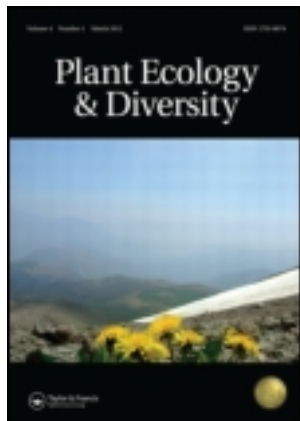


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The ecosystem dynamics of Amazonian and Andean forests

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EDITORIAL

The ecosystem dynamics of Amazonian and Andean forests

The importance of Amazonian and Andean rain forests in the Earth System cannot be overstated. They store ca. 100 billion tonnes of carbon in their biomass (Malhi et al. 2006; Saatchi et al. 2007), are responsible for 10–15% of global net primary productivity (Melillo et al. 1993; Zhao and Running 2010) and recycle 25–50% of the rainfall that they receive (Salati and Vose 1984; Costa and Foley 2000). Furthermore, these rainforests house a large fraction of global biodiversity and provides a host of ecosystem services of inestimable local, regional and global value. In recent decades, great strides have been made in understanding how these forests vary over space in terms of tree diversity (ter Steege et al. 2006), biomass storage (Baker et al. 2004b; Malhi et al. 2006), wood production (Malhi et al. 2004) and soil properties (Quesada et al. 2013). Considerable progress has also been made in understanding how above-ground biomass (Baker et al. 2004a), tree mortality and recruitment (Phillips et al. 2004) and some aspects of species composition (Phillips et al. 2002) of tropical forests have been changing over time. Despite these significant advances, much less progress has been made in understanding other fundamental ecosystem processes, such as internal carbon cycling, forest successional pathways and the impacts of disturbance events on forest structure. Knowledge of these processes is essential to better understand the functioning of Amazonian rain forests and predict how they may respond to global environmental change. This Special Issue includes papers that help to bridge these and other important knowledge gaps in our understanding of the ecological functioning of Amazonian and Andean rainforests. This issue also showcases the current strength of South American ecology as 21 out of the 28 articles in the edition were led by South American scientists. The issue brings together work related to two general strands of Amazonian ecosystem ecology, namely biogeochemical cycling (13 studies) and forest community dynamics and structure (15 studies).

Biogeochemical cycles

This section contains eight papers presenting a detailed account of carbon cycling within different Amazonian forests, one paper on woody debris dynamics along an elevational transect, one paper comparing forest structural properties across three elevational transects, one paper on nitrogen cycling across the Amazon, one paper on the seasonality of leaf gas exchange in an eastern Amazonian forest, and one paper exploring dissolved organic carbon transport via forested blackwater streams in central Amazonia.

The eight carbon cycling studies are the first to be published from the recently established Global Ecosystems Monitoring (GEM) network (<http://gem.tropicalforests.ox.ac.uk/>), a subset of sites of the Red Amazonica de Inventarios Forestales (RAINFOR) and Andes Biodiversity and Ecosystem Research Group (ABERG) forest inventory networks. These studies use a standardised methodology that involves quantifying the component terms (e.g. leaves, wood and roots) of net primary productivity (Aragão et al. 2009; Girardin et al. 2010) and autotrophic respiration (Malhi et al. 2009) to construct a detailed bottom-up carbon budget for individual sites. Furthermore, as measurements have been repeated at regular intervals throughout the year, they have allowed, for the first time, the seasonal cycle of individual components of the carbon cycle to be described. By providing essential data on previously little-understood internal carbon cycling within Amazonian and tropical Andean montane forests, these studies have significantly advanced our understanding of how carbon use efficiency (the ratio of net primary productivity (NPP) to gross primary productivity (GPP)) and carbon allocation processes vary from Amazonian lowlands to the Andean slopes of the Basin. Each study consisted of a paired set-up, where the internal carbon cycling of two plots, differing in some key feature, was compared.

Da Costa et al. (2014) and Rocha et al. (2014) considered the effects of prolonged experimental drought and experimental burning, respectively, on carbon cycling in Amazonian forests. Da Costa et al. (2014) compared comprehensive carbon budgets of an eastern Amazonian forest exposed to intense drought (~50% reduction in throughfall) for 10 years with those of a control plot without rainfall exclusion and with previous carbon budget measurements made at the same site following five years of experimental drought. They found that some of the differences reported previously, such as increased levels of autotrophic respiration in the droughted plot, had been maintained. However, there was also evidence that the forest was regaining stability following previous large increases in tree mortality as some processes, such as leaf area index, growth of small trees and soil respiration, all appeared to have increased in the droughted plot over recent years. There appeared to be a surge of growth of small and medium trees that took advantage of the light gaps created by the fall of large trees. Rocha et al. (2014) compared an annually-burned transitional forest plot in Mato Grosso, southern Amazonia, with an adjacent unburned plot and found that, although productivity was generally lower in the burned plot, the magnitude of the reduction was relatively small. For example, total net primary productivity in the burned plot was ca. 15% lower

than that in the control. The general finding of the study therefore was that these forests were relatively resistant to the fire regime imposed on them. However, as Balch et al. (2008) demonstrated, more infrequent, three-yearly burns could have more severe impacts because of greater fuel loads building up on the forest floor.

Lowland Amazonian forests occur across a wide range of climate and soil conditions. Four studies in this volume explored how carbon cycling varied across a diverse range of lowland forest types. Doughty et al. (2014) compared the carbon budgets of a highly fertile eastern Amazonian *terra preta* ('black earth') forest with that of a nearby forest on an infertile, highly weathered soil; Araujo-Murakami et al. (2014) examined carbon cycling in two seasonally dry forest plots located close to the Amazon forest–dry forest ecotone in Bolivia; Pasquel et al. (2014) compared the carbon budgets of a white sand forest and a nearby forest on more fertile soil in north-western Amazonia; and Malhi et al. (2014) compared two plots in south-western Amazonia that differed in geological history and fertility. The studies reported some unexpected results. Doughty et al. (2014) found that, although net primary productivity was ca. 15% higher in the *terra preta* plot than the control plot, most of the difference between plots could be attributed to much greater fine root production in the *terra preta* plot. This result is surprising as it contradicts expectations arising from resource allocation theory, whereby forests on nutrient-poor soils would be expected to show increased investment to roots to maximise nutrient uptake. Araujo-Murakami et al. (2014) reported surprisingly high net primary productivity (ca. 15 t C ha⁻¹ year⁻¹) for a seasonally dry forest at the forest–savanna ecotone but lower productivity (ca. 11 t C ha⁻¹ year⁻¹) in a nearby plot, which had a more xeric species composition, possibly due to poorer soil drainage characteristics and potentially less plant-available water. Pasquel et al. (2014) found that GPP and NPP in two plots near Iquitos, north-western Amazonia, were among the highest ever reported for Amazonian rain forests. The high fertility of the soils and lack of a dry season at these sites are thought to be important for sustaining such high rates of productivity. Surprisingly, the white sand forest in that study was found to be as productive as the nearby forest on clay soils with much better physical structure; however, this white sand soil sits on highly fertile Pebas formation and, in terms of species composition, the plot is akin to the forests on the surrounding clay soils. Hence, it is unlike typical white sand soil forests. Another important finding from this study was that there was a surprisingly high degree of seasonality in productivity even though there was no seasonality in rainfall, which was apparently related to the seasonality of solar radiation at this site. Malhi et al. (2014) also reported considerable seasonality in productivity at two forest plots in Tambopata, south-western Amazonia, and presented the first budgets for how NPP and total carbon expenditure in a tropical forest varied at seasonal scales. Another surprising outcome of this study was that differences in GPP between these relatively fertile western Amazonian

forests and less fertile plots in eastern Amazonia were quite small.

Four papers in this volume considered carbon dynamics in Andean montane forests or elevation transects that included montane forests. Girardin et al. (2014a) evaluated internal carbon cycling at two plots located at an altitude of ca. 3000 m, close to the climatic treeline. Huasco et al. (2014) compared internal carbon cycling of two mid-elevation forests (1500–1750 m) straddling the montane/lowland forest ecotone. Gurdak et al. (2014) considered how woody debris dynamics varied along an elevational gradient ranging from 210 to 3025 m, while Girardin et al. (2014b) evaluated how above-ground biomass storage, tree height and species composition varied along the same gradient. Girardin et al. (2014a) found substantially lower NPP values for two upper montane forests (ca. 7–8 Mg C ha⁻¹ year⁻¹ compared to 14–15 Mg C ha⁻¹ year⁻¹ in lowland forests in the Peruvian Amazon) and values of carbon use efficiency similar to those in lowland forests. They also found some very interesting seasonal patterns, with NPP displaying more seasonality than autotrophic respiration and peaking in the warmer and rainier season. Huasco et al. (2014) found very large differences in productivity between a forest plot located at 1500 m and a forest plot located at 1750 m: the lower elevation plot was found to be 50% more productive than the higher one at 1750 m. The authors hypothesised that these large differences between plots were due to differences in cloud immersion as the plot at 1750 m was likely to be more frequently immersed in clouds. Thus, a distinct ecological shift may be occurring near this elevation so that forests at 1500 m are similar in ecology and ecosystem function to lowland forests, whereas those at 1750 m are more similar in ecology to montane forests. It is notable that the productivity of the 1500 m plot was similar to that of lowland plots, suggesting little decline with elevation until cloud base is reached. Gurdak et al. (2014) found little relationship between woody debris stocks and elevation, but found that woody debris respiration was significantly correlated with soil moisture, temperature and wood density. An important finding of this study with implications for understanding the impacts of climate change on Andean forests was that woody debris respiration was consistently more sensitive to temperature changes (higher Q_{10}) at high than at low elevations. Girardin et al. (2014b) found that above-ground biomass and tree height both decreased significantly with elevation in three elevational transects in Bolivia, Peru and Ecuador, but that stem density increased. Tree species richness, on the other hand, showed a humped relationship with elevation, increasing until ca. 1750 m and declining thereafter, following increasing cloud immersion.

Two papers in the biogeochemical cycling section of the Special Issue focused on nitrogen cycling and the seasonality of photosynthetic parameters. Nardoto et al. (2014) studied nitrogen cycling patterns across Amazonia by analysing data on $\delta^{15}\text{N}$ concentrations in top-of-canopy leaves from 65 rainforest plots. This study has advanced our understanding of the nitrogen cycle in Amazonia

by showing that dry season precipitation and soil age exerted important controls on plant nitrogen availability in Amazonia. The study also showed that most Fabaceae species in Amazonia do not fix nitrogen, despite having the ability to do so. Domingues et al. (2014) examined seasonal variation in leaf-level gas exchange in the Tapajós forest in eastern Amazonia. They found little evidence of dry season limitation of leaf-level stomatal conductance or photosynthetic capacity, providing support for previous findings which suggested that photosynthesis remained high in the dry season in deep-rooted eastern Amazonian forests. Finally, Monteiro et al. (2014) explored dissolved organic carbon (DOC) export in blackwater streams in central Amazonia. They demonstrated that electrical conductivity was a good and low-cost proxy for DOC concentration, and used their multi-year monitoring to estimate that carbon export via DOC per unit area of watershed was 8.7 g m^{-2} . This is a rarely quantified term in carbon budgets, and this study showed that this DOC export flux was likely to be too small to substantially affect forest carbon balance estimates.

Forest community dynamics and structure

This section of the Special Issue contains 15 papers, which can be divided into four general themes: (1) drivers and patterns of forest structure and composition (four papers); (2) temporal changes in composition, dynamics and structure (three papers); (3) successional and disturbance dynamics (six papers); and (4) plant traits (two papers).

Emilio et al. (2014) investigated the role of soil physical properties in determining tree and palm basal area across 77 forest plots spread across Amazonia. Their findings showed that soil physical properties were indeed important, with the basal area of dicot trees highest in well-drained, well-structured and deep soils, while palm basal area was higher in poorly drained, less structured and shallow soils. De Oliveira et al. (2014) investigated the diversity and distribution of lianas in different types of vegetation at the Cerrado–Amazon rain forest transition. Their findings suggested a high degree of specificity between liana species composition and vegetation type, likely related to environmental gradients. Flooded forests were found to have particularly high liana abundance, although liana species richness was generally low in these forests. Schiatti et al. (2014) developed a proxy for water table depth (terrain height above nearest drainage) and used this to predict plant community composition in 72 different forest plots in central Amazonia. They found that plant composition was highly correlated with vertical distance from the water table. Furthermore, they also found high species turnover extending up to 350 m horizontally from river margins. This result has implications for Brazilian conservation laws, which only require that riparian zones extending up to 30 m from river courses be protected. Stropp et al. (2014) investigated whether there was an interaction between soil

nutrients and herbivory on seedling growth rates in the upper Rio Negro, Amazonia. To test this, they transplanted seedlings associated with white sand soils into forests with clay-rich soils and vice versa, while also controlling for the presence of herbivores. They found that the growth of seedlings was similar regardless of presence/absence of herbivore or the type of soil on which they were grown.

Butt et al. (2014) investigated changes in tree composition over a 20-year period in 46 Amazonian forest plots. Three functional groupings were used in the analysis: dry affiliates (species with a preference for dry conditions), wet affiliates (species with a preference for wet conditions) and climate generalists. The results showed that wet affiliates and climate generalists moved from a state of net basal area gain to dynamic equilibrium, where gains and losses were equivalent, over the 20-year period of the study. Dry affiliates, on the other hand, showed a strong increase in stem recruitment and net basal area gain. The results therefore hint at a climate-related shift in functional composition in some parts of the Amazon. Marimon et al. (2014) compared mortality and recruitment rates of trees species in plots in the rainforest–savanna ecotone of southern Amazonia with those in the core area of the Amazon. Turnover rates in these transitional ecotone forests were found to be considerably greater than those in core regions of the Amazon. The results are especially surprising as these forests are found on deep, infertile soils usually associated with low dynamism. However, the occurrence of recent drought events in the forest–savanna transition region of the Amazon confounds the results somewhat and more work is needed to ascertain whether this is an intrinsic feature of these forests or a response to recent drought events. Nascimento et al. (2014) examined compositional changes in three compositional variants of rain forest in Maracá Island, Roraima, Brazil, over the last 20 years. One was *Peltogyne gracilipes* monodominant forest, one had low abundance of *Peltogyne gracilipes* and in another forest this species was absent altogether. The three forest types exhibited considerable stability in terms of dynamics (mortality/recruitment) and floristic composition over the period of the study.

Espirito-Santo et al. (2014) used remote-sensing analysis to quantify the area affected by gaps and the carbon flux-associated gap disturbances in an eastern Amazonian forest. Comparison with ground measurements, however, showed that the remote-sensing approach greatly overestimated the canopy gap fraction. The authors found that only 30% of tree mortality was associated with canopy gaps. These results demonstrate the importance of maintaining long-term plots to accurately quantify mortality rates. Flores et al. (2014) used a combination of remote sensing and field studies to investigate the impact of fire disturbance on floodplain forests of the Rio Negro. They found that the fires resulted in catastrophic loss of forest area (88% reduction) and mortality (91% of trees died). Furthermore, forest recovery was much lower in the floodplain forests than in normal *terra firme* forests. Overall, the

results suggested very low resilience of blackwater floodplain forests to fire. Oliveras et al. (2014) examined the effects of fires on forest structure and composition at the treeline (ca. 3500 m elevation asl) of the Andes in southern Peru. They found that fires had a strong effect upon forest structure up to 15 years after fire. The species-level features most associated with fire tolerance were the ability to resprout after fire, and tree biomass (with large trees being more resistant to fire damage).

Williamson et al. (2014) compared changes in woody vegetation following regrowth on abandoned pastures with those following regrowth on abandoned clearcuts. Differences in land-use history led to different successional pathways with species of *Vismia* dominating following pasture abandonment and species of *Cecropia* dominating on abandoned clearcuts. The authors found that stem densities exhibited no trend during the first 25 years of secondary succession, irrespective of land-use history. Species diversity increased at a much faster rate following regrowth on abandoned clearcuts, dominated by *Cecropia*, than on abandoned pastures dominated by *Vismia*. Jakovac et al. (2014) examined how controls on seedling growth under these two different successional pathways differed. They found that successional age and light intensity affected seedlings differently in the two successional pathways. In *Cecropia*-dominated successions, seedlings were limited by light, but this was not the case in *Vismia*-dominated successions. Aguilar Jr et al. (2014) investigated the process of invasion of *Acacia mangium* in savannas adjacent to a forestry plantation in Roraima, northern Amazonia. They found that individuals of *A. mangium* were dispersed up to 900 m from the plantation border 8–9 years after planting and found evidence that adult savanna trees might be facilitating the establishment of *Acacia*. Given these characteristics, *A. mangium* could rapidly become a serious invasive threat to Amazonian savannas.

Bentos et al. (2014) investigated whether the trade-off between seed mass and number was related to fruit variables (fruit mass and fruit number per tree) for 12 commonly-occurring pioneer species in Amazonia. Seed mass, fruit mass and fruit number explained most of the variation in seed number. They concluded that biomass trade-offs between seed size and number were partly determined by packaging (seeds per fruit, number of fruits, fruit mass). Queenborough and Porras (2014) explored the potential of extracting specific leaf area (SLA) measurements from herbarium samples. More specifically, they looked at the effect of pressing and drying on leaf area to ascertain whether this introduced error into SLA estimates from herbarium specimens. They found a significant decrease in leaf area following drying (ca. 8%), but this decrease in leaf area had no overall statistically significant effect on SLA. Family-level responses, however, varied widely, suggesting that herbarium samples can be used if shrinkage is quantified properly.

The papers contained in this Special Issue span a wide range of topics within the overarching field of ecosystem ecology of Amazonian lowland and Andean montane forest

ecosystems. As a whole, they have substantially added to our knowledge in many areas. The issue includes many important pieces of work that have the potential to be highly cited. Each of the papers in the issue contributes to our knowledge of the functioning of these diverse ecosystems, and as a whole they demonstrate the sheer diversity of functioning in Amazonian Basin forests, as well as pointing to some commonalities in their emergent properties, such as total primary productivity. Importantly, the studies included in the issue raise a number of intriguing questions, including: Why do *terra firme* forests allocate so much of their NPP to roots? Why are forests at the rainforest–savanna ecotone so dynamic? Why do blackwater floodplain forests take so long to recover from fire? Such questions should inspire follow-on research that will further deepen our understanding of Amazonian and Andean ecosystems.

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