forests can also be further divided into two major groups: Alluvial terrain forests with textural characteristics (in the satellite images) of *Terra Firme* areas, and alluvial terrain forests with textural characteristics of permanently or seasonally inundated areas. This landscape forest physiognomy differentiation is an effective way to characterize the heterogeneous mosaic of forest composition and structure in *Terra Firme* areas associated with differences in edaphic conditions (Table 3).

Terra Firme forests encompass a number of ecologically different forest types (Duque et al., 2003; Phillips et al., 2003; Malhi et al., 2004; Aragão et al., 2005). A large diversity of soils is found beneath *Terra Firme* forests in Amazonia (Quesada et al., 2008a), with Ferralsols, Acrisols, Leptosols, Cambisols and Plinthosols accounting for more than 80% of the soils types, and the forests' textural properties observed in remote sensing imagery are generally more homogeneous than those of alluvial terrain forests, on Fluvisol soil type.

In addition to this main differentiation of *Terra Firme* and Alluvial terrain forests physiognomies, the SRTM data was used to further characterize the altitudinal range of each one of the vegetation classes depicted by the classification algorithms.

Map algebra were carried out by running a script written in Spatial Language for Algebra Geoprocessing (LEGAL) by using Boolean operations for integrating the forest physiognomy classes and the elevation layers.

3.4 Wood productivity, wood specific density and above ground biomass (AGB) of the field plots in the landscape context

To evaluate which land cover types have been sampled in field inventories and the representativeness of these samples in the landscape mosaic we analyzed the propor-

tional contribution of each land cover type and the spatial location of the field plots.

The objective of this study was to assess the representativeness of forest properties of the sample plots in relation to the wider landscape. This was done by assigning a measured value of forest parameters to each forest class mapped in the remote sensing images, and then scaling to the landscape by weighting according to the area covered by each forest class. The weighted analysis was carried out only on sites with field measurements in more than one forest physiognomy (Allpahuayo, Cuzco Amazonico, Jenaro Herrera and Tambopata). Specifically, we use the relative area within the landscape of the physiognomies that characterizes the plots within a site to calculate a weighted average for the three biophysical variables. This was then compared with the forest properties obtained by simple, non-weighted average across the forest plot data. Any significant discrepancies between weighted and un-weighted values would indicate a degree of landscape bias. The forest variables assessed were the updated estimates of above ground wood productivity (Malhi et al., 2004), wood specific density (Baker et al., 2004b) and above ground biomass (Malhi et al., 2006). The first census data is from 1981 (Manaus site), and the most recent ones are from 2006 (Jenaro Herrera site). As the time interval and the total number of years monitored between the forest census can affect the above ground wood productivity estimates, two rules were applied for calculating the final values: a) the 2005 year forest census was not taken into account, as it was an anomalous dry year and there was an increase in trees mortality (Phillips et al., 2009), and b) a time-weighted procedure (multiplying the number of years in the time-interval by the wood productivity for that interval and dived the result by the length of the interval) for calculating the final estimates was used.

4 Results

4.1 Landscape maps and field plot representativeness

4.1.1 Allpahuayo

The Allpahuayo "landscape" map has 5% of the total area covered by land use (roads, agriculture, pastures, villages), 25% covered by disturbed forest and 70% classified as *Terra Firme* (Fig. 2a, b). Within the Terra Firme forest class, the classification algorithms detected three spectrally distinct Terra Firme forest types (Table 3), here denominated *Terra Firme* 1, *Terra Firme* 2 and *Terra Firme* 3 (73%, 6% and 21%, respectively). These three *Terra Firme* forest types occur in the same elevation range, varying from about 96 m to 166 m (Fig. 2c).

The characteristics of the three sample plots in Allpahuayo are described in Table 4. The ALP A and ALP B plots are transects that crosses both sandy and clay soils (Quesada et al., 2009a); however only the area around plot B was classified by the algorithms as picking up this variability. Based on the field descriptions of these two plots, it appears that the *Terra Firme* 2 and *Terra Firme* 3 classes are related to sandy soils, while *Terra Firme* 1 class reflects the forests on clay soil. The biophysical parameters also support this approach: ALP-03 has higher above-ground biomass and wood density than ALP A and ALP B. However ALP-03 has higher wood productivity, exhibiting more dynamism than expected. The field plots are representative of two of the identified forest types (*Terra Firme* and *Terra Firme* 3) covering 93% of the natural landscape units mapped in this study.

Application of an area-weighted approach results in the mean value of wood productivity, wood specific density and above ground biomass being 10%, 1.5% and 8.2% higher than with the simple mean (Table 4).

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4.1.2 Cuzco Amazonico

The Cuzco Amazonico landscape is located in a predominantly alluvial region in the vicinity of the Madre de Dios River, where the Cambisol soil type dominates. It has 2% of the area classified as land use, 10% of the area is covered by rivers and 6% is flooded area. Excluding these areas, there are four spectrally different forest physiognomies detected by the algorithms (Fig. 3a, b). *Terra Firme* forests are located in northern and southern extremes of the Landscape map, representing 5% of the area. The alluvial terrain forest type 1 (occasionally inundated region – Table 3) represent 40% of the area, while the alluvial forest type 2 (non inundated areas) covers 37% of the region. As would be expected, the alluvial forest type 1 is located in lower areas (Fig. 3c). There is a homogeneous and spectrally distinct area covering 8% of the landscape characterized by *Heliconia sp*. mono-dominance previously verified in the field (T. R. Baker, personal communication, 2006). The last forest class is an alluvial forest type presenting a very low density of individuals with patches of bare soils evident, representing 10% of the area.

There are four field plots in Cuzco Amazonico region. The plots CUZ-01 and CUZ-02 are located in the non-flooded terrace and have a mean value of above ground biomass, wood productivity and wood density lower than the plots CUZ-03 and CUZ-04, which present small sections that can get flooded (T. R. Baker, personal communication, 2006). Considering the primary forests land cover physiognomies, the field transects cover two of the five classes, covering 77% of the landscapes units mapped.

The weighted analysis showed minor changes in wood productivity (an increase of 0.8%) and no changes in wood density and above ground biomass in relation to the un-weighted mean (Table 4).

4.1.3 Jenaro Herrera

The landscape of Jenaro Herrera has 11% of its area covered by rivers and water bodies, 12% covered by disturbed forests and 15% covered by land use class. Exclud-

ing these classes, the primary forest physiognomies are composed of alluvial terrain forests type 1 in the lower terrace (Table 3), representing 30% of the mapped area, and 40% covered by *Terra Firme* forests (Fig. 4).

There are six plots in this region, three of them in the alluvial terrain forests located in different elevation (Fig. 4c), two plots located in the *Terra Firme* physiognomy, and one plot in the disturbed forest class. The mean value of above ground biomass is higher in the *Terra Firme* plots than in the alluvial terrain plots, and the latter have mean AGB higher than the plot located in the disturbed forest (JEN-10). The JEN-10 plot location might be affected by errors on the geocorrection of the image and GPS measurements, as it is just in the limit of the disturbed forest class and *Terra Firme* class.

The weighted analysis showed an increase in 3% for above ground biomass and 7% increase for the overall wood productivity for this site. Wood density was not evaluated due to the limited number of plots with this measurement (Table 4). Considering the forests physiognomies, the field plots in this region cover 81% of the landscape classes mapped for this site.

4.1.4 Sucusari

The Sucusari site has 12% of the mapped area covered by river and streams, 11% is disturbed forests and 1% is land use classes. The primary forests physiognomies are divided into *Terra Firme* class (90%) and 10% covered by alluvial terrain forests type 2 (Table 3).

There are five plots in Sucusari, all located in the Terra Firme physiognomy, except plot SUC-03 which is a seasonally flooded forest (Fig. 5a, b). The Landsat/ETM+ image classification was not able to distinguish the seasonally flooded region from other regions; however, according to the field characterization of the plot SUC-03 and the elevation gradient of the region derived from the SRTM data, it is possible to distinguish two types of Terra Firme: the plateau and the river valley. Plot SUC-03 is located very close to a river and is seasonally inundated, suggesting a threshold around 110m elevation to separate both physiognomies (Fig. 5c). This site has lower wood productivity

and higher above ground biomass than the other plots in this site (Table 4).

The weighted analysis for the Sucusari was not carried out, as all the plots are located in the same forest physiognomy (as far as the Landsat/ETM+ analysis could distinguish).

4.1.5 Tambopata

In the Tambopata landscape map (Fig. 6), 7% of the area corresponds to land use, 6% is covered by rivers and water bodies, and 4% is covered by disturbed forest. The non-disturbed vegetation type is divided into 10% of *Terra Firme* class and 75% of alluvial terrains forests type 3 (Table 3). Palm tree forests (1% of the forest area), Bamboo forest (2 types, representing 2% and 4% of the forest area) and the Swamp class (5% of the area) were spectrally distinguishable and were characterized by using a combination of high resolution imagery (Palm tree forest and swamp), field data (swamp area) and the literature (bamboo areas – in Foody and Hill, 1996).

There are seven plots in this site. The TAM-01, TAM-02, and TAM-06 are located on a Pleistocene terrace, and this area was classified as alluvial terrain type 3. The plots TAM-07 and TAM-08 are located in a Pleistocene terrace, and the vegetation type was classified as *Terra Firme* forest physiognomy. There is also one plot located in the swamp region, TAM-04, which presents higher above ground biomass and wood productivity then the other plots in this site. The Terra Firme plots have a mean wood density value higher than the alluvial terrain forest type 3 in this site, but lower mean values of above ground biomass and wood productivity. Taking into account all the undisturbed forested physiognomies, the field plots are representative of 90% of the total landscape studied in this site.

The weighted analysis estimates a decrease in the values of the three biophysical parameters in relation to the published data, with 1.2% lower above ground biomass, 2.9% lower wood productivity and 3.5% lower wood density (Table 4).

4.1.6 Manaus

The landscape map generated for Central Amazonia (Manaus region) has less than 1% of the area covered by clouds, cloud shade and water bodies, 7% is covered by disturbed forests and 2% covered by land use. The undisturbed forests were classified as 98% of Terra Firme and 2% alluvial. The Terra Firme class did not present spectral differentiation in the elevation range; however it is possible to assume that from 70 m to 80 m elevation there is a cut off and the landscape can be subdivided into river valleys and plateau (Fig. 7). Using this elevation range as a threshold, 17% of the *Terra Firme* forests in this landscape can be considered as river valley vegetation type.

There are 16 plots in the Manaus area (Table 4). They are located in the *Terra Firme* forest from 90 m to 160 m altitude, representing 98% of the area mapped. The plots JAC-01 and JAC-02 are transect measuring 20×2500 m, ranging across plateau and lowland areas associated with streams valleys. This variation is reflected in the landscape map in *Terra Firme* class in association with the SRTM data. The vegetation structure (Higuchi et al., 1998) has been previously published for these plots. Soils vary from very clay-rich Ferralsols in the plateau to very sandy Podzols in the lowland (Quesada et al., 2009a). The two JAC plots are characterized by relatively lower above ground biomass and relative higher wood productivity in comparison to the other plots in this site.

In general, the Manaus field plots have been intensively studied and described in the literature evaluating AGB, wood productivity (Chambers et al., 2001; Clark et al., 2001) and forest edge effects (Laurance et al., 1997; Nepstad et al., 1999). Considering the field sites that can be affected by edge effects (Laurance et al., 1997, 1998), the plots BDF-01, BDF-10 and BDF-14 are located in less than 500 m from a disturbed or anthropogenic area. These plots show a mean wood productivity and biomass of 2.33 Mg C ha^{-1} $year^{-1}$ and 274 Mg C ha^{-1}, respectively. The wood productivity value is higher than the mean value for the other plots in this site suggesting that forest disturbance affects these biophysical parameters.

The Manaus plots can be therefore considered to cover Terra Firme plateau and river valleys, as well as disturbed forests. The forest physiognomies not being sampled are the seasonally inundated areas, which represent less then 3% of the landscape.

4.1.7 Caxiuanã

The Caxiuanã landscape has two anthropogenic classes (land use and disturbed forest, covering less than 1% of the area), a river covering 4% of the landscape map and clouds and clouds shadows that covers 21% of the mapped area. The undisturbed forest is composed mainly by *Terra Firme* class (74% of the total area) with homogeneous spectral response (Fig. 8). However, the *Terra Firme* forest can be sub-classified into plateau and river valleys if a threshold around 30–40 m elevation is considered (Fig. 8a). In this case, 36% of the landscape region evaluated can be considered as river valley vegetation type.

In Caxiuanã we utilised four field plots: CAX-01, CAX-02, CAX-06 and TEC-02 (Table 4). The transects CAX-01 and CAX-02 cover part of the elevation range, from 29 m to 35 m. These two plots present higher wood productivity and lower above ground biomass than the other plots located in the plateau.

4.2 Regional variation in wood productivity, wood specific density and above ground biomass

Wood productivity did not show a clear regional pattern from the south-western sites to the north-eastern sites (Fig. 9a), but wood density and above ground biomass mean values were higher in the north-east (Fig. 9b and c). These patterns did not change according to the result of the area weighted-analysis (Fig. 9).

In this study, the Peruvian plots were considered as western Amazonia sites, the Manaus plots in Brazil were considered central Amazonia site and the Caxiuanã plots were considered eastern Amazonia site for a macro-regional analysis. An evaluation of the plots located only in the *Terra Firme* physiognomy showed that the three variables

are clearly distinguishable from Western to Eastern Amazonia (Fig. 10).

The variation in the spatial heterogeneity of the landscape observed in the alluvial terrain forests is characterized by differences in texture observed in the remote sensing data that reflects differences in geomorphology, vegetation, soil chemical and physical characteristics and inundation pulse. The three alluvial types classified in this study also reflect these differences. The physiognomy type 1, characteristic of Jenaro Herrera (plots 3, 6 and 9) and Cuzco Amazonico (plots 03 and 04), is composed of younger soils, probably from the Holocene period. This physiognomy is characterized by higher above ground biomass and is more productive than the other two types (Fig. 11). The type 2 physiognomy is also located in the same geomorphological area as the type one (Cuzco Amazonico, plots 01 and 02), but without the potential for inundation. It presents lower mean values for the three parameters evaluated. The alluvial terrain forest type 3 is located in older terraces, assumed to be from the Pleistocene, and presents higher values of above ground biomass and wood productivity than type 2 and lower values of those parameters than type 1.

5 Discussion

5.1 Landscape mapping

Remote sensing data can be an important source of information on the spatial distribution of different vegetation physiognomies in tropical forests. In this study, we distinguished three types of *Terra Firme* forests, three types of alluvial terrain forests, swamp areas, palm forest, two types of bamboo dominated forests and seasonally inundated areas.

Salovaara et al. (2004) produced a map based on field work data with four main forest classes separated by floristic characteristics in Northeastern Peruvian Amazonia. The same authors then investigated the possibility of aggregating a Landsat/ETM+ image with altimetry data derived from SRTM to achieve the same results as found for the

map solely based on field data (Salovaara et al., 2005). They succeeded in separating inundated areas from *Terra Firme*; however *Pebas* formation forests and intermediate *Terra Firme* forests were misclassified by the algorithms. Due to the characteristics of the forest types evaluated in this study, alluvial terrain forests (inundated and non-inundated) were generally successfully separated automatically from *Terra Firme* areas (with the exception of one site, Sucusari plot SUC-03). Moreover, in the *Terra Firme* forests in the Allpahuayo site, it was possible to automatically separate three *Terra Firme* sub-classes due to the presence of forests over sandy soil and regions with high palm tree density, a feature which is visually darker in the satellite image due to the higher proportion of canopy shade. Previous studies reported that sandy soil forests could not be automatically separated using satellite images due to limitations of the algorithms (Foody and Hill, 1996; Hill, 1999). At this site, the forest characteristics of the sandy soils appear to be sufficient distinct from those of the surrounding clay areas.

Foody and Hill (1996) have studied the Tambopata region on a larger geographic scale, and using automatic classification they were able to separate the swampy areas from the other land cover types (*Bamboo* and lowland forests). In spite of using different classification algorithms to Foody and Hill (1996), in this study we still expected that the swamp areas would produce a distinguishable spectral characteristic. However, this was not the case. One possible explanation for this lack of differentiation might be that the images in the two studies were acquired on different dates. Thus, it is probable that the water level may have been different; thereby changing the swamp's spectral properties and the ability to distinguish swamps from *Terra Firme* forests.

5.2 Wood productivity, wood density and above ground biomass patterns across Amazonia

Our results generally support previous findings about the regional variation in forest wood productivity, wood specific density and above ground biomass in Amazonia revealed by the RAINFOR network (Malhi et al., 2004; Phillips et al., 2004; Lewis et al., 2004; Baker et al., 2004a, b). The RAINFOR sites in this study have been used to

demonstrate that forest productivity is higher in Western Amazonia than the Central and Eastern regions. This pattern follows a gradient of soil structural and chemical composition and number of dry months (Quesada et al., 2009b). It has also been suggested that the absolute wood specific density value of the species declines with increasing soil fertility similarly for both trees and saplings/shrubs (Huston, 1980; Swaine and Becker, 1999), and that there is no robust relationship between soil fertility and wood specific density of tropical forest tree species (Wright, 1992; Clinebell et al., 1995). In this study, Western Amazonia had the lowest mean value for wood specific density. Muller-Landau (2004) and Baker et al. (2004) reported higher wood specific density in nutrient-poor soils in central Amazonia and lower values in Western Amazonia with richer soils, independent of rainfall, seasonality and temperature. However, it has been generally noted that within the RAINFOR sites, wood specific gravity varies widely among species and that within-species variations can also be significant (Patiño et al., 2009).

Nebel et al. (2001) found a significant relationship between forest productivity and biomass and the period of flooding in seasonally inundated forests. Therefore, as we showed that some of the RAINFOR plots are located in alluvial terrains, it might be expected that these sites could be driving the observed east-west variation (Fig. 12). For instance, within the Cuzco Amazonico site all four plots are characterized by alluvial terrain forests physiognomy. Similarly, Tambopata and Jenaro Herrera sites have the majority of their plots in Holocene alluvial terrains. Although very few of these plots located in the alluvial terrain forests are seasonally flooded, the mean wood productivity of these sites is about the same as the Western *Terra Firme* sites, and the absolute mean value is higher than the mean values for all *Terra Firme* sites (Fig. 12a). It is pertinent to note that the seasonally flooded plots show a wide range of coarse wood productivities, possibly related to sediment loading and flooding period (Malhi et al., 2004).

A previous study quantifying the flooded forests in Central Amazonia estimated a total area of 187×10^3 km^2 (Hess et al., 2003) – a substantial region with high impor-

tance for the carbon fluxes. Therefore, more studies on quantifying the dynamics of the flood plain forests would provide valuable and more accurate information on the variation of the amount of carbon stored in these areas and its dynamics. In their analysis of the RAINFOR plots, Baker et al. (2004b) found that ABG and stand-level wood specific gravity of the floodplain plots are structurally the same as the non-floodplain Western Amazonian plots. Our results showed that there is a significant difference in wood density from more recent alluvial terrain forest sites and Western *Terra Firme* sites (Fig. 12b) but no significant difference in the above ground biomass (Fig. 12c).

6 Conclusions

In this paper we have precisely located many key RAINFOR plot clusters covering western, central and eastern Amazonia for a landscape evaluation of the representativeness of those plots and its implications for a apparent regional variation in forest biophysical parameters.

We conclude that the plots were generally representative of the forest physiognomies in the landscape in which they are located, and the forest parameters analysis supports the observed regional trends.

The landscape maps generated here can be used as a basis for defining different vegetation types to be sampled, and future work involving radar remote sensing data could be used in combination for improving of the capturing the forest structural parameters.

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Table 1. General characteristics of the sites studied. Data compiled from Malhi et al. (2004). The soil type classes are from the World Reference Base soil classification; for detailed information, see Quesada et al. (2009b).

Site	Location	Mean Precipitation (mm)	Mean Temperature (°C)	Soil Type
Allpahuayo	Northern Peruvian Amazon 73°25′ W, 3°56′ S	2760	26.3	Arenosols, Alisol, Gleysol and Plinthosol
Cuzco Amazonico	Southern Peruvian Amazon 68°57′ W, 12°30′ S	2420	25.5	Cambisols
Jenaro Herrera	Northern Peruvian Amazon 73°41′W, 4°55′ S	2700	26.6	Cambisols, Arenosols
Sucusari	Northern Peruvian Amazon 72°54′ W, 3°15′ S	2670	26.2	Plinthosols, Acrisols, Gleysols
Tambopata	Southern Peruvian Amazon 69°17′ W, 12°50′ S	2420	25.2	Alisol, Cambisols, Gleysols
Manaus	Centre of the Brazilian Amazon 60°01′ W, 2°28′ S	2170	26.8	Ferralsols, Podzols
Caxiuanã	Eastern Brazilian Amazon 51°27′ W, 1°43′ S	2300	26.8	Acrisols, Ferralsols

Table 2. Field plots characteristics. TF=Terra Firme, TF 2=Terra Firme 2, TF 3=Terra Firme 3, AT 1=alluvial terrain forests type 1, AT 2=alluvial terrain forests 2, AT 3=alluvial terrain forests 3, DF=disturbed forest, SW=swamp. The forest type is derived from the landscape maps in this study; detailed description is presented in Table 3.

Site	Plot code	Country	Central Latitude	Central Longitude	SRTM Altitude (Mean value, in meters)	Plot shape (m×m)	Forest type	Landsat Path/Row	Image date
Allpahuayo	ALP-03	Peru	−3°57′15.57″	−73°25′32.93″	145	40×250	TF	006/063	23/09/2003
	ALP A		−3°56′57.94″	−73°26′2.81″	128	40×500	TF 3		
	ALP B		−3°57′10.62″	−73°26′14.64″	136	40×250	TF, TF3		
Caxiuanã	CAX-01	Brazil	−1°44′14.65″	−51°27′46.46″	45				
	CAX-02		−1°44′36.51″	−51°27′41.34″	42	100×100	TF	225/061	20/08/2002
	CAX-06		−1°44′12.55″	−51°27′42.52″	47				
	TEC-02		−1°42′24.07″	−51°27′33.12″	42				
Cuzco	CUZ-01	Peru	−12°29′56.34″	−68°58′25.63″	200		AT 2	002/069	23/08/2001
Amazônico	CUZ-02		−12°29′56.81″	−68°58′14.54″	199	20×500	AT 2		
	CUZ-03		−12°29′58.81″	−68°57′46.65″	198		AT 1		
	CUZ-04		−12°29′57.18″	−68°57′35.21″	196		AT 1		
Jenaro	JEN-03	Peru	−4°54′51.14″	−73°44′32.98″	114	100×100	AT 1	006/063	23/09/2002
Herrera	JEN-06		−4°54′45.84″	−73°44′46.94″	112		AT 1		
	JEN-09		−4°57′29.21″	−73°43′18.32″	102		AT 1		
	JEN-10		−4°53′56.37″	−73°38′50.42″	135		DF		
	JEN-11		−4°52′41.56″	−73°37′46.25″	131		TF		
	JEN-12		−4°53′57.36″	−73°37′40.97″	128	50×200	TF		
Manaus	BDF-01	Brazil	−2°20′33.93″	−60°05′47.24″	116			230/062	08/09/2002
	BDF-03		−2°25′26.96″	−59°51′18.08″	105	100×100			
	BDF-04		−2°25′38.90″	−59°51′10.75′	120				
	BDF-05		−2°25′32.80″	−59°51′2.82″	120				
	BDF-06		−2°24′53.94′	−59°51′24.09′	111				

Table 2. Continued.

Site	Plot code	Country	Central Latitude	Central Longitude	SRTM Altitude (Mean value, in meters)	Plot shape (m×m)	Forest type	Landsat Path/Row	Image date
	BDF-09		−2°23′48.92″	−59°50′47.03″	114				
	BDF-10		−2°23′19.92″	−59°51′18.50″	123				
	BDF-11		−2°23′4.72″	−59°50′59.77″	119		TF		
	BDF-12		−2°23′30.15″	−59°51′10.87″	110				
	BDF-13		−2°23′55.07″	−59°54′49.18″	153				
	BDF-14		−2°21′51.22″	−59°58′27.25″	137				
	BNT-01		−2°38′33.34″	−60°09′27.44″	118				
	BNT-02		−2°38′29.46″	−60°09′1.66″	119				
	BNT-04		−2°37′45.25″	−60°09′15.05″	117				
	JAC-01		−2°36′23.27″	−60°12′23.53″	90				
	JAC-02		−2°36′54.20″	−60°11′46.58″	101				
Sucusari	SUC-01	Peru	−3°15′7.60″	−72°54′26.77″	123			006/062	23/09/2003
	SUC-02		−3°15′4.11″	−72°54′12.94″	128				
	SUC-03		−3°14′49.02″	−72°55′20.76″	101	20×500	TF		
	SUC-04		−3°15′1.29″	−72°53′31.51″	125				
	SUC-05		−3°15′37.68″	−72°53′58.02″	129				
Tambopata	TAM-01	Peru	−12°50′38.81″	−69°17′18.18′	211		AT 3	002/069	23/08/2001
	TAM-02		−12°50′5.11″	−69°17′9.89″	214		AT 3		
	TAM-04		−12°50′11.47″	−69°16′42.61″	211	100×100	SW		
	TAM-05		−12°49′49.04″	−69°16′13.92″	210		TF		
	TAM-06		−12°50′18.59″	−69°17′45.65″	194		AT 3		
	TAM-07		−12°49′32.45″	−69°15′39.72″	227		TF		
	TAM-08		−12°49′34.70″	−69°16′9.95″	220		TF		

Table 3. Land cover classes description.

Land Cover Classes	Description
Land use	Bare soil, pasture areas, croplands and roads
Disturbed forest	Disturbed forest, secondary forest and logging areas
Clouds	Cloud
Cloud shade	Cloud shadow
Water	Rivers and water bodies
Terra Firme	Typical *Terra Firme* area, with the elevation data showed
Terra Firme 2	*Terra Firme* area with darker spectral characteristics than the *Terra Firme*; presence of palm trees, with sandy soil
Terra Firme 3	*Terra Firme* area with the spectral characteristic between *Terra Firme* and *Terra Firme* 2; presence of palm trees, with sandy soil
Alluvial terrain forests 1 (AT1)	Forest physiognomy in seasonal inundated area located in Holocene/Pleistocene alluvial formation
Alluvial terrain forests 2 (AT2)	Forest physiognomy with the spectral property close to seasonal inundated area, however without inundation periods also located in Holocene/Pleistocene alluvial formations
Alluvial terrain forests 3 (AT3)	Forest physiognomy of *Terra Firme*, however located in Holocene/Pleistocene alluvial formations, non-flooded
Alluvial terrain forests low density	Alluvial terrain forests with low density of individuals Patches of bare soil are sometimes evident
Bamboo	Bamboo dominant physiognomy; spectrally it was possible to differentiate 2 types
Heliconia	*Heliconia sp.* monodominant physiognomy (T. R. Baker, personal communication, 2006)
Flooded area	Permanent flooded area
Seasonally inundated	Seasonally inundated area over streams

Table 4. Detailed site parameters. Mean values of wood productivity wood density and above ground biomass updated from Baker et al. (2004a); Malhi et al. (2004, 2006). Forest censuses are pre-2005 year, except for the following plots: JEN 10, JEN 11, SUC 03 SUC 04, SUC 05, CAX 06. Mean values/Weighted mean values presented with ± one standard error.

Site	Field plot	Mean Productivity ($Mg\,C\,ha^{-1}\,y^{-1}$)	Mean Density ($g\,cm^{-3}$)	Mean Biomass ($Mg\,DW\,ha^{-1}$)
Allpahuayo	ALP-03	2.00	0.66	265
	ALP A	1.45	0.64	225
	ALP B	1.68	0.62	209
	Mean value	1.716 (±0.19)	0.64 (±0.01)	233 (±20)
	Weighted mean value	1.90	0.65	254
Cuzco Amazonico	CUZ-01	1.91	0.55	262
	CUZ-02	2.10	0.52	225
	CUZ-03	2.15	0.55	231
	CUZ-04	3.14	0.58	280
	Mean value	2.32 (±0.31)	0.55 (±0.01)	250 (±15)
	Weighted mean value	2.34	0.55	250
Jenaro Herrera	JEN-03	2.55		257
	JEN-06	2.72		269
	JEN-09	2.55		279
	JEN-10	1.29		233
	JEN-11	4.07	0.67	295
	JEN-12	0.59	0.67	266
	Mean value	2.29 (±0.54)	0.67	267 (±9)
	Weighted mean value	2.47		275
Sucusari	SUC-01	3.53	0.60	287
	SUC-02	4.11	0.61	284
	SUC-03	2.10	0.70	322
	SUC-04	3.33	0.62	298
	SUC-05	2.93	0.61	287
	Mean value	3.2 (±0.37)	0.63 (±0.01)	296 (±7)

Table 4. Continued.

Site	Field plot	Mean Productivity ($Mg\,C\,ha^{-1}\,y^{-1}$)	Mean Density ($g\,cm^{-3}$)	Mean Biomass ($Mg\,DW\,ha^{-1}$)
Tambopata	TAM-01	2.75	0.51	235
	TAM-02	2.16	0.53	245
	TAM-04	2.98	0.61	290
	TAM-05	2.47	0.61	250
	TAM-06	1.70	0.49	255
	TAM-07	2.79	0.61	260
	TAM-08	1.81	0.58	219
	Mean value	2.38 (±0.20)	0.56 (±0.02)	251(±9)
	Weighted mean value	2.26(±0.67)	0.52(±0.15)	248 (±75)
Manaus	BDF-01	2.40	0.72	289
	BDF-03	2.20	0.66	358
	BDF-04	1.90	0.67	277
	BDF-05	2.24	0.69	322
	BDF-06	2.28	0.68	306
	BDF-09	2.39	0.71	405
	BDF-10	2.39	0.70	328
	BDF-11	1.16	0.70	395
	BDF-12	2.17	0.70	380
	BDF-13	1.73	0.71	365
	BDF-14	2.31	0.71	406
	BNT-01	1.26	0.69	376
	BNT-02	1.32	0.70	398
	BNT-04	2.15	0.71	337
	JAC-01	2.21	0.67	302
	JAC-02	2.02	0.68	292
	Mean value	2.01(±0.16)	0.70(±0.00)	346 (±12)
Caxiuanã	CAX-01	1.39	0.73	394
	CAX-02	2.88	0.71	376
	CAX-06	0.49	0.71	416
	TEC-02	0.30	0.74	446
	Mean value	1.27 (±0.68)	0.73 (±0.00)	408 (±17)

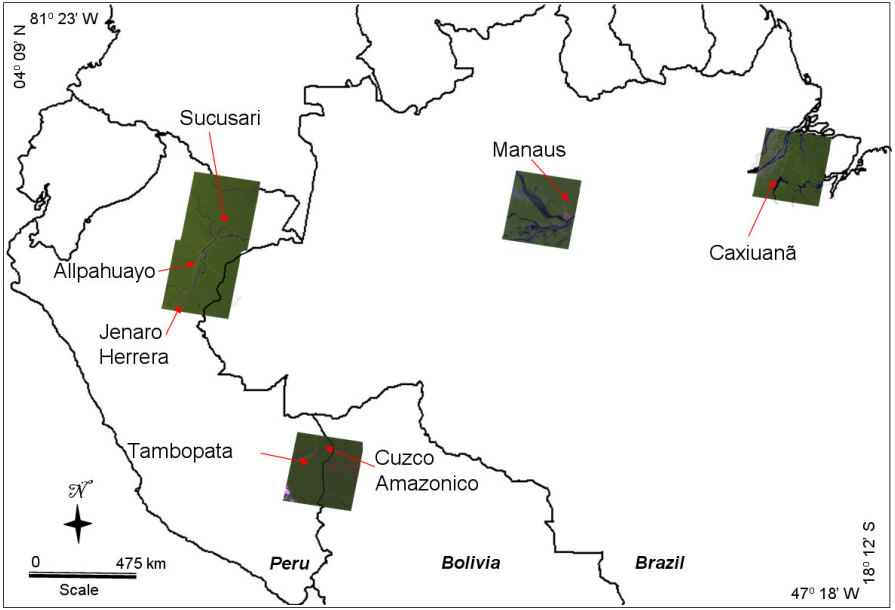

Fig. 1. Location of the 7 study sites: Western Amazonia is covered by Peruvian sites, Central Amazonia is represented by Manaus region and Eastern Amazonia encompasses Caxiuanã plots. The country limits are in black lines and the sites are indicated in an ETM+ colour composite image.

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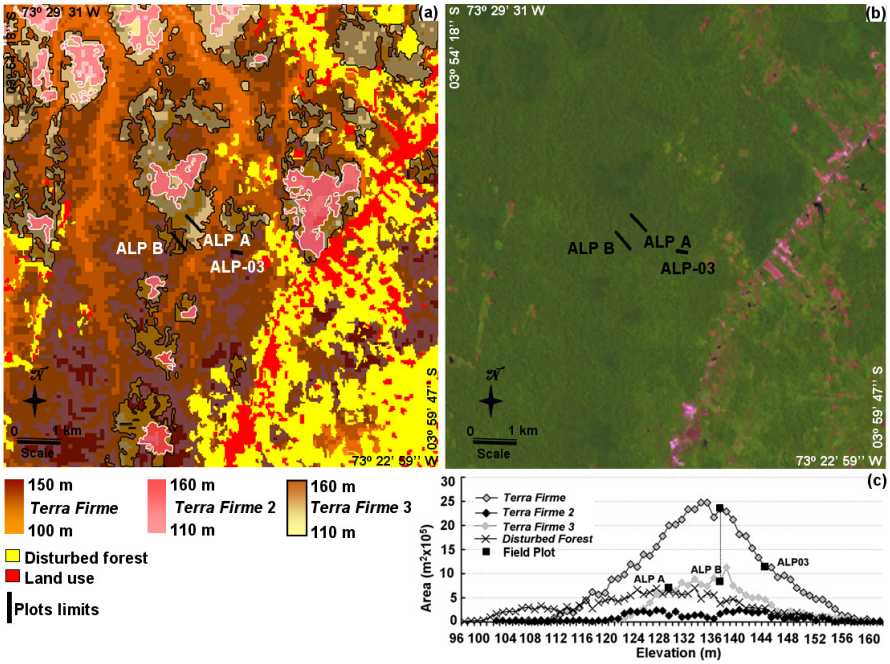

Fig. 2. Allpahuayo site: **(a)** Landscape map; **(b)** Landsat image for the field site (RGB channels in band 5, band 4 and band 3), the black rectangles represent the transects limits; **(c)** histogram of the elevation distribution per land cover class, with the field transects.

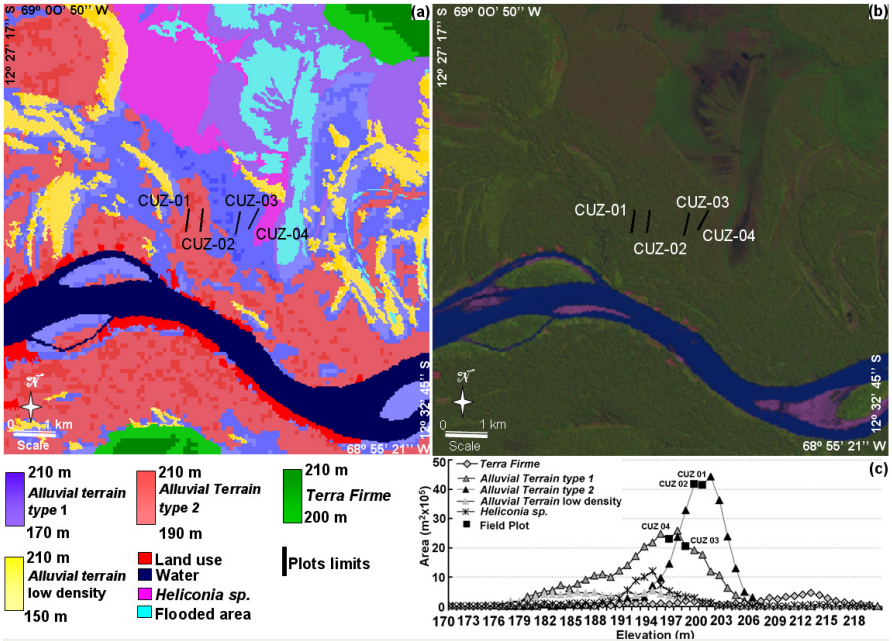

Fig. 3. Cuzco Amazonico site: **(a)** Landscape map; **(b)** Landsat image for the field site (RGB channels in band 5, band 4 and band 3), the black rectangles represent the transects limits; **(c)** histogram of the elevation distribution per land cover class, with the field transects.

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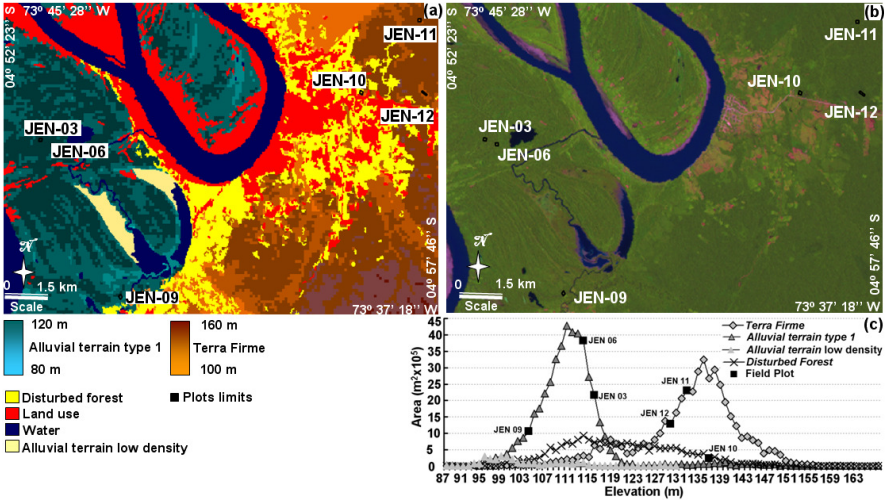

Fig. 4. Jenaro Herrera site: **(a)** Landscape map; **(b)** Landsat image for the field site (RGB channels in band 5, band 4 and band 3), the black rectangles represent the transect limits; **(c)** histogram of the elevation distribution per land cover class, with the field transects.

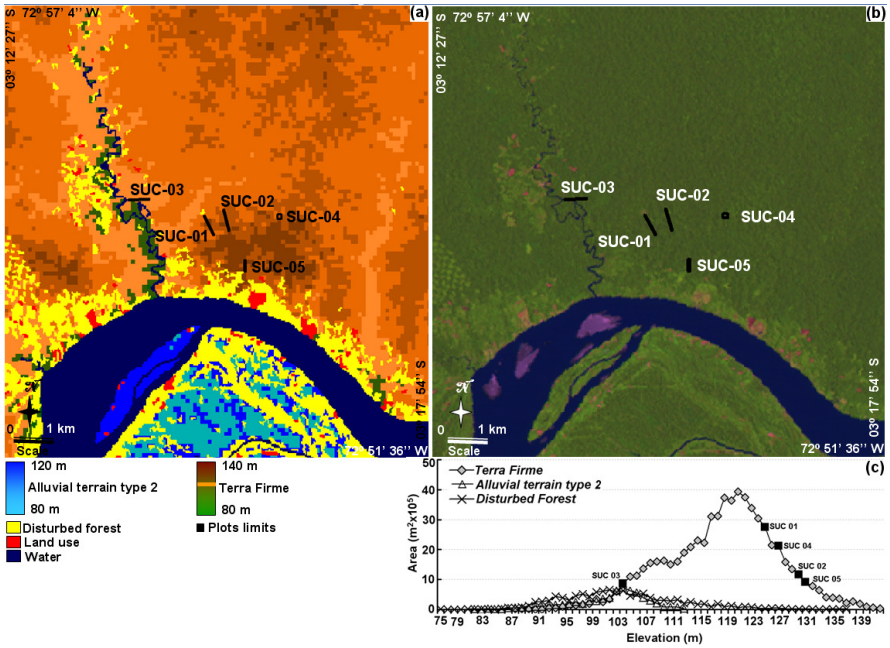

Fig. 5. Sucusari site: **(a)** Landscape map; **(b)** Landsat image for the field site (RGB channels in band 5, band 4 and band 3), the black rectangles represent the transect limits; **(c)** histogram of the elevation distribution per land cover class, with the field transects.

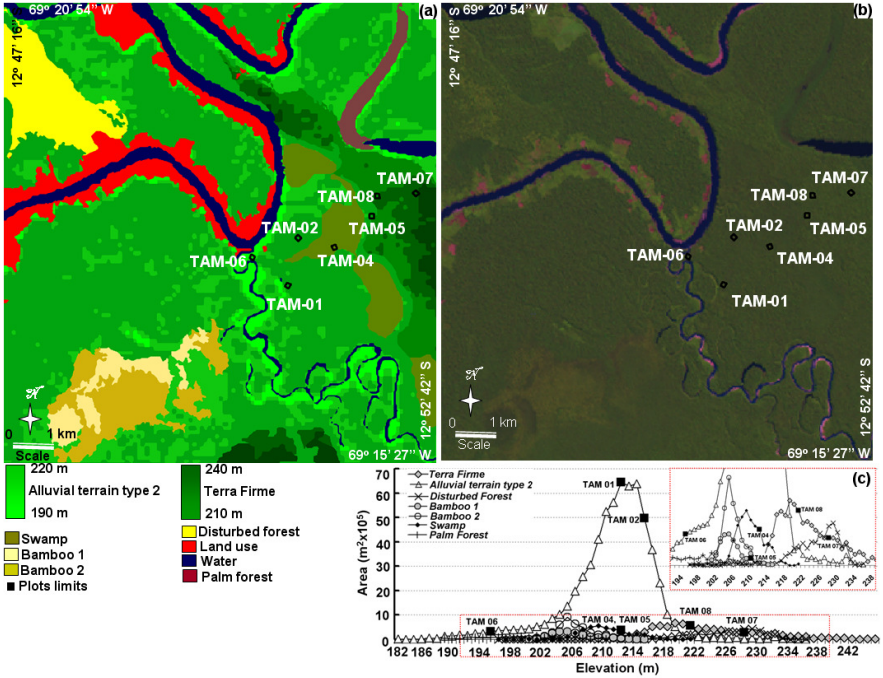

Fig. 6. Tambopata site: **(a)** Landscape map; **(b)** Landsat image for the field site (RGB channels in band 5, band 4 and band 3), the black rectangles represent the transect limits; **(c)** histogram of the elevation distribution per land cover class, with the field transects – the red rectangle in x-y axis is presented in a zoom.

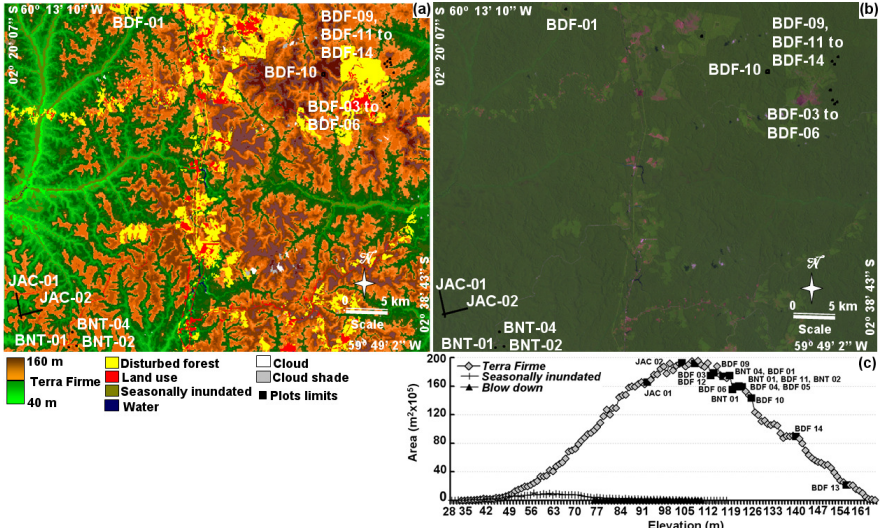

Fig. 7. Manaus site: **(a)** Landscape map; **(b)** Landsat image for the field site (RGB channels in band 5, band 4 and band 3), the black rectangles represent the transect limits; **(c)** histogram of the elevation distribution per land cover class, with the field transects.

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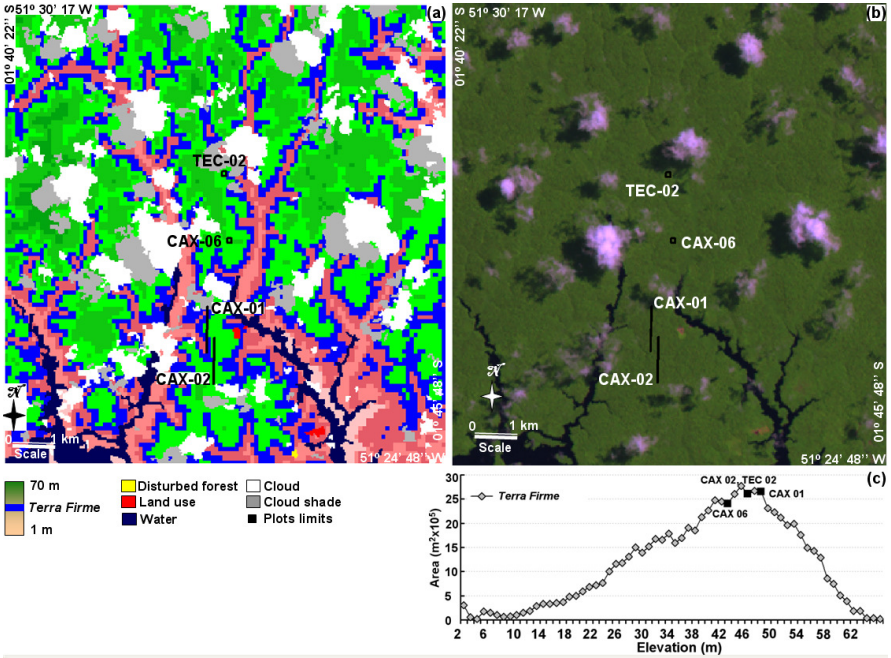

Fig. 8. Caxiuanã site: **(a)** Landscape map; **(b)** Landsat image for the field site (RGB channels in band 5, band 4 and band 3), the black rectangles represent the transect limits; **(c)** histogram of the elevation distribution per land cover class, with the field transects.

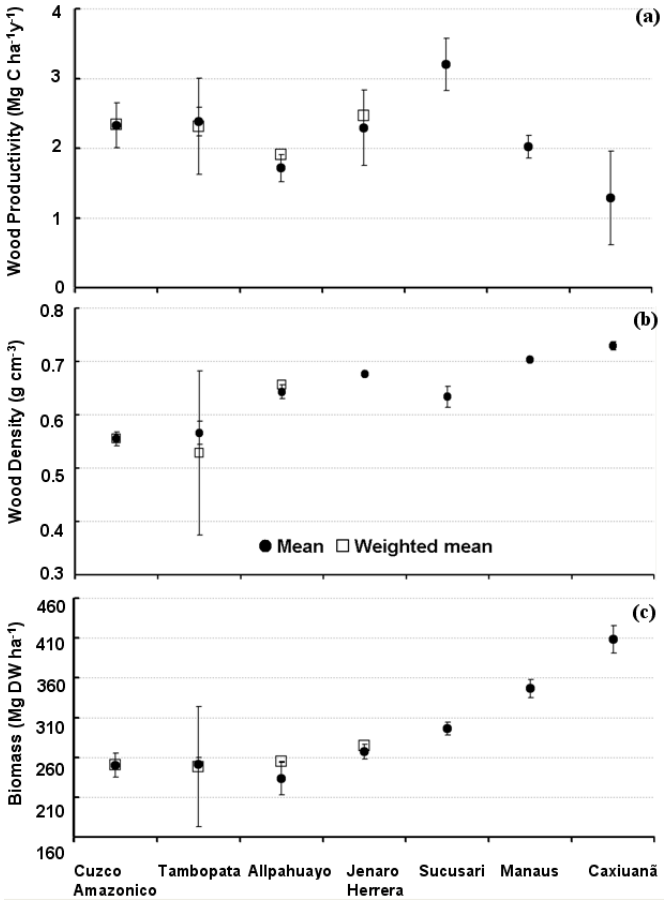

Fig. 9. Mean and weighted mean values evaluation per site: **(a)** Wood productivity, **(b)** wood density and **(c)** above ground biomass.

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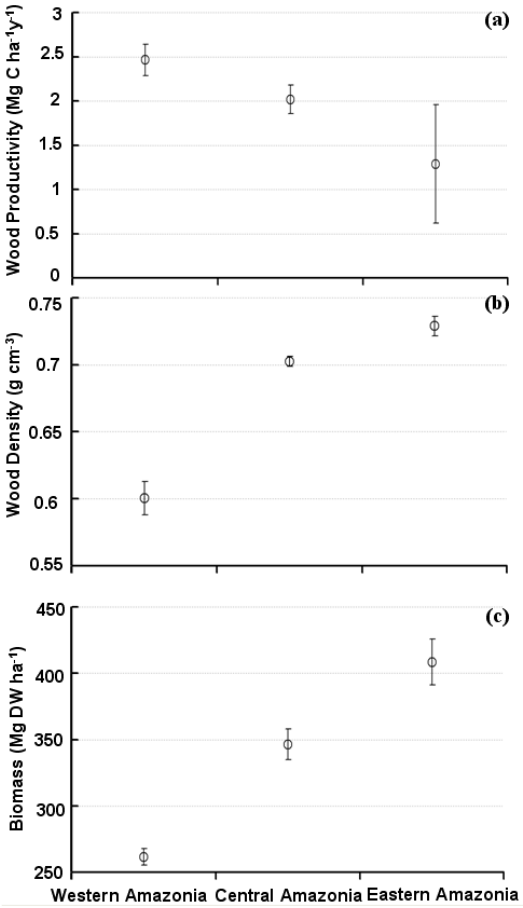

Fig. 10. Macro-regional variability of **(a)** Wood productivity, **(b)** wood density and **(c)** above ground biomass mean values (± one standard error) for the plots located in the *Terra Firme* physiognomy.

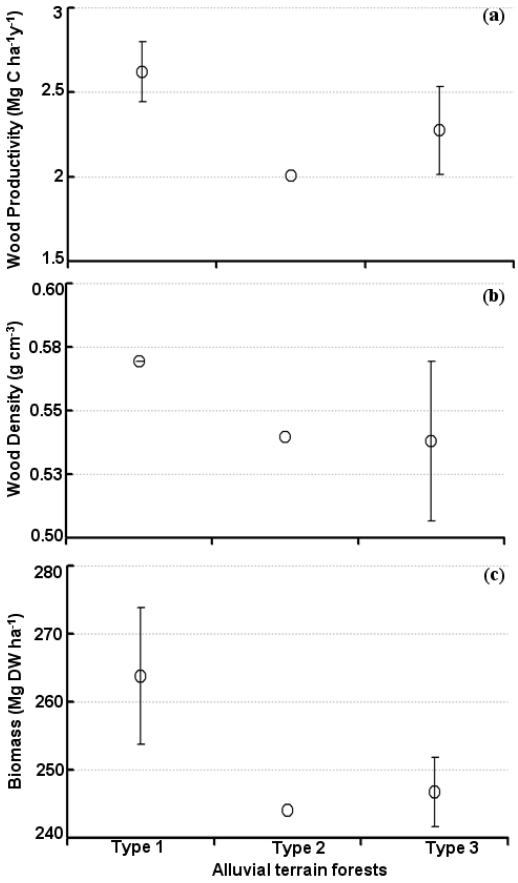

Fig. 11. Variability within the alluvial terrain forests physiognomy mean values with ± one standard error: **(a)** Wood productivity, **(b)** wood density, **(c)** above ground biomass.

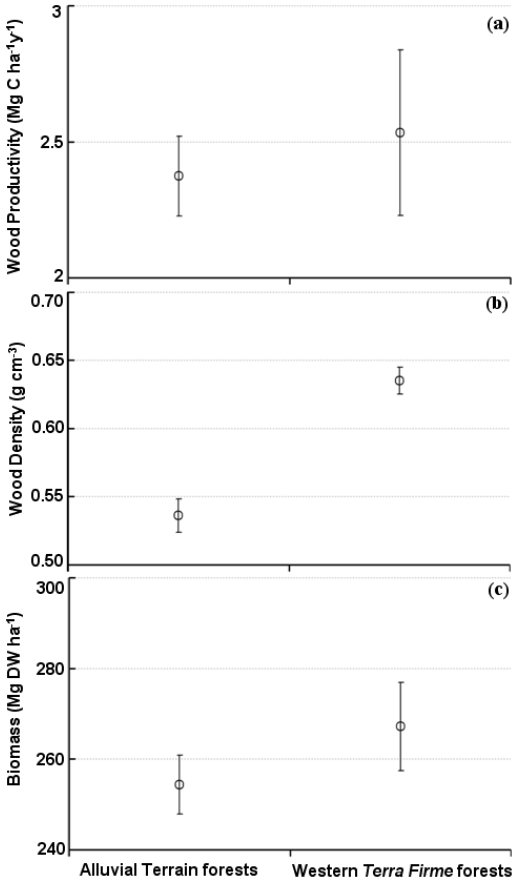

Fig. 12. Comparison of the forest variables in alluvial terrain with the Western *Terra Firme* sites. **(a)** Wood productivity, **(b)** wood density and **(c)** above ground biomass (±) one standard error.

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