

3

Plants and Vegetation — Update 2014

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The Monteverde area is home to a large and unique flora, thanks to the topography of the mountains and the rare cloud forest that sits atop them. The original chapter in this book (Haber, 2000) contains a thorough description of the diversity and ecology of Monteverde's flora. Here, I review a selection of recent research on plants and vegetation from the Monteverde area.

The abundance of epiphytes, plants that grow perched on other plants, is one of the most distinctive and striking aspects of cloud forest vegetation. Monteverde has remained an important location for research on epiphytes and canopy biology, led by the efforts of Nalini Nadkarni, who first ascended the canopy in 1980 and began describing the rich flora found high above the forest floor. Recent research has illuminated more details about the ecology and life history of the once-mysterious epiphytes, as well as their important interactions with the environment.

A particularly characteristic family of epiphytes, the bromeliads (Bromeliaceae), has received substantial research attention in Monteverde recently. Evidence for arbuscular-mycorrhizal fungal associations was found in the

bromeliad species *Werauhia werkleana* (previously identified as *Vreisia werkleana*; W. Haber, pers. comm.; Hammel *et al* eds, 2000) (Rowe & Pringle 2005). The reproductive traits of several species have also been studied in depth. *Pitcairnia brittoniana* is hummingbird-pollinated (Bush & Guilbeau 2009), while *Werauhia gladioliflora* in the upper San Luis valley is pollinated by bats; *W. gladioliflora* flowers in the rainy season, with fruit maturation and seed dispersal occurring during the dry season (Cascante-Marín *et al* 2005). Both species, however, were shown to be capable of successful self-pollination, implying that these plants are flexible in their reproductive strategies and can continue reproducing independently of pollinator abundance (Cascante-Marín *et al* 2005, Bush & Guilbeau 2009). From a community standpoint, the composition of bromeliad species differs between primary and secondary forest (Cascante-Marín *et al* 2006), but this was not explained by variation in seed establishment success between species (Cascante-Marín *et al* 2008). Further studies on population and community ecology of bromeliads are listed at the end.

Monteverde's epiphyte flora interacts greatly with both climate and nutrient cycles (Nadkarni 1986, Nadkarni and Matelson 1991, Hietz et al 1999), and these relationships are becoming even better understood. For example, epiphytic plants seem to absorb and retain a substantial proportion of their nitrogen from atmospheric inputs, such that the nitrogen cycle of arboreal plant communities is relatively independent from that of the trees and terrestrial soil (Hietz *et al* 2002, Clark *et al* 2005). In addition to *W. werkleana*, associated mycorrhizal fungi were found in species from the families Araceae, Clusiaceae, and Ericaceae, with first records in *Cavendishia melastomoides*, *Disterigma humboldtii*, and *Gaultheria erecta*. Mycorrhizas were not found in epiphytes from the common genus *Peperomia* (family Piperaceae) (Rains *et al* 2003). These fungi, known mostly from association with ground-dwelling plants, aid nutrient and water absorption.

Epiphyte communities contribute hugely to water and nutrient cycling, overall biomass (Nadkarni 1984, Nadkarni *et al* 2004), and species diversity of Monteverde's forests (Haber 2000), but this valuable flora may be particularly sensitive to ongoing environmental changes, especially in climate. Recolonization of epiphytes proceeded extremely slowly after branches were experimentally stripped, suggesting that it is difficult and slow for canopy communities to recover after unnatural disturbance (Nadkarni 2000). Additional evidence implies that cloud forest epiphytes depend on the frequent cloud immersion for survival, presumably because they receive water and nutrients from the enveloping mist. When epiphytes in intact canopy mats were transplanted from the cloud forest at 1480m to trees only 70-140m lower in elevation, but below the base height of the clouds, they suffered significant decreases in size and season-dependent mortality (Nadkarni and Solano 2002). Models of climate change predict that cloud height will rise in the coming decades (Still *et al* 1999), which would have serious implications for a cloud forest such as Monteverde, which resides at the top of its local elevation gradient. Ongoing research in the Monteverde area is further exploring the relationship between epiphyte ecology and

climate, in order to understand the effects that these impending changes will have on the epiphytic flora and the biotic and abiotic processes they affect.

Of course, the unique climatic conditions in Monteverde have affected more than just the "air plants." Various species of cloud forest trees perform foliar uptake, an unusual trait by which plants absorb water through their leaves, in reverse of the canonical water transpiration pathway. Finding this syndrome is perhaps not entirely surprising in the cloud forest; indeed, tree species found just below the cloud base in Monteverde showed more limited capacity for foliar uptake, implicating it as an important adaptation to the specific mist-shrouded conditions that define cloud forest (Goldsmith *et al* 2013).

Comparative studies between different forest types are becoming increasingly common, and ever more relevant. To understand the ongoing and future impacts of global change on the forests of Monteverde and elsewhere, it is crucial to know how different environmental conditions affect species and communities. Plants form the base of all ecosystems, and usually interact more directly with the abiotic environment than do animals; thus, understanding their responses to environmental change is paramount.

Currently, ample area is being left for forest regeneration, prompting deserved interest in the dynamics of these young secondary forests, how they differ from and interact with old growth habitats, and the advantages and disadvantages of secondary forest for biodiversity conservation. In Monteverde, the differences between primary and secondary forests have been measured in several ways. For example, canopy-held biomass in old growth forests around Monteverde has been variously measured to be 15 times (Köhler *et al* 2007) and 50 times (Nadkarni *et al* 2004) greater than in nearby secondary forests, as well as offering different nutrient balances (Nadkarni *et al* 2004) and significantly greater water storage capacity in the primary forest (Köhler *et al* 2007).

Similarly, comparing plant species across different climatic zones is moving from an interesting description of community turnover to an urgent need to understand where, why, and

how plants are limited, enabled, or controlled by climate. Monteverde is an excellent place to study the biotic effects of variations in climate, because the unique topography of the area yields a wide range of temperature, precipitation, seasonality, and other conditions, encompassing six Holdridge life zones in a relatively small area (Haber 2000; Bolaños *et al* 2005). An analysis of tree species composition and turnover across two 300m elevational transects in Monteverde revealed that species turnover corresponds with gradients in climatic conditions (precipitation, temperature, and soil), suggesting that many species respond strongly to the diverse microclimates created by complex topography and sharp elevational relief, which yields the high beta diversity found in the area (Häger 2010). The discovery of foliar water uptake by Goldsmith *et al* (2013) emphasized that the ability to absorb water from the clouds was stronger in tree species native to the cloud forest compared to other species found at only slightly lower elevations, below the cloud base. Forthcoming elevational gradient analyses in Monteverde include epiphyte species' distributions and microbial characteristics of both terrestrial and arboreal soil.

Population studies of the Lauraceae tree *Ocotea ternera* have deepened our understanding of this important species, which serves as a primary food source for many cloud forest birds. A long-term study with 20 years of measurements on a natural population of *O. ternera*, a species with sexually dimorphic individuals, revealed that female trees suffer a cost of reproduction, observed via reduced lifetime growth and lower photosynthetic capacity in the year following reproduction. Females also had overall slower growth rates and photosynthetic capacity than males (Wheelwright and Logan 2004), but larger leaf size, possibly to make up for their lower photosynthetic capacity (Wheelwright *et al* 2012).

Seed dispersal is another crucial aspect of plant reproduction, and this life history feature has been examined in depth in several species and communities in Monteverde. Seed survival in the bird-dispersed tree *Beilschmiedia pendula* (Lauraceae) was found to be optimal in the zone between 10-20m from the tree crown, although

only 10% of seeds were dispersed into this "high-quality" zone; over 70% of seeds ended up within 10m of a conspecific adult, where they suffer higher mortality from predation and fungal infection (Wenny 2000b), consistent with the Janzen-Connell hypothesis (Janzen 1970, Connell 1971). There is evidence that different species of birds create different seed shadows through dispersal. Bellbirds tended to deposit over half of *Ocotea endresiana* seeds >25m from the parent tree, and more often in gaps, whereas other species of birds only dispersed 6% of seeds so far away, and less than 3% in gaps (Wenny 2000a). Two trees in the Meliaceae family, *Guarea glabra* and *G. kunthiana*, are also bird dispersed, but the secondary dispersal caused by rodents hoarding the seeds may actually be another important component of their dispersal syndrome. The rodents tended to bring the seeds to microsites more beneficial for germination success, due to increased distance from conspecifics as well as ecological characteristics such as lower leaf litter and vegetation density (Wenny 1999).

From a community standpoint, seed rain was compared between canopy branches and ground soil in Monteverde. The canopy seed rain was dominated by epiphytic species, while seeds found on the ground were most commonly from large trees, indicating successful adaptation of directed dispersal for both groups. The majority of all seeds was dispersed by birds (Sheldon and Nadkarni 2013). Within seed banks of pioneer species, seeds that have greater chemical defenses tend to persist for longer in the soil (Veldman 2007).

Due to the unique and incredibly diverse composition of Monteverde's flora, new species and taxonomic revisions are constantly augmenting what is known. Recent newly described species include, but are far from limited to, *Dioscorea natalia* (Dioscoreaceae) (Hammel 2000), *Eugenia haberi* (Myrtaceae) (Barrie 2006), and *Mucuna monticola* (Leguminosae-Papilionoideae-Phaseoleae) (Moura *et al* 2012). For the most updated plant taxonomy, readers should consult the *Manual de Plantas de Costa Rica* (Hammel *et al*, 2010) or the TROPICOS database at <http://www.tropicos.org>.

In addition to the above discussed studies, here I provide a list of other papers published since 2000 on plant topics from the Monteverde area.

- Cascante-Marín, A., M. de Jong, E. D. Borg, J. C. B. Oostermeijer, J. H. D. Wolf, J. C. M. den Nijs. 2006a. Reproductive strategies and colonizing ability of two sympatric epiphytic bromeliads in a tropical premontane area. *International Journal of Plant Sciences* 167:1187-1195.
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- Harvey, C. A. 2000. Windbreaks enhance seed dispersal into agricultural landscapes in Monteverde, Costa Rica. *Ecological Applications*, 10:155-173.
- Harvey, C. A. 2000. Colonization of agricultural windbreaks by forest trees : Effects of connectivity and remnant trees. *Ecological Applications*, 10:1762–1773.
- Kohlmann, B., D. Roderus, O. Elle, X. Soto, & R. Russo. 2010. Biodiversity conservation in Costa Rica: a correspondence analysis between identified biodiversity hotspots (Araceae , Arecaceae , Bromeliaceae , and Scarabaeinae) and conservation priority life zones. *Revista Mexicana de Biodiversidad*, 2:511–559.
- Krings, A. 2000. Floristics and ecology of Mesoamerican montane climber communities: Monteverde, Costa Rica. *Selbyana*, 21:156–164.
- Lawton, R. M. & R. O. Lawton. 2010. Complex spacial structure in a population of *Didymopanax pittieri*, a tree of wind-exposed lower montane rain forest. *Plant Ecology*, 210:125–135
- Moran, R. C., K. Klimas, & M. Carlsen. 2003. Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. *Biotropica*, 35:48–56.
- Muchhala, N. 2003. Exploring the boundary between pollination syndromes: Bats and hummingbirds as pollinators of *Burmeistera cyclostigmata* and *B . tenuiflora* (Campanulaceae). *Oecologia*, 134:373–380.
- Murray, K.G., and J. Mauricio Garcia-C. 2002. Contributions of seed dispersal and demography to recruitment limitation in a Costa Rican cloud forest. Pp. 323-338, in: Levey, D. J., W. R. Silva, and M. Galetti. (eds) *Seed dispersal and frugivory: Ecology, evolution, and conservation*. CABI Publishing, Wallingford, UK.
- Nadkarni, N. M., D. Schaefer, T. J. Matelson, & R. Solano. 2002. Comparison of arboreal and terrestrial soil characteristics in a lower montane forest, Monteverde, Costa Rica. *Pedobiologia*, 46:24–33.
- Papes, M., A. T. Peterson, & G. V. N. Powell. 2012. Vegetation dynamics and avian seasonal migration: clues from remotely sensed vegetation indices and ecological niche modelling. *Journal of Biogeography*, 39:652–664.
- Piper, J. 2006. Colonization of tubu (*Montanoa guatemalensis*, Asteraceae) windbreaks by woody species. *Biotropica*, 38:122–126
- Stone, J. L., E. E. Wilson, & A. S. Kwak. 2010. Embryonic inbreeding depression varies among populations and by mating system in *Witheringia solanacea* (Solanaceae). *American Journal of Botany*, 97:1328–33.
- Waring, B. 2008. Light exposure affects secondary compound diversity in lichen communities in Monteverde, Costa Rica. *Pennscience*, 6:11–13.

- Yanoviak, S. P., H. Walker, & N. M. Nadkarni. 2003. Arthropod assemblages in vegetative vs humic portions of epiphyte mats in a neotropical cloud forest. *Pedobiologia*, 48:51–58.
- Yanoviak, S. P., N. M. Nadkarni, R. Solano. 2007. Arthropod assemblages in epiphyte mats of Costa Rican cloud forests. *Biotropica*, 39:202–210.