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Factors controlling the productivity of tropical Andean forests: Climate and soil are more important than tree diversity

Jürgen Homeier[1,2], Christoph Leuschner[1,2]

[1]Plant Ecology and Ecosystems Research, University of Goettingen, Untere Karspüle 2, 37073 Goettingen, Germany
[2]Centre for Biodiversity and Sustainable Land Use, University of Goettingen, Untere Karspüle 2, 37073 Goettingen, Germany

Correspondence to: Jürgen Homeier (jhomeie@gwdg.de)

Abstract. Theory predicts positive effects of species richness on the productivity of plant communities through complementary resource use and facilitative interactions between species. Results from manipulative experiments with tropical tree species indicate a positive diversity-productivity relationship (DPR), but the existing evidence from natural forests is scarce and contradictory. We studied forest aboveground productivity in more than 80 humid tropical montane old-growth forests in two highly diverse Andean regions with large geological and topographic heterogeneity, and related productivity to tree diversity and stand structural, edaphic and climatic factors with likely influence on productivity. Main determinants of aboveground productivity in the perhumid study regions were elevation (as a proxy of temperature), soil nutrient (N, P and base cation) availability, and forest structural parameters (wood specific gravity, aboveground biomass). Tree diversity had only a small positive influence on productivity, even though tree species numbers varied largely (6-27 species per 0.04 ha). We conclude that the productivity of Neotropical humid montane forests is primarily controlled by thermal, edaphic and stand structural factors, while tree diversity is of minor importance.

1 Introduction

Research into the diversity-productivity relationship (DPR) is of theoretical importance, and has recently focused on forests because of their importance for the global carbon cycle and the high biodiversity especially of tropical forests Mori et al., 2017; Fei et al., 2018). Results from the few experimental plantations with variable tree species richness in the tropics and subtropics show that DPRs are positive (Sapijanskas et al. 2014; Huang et al., 2018; Schnabel et al., 2019), likely due to complementary resource use and facilitative interactions between different tree species (McIntire et al., 2014; Chen et al., 2016). On the other hand, results from observational studies on correlations between tree diversity and productivity in natural or near-natural tropical forests are more contradictory. On Mt. Kinabalu, Malaysia, aboveground NPP was higher in more diverse tropical montane forest plots (Aiba et al., 2005), but no effects of species richness on productivity were found in logged tropical lowland forests in Guyana (van der Sande et al., 2018). Chisholm et al. (2013) analyzed the tree diversity-productivity relation in 25 permanent forest plots from temperate to tropical regions and found a positive diversity effect when plot size was small (0.04 ha), but the effect disappeared at larger spatial scales (0.25 and 1 ha). Finally, in a global analysis, Liang et al. (2106) found that positive tree species richness–productivity relationships predominate, but negative relations do also exist, though restricted to a few of the tested data sets.

The existing observational data from tropical forests thus suggest that (i) tree diversity seems to enhance productivity under certain conditions, and (ii) a positive DPR might be more prominent in small plots. To date, it is not clear under which abiotic conditions and stand structural settings a positive DPR does emerge, and how important tree diversity is compared to abiotic and other biotic determinants of productivity.

The search for abiotic determinants of tropical forest productivity has concentrated on precipitation and solar irradiance, revealing clear dependencies in studies along environmental gradients (Schuur, 2003; Girardin et al., 2014; Malhi et al., 2017). Also seasonal variation of precipitation seems to have a major influence on forest productivity (Wagner et al., 2016). Less clear is the role of temperature. Although the majority of studies along elevation transects found the expected productivity decline with decreasing temperature in tropical mountains (Kitayama & Aiba, 2002; Cleveland et al.; 2011; Leuschner et al., 2013), some studies failed to show a temperature dependence of net primary production in tropical forests (Luyssaert et al., 2007; Selmants et al., 2014). There is wide agreement that the productivity of tropical forests tends to increase with soil fertility, notably N and availability and base cation supply (Kitayama & Aiba, 2002; Cleveland et al.; 2011; Malhi et al., 2004; Homeier et al., 2010; Unger et al., 2012; Banin et al., 2014; Hofhansel et al., 2015).

With few exceptions, productivity also increases with standing aboveground biomass (AGB) (Keeling & Phillips, 2007; Pan et al., 2013; Lohbeck et al., 2015), but this relation does not always seem to be very close (Chisholm et al., 2013). In conclusion, a multi-factorial approach is needed to understand the driving factors of tropical forest productivity, whereas most of the existing studies have investigated only one or two of the mentioned factors.

Tropical montane forests occur along steep thermal and edaphic gradients, which predestines them for the study of abiotic controls of tropical forest productivity. They also play important roles for the provision of water and as stores of carbon (Bruijnzeel et al., 2010; Spracklen & Righelato, 2014).

In this study in two Andean elevation transects, we combine biomass, production and tree diversity data with comprehensive soil chemical data to identify the most important drivers of forest productivity in Neotropical montane forests (Figure 1). In permanent plots in old-growth forests, we measured coarse wood production (WP) and fine litter production (only one of the transects) and related these components of aboveground primary production to the availability of N, P, Ca, K and Mg in the soil, to elevation as a proxy of temperature, and to stand structural properties and the rarefied number of tree species per plot. We chose a plot size of 0.04 ha (20 m × 20 m) in both transects because assumed diversity effects are more likely to emerge at small spatial scales (Chisholm et al., 2013). This allowed us to investigate a larger number of plots across extended environmental gradients (2000 m of elevation distance or ~10 K variation in mean annual temperature; large bedrock, topographic and soil variation) and to encounter considerable variation in tree diversity (6 to 27 species per plot). The analyses were restricted to old-growth forests with closed canopy in order to exclude variation in stand structure and species composition related to successional processes. We employed structural equation modeling for exploring mutual inter-relationships between the likely abiotic and biotic drivers of productivity.

Based on the assumption that precipitation is not a growth-limiting factor in this humid to perhumid study region, we hypothesized in accordance with the existing literature that (i) temperature is the principal productivity-determining factor in the study regions, (ii) soil nutrient availability is another, but secondary, influential abiotic factor, acting in TMFs mainly through N availability, and (iii) tree diversity is a less important driver of productivity than abiotic factors.

2 Methods

2.1 Study transects

The study was conducted in permanent plots in old-growth montane forests established along two elevation transects on the eastern slope of the Ecuadorian Andes in the provinces Napo (Napo transect) and Loja and Zamora-Chinchipe (Loja transect) (Figure A1). The chosen plot area was 20 m x 20 m (400 m^2), a size that has previously been used in surveys of tropical forest diversity, because the area is large enough to give representative information on stand structure and species composition, while the patch size is in tropical montane old-growth forests small enough to guarantee sufficient stand structural and edaphic homogeneity on the plot level. All plots were placed in forest patches without signs of recent disturbance and in sufficient distance to special microhabitats such as ravines and ridges. By selecting small-sized plots solely in old-growth portions of the forest, we attempted to reduce the variation in structural and biological parameters resulting from the mosaic of different successional stages typically present in natural forests.

The climate in both transect regions is perhumid throughout the year with a mean annual precipitation >2000 mm at all elevations and without a distinct dry season (Bendix et al., 2008; Salazar et al., 2015). All study sites are characterized by aridity index values >0.74 after (Trabucco et al., 2009).

Soil properties vary with elevation and differ between the two transects. The Loja transect is characterized by relatively nutrient-poor soils mostly on metamorphic schists and sandstones with a slightly better nutrient supply at lower elevations and in valleys and less favorable supply of N and P on upper slopes and at higher elevations (Wilcke et al., 2008; Werner & Homeier, 2015). In contrast, the Napo transect has more fertile soils, which developed on volcanic deposits or limestone. In this transect, N mineralization rate decreased with elevation, while plant-available P increased (Unger et al., 2010). The availability of the five plant macronutrients N, P, Ca, K and Mg was analyzed in the soil of all study plots together with soil acidity. For characterizing N availability, incubation experiments to determine the net release of NH_4^+ and NO_3^- through mineralization and nitrification (N_{min}) were conducted in the topsoil. In addition, the bulk soil C/N ratio was determined in the topsoil for characterizing the decomposability of soil organic matter and thus give an independent measure of potential N supply (Pastor et al., 1984). P availability was estimated as resin-exchangeable P, i.e. the exchange of phosphate ions by anion exchange resins, which may give a minimum estimate of plant-available P (P_{av}). The plant availability of Ca, K and Mg ($CaKMg_{ex}$), and also of potentially toxic Al^{3+}, was quantified by salt exchange (0.2 N $BaCl_2$ solution), applying a standard protocol for the chemical analysis of forest soils (for analytical details see Unger et al. (2010) and Wolf et al. (2011)). Soil pH was measured in soil suspended in 1 M KCl. Since most fine roots are concentrated in the topsoil (Soethe et al., 2006), where

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also the vegetation effect on the soil is largest, the statistical analyses focus on the chemistry of the 0-10 cm layer and its importance for the vegetation (see Appendix A2 for the soil chemical properties of the plots**)**.

2.2 Plot inventory and forest productivity

The Loja transect consists of 54 plots that are equally spread over the three elevation levels (18 plots each at ~1000, ~2000 and ~3000 m a.s.l.) (see Appendix A3 for the stand properties of the plots**)**. From the Napo transect**,** we included data from 66 plots that were located in a comparable elevation range (960 – 3100 m asl). In both transects, all trees with diameter at breast height (dbh) ≥10 cm in the 400 m^2–plot were recorded with their dbh and identified to species. From unknown tree species, specimens were collected for later identification at Ecuadorian herbaria (HUTPL, LOJA, QCA, QCNE) or by international specialists for difficult groups.

Data on aboveground woody biomass (AGB), annual AGB increment (WP) and WSG (wood specific gravity) of all trees ≥10 cm dbh in the plots were available from earlier studies (Loja transect: Wolf et al. (2011), Leuschner et al. (2013); Napo transect: Unger et al. 2012), Kessler et al. (2014)). For the Loja transect we additionally calculated net aboveground productivity (NPP_a) as the sum of WP and annual fine litter production (data available from Wallis et al., 2019).

Leaf area index (LAI) was estimated by synchronous measurement with two LAI 2000 Plant Canopy Analyzers (LI-COR Inc., Lincoln, NE, USA) that were operated in the remote mode during periods of overcast sky. Simultaneous readings were taken below the canopy at 2 m height above the ground and in nearby open areas (“above-canopy” reading) to record incoming radiation. Data for the Napo transect were taken from Unger et al. (2013). For the Loja transect, the LAI measurements were conducted in 2011, following the same methods described in detail in Unger et al. (2013).

2.3 Data analysis

Tree diversity was calculated according to the individual-based rarefaction method (Gotelli & Colwell, 2001) as the number of species (stems with dbh ≥10 cm) expected in a random sample of 14 trees in a 400 m^2-plot (14 being the smallest number of tree individuals recorded in our plots). Linear regression analyses were applied to identify significant relationships between AGB, WP, tree diversity, LAI, stem density, WSG and soil properties as dependent variables, and elevation (as a proxy of temperature) as independent variable.

We used principal components analysis (PCA) to reduce the number of soil variables and to ensure that the subsequent analyses were not affected by the problem of multi-collinearity. We conducted two PCAs using the R package ‘pcaMethods’, one with the merged data from both transects, and another one for the Loja transect. The following ten soil variables were included in the PCAs: organic layer depth, mineral soil pH (KCl), exchangeable K, Mg, Ca, and Al, resin-exchangeable P, C/N ratio, topsoil N mineralization and nitrification rate. The plot scores on the first two resulting principal components (PC 1 and PC 2) were included in the subsequent analyses.

Structural equation modeling was used for identifying the direct influence of abiotic factors (elevation, soil PCs) on forest stand properties and tree diversity and to assess the direct and indirect influences of these factors on productivity. For each

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initial structural equation model (SEM), we included the two principal soil components (PC1 and PC2) from the respective PCA, and the factors elevation, WSG, and tree diversity to predict AGB and stand productivity (wood production WP or NPP_a). WSG was selected from the stand structural variables, as it showed a stronger correlation to stand productivity than the other measured structural variables (stem density and LAI).

Based on the existing knowledge about the dependency of productivity and AGB on environmental and stand structural properties, and assumed diversity effects on productivity, we developed an initial model of interaction paths between the environmental parameters (elevation, soil PC 1 and PC 2), WSG and tree diversity, and the target variables (AGB and WG or NPP_a) (Figure 1). We then fitted two different SEMs, one for the complete set of 83 plots from both transects (where all information was available: 54 Loja plots and 29 Napo plots), and another one for the Loja transect (54 plots), where NPP_a (and not only WP) data are available.

IBM SPSS AMOS 24 software (Arbuckle 2016) was used to fit the normalized data to the hypothesized path model and to determine path coefficients using the maximum likelihood method. We assessed the goodness of model fit using the χ^2 value, the associated p value, AIC, RMSEA, and the CFI. Since we used SEM in an explorative way, the original model has been subject to modification. We iteratively removed insignificant paths to test whether incorporation of those paths in the model significantly increased the χ^2 value and CFI, and reduced the AIC and the RMSEA of the model. For all dependent variables, we calculated R^2 values that indicate the proportion of variance explained by the model.

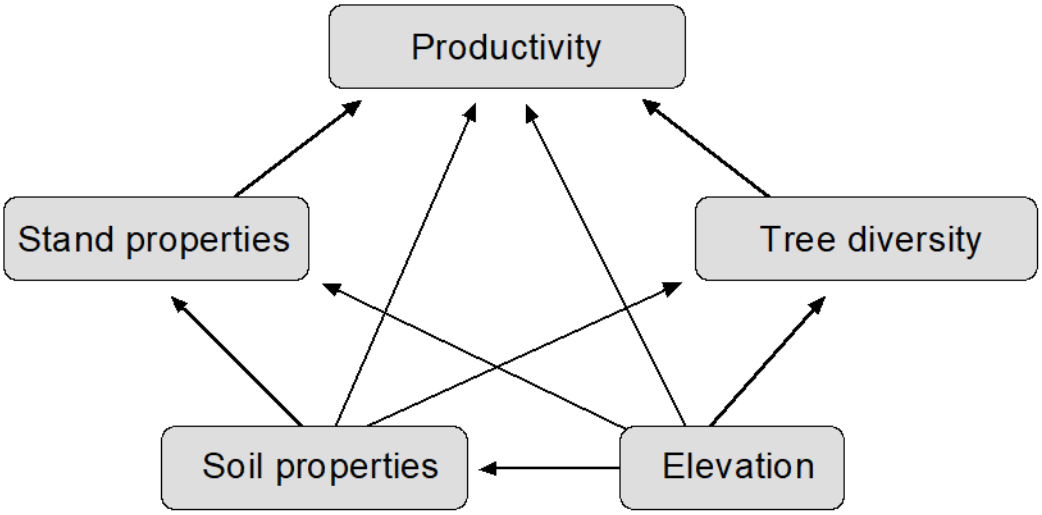

Figure 1. Conceptual model of plausible interaction pathways between environment (elevation, soil) and forest structure as drivers of productivity. Arrows drawn from the two boxes Forest stand properties and Soil properties indicate that pathways from the respective variables (Forest stand properties: wood specific gravity, stem density, LAI; Soil properties: first two PCA axes) were included in the models.

3 Results

3.1 Patterns of tree diversity and productivity

The two transects differed considerably with respect to floristic composition. Most important tree families in the Loja transect (in order of abundance) were Lauraceae, Melastomataceae, Cunoniaceae, Moraceae and Clusiaceae, in the Napo transect Euphorbiaceae, Fabaceae, Lauraceae, Moraceae and Rubiaceae. The number of stems per plot varied between 14 and 61 and the number of tree species between 6 and 27 (Supplement S1). Tree species richness showed no significant decline with elevation (Figure 2a). AGB decreased on average by 50-90 Mg ha^{-1} per km elevation in both transects (Figure 2b). Biomass was between 200 Mg ha^{-1} (lower elevations) and 100 Mg ha^{-1} (upper elevations) higher in the Napo transect on more fertile soil than in the Loja transect. The AGB decrease was linked to a decline in WP between 1000 and 3000 m by about 1.3 - 1.5 Mg ha^{-1} yr^{-1} per km elevation with a generally lower productivity (by about 1.0 - 1.5 Mg ha^{-1} yr^{-1}) in the Loja transect compared to the Napo transect (Figure 2c). LAI decreased with elevation in both transects by about 1 m^{2} m^{-2} per km elevation with slightly higher LAI values in the Loja transect (Figure 2d). WSG showed no systematic variation with elevation (Figure 2e). The expected stem density increase with elevation was only observed in the Loja transect (Figure 2f).

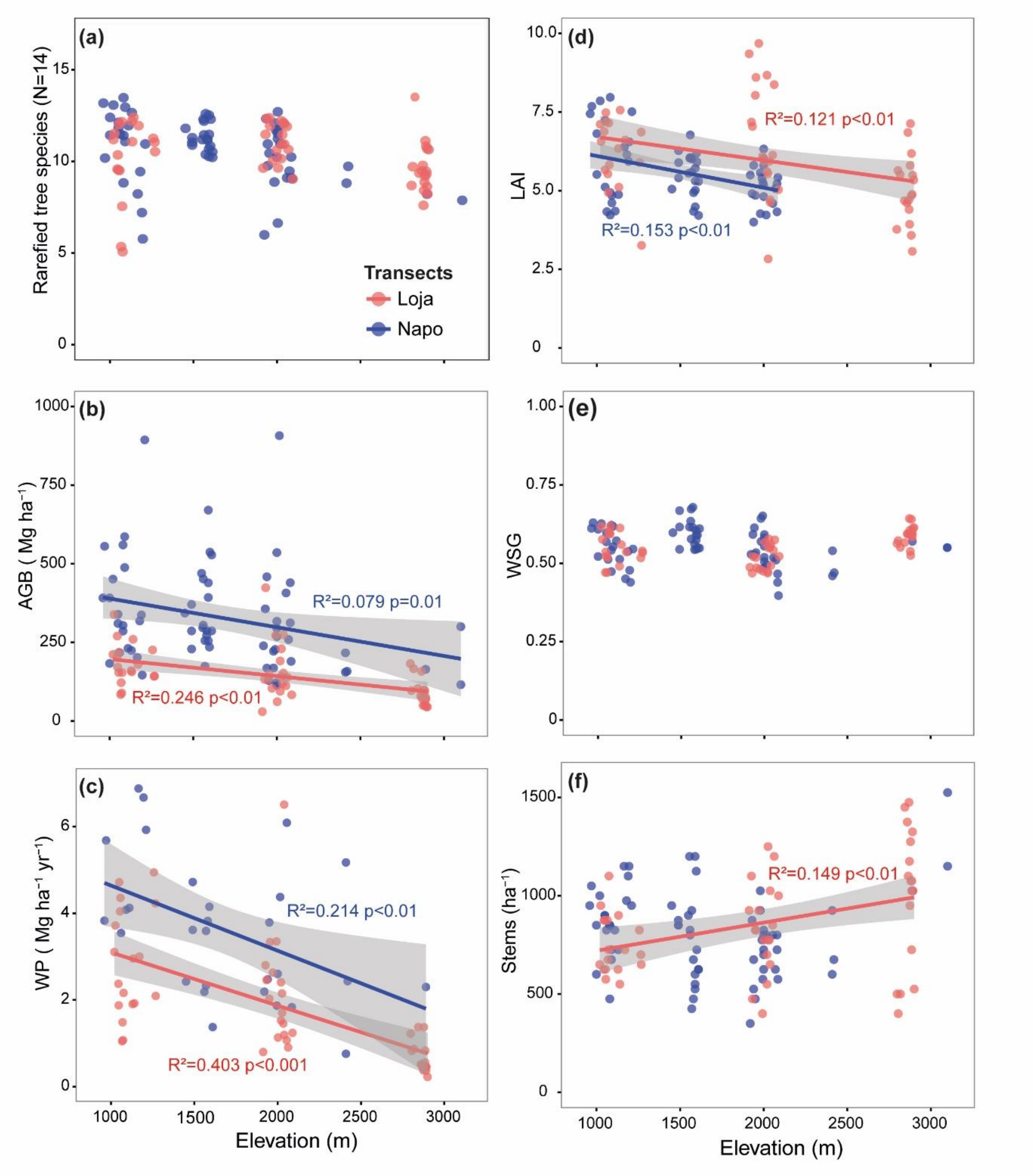

Figure 2. Variation of tree diversity (a), aboveground biomass (b), wood production (c), LAI (d), wood specific gravity (e), and stem density (f) along the two studied forest transects (red dots: Loja-transect, blue dots: Napo-transect). The number of plots available for a given parameter and transect varies, as not all parameters were measured in all plots (a: Loja 54 plots / Napo 64 plots; b: 54/66; c: 54/29; d: 53/60; e: 54/66; f: 54/66). Data presented in b, c, e and f were compiled from Unger et al. (2012), Leuschner et al. (2013), Kessler et al. (2014); data from the Napo transect in d are from Unger et al. (2013). 170

3.2 Identification of principal soil factors

175 In the two data sets (both transects merged; Loja transect only), the first two PCA axes explained 63 % and 61 %, respectively, of the variation in soil factors across all plots. In the merged data set (Figure 3, Figure B1 and Table B1), the first axis represented mainly the basic cations Mg, Ca and K, soil pH and organic layer depth, whereas the second axis stood for N supply and P_{av}. In the PCA of the Loja transect (Figure B2 and Table B2), soil parameters were represented similarly, but P_{av} had a higher loading on the first axis. In general, the soils of the Napo transect were characterized by higher fertility, as 180 indicated by on average markedly higher topsoil net N mineralization rates and higher P availability in the mineral topsoil (see Supplement S2).

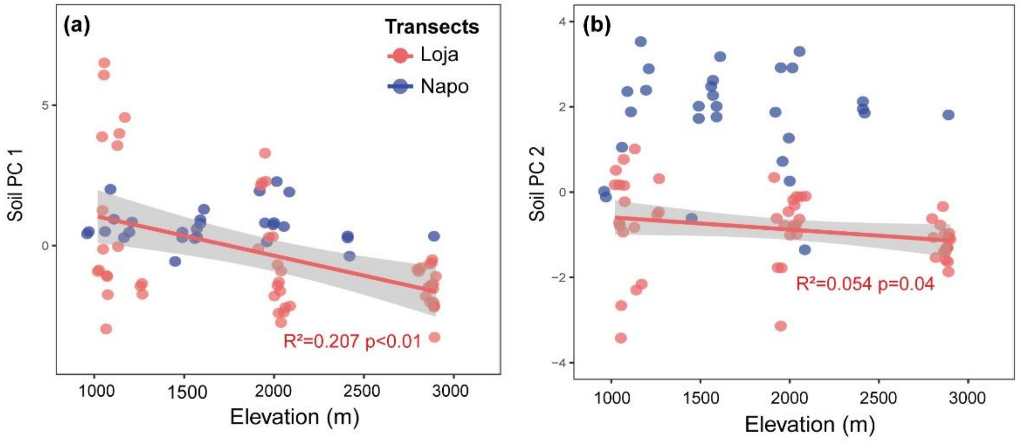

Figure 3. Variation of soil properties along the two forest transects (red dots: Loja-transect, blue dots: Napo-transect). Shown are the (a) first and (b) second principal components of the soil PCA (see Figure B1 and table B1).

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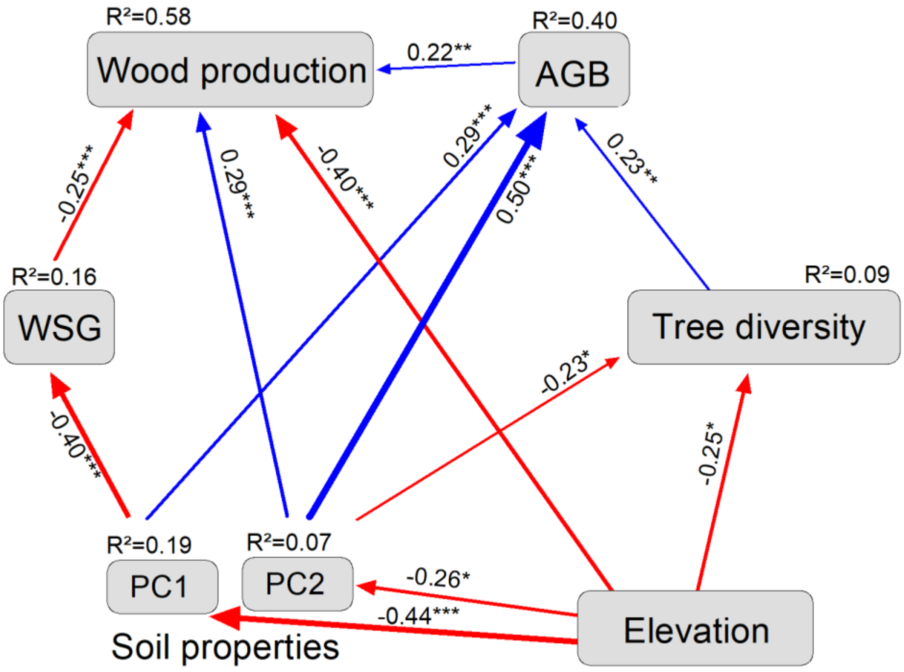
3.3 Factors determining wood production in the merged data set

In the merged data set (83 plots; Figure 4, Table 1), aboveground tree biomass (AGB) was positively influenced by soil fertility (standardized total effects of PC1 and PC2, 0.30 and 0.45, respectively) and tree diversity (0.23). The three most important determinants of WP were elevation (negative influence, standardized direct effect -0.58), soil PC2 (0.29) and WSG (-0.25). 190 The direct negative effect of elevation on WP was prominent and this influence was enhanced through indirect relationships via negative effects of elevation on soil properties and tree diversity (standardized indirect effect -0.18). However, soil factors were also important drivers of wood production, either directly (in case of PC2, which was related to N mineralization, 0.29), or indirectly through a soil N effect (PC2) on AGB and diversity (together 0.10), and effects of base cation availability and pH (PC1) on WSG and AGB. Tree diversity itself had only a relatively weak indirect positive effect on WP through its influence 195 on AGB (standardized total effect 0.05).



200 **Figure 4.** Final model for wood production (Loja-transect and Napo-transect: 83 plots). Structural equation model (chi-square = 8.4, 9 df, p = 0.50, AIC 60.4, RMSEA < 0.01, CFI = 1.00) with standardized path coefficients. The size of the arrows is proportional to the strength of the paths, their significance is indicated by asterisks (* P < 0.05, **P < 0.01, *** P < 0.001), blue arrows indicate positive and red negative estimates. AGB: aboveground biomass; WSG: wood specific gravity; PC1, PC2: first two axes of the soil PCA (Figure B1 and Table B1).

Table 1. Standardized direct, indirect and total effects of elevation, various stand structural and soil chemical parameters on coarse wood production (WP) and aboveground biomass (AGB) according to the SEM analysis in Figure 4. Standardized path coefficients are shown.

Factors	Direct	Indirect	Total
WP			
Elevation	-0.397	-0.183	-0.580
PC1		0.163	0.163
PC2	0.285	0.099	0.385
AGB	0.222		0.222
WSG	-0.245		-0.245
Tree diversity		0.051	0.051
AGB			
Elevation		-0.302	-0.302
PC1	0.295		0.295
PC2	0.447		0.447
Tree diversity	0.230		0.230

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205 ### 3.4 Factors determining NPP$_a$ in the Loja transect

The model for aboveground net primary production (i.e. WP plus fine litter production), built only with the Loja transect data, identified elevation and WSG as the main direct determinants of NPP$_a$ (both effects negative; standardized direct effects of -0.67 and -0.39, respectively; Figure 5, Table 2). Soil properties were also influential (mainly PC1 with N availability), but only indirectly through a negative effect on WSG and a positive effect on diversity (standardized total effect 0.30). Tree diversity 210 had a significant positive, but relatively weak direct effect on NPP$_a$ (0.18), which was enhanced by an indirect influence via AGB (standardized total effect 0.27).

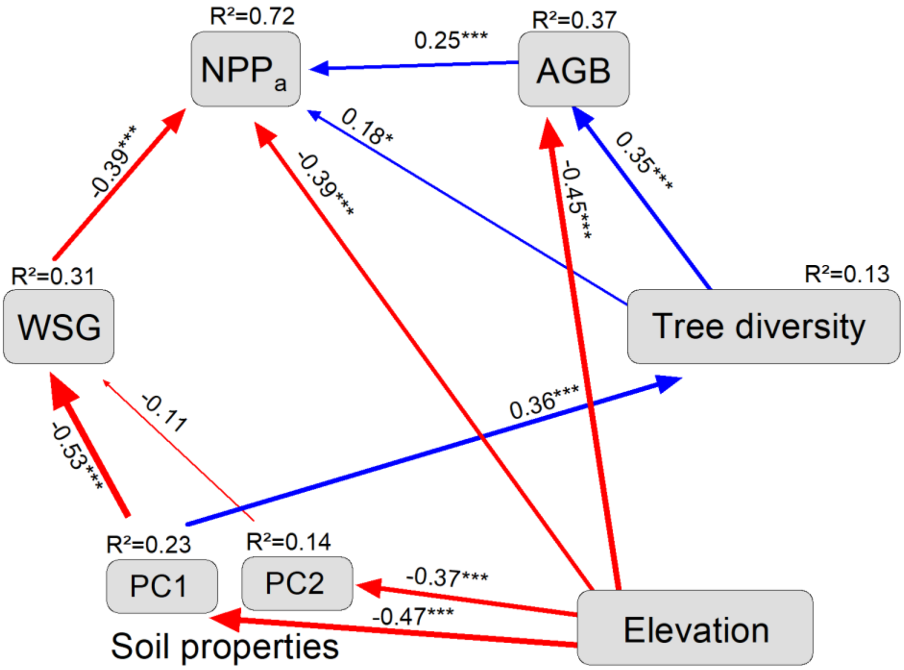

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Figure 5. Final model for NPP$_a$ (Loja-transect: 54 plots). Structural equation model (chi-square = 9.9, 10 df, p = 0.45, AIC 59.9, RMSEA < 0.01, CFI = 0.99) with standardized path coefficients. The size of the arrows is proportional to the strength of the paths, their significance is indicated by asterisks (* P < 0.05, **P < 0.01, *** P < 0.001), blue arrows indicate positive and red negative estimates. AGB: aboveground biomass; WSG: wood specific gravity; PC1, PC2: first two axes of the soil PCA (see Figure B2 and Table B2).

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Table 2. Standardized direct, indirect and total effects of elevation, various stand structural and soil chemical parameters on NPP_a and aboveground biomass (AGB) (Loja transect) according to the SEM analysis in Figure 5. Standardized path coefficients are shown.

Factors	Direct	Indirect	Total
NPP_a			
Elevation	-0.393	-0.272	-0.665
PC1		0.304	0.304
PC2		0.042	0.042
AGB	0.253		0.253
WSG	-0.391		-0.391
Tree diversity	0.178	0.088	0.266
AGB			
Elevation	-0.447	-0.60	-0.506
PC1		0.126	0.126
PC2			
Tree diversity	0.346		0.346

4 Discussion

In general, forest productivity increases with temperature in cooler regions, and with precipitation in drier regions (Reich & Bolstad 2001; Schuur 2003). In the absence of temperature and precipitation measurements and soil moisture data from the plots, we used elevation as a proxy for the thermal conditions. We further assumed that soil moisture is rarely constraining forest productivity in both study regions, as precipitation totals range well above 2000 mm yr^{-1} throughout the Napo and Loja transects (Bendix et al. 2008; Salazar et al., 2015). Our assumption is supported by the highly significant negative influence of elevation on WP, suggesting that the temperature decrease with elevation was physiologically much more important than a possible water shortage effect on productivity. Both the SEMs and correlation analyses show that tropical forest productivity largely decreases (by 1.3 - 1.5 Mg ha^{-1} yr^{-1} km^{-1}) with a concurrent decrease in mean annual temperature from ~20 to ~10 °C in the two transects, confirming earlier observations (Aiba et al., 2005; Cleveland et al., 2011). Temporal water limitation, if it were relevant in the two regions, should be more prominent at lower elevations with lower rainfall, which should lead to a positive, and not a negative, elevation effect on productivity. We cannot exclude, however, that high soil moisture in combination with temporal hypoxia in the rhizosphere of the high-elevation stands is contributing to the productivity decline toward the timberline (Moser et al., 2011).

Other climatic factors with potential impact on productivity such as solar radiation, air humidity and leaf wetness were not considered in our analysis due to lack of suitable local data. Solar radiation typically reaches a minimum at montane or upper montane elevation due to cloud immersion, which can reduce carbon gain (Malhi et al., 2017). Including these factors in the analysis may lead to somewhat different conclusions on the key determinants of forest productivity (Fyllas et al., 2017). Our study in two regions of the northern Andes is the first worldwide to analyze the dependence of tropical montane forest production on the availability of all five quantitatively most important plant nutrients (N, P, Ca, K, Mg). P availability has been reported to limit or co-limit forest productivity at many tropical lowland sites (Tanner et al., 1998; Paoli & Curran, 2007; Cleveland et al., 2011; Wright et al., 2011; Dalling et al., 2016b), whereas N seems to limit tropical forest productivity more often at higher elevations (Tanner et al., 1998; Benner et al., 2010; Wolf et al., 2011; Dalling et al., 2016a). The prominent direct and indirect effects of PC1 and PC2 on productivity suggest that all three nutrient components (N, P and base cations) play roles in the limitation of forest productivity in the study regions.

A high net N mineralization rate positively influenced WP in the merged dataset, but the indirect effect through AGB dominated. The large difference in N mineralization rates between the two transects with high values on the predominantly volcanic soils in the Napo region but low values on the non-volcanic soils of the Loja region probably explains also the considerably higher AGB and consequently WP in the Napo transect as compared to the Loja transect (Figure 2). The trees in the less fertile Loja transect most likely allocate a higher proportion of their photosynthates to root production and to root symbionts (Vicca et al., 2012; Doughty et al., 2017), which must reduce wood production. The availability of base cations and soil acidity influenced productivity in both models only indirectly, mainly through an effect on WSG (higher wood density on acidic, base-poor soils).

The PCAs also showed that the three main nutrient categories (P, N, base cations) varied more or less independently from each other across the plots. Moreover, their relative importance varied between the Loja and Napo data sets, suggesting that soil nutrient limitation of forest productivity is depending more on region, bedrock type and soil age than on elevation. The different paths from soil nutrients to productivity and the weak correlations among P_{av}, N_{min} and base cations across our data set imply that no single nutrient element can serve as a good indicator of overall nutrient availability or soil fertility in the study regions. This is also valid for pH, which showed the tightest relation to $CaKMg_{ex}$ (Loja transect) or organic layer depth (merged transects), but weaker or no association to P_{av}, N_{min} and soil C/N ratio. Soil fertility assessments in Andean montane forests should consider N, P and basic cations, when forest productivity shall be related to soil fertility.

Various studies have identified WSG as a good predictor of the diameter increment of tropical trees, and high WSG has been linked to low aboveground productivity in tropical lowland forests (Malhi et al., 2004; Poorter et al., 2008; Finegan et al., 2015). In the Ecuadorian Andes, the negative effect of average WSG on productivity was as strong as the positive biomass (AGB) influence, suggesting that negative edaphic effects on productivity, notably high soil acidity and low availability of basic cations, are exerted in part indirectly through an increase in wood specific gravity (Unger et al., 2012). Moreover, our data support a causal link from higher N availability through lower WSG to higher productivity, which is suggested by N fertilization experiments (Jozsa & Brix, 1989) and a negative correlation between wood density and soil fertility in continent-wide wood property analyses (Chave et al., 2009).

Unexpected is the insignificant effect of LAI on WP in both transects, visible in the exclusion of leaf area from the models. This is difficult to reconcile with the fact that canopy carbon gain depends on the amount of intercepted light and that the LAI-productivity relationship is usually tight in forests (Reich 2009). A possible explanation could be that LAI measurements with the LAI2000 Canopy Analyzer tend to underestimate true leaf area in complex canopies with abundant leaf clumping (Moser et al., 2007), the effect of which likely is greater at lower elevation where LAI is higher (Unger et al., 2013). This may have blurred LAI differences between stands differing in productivity.

Tree diversity apparently has only a small influence on productivity in the studied tropical montane forests, even though tree species numbers varied largely across the plots (6-27 species per 0.04 ha) and plot size was small, so that effect should be better visible. A positive diversity effect apparently was confined to the component fine litter production (in the Loja transect), as the effect became more visible when NPP_a (which includes fine litter production) was considered and not wood production alone (Figure 4). A possible explanation of the weak diversity effect is that the species richness in our plots may have been too high to show a positive DPR, as diversity effects on productivity generally are more pronounced at lower species numbers (Tilman et al., 2012).

Our results support our third hypothesis and fit the controversial picture that emerges from the existing studies on the DPR in tropical forests. Chisholm et al. (2013) systematically explored the role of diversity for productivity in natural tropical forests and found only a small absolute effect: When controlling for stem density effects in the 0.04 ha plots, a doubling of species richness corresponded in their study only to a 5% increase in WP on average. This matches findings from more than 100,000 forest plots in the United States, where the predominant DPR was concave-negative in humid climates and primarily non-significant in harsh climates (Fei et al., 2018).

A key finding of our study is that a diversity effect, even if significant, is of minor importance in comparison with other productivity-influencing factors. In our case, it ranged behind effects of elevation (temperature), soil nutrient availability and wood specific gravity. For understanding the controls of forest productivity, it is more important to study the influences of environmental factors and stand structural and functional properties in more detail.

5 Conclusions

From the analysis of more than 80 old-growth forest plots in two highly diverse Andean regions with large geological and topographic heterogeneity, we conclude that the main determinants of aboveground productivity in tropical montane forests are elevation (primarily as a proxy of temperature), nutrient supply and stand structural properties, given non-limiting moisture conditions. Nutrient availability seems to affect productivity not only directly but also indirectly through stand properties and tree diversity has only a small influence on productivity. This finding is of practical relevance, as our analysis addresses spatial scales relevant for old-growth forest conservation and management.

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Appendix A: Study sites and plots

Figure A1. Map showing the location of the two study sites in Ecuador.

Appendix B: PCAs of soil properties

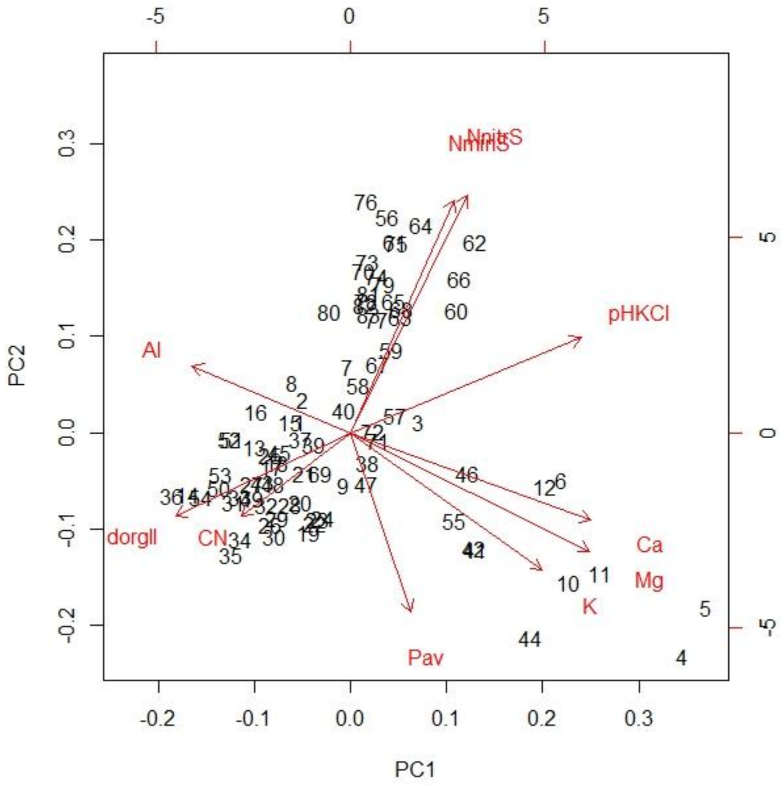

Figure B1. Principal component analysis of the soil properties of 83 study plots (Loja transect and Napo transect), PC1 and PC2 explained 37.4% and 26.1% of variance, respectively.

Table B1. Factor loadings of the variables in the PCA (Figure B1).

Variable	PC1	PC2
org. layer depth	-0.319	-0.182
pH KCl	0.421	0.208
K	0.349	-0.300
Mg	0.436	-0.258
Ca	0.438	-0.192
Al	-0.289	0.146
CN	-0.199	-0.181
Pav	0.111	-0.390
NminS	0.189	0.507
NnitrS	0.212	0.517

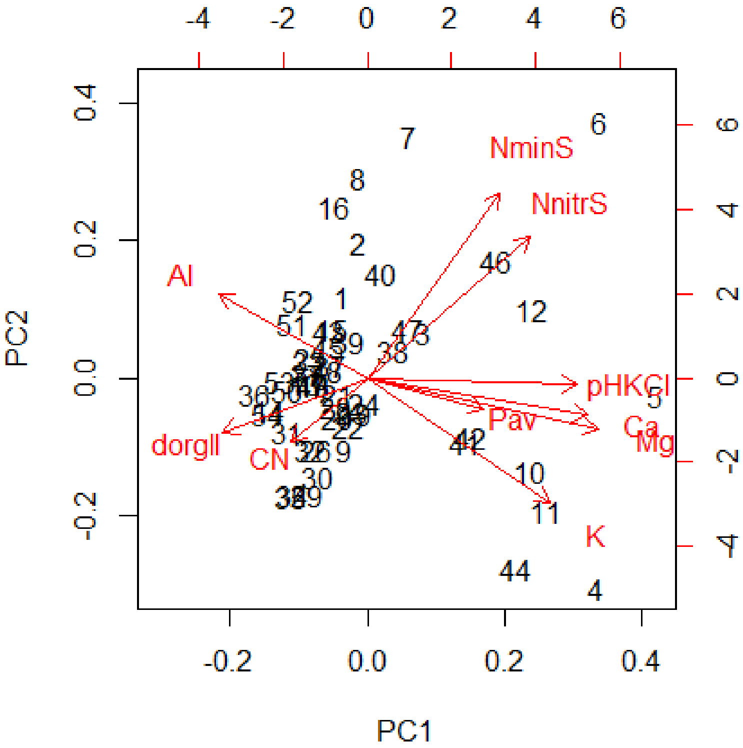

Figure B2. Principal component analysis of the soil properties of 54 study plots of the Loja transect, PC1 and PC2 explained 46.9% and 14.6% of variance, respectively.

Table B2. Factor loadings of the variables in the PCA (Figure B2).

Variable	PC1	PC2
org. layer depth	-0.270	-0.182
pH KCl	0.392	-0.020
K	0.343	-0.419
Mg	0.431	-0.173
Ca	0.413	-0.125
Al	-0.278	0.280
CN	-0.144	-0.214
Pav	0.218	-0.104
NminS	0.248	0.621
NnitrS	0.305	0.475

Data availability

All relevant data are within the paper and its appendices.

Supplement

Supplement S1: Plot forest parameters

Supplement S2: Plot soil parameters

Author contribution

JH and CL designed the study, JH performed research and analyzed the data, JH and CL wrote the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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