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Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties

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Abstract

Forest structure and dynamics have been noted to vary across the Amazon Basin in an east-west gradient in a pattern which coincides with variations in soil fertility and geology. This has resulted in the hypothesis that soil fertility may play an important role in explaining Basin-wide variations in forest biomass, growth and stem turnover rates.

To test this hypothesis and assess the importance of edaphic properties in affect forest structure and dynamics, soil and plant samples were collected in a total of 59 different forest plots across the Amazon Basin. Samples were analysed for exchangeable cations, C, N, pH with various *P* fractions also determined. Physical properties were also examined and an index of soil physical quality developed.

Overall, forest structure and dynamics were found to be strongly and quantitatively related to edaphic conditions. Tree turnover rates emerged to be mostly influenced by soil physical properties whereas forest growth rates were mainly related to a measure of available soil phosphorus, although also dependent on rainfall amount and distribution. On the other hand, large scale variations in forest biomass could not be explained by any of the edaphic properties measured, nor by variation in climate.

A new hypothesis of self-maintaining forest dynamic feedback mechanisms initiated by edaphic conditions is proposed. It is further suggested that this is a major factor determining forest disturbance levels, species composition and forest productivity on a Basin wide scale.

1 Introduction

There is a coincident semi-quantitative correlation between forest above ground biomass gain (AGB) and soil fertility observed across the Amazon Basin (Malhi et al., 2004). But what controls Amazon forest productivity and function, either at a Basin wide scale or regionally remains to be accurately determined.

Stem turnover, viz. the rate in which trees die and are recruited in a forest population,

also varies across the Amazon Basin (Phillips et al., 2004) with an east-west gradient coinciding with gradients of soil fertility and geology as first described by Sombroek (1966) and Irion (1978). An average turnover rate of $1.35\% \text{ yr}^{-1}$ is observed in the infertile eastern and central areas whilst the average turnover rate of $2.60\% \text{ yr}^{-1}$ occurs in the more fertile west and south-west portion of Amazonia. This pattern has resulted in the hypothesis that soil fertility may play an important role in explaining the almost two-fold difference in stem turnover rates between the western and central-eastern areas (Phillips et al., 2004; Stephenson and Van Mantgen, 2005).

Nevertheless, in addition to soil fertility per se, soil physical properties such as a limited rooting depth, low drainage capacity, low water holding capacity, the presence of hardpans, bad soil structure and topographic position have also long been known to be an important limitations to forest growth, directly or indirectly influencing tree mortality and turnover rates across both temperate and tropical forest ecosystems (Arshad et al., 1996; Dietrich et al., 1996; Gale and Barford, 1999; Schoenholtz et al., 2000). Variations in soil fertility and physical properties across the Amazon Basin are similarly related to variations in soil age and type of parent material (Quesada et al., 2009).

Specifically, highly weathered soils are generally of depths several metres above the parent material and usually have very good physical conditions as a result of millenniums of soil development (Sanchez, 1987). On the other hand, the more fertile soils in Amazonia are closely related to lower levels of pedogenesis with the parent material still a source of nutrients, or often as a consequence of bad drainage and/or deposition of nutrients by flooding waters (Irion, 1978; Herrera et al., 1978; Quesada et al., 2009). It is for this reason that soil fertility is to some extent correlated with physical limiting conditions (Quesada et al., 2009).

This gives rise to the idea that the previously identified relationship found between soil fertility and turnover rates might, at least to some extent, reflect physical constraints, or at least a combination of chemical and physical factors. Other forest traits such as wood density, forest production and above ground biomass could also be influenced by physically adverse soil conditions.

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In any case, relationships of forest dynamics and structure with soil fertility are not clear. For example, the effect of soil properties on tropical forest above ground biomass have been contradictory: Some studies have found interactions between soil fertility and above ground biomass (Laurance et al., 1999; Roggy et al., 1999), but most other studies have found no relationship with soil fertility (Proctor et al., 1983; Clark and Clark 2000; Chave et al., 2001; DeWalt and Chave, 2004), with climate then being invoked as a causative factor.

An important step forward was made by Baker et al. (2004) who found that the variations in above ground biomass are mostly related to stand wood specific gravity differences. Thus what causes variations in wood specific gravity has a direct influence on the above ground biomass variations.

Here we look in some detail at the relationship between Amazon forest soil physical and chemical conditions and forest turnover rates, above ground biomass gain, average plot wood density and above ground biomass. We use both previously published data (Phillips et al., 2004; Malhi et al., 2004; Baker et al., 2004) and newly calculated estimates of these parameters from the RAINFOR database (Peacock et al., 2007), all estimates used were prior to 2005.

2 Material and methods

2.1 Study sites

From the complete soils dataset found in Quesada et al. (2009, Table 1), a subset of 59 primary forest plots across the Amazon basin was used in the analysis here. The selected areas account for sites where forest parameters and complete soil data was available. Therefore, the following sites have been excluded in this analysis: MAN-03, MAN-04, MAN-05, TAP-04, TIP-05 and CPP-01 did not have forest data available. CAX-06, SUC-03, ELD-34, SCR-04 and CAX-04 had incomplete soil data, and SUM-06 was excluded since it is a montane forest above 500 m altitude.

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2.2 Soil sampling and determination of chemical and physical properties

Soil sampling and determination methods are described in detail in Quesada et al. (2009) and are thus only briefly summarized here.

For each one hectare plot, five to twelve soil cores were collected and soil retained over the depths 0–0.05, 0.05–0.10, 0.10–0.20, 0.20–0.30, 0.30–0.50, 0.50–1.00, 1.00–1.50 and 1.50–2.00 m using an undisturbed soil sampler (Eijkelkamp Agrisearch Equipment BV, Giesbeek, The Netherlands).

Each plot usually had one soil pit dug to the depth of 2.0 m with samples collected from the pit walls. All sampling was done following a standard protocol (see <http://www.geog.leeds.ac.uk/projects/rainfor/pages/manualstodownload.html>) in such way to account to spatial variability within the plot.

Soil samples were air dried, usually in the field, and then once back in the laboratory had roots, detritus, small rocks and particles over 2 mm removed. Samples were then analysed for: pH in water at 1:2.5, exchangeable cations by the silver-thiourea method (Pleysier and Juo, 1980), complete phosphorus fractionation (modified from Hedley et al., 1982), and carbon and nitrogen (Pella, 1990; Nelson and Sommers, 1996). Here results from the top soil layer (0–0.3 m) are presented.

For quantifying the magnitude of limiting soil physical properties, a score table was developed, and sequential scores assigned to the different levels of physical limitations. This was done by simply scoring a soil going through the field descriptions with the help of the score table (details in Quesada et al., 2009) with this providing information on soil depth, soil structure quality, topography and anoxic conditions in a semi-quantitative format. This data was also combined in two indexes of soil physical quality by adding up the scores of each physical property. Therefore INDEX–1 was created by the adding up of soil depth, structure, topography and anoxic scores, and INDEX–2 by the adding up of only soil depth, structure and topography scores. INDEX–1 was shown to be strongly related to soil's weathering degree, reflecting broad geographical patterns of soil quality in Amazonia (Quesada et al., 2009). In addition, soil bulk density was determined

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and included in the assessment of soil structure scores. Particle size analysis was performed using the Boyoucos method (Gee and Bauder, 1986).

Available water content (AWC) was determined as a function of potential evaporation, depth of root system (as noted from soil pit descriptions) and by an estimation of soil available water content based on the particle size pedotransfer functions given by Hodnett and Tomasella (2002). AWC was integrated to the maximum rooting depth for each area or integrated to four meters were roots were not observed to be constrained in any way. This was then modelled to vary following daily rainfall inputs and losses estimated by potential evaporation, with the time (months) in which less than 20% AWC was attained recorded using standard soil "water bucket" calculations.

2.3 Statistical methods

Analyses of ecological processes have usually been done using multiple regressions in which a desired response variable is regressed against sets of environmental variables (see Paoli and Curran, 2007 for a recent relevant example). However, the lack of independence between pairs of observations across geographical space (spatial autocorrelation), results in the need for more complex strategies for data analyses (Legendre, 1993). This is because spatial autocorrelation generates redundant information on data and overestimation of actual degrees of freedom (Dutilleul, 1993). Therefore, autocorrelation in multiple regression residuals results in the underestimation of standard errors of regression coefficients, consequently inflating Type I errors. Thus models that incorporate the spatial structures into model structure or regression residuals should be used to provide unbiased regression coefficients (Diniz-Filho and Bini, 2005).

In this paper eigenvector-based spatial filtering (extracted by Principal Component of Neighbour Matrices: PCNM, Borcard and Legendre, 2002) was thus used to help us understand our observed spatial patterns in forest structure and dynamics. Spatial filters were then used in multiple partial regressions specifically designed to partition between purely environmental and geographical effects. To aid the detection of spatial structures in the data, Moran's *I* correlograms were performed for each variable of

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interest. Spearman correlations were then adjusted to account for spatial autocorrelation, following Dutilleul's method (Dutilleul, 1993), which adjusts degrees of freedom and p values. All spatial statistics were performed using the software Spatial Analysis in Macroecology – SAM (Rangel et al., 2006).

5 3 Results

3.1 Forest structure and dynamics in the geographic space

Figure 1 shows the geographical distribution of tree turnover rates (Fig. 1a); above ground biomass gain (AGB gain, Fig. 1b) and above ground biomass (Fig. 1c). Forest structure and dynamics are remarkably conditioned by spatial location. Tree turnover rates vary substantially across Amazonia, ranging from as little as 0.7 to 4.3% yr⁻¹. Tree turnover rates are systematically higher in the western areas of Amazonia while much lower rates occur in central and eastern sedimentary areas as well as in the north part (Guyana Shield) as has been reported before (Phillips et al., 2004). This geographical pattern is similar to that of AGB gain, which also varies with a similar pattern ranging from 2.7 to 10.3 Mg ha⁻¹ yr⁻¹, also being noticeably higher in the proximity of the Andean cordillera, intermediary in the Guyana Shield area and lowest in the central and eastern Amazonian areas (Malhi et al., 2004). By contrast, above ground biomass is higher in the east and central areas as well as in the north, but also having an east-west gradient with lower above ground biomass occurring in west and south-west areas of Amazonia (Baker et al., 2004; Malhi et al., 2006). Above ground biomass ranged from 138.6 to 458.1 Mg ha⁻¹ across the basin. Growth and turnover patterns are congruent with the geological history of the area (Irion, 1978) and thus have generated the idea that broad edaphic and geological variations across the region might account for the regional variation in forest structure and dynamics (Stephenson and Van Mantgen, 2005; Malhi et al., 2004; Baker et al., 2004; Phillips et al., 2004). For biomass geographical association are less clear.

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Though the relationship is different all three forest properties correlate with latitude and longitude. Thus spatial structures influence the data, because closely spaced plots are essentially replicate measures of the same conditions. Variations in forest structure and dynamics may also be affected by plant population processes which may have local variation. Moran's I correlograms in Fig. 2 (Fig. 2c, f and i, for tree turnover, biomass and AGB gain, respectively) demonstrate that all three forest variables are positively spatially autocorrelated, until an approximate distance of 900–1200 km (geographical distance among areas) then becoming negatively autocorrelated at larger distances. This suggests a need to adopt adequate strategies to perform statistical analysis for such data. This is because in such situations the usual statistical protocols such as ordinary multiple least square regressions (OLS) generate autocorrelated residuals, underestimating the uncertainty of regression coefficients and consequently inflating Type I errors. This results in too liberal tests of hypothesis (Legendre, 1993; Diniz-Filho and Bini, 2005).

To account for spatial autocorrelation, eigenvector-based spatial filters (Bocard and Legendre, 2002), were therefore calculated for each of the variables analysed in this study, and then used in a multiple regression framework as additional predictors. This approach, based on principal coordinate analysis of truncated geographical distance matrices provides, in principle, unbiased regression coefficients (Diniz-Filho and Bini, 2005). Following that method, three eigenvector filters were extracted to account for the spatial structures in tree turnover rates, four were selected to correct for spatial autocorrelation in AGB gain, and five for above ground biomass. The selection of eigenvector filters was done according to the framework suggested by Diniz-Filho and Bini (2005). Spatial filters alone explained 44.2% of the variation in tree turnover rates, about 40% of the variation in AGB gain and, remarkably, 72% of the variation in above ground biomass. The application of such spatial filters results in the effective removal of spatial autocorrelation problems from regression residuals as seen in the Moran's I correlograms in Fig. 2. In theory, this should allow for the correct estimation of the effects of each variable, unbiased by spatial autocorrelation in residuals.

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3.2 Relationships between environment and forest stem turnover rates. Effects of soil fertility, soil physical constraints and climate

In order to investigate relationships between tree turnover rates and environmental factors, spatially adjusted Spearman correlations (Dutilleul, 1993) as described above (Table 1) for a total of 28 predictors. Associated p values and degrees of freedom were adjusted to account for spatial autocorrelation. Among the soil fertility predictors, best correlations were with the different soil phosphorus pools (organic, readily available, total extractable, total and inorganic P , in decreasing order of correlation) and exchangeable Ca, Mg and K and also their combined forms sum of bases, SB, and effective cation exchange capacity, ECEC. Soil nitrogen was also relatively well correlated to tree turnover rates with soil C:N ratio negatively correlated to it. Relationships between soil fertility parameters and tree turnover rates are graphed in Fig. 3 showing that indeed tree dynamics are strongly associated with soil fertility. This association is also related to gradients in soil type as detailed elsewhere (Quesada et al., 2009). Noting that the validity of ECEC as a fertility indicator is arguable due to the inclusion of aluminium into its calculation, sum of bases (SB) has been taken to represent the a base cation availability and is thus plotted against tree turnover in Fig. 3 instead of the better correlated ECEC, though the latter might, in fact, be a surrogate for soil development (Quesada et al., 2009).

Soil physical properties were also highly correlated to tree turnover rates. Soil structure, depth and topography scores provided the best individual correlated factors, while the indexes of soil physical properties INDEX-1 and INDEX-2 were also well correlated. Relationships between physical properties and tree turnover rates are graphed in Fig. 4. Soil depth, structure and topography showed a strong relationship with tree turnover rates while no clear pattern could be seen with soil anoxic conditions. The indexes of soil physical properties were both strongly related to tree turnover but the INDEX-2 remarkably so. Climatic predictors on their own only resulted in poor correlations, but a close examination of the relationships between these variables and tree

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turnover rates (Fig. 5) suggests that tree turnover is related to average annual precipitation and minimum dry season precipitation for many study sites. Tree turnover rates are generally low in relatively dry areas and higher in the wetter places. However, a small group of sites bearing high tree turnover rates consistently appear as deviants in these relationships, with higher turnover rates in the driest areas. Perhaps these constitute areas where water shortage may influence tree turnover rates. This is best depicted by looking at the relationship between tree turnover rates and the time in which available water content was modelled to fall below 20% (# months < 20% AWC). This water stress condition only occurred in a limited number of study sites but these mostly account for the "deviant" group of sites, plus a few others.

To verify the above ideas, variables were subjected to multiple partial regression analysis with and without the inclusion of spatial filters as predictors. Despite having reasonable correlations, fertility predictors emerged with a limited capacity to explain variations in tree turnover rates. Well correlated variables such as soil C:N ratio, exchangeable cations and ECEC did not appear as significant in any regression model. The best soil fertility model (Fig. 6a), chosen by maximising model R^2 and minimising the Akaike information criterion (AICc), had as predictors; soil nitrogen, sum of bases and readily available phosphorus, left only readily available P as significant ($p < 0.01$). But once spatial filters were included, phosphorus lost its significance but with SB becoming marginally significant at $p < 0.1$ level. Indeed, the partitioning between purely soil fertility and geographical effects resulted in spatial structures explaining more variation in tree turnover rates than did soil fertility parameters. Space explained 44.2% of the variation while soil predictors explained a total of 32.9%, and both together explained about 49% of the variation in tree turnover rates. Further partitioning for the effect of predictors and space resulted in fertility predictors alone explaining only about 5% of the variance with space alone explaining about 16%. The shared variance between space and soil fertility was the largest factor being 28%, indicating that most of the relationship between soil fertility and tree turnover rates is integrated in common spatial structures.

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Indeed, as shown in Fig. 6b, soil physical properties have a larger capacity to explain the observed variation in tree turnover rates, with no soil fertility parameter attaining significance when included in regression models containing soil physical predictors as well. The best model explaining tree turnover rates formed by a mixture of climatic and soil physical properties, with predictors alone explaining 52.2% of the variation in tree turnover rates. This regression model included average annual precipitation, soil structure, topography and time under <20% AWC as predictors and all these variables were significant with confidence intervals varying from $p < 0.001$ to < 0.1 (Fig. 6b). Nevertheless, after inclusion of spatial filters into the regression model only soil structure remained significant ($p = 0.002$). Both environment and space together, explained 56.2% of variance in turnover rates, with environment alone explaining 12% of variation and space alone explaining only 4%. The shared variance between space and environment was also the largest term explaining as much as 40% of variance.

However, interactions among physical constraints in soils and environment would be expected to occur and this should increase the tendency of disturbance to increase forest dynamics. One example of this is that the effect of short soil depth and/or deficient structure over tree stability should be stronger when associated to steep topographies. It is thus likely that combined indexes of physical constraints might actually best describe the effect of soil physical properties to influence tree turnover rates. Therefore another regression model was selected, but this time having the (summed) INDEX variables as the soil physical predictor. The regression model yielding the highest R^2 and lowest AICc had the variables INDEX-2 (formed by soil depth, structure and topography scores) and time under <20% available water content as predictors, with these two variables explaining 49% of the variation in tree turnover (Fig. 6c). Inclusion of spatial filters in the regression model did not change the overall result and both variables were significant both before and after the application of corrections for spatial autocorrelation, although time under <20% AWC had its level of significance reduced from $p < 0.001$ to $p = 0.057$. Both space and environment together explained about 54% of variation.

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3.3 Environmental and edaphic controls over forest biomass growth rates

Spatially adjusted Spearman correlations between forest biomass gain and edaphic and climatic variables are shown in Table 2. From the soil fertility predictors, the best correlations with AGB gain came from the different pools of phosphorus, with correlations decreasing from 0.459 to 0.371 in the order total organic P > total extractable > readily available > total inorganic, with all correlations remaining significant after adjusting significance for spatial autocorrelation (Table 2). In addition, soil nitrogen and soil C:N ratio were strongly correlated to AGB gain, with soil exchangeable cations and sum of bases were also relatively well correlated to it. Effective cation exchange capacity was also remarkably well correlated to ABG gain. Relationships between soil fertility parameters and AGB gain are plotted in Fig. 7. Overall there is the strong suggestion of a close relationship between soil phosphorus and growth.

But in contrast to tree turnover rates, soil physical properties had much less of a correlation with AGB gain; the only exception being topography. The relationships between soil physical properties and AGB gain are shown in Fig. 8. Soil depth and anoxic conditions showed little relationship, but soil structure does show a different and interesting behaviour from other physical variables. AGB gain apparently increases slightly with soil structure scores but seems to decline when soil structure becomes more limiting (scores 4).

Of the climatic variables, mean annual temperature showed a relatively weak negative correlation with AGB gain, but with variables related to water availability such as average annual precipitation and minimum dry season precipitation having stronger effects (Fig. 9). AGB gain also increases with increasing average annual precipitation, and has some sort of relationship with minimum dry season precipitation, suggesting an effect of both amount and distribution of rainfall in AGB gain. However, a few areas have their rates of biomass gain not directly related to rainfall amount and distribution and stand out as deviants from the main relationship, with high biomass production at low rainfall. Interestingly, these are also areas which show increasing AGB gain

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as water becomes more limiting in the plot of time (months) in which <20% AWC. Almost all of these sites occur in the southern fringe of Amazonia, in the transition zone with savannah areas in Bolivia. Their biomass production rates may be controlled by factors other than water and nutrient availability, perhaps being related to disturbance recovery.

Variables were then included into multiple regression analysis, with and without the inclusion of spatial filters. Figure 10 shows the result for the best regression model describing AGB gain, including climatic variables and soil fertility parameters. All variables shown were significant in the regression model without spatial correction. As opposed to tree turnover, the inclusion of spatial filters into the regression model did not change the level of significance of edaphic predictors, and so with phosphorus and sum of bases remaining significant at the same levels as in the unfiltered model. Phosphorus and sum of bases both had the highest regression coefficients both in filtered and unfiltered models. Nevertheless, after correction for spatial autocorrelation, all climatic variables showed changed levels of significance, with average annual precipitation decreasing from $p < 0.001$ to $p = 0.063$ while mean annual temperature increased the level of significance from $p < 0.1$ to $p = 0.056$. Minimum dry season precipitation which was significant at $p < 0.001$ before spatial filters being added to the model was not significant after spatial correction. The partitioning of effects of environment and spatial structure shows that environment accounted to 52.4% of variation in AGB gain, from which P alone accounts for about half of the variation. Space explained almost 40% of that variation and environment and space together explained about 61% of the variance in AGB gain. Further partitioning resulted in environmental predictors alone accounting for 20.7% of variation in AGB gain while spatial structures alone explained only 7.9%. The interaction between space and environmental predictors was again the largest term explaining 31.7% of variation in AGB gain, resulting from interactions between spatial structures and predictors.

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3.4 Forest above ground biomass

Spearman correlations between above ground biomass and edaphic and climatic variables are listed in Table 3. Forest biomass was generally negatively correlated to soil fertility (Fig. 11), with higher values in the lower fertility regions. The best correlations among soil fertility parameters were again with soil phosphorus pools, which varied from $\rho = -0.483$ to $\rho = -0.279$, with correlations decreasing in the order readily available > total extractable > total organic > total inorganic > total phosphorus. Exchangeable cations also had strong negative correlations with forest above ground biomass, with exchangeable K and Mg showing the best correlations ($\rho = -0.449$ and $\rho = -0.308$, respectively). Sum of bases was also relatively well correlated to forest above ground biomass ($\rho = -0.294$). Correlations with both soil phosphorus pools and exchangeable cations remained significant after correction for spatial autocorrelation, with significance levels of exchangeable cations generally increasing after correction. However, ECEC which was well correlated with tree turnover rates and AGB gain showed no relationship with forest biomass.

Soil physical properties varied in their ability to correlate with forest biomass. Soil depth and structure were the best correlated factors, with biomass decreasing as depth and structure scores increased (Fig. 12). Topography on the other hand had a weak but positive correlation with forest biomass. Nevertheless, biomass can be seen to decline once topography becomes very steep (scores 4). Anoxic conditions also had a negative but weak correlation with forest biomass, as did both indexes of physical properties. Correlations between physical properties and forest biomass also remained significant after spatial correction with the exception of topography and INDEX-1.

Above ground biomass had stronger correlations with climatic variables than did tree turnover rates or AGB gain, being positively correlated with mean annual temperature, average annual precipitation, and minimum dry season precipitation, and strongly negatively correlated to the time (number of months) for which $AWC < 20\%$. The relationships between forest biomass and climatic variables are shown in Fig. 13, suggesting

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some response to rainfall amount as well as to its distribution during the dry season.

However, despite strong correlations with both edaphic and climatic variables, multiple regression analysis did not result in significant relationships, especially after the inclusion of spatial filters. For instance, a regression model containing total extractable P and soil structure resulted in significance at $p < 0.05$, explaining about 26% of variance in forest biomass, but once spatial filters were added to the regression model these variables were not significant at all. Actually, spatial filters by themselves explain 72% of variation in above ground biomass. So, when added to any regression model, it is not all that surprising that soil predictors could not explain any fraction of the variation which was not explained by space alone, with the fraction explained by edaphic properties being actually due to a bias resulting from the integration of edaphic properties into the spatial structure (Fig. 14).

It turns out, however, that environmental variables which do not have a direct influence on above ground biomass in a Basin wide scale, may still have some indirect influence on it. For instance, Baker et al. (2004) suggested that regional variations in stand wood density could explain a large fraction of the variation in above ground biomass. Average plot wood density varies considerably across Amazonia, and with a remarkable relationship with forest biomass (Fig. 15). This may be related to species composition and their intrinsic genetic characteristics, but a fraction of wood density variations may also be related to resource availability.

Looking more closely at this question, average plot wood density is generally negatively correlated with soil fertility and physical properties as well as with climatic variables such as average annual precipitation and minimum dry season precipitation (Table 4). Relationships between average plot wood density and various edaphic predictors are shown in Figs. 16 (soil fertility) and 17 (physical properties). Figure 16 suggests that of all fertility variables, soil phosphorus pools and sum of bases show the strongest relationships with average wood density. Physical properties are also strongly related to wood density, with soil depth, soil structure and topography being negatively correlated to it, but with anoxic conditions showing no clear relationship with

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it. The combined indexes of physical properties showed the strongest relationships with wood density, with INDEX-1 being highly correlated ($\rho = 0.662$). Figure 18 shows that average plot wood density was also related to climatic variables, with a strong relationship with mean annual temperature. Average annual precipitation and minimum dry season precipitation also had strong negative relationships suggesting an effect of both amount and distribution of rainfall.

With total extractable phosphorus, sum of bases, INDEX-1 and minimum dry season precipitation selected and used in a multiple regression model (Fig. 19), INDEX-1 emerged as significant (at $p < 0.001$) but all other variables not. This regression model explained 53% of variation in wood density. But after the inclusion of spatial filters into the regression model these results changed dramatically with soil phosphorus, sum of bases and dry season minimum rainfall becoming significant with INDEX-1 not. The inclusion of spatial filters into the model along with the other predictors explained 82% of variation in average plot wood density. Partitioning between the effect of predictors and space resulted in space alone explaining 72% of variation and predictors alone explaining 53%. Further partitioning resulted in predictors alone explaining 10.1% of the variation, space alone explaining 29.1% and both space and predictors together explained an additional 42.9% which accounts for common spatial structures between space and predictors. Figure 19 also includes a Moran's I correlogram for wood density which shows a remarkable level of spatial autocorrelation but with spatial filters being able to effectively remove its effect from regression residuals.

It thus seems that above ground biomass may be indirectly affected by environmental variables controlling variations in wood density such as soil fertility and rainfall distribution during the dry season.

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4 Discussion

4.1 Accounting for spatial autocorrelation

Environmental data collected over wide areas such as the Amazon Basin are likely to produce a high level of correlated spatial structures. This is of significance, as inclusion of spatial filters into statistical analyses have demonstrated that spatial autocorrelation creates a bias in regression coefficients which inflates tests of hypothesis and thus may eventually change interpretations of ecological processes in question (Diniz-Filho and Bini, 2005). In the study here, the inclusion of spatial filters changed the level of significance of regression predictors, and there should certainly be an overestimation of their capacity to influence response variables if no correction was applied to it. Also, at least two central results of this study may have been completely misjudged if no correction for spatial autocorrelation had been applied; above ground biomass would have been inferred to be significantly affected by soil structure and *P* availability, whereas no relationship was found with any edaphic variable when spatial filters were applied. Also wood density would have been taken as solely influenced by soil physical properties, but after the removal of spatial structures associated with it, physical properties did not emerge as an important variable at all, but soil fertility and dry season precipitation did. Therefore, it is noteworthy that any analysis of forest biomass and/or wood density would be wrong in principle if spatial structures were not taken into account. Geographical space itself explains >70% of their variation.

4.2 Tree turnover rates

Results from Sect. 3.2 show that tree turnover rates are strongly correlated to soil fertility and soil-landscape physical conditions as well as to climatic variables such as amount and distribution of precipitation. Nevertheless, despite soil fertility parameters such as soil *P* and exchangeable base cations being highly correlated with tree turnover, multiple-regression analysis showed that no soil fertility parameter was sig-

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nificant. Rather, the analysis performed in Sect. 3.2 indicates that tree turnover rates are controlled mainly by variations in soil physical properties, implying that the actual correlation with soil nutrient availability may be a result of inter-correlations between fertility and soil physical conditions as discussed in Quesada et al. (2009).

Soil physical properties are thus suggested to have a direct influence over disturbance levels and hence turnover rates. For example, the proportion of trees which die standing, uprooted and snapped is related to soil physical properties such as topographic position, slope angle, soil depth, soil shear strength, flooding and drought, and to biological effects as herbivory, diseases and pathogens (Gale and Barfod, 1999; Chao et al., 2008). Causes for tree uprooting are predominantly physical, due to bad soil anchorage, short soil depth, steep topography and slope position, storms, wind-blown, and the effect of other fallen trees. On the other hand, standing death is most strongly related to biological agents such as senescence, diseases and competition for resources (Gale and Barfod, 1999; Gale, 2000; Gale and Hall, 2001).

Individual soil physical properties could influence tree turnover in many different ways. For instance, shallow soil depth implies a limited root space which often leads to short and stunted root systems, this most likely having a major influence on plant growth and survival (Schoenholtz et al., 2000; Arshad et al., 1996). This problem is often associated with steep topographies, which can greatly increase the probability of tree death by wind throw (Dietrich et al., 1996). In addition to possible constraints of nutrient supply due to limited rooting depth, hydrological constraints may also occur, either by low drainage capacity or due to low water availability or seasonal drought (Arshad et al., 1996). As well as occurring for young soils such as Leptosols and Cambisols, a shallow effective rooting depth should also occur in many soils which have large and shallow hardpans or soils that have severe structural problems, such as massive and compact subsoil horizon. Hardpans are found all over the Amazon Basin and have different natures. The most common are continuous and hardened clusters of iron and aluminium oxides, often known as ironstones (hardened plinthite) and similar continuous gravel and rock layers. These layers can be a few centimetres

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or more than one metre thick; sometimes allowing roots to go through and sometimes not. The depth of occurrence and the nature of a hardpan are the best determinants of its capacity to limit plant growth (Sombroek, 1966). Nevertheless, soil depth was not significant in multiple regressions, but it may have a strong effect on turnover rates through interactions with other soil properties.

Poor soil structure is another important factor affecting tree turnover, expected to lead to problems that are similar to those caused by a limited soil depth because both are physical impediments to root growth. Subsoil structure development occurs in line with the soil weathering process. Thus poor soil structure is generally a feature in soils with low pedogenic status such as Gleysols and Regosols, also occurring in soils with argic horizons such as Alisols, Lixisols and Acrisols as a consequence of increasing clay contents through the profile. Poor soil structure may also result in weak aeration in clay rich soils, particularly when soil is moist, with most of the pore space filled with water (Korning et al., 1994). Structural problems are also strongly related to hydrological constraints and water movement due to its relationship with soil porosity (in especially macro-porosity) which influences water infiltration as well as aeration (Schoenholtz et al., 2000; Arshad et al., 1996). Root proliferation is also highly affected by soil structure and soil bulk density. High bulk density which is characteristic of soils with deficient structure, is often reported to restrict root growth at density values above 1.35 g cm^{-3} (Van Wambeke, 1992; Arshad et al., 1996) being associated with reductions in the productivity of tree plantations in the tropics (Dedecek et al., 2001; Hirai et al., 2003).

Topography is another factor that is closely associated with soil physical constraints as it is highly related to the pedogenetic status of tropical soils. Soils with steep topography are usually shallow and thus mechanical instability is often a problem for trees. For instance, Gale and Barfod (1999) reported that steep topography was an important factor influencing tree mortality in tropical forests due to its association with thin soils and strong lateral forces which favour tree uprooting. However, deep soils may also occur in steep areas and this has been shown to provide better tree anchorage and consequently lead to lower tree mortality rates in steep slopes, for example in the Man-

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aus region of Brazil (Rocha et al., 2003). Lieberman and Lieberman (1987) reported that steep slopes may lead to a threshold in tree size above which tree is much more probable to collapse. Such a relationship is thought to explain differences in mortality rates among forests in Costa Rica.

Drainage capacity has two implications. Firstly, badly drained soils may become anoxic, which depending on the severity, could exclude most plant species in areas where it occurs as very few species can cope with such conditions. Seasonally flooded soils are related to high rates of tree uprooting because anaerobic conditions inhibit deep root growth and tree anchorage is limited in hard subsoils (Gale and Barfod, 1999; Gale and Hall, 2001). Gale and Hall (2001) also showed that, in poorly drained soils, young trees tend to die standing, possibly suffering from anoxia, whilst larger trees tend to die uprooted; not having enough anchorage in soft waterlogged soils. On the other hand, excessively drained soils such as white sands (Arenosols) could lead to drought problems in seasonal areas. Soil texture is a less direct but important factor as it interacts with almost all process of physical limitation. Considering soil depth for instance, sandier textures can increase problems of mechanical instability and drastically reduce water holding capacity.

The relationship between tree turnover and amount and distribution of precipitation is a function of regional patterns in rainfall, with more and better distributed precipitation in western Amazonia. As it seems unlikely that more and evenly distributed rainfall would increase tree turnover rates, this correlation is taken here as an indication of regional patterns of rainfall distribution. Specifically, most areas included in this study do not suffer strong water deficits, as the great majority of sites never reach modelled AWC values below 20% (Fig. 5). However, the time (months) in which <20% AWC was attained had some potential to explain tree turnover rates in some specific areas. Soils located in seasonal areas (mostly at southern and northern borders of Amazonia); especially those having shallow soil depths, or constrained root systems were the most affected by soil water deficits. For the remaining sites, it was a case of either being located in aseasonal areas or in soils with enough available water capacity to survive

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dry spells. Nevertheless, results shown here indicate that one cannot exclude water deficit as a potential driver affecting tree turnover rates, especially in seasonal areas of Amazonia.

On the other hand, there seems to be little influence of anoxic conditions over turnover rates. This may be because only well adapted species tend to occur on severely anoxic soils, such as occur under permanent water saturation. Most species would have limited success in such environments as very few can cope with a limited availability of soil O₂. Thus, permanent flooding may have limited impact on turnover as the vegetation formed on such soils consists of well adapted trees. Seasonal flooding or fluctuations of the water table are however more likely to cause stress and mortality in trees (Cannel, 1979). Such conditions affected only a small fraction of the study sites.

Although single physical constraint scores showed an important indication of their relationships with tree turnover rates, it is also the case that only the most extreme conditions are likely to show a significant influence independently. As argued above, interactions among field characteristics are likely to occur which should increase their effect on the tree community. A simple example is that tree mechanical instability caused by steep topography will be made worse by occurring in conjunction with shallow soil depth. Therefore, physical constraints should be considered jointly to allow for the interaction among such characteristics (Muchena, 1979). An approach to represent the interactions among factors, the INDEX-1, emerged as a good explanatory factor for tree turnover rates. But it was a simplified index model consisting of soil depth, soil structure and topography only (INDEX-2) that best described the influence of physical properties on tree turnover rates.

Indexes of soil quality are a common tool both for agriculture and forestry, usually including soil physical constraints, chemical properties and meteorological data as predictors. Examples of site quality indexes are the USDA Land Capability Classification system, the Fertility Capability Classification system (Sanchez et al., 2003), the Brazilian Land Capability system (Ramalho Filho and Beek, 1995) and the Storie Index Rat-

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ing for timber production (Storie and Wieslander, 1948). All these systems are based more or less on the same soil physical constraints thought to result in a harmful environment to plants; aiming to classify lands for agricultural and/or timber production. However, as such a system that could be used for natural rainforest soils is lacking, the indexes shown here could also be used as such an index. Moreover, the simplicity of the index proposed and the fact it is almost entirely based on soil descriptions may prove to be an advantage as soil physical data is seriously lacking in Amazonia. Nevertheless, extensive soil survey description data is available (i.e. RADAMBRASIL, 1978).

Previous studies of tree turnover rates in Amazonia have resulted in the hypothesis that soil fertility plays an important role in explaining the almost two-fold difference in stem turnover rates between the western and central-eastern areas of Amazonia (Phillips et al., 2004; Stephenson and Van Mantgen, 2005). However, the results here suggest that this relationship between turnover rates and soil fertility may, to a large degree, be an effect of soil physical constraints. Nevertheless, this does not completely rule out a role of soil fertility in influencing turnover rates, as interactions between the effect of soil fertility and soil physical properties may occur. Nevertheless, factors that can cause continuous high abiotic disturbances seem more likely to affect stem turnover rate than those related to soil fertility alone. The most likely factors that could explain a soil fertility influence on turnover rates are high levels of competition for resources, increased fecundity and subsequent higher mortality due to strong competition; biotic factors such as insect damage, herbivory and plagues which could be higher in more resource abundant areas; perhaps fertility effects on forest floristic composition (pioneers and light demanding taxa) and life cycles (Phillips et al., 2004). From all those possibilities it seems that the competition for resources and the effect of different species composition are likely and should influence on turnover rates.

Forest floristic composition is certainly a key factor influencing turnover rates. Forests in western Amazon are dominated by fast growing, light demanding taxa while the central and eastern areas of Amazonia are dominated by slower growing, shade

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tolerant trees (Phillips et al., 2004; Baker et al., 2004). This implies that these forests have different “life cycles”, western forests being much more dynamic as fast growing species also tend to die young. However, it is quite likely that species composition could also be indirectly affected by soil physical conditions; as adverse soil physical conditions should also favour the dominance of pioneer species with short lifetimes. An example of this process could be the maintenance of light demanding taxa recruitment after disturbance events such as induced by a limited rooting depth and steep topography or other combinations of processes. This in turn would affect the turnover rates due to intrinsically higher mortality rates, resulting in a wave like continuum driven both by soil and species composition (Phillips et al., 2004). Thus, soil physical limitations may short-circuit the successional process by promoting a continued pattern of high disturbance, with forest succession never proceeding towards climax state, unless dramatic changes in the landscape and species composition occur.

Wood density is also another important factor involved in disturbance regime. As discussed already, there is a broad gradient in wood density across the Basin with higher wood density values occurring in infertile soils of central and eastern Amazonian areas while the lowest wood density values are found in the more fertile western areas (Baker et al., 2004). Apparently the role of wood density affecting turnover rates can be a function of two interacting factors, these being environmental conditions and stand floristic composition. Firstly, high wood density seems to be part of the slow growth/shade tolerant strategy which would obviously be favoured on soils of little disturbance due to soil limitations. Forests with slow growth/shade tolerant strategies need a higher investment in long-term structures to support taller and large and heavy canopies. For water transport in taller trees stronger vessels walls may also be needed to cope with lower tensions. The residence time of such structures must naturally be higher and all those features clearly fit with having a good physical soil environment to grow in for a long period of time. On the other hand, low wood density apparently is part of the fast growing – high turnover strategy suggesting an adaptation to highly disturbed environments. In such forests, there is a need to grow fast and rapidly com-

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plete one's life-cycle. Generally higher fertility levels should fulfil nutrient requirements for fast growth. This results in a lower level of investment in structure and in a lower residence time as well.

Floristic composition influences wood density as slow growing taxa tend to have higher wood densities while fast growing trees have lighter wood. As there is a gradient of floristic composition across the Amazon, wood density can be a result of the regional scale of species composition and abundance (Baker et al., 2004). Furthermore, similar spatial patterns of wood density across Amazon regions suggest that the differences in stand-level wood density may be caused by ecological factors that regulate the abundance of taxa that share similar values of wood density (Baker et al., 2004). Thus, floristic composition may be intrinsically related to what happens in the soil as well. Thus, Fig. 20 shows how soil physical and chemical conditions might take part in positive feedback mechanisms which would maintain the patterns of slow growth strategy in the eastern and central areas of Amazonia (top) as well as the fast growth – light demanding in the western and southern areas of Amazonia (bottom).

The strong relationships between soil physical quality and turnover as well as its coincident pattern with wood density are therefore interpreted here to suggest that soil physical structure may be a key factor directing the mechanisms that regulate Amazon forest floristic composition, wood density and stem turnover rates. Soil physical quality is proposed to initiate a positive feedback mechanism that maintains the patterns of slow growth – fast growth across Amazonia. In other words, the absence of disturbance coming from soil physical properties is intrinsically a key component in a self-maintaining system (Fig. 20). Where low disturbance leads to shade environments, these together with a limited nutrient supply favour a slow growth strategy. This in turn increases investment in structures to support taller and bigger trees, increasing residence time, with reduced disturbance levels and so on. Low nutrient availability in soils also influence forest growth rates as clearly demonstrated here, with the opposite system is found in western Amazonia where high disturbance levels are initiated by soil physical constraints, thus increasing mortality rates, gap formation and light lev-

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els lower down inside the forest. Together with higher nutrient availability, this favours fast growth with species with a lower investment in structures (low wood density) being favoured. This then reduces mean tree life-times, increasing disturbance frequencies and so on.

5 Differences in mortality mode and gap formation, themselves related to soils physical properties also support the idea of feedbacks controlling forest growth and dynamics at an Amazon Basin wide scale. For example, gaps from fragmentation of standing dead trees, usual in sites with favourable physical conditions, are usually smaller and formed over a more extended period than gaps formed by uprooted and snapped trees;
10 these being mostly found in association with bad soil physical conditions being larger and produce a more dense layer of debris, resulting in much higher disturbance level (Gale and Barfod, 1999; Carey et al., 1994; Sugden et al., 1985). This is thought to favour low wood density pioneer species (Gale and Hall, 2001), and maybe lianas as well (van der Heijden and Phillips, 2008).

15 **4.3 Forest growth rates: above ground biomass gain**

Results from Sect. 3.3 point to an effect of soil fertility as the most important factor affecting AGB gain, but with this being also associated with other environmental factors such as amount and distribution of rainfall and soil physical properties. Of all fertility parameters soil phosphorus pools and sum of bases were those best related with AGB
20 gain.

Despite being the best correlated variable, soil *P* pools varied in their relationship with AGB gain. For instance, readily available *P* (the adding up of resin and bicarbonate *P* fractions) which is often referred to as being essentially available for plants (Cross and Schlesinger, 1995; Johnson et al., 2003) was not significant in regression
25 analysis. The ability of *P* pools to explain variations in AGB gain increased with the inclusion of more stable, slow turnover forms of *P*, with the total extractable and total *P* yielding the highest R^2 and regression coefficients. This suggests that it is not only the immediately available *P* forms, but probably the entire *P* pool that interacts actively with

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forest growth on longer timescales. This is most likely due to a transiting through buffer pools to the immediately available forms (Tiessen et al., 1984; Hinsinger, 2001), and/or due to the effect of mycorrhizal infections (Alexander, 1989). Mycorrhizal association raise the affinity of infected roots for *P* in solution lowering its threshold concentration
5 to absorption (Mosse et al., 1973), leading to more desorption of *P* from the labile pools. Mycorrhizal association can also release *P* phosphorus that is adsorbed by iron oxides and otherwise unavailable to plant roots (Alexander, 1989). In agreement with results reported here, Kitayama et al. (2000), showed that total extractable *P* (total – residual) was a better estimate of *P* availability for plants in Borneo. As discussed
10 in detail in Quesada et al. (2009), there is also evidence that more stable *P* fractions such as organic, hydroxide and hydrochloric forms may become available for plants when *P* is in relatively short supply (Adepetu and Corey, 1976; Tiessen et al., 1984; Gahoonia et al., 1992; Sattell and Morris, 1992; Hedley et al., 1994; Saleque and Kirk, 1995; Magid et al., 1996; Hinsinger and Gilkes, 1996; Trollove et al., 1996; Zoysa et al.,
15 1997, 1998, 1999; Guo and Yost, 1998; Bertrand et al., 1999; Frossard et al., 2000). An important implication of this result is that the true importance of *P* may have been underestimated as most studies of soil fertility have usually only taken into account the immediately available *P* in the soil solution. (e.g. Chambers and Silver, 2004)

Soil phosphorus has been considered the most likely nutrient to limit forest productivity (Vitousek, 1982, 1984, 2004; Cuevas and Medina, 1986; Vitousek and Sanford, 1986; Silver, 1994; Reich et al., 1995; MacGrath et al., 2001; Paoli and Curran, 2007) and a limitation of tropical forest productivity by phosphorus is conceptually attractive. This is because *P* is almost exclusively supplied by parent material and tropical forest soils are often of considerable age as outlines elsewhere (Quesada, 2009). In addition,
25 the evolution of soils during weathering tends to reduce plant available *P* pools either by parent material weathering and leaching and/or modification to the chemical state of both organic and inorganic *P* towards non available forms as the *P* occluded by Fe and Al oxides (Walker and Syers, 1976). Also, because *P* is essential for high energy *P* bounds and triose *P*, deficiency of this nutrient could potentially limit carboxylation

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in photosynthesis and thus community level primary production (Raaimakers et al., 1995; Crews et al., 1995; Herbert and Fownes, 1995; Raich et al., 1996; Kitayma et al., 2004).

Indeed, for the majority of lowland tropical forests studied so far, soil *P* has been considered the most likely limiting factor for primary production. For instance, Paoli and Curran (2007) showed that basal area and biomass growth and forest NPP (defined as litterfall+biomass growth) showed a strong positive relationship with soil nutrients, particularly with Olsen *P* (bicarbonate extracted *P*) in Borneo. Litterfall production was also positively related to Olsen *P* and sum of bases. They concluded that soil *P* supply was the main driver of spatial variation of NPP in their study area.

Physical properties were relatively well correlated with AGB gain but had much lower capacity than soil fertility to explain the variations observed. The one exception was topography scores which had a reasonable relationship with AGB gain. This may reflect a positive influence of topography on forest growth as crow illumination may be favoured on slopes. In addition, continuous erosion processes may aid the maintenance of mineral nutrient inputs bringing less weathered soil layers to the proximity of soil surface and thus within the reach of nutrient absorbing roots.

Although appearing contradictory at first, it is also possible that harsh soil physical properties could lead to faster rates of forest growth. As discussed in Sect. 4.2, a harsh soil environment is likely to increase forest dynamics (tree turnover rates) and through this, a change the structure of the forest giving rise to more open physiognomies, with more available light interception than for more "stable" forests with tall, closed canopies. Also, disturbance may short-circuit vegetation succession and favour the dominance of pioneer species over late successional ones. Thus higher growth rates typical of light wooded, light demanding pioneer species may dominate. Therefore, despite that a favourable soil physical quality may be important for root development and tree stability (Kiniry et al., 1983; Burger and Kelting, 1999); increased light conditions generated by frequent disturbance events, coupled with more favourable fertility conditions typical for soils with a lower degree of weathering may both enhance tree growth rates in the

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most fertile areas of Amazonia.

On the other hand, low disturbance levels seems to be intrinsically related to favourable soil physical properties, which is also associated to low fertility. These conditions lead to the dominance of late successional shade tolerant species, in which slow growth strategies dominate. Such contrasting but characteristic conditions occurring between soils with different pedogenic development may thus be integrated into the positive feedback mechanisms described in the above section.

4.4 Above ground biomass

Basin wide variations in forest biomass across Amazonia were negatively correlated with soil fertility and physical properties. In broad terms, above ground biomass is lower in areas having fertile soils with low pedogenic development and having a higher incidence of physical constraints. And by corollary, higher in infertile areas, with more developed soils and better physical conditions. Nevertheless, despite being well correlated with individual soil and climate variables, forest biomass did not show significant relationships with soil or climate conditions once corrections for spatial autocorrelation were applied. But we also note that forest above ground biomass seems not directly influenced by edaphic conditions, unless the most extreme cases of low fertility and/or extremely bad physical environment are encountered (Vitousek and Sanford, 1986). On the other hand, average plot wood density is a prime factor determining variations of above ground biomass (Baker et al., 2004; Malhi et al., 2006), and variations in species composition and relative abundance across Amazonia have been shown to account for a large fraction of wood density variations (Baker et al., 2004). Results shown here suggest that average plot wood density is significantly related to soil fertility, in accord with previous results from Muller-Landau (2004), who found negative correlations between wood density and estimated soil fertility among tropical forests in Brazil, Peru, Panama, and Costa Rica. On the other hand, Woodcock (2000) found no difference in wood density among different soil types in the Peruvian Amazon and ter Steege and Hammond (2001) also found no relationship between wood density

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and soil fertility in the Guyanas. They suggested that differences in wood density may have been related to disturbance. Indeed, associations between disturbance level and wood density are commonly found (Muller-Landau, 2004). However, physical properties, which have been shown to account significantly for disturbance, were not found to be significant predictors of wood density when spatial filtering was included in regression analysis, most likely due to the strong regional pattern already existing. It seems then that the association between low wood density and high disturbance levels may be more a consequence of the selection for fast growth species under such conditions than a direct effect of soil physical constraints. Although drought stress may also affect wood density through the relationship between xylem structure and wood density (Muller-Landau, 2004), studies on the effect of environmental factors over wood density suggest that there is little relationship between amount and distribution of rainfall and wood density (ter Steege and Hammond, 2001; Muller-Landau, 2004). Nevertheless, the much wider analysis of stand level wood densities analysed here (59 plots across Amazonia) shows that the distribution of rainfall during the dry season is the best predictor of average plot wood density. This challenges the notion that seasonality and amount of rainfall do not explain large-scale variations in wood density in the tropics.

Apparently, above ground biomass might be more closely related to factors controlling general forest structure, such as the factors integrated in the positive feedback. If disturbance levels are reduced, larger and long living shade tolerant trees, typical of late successional environments may dominate with their inherent slow growth rates, which in turn are tuned with low nutrient availability from soils. Wood density is higher as affected by genetic characteristics of such species, but also due to slow growth and low resource availability.

The association of larger, long lived trees with higher wood density, and associated low turnover rates, may lead to accumulation of bigger and heavier trees, which on longer time scales may have resulted in larger biomass pools. On the other hand, higher disturbance on physically more demanding soils but with higher nutrient levels may favour the dominance of fast growing tree species, which usually have shorter life

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spans and low wood density. High disturbance levels may lead to the maintenance of self-thinning process in which forests may be dominated by relatively smaller and thinner trees, thus suggesting that the contrasting dynamics of eastern and western areas of Amazonia could account for a fraction of the variation in above ground biomass.

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Table 1. Spearman correlations between tree turnover rates and different predictors, adjusted for spatial autocorrelation by Dutilleul's method (Dutilleul, 1993).

Variable Spearman	rho ρ	value p	value adj	df adj
Sand	-0.141	0.243	0.250	52.25
Clay	0.095	0.876	0.885	46.03
Silt	0.272	0.034	0.064	41.17
Soil depth	0.381	0.001	0.008	35.06
Soil structure	0.526	<0.001	0.002	28.75
Topography	0.311	0.040	0.125	30.39
Anoxic	0.183	0.082	0.089	51.73
INDEX-1	0.527	<0.001	0.002	24.57
INDEX-2	0.554	<0.001	0.001	24.64
Temperature	-0.145	0.101	0.179	36.39
Precipitation	-0.06	0.626	0.773	19.21
Dry s. min. precip	-0.046	0.915	0.956	15.09
# month <20% AWC	0.265	0.027	0.189	19.38
pH	0.332	0.004	0.022	35.28
P _{TE}	0.559	<0.001	0.002	26.76
P _{readilyavailable}	0.561	<0.001	0.003	26.14
P _{inorg}	0.469	<0.001	0.009	29.48
P _{org}	0.568	<0.001	0.001	26.63
P _{total}	0.489	<0.001	0.001	33.01
Nitrogen	0.252	0.051	0.119	34.58
Carbon	-0.077	0.880	0.899	38.72
C:N	-0.570	<0.001	<0.001	32.60
Ca	0.336	<0.001	0.003	40.79
Mg	0.449	<0.001	0.001	39.82
K	0.442	<0.001	0.009	31.60
Al	0.036	0.812	0.828	44.85
Sum of bases	0.368	<0.001	0.002	39.45
ECEC	0.587	<0.001	<0.001	41.56

4032

Table 2. Spearman correlations between above ground biomass gain and different predictors, adjusted for spatial autocorrelation by Dutilleul's method (Dutilleul, 1993).

Variable	Spearman rho	p value	p value adj	df adj
Sand	0.031	0.763	0.793	39.60
Clay	0.000	0.788	0.812	40.99
Silt	0.156	0.429	0.494	38.93
Soil depth	0.142	0.131	0.250	30.44
Soil structure	0.108	0.396	0.424	46.67
Topography	0.451	<0.001	0.010	30.66
Anoxic	0.162	0.376	0.330	62.82
INDEX-1	0.380	0.007	0.037	30.75
INDEX-2	0.373	0.006	0.028	33.60
Temperature	-0.091	0.042	0.085	37.33
Precipitation	0.195	0.208	0.318	32.94
Dry s. min. precip	0.258	0.015	0.187	15.70
# month <20% AWC	0.062	0.518	0.657	24.79
pH	0.315	0.054	0.194	23.93
P _{TE}	0.430	0.002	0.026	25.86
P _{readilyavailable}	0.409	0.004	0.047	25.62
P _{inorg}	0.371	0.019	0.090	27.24
P _{org}	0.459	<0.001	0.010	25.68
P _{total}	0.451	<0.001	0.017	27.25
Nitrogen	0.406	0.004	0.068	21.64
Carbon	0.126	0.232	0.394	26.74
C:N	-0.421	0.002	0.013	31.91
Ca	0.311	0.029	0.126	25.80
Mg	0.287	0.048	0.151	27.56
K	0.196	0.239	0.273	45.21
Al	0.121	0.694	0.720	43.29
Sum of bases	0.287	0.040	0.146	26.27
ECEC	0.462	0.001	0.007	36.23

4033

Table 3. Spearman correlations between above ground biomass and different predictors, adjusted for spatial autocorrelation by Dutilleul's method (Dutilleul, 1993).

Variable	Spearman rho	p value	p value adj	df adj
Sand	0.161	0.346	0.293	61.94
Clay	-0.045	0.463	0.411	62.52
Silt	-0.343	0.017	0.071	29.12
Soil depth	-0.341	0.019	0.072	16.49
Soil structure	-0.355	<0.001	0.067	29.48
Topography	0.162	0.570	0.664	45.90
Anoxic	-0.184	0.024	0.030	18.77
INDEX-1	-0.221	0.030	0.188	18.28
INDEX-2	-0.283	0.004	0.088	32.21
Temperature	0.135	0.774	0.818	10.25
Precipitation	0.276	0.246	0.641	12.89
Dry s. min. precip	0.257	0.459	0.711	11.51
# month <20% AWC	-0.314	0.030	0.307	42.53
pH	-0.255	0.158	0.123	48.01
P _{TE}	-0.472	0.002	0.016	29.56
P _{readilyavailable}	-0.483	<0.001	0.004	30.02
P _{inorg}	-0.418	0.004	0.024	32.55
P _{org}	-0.438	0.003	0.023	29.84
P _{total}	-0.279	0.156	0.199	42.66
Nitrogen	-0.198	0.102	0.095	52.19
Carbon	-0.018	0.524	0.615	31.36
C:N	0.345	0.033	0.160	22.05
Ca	-0.255	0.080	0.018	91.13
Mg	-0.308	0.050	0.035	57.80
K	-0.449	<0.001	0.003	26.24
Al	0.105	0.764	0.758	52.47
Sum of bases	-0.294	0.047	0.015	75.25
ECEC	-0.187	0.146	0.177	30.02

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Table 4. Spearman correlations between average plot wood density and different predictors, adjusted for spatial autocorrelation by Dutilleul's method (Dutilleul, 1993).

Variable	Spearman rho	p value	p value adj	df adj
Sand	0.069	0.536	0.520	55.10
Clay	0.038	0.125	0.058	77.49
Silt	-0.430	<0.001	0.064	15.98
Soil depth	-0.450	<0.001	0.040	16.98
Soil structure	-0.523	<0.001	0.052	11.37
Topography	-0.520	<0.001	0.121	9.64
Anoxic	-0.142	0.265	0.337	37.89
INDEX-1	-0.662	<0.001	0.036	7.58
INDEX-2	-0.542	<0.001	0.045	7.49
Temperature	0.499	<0.001	0.007	25.93
Precipitation	-0.257	0.006	0.296	7.82
Dry s. min. precip	-0.300	<0.001	0.304	5.43
# month <20% AWC	-0.167	0.828	0.928	9.16
pH	-0.333	0.057	0.071	45.10
P _{TE}	-0.552	0.007	0.104	19.03
P _{readilyavailable}	-0.538	<0.001	0.076	15.66
P _{inorg}	-0.497	0.008	0.073	23.70
P _{org}	-0.535	0.014	0.140	18.65
P _{total}	-0.470	<0.001	0.031	19.65
Nitrogen	-0.330	0.263	0.436	24.94
Carbon	0.019	0.680	0.766	26.82
C:N	0.633	<0.001	0.025	9.45
Ca	-0.518	<0.001	0.026	20.80
Mg	-0.551	<0.001	0.019	22.47
K	-0.457	<0.001	0.041	17.23
Al	0.086	0.987	0.990	31.25
Sum of bases	-0.552	<0.001	0.022	20.73
ECEC	-0.489	<0.001	0.048	14.11

4035

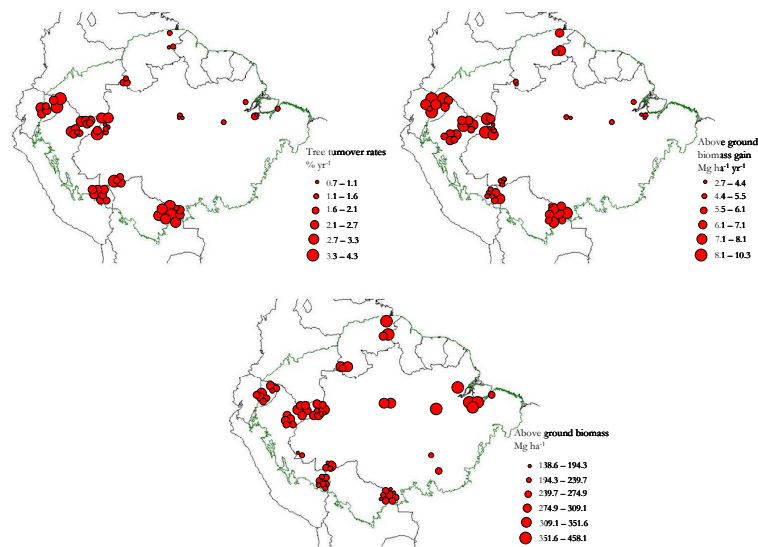


Fig. 1. Geographical distribution of tree turnover rates (a); above ground biomass gain (b) and above ground biomass (c) across Amazonia. Size of circles represents variations among sites, see legend for details.

4036

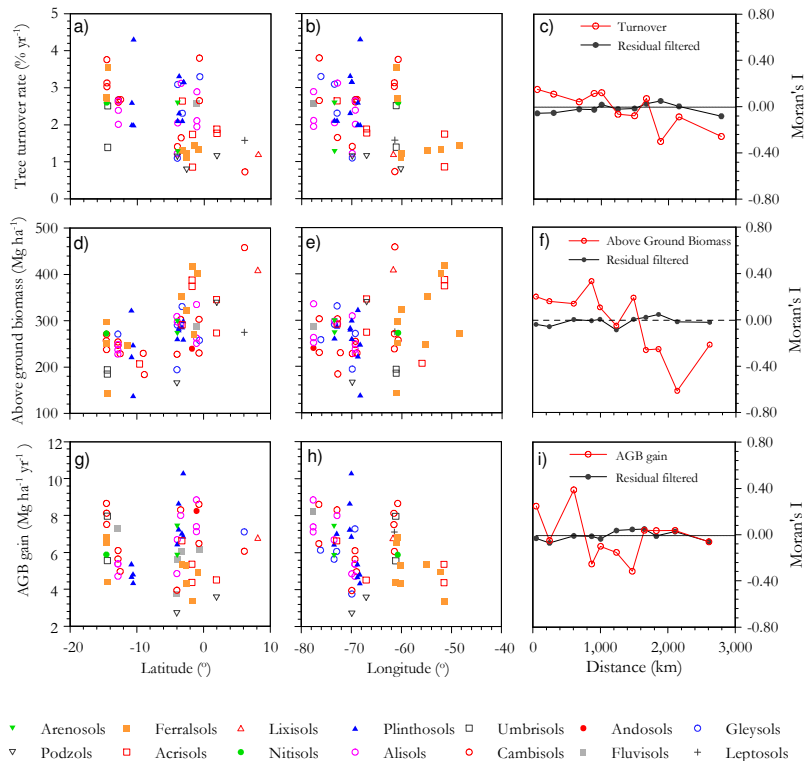


Fig. 2. Correlations of tree turnover, above ground biomass gain and above ground biomass with the geographic space. Moran's / correlograms are also given showing spatial autocorrelation but with spatial filters being able to effectively remove its effect from regression residuals.

4037

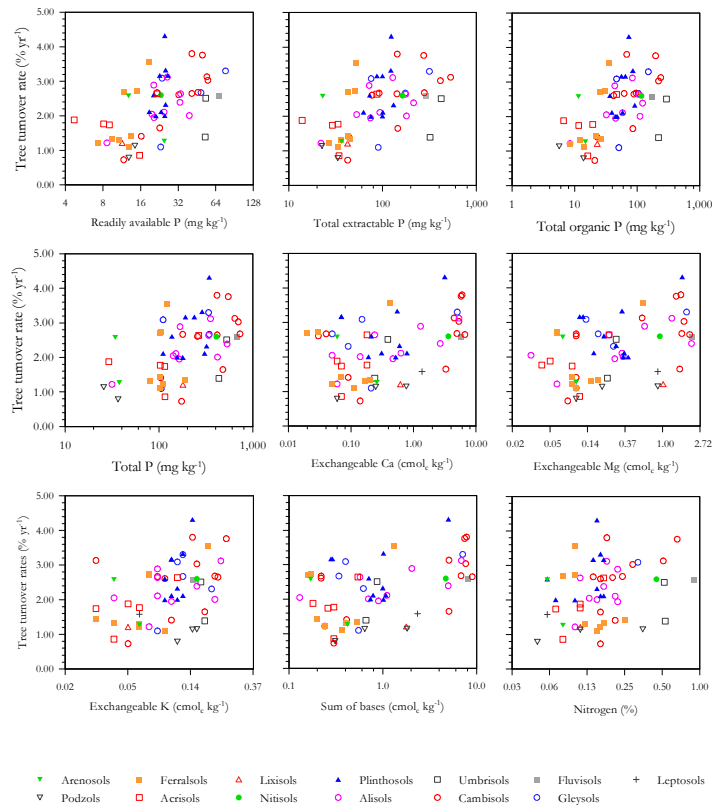


Fig. 3. Relationships between tree turnover rates and different soil fertility parameters.

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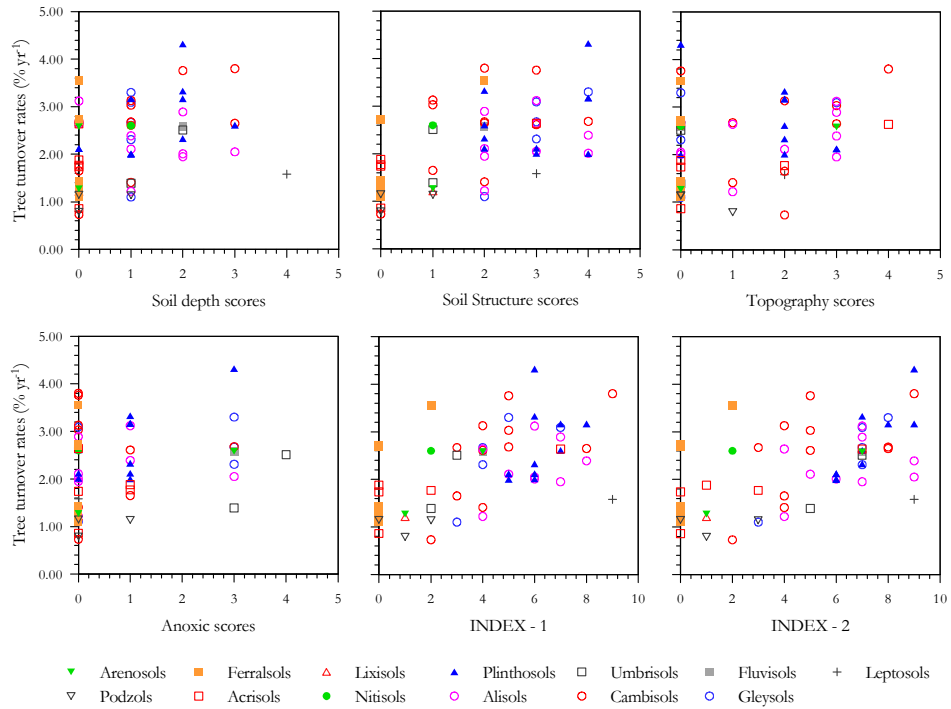


Fig. 4. Relationships between tree turnover rates and soil physical properties.

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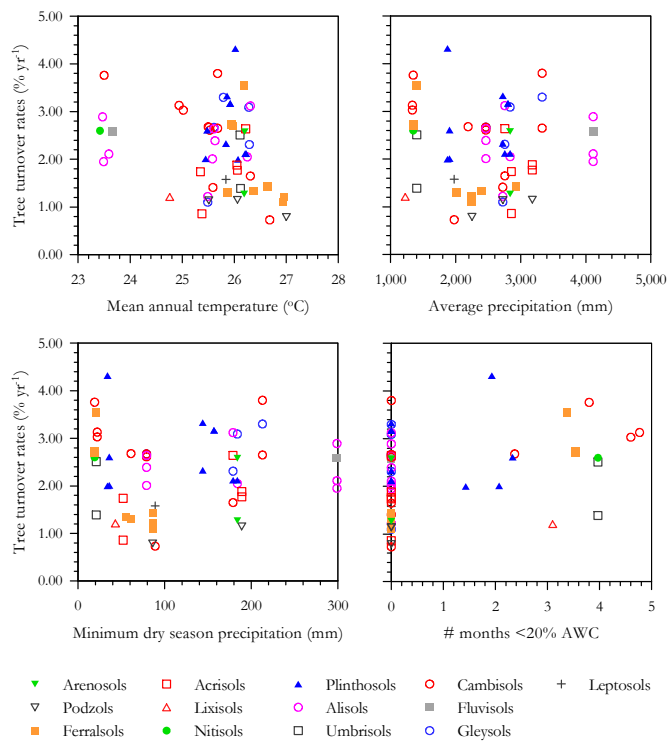


Fig. 5. Relationships between tree turnover rates and climatic factors.

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Variables	Unfiltered			Filtered		
	Std coeffic	t	p value	Std coeffic	t	p value
Nitrogen	-0.133	-0.913	0.366	-0.084	-0.596	0.554
Readily available P	0.449	2.818	0.007	0.050	0.260	0.796
Sum of bases	0.258	1.658	0.104	0.252	1.790	0.080
Spatial filter 1				-0.225	-1.835	0.073
Spatial filter 2				-0.465	-3.267	0.002
Spatial filter 3				-0.193	-1.863	0.069

Partial regression:

Total explained by predictors:	0.329
Total explained by space:	0.442
Total explained by both together (R ²):	0.491
Predictors only (a):	0.049
Shared variance (b):	0.280
Space only (c):	0.162
Unexplained (d):	0.509

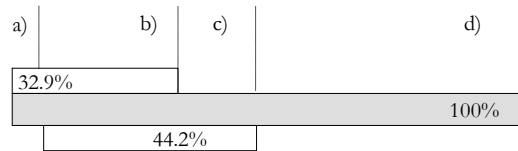


Fig. 6a. Multiple regressions between tree turnover rate and soil fertility parameters, with partitioning for the effect of spatial autocorrelation and soil predictors.

4041

Variables	Unfiltered			Filtered		
	Std coeffic	t	p value	Std coeffic	t	p value
Precipitation	0.283	1.693	0.097	0.025	0.119	0.906
# months <20% AWC	0.635	3.975	<0.001	0.287	1.166	0.250
Soil structure	0.514	5.390	<0.001	0.514	3.315	0.002
Topography	0.213	1.998	0.051	0.167	1.491	0.143
Spatial filter 1				0.077	0.543	0.590
Spatial filter 2				-0.259	-1.633	0.109
Spatial filter 3				-0.132	-1.158	0.253

Partial regression:

Total explained by predictors:	0.522
Total explained by space:	0.442
Total explained by both together (R ²):	0.562
Predictors only (a):	0.120
Shared variance (b):	0.402
Space only (c):	0.040
Unexplained (d):	0.438

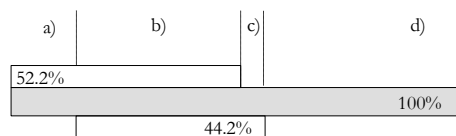


Fig. 6b. Multiple regressions between tree turnover rate and soil physical parameters, with partitioning for the effect of spatial autocorrelation and soil predictors.

4042

Variables	Unfiltered			Filtered		
	Std coeffic	t	p value	Std coeffic	t	p value
INDEX - 2	0.639	6.419	<0.001	0.508	3.156	0.003
# months <20% AWC	0.362	3.702	<0.001	0.230	1.953	0.057
Spatial filter 1				0.012	0.089	0.930
Spatial filter 2				-0.257	-1.880	0.066
Spatial filter 3				-0.125	-1.224	0.227

Partial regression:

Total explained by predictors: 0.491
Total explained by space: 0.442
Total explained by both together (R^2): 0.541
Predictors only (a): 0.099
Shared variance (b): 0.392
Space only (c): 0.050
Unexplained (d): 0.459

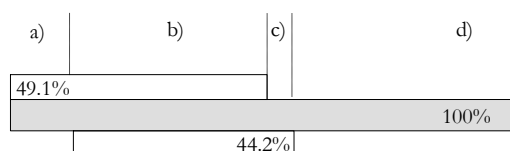


Fig. 6c. Multiple regressions between tree turnover rate and the index of physical properties INDEX-2, with partitioning for the effect of spatial autocorrelation and soil predictors.

4043

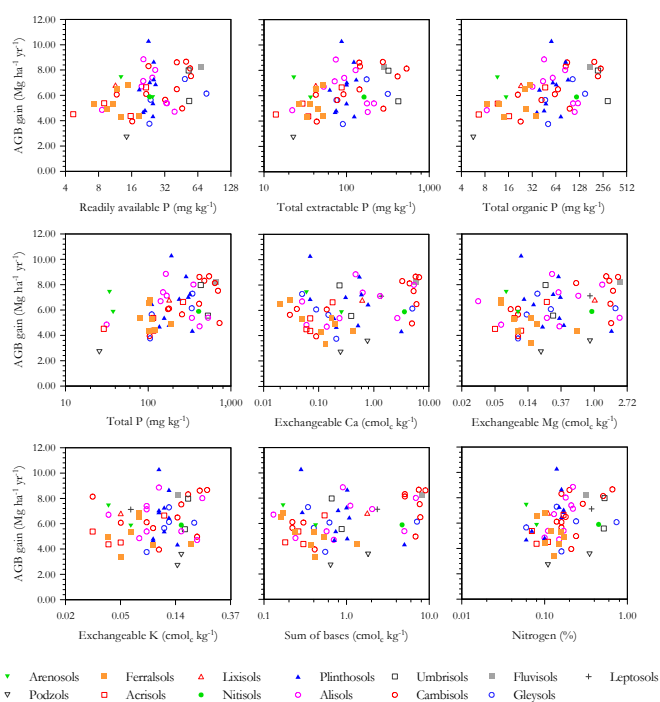


Fig. 7. Relationships between above ground biomass gain and different soil fertility parameters.

4044

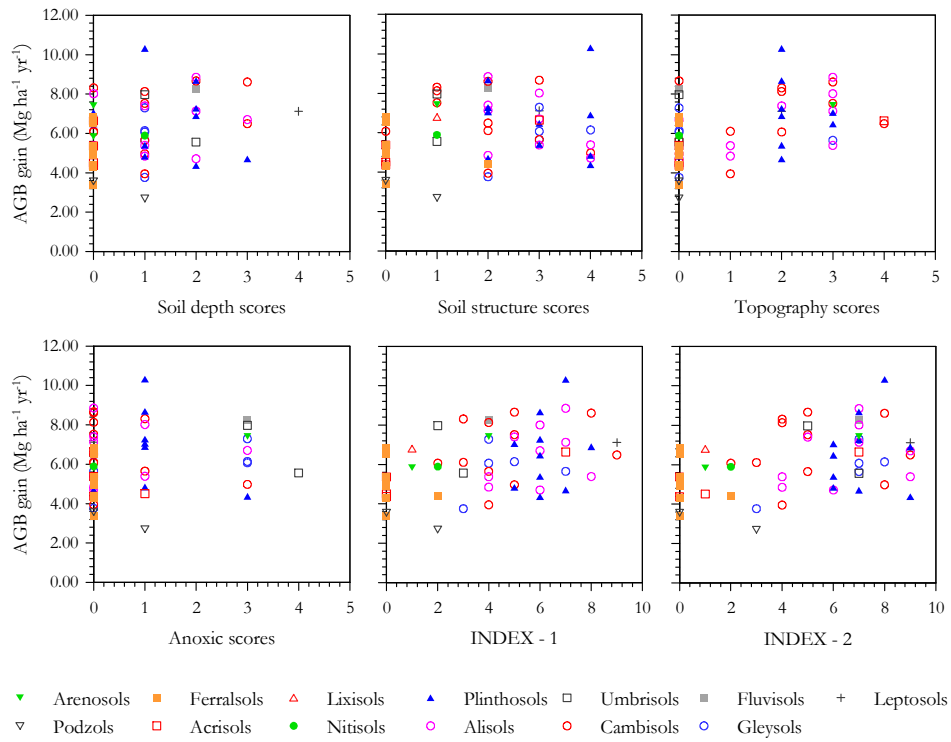


Fig. 8. Relationships between above ground biomass gain and soil physical properties.

4045

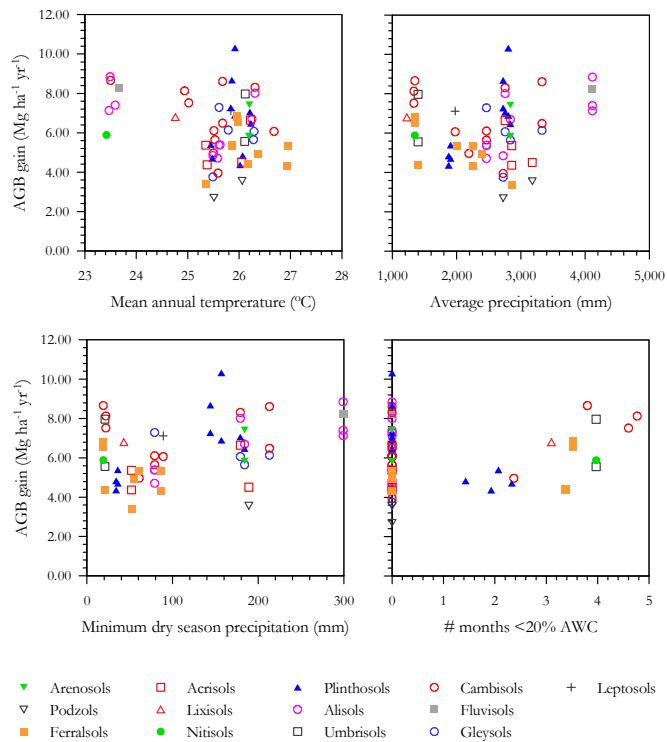


Fig. 9. Relationships between above ground biomass gain and climatic factors.

4046

Variables	Unfiltered			Filtered		
	Std coeffic	t	p value	Std coeffic	t	p value
Mean annual temperature	-0.192	-1.699	0.096	-0.250	-1.965	0.056
Average precipitation	-1.016	-3.707	<0.001	-0.733	-1.910	0.063
Minimum dry season precip.	1.367	4.926	<0.001	0.417	0.853	0.398
Total phosphorus	0.703	4.829	<0.001	0.651	3.896	<0.001
Sum of bases	-0.395	-2.556	0.014	-0.384	-2.520	0.016
Spatial filter 1				-0.658	-2.422	0.020
Spatial filter 2				0.139	1.357	0.182
Spatial filter 3				0.211	1.383	0.174
Spatial filter 4				-0.209	-1.319	0.194

Partial regression:

Total explained by predictors: 0.524
 Total explained by space: 0.396
 Total explained by both together (R^2): 0.606
 Predictors only (a): 0.207
 Shared variance (b): 0.317
 Space only (c): 0.079
 Unexplained (d): 0.397

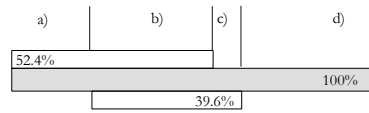


Fig. 10. Multiple regressions between above ground biomass gain and soil fertility parameters total phosphorus and sum of bases, with partitioning for the effect of spatial autocorrelation and soil predictors.

4047

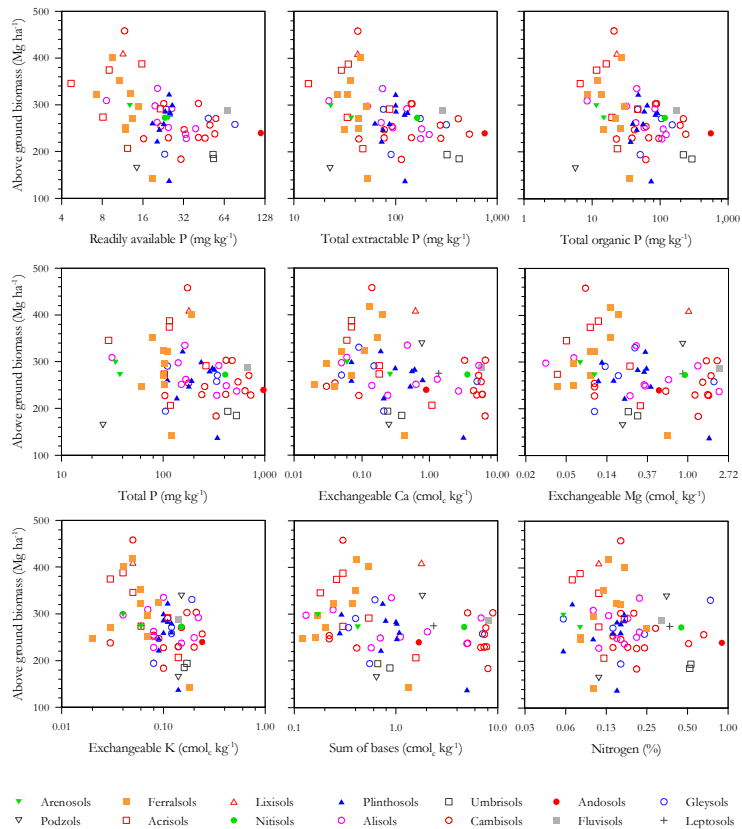


Fig. 11. Relationships between above ground biomass and different soil fertility parameters.

4048

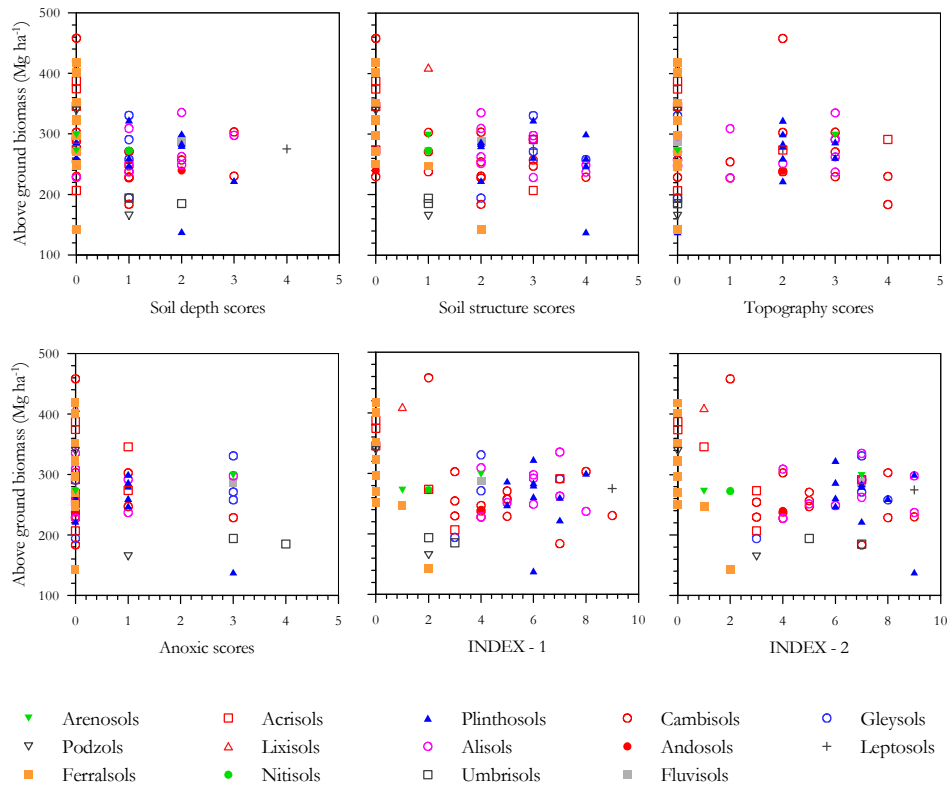


Fig. 12. Relationships between above ground biomass and soil physical properties.

4049

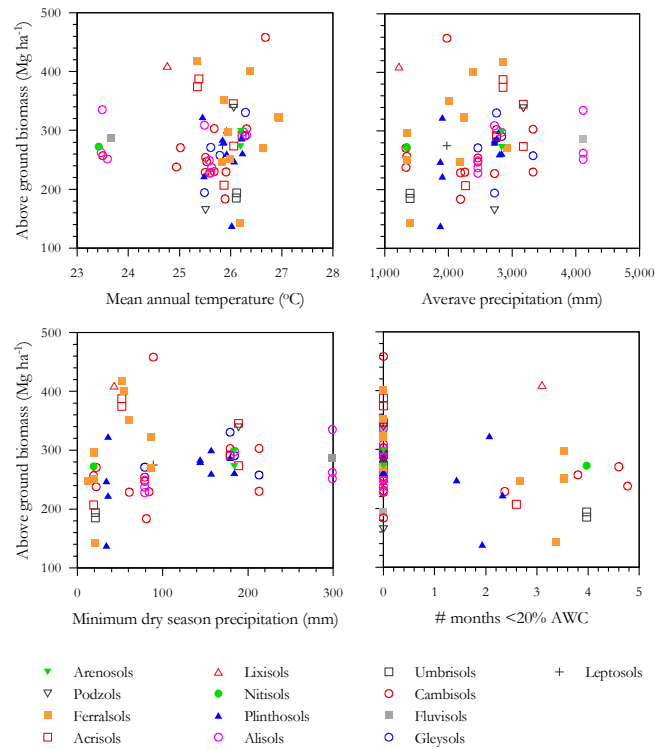


Fig. 13. Relationships between above ground biomass and climatic factors.

4050

Variables	Unfiltered			Filtered		
	Std coeffic	t	p value	Std coeffic	t	p value
Total extractable P	-0.209	-2.096	0.041	0.030	0.236	0.815
Soil structure	-0.308	-2.223	0.031	0.005	0.044	0.965
Spatial filter 1				-0.231	-2.604	0.013
Spatial filter 2				0.497	4.423	<0.001
Spatial filter 3				-0.556	-5.782	<0.001
Spatial filter 5				0.212	2.596	0.013
Spatial filter 6				0.311	3.764	<0.001

Partial regression:

Total explained by predictors:	0.257
Total explained by space:	0.720
Total explained by both together (R ²):	0.720
Predictors only (a):	0.000
Shared variance (b):	0.257
Space only (c):	0.463
Unexplained (d):	0.280

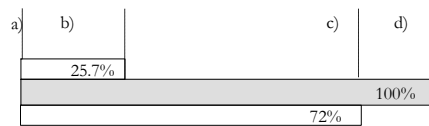


Fig. 14. Multiple regressions between above ground biomass and total extractable phosphorus and soil structure, with partitioning for the effect of spatial autocorrelation and soil predictors.

4051

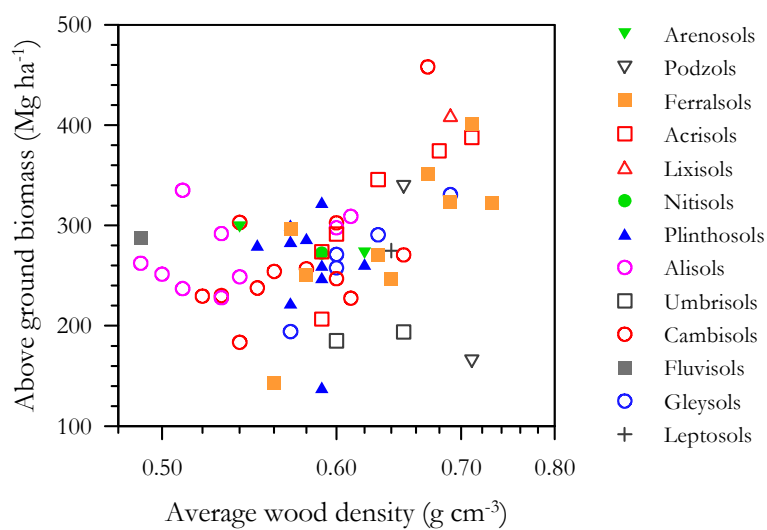


Fig. 15. Relationship between above ground biomass and average plot wood density.

4052

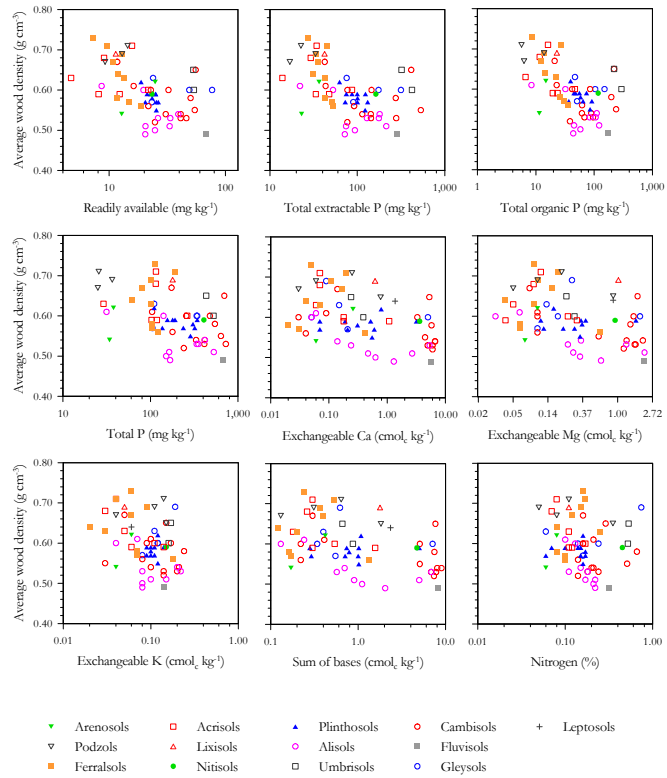


Fig. 16. Relationships between wood density and different soil fertility parameters.

4053

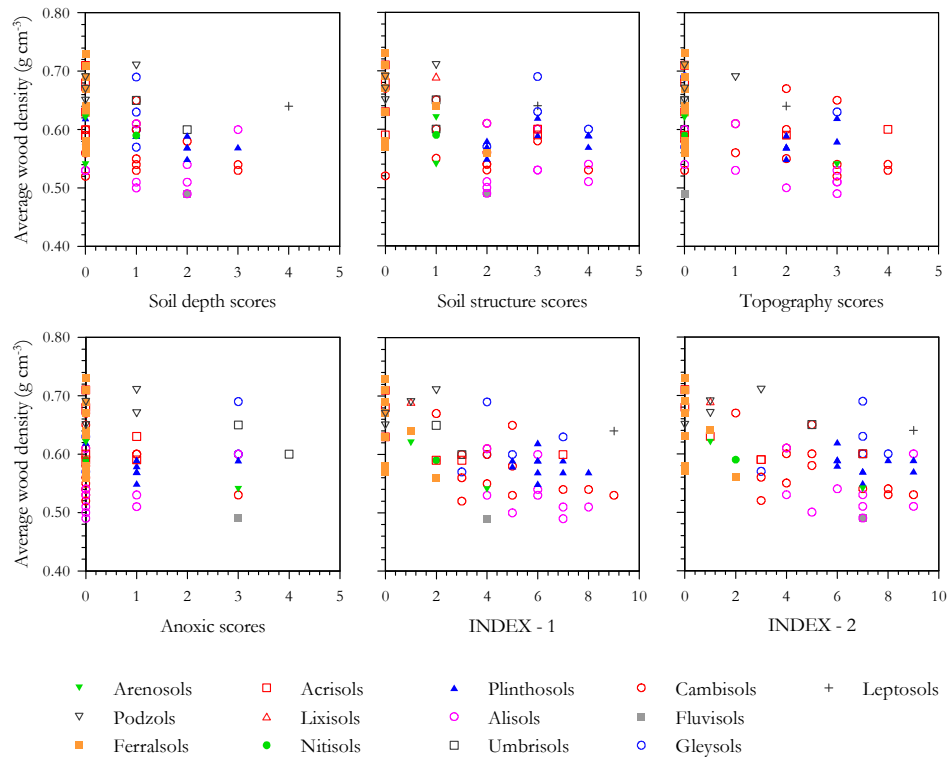


Fig. 17. Relationships between wood density and soil physical properties.

4054

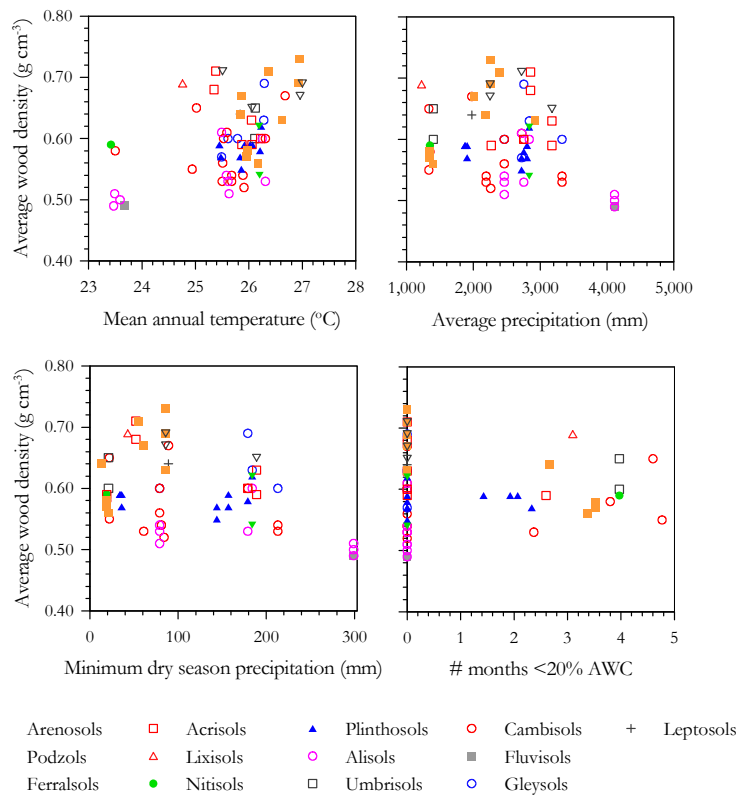


Fig. 18. Relationships between wood density and climatic factors.

4055

Variables	Unfiltered			Filtered		
	Std coeffic	t	p value	Std coeffic	t	p value
Total extractable P	-0.100	-0.826	0.413	0.156	1.727	0.092
Sum of bases	-0.197	-1.623	0.111	-0.251	-2.983	0.005
Dry s. minimum precip.	-0.160	-1.342	0.186	-0.677	-3.100	0.004
INDEX - 1	-0.484	-3.758	<0.001	-0.184	-1.565	0.125
Spatial filter 1				-0.399	-1.853	0.071
Spatial filter 2				-0.193	-2.521	0.016
Spatial filter 3				0.606	7.034	<0.001
Spatial filter 4				0.103	1.370	0.178
Spatial filter 5				0.027	0.287	0.776
Spatial filter 6				0.170	2.091	0.043

Partial regression:

Total explained by predictors: 0.530
 Total explained by space: 0.720
 Total explained by both together (R²): 0.821
 Predictors only (a): 0.101
 Shared variance (b): 0.429
 Space only (c): 0.291
 Unexplained (d): 0.179

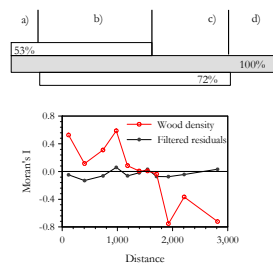


Fig. 19. Multiple regressions between wood density and edaphic and climatic parameters, partitioned for the effect of spatial autocorrelation and soil predictors.

4056

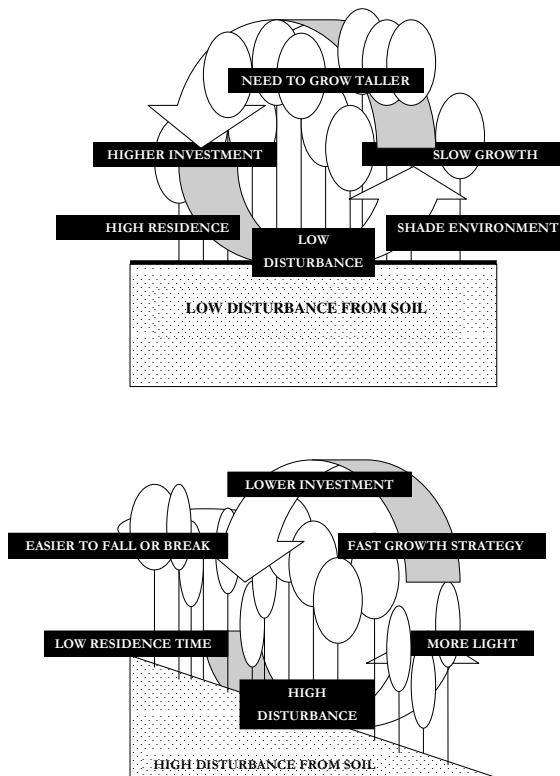


Fig. 20. Positive feedback mechanisms acting over floristic composition, wood density and tree turnover rates. In the top the interacting mechanisms tend to select slow growth strategy while in the bottom it tends to select fast growth strategy.