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FORUM

Driving factors of forest growth: a reply to Ferry *et al.* (2012)

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Summary

1. In a recent paper, we analysed the effects of climate, soil and logging disturbance on tree and forest growth (Toledo *et al*. 2011a). We took advantage of one of the largest data sets in the Neotropics, consisting of 165 1-ha plots and over 62 000 trees distributed over an area of *c*. 160 000 km^2, across large environmental gradients in lowland Bolivia. The main findings were that climate was the strongest driver of spatial variation in tree growth, whereas soils had only a modest effect on growth and that the effect of logging disappeared after a few years.

2. Ferry *et al*. (2012) suggest that we underestimated the disturbance effects on growth because of a supposedly wrong coding of Time After Logging (TAL) for unlogged plots. Although we have good biological reasons why we coded TAL like we did, we checked Ferry *et al*.'s suggestions for recoding and found no differences in variables that significantly explained tree and forest growth. We agree, however, that for future research, it is important to go beyond simple descriptors such as time after logging and basal area logged, to better describe the variation in logging impact found in areas under forest management.

3. Ferry *et al*. claim that we did not define basal area growth properly. We believe this is a semantic issue, as we clearly defined basal area growth as the net change in basal area. This net basal area change in Bolivian forests is indeed relatively high compared to other studies, which may be attributed to the higher soil fertility and biogeographic differences in species composition and their traits.

4. *Synthesis*. Many apparent discrepancies in the ecological literature arise because tropical forest ecologists tend to see the world from the perspective of their 'own' forest (despite clear biogeographic differences) and try to capture the same ecological processes using different variables and measurement protocols. To advance our understanding and go beyond single-case studies, we need to assemble large databases, quantify forest dynamics and disturbances in similar ways, be aware of differences among forests and analyse environmental dose–response curves.

Key-words: Bolivia, climate, disturbance, logging, plant-climate interactions, tree growth, tropical forest

Introduction

In a recent paper, we analysed the effects of climate, soil and logging disturbance on tree and forest growth (Toledo *et al.* 2011a). We took advantage of one of the largest data sets in the Neotropics, consisting of 165 1-ha plots and over 62 000 trees distributed over an area of *c.* 160 000 km^2, across large environmental gradients in lowland Bolivia. The main findings were that climate was the strongest driver of spatial variation in tree growth, whereas soils had only a modest effect on growth, and the effect of logging was apparently temporary. In their commentary, Ferry and co-workers focused on some potential methodological and conceptual constraints they thought would jeopardize the generality of our conclusions. Their main concerns were related to (i) the impact of logging on growth rates and specifically the use of the variable 'time after logging', (ii) the effect of species composition on growth rates, (iii) the use of 'short' measurement periods and (iv) the calculation of stand basal area growth. Our main research question ('what are the effects of climate, soils and disturbance

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on lowland tropical forest growth?') is of wide importance, for both theoretical and applied reasons, which has also clearly been underlined by Ferry *et al.* Despite the vast area covered by tropical lowland forests, there is surprisingly little data available on how they respond at larger spatial scales, which warrants further discussion and research. Ferry *et al.* critically evaluated our study and provided suggestions for its improvement. Without doubt, there is a trade-off between the scale and the precision of the data analysed and the questions addressed. We opted for the larger scale because it allows novel questions to be addressed and for wider generalization of the results. Some of Ferry *et al.*'s suggestions concern relevant but different questions that require more detailed analyses and different papers. Some aspects have been dealt with already in companion papers on the effect of soil and climate on forest structure, species composition and distribution (Toledo *et al.* 2011b,c, 2012). Here, we will respond to their major concerns and provide suggestions for advancing our scientific understanding with similar kinds of studies.

How to evaluate the impact of logging on growth rate?

Ferry *et al.* suggest that disturbance effects might be much more important for forest growth than our results show. We analysed the effect of logging disturbance, which we quantified in various ways [logging presence, logging impact, basal area removed and the amount of time passed after logging (TAL)]. We found that growth rates increased just after logging, but that this disturbance effect disappeared after several years. Ferry *et al.* suggest that we 'severely' underestimated the disturbance effects on average diameter growth because of a supposedly wrong coding of TAL. Where we set the TAL of unlogged plots to zero, Ferry *et al.* recommend setting the TAL of unlogged plots to a very high number of years (thus indicating an old-growth forest). Although such an approach has indeed been used in several studies of secondary forest succession (e.g. Peña-Claros 2003; Lebrija-Trejos *et al.* 2010), we did not use it here for two reasons: First, properly modelling forest responses to disturbance require the background growth rates before release. We argue, therefore, that old-growth forest is the situation just before logging, and TAL should be a very small negative value, which we rounded-off to 0. Not including these background growth rates set at a time close to zero, erroneously, suggests that directly after logging the growth rates are very high, whereas trees in fact respond with a time-lag to the new high irradiance conditions. Second, determining the age of a mature forest is an educated guess, and this value would also have to vary according to the forest's location along the fertility and climate gradient, given that forests differ in their resilience to disturbance (e.g. Dauber, Fredericksen & Peña-Claros 2005). Nonetheless, we have checked Ferry *et al.*'s suggestion by carrying out a backward multiple regression analysis with average diameter growth as the dependent variable, including the climatic and soil variables, and TAL as a simple factor. For unlogged forests, we used a TAL of −0.001, 100 and 200 years, respectively. When using a TAL of −0.001, the amount of explained variation, significance level for TAL and standardized regression coefficient were identical to those of Toledo *et al.* (2011a), where a TAL of 0 was used for unlogged plots. When using a TAL of 100 or 200 years, it was excluded from the regression model, suggesting that the use of a longer TAL for unlogged plots does not improve the regression model. We have also analysed the logged plots only and looked at their relationship with TAL, without considering the potential confounding effect of climatic variables and soil variables. The relationship between diameter growth rate and TAL can be equally well described by a logarithmic, power or exponential relationship (r^2 ranges from 0.269 to 0.223, d.f. = 85, $P < 0.001$ in all three cases). Hence, TAL alone can describe a reasonable amount of variation in growth. The logarithmic relationship (which had the highest r^2) indicates that diameter growth is equal to 0.465–0.111 ln (TAL). Based on this relationship, diameter growth rates 1 year after logging are predicted to be as high as 0.47 cm year^{-1}, whereas 6 years after logging, this is 0.27 cm year^{-1}, which is very similar compared to growth rates in non-logged plots (their average diameter growth rate = 0.28 cm year^{-1} ± 0.08). Hence, the growth-stimulating effect of logging disappears in these forests after a few years. We do agree, of course, that TAL is unlikely to be linear, nor independent of logging impact. We therefore used three additional variables to better describe the logging impact that each specific plot was subjected to (see table 2 in Toledo *et al.* 2011a). We believe this is crucial because of the large variation in conditions found in logged areas, which may vary from plots in a matrix of logged forests, but without logging inside them, to plots that have been heavily logged. Consequently, we suggest that future studies quantifying the effects of logging should better describe the variation in logging impact found in areas under forest management and go beyond simple descriptors such as time after logging and basal area logged to include additional variables such as total area in gaps and skid trails, total basal area damaged during logging operations and canopy openness.

Ferry *et al.* propose a new formula to calculate the decreasing effect of logging through time. Such an approach may be helpful as there is very little data in the literature indicating the time to return to baseline growth rates. This is a relevant question not only when assessing the impact of logging on growth rates but also to fine-tune the timing of silvicultural treatment application to enhance growth rates (e.g. Silva *et al.* 1995; Gourlet-Fleury *et al.* 2005). Current discussions on REDD+ schemes will also benefit from such information, as forests that grow faster in terms of basal area or biomass recover more rapidly to pre-disturbance characteristics than forests with low growth rates.

Given that tree growth rates are correlated to soil and climatic conditions (Baker, Burslem & Swaine 2003; Toledo *et al.* 2011a) and management practices (e.g. logging intensity; de Graaf, Poels & Van Rompaey 1999; Finegan *et al.* 1999; Peña-Claros *et al.* 2008; Villegas *et al.* 2009), we expect a large variation in the time required to return to pre-logging growth rates. We were, therefore, not surprised that French Guianan forests take more time to return to unlogged growth rates

(15 years) than Bolivian forests (6 years). The plots for which Ferry *et al.* present their calculations are most likely the Paracou plots, which have been more intensively logged (5.8–41.7 trees ha^{-1}, depending on treatment, Gourlet-Fleury *et al.* 2004; Blanc *et al.* 2009) than ours (1–13 trees ha^{-1}). The Paracou plots have also received heavy silvicultural treatments (on average 16.6 trees ha^{-1} were thinned, compared to no additional silvicultural treatments applied in the database we used), and the forests on the Guyana shield are known to have slower dynamics (Lewis *et al.* 2004; ter Steege *et al.* 2006; Hoorn *et al.* 2010).

Many apparent discrepancies arise in the ecological literature because tropical forest ecologists tend to see the world from the perspective of the forest in which they work (despite clear biogeographic differences, for example ter Steege *et al.* 2006) and try to capture the same ecological processes using different variables and measurement protocols. To advance understanding and go beyond single case studies, large databases need to be assembled; forests and disturbances (including human interferences and management actions) need to be quantified in similar ways; studies should recognize that forests are different, and should analyse environmental response curves. The forest plot networks (e.g. CTFS, RAINFOR, ATDN), the suggestions made by Ferry *et al.* and our work provide important steps towards reaching this goal.

The effect of floristic composition on growth rates

Ferry *et al.* argued that we underestimated the growth-stimulating effect of logging because our calculation of diameter growth rates only included trees that were alive during the whole survey period, and hence, did not include the effect of fast-growing pioneers that recruited later in the plot. We fully recognize that floristic changes are likely to occur after logging and that it would have been more appropriate to account for this in our analysis. However, the increase in pioneer abundance will take some time as, first, there is a response time-lag after logging, and second, the minimum diameter at breast height of evaluated trees was 10 cm. Consequently, we expect that the proportion of pioneer trees among the newly recruited individuals (diameter > 10 cm) will be low because, despite their fast growth rates, they may have not had sufficient time to establish from seed and attain 10 cm d.b.h. (the evaluation period after logging ranged from 2 to 11 years; mean = 4.3, median = 3.9). Additionally, to take into account the effect of floristic composition changes on growth rates, it is necessary to have more than two censuses (which was lacking for 16% of our plots), have longer monitoring periods with shorter intervals and have more precise taxonomic identification of several of the plant species (which is lacking for most of the plots).

For a selection of the plots (that are part of the Long-term Silvicultural Research Program; Peña-Claros *et al.* 2008), we have data available that fulfil the abovementioned requirements (almost 10 years of data, censuses every 1–2 years). Using this database, G. Carreño-Rocabado (unpublished data) analysed the effect of logging on functional diversity 8 years after logging. Indeed, she found that recruits from logged areas tend to have more acquisitive characteristics than recruits from unlogged areas. Acquisitive recruit characteristics, however, increased with logging intensity (i.e. higher logging intensity plus application of silvicultural treatments). Therefore, we expect that the contribution of newly recruited pioneer trees to overall diameter growth rates will vary with management intensity and will certainly have a smaller effect in areas logged at low intensities (as in the plots included in this study). Consequently, although we fully agree with the argument of Ferry *et al.* and with the need to explore these questions further, we are confident that although we did not take the relatively few new pioneer recruits into account, this would have led to a small underestimation of changes in diameter growth after logging.

Shorter-term growth rates versus long-term climate data

Ferry *et al.* are concerned that the average monitoring period is 4.3 years, which would lead to reduced precision of tree growth estimates and increased sensitivity to climatic events. Although tropical trees are known to grow slowly, the average diameter growth rate in our study (0.31 cm year^{-1}) is sufficiently fast to be precisely quantified over the monitoring period (with an average diameter increase of 1.33 cm over the monitoring period). Moreover, average diameter growth rates and stand basal area growth rates were calculated per 1-ha plot, using growth data of on average 378 trees per plot. Hence, small measurement errors may lead to under- or over-estimates of growth rates of individual trees, but they are likely to cancel out at the stand level. Similarly, by using growth rates over 4.3 years, inter-annual variation in growth because of climatic variation is smoothed out.

We related mid-term growth to longer-term climatic conditions (30 years), based on the rationale that with longer-term data both the average growth and average climate can be quantified more precisely than by using data from individual years. Ideally, we would have used year to year variation in climate and in forest growth. However, such data are not available for Bolivia, neither for climate nor for forests. Few weather stations occur in the forest area and making interpolations for each year separately would also have increased the biases and errors. In contrast to what Ferry *et al.* suggest, we did not want to evaluate climate change effects, but we wanted to evaluate the effect of spatial variation in climate on spatial variation in growth. Based on these spatial results, we speculated on the possible consequences of climate change, as explicitly stated in both the discussion and the summary of our paper. This assumes that one can substitute space for time. Relating temporal variation in climate to temporal variation in growth (e.g. Clark, Clark & Oberbauer 2010) would provide an initial indication of the validity of these predictions. We are currently analysing these data for several sites with sufficient long-term data, measured at 1–2 year intervals.

Evaluating basal area growth

Ferry *et al.* claim that we made a mistake in how we defined basal area growth. In our methods, we clearly define basal area growth rate *at the stand level* (hereafter BAGRstand) as the *net* yearly basal area change per plot, which includes the effects of growth, mortality and recruitment. Ferry *et al.* suggest that we should have used the expression 'basal area change', following Lewis *et al.* (2004). Clearly, this is a semantic issue.

Ferry *et al.* are right in pointing to the erroneous comparison that we made of our BAGRstand with the 'basal area growth rate' values of Lewis *et al.* (2004) as the latter refer to the basal area growth of surviving individuals plus the basal area of the recruited trees. That value did not include the basal area lost because of trees dying during the monitoring period, whereas our BAGRstand values did. The correct comparison of our estimates of stand level net change in basal area (BAGRstand) with the corresponding values of Lewis *et al.* (2004) shows higher basal area change in Bolivian forests during our study. This discrepancy may be caused by the higher soil fertility of Bolivian (and other western Amazonian) forests and more fast-growing species with low-density wood, leading to faster stand-level growth rates than eastern Amazonian or Guianan forests (ter Steege *et al.* 2006). Lewis *et al.* (2004) also distinguished fast and slow forests.

Ferry *et al.* implicitly attributed the higher basal area growth found in our study to 'secondarization of unlogged forests' and measurement errors. Unlike their suggestion, our unlogged plots were definitely unlogged, or at least there was no evidence of human disturbances for the last few decades. Plots logged in the past decades (mostly for *Swietenia macrophylla,* nine plots) were included in our analysis as logged forests, even when the logging occurred in the surrounding matrix.

Ferry *et al.* suggested that another possible bias could be that 'many different teams' have taken the field measurements. This is unavoidable when working with large databases such as this one. We were as careful as possible: (i) part of the plots was established by or with support of the BOLFOR project that provided training and technical assistance, (ii) between 2001 and 2003, all 1-ha plots in areas under forest management in the country were visited by BOLFOR technicians, data were standardized, a protocol was defined, and additional plots were established, (iii) A total of 117 ha of permanent plots were identified as plots in good conditions for further monitoring (representing only about 60% of the plots that were established in areas under forest management; Dauber, Fredericksen & Peña-Claros 2005), (iv) new plots were established by IBIF staff, (v) part of the 1-ha plots included in the database area part of the Long-Term Silvicultural Research Program, which are measured by largely the same team, (vi) for the present study, M. Toledo personally visited 220 1-ha plots contained in the database to collect soil samples, evaluate logging impact, assess plot condition and re-measured 55% of the plots. Plots with a different layout and problems with data management or establishment were not included in any analyses using this database (Toledo *et al.* 2011a,b,c, 2012). We are aware that continued database improvement is needed (e.g. species identification, measurement of large diameters), as is the case with all large databases, but we have been as conservative as possible when deciding which plots to include in the analyses. Therefore, we are convinced that measurement error is not a main factor explaining the differences in basal growth rate found in our study.

Within the frame of our study, we have taken care to consider potential problems, and although we acknowledge that we were not able to solve all of them, we are convinced that our message (climate is a stronger driver of forest growth than soil or disturbance) firmly holds for Bolivian lowland forests. The Bolivian lowland forests cover the drier end of the rainfall gradient (average: 1100–2200 mm year^{-1}), and water availability is clearly a more limiting factor here than for forests at the wetter part of the rainfall gradient, where nutrient availability might become a limiting factor for growth. We did not include extreme soils such as limestone karsts, granitic outcrops and white sands in our study, because they are relatively rare in our region. However, inclusion of such soils would extend the sampled soil gradient and may lead to different results. Finally, to evaluate whether our results can be extended over the wider tropical forest zone, it would be important to join plot networks, bring together data sets from different regions, extend the geographic range and hence the range in environmental conditions and logging intensity, and analyse environmental response curves. This would shed further light on these issues and substantially advance the field of comparative forest ecology.

We thank Ferry *et al.* for their thoughtful comments and suggestions, which do not only address possible biases in our study but also have a more general application. In this reply, we not only answered the issues they raised, but we also evaluated these in the light of the recently increased attention to merged large comparative databases. We are convinced that the scientific community will need to make additional steps in that direction to solve some of these issues.

References

Baker, T.R., Burslem, D.F.R.P. & Swaine, M.D. (2003) Associations between tree growth, soil fertility and water availability at local and regional scales in Ghanaian tropical rain forest. *Journal of Tropical Ecology*, **19**, 109–125.

Blanc, L., Echard, M., Herault, B., Bonal, D., Marcon, E., Chave, J. & Baraloto, C. (2009) Dynamics of aboveground carbon stocks in a selectively logged tropical forest. *Ecological Applications*, **19**, 1397–1404.

Clark, D.B., Clark, D.A. & Oberbauer, S.F. (2010) Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO_2. *Global Change Biology*, **16**, 747–759.

Dauber, E., Fredericksen, T.S. & Peña-Claros, M. (2005) Sustainability of timber harvesting in Bolivian tropical forest. *Forest Ecology and Management*, **214**, 294–304.

Ferry, B., Bontemps, J.-D., Blanc, L. & Baraloto, C. (2012) Is climate a stronger driver of tree growth than disturbance? A comment on Toledo *et al.* (2011). *Journal of Ecology*, doi: 10.1111/j.1365-2745.2011.01895.x.

Finegan, B., Camacho, M. & Zamora, N. (1999) Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest. *Forest Ecology and Management*, **121**, 159–176.

Gourlet-Fleury, S., Favrichon, V., Schmitt, L. & Petronelli, P. (2004) Consequences of silvicultural treatments on stand dynamics at Paracou. *Ecology and Management of a Neotropical Rainforest: Lessons Drawn from Paracou,* *A Long-Term Experimental Research Site in French Guiana*, (eds S. Gourlet-Fleury, J.-M. Guehl & O. Laroussinie), pp. 254–280. Elsevier, Paris.

Gourlet-Fleury, S., Cornu, G., Jésel, S., Dessard, H., Jourget, J.-G., Blanc, L. & Picard, N. (2005) Using models to predict recovery and assess tree species vulnerability in logged tropical forests: a case study from French Guiana. *Forest Ecology and Management*, **209**, 69–85.

de Graaf, N.R., Poels, R.L.H. & Van Rompaey, R.S.A.R. (1999) Effect of silvicultural treatment on growth and mortality of rainforest in Surinam over long periods. *Forest Ecology and Management*, **124**, 123–135.

Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J. *et al.* (2010) Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, **330**, 927–931.

Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F. & Poorter, L. (2010) Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, **91**, 386–398.

Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S. *et al.* (2004) Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **359**, 421–436.

Peña-Claros, M. (2003) Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. *Biotropica*, **35**, 450–461.

Peña-Claros, M., Fredericksen, T.S., Licona, J.C., Blate, G.M., Choque, U., Leaño, C., Alarcón, A., Mostacedo, B., Pariona, W., Villegas, Z. & Putz, F.E. (2008) Beyond reduced-impact logging: silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management*, **256**, 1458–1467.

Silva, J.N.M., de Carvalho, J.O.P., Lopes, J., Do, C.A., de Almeida, B.F., Costa, D.H.M., de Oliveira, L.C., Vanclay, J.K. & Skovsgaard, J.P. (1995) Growth and yield of a tropical rain forest in the Brazilian Amazon 13 years after logging. *Forest Ecology and Management*, **71**, 267–274.

ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.-.F., Prévost, M.-.F., Spichiger, R., Castellanos, C., von Hildebrand, P. & Vasquez, R. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, **443**, 444–447..

Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leaño, C., Licona, J.C., Llanque, O., Vroomans, V., Zuidema, P. & Bongers, F. (2011a) Climate is a stronger driver of tree and forest growth rates than soil and disturbance. *Journal of Ecology*, **99**, 254–264.

Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Chuviña, J., Leaño, C., Licona, J.C., ter Steege, H. & Bongers, F. (2011b) Patterns and determinants of floristic variation across lowland forests of Bolivia. *Biotropica*, **43**, 405–413.

Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leaño, C., Licona, J.C. & Bongers, F. (2011c) Climate and soil drive forest structure in Bolivian lowland forests. *Journal of Tropical Ecology*, **27**, 333–345.

Toledo, M., Peña-Claros, M., Bongers, F., Alarcón, A., Balcázar, J., Chuviña, J., Leaño, C., Licona, J.C. & Poorter, L. (2012) Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *Journal of Ecology*, **100**, 253–263.

Villegas, Z., Peña-Claros, M., Mostacedo, B., Alarcón, A., Licona, J.C., Leaño, C., Pariona, W. & Choque, U. (2009) Silvicultural treatments enhance growth rates of future crop trees in a tropical dry forest. *Forest Ecology and Management*, **258**, 971–977.

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