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Physical Environment — Update 2014

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The original chapter on the “Physical Environment” had two goals: 1) review what is known about the climate and weather, geology, geologic history, geomorphology, soils, and hydrology of Monteverde, and 2) identify areas where our knowledge is incomplete and further investigations will be fruitful. Since its publication, our overall understanding of tropical montane regions has benefitted from global-scale comparative data. Recent quantitative information on how variation in the physical environment interacts with biotic processes at the population, community and ecosystem scales are beginning to be addressed. Here, I summarize some of the recent research on: a) climate and hydrology of Monteverde; b) recent information on geology and geomorphology, including more accurate ages for recent volcanism, the large granodiorite pluton in the Monteverde area, and a refinement of the tectonic interpretation of the region; c) carbon, nutrients and enzymes in soils; d) the impacts of deforestation on soil carbon and nutrients, and e) comparisons between terrestrial and arboreal soils in the Monteverde area. I

briefly review selected studies at the end of each section.

Climate and Hydrology of Monteverde

We still lack complete information on climate and hydrologic cycling for Monteverde, especially long-term data on changes in wind-driven cloud and precipitation inputs, evapotranspiration, and stream flow. However, recent studies are closing these information gaps. Our understanding of hydrologic cycling in Monteverde has benefitted from a more complete understanding of the biophysical controls of cloud formation and persistence, and recent measurements of cloud water and wind-driven precipitation inputs across the Caribbean and Pacific slopes (Lawton *et al.*, 2001, 2010, Frumau *et al.* 2011, Hager and Dohrenbusch 2011, Schmid *et al.* 2011). Estimates of evapotranspiration and stream outputs have been refined using isotopic analyses of inputs, outputs, and isotopic signatures in tree rings (Anchukaitis *et al.* 2008, Guswa *et al.* 2007, Rhoades *et al.* 2010, Sanchez-Murillo *et al.* 2013). In addition, comparative information on hydrology in tropical montane cloud forests

(TMCF) has been advanced by recent syntheses (Bruijnzeel *et al.* 2010, Jarvis and Mulligan 2011). Some of these investigations have been driven by the realization that TMCF are especially susceptible to climate change (Pounds *et al.* 1999, 2006). Recent climate change model simulations indicate that mean dry season surface air temperatures along the Pacific slope of Costa Rica will increase 3.8 °C by 2100, in concert with increased variability in surface air temperatures and a projected decrease in dry season precipitation of approx. 14% (Karmalkar *et al.* 2011).

Information from remote sensing applications and simulation models have more accurately documented the biophysical controls over cloud base heights and the incidence of cloud immersion during the dry season in Monteverde (Lawton *et al.* 2001, 2010, Nair *et al.* 2008). Conversion of Caribbean lowland forest to pasture and agricultural lands has resulted in greater surface air temperatures and sensible heat flux, and lower latent heat flux and evapotranspiration rates. Reduced evapotranspiration over pastures raises the cloud condensation level in comparison to that over forest, and decreases the moisture content in air parcels during the dry season. Satellite imagery indicates that deforested areas of Costa Rica's Caribbean lowlands remain relatively cloud-free, while forested regions have well-developed dry season cumulus cloud fields (Lawton *et al.* 2001, Nair *et al.* 2008, Welch *et al.* 2008). Changes in surface energy balance in the Caribbean lowlands have resulted in an increase in cloud base height, a decrease in cloud immersion (Lawton *et al.* 2001; Nair *et al.* 2003), and a reduction in the number of consecutive days with precipitation during the dry season in Monteverde (Pounds *et al.* 1999, 2006, Lawton *et al.* 2010). Regional atmospheric model simulations have further linked changes in surface energy balance to the incidence and height of cloud immersion over the continental divide in the Monteverde region. Overall, these results suggest that land use change in lowland forests can have large impacts on the climate of adjacent mountains, although larger, global scale phenomena such as the El Niño-Southern Oscillation also contribute to variability in climate in TMCF (e.g., Anchukaitis *et al.* 2010).

However, limitations to our understanding of these processes still exist (Nair *et al.* 2003, Ray *et al.* 2006, 2009, 2010).

Variability in cloud immersion and wind-driven precipitation have been linked to a number of changes in Monteverde, e.g., decreases in populations of anoline lizards and anurans (Pounds *et al.* 1999), potential interactions with pathogens (Pounds *et al.* 2006), and increased drought stress in plants (Anchukaitis *et al.* 2008, Goldsmith *et al.* 2013). Experimental transplants of upper cloud forest epiphyte mats to tree canopies at slightly lower elevations that experience longer dry season conditions suggest that vascular epiphytes are vulnerable to the drier environments predicted for the bioregion due to climate change (Nadkarni and Solano 2002).

The inputs of cloud water and wind-driven precipitation to forest canopies have been further investigated since the work of Clark *et al.* (1998a,b, 2005). 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). They reported cloud water deposition rates of $1.2 \pm 0.1 \text{ mm day}^{-1}$, within the range of estimates from other TMCF sites (reviewed in Bruijnzeel *et al.* 2010). Cloud water measured directly averaged 5% of precipitation during the dry season, while use of a canopy hydrology model based on the use of $\delta^{18}\text{O}$ isotope content as a tracer for cloud water deposition (see below) represented 9% of dry season precipitation. Schmid *et al.* (2011) noted that $\delta^{18}\text{O}$ was a reliable tracer for cloud water deposition, but also acknowledged the difficulties in separating cloud water vs. precipitation during events characterized by a significant amount of wind-driven horizontal precipitation. High collection efficiencies for different cloud water collector designs corroborated the investigations of Schmid *et al.* (2011), including those used in previous research efforts in Monteverde (Clark *et al.* 1998a,b, Frumau *et al.* 2011).

Cloud and wind-driven precipitation inputs in the MVCFR were monitored at seven climate stations that measured rainfall, horizontal precipitation, throughfall, temperature and soil moisture along a 2.5 km transect across the Atlantic (windward) slope and the Pacific

(leeward) slopes (Hager and Dohrenbusch 2011). Annual precipitation ranged from 3690 mm on the leeward slope (similar to the amount measured by Clark *et al.* (1998a) of 4077 mm, but above the long term average measured by J. Campbell lower in the community of 2519 mm) to 6390 mm on the windward slope. Horizontal precipitation was 3560 mm at the ridge, where it exceeded rainfall during the dry season, compared to 330 mm and 28 mm at the lowest windward and leeward plots, respectively. For comparison, Clark *et al.* (1998b) estimated 886 mm of wind-driven cloud water and precipitation at a leeward forest site in the MVCFR. Throughfall amounts remained below rainfall on the lower slopes, but exceeded rainfall amounts on the ridge because of the additional wind-driven precipitation (Hager and Dohrenbusch 2011). Forest census measurements made along their transect further confirmed that strong hydrologic and topographic gradients correspond to differences in soil conditions and the occurrence of distinctive forest types across the continental divide in Monteverde (Hager and Dohrenbusch 2011).

Additional information on precipitation inputs and hydrologic cycling has been facilitated by an analysis of the isotopic composition of precipitation throughout Costa Rica (Rhoades *et al.* 2006, 2010, Sanchez-Murillo *et al.* 2013; method reviewed in Scholl *et al.* 2011). Precipitation samples collected from 2003 to 2005 had seasonal signals in $\delta^{18}\text{O}$ and $\delta^2\text{H}$ that were more negative (indicating that relatively higher concentrations of heavier ^{18}O and ^2H isotopes occurred compared to the more abundant lighter ^{16}O and ^1H isotopes of oxygen and hydrogen) during the dry and transitional seasons than during the wet season. In addition, cloud water has distinct $\delta^{18}\text{O}$ and $\delta^2\text{H}$ signals compared to rainfall (Schmid *et al.* 2011).

Attenuated signals of these heavy isotopes propagate through forests to streamflow, and provide a tracer for estimating cloud water and wind-driven precipitation inputs to watersheds during the dry and transitional seasons. For example, Guswa *et al.* (2007) used $\delta^{18}\text{O}$ data in precipitation and streamflow to partition baseflow (i.e., the portion of streamflow that is derived from the seepage of water from the

ground into a channel slowly over time, rather than direct runoff; see Clark *et al.* 2000) sources during the dry season. They reported that dry season precipitation contributed from 0% to 31% of baseflow for streams in the Monteverde area, with the highest proportions occurring for Río San Luis (31%) with headwaters along the Brillante Gap. The contribution of dry-season precipitation to stream baseflow peaked near the end of the transitional for most streams, whereas the water in the Río San Luis remained enriched throughout the transition and dry seasons. Additional analyses of $\delta^2\text{H}$ in precipitation allow for an estimate of recycling of precipitation between forests and the atmosphere before deposition (Sanchez-Murillo *et al.* 2013). Air mass trajectory analyses for Monteverde further indicated the input of “recycled” precipitation from the Caribbean lowlands.

The effects of cloud deposition on vascular plant water status and epiphytes have been further investigated. Goldsmith *et al.* (2013) used satellite and ground-based observations to study cloud and leaf wetting patterns in pre-montane and montane forests in Monteverde, and evaluated the importance of direct uptake of water accumulated on leaf surfaces to plant water status during the dry season. Although 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, leaf wetting events resulted in foliar water uptake in all species studied. They concluded that foliar water uptake is common in Monteverde, and improves plant water status during the dry season. Isotopic analyses of $\delta^{18}\text{O}$ in tree rings of dominant species has allowed an estimate of seasonality of the sources of water used and of water stress of trees in Monteverde (Anchukaitis *et al.* 2008). Further, $\delta^{18}\text{O}$ analyses in main stems of *Pouteria* sp. have been linked to long-term climate variability in the Monteverde (Anchukaitis *et al.* 2010).

The role of epiphytic vegetation in stand hydrology 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 (323 ± 106 % dry

weight; Tobon *et al.* 2010). Evaporation following cloud water events followed a logarithmic decay pattern. Tobon *et al.* (2010) noted that uptake and evaporation of cloud water was highly dynamic. 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.

Geology of Monteverde

I summarize recent information on the geology of Monteverde, including more accurate paleomagnetic analyses of recent volcanic flows, further research on the large granodiorite pluton in the Monteverde area, and an overall refinement of the tectonic interpretation of the region. These new dates better constrain the magmatic and structural history of Costa Rica. Volcanic activity has occurred over a broad area known as the Central American volcanic arc for at least the past 24 Ma. Cromwell *et al.* (2013) conducted a comprehensive field and age determinations using paleomagnetic and $^{40}\text{Ar}/^{39}\text{Ar}$ analyses to date lava flows in Costa Rica. They determined that modern composite volcanoes (those active today include Rincón de la Vieja, Arenal, Platanar, Poás, Barva, Miravalles, Irazú, and Turrialba) have mainly been built during two recent peaks in volcanism dating (0.4–0.6 and <0.1 Ma), and are superimposed on older volcanic formations.

Igneous rocks in Costa Rica older than about 8 Ma have chemical compositions typical of ocean island basalts and intra-oceanic arcs. In contrast, younger igneous deposits contain abundant silicic rocks, which are significantly enriched in SiO_2 , alkalis, and light rare-earth elements, and are geochemically similar to the average upper continental crust (Deering *et al.* 2012, Hayes *et al.* 2013). Žacek *et al.* (2011) provided an account of the gabbro to granodiorite Guacimal pluton in the Cordillera de Tilarán. Plutons are exposed in all three major ranges (Talamanca, Central, and Tilarán ranges) and were emplaced from approximately 17 to 3.5 Ma, and mainly from 7–10 Ma during an apparent gap in volcanism. The Guacimal pluton intruded into mafic volcanic rocks of the

Aguacate group during this time, and is overlain by younger andesite lava of the Pleistocene Monteverde Formation along its northeastern boundary.

Recent tectonic interpretations and more refined estimates for the rates and direction of movement for Cocos plate subduction beneath the Caribbean plate occur in the literature. MacMillan *et al.* (2004) present the plate tectonic history for the southern Central American volcanic arc since the mid-Miocene. Geophysical, geochemical, and petrographic studies have contributed to a better understanding of regional geologic history (Derring *et al.*, 2012, Hayes *et al.* 2013). Using isotope geochemistry and seismic velocity analyses, Hoernle *et al.* (2008) indicated flow in the mantle wedge beneath Costa Rica and Nicaragua is trench-parallel rather than trench-normal as in classical plate subduction models, and that parallel flow needs to be taken into account in models evaluating thermal and chemical structure and melt generation in subduction zones. They also noted that the isotopic signature in volcanic rocks in Costa Rica is consistent with seamounts along the Galapagos hotspot track on the subducting Cocos plate, rather than from the mantle wedge or eroded volcanic fore-arc material. This isotopic signature decreases continuously from central Costa Rica to northwestern Nicaragua. They estimated minimum northwestward flow rates of 63–190 mm yr^{-1} , comparable to the magnitude of subducting Cocos plate motion (85 mm yr^{-1}).

Soils of Monteverde

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 the properties of soils 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, while no trend occurred

for soil nitrogen (Tanner *et al.* 2014). Soil CO₂ flux followed the same trend as soil carbon; mature forest soils exhibit slightly higher CO₂ flux, but greater spatial variability, and secondary forest soils have a higher flux than pasture soils. They suggested that differences in soil CO₂ flux between sites were due to differences in root respiration, controlled by the size and abundance of plant roots in the subsurface. Comparing canopy and terrestrial soils in the MVCFR, Nadkarni *et al.* (2002) reported that the carbon content of canopy organic matter 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.

Suggestions for Future Research

We are beginning to understand some of the complex relationships between climate, microclimate, the distribution of species and ecosystem functioning at Monteverde. These recent data lead to key questions that should be addressed in future research efforts. How will

interactions of climate change and land use change in the Caribbean lowlands affect cloud formation and dry season precipitation in Monteverde? How closely coupled is the maintenance of biodiversity to changes in climatic and micro-climatic variables? Will changes in climate and precipitation drive further local extinctions, and how could extinctions lead to changes in community-level interactions and ecosystem functioning? Addressing these questions will involve the integration of field observations with simulation studies, based on the abundant research conducted previously in Monteverde and other TMCs.

Geological interpretation of Monteverde and Costa Rica is continuing to evolve. Regional simulation studies of the plate boundaries incorporating rates and direction of movement of tectonic plates derived from isotopic studies, a more realistic treatment of mantle convection processes, and mechanisms of incorporation of basaltic oceanic material vs. more andesitic continental plate material will further these research efforts. Increased use of seismic sounding studies could help resolve some of these questions.

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