

1. BIODIVERSITY AND CARBON FLUX IN TROPICAL ECOSYSTEMS

BIODIVERSITY INCREASES THE RESILIENCE OF TROPICAL FORESTS TO CLIMATE CHANGE: IMPLICATIONS FOR CONSERVATION POLICY

Tim Baker, School of Geography
University of Leeds, UK

ABSTRACT

Understanding how biodiversity affects ecosystem functions such as carbon storage and productivity is a major research field with potentially important implications for conservation policy. However, studies of the links between biodiversity and ecosystem function (BEF) in carbon-rich and diverse moist tropical forests are only just emerging. Here, I therefore review the findings of large-scale, field-based and modelling studies of BEF in tropical forests and identify how the results might best inform conservation policy.

BEF relationships comprise the effect of variation in both *composition* (the identity and traits of different species) and *diversity* (the number of species and their relative abundances) among sites, on processes such as carbon storage and productivity. Variation in the tree *composition* of tropical forests has an important role in determining aboveground carbon stocks and productivity at continental and pan-tropical scales. These relationships are mediated by variation in community-level average trait values for wood density and maximum height. The presence of species with different traits also increases the resilience of the carbon stocks of tropical forests to environmental changes, such as drought, over decadal and centennial time-scales. However, tree *diversity* is less strongly related to patterns of carbon cycling than variation in composition and may only be important at small, sub-hectare, spatial scales. These findings suggest that the strongest justification for conserving the biodiversity of tropical forests in terms of carbon cycling is that higher biodiversity increases the resilience of forest structure and biomass to environmental change. More practically, this view suggests that connected networks of protected areas that encompass wide environmental gradients will be most valuable for maintaining ecosystem function under climate change by allowing shifts in tree species distributions. Although the idea of such ecological corridors is not a new policy measure, the new evidence on how biodiversity promotes the resilience of carbon stocks to climate change may help to promote conservation amid the shrinking opportunities for protecting intact tropical forest.

INTRODUCTION

The intensive search for convincing relationships between biodiversity and ecosystem function over the last twenty five years has been stimulated by the desire to understand the impacts of species loss due to human activities, including climate change, on the services that ecosystems provide (Chapin et al., 1998, Schulze and Mooney, 1994). The findings of experimental studies, for example, indicate that extinction can lead to reductions in the delivery of ecosystem services that are similar to the direct effect of many pollutants (Hooper et al., 2012). However, BEF research in the highest diversity terrestrial ecosystem and arguably the greatest global conservation priority - tropical forests - remains scarce. Studies at landscape scales, which are most relevant to informing management decisions, are particularly rare: for example, a previous policy-facing review of BEF relationships in forest ecosystems contained no large-scale, observational studies from tropical forests of how biodiversity affects ecosystem function or resilience (Thompson et al., 2009). As a result, the integration of BEF relationships within arguments for conservation in the tropics is poorly articulated. The purpose of this chapter is to review recent studies concerning the importance of biodiversity for ecosystem function in tropical forests and reflect on the implications for future research and conservation policy. I emphasise large-scale, field-based

and modelling BEF studies, which have the most relevance for informing management decisions, as they explore the role of biodiversity in the context of wide spatial and temporal environmental gradients. My focus is on aboveground carbon biomass (AGB) and wood productivity as ecosystem functions, as they are the cornerstone of efforts to generate payments for ecosystem services to support conservation in tropical forests (Baker et al., 2010).

HOW BIODIVERSITY PROMOTES ECOSYSTEM FUNCTION IN TROPICAL FORESTS

BEF relationships comprise the effect of variation in both *composition* (the identity and traits of different species) and *diversity* (the number of species and their relative abundances) among sites, on processes such as carbon storage and productivity. Variation in composition undoubtedly has an important role for determining spatial variation in carbon stocks and aboveground wood production at both continental and pan-tropical scales (Baker et al., 2004, Banin et al., 2014). These relationships are mediated by variation in community-level average trait values for wood density and maximum height among forests. For example, above ground carbon stocks are approximately 15 % higher in forest plots in central compared to western Amazonia, because they comprise species that have denser wood which contains more carbon per unit volume (Baker et al., 2004). Variation in the abundance of species which have different allometric relationships – achieve greater or lesser height for a given diameter - also affects aboveground carbon stocks. The clearest example of this mechanism is found in forests in SE Asia where dominance of forests by very tall-statured individuals of the Dipterocarpaceae (Banin et al., 2012) leads to wood productivity which is 49 % higher than forests growing in similar environmental conditions in Amazonia (Banin et al., 2014). Less well-appreciated is that this process is also important within some tropical forest regions: many upland forests on clay-rich soils in the Guianas in South America are dominated by a group of caesalpinoid legumes which achieve higher statures than many other species found in Amazonia (ter Steege et al., 2006). The forests in this region therefore have high canopy heights (Feldpausch et al., 2011), and this distinctive composition is one reason for the particularly high (>400 Mg ha⁻¹) AGB values in this region (Feldpausch et al., 2012, Johnson et al., 2016). Finally, as variation in the maximum diameter that different species attain is strongly related to their contribution to forest biomass and woody productivity (Fauset et al., 2015), the abundance of tree species and individuals that reach large diameters is strongly related to variation in AGB (Baker et al., 2004, Slik et al., 2013). As a result of all these patterns, it is simple to demonstrate that changes in species composition, particularly losses of large diameter, tall-statured, heavy wooded species, can lead to substantial reductions in aboveground biomass of tropical forests (e.g. Bunker et al., 2005): species composition matters for patterns of biomass and woody productivity in tropical forests.

The underlying reasons for the variation in species composition that leads to such differences in ecosystem structure and function include both current ecological processes, as well as the legacy of historical events. For example, differences in mean wood density between western and central Amazonian forests is associated with underlying differences in soil physical and chemical properties that favour either fast-growing species with high mortality rates and low wood density, or slow-growing species with low mortality rates and high wood density (Baker et al., 2004, Quesada et al., 2012, Baker et al., 2014). However, variation in the distribution of species with different height diameter allometries may be due to the legacy of historical processes that have resulted in the dominance of certain families in certain tropical regions (Banin et al., 2012, Johnson et al., 2016).

A second way in which biodiversity is related to ecosystem service delivery within tropical forests is by increasing their resilience to environmental change. Over decadal timescales, resilience (the ability of ecosystem function to resist and bounce back from perturbation; Oliver et al., 2015) relies on the presence of a wide range of species with different characteristics within the regional species pool. Larger species pools are more likely to contain taxa that have adaptations that allow them to persist and thrive as a result of changing environmental conditions. A simple example is how Amazonian forests transitioned to an alternative, but still tree-dominated, state during the last glacial maximum despite cooler and drier conditions (Colinvaux et al., 2000). Such resilience has also been demonstrated in tropical forests over recent decades (Fauset et al., 2012): in Ghana, a long term reduction in rainfall since the 1970s has led to an increase in the abundance of species characteristic of drier tropical forests, and the AGB of these forests has actually increased during the same period (Fig. 1; Fauset et al., 2012). In this case, alterations in species composition have contributed to maintaining a stable forest structure, despite a shift in climate. Similarly, modelling studies have demonstrated how greater diversity could help to maintain high carbon stocks in the face of predicted climate change over coming centuries

(Sakschewski et al., 2016). Of course, the resilience that biodiversity offers for maintaining forests in the face of climate change should not be overstated. Substantial changes in climate, or strong interactions between climate change with direct human degradation will doubtless cause major biome shifts: areas at the fringe of Amazonia became open habitats during the last glacial maximum (Anhuf et al., 2006) and strong drought in 1982/3 in Ghana coupled with human-caused fire, caused the savannisation of large areas of forest (Swaine et al., 1997). However, biodiversity can clearly increase the resilience of tropical forest structure to environmental change.

WHERE BIODIVERSITY HAS LIMITED IMPORTANCE FOR ECOSYSTEM FUNCTION IN TROPICAL FORESTS

In contrast to the importance of composition, variation in diversity is a weaker correlate of aboveground carbon stocks in tropical forests. An analysis of 360, one hectare forest plots from all three tropical continents that accounted for variation in environmental factors and spatial auto-correlation, indicated that there was no significant relationship between diversity and carbon stocks across tropical forests (Sullivan et al., in review). This result contrasts with prior studies of 58 sites in the neotropics (Poorter et al., 2015), and 59, one hectare plots across the tropics (Cavanaugh et al., 2014) which hinted at a positive relationship between diversity and AGB, using similar plot sizes. However, the larger scale study indicates that the results at a one hectare scale from these previous analyses cannot be generalised across the moist tropical forest biome (Sullivan et al., in review). In contrast, positive relationships between diversity and AGB are more consistently significant at small scales (e.g. 0.1 ha plots, Poorter et al. (2015); 0.04 ha plots Sullivan et al. (in review)). These relationships are consistent with how mechanisms such as selection effects and niche differentiation might operate (Sullivan et al., in review, Poorter et al., 2015). However, as these relationships have only been detected at very small scales where there is little environmental variation and few species interact, it is unlikely that these mechanisms are important determinants of variation in biomass at landscape and regional scales.

The effect of biodiversity on forest productivity has been less well studied than relationships with AGB. At large spatial scales, variation in composition may be an important control of productivity, in addition to the effect of environmental variables, such as rainfall and soil physical and chemical properties, which control tree growth (Quesada et al., 2012, Baker et al., 2003). However, the importance of environmental variables may be far stronger than any effect of composition and/or diversity. For example, variation in the functional composition of western and central Amazon forests does not cause the higher productivity of western Amazon forests: within the same functional group of tree, higher productivity is observed in western compared to central Amazon forests, suggesting that environmental factors play a more important role than variation in composition (Baker et al., 2009).

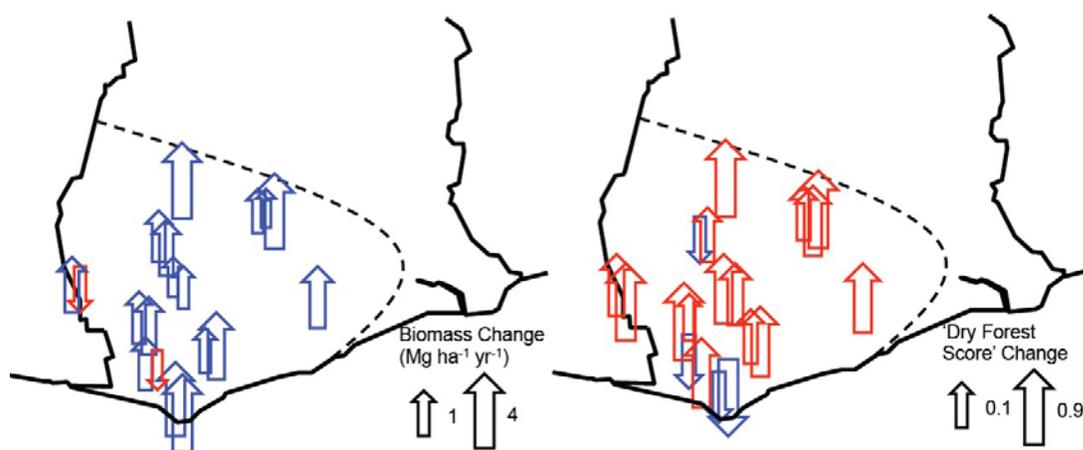


Figure 1: Changes in (left) aboveground biomass and (right) tree species composition in relation to the abundance of species with preferences for wet or dry forests, quantified as 'Dry Forest Score' (Fauset et al., 2012), over a 20 year period in 19 intact forest plots in Ghana. For most plots, aboveground biomass increased and forest composition shifted to favour more drought-tolerant species, shown by the increase in 'Dry Forest Score' over time. Redrawn from Fauset et al. (2012).

OPPORTUNITIES FOR STUDYING BIODIVERSITY AND ECOSYSTEM FUNCTION RELATIONSHIPS IN TROPICAL FORESTS

Current knowledge of BEF relationships in intact tropical forests demonstrates how variation in composition defines spatial patterns of carbon stocks and the importance of biodiversity for the resilience of these ecosystems. However, there are many opportunities for further research. As noted above, studies of the effect of biodiversity on productivity are largely lacking in tropical forests. In addition, the role of phylogenetic diversity for determining ecosystem function (Cadotte, 2013) may reveal useful relationships in ecosystems where high diversity precludes easy measurement of the functional properties of thousands of species. In general terms, there is also much work to be done understanding the species, community and landscape-scale mechanisms that underpin the role of biodiversity in augmenting the resilience of ecosystem function in tropical forests (Oliver et al., 2015). For example, we know that rare species in tropical forests may have unusual combinations of functional traits, but we do not understand how that links to their performance and therefore their overall importance for ecosystem function and resilience (Mouillot et al., 2013). In particular, we need to understand the nature (e.g. which ecosystem functions are most resilient and which are most sensitive?) and limits (e.g. what are the thresholds where biome collapse is unavoidable?) of the resilience that biodiversity affords tropical forests in much more detail. For example, there is compelling evidence for upward altitudinal shifts in species distributions in the Andes as a result of warming temperatures (Feeley et al., 2011, Duque et al., 2015), but we do not know how these shifts are related to changes in forest structure or function. High-quality, standardised forest plot datasets with information on the identity, traits, sizes and population dynamics of tropical trees, linked with measurements using LiDAR and hyperspectral remote sensing technology (e.g. Asner et al., 2015) that provide a landscape-scale perspective, will be essential for understanding the role that biodiversity will play in the future trajectory of ecosystem function in this biome.

BEF AND CONSERVATION IN TROPICAL FORESTS

The first way in which the BEF research described above links to conservation policy is related to the design of carbon-based payments for ecosystem services. This topic has been particularly prominent in debates about the design of REDD+ (Reducing Emissions from Deforestation and Degradation) schemes which aim to reduce carbon emissions from land-use change (Angelsen, 2008). One aspect of the debate is whether biodiversity conservation should be an integral part of carbon-based conservation because there are mechanistic reasons that lead higher biodiversity to generate greater carbon stocks in tropical forests (Poorter et al., 2015). However, the lack of a relationship between diversity and carbon storage among a comprehensive sample of one hectare plots (Sullivan et al., in review) indicates that such mechanisms may, at best, only operate at very small spatial scales. At landscape-scales relevant to conservation, there is therefore no evidence that tropical forest landscapes containing thousands of tree species have higher carbon stocks than landscapes with a few hundred different taxa. A second related aspect of the debate is whether effective biodiversity conservation can be achieved with a carbon-based approach, because spatial patterns of both parameters are broadly correlated rather than because there is a direct mechanistic link between biodiversity and carbon storage (Cavanaugh et al., 2014). However, again, the lack of correlation between diversity and carbon stocks among tropical forests suggests the conservation of carbon and species require, broadly-speaking, independent strategies (Sullivan et al., in review). In general, this finding emphasises the importance of including substantial incentives within carbon-based strategies to optimise the contribution they make to biodiversity conservation (Venter et al., 2009, Grainger et al., 2009, Miles and Kapos, 2008). Overall, the lack of consistent 'win-win' outcomes for both carbon and biodiversity if conservation policy solely focuses on just one of these parameters is exemplified by considering that the most carbon-dense tropical ecosystems in the neotropics – the peatlands of northwest Amazonia – contain some of the least diverse tree communities (Draper et al., 2014, Pitman et al., 2014) and that the remarkable beta diversity of neotropical dry forests is associated with generally low carbon stocks (DRYFLOR, 2016, Becknell et al., 2012). Conservation strategies will need to value carbon and biodiversity independently to protect both of these vegetation types.

A second, perhaps more compelling, way in which BEF research could strengthen conservation policy is through the increased resilience that biodiversity provides for forest structure, and therefore the ecological functions that forests perform, in the face of environmental change. Biodiversity provides this resilience because species can change in abundance depending on changing environmental conditions (Fauset et al., 2012, Sakschewski et al., 2016). Realising this resilience depends on conserving a connected protected area network that encompasses the regional species pool. The idea of connected networks of protected areas is not a new idea; ecological networks and corridors are well established as a key conservation strategy in response to land-use change which can be beneficial for both biodiversity and carbon (Jantz et al., 2014, Bennett and Mulongoy, 2006). The idea that such networks might allow species to persist in the face of the interacting effects of changes in both land-use and climate is also now widely appreciated (Bennett and Mulongoy, 2006, Brodie et al., 2012) and the concept has been influential in the design of a range of specific, large-scale conservation initiatives in tropical forest landscapes such as the Vilcabamba-Amboró corridor in Bolivia and Peru (Bennett and Mulongoy, 2006, Ibisch et al., 2007). However, the idea that *both* biodiversity and carbon conservation is ensured over time by the existence of such networks because biodiversity increases the resilience of carbon stocks to environmental change is not well integrated within existing conservation planning in the tropics. For example, the designation of the Sierra del Divisor as a National Park in Peru in 2015 acknowledged the role that these forests have for supplying ecosystem services - their overall large carbon stocks and protection of watersheds - as well as the presence of high-profile species and their importance as ancestral lands of indigenous groups (SERNANP, 2012). However, the importance of biodiversity conservation to increase the resilience of the ecosystem services provided by the protected area network in Peru, or across Amazonia, was not used as a reason to protect this region. The Sierra del Divisor National Park is located along a key north-south precipitation gradient, between a set of other protected areas in Peru and Brazil. Conserving this area therefore ensures connectivity along an environmental gradient that is highly likely to be affected by climate change, and where species migration is likely. Overall, the greater resilience that biodiversity gives to forest carbon stocks is considered an important link between biodiversity conservation and ecosystem service provision (Thompson et al., 2009). Firm evidence now exists to support this argument from the tropical forest biome. Overall, this concept shows the importance of integrating the impact of climate change fully within conservation planning (cf Freudenberger et al., 2013) and the new evidence potentially provides powerful support to use this argument for justifying the protection of networks of intact tropical forest in the face of increasing threats from land-use and climate change.

ACKNOWLEDGEMENTS

I thank Lily Rodriguez and Ione Anderson for their tireless efforts to organise the pre-UNFCCC COP conference 'Biodiversity and Climate Change: from science to policymakers' in Lima, Peru and bring this volume to publication. I also thank two anonymous reviewers for their helpful comments and acknowledge the project 'Monitoring Protected Areas in Peru to Increase Forest Resilience to Climate Change' funded by the Gordon and Betty Moore Foundation (grant number 5349) which has been influential in the development of the ideas presented in this manuscript.

REFERENCES

- Angelsen, A. (2008) Moving ahead with REDD: issues, options and implications. Bogor, Indonesia.
- Anhuf, D., Ledru, M. P., Behling, H., Da Cruz, F. W., Cordeiro, R. C., Van Der Hammen, T., Karmann, I., Marengo, J. A., De Oliveira, P. E., Pessenda, L., Siffedine, A., Albuquerque, A. L. & Dias, P. L. D. (2006) Paleo-environmental change in Amazonian and African rainforest during the LGM. *Palynology, Palaeogeography & Palaeoclimatology*, **239**, 510-527.
- Asner, G. P., Anderson, C. B., Martin, R. E., Tupayachi, R., Knapp, D. E. & Sinca, F. (2015) Landscape biogeochemistry reflected in shifting distributions of chemical traits in the Amazon forest canopy. *Nature Geoscience*, **8**, 567-573.
- Baker, T. R., Swaine, M.D. & Burslem, D.F.R.P. (2003) Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. *Perspectives in Plant Ecology, Evolution and Systematics* **6**, 21-36.

- Baker, T. R., Jones, J. P. G., Rendón Thompson, O. R., Román Cuesta, R. M., del Castillo, D., Chan Aguilar, I., Torres, J. & Healey, J. R. (2010) How can ecologists help realise the potential of payments for carbon in tropical forest countries? *Journal of Applied Ecology*, **47**, 1159-1165.
- Baker, T. R., Pennington, R. T., Magallon, S., Gloor, E., Laurance, W. F., Alexiades, M., Alvarez, E., Araujo, A., Arets, E. J., Aymard, G., Alves de Oliveira, A., Amaral, I., Arroyo, L., Bonal, D., Brienen, R. J. W., Chave, J., Dexter, K. D., Di Fiore, A., Eler, E., Feldpausch, T. R., Ferreira, L., Lopez-Gonzalez, G., van der Heijden, G., Higuchi, N., Honorio, E., Huamantupa, I., Killeen, T., Laurance, S., Leano, C., Lewis, S. L., Malhi, Y., Schwantes Marimon, B., Marimon Junior, B. H., Monteagudo Mendoza, A., Neill, D., Penuela-Mora, C., Pitman, N., Prieto, A., Quesada, C. A., Ramírez, F., Ramírez Angulo, H., Rudas, A., Ruschel, A. R., Salomao, R. P., Segalin de Andrade, A., Silva, N. M., Silveira, M., Simon, M. F., Spironello, W., ter Steege, H., Terborgh, J., Toledo, M., Torres-Lezama, A., Vasquez, R., Vieira, I. C. G., Vilanova, E., Vos, V. A. & Phillips, O. L. (2014) Fast demographic traits promote high diversification rates of Amazonian trees. *Ecology Letters*, **17**, 527-536.
- Baker, T. R., Phillips, O. L., Laurance, W. F., Pitman, N. C. A., Almeida, S., Arroyo, L., DiFiore, A., Erwin, T., Higuchi, N., Killeen, T. J., Laurance, S. G., Nascimento, H., Monteagudo, A., Neill, D. A., Silva, J. N. M., Malhi, Y., Gonzalez, G. L., Peacock, J., Quesada, C. A., Lewis, S. L. & Lloyd, J. (2009) Do species traits determine patterns of wood production in Amazonian forests? *Biogeosciences*, **6**, 297-307.
- Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Lloyd, J., Monteagudo, A., Neill, D. A., Patino, S., Pitman, N. C. A., Silva, J. N. M. & Martinez, R. V. (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**, 545-562.
- Banin, L., Feldpausch, T., Phillips, O., Baker, T., Lloyd, J., Affum-Baffoe, K., Arets, E., Berry, N., Bradford, M. & Brienen, R. (2012) What controls tropical forest architecture? Testing environmental, structural and floristic drivers. *Global Ecology and Biogeography*, **21**, 1179-1190.
- Banin, L., Lewis, S. L., Lopez Gonzalez, G., Baker, T. R., Quesada, C. A., Chao, K. J., Burslem, D. F., Nilus, R., Abu Salim, K. & Keeling, H. C. (2014) Tropical forest wood production: a cross-continental comparison. *Journal of Ecology*, **102**, 1025-1037.
- Becknell, J. M., Kucek, L. K. & Powers, J. S. (2012) Aboveground biomass in mature and secondary seasonally dry tropical forests: A literature review and global synthesis. *Forest Ecology and Management*, **276**, 88-95.
- Bennett, G. & Mulongoy, K. J. (2006) Review of experience with ecological networks, corridors and buffer zones. *Technical Series no. 23*, pp. 100. Secretariat of the Convention on Biological Diversity, Montreal.
- Brodie, J., Post, E. & Laurance, W. F. (2012) Climate change and tropical biodiversity: a new focus. *Trends in Ecology & Evolution*, **27**, 145-150.
- Bunker, D. E., DeClerck, F., Bradford, J. C., Colwell, R. K., Perfecto, I., Phillips, O. L., Sankaran, M. & Naeem, S. (2005) Species loss and aboveground carbon storage in a tropical forest. *Science*, **310**, 1029-1031.
- Cadotte, M. W. (2013) Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences*, **110**, 8996-9000.
- Cavanaugh, K. C., Gosnell, J. S., Davis, S. L., Ahumada, J., Boundja, P., Clark, D. B., Mugerwa, B., Jansen, P. A., O'Brien, T. G. & Rovero, F. (2014) Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale. *Global Ecology and Biogeography*, **23**, 563-573.
- Chapin, F. S., Sala, O. E., Burke, I. C., Grime, J. P., Hooper, D. U., Lauenroth, W. K., Lombard, A., Mooney, H. A., Mosier, A. R. & Naeem, S. (1998) Ecosystem consequences of changing biodiversity. *Bioscience*, 45-52.
- Colinvaux, P. A., de Oliveira, P. E. & Bush, M. B. (2000) Amazonian and neotropical plant communities on glacial timescales: the failure of the aridity and refuge hypothesis. *Quaternary Science Reviews*, **19**, 141-169.

- Draper, F. C., Roucoux, K. H., Lawson, I. T., Mitchard, E. T., Coronado, E. N. H., Lahteenoja, O., Montenegro, L. T., Sandoval, E. V., Zarate, R. & Baker, T. R. (2014) The distribution and amount of carbon in the largest peatland complex in Amazonia. *Environmental Research Letters*, **9**, 124017.
- DRYFLOR (2016) Plant diversity patterns in neotropical dry forests and their conservation implications. *Science*, **353**, 1383-1387.
- Duque, A., Stevenson, P. R. & Feeley, K. J. (2015) Thermophilization of adult and juvenile tree communities in the northern tropical Andes. *Proceedings of the National Academy of Sciences*, **112**, 10744-10749.
- Fauset, S., Baker, T. R., Lewis, S. L., Feldpausch, T. R., Affum-Baffoe, K., Foli, E. G., Hamer, K. C. & Swaine, M. D. (2012) Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecology Letters*, **15**, 1120-1129.
- Fauset, S., Johnson, M. O., Gloor, M., Baker, T. R., Monteagudo, A., Brienen, R. J., Feldpausch, T. R., Lopez-Gonzalez, G., Malhi, Y. & ter Steege, H. (2015) Hyperdominance in Amazonian forest carbon cycling. *Nature Communications*, **6**, 6857.
- Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., Meir, P., Revilla, N. S., Quisiyupanqui, M. N. R. & Saatchi, S. (2011) Upslope migration of Andean trees. *Journal of Biogeography*, **38**, 783-791.
- Feldpausch, T., Banin, L., Phillips, O., Baker, T., Lewis, S., Quesada, C., Affum-Baffoe, K., Arets, E., Berry, N. & Bird, M. (2011) Height-diameter allometry of tropical forest trees. *Biogeosciences*, **8**, 1081-1106.
- Feldpausch, T. R., Lloyd, J., Lewis, S. L., Brienen, R. J., Gloor, M., Monteagudo Mendoza, A., Lopez-Gonzalez, G., Banin, L., Abu Salim, K. & Affum-Baffoe, K. (2012) Tree height integrated into pantropical forest biomass estimates. *Biogeosciences*, **9**, 3381-3403.
- Freudenberger, L., Hobson, P., Schluck, M., Kreft, S., Vohland, K., Sommer, H., Reichle, S., Nowicki, C., Barthlott, W. & Ibsch, P. L. (2013) Nature conservation: priority-setting needs a global change. *Biodiversity and Conservation*, **22**, 1255-1281.
- Grainger, A., Boucher, D. H., Frumhoff, P. C., Laurance, W. F., Lovejoy, T., McNeely, J., Niekisch, M., Raven, P., Sodhi, N. S. & Venter, O. (2009) Biodiversity and REDD at Copenhagen. *Current Biology*, **19**, R974-R976.
- Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L. & O'Connor, M. I. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, **486**, 105-108.
- Ibsch, P. L., Araujo, N. & Nowicki, C. (2007) Visi3n de Conservaci3n de la Biodiversidad del Corredor Ambor3 - Madidi. FAN/WWF/TNC/CI. Editorial FAN, Santa Cruz de la Sierra - Bolivia.
- Jantz, P., Goetz, S. & Laporte, N. (2014) Carbon stock corridors to mitigate climate change and promote biodiversity in the tropics. *Nature Climate Change*, **4**, 138-142.
- Johnson, M. O., Galbraith, D., Gloor, M., De Deurwaerder, H., Guimberteau, M., Rammig, A., Thonicke, K., Verbeeck, H., Randow, C., Monteagudo, A., Phillips, O. L., Brienen, R. J. W., Feldpausch, T. R., G., L. G., Fauset, S., Quesada, C. A., Christoffersen, B., Ciais, P., Gilvan, S., Kruijt, B., Meir, P., Moorcroft, P., Zhang, K., Alvarez, E., Alves de Oliveira, A., Amaral, I., Andrade, A., L.E.O.C., A., Araujo-Murakami, A., Arets, E. J. M. M., Arroyo, L., Aymard, G. A., Baraloto, C., Barroso, J., Bonal, D., Boot, R., Camargo, J., Chave, J., Cogollo, A., Cornejo Valverde, F., da Costa, L., di Fiore, A., Ferreira, L., Higuchi, N., Honorio, E., Killeen, T. J., Laurance, W. G., Laurance, S. F., Licona, J., Lovejoy, T., Malhi, Y., Marimon, B., Marimon Junior, B. H., Matos, D. C. L., Mendoza, C., Neill, D. A., Pardo, G., Pena-Claros, M., Pitman, N. C. A., Poorter, L., Prieto, A., Ramirez-Angulo, H., Roopsind, A., Rudas, A., Salomao, R. P., Silveira, M., Stropp, J., ter Steege, H., Terborgh, J., Thomas, R., Toledo, M., Torres, A., van der Heijden, G. M. F., Vasquez, R., Vieira, I., Vilanova, E., Vos, V. A. & Baker, T. R. (2016) Variation in stem mortality rates determines patterns of aboveground biomass in Amazonian forests: implications for dynamic global vegetation models. *Global Change Biology*.

- Miles, L. & Kapos, V. (2008) Reducing greenhouse gas emissions from deforestation and forest degradation: global land-use implications. *Science*, **320**, 1454-1455.
- Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C. E. T., Renaud, J. & Thuiller, W. (2013) Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology*, **11**, e1001569.
- Oliver, T. H., Heard, M. S., Isaac, N. J., Roy, D. B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C. D. L. & Petchey, O. L. (2015) Biodiversity and resilience of ecosystem functions. *Trends in Ecology & Evolution*, **30**, 673-684.
- Pitman, N. C., Andino, J. E. G., Aulestia, M., Cerón, C. E., Neill, D. A., Palacios, W., Rivas-Torres, G., Silman, M. R. & Terborgh, J. W. (2014) Distribution and abundance of tree species in swamp forests of Amazonian Ecuador. *Ecography*, **37**, 902-915.
- Poorter, L., Sande, M., Thompson, J., Arets, E., Alarcón, A., Álvarez-Sánchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G. & Boit, A. (2015) Diversity enhances carbon storage in tropical forests. *Global Ecology and Biogeography*, **24**, 1314-1328.
- Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., Fyllas, N. M., Hodnett, M., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneth, A., Arroyo, L., Chao, K.-J., Deuzeo, N., Erwin, T., di Fiore, A., Higuchi, N., Honorio Coronado, E., Jiménez, E. M., Killeen, T., Lezama, A. T., Lloyd, G., López-González, G., Luizão, F. J., Malhi, Y., Monteagudo, A., Neill, D. A., Núñez Vargas, P., Paiva, R., Peacock, J., Peñuela, M. C., Peña Cruz, A., Pitman, N. C. A., Priante Filho, N., Prieto, A., Ramírez, H., Rudas, A., Salomão, R., Santos, A. J. B., Schmerler, J., Silva, N., Silveira, M., Vásquez, R., Vieira, I., Terborgh, J. & Lloyd, J. (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate *Biogeosciences*, **9**, 2203-2246.
- Sakschewski, B., von Bloh, W., Boit, A., Poorter, L., Peña-Claros, M., Heinke, J., Joshi, J. & Thonicke, K. (2016) Resilience of Amazon forests emerges from plant trait diversity. *Nature Climate Change*.
- Schulze, E.-D. & Mooney, H. A. (1994) Ecosystem function of biodiversity: a summary. *Biodiversity and ecosystem function* (eds E.-D. Schulze & H. A. Mooney), pp. 497-510. Springer.
- SERNANP (2012) Expediente tecnico Zona Reserva Sierra del Divisor. pp. 125. SERNANP, Lima.
- Slik, J., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P. & Clark, C. (2013) Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*, **22**, 1261-1271.
- Sullivan, M. J. P., Talbot, J., Lewis, S. L. & Phillips, O. L. (in review) Diversity and carbon storage across the tropical forest biome. *Scientific Reports*.
- Swaine, M. D., Agyeman, V. K., Kyereh, B., Orgle, T. K., Thompson, J. & Veenendaal, E. M. (1997) *Ecology of Forest Trees in Ghana*. ODA, London, U.K.
- ter Steege, H., Pitman, N., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., Molino, J.-F., Prévost, M.-F., Spichiger, R., Castellanos, H., von Hildebrand, P. & R., V. (2006) Continental scale patterns of canopy tree composition and function across Amazonia. *Nature*, **443**, 444-447.
- Thompson, I., Mackey, B., McNulty, S. & Mosseler, A. (2009) Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. *Technical Series no. 43*, pp. 67. Secretariat of the Convention on Biological Diversity, Montreal.
- Venter, O., Laurance, W. F., Iwamura, T., Wilson, K. A., Fuller, R. A. & Possingham, H. P. (2009) Harnessing carbon payments to protect biodiversity. *Science*, **326**, 1368.