

# 9

## Ecosystem Ecology and Forest Dynamics — Update 2014

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The original chapter on the “Ecosystem Ecology and Forest Dynamics” summarized research on four areas of ecosystem ecology. The authors: a) described forest structure, composition, and dynamics of two primary forest stands, a windward elfin woodland and a leeward cloud forest; b) reviewed research efforts that focused on ecological roles of canopy biota in forest nutrient cycles; c) compared ecosystem-level data collected at Monteverde to other tropical montane forests; and d) identified areas where our knowledge is incomplete and further investigations were warranted. Since its publication, our overall understanding of ecosystem ecology in tropical montane regions has benefitted greatly from global-scale syntheses (Bruijnzeel *et al.* 2010, Giambelluca and Gerold 2011, Dalling *et al.* 2015). Here, I summarize some of the recent research on: a) forest structure and biomass in Monteverde, including new mass estimates for epiphytes and hemi-epiphytes; b) linkages between climate, hydrology and forest structure and functioning; c) more complete comparisons

of carbon and nutrient content between terrestrial and epiphytic vegetation; d) the processing of atmospheric deposition of nitrogen and other nutrients by epiphyte-laden canopies; and e) carbon, nutrient and enzymes in soils, and the impacts of deforestation on soil carbon and nutrients. I then suggest future research directions that will help fill some of the gaps in ecosystem level information at Monteverde.

**A. Forest Structure and Biomass.** Recent data on forest structure and biomass have been published since the original chapter (Nadkarni *et al.* 2004, Hager and Dohrenbusch 2011, Kohler *et al.* 2007). Forest census measurements made at seven stands along a 2.5 km transect across the Atlantic (windward) and Pacific (leeward) slopes indicated maximum canopy heights ranged from 6 to 20 m, number of stems from 1160 to 3280 ha<sup>-1</sup>, and basal area from 33 to 99 m<sup>2</sup> ha<sup>-1</sup> (Hager and Dohrenbusch 2011). Estimated aboveground biomass ranged from 84 t ha<sup>-1</sup> in the wettest, most wind-exposed site, to 431 t ha<sup>-1</sup> in a lower elevation stand (assuming a

wood density of  $0.56 \text{ g cm}^{-3}$ ; Nadkarni *et al.* 2000). In a 4-ha leeward cloud forest stand, canopy height was 18-25 m and stem density was  $2062 \text{ individuals ha}^{-1}$ , with large ( $>30 \text{ cm DBH}$ ), medium (10-30 cm DBH) and small (2-10 cm DBH) stems totaling 159, 396, and 1507, respectively (Nadkarni *et al.* 2000). Stand biomass was  $490 \text{ t ha}^{-1}$ , with approx. 95% of this in stem and branch wood (Nadkarni *et al.* 2004). Aboveground biomass in a secondary forest dominated by *Conostegia oerstediana* was  $152 \text{ t ha}^{-1}$  (Nadkarni *et al.* 2004).

Recent research efforts have also quantified epiphyte mass in a number of forests in Monteverde, with estimates from primary forests ranging between  $16 \text{ and } 39 \text{ t ha}^{-1}$ . Nadkarni *et al.* (2004) reported an epiphyte mass value of  $33.1 \text{ t ha}^{-1}$  for an intensively-studied leeward cloud forest. Approximately 60% of the epiphyte mass was dead organic matter (DOM;  $20.7 \text{ t ha}^{-1}$ ), and mass of epiphytic bryophytes, roots, stems and foliage was 4.1, 5.2, 2.1 and  $0.7 \text{ t ha}^{-1}$ , respectively (Nadkarni *et al.* 2004). The sum of bryophytes and epiphyte foliage in the canopy represented 67 % of the sum of canopy and understory foliage. Values of  $26 \text{ and } 32 \text{ t ha}^{-1}$  for epiphyte mass, and  $6 \text{ and } 7 \text{ t ha}^{-1}$  for hemi-epiphytes and lianas were reported for two stands at 1200 and 1450 m elevation, respectively (Hager and Dohrenbusch 2011). DOM averaged 23.6% and 26.4% of epiphyte mass in these two stands. Epiphyte mass in primary forest near San Gerardo was estimated to be  $16.2 \text{ t ha}^{-1}$  (Kohler *et al.* 2007), with epiphytic bryophytes, vascular epiphytes, and DOM estimated at 11.5, 3.9 and  $2.1 \text{ t ha}^{-1}$ , respectively. Epiphyte mass, primarily epiphytic bryophytes, was much lower in a secondary forest stand dominated by *Conostegia oerstediana*, totaling only  $0.2 \text{ t ha}^{-1}$  (Nadkarni *et al.* 2004).

Many of the pools and fluxes needed to calculate productivity of terrestrial and epiphytic vegetation have been measured at Monteverde. For example, litterfall and epiphyte litterfall (Nadkarni *et al.* 1992a,b, 1995), litter decomposition (Gholz *et al.* 2000, Cusack *et al.* 2009, Currie *et al.* 2010), production and decomposition of epiphytic bryophytes (Clark *et al.* 1998a), and colonization of branches by epiphytes (Nadkarni 2000, *et al.* 2002).

Unfortunately, few stands have been censused at regular and long enough intervals to estimate tree and understory production, although gap dynamics measurements in the windward cloud forest described in Nadkarni *et al.* (2000), and tree turnover measurements in the intensively studied leeward cloud forest stand described in Nadkarni *et al.* (2000, 2004) come close. In the later stand, trees in a 4-ha plot have been measured and tagged, and tree increments have been measured, but results have not been reported yet (G. Goldsmith, pers. comm.). Other processes have not been measured at any study site with sufficient resolution to calculate a complete forest carbon budget.

One limitation to estimate net primary production in tropical montane cloud forests is that although canopy height and diameter at breast height (dbh; 1.37 meters) measurements are relatively straightforward, allometric equations to calculate biomass, and with repeated measurements, biomass increment, for cloud forest trees are rare in the literature. In addition, unlike many tree species in temperate forests, tree ages cannot be estimated reliably from tree cores and counts of annual rings for many tropical tree species. A potential alternate method for estimating stem production is to use annual growth increments estimated from  $\delta^{18}\text{O}$  isotope signals in tree stems. Seasonal isotopic signals of  $\delta^{18}\text{O}$  occur in tree stems of dominant species in Monteverde, and this has allowed an estimate of seasonality of the sources of water used (Anchukaitis *et al.* 2008). This technique could be extended to estimate annual growth increments from tree cores.

**B. Linkage of forest structure and ecosystem processes to abiotic factors.** Recent studies have further linked patterns of cloud, wind-driven precipitation and soil water content across the Monteverde area to forest structure, epiphyte abundance and plant water status, and soil microbial biomass and functioning. Hager and Dohrenbusch (2011) measured rainfall, horizontal precipitation, throughfall, temperature and soil moisture at seven forest stands along the same 2.5 km transect across the Atlantic slope and the Pacific slopes that they measured forest structure. Patterns of forest structure and biomass along their transect corresponded to the

strong hydrologic and topographic gradients, and to differences in soil moisture conditions across the continental divide in Monteverde. Nadkarni and Solano (2002) used experimental transplants of upper cloud forest epiphyte mats to tree canopies at slightly lower elevations that experience longer dry season conditions, demonstrating the importance of cloud and wind-driven precipitation to vascular epiphytes during the dry season. Similarly, Heitz *et al.* (2002) reported that epiphytes on small branches also had less negative  $\delta^{13}\text{C}$  values, indicating more frequent water stress occurred, compared to vascular epiphytes rooted in canopy DOM or terrestrial vegetation. Variability in microbial biomass, fungal and bacterial abundance and diversity, and the abundance of key functional genes for lignin degradation and bacterial N-fixation, as well as soil nitrogen fixation activity, have been linked to patterns of soil moisture in forest stands along the Caribbean and Pacific slopes of Monteverde (Eaton *et al.* 2012).

**C. Comparisons of nutrient content of terrestrial and epiphytic vegetation.** More complete nutrient analyses of terrestrial and epiphytic vegetation have been reported in the literature (Heitz *et al.* 2002, Nadkarni *et al.* 2004, Cardelús and Mack 2010). Although epiphytic bryophytes and vascular epiphyte foliage were lower in nitrogen (N) and phosphorus (P) content than tree foliage in the intensively-studied leeward cloud forest stand (1.4, 1.4 and 2.3 % N, and 0.08, 0.09 and 0.10 % P, respectively), N and P mass in bryophytes and epiphytic foliage represented 45 and 61 % of the mass in canopy foliage (Nadkarni *et al.* 2004).

The natural abundance of  $^{15}\text{N}$  in epiphyte bryophytes more closely matched those in precipitation compared to host tree foliage, indicating that atmospherically deposited N was retained by epiphytes (Heitz *et al.* 2002). They also reported that vascular epiphytes on small branches without canopy soil had lower N foliar concentrations and  $\delta^{15}\text{N}$  signals than those rooted in canopy DOM, suggesting that epiphytes on smaller branches also retained a greater proportion of N directly from cloud water and precipitation. Overall, epiphytes had lower  $\delta^{15}\text{N}$  values than host tree foliage, and canopy DOM had lower values than terrestrial

soil. Hietz *et al.* (2002) indicated that canopy DOM is derived primarily from epiphytes, with only minor inputs from host tree litter matter. They concluded that the epiphyte N cycle appears to be largely detached from the tree-soil cycle. However, Matson *et al.* (2014) reported that rates of N cycling in canopy DOM were sensitive to slight changes in forest floor nutrient availability in an Andean tropical montane forest, indicating a greater coupling between epiphytic and terrestrial N cycling. Their results indicated that canopy DOM was a significant N source for epiphytes, and N mineralized in canopy DOM contributed up to 23% of total (canopy + forest floor) mineral N production in tropical montane forests. Cardelús and Mack (2010) reported comparisons of epiphytic vegetation along an elevational transect on Volcan Barva. They reported that epiphytes rooted in canopy DOM had higher N concentrations than “atmospheric” epiphytes, while P content did not vary among groups. They also reported higher variability in foliar  $\delta^{15}\text{N}$  values, with no differences between epiphytes rooted in canopy DOM and atmospheric epiphytes. Their data indicated significant correlations between P concentrations of ferns and orchids and host tree foliage, supporting the results of Matson *et al.* (2014). Nadkarni *et al.* (2002) reported that the carbon content of canopy DOM was significantly higher than terrestrial soil, but similar for phosphorus and calcium. Canopy humus had very low pH compared to terrestrial soils. Terrestrial soil had a tenfold greater amount of extractable cations, but the C/N ratios and cation exchange capacity of canopy humus and the upper soil horizon did not differ significantly.

**D. Processing of atmospheric deposition of nitrogen and other nutrients by epiphyte-laden canopies.** Our understanding of nutrient inputs via atmospheric deposition has benefitted from recent measurements of cloud water and wind-driven precipitation at Monteverde (Frumau *et al.* 2011, Hager and Dohrenbusch 2011, Schmid *et al.* 2011), in addition to isotopic analyses of precipitation and streamflow (Rhodes *et al.* 2010; see Chapter 2). Eddy covariance data and cloud water impactors were

used to estimate hydrologic inputs to Santa Elena Cloud Forest Reserve in Monteverde (Schmid *et al.* 2011), and they reported cloud water deposition rates of  $1.2 \pm 0.1$  mm day<sup>-1</sup>. Cloud water measured directly averaged 5% of precipitation during the dry season, while use of a canopy hydrology model based on  $\delta^{18}\text{O}$  isotope content as a tracer indicated that cloud water deposition represented 9% of precipitation during the same period (see Chapter 2). Because cloud water is approximately 19, 24 and 8 times enriched in  $\text{NO}_3^-$ ,  $\text{NH}_4^+$  and  $\text{H}^+$  compared to precipitation, deposition represents a significant input of these and other ions to forest canopies in Monteverde (Clark *et al.* 1998a,b, 2005).

The effects of cloud deposition on vascular plant water status and epiphytes have been investigated recently. Using satellite and ground-based observations to study cloud and leaf wetting patterns in pre-montane and montane forests in Monteverde, Goldsmith *et al.* (2013) evaluated the importance of direct uptake of water accumulated on leaf surfaces to plant water status during the dry season. The capacity for foliar water uptake differed significantly between plants in montane and premontane forest plant communities, as well as among species within a forest type. However, leaf wetting events resulted in foliar water uptake in all species studied. Although Clark *et al.* (2005) measured little inorganic N retention from tree foliage characterized by relatively thick, waxy cuticles, other leaf types were not investigated. Goldsmith *et al.* (2013) and more recently Gotsch *et al.* (2015) investigating vascular epiphytes and hemi-epiphytes concluded that foliar water uptake is common in Monteverde, and improves plant water status during the dry season. It is possible that cloud water and canopy throughfall also result in available nutrients for some vascular plants.

The role of epiphytic vegetation in stand hydrology and nutrient retention from atmospheric deposition has been further quantified by Kohler *et al.* (2007) and simulated by Clark *et al.* (2005). Epiphyte assemblages exposed to cloud water wetted up asymptotically, and began to generate throughfall well below their water storage capacity at saturation (Tobon *et al.* 2010). Clark *et al.* (2005) modeled this process as a “leaky

cup” in their canopy hydrology model (see below). Tobon *et al.* (2010) noted that uptake and evaporation of cloud water was highly dynamic, leading to relatively long residence times of ions in cloud water and mist in epiphytic bryophyte mats, facilitating nutrient retention.

A canopy model was developed and evaluated to estimate inorganic nitrogen (N) retention from atmospheric deposition by canopy components in a leeward cloud forest (Clark *et al.* 2005). They first estimated net retention of inorganic N by samples of epiphytic bryophytes, epiphyte assemblages, vascular epiphyte foliage, and host tree foliage that were exposed to cloud water and precipitation solutions. Leaching experiments indicated that  $\text{NO}_3^-$  was strongly retained by epiphytic bryophytes, but not by vascular plant foliage. Net retention of  $\text{NH}_4^+$  by epiphytic bryophytes and epiphyte assemblages was somewhat lower, and reflected the internal cycling of  $\text{NH}_4^+$  in DOM (Clark *et al.*, 2005). Results were then scaled up to the ecosystem level using a multi-layered model of the canopy derived from measurements of forest structure and epiphyte mass in Nadkarni *et al.* (2004). Their model was driven with hourly meteorological and event-based atmospheric deposition data, and model predictions were evaluated against measurements of throughfall collected at the site (Clark *et al.* 1998b). Model predictions were similar to field measurements for both event-based and annual hydrologic and inorganic N fluxes in throughfall. Simulation of individual events indicated that epiphytic bryophytes and epiphyte assemblages retained 33 to 67% of the inorganic N deposited in cloud water and precipitation. On an annual basis, the model predicted that epiphytic components retained 3.4 kg N ha yr<sup>-1</sup>, approx. 50% of the inorganic N in atmospheric deposition (6.8 kg N ha yr<sup>-1</sup>). Thus, epiphytic bryophytes play a major role in N retention and cycling in the canopy by transforming highly mobile inorganic N (ca. 50% of atmospheric deposition is  $\text{NO}_3^-$ ) to less mobile (exchangeable  $\text{NH}_4^+$ ) and recalcitrant forms in biomass and remaining litter and canopy humus.

Overall, these studies provide a much better understanding of the role of epiphytes in N and

P cycling in tropical montane forests. N retention and cycling by epiphyte bryophytes and canopy DOM can provide an important source of N for forest ecosystems. In the canopy, N cycling in DOM is a significant N source for vascular epiphytes, although the activity of canopy roots remains to be determined (e.g., Hertel *et al.* 2011). Canopy DOM could be important in overall stand N cycling where N cycling rates in soil on the forest floor is relatively low (e.g., due to waterlogging) and the mass of canopy DOM is relatively large. These research efforts further confirm the linkage of bryophytes and vascular epiphytes to microclimatic conditions in Monteverde, and suggest that they will likely be some of the first organisms affected by changes in climate and wind-driven cloud and precipitation amounts.

#### **E) Carbon, nutrients, and enzymes in soils.**

The variability of soil nitrogen fixation activity, microbial biomass, fungal and bacterial abundance and diversity, and the abundance of key functional genes for lignin degradation and bacterial N-fixation in forests on the Caribbean and Pacific slopes of Monteverde have been correlated with soil moisture (Eaton *et al.* 2012). Investigation of soil properties in and near the Santa Elena Forest Reserve indicated that pastures created by forest clearing of the cloud forest contained 20% less carbon at 0 to 30 cm depth than mature forest soils, and that 30 year old secondary forest contained intermediate amounts of soil carbon, whereas no trend for soil nitrogen occurred (Tanner *et al.* 2014). Soil CO<sub>2</sub> flux followed the same trend as soil carbon; mature forest soils exhibit slightly higher CO<sub>2</sub> flux, but greater spatial variability, and secondary forest soils have a higher flux than pasture soils. They suggested that differences in soil CO<sub>2</sub> flux between sites were due to differences in root respiration, controlled by the size and abundance of plant roots in the subsurface.

#### **Suggestions for Future Research**

A developing technology that could be useful to scaling up from plot measurements is the use of light detection and ranging (LiDAR) systems. Although the digital elevation model (DEM) of the forest floor would be challenging to accurately generate in some areas of Monteverde, this technique has estimated biomass and canopy structure in other tropical forest ecosystems (e.g., Clark *et al.*, 2011, Asner *et al.* 2012, Vaughn *et al.* 2013).

A second fruitful area of investigation would be the use of eddy covariance to measure net CO<sub>2</sub> exchange (NEE<sub>c</sub>) and forest productivity. Although eddy covariance have been used to estimate CW deposition in the Santa Elena cloud forest (Schmid *et al.* 2011), this technique has not been used to estimate long-term net CO<sub>2</sub> exchange in Monteverde. One limitation to this approach in the complex terrain, although some locations in the lower MV community would be appropriate. Even discontinuous NEE<sub>c</sub> data could be integrated with various forest productivity models such as PnetCN (Thornton *et al.* 2002) or ED2 (Medvigy *et al.* 2013) to estimate net primary productivity of forests in Monteverde. Some satellite datasets (such as the MODIS NPP algorithms) may be difficult to apply to Monteverde because of cloudiness. However, CO<sub>2</sub> exchange and fluorescence data collected from the recently launched NASA Orbiting Carbon Observatory 2 satellite may provide useful information for remote areas such as Monteverde.

Finally, the impact of reduced cloud water deposition during the dry season may affect canopy N cycling. The global trend has been towards enhanced N deposition due to vehicle emissions, fertilizer use and agriculture practices, leading to greater NH<sub>3</sub> and NO<sub>x</sub> emission and ultimately higher rates of N deposition. However, if the mechanism of delivery to epiphyte laden canopies change, little is known about canopy processing of dry deposition in Monteverde, or how this may impact both non-vascular and vascular epiphytes.

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