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Monteverde: Ecology and Conservation of a Tropical Cloud Forest - 2014 Updated Chapters

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Introduction — Update 2014

Nalini M. Nadkarni & Nathaniel T. Wheelwright

In the last three decades, Monteverde, Costa Rica has emerged as a critical venue for research in tropical montane biology. Over 350 scientific articles and 10 scholarly books have been generated. In terms of conservation and training young biologists, Monteverde is considered one of the premier tropical cloud forest sites in the world.

This rich research, conservation, and education legacy exists even though the research infrastructure has been extremely limited, relative to many other major tropical field stations. Research has mostly been conducted by single investigators, often with little or no extramural support, and there have been few large-scale, long-term, multi-institutional projects.

Synergistic interactions between several distinctive features of Monteverde appear to explain the high research productivity in the face of limited research support: a long-time emphasis on watershed protection and conservation; a commitment to education, from bilingual local grade schools to graduate field courses offered by the Organization for Tropical Studies and other groups; outstanding natural attractions to attract ecotourism as an economic driver, and good infrastructure to support it; and a rare degree of civic awareness and community engagement (Nadkarni *et al.* 2013).

For example, the presence of a strong scientific understanding of the negative effects of deforestation on soil erosion, water quality, and biodiversity prompted the early conservation movement. This helped raise awareness about the presence of remarkable species such as the Resplendent Quetzal and Golden Toad and the threats they faced from fragmented landscapes, introduced species, and changing climates. The presence of such charismatic species, living in such charismatic habitats, attracted student groups and tourists to the area. This led to an income flow that could support continued preservation and additions to cloud forest preserve areas, which expanded opportunities for scientific research. The sense of civic awareness and spirituality of this Quaker-originated community fostered a sense of personal responsibility to carry out actions to benefit people, wildlife, and plants.

Because montane forests comprise a much smaller land area and have a lower economic value than lowland forests, they have tended to attract fewer scientists and less funding and research infrastructure. Monteverde provides an example – and potentially a model – for scientists in other montane cloud forests and other tropical ecosystem types that do not attract large funding and yet still can produce excellent science (Nadkarni *et al.* 2013).

It has been 14 years since *Monteverde: Ecology and Conservation of a Tropical Cloud Forest* was first published (Nadkarni and Wheelwright 2000). Given the many new research projects that have appeared in the interim, we felt it was time to update the book. More importantly, the book's cost and the fact that it was published only in English effectively put the book out of reach for many readers in Latin America. Clearly, it is time to translate the book into Spanish, particularly in light of accelerating rates of biodiversity loss — "defaunation" — and the paucity of conservation monitoring studies in the neotropics (Fig. 1; Dirzo et al. 2014). In addition to translating the original book, we requested representatives of the Monteverde research, conservation, and education communities to write an actualización for each chapter. The actualizaciones are not meant to describe in detail everything that has transpired in each field since the original book was published, but rather to inform the reader of significant advances and relevant literature on that topic.

In the spirit of Monteverde research, education, and education, we drew upon grass-roots support — rather than applying to traditional funding sources — to fund the translation of this translation. We had two main objectives. The first objective was to educate, inspire and engage as many people as possible in the effort to protect tropical cloud forests. When we were in graduate school, the standard model of conservation was this: acquire a lot of land, put a big fence around it, and keep people out. That approach has been discredited over the years, and now everyone realizes the importance of having people "buy in" on conservation projects. Our second objective was to attempt to shift the culture of scientists who conduct research in developing countries, then return home to publish their work in English in scholarly journals. "Education" literally means "leading outward" — in this case, taking information about tropical biology and conservation that is currently sequestered in expensive books in privileged libraries and making it freely available on the web to anyone who speaks Spanish.

Within six weeks of initiating a Kickstarter campaign (www.kickstarter.com/projects/768016193/rainforest-conservation-making-science-available-i) in December, 2014, we received contributions from 185 individuals from all walks of life and from all over the world—Costa Rica, of course, but also New Zealand, France, Canada, the Netherlands, Spain, Switzerland, Mexico and other countries, which has made the translation, updating and publication of this book possible. We hope that readers will find it a useful resource for understanding and protecting tropical cloud forests not just in Monteverde but throughout Latin America.

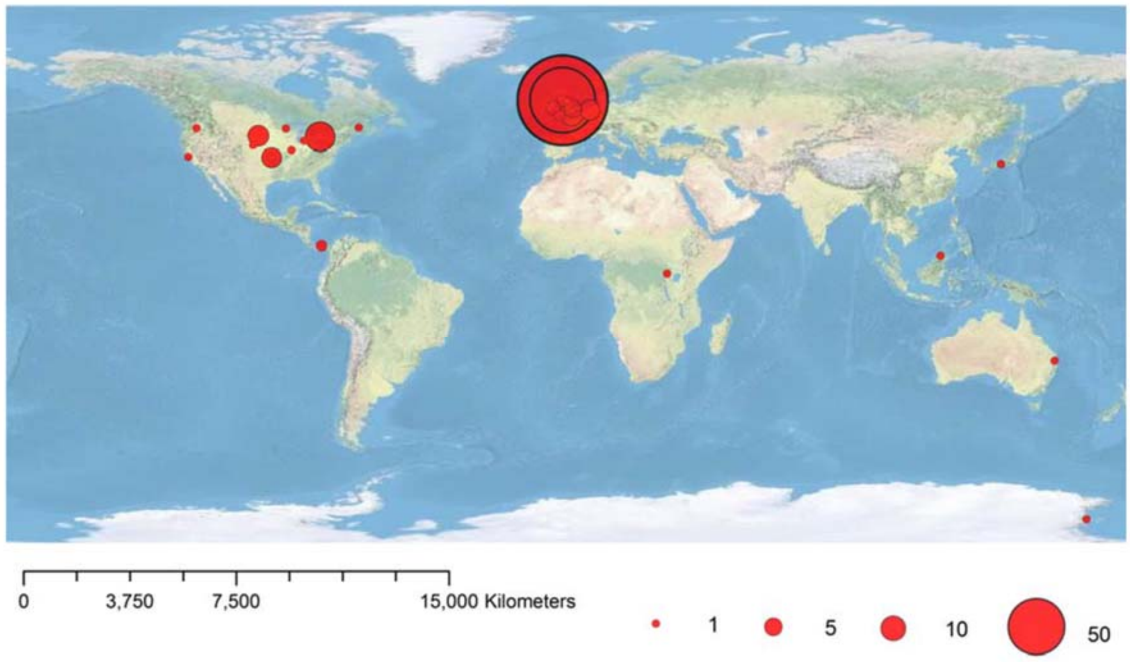

Fig. 1. Locations of all sources of invertebrate abundance time series data. The size of the circle is relative to the number of species studied in a given location. Note the paucity of studies in Latin America and the tropics in general (figure from Supplementary Material in Dirzo et al. 2014).

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Physical Environment — Update 2014

Kenneth L. Clark, Robert O. Lawton & Paul R. Butler

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 ± 0.1 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 δ^{18}O isotope content as a tracer for cloud water deposition (see below) represented 9% of dry season precipitation. Schmid *et al.* (2011) noted that δ^{18}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 $\delta^{18}O$ and $\delta^{2}H$ that were more negative (indicating that relatively higher concentrations of heavier ^{18}O and ^{2}H isotopes occurred compared to the more abundant lighter ^{16}O and ^{1}H isotopes of oxygen and hydrogen) during the dry and transitional seasons than during the wet season. In addition, cloud water has distinct $\delta^{18}O$ and $\delta^{2}H$ 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 $\delta^{18}O$ 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 $\delta^{2}H$ 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 premontane 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 $\delta^{18}O$ 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). Futher, $\delta^{18}O$ 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}Ar/^{39}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 CO_2 flux followed the same trend as soil carbon; mature forest soils exhibit slightly higher CO_2 flux, but greater spatial variability, and secondary forest soils have a higher flux than pasture soils. They suggested that differences in soil CO_2 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 TMCFs.

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 sesmic sounding studies could help resolve some of these questions.

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3

Plants and Vegetation — Update 2014

Emily Hollenbeck

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.

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4

Insects and Spiders — Update 2014

Paul Hanson

In the last 15 years there have been a number of publications on the insects of cloud forests, and it is impossible to include all of them in this update. In particular, it has not been possible to compile all the taxonomic publications that include species occurring in Monteverde, a compilation that would be useful since identification is the principal impediment to studying insects. Nonetheless, I have attempted to mention the most important taxonomic publications (of an order, family or subfamily) as well as some examples of specific investigations.

As in Hanson (2000), this update is organized by taxonomic group. Nonetheless, some publications deal with distinct groups and therefore do not fit this organization, for example the studies of arthropods associated with epiphytes (Yanoviak et al. 2004, 2006). Before commencing with the individual groups, two general comments should be made. First, the estimations of species numbers in each order are too low, but updated estimations are not attempted here. Second, it is important to emphasize that despite the advances reported here, there is still much to learned about the arthropods of cloud forests.

Small insect orders

For dragonflies and damselflies (Odonata) there is a very useful website that provides keys and descriptions of the families, as well as photos of all the species known from Monteverde (Haber 2014).

For the order Orthoptera there are two general publications, one on katydids (Tettigoniidae: subfamily Conocephalinae) (Naskrecki 2000) and another on grasshoppers (suborder Caelifera) (Rowell 2013), which provide valuable resources for future research on these groups of insects.

True bugs, spittlebugs, leafhoppers, treehoppers, etc. (order Hemiptera)

The vast majority of true bugs (suborder Heteroptera) are predatory or phytophagous, but species in the subfamily Triatominae (Reduviidae) suck blood from vertebrates. In Costa Rica, one species, *Triatoma dimidiata,* is the vector of Chagas disease. One of the few studies of this species in the wild was carried out in Monteverde (Salas Peña 2010), where it was found principally on trunks of live trees, although it was more abundant in residential areas.

With respect to the suborder Auchenorrhyncha, the principal publication in recent years is one on treehoppers (Membracidae), which includes a guide for identification, photos of all the genera, and summaries of their biology (Godoy et al. 2006). This book should greatly facilitate future studies of these gaudy insects. A publication on the spittlebugs (Cercopidae) associated with pastures (Thompson & León-González 2005) will assist in identifying Monteverde species associated with grasses.

Recently, a study was carried out in Monteverde which examined the responses of six species of Auchenorrhyncha to a model of a redstart (*Myioborus*, Parulidae), a bird species that hunts insects by first frightening and then pursuing them. Two Membracidae (with structural defenses) were the most sensitive, whereas two Cixiidae (defended by camouflage) were the last to flee; two Cercopidae (with aposematic coloration) showed an intermediate response (Galatowitsch & Mumme 2004).

Beetles (order Coleoptera)

Some general works that include aids for identification and summaries of biology are available for Staphylinidae (Navarette-Heredia et al. 2002), Scarabaeidae-Dynastinae (Ratcliffe 2003), Scarabaeidae-Cetoniinae (Solís 2004), Chrysomelidae-Cassidinae (Chaboo 2007) and Chrysomelidae-Chrysomelinae (Flowers 2004).

One of the largest families of beetles is Curculionidae, which includes the phytophagous weevils. Two groups that are found in Monteverde and which have been the subjects of research in recent years are members of the subfamily Baridinae associated with Piperaceae (Prena 2010) and those in the tribe Derelomini (now known as Acalyptini; subfamily Curculioninae). Various members of the latter group are pollinators of palms, but some species have changed host plants and can be pollinators of Cyclanthaceae and *Anthurium* (Araceae) (Franz 2006).

Butterflies and moths (order Lepidoptera)

For butterflies (superfamily Papilionoidea) there is a website providing a list of species known from Monteverde, with more detailed information and photos of the glasswing butterflies (Nymphalidae: Ithomiini) (Haber 2001).

In Hanson (2000) there is a summary of the biology of *Manataria maculata* (Nymphalidae-Satyrinae; now classified as a subspecies of *M. hercyna*), which lays eggs on bamboo in the Pacific lowlands (Murillo & Nishida 2003), but spends most of the year in reproductive diapause at higher altitudes, including Monteverde. This is an unusual butterfly in that it is crepuscular and uses different communal roosts—protected sites near the ground during the day and in the canopy at night, probably to avoid birds during the day and mice during the night (Hedelin & Rydell 2007). Its Vogel's organ, situated at the base of the front wing, detects ultrasounds of insectivorous bats, allowing this butterfly to respond with evasive flight (Rydel et al. 2003). Although Vogel's organ is found in the majority of Satyrinae, this is the first case where sensitivity to ultrasound has been demonstrated (other Satyrinae probably use this organ to detect the sounds associated with birds in flight).

As mentioned in Hanson (2000), the only Satyrinae in Monteverde with transparent wings is *Cithaerius pireta* (cited as *C. menander*). Recently, the larval host plant of this species has been discovered, *Philodendron herbaceum* (Araceae) (Murillo-Hiller 2009).

Most families of Lepidoptera are microlepidopterans, but their biology is relatively poorly known. The larvae of many species are leaf miners or leaf rollers. The larvae of a few species induce galls on plants; for example, an undescribed species of Momphidae produces quite large stem galls on *Conostegia oerstediana* (Melastomataceae).

Flies (order Diptera)

Of all the principal insect orders, the inventory of flies is the most advanced, both in Costa Rica as a whole and in cloud forests in particular. The two volumes by Brown et al. (2009, 2010) provide keys for the identification of fly genera and summaries of our knowledge of each genus. This valuable work opens doors for future research on flies.

Many of the specialists who collaborated in the production of the two volumes mentioned above are currently carrying out an inventory of the flies found in a cloud forest at Zurquí de Moravia (Zurqui All-Diptera Biodiversity Inventory, ZADBI 2014). Although this cloud forest is located in a different mountain range, the results of this project will be very applicable to the Monteverde cloud forest. When the results of the Zurqui project become available we should have a significantly better understanding of the fly fauna of Costa Rican cloud forests.

The biology of fly larvae is extremely diverse. This order includes the most species-rich family of gall-inducers, Cecidomyiidae (Hanson & Gómez-Laurito 2005). Although there is a large diversity of plant galls in Monteverde, there are very few studies of these insects. In large part this is due to the fact that Cecidomyiidae is probably the largest family of insects and at the same time probably harbors the greatest proportion of undescribed species (more than 99%). Other phytophagous fly larvae include leaf miners, for example, two species of Agromyzidae on *Bocconia frutescens* (Papaveraceae) (Boucher & Nishida 2014).

The larvae of other flies are predators, one of the best studied families being Syrphidae. The literature gives the impression that nearly all predatory syrphid larvae feed on aphids and other Sternorrhyncha (Hemiptera) on plants. Nonetheless, the biology of predatory syrphids is probably much more diverse in the Neotropics. For example, *Ocyptamus luctuosus*, a species found in Monteverde, is a predator in the water that accumulates in epiphytic bromeliads (Rotheray et al. 2000). *Ocyptamus* is one of the most diverse genera of Syrphidae and the evidence suggests that it is not a monophyletic group (Mengual et al. 2012).

Some adult flies are pollinators of certain plants. An unusual example from Monteverde is the fungus gnat, *Bradysia floribunda* (Sciaridae), which pollinates *Lepanthes glicensteinii* (Orchidaceae) via a mechanism known as pseudocopulation. This orchid attracts and dupes the male fungus gnats, which confuse the flower for a female gnat and then copulate with it, in the process receiving a pollinarium that becomes attached to its abdomen (Blanco & Barboza 2005).

Wasps, ants and bees (order Hymenoptera)

There are two books in Spanish on the Hymenoptera of the Neotropical region, one that emphasizes identification (Fernández & Sharkey 2006) and the other with detailed summaries of the biology of the order (Hanson & Gauld 2006). Although these books cover the entire region, they provide a good introduction for studies of Monteverde hymenopterans.

The vast majority of hymenopterans are parasitoids of other insects, but in recent years several species have been discovered that have made an evolutionary transition to phytophagy. For example, in Monteverde the larvae of *Eurytoma werauhia* (Eurytomidae) feed on the floral buds of *Werauhia gladioliflora* (Bromeliaceae) (Gates & Cascante-Marín 2004). In the Central Valley of Costa Rica the larvae of *Allorhogas conostegia* (Braconidae) induce galls in the fruits of *Conostegia xalapensis* (Melastomataceae), but it is possible that in Monteverde another (undescribed) species of the same genus produces these galls (Chavarría et al. 2009a). This deserves more research, and if this hypothesis is correct, it could represent an interesting case of speciation.

The wasps that are best known to the general public are the eusocial wasps which construct paper (carton) nests (Vespidae, subfamily Polistinae). The best studied species in Monteverde is *Polybia aequatorialis* (O'Donnell et al. 2004, Jones et al. 2009), which is the only species of Polistinae that occurs at very high elevations (more than 3000 m), where they have enormous colonies (Chavarría et al. 2009b).

Ants (Formicidae) continue to be one of the best studied hymenopteran families in Monteverde. Some research deals with the entire ant fauna. For example, utilizing canopy fogging, fewer species were found in secondary forest than in primary forest, but the number of species in pasture trees was similar to that in primary forest (Schonberg et al. 2004). A study of leaf litter ants showed that the complex of species was not very affected by the formation of forest clearings (Patrick et al. 2012). Other studies deal with particular groups of ants and in recent years army ants (Ecitoninae, now placed in Dorylinae) have received considerable attention, especially with respect to the effects of altitude/temperature and forest fragmentation on the ants (O'Donnell & Kumar 2006, Kumar & O'Donnell 2009, Soare et al. 2014), and the birds that accompany these ants (Kumar & O'Donnell 2007).

Spiders (order Araneae)

A recent study of the arboreal spiders in Monteverde found no differences in the abundance or number of species in primary versus secondary forest. Nonetheless, in both forest types vertical differences were observed, with greater abundance and a greater number of species on tree trunks (from zero to two meters above the ground) than in the canopy (Yanoviak et al. 2003).

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6

Birds — Update 2014

Bruce E. Young

Although the pace of research on birds in Monteverde may have slowed during the 14 years since the last synopsis (Young and McDonald 2000), researchers continue to make important contributions to tropical avian biology and other scientific disciplines. Elevational gradients and migrations of birds along them still inspire research in Monteverde, where field study at varying elevations is facilitated by the steep topography and easy access. These gradients are also useful for studying biotic responses to climate change, a growing threat to biodiversity, especially in the tropics (Colwell et al. 2008). Ornithologists completed two new autecological studies and finished two long-term studies initiated in the 20th century, continuing a long and valuable tradition in Monteverde. Other scientists tackled new research topics in bird-army ant interactions and behavior. Finally, careful observation continues to extend our knowledge of natural history, such of the first nest description for Silvery-fronted Tapaculo (*Scytalopus argentifrons*; Young and Zuchowski 2003) and an observation of a Slaty-backed Nightingale Thrush (*Catharus frantzii*) foraging on a frog (Acosta and Morún 2014). The following summarizes the major findings of the 27 publications that encompass this new research.

Elevational Gradients, Migration, and Conservation

New research has shed light on the remarkable biotic turnovers associated with elevational gradients that characterize Monteverde and many tropical mountain slopes. A new statistical analysis revealed that the beta diversity (the increase in species richness across habitats) of birds on the Pacific slope of Monteverde is twice as high as that at the same elevations on temperate mountains (Jankowski et al. 2009). Moisture gradients, rather than elevation per se, best explained the rapid species turnover. The Caribbean slope of Monteverde, with a less dramatic moisture gradient, has substantially lower beta diversity than that of the Pacific slope, where a rain shadow accentuates moisture differences. One mechanism leading to narrow ranges of Monteverde birds appears to be behavior. A series of song playback experiments demonstrated that congeneric species that replace each other along elevational gradients show interspecific territorial behavior toward one other (Jankowski et al. 2010).

How does abundance correlate with range size in birds occupying Monteverde's different elevational zones? An extensive analysis using both mist-net and point count data revealed that species occupying fewer sites also tend to be less abundant in those sites than those occupying more sites (Jankowsli and Rabenold 2007). At a broader scale, species with larger range sizes occupied more habitat zones in Monteverde than those with smaller range sizes. Species endemic to Costa Rica and western Panama tended to occur at the highest elevations and have lower abundance. These results highlight the conservation challenges posed by this and other endemic highland avifaunas: most species are relatively rare at both geographical and local scales.

Seasonal migration across elevational gradients continues to attract scientific attention. A study of eight large frugivorous bird species, including guans, trogons, toucans, and cotingas, confirmed the results of earlier studies on seasonal movements (Chaves-Campos 2004). The birds generally nest at higher elevations and move to lower elevations when not breeding, although some individuals remain at high elevations year round. This pattern may be partially explained by seasonal changes in fruit abundance and precipitation, but additional factors may also be involved. A separate study of vegetation seasonality did not detect a link between vegetation changes and the migration of one of the species that Chaves-Campos studied, the Bare-necked Umbrellabird (*Cephalopterus glabricollis*; Papes et al. 2012)

Radio-tracking of two of these large, migrant frugivores, the Bare-necked Umbrellabird and Three-wattled Bellbird (*Procnias tricarunculatus*), revealed more details about the annual movements of the two species. These species are important from a conservation standpoint because both are categorized as threatened on the IUCN Red List of Threatened Species. The Bare-necked Umbrellabird appears to make a straightforward migration between breeding areas at 800-1400 m, and lower elevations (600-800 m) during the nonbreeding season (Chaves-Campos et al. 2003). The bellbird, on the other hand, makes a spectacular four-part migration that spans 200 km (Powell and Bjork 2004). Radio-collared individuals migrated from Monteverde to the Caribbean lowlands of northwestern Costa Rica and southeastern Nicaragua during the period of September to December, then flew to southeastern Costa Rica where they remained until March. Then they migrated to their breeding area at 1000-1800 m on the Caribbean slope of Monteverde. Finally, in June and July, the birds migrated back across the continental divide to mid-elevation Pacific slopes in Monteverde, where they remained until September. The migrations of bellbirds and umbrellabirds highlight pressing conservation needs. Although the breeding areas of both are well protected in Monteverde, each spends significant periods of time in unprotected habitats. Umbrellabirds descend to the lowest elevation where intact forest remains on the Caribbean slope of Monteverde. Loss of lowland habitat may be a limitation for the Monteverde population as this species is known to occur at much lower elevations elsewhere in Costa Rica where lowland forests persist. Bellbirds are also vulnerable because they spend at least half of their annual cycle on unprotected lands.

Climate Change

Ongoing climate change threatens species and ecosystems worldwide. Sensitivity of Monteverde habitats to climate and dramatic climate differences over small spatial scales combine to make the area ideal for studying the effects of climate change on natural systems. Careful monitoring of the breeding birds in a small study plot near the entrance of the Monteverde Cloud Forest Preserve revealed that lower elevation species were colonizing and that higher elevation species were declining (Pounds et al. 1999). Annual colonizations were closely tied to the annual number of precipitation-free days, which result from increasing temperatures that raise cloud-bank levels.

A subsequent study modeled the effects of future climates on the community of montane birds. Using data on current population sizes, fine spatial-scale models predicted the decline of nearly half of 77 species currently occurring in the higher elevation forests of Monteverde during the next 100 years (Gasner et al. 2010).

More sobering was the finding that seven of the eight species predicted to become extirpated in the region already have small ranges restricted to Costa Rican and western Panamanian highlands.

Birds and Army Ants

A new area of study for Monteverde is the interaction between birds and army ants. The bird-army ant relationship is well known in tropical lowland forests, where several specialist species forage on insects and other invertebrates as they flee advancing army ant foraging raids. Recent observations in Monteverde reveal that a surprising diversity of montane birds also follow army ants when they swarm. During two months of opportunistic observations at 1200-1650 m elevation, researchers identified 41 bird species attending army ant raids (Kumar and O'Donnell 2007). Neither the diversity nor the abundance of ant-following birds was influenced by elevation, but both factors were affected by forest patch size. More bird species and more individuals followed army ants in continuous forest than in small forest fragments. More extensive observations showed that resident species are more likely to follow raids than long-distance migrants, and eight resident species regularly visit army ant bivouacs to determine when raids begin (O'Donnell et al. 2010). Although no montane species rely on army ants as extensively as some lowland specialists, attending army ant raids is an important foraging activity for several montane bird species.

Autecological Studies

A major contribution of ornithological research in Monteverde has been a series of autecological studies that provide detailed aspects of the life cycle and behavior or montane tropical birds (Young and McDonald 2000). Over the last 14 years, new results became available from two of those studies, on Brown Jays (*Cyanocorax morio*) and Long-tailed Manakins (*Chiroxiphia linearis*), while researchers initiated studies of two additional species, the Black-Breasted Wood-Quail (*Odontophorus leucolaemus*) and Slate-throated Redstart (*Myioborus miniatus*). In an epilogue to a long-term study of Long-tailed Manakins, a genetic study found little differentiation between manakins in Monteverde and those in Santa Rosa National Park, 115 km away in the Pacific lowlands (McDonald 2003). Although gene flow appears to be greater up from Santa Rosa to Monteverde than in the reverse direction, the intense sexual selection on this lek-breeding species appears to be insufficient to create significant genetic isolation to lead to speciation.

Brown Jays are known for their cooperative breeding system in which multiple females and males contribute to the rearing of young. Use of multi-locus DNA fingerprinting has shown that virtually all chicks in a nest are the offspring of a single primary female breeder that is able to suppress breeding by other females in her group (Williams 2004). Males have much less skewed breeding success, with multiple paternity occurring in 33-40% of nests, and extra-group paternity occurring in at least 20% of nests. Group size is important in determining the breeding success of a group. Larger groups are better able to defend territories with isolated nesting trees, which are key to preventing nest predation, the leading cause of nest failure (Williams and Hale 2006). Increased nesting success and post-fledging survival were also correlated with group size. The benefit to non-reproductive helpers in a group appears to be access to future breeding opportunities. Observation of marked individuals showed that breeding females and their social mates maintain their bond across years and have higher nest attendance and nestling feeding rates than helpers (Williams and Hale 2007). Compared to other New World jays, however, social mates invested relatively less in nesting activities, suggesting that mate guarding may not be an effective strategy (Williams and Hale 2008).

The Slate-throated Redstart is a common resident in all but the highest elevation forests in Monteverde, calling attention to itself with its constantly flashing white outer tail feathers. A set of ingenious experiments and observations confirmed a hypothesis that the adaptive value of this plumage coloration is to startle invertebrate prey during flush-pursuit foraging. Individuals that had their white outer tail feathers experimentally blackened foraged with only one-third the success of controls in which inner, black tail feathers where colored with a black marker (Mumme 2002). Further tail-coloring experiments that mimicked the natural variation in the extent of white tail feathers in geographic subspecies of the Slate-throated Redstart ranging from Mexico to Bolivia suggested that white tail feathers are adaptive for increasing foraging success, but the extent of white is constrained by regional habitat characteristics (Mumme et al. 2006).

Breeding in the Slate-throated Redstart is typical for Monteverde birds, spanning the late dry and early wet seasons from late May to early June during a five-year observation period (Mumme 2010). Females incubate clutches that average 2.9 eggs, but both parents feed young. Fledging occurred at an average age of 11 days, and parents subsequently provisioned fledglings for an additional four weeks. Nesting success was 40%, with predation the cause of 85% of nest failures (Mumme 2010).

Black-Breasted Wood-Quail live year-round in coveys of an average of four individuals (range 2-9) at similar densities (about one covey per 3.3 ha) in both fragmented and intact forest (Hale 2006). This species also breeds at the dry-wet season transition. Larger coveys produce more offspring than small coveys, hinting that the species may have a cooperative breeding system (Hale 2006). Sampling of 50 individuals from Monteverde revealed nine polymorphic microsatellite loci, providing useful markers for future genetic studies of this and other *Odontophorus* species (Hale and Hughes 2003).

Behavior

Several lines of evidence now indicate that Three-wattled Bellbirds learn their songs, making this species the first sub-oscine passerine known to learn songs (Saranathan et al. 2007, Kroodsma et al. 2013). Song learning has previously been documented only in hummingbirds, parrots, and oscine passerines. First, variation in mitochondrial DNA sequences and nuclear microsatellite loci does not correspond with the three vocal dialects of the species, which occur in Nicaragua, Monteverde, and Talamanca in southern Costa Rica (Saranathan et al. 2007). In addition, Monteverde birds appear to be bilingual, using the Talamanca as well as Monteverde dialects; a captive male raised in isolation developed abnormal songs that more closely resembled birds that occurred nearby. The lengthy (six year) song development period also strengthens the argument that bellbirds learn their songs, as does the fact that adults continually relearn songs (Kroodsma et al. 2013).

Landscape Ecology

One novel study developed land-cover models of bird use of habitats in forest fragments in Coto Brus, in southern Costa Rica, and then tested the models' ability to predict bird diversity and abundance in Monteverde habitats at similar elevations and life zones, 230 km away (Lindell et al. 2006). The results were mixed. Coto Brus models for canopy insectivores, understory insectivores and non-insectivores, and edge non-insectivores were successful for characterizing abundance of Monteverde birds in these habitats. However, Coto Brus models for open-country birds did not predict abundances of open-country birds in Monteverde. None of the predictions for species richness developed from the Coto Brus data set were more accurate than null models at predicting species richness in Monteverde communities. These findings indicate that land cover models are best extrapolated over the region where parameters are measured.

On a finer spatial scale, one observer asked what influenced bird visits to *Sapium glandulosum* trees isolated in pastures. Fifty-two bird species visited focal trees, preferentially visiting larger, more isolated trees with higher epiphyte loads (Sheldon and Nadkarni 2013). Although epiphyte loads helped attract birds, most foraging activity was focused on the host tree itself. Visitation was not affected by the distance of trees from forest edges, suggesting that Monteverde pastures are small relative to distances birds are willing to travel for foraging opportunities.

Conclusions

Study of Monteverde's avifauna continues to provide new perspectives on tropical birds. Although the area will continue to provide ready access to protected study sites, the future is uncertain for some members of the bird community. Climate change threatens to reduce the diversity of endemic species, and the shortage of protected habitats outside of Monteverde may compromise the persistence of some regional migrant species. Colonization by lowland species may serve to maintain species richness, consistent with observations of assemblages in which species richness remains despite declining temporal beta-diversity (Dornelas et al. 2014). The new body of research from Monteverde extends the outsized role that the region's avifauna has played in shaping our understanding of tropical avian biology.

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7

Mammals — 2000–2017

Robert M. Timm
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Mammalogists currently recognize nearly 6,400 species of Recent mammals worldwide and the number of new species being recognized has increased dramatically in recent decades. It is estimated that perhaps as many as 7,500 species might occur when additional studies are completed. This increase in the number of mammal species known is a result of exciting new discoveries in the field, as well as additional study of scientific specimens housed in museums. Using new techniques, including genetic data, as well as traditional morphological studies, scientists are undertaking taxonomic revisions that significantly increase our understanding of the diversity of mammals and the relationships among species.

We are fortunate that a number of biologists have worked at Monteverde beginning in the 1960s and considerable information and voucher material are available for study. We now know that at least 90 of mammals occur in the greater Monteverde area. However, one of the outcomes of these studies is that a number of name changes are proposed each year. These better reflect relationships between species; however, a bewildering array of new names often makes it difficult to understand what is happening when authors refer to an animal for which more than one scientific name exists, sometimes surrounded by controversy. A scientific name associated with a species is a hypothesis. Eventually, usage of these new names in scientific publications will lead to their acceptance (or refinement, in some cases). Meanwhile, it is up to researchers to make the sometimes difficult decisions as to whether to use the new names in our publications. Herein, our decisions are based on the current literature, our experience with these species both in the field and in study of museum specimens, and the best information currently available to us. Many of the name changes we provide below to the list of mammals of Monteverde appear in specialized systematic revisions; to assist researchers interested in Monteverde mammals, we provide the new name as well as a footnote to the older name.

At present, only one species of mammal, a newly described small-eared shrew, is apparently endemic to Monteverde. A single specimen of shrew found in the Reserve in 1973 was described recently as *Cryptotis monteverdensis*; extensive efforts to obtain additional specimens have proven futile to date (Woodman and Timm 2017). A species of harvest mouse of the genus *Reithrodontomys* found in the cloud forest also represents an undescribed species (see below). Additionally, intriguing observations suggest that one or more unrecognized species of rodents might be found in the cloud forest (LaVal, pers. obs.).

Researchers who wish to make comparisons between regions, habitats, or elevations should use this English version or the Spanish updated version (LaVal and Timm 2014; Apéndice 11) of our species lists of Monteverde mammals because a significant number of changes have been made since 2000. These changes are due in part to a more refined understanding of distributions and systematic relationships of the mammals, but also to improved ability to detect species and distributional changes due to climatic change. Because six life zones are represented in the updated species lists, comparisons should be made for each zone and not the entire list as representative of Monteverde. Comparisons are best made with specific habitats (life zones) within the greater Monteverde area.

LaVal's (in press) extensive use of Anabat detection systems has added a number of species of bats new to the various life zones that were not detected via standard mist nets. This has been especially true for the emballonurid and molossid bats.

Life zones are generally agreed to be biologically defined areas in which there is notable similarity between the flora and fauna throughout the zone. These are often defined by the species of birds and plants that occur there because these are easily observed and that has been especially true at Monteverde. On mountain slopes, upper and lower elevational limits can help to define the zones, but it is generally agreed now that any boundaries between two adjacent zones are poorly defined and flexible over time. When climate change leads to warmer (or cooler or drier) conditions, these elevational limits may move up or down the mountain as organisms attempt to remain within the temperature and humidity limits to which they are adapted. Thus, a bat for example originally restricted to Zone 1 in Monteverde, might move up to Zone 2 under warming conditions (see LaVal 2004). In our 2000 list of distributions of mammals in the Monteverde region, we listed southern cotton rats as rare in zones 1 and 2. Today, cotton rats are abundant in those zones in disturbed habitats. The rain shadow on the Pacific slope, heavily disturbed grassy areas, and climate change have seemly created abundant habitat for this grassland species at Monteverde as well as elsewhere on Costa Rica's Pacific slopes. At Monteverde, plants and birds were originally used to define the life zones, whereas most species of mammals were distributed across two or more life zones (see Timm and LaVal 2000a, b, c).

Owing to our ever-increasing knowledge of Monteverde mammals and the long-term work that has been done there, interesting changes in distributional and ecological patterns are being discovered. Distributions of mammals across the elevational zones clearly are changing. LaVal documented that vampire bats moved up into the Monteverde area in the 1990s and cotton rats moved up and became abundant in the past decade. LaVal noted that cotton rats first started appearing in zone 2 in the early 2000s, whereas they were previously known only from zone 1. An intriguing example of a truly sympatric distribution is the discovery of the two species of mouse opossums—*Marmosa mexicana* and *M. zeledoni*—in LaVal's home. The observations were made years apart so the two similarly appearing species may not be temporally sympatric, but the dry forest species (*M. mexicana*) and the wet forest species (*M. zeledoni*) are now documented from a single residence in Monteverde. Three similarly-sized species of small-eared shrews are known from the Reserve with *Cryptotis nigrescens* widespread and common throughout the area, whereas *C. merriami* and *C. monteverdensis* are known only in the reserve and are both rare. Considerable differences in the forearm bones of the three similarly-appearing shrews were documented by Woodman and Timm (2017), and they speculated that the differences reflected more ambulatory above ground versus more semi-fossorial foraging.

This chapter was undertaken along with two companion chapters (apéndices 10, 11) to update the research and findings in the field of mammalogy that have taken place since the publication of the Monteverde book in 2000. The first in this series, Apéndice 10 (Timm and LaVal 2014), is a Spanish translation of the original Appendix 10 from the Monteverde book. The second (LaVal and Timm 2014) is a Spanish updated version of that original listing of Monteverde mammals and their distributions and abundance. Herein, we update the distributions of mammals in the six life zones represented in the greater Monteverde region, add species newly discovered in the region, and provide literature updates. In these updated versions, we provide brief comments explaining taxonomic changes that have occurred since the original listing was published in 2000 provided as footnotes to the original appendix. In the References below, we include the 25 publications that have appeared based on the study of mammals at Monteverde since our 2000 overview, as well as references that we cite in preparation of these updated versions.

Keys to the bats of Costa Rica based extensively on our experience at Monteverde were provided in English (Timm and LaVal 1998) and Spanish (Timm et al. 1999). A very useful and beautifully illustrated key to the rodents of Costa Rica was provided by Villalobos-Chaves et al. (2016).

On a positive note, two factors favor a bright future for Monteverde mammals: 1) An immense area of contiguous pristine habitat and regenerating forest, around 50,000 hectares, has been preserved and is relatively well-protected in the Monteverde area; 2) Most, although not all, Monteverde mammals have distributional and ecological ranges that cover several life zones and thus are less threatened by climate change than many birds and herps that may be restricted to one or two life zones.

Table 1. Mammal distributions and abundances in the Monteverde region—2017.

Richard K. LaVal and Robert M. Timm

Scientific Name	Common Name	Abundance [1]	Life Zone [2]
Didelphimorpha	**Marsupials**		
Didelphidae	American Opossums		
Caluromys derbianus	Woolly Opossum	uncommon	1, 2, 3
Chironectes minimus	Water Opossum	uncertain	1
Didelphis marsupialis	Common Opossum	abundant	1, 2, 3, 4, 5, 6
Marmosa mexicana	Mexican Mouse Opossum	uncommon	1
Marmosa zeledoni	Mouse Opossum	common	2, 3, 5, 6
Metachirus nudicaudatus	Brown Four-eyed Opossum	rare	6
Micoureus alstoni	Alston’s Opossum	uncommon	2, 3, 6
Philander opossum	Gray Four-eyed Opossum	uncommon	1, 2, 3, 5, 6
Eulipotyphla	**Shrews**		
Soricidae	Shrews		
Cryptotis merriami	Merriam’s Small-eared Shrew	rare	3
Cryptotis nigrescens	Blackish Small-eared Shrew	common	2, 3, 4, 5, 6
Cryptotis monteverdensis [3]	Monteverde Small-eared Shrew	rare	3
Chiroptera	**Bats**		
Emballonuridae	Sac-winged Bats		
Balantiopteryx plicata	Gray Sac-winged Bat	uncommon	1, 2
Cormura brevirostris	Wagner’s Sac-winged Bat	rare	6

Cyttarops alecto	Short-eared Bat	rare	3
Diclidurus albus	Northern Ghost Bat	rare	2, 4, 6
Peropteryx kappleri	Greater Dog-like Bat	uncommon	2, 6
Peropteryx macrotis	Lesser Dog-like Bat	rare	2
Rhynchonycteris naso	Proboscis Bat	rare	2
Saccopteryx bilineata	Greater White-lined Bat	common	1, 6
Mormoopidae	Mustached Bats		
Pteronotus davyi	Lesser Naked-backed Bat	uncommon	2, 5
Pteronotus gymnonotus	Big Naked-backed Bat	uncommon	1, 2, 3, 4, 5, 6
Pteronotus mesoamericanus [4]	Mesoamerican Mustached Bat	uncommon	1, 2, 3, 4, 5, 6
Pteronotus personatus	Lesser Mustached Bat	uncommon	5
Phyllostomidae	American Leaf-nosed Bats		
Phyllostominae	Gleaning Bats		
Glyphonycteris sylvestris	Tri-colored Big-eared Bat	rare	2
Lonchorhina aurita	Sword-nosed Bat	uncommon	5, 6
Lophostoma brasiliense	Pigmy Round-eared Bat	rare	1, 6
Micronycteris hirsuta	Hairy Big-eared Bat	rare	2, 6
Micronycteris microtis	Little Big-eared Bat	uncommon	1, 2, 3, 4, 6
Micronycteris minuta	Tiny Big-eared Bat	rare	6
Micronycteris schmidtorum	Schmidt’s Big-eared Bat	uncertain	5, 6
Mimon cozumelae	Cozumel Spear-nosed Bat	rare	2
Phylloderma stenops	Northern Spear-nosed Bat	rare	6
Phyllostomus discolor	Pale Spear-nosed Bat	common	1, 2
Phyllostomus hastatus	Greater Spear-nosed Bat	rare	5, 6
Tonatia saurophila	Stripe-headed Bat	rare	6

Trachops cirrhosus	Frog.eating Bat	uncommon	1, 2, 3, 4, 5, 6,
Vampyrum spectrum	False Vampire Bat	rare	1, 2, 3, 4, 6
Glossophaginae	Pollen- and Nectar-feeding Bats		
Anoura cultrata	Handley's Tailless Bat	uncommon	2, 3, 4, 5, 6
Anoura geoffroyi	Geoffroy's Tailless Bat	common	1, 2, 3, 4, 5, 6
Choeroniscus godmani	Godman's Long-nosed Bat	rare	1, 2, 3, 4
Glossophaga commissarisi	Commissaris' Long-tongued Bat	common	1, 2, 3, 4
Glossophaga soricina	Pallas' Long-tongued Bat	common	1, 2, 3, 6
Hylonycteris underwoodi	Underwood's Long-tongued Bat	common	2, 3, 4, 5
Lonchophyllinae	Long-tongued Bats		
Lonchophylla robusta	Panama Long-tongued Bat	rare	2, 3, 4, 5, 6
Carolliinae	Short-tailed Bats		
Carollia castanea	Allen's Short-tailed Bat	uncommon	1, 2, 5, 6
Carollia perspicillata	Short-tailed Fruit Bat	uncommon	1, 2, 3, 5, 6
Carollia sowelli [5]	Silky Short-tailed Bat	common	1, 2, 3, 4, 5, 6
Carollia subrufa	Gray Short-tailed Bat	rare	1
Stenoderminae	Fruit-eating Bats		
Artibeus intermedius	Davis' Fruit Bat	uncommon	1, 2
Artibeus jamaicensis	Jamaican Fruit Bat	common	1, 2, 3, 4, 5, 6
Artibeus lituratus	Big Fruit Bat	common	1, 2, 3, 4, 6
Dermanura azteca	Highland Fruit-eating Bat	rare	2, 6
Dermanura phaeota	Pygmy Fruit-eating Bat	uncommon	4, 5, 6
Dermanura tolteca	Toltec Fruit-eating Bat	abundant	1, 2, 3, 4, 5, 6
Dermanura watsoni	Thomas' Fruit-eating Bat	uncommon	2, 4, 6
Centurio senex	Wrinkle-faced Bat	rare	1, 2, 3

Chiroderma salvini	Salvin’s White-lined Bat	rare	2
Chiroderma villosum	Shaggy-haired Bat	rare	2
Ectophylla alba	Caribbean White Bat	rare	6
Enchisthenes hartii	Velvety Fruit-eating Bat	rare	1, 2, 3, 4
Platyrrhinus helleri	Heller’s Broad-nosed Bat	uncommon	1, 2, 5
Platyrrhinus vittatus	Greater Broad-nosed Bat	common	1, 2, 3, 4, 5, 6
Sturnira hondurensis [6]	Highland Yellow-shouldered Bat	abundant	1, 2, 3, 4, 5, 6
Sturnira mordax	Talamancan Bat	uncommon	2, 3, 4, 5, 6
Sturnira parvidens [7]	Little Yellow-shouldered Bat	uncommon	1, 2
Vampyressa thyone	Little Yellow-eared Bat	rare	2, 3, 5, 6
Vampyrodes major	Great Stripe-faced Bat	rare	2, 5
Desmodontinae	Vampire Bats		
Desmodus rotundus	Common Vampire Bat	uncommon	1, 2, 3, 5, 6
Diphylla ecaudata	Hairy-legged Vampire Bat	rare	2
Natalidae	Funnel-eared Bats		
Natalus lanatus [8]	Highland Funnel-eared Bat	rare	2
Thyropteridae	Disk-winged Bats		
Thyroptera tricolor	Spix’s Disk-winged Bat	common	2, 3, 4, 6
Vespertilionidae	Vespertilionid Bats		
Bauerus dubiaquercus	Doubtful Oak Bat	rare	2, 3, 5
Dasypterus ega	Southern Yellow Bat	common	2, 4, 6
Dasypterus intermedius	Northern Yellow Bat	rare	2, 6
Eptesicus brasiliensis	Brazilian brown Bat	common	2, 3, 4, 5, 6
Eptesicus furinalis	Argentine Brown Bat	uncommon	1, 6
Eptesicus fuscus	Big Brown Bat	uncommon	2, 3, 4

Lasiurus castaneus	Tacarcuna Bat	rare	4, 5
Lasiurus frantzii	Central American Red Bat	common	2, 3, 4, 5, 6
Myotis albescens	Silver-haired Myotis	uncommon	6
Myotis elegans	Elegant Myotis	uncommon	6
Myotis nigricans	Black Myotis	common	1, 2, 3, 4, 6
Myotis oxyotus	Montane Myotis	uncommon	2, 3, 4
Myotis pilosatibialis [9]	Hairy-legged Myotis	abundant	1, 2, 3, 4, 5, 6
Myotis riparius	Riparian Myotis	uncommon	1, 2, 6
Rhogeessa io [10]	Rainforest Yellow Bat	uncommon	6
Molossidae	Free-tailed Bats		
Eumops auripendulus	Shaw’s Mastiff Bat	uncommon	1, 2, 4, 6
Molossus molossus	Little Mastiff Bat	common	1, 2, 6
Molossus rufus	Black Mastiff Bat	uncommon	1, 2, 5
Molossus sinaloae	Sinaloan Mastiff Bat	common	1, 2, 6
Nyctinomops laticaudatus	Broad-eared Bat	uncertain	2
Promops centralis	Big Crested Mastiff Bat	rare	2, 6
Tadarida brasiliensis	Brazilian Free-tailed Bat	uncommon	1, 2, 6
Primates	**Primates**		
Atelidae	Howler and Spider Monkeys		
Alouatta palliata	Mantled Howler Monkey	common	1, 2, 3, 4, 5, 6
Ateles geoffroyi	Black-handed Spider Monkey	uncommon	2, 3, 4, 5, 6
Cebidae	Capuchin Monkeys		
Cebus capucinus [11]	White-faced Capuchin	common	1, 2, 3, 4, 5

Cingulata	**Armadillos**		
Dasypodidae	Armadillos		
Cabassous centralis	Northern Naked-tailed Armadillo	rare	2, 3, 4, 6
Dasypus novemcinctus	Nine-banded Armadillo	abundant	1, 2, 3, 4, 5, 6
Pilosa	**Anteaters and Sloths**		
Bradypodidae	Three-toed Sloths		
Bradypus variegatus	Brown-throated Three-toed Sloth	rare	1
Megalonychidae	Two-toed Sloths		
Choloepus hoffmanni	Hoffmann’s Two-toed Sloth	common	1, 2, 3, 4, 5, 6
Cylopedidae	Silky Anteater		
Cyclopes didactylus	Silky Anteater	uncertain	2, 6
Myrmecophagidae	Anteaters		
Myrmecophaga tridactyla	Giant Anteater	originally here, but now extirpated	1
Tamandua mexicana	Northern Tamandua	uncommon	1, 2, 3, 5, 6
Lagomorpha	**Rabbits**		
Leporidae	Rabbits and Hares		
Sylvilagus floridanus	Cottontail Rabbit	uncommon	1, 2, 3
Sylvilagus gabbi [12]	Forest Rabbit	rare	2, 3
Rodentia	**Rodents**		
Geomyidae	Pocket Gophers		
Orthogeomys cherriei	Cherrie’s Pocket Gopher	common	2, 3, 6
Sciuridae	Squirrels		

Microsciurus alfari	Alfaro's Pygmy Squirrel	common	2, 3, 4, 5, 6
Sciurus granatensis	Neotropical Red Squirrel	common	1, 2, 3, 4, 5, 6
Sciurus variegatoides	Variegated Squirrel	abundant	1, 2, 3, 6
Heteromyidae	Pocket Mice		
Heteromys desmarestianus	Desmarest's Spiny Pocket Mouse	common	5, 6
Heteromys nubicolens [13]	Cloud-dwelling Spiny Pocket Mouse	common	1, 2, 3, 4
Cricetidae	Long-tailed Rats and Mice		
Handleyomys alfaroi	Alfaro's Rice Rat	uncommon	2, 3, 5
Melanomys chrysomelas [14]	Dusky Rice Rat	uncommon	5, 6
Nephelomys devius [15]	Tome's Rice Rat	common	2, 3, 4, 5
Nyctomys sumichrasti	Sumichrast's Vesper Rat	uncommon	1, 2, 3, 5, 6
Oligoryzomys fulvescens	Pygmy Rice Mouse	rare	2, 3, 5
Oligoryzomys vegetus	Pygmy Rice Mouse	rare	2, 3, 4
Ototylomys phyllotis	Big-eared Climbing Rat	rare	1, 2
Peromyscus nudipes [16]	Naked-footed Mouse	abundant	1, 2, 3, 4, 5
Reithrodontomys brevirostris	Chiriquí Harvest Mouse	common	1, 2, 3, 4, 5, 6
Reithrodontomys creper	Chiriquí Harvest Mouse	uncommon	4
Reithrodontomys sp.[17]	Harvest Mouse	rare	4
Rheomys raptor	Goldman's Water Mouse	rare	3, 4, 5
Scotinomys teguina	Alston's Brown Mouse	common	2, 3, 4, 5, 6
Sigmodon hirsutus	Southern Cotton Rat	common	1, 2
Transandinomys bolivaris [18]	Long-whiskered Rice Rat	rare	6
Tanyuromys aphrastus [19]	Long-tailed Montane Rat	rare	4, 5
Tylomys watsoni	Watson's Climbing Rat	common	2, 3, 4, 5, 6

Erethizontidae	Porcupines		
Coendou mexicanus	Prehensile-tailed Porcupine	common	1, 2, 3, 4, 5, 6
Cuniculidae	Pacas		
Cuniculus paca	Paca	uncommon	1, 2, 3, 4, 5, 6
Dasyproctidae	Agoutis		
Dasyprocta punctata	Agouti	common	1, 2, 3, 4, 5, 6
Carnivora	**Carnivores**		
Canidae	Coyotes, Foxes, and Dogs		
Canis latrans	Coyote	uncommon	1, 2
Urocyon cinereoargenteus	Gray Fox	common	1, 2, 3, 5
Mephitidae	Skunks		
Conepatus semistriatus	Striped Hog-nosed Skunk	uncommon	1, 2, 3, 4, 6
Spilogale angustifrons	Southern Spotted Skunk	rare	2
Mustelidae	Weasels and Otters		
Eira barbara	Tayra	common	1, 2, 3, 4, 5
Galictis vittata	Grison	rare	2, 3, 5, 6
Lontra longicaudis	Southern River Otter	rare	1, 2, 3, 4, 5, 6
Mustela frenata	Long-tailed Weasel	uncommon	1, 2, 3, 4, 5, 6
Procyonidae	Raccoons and allies		
Bassaricyon gabbii	Olingo	common	1, 2, 3, 5, 6
Bassariscus sumichrasti	Central American Cacomistle	uncertain	3
Nasua narica	White-nosed Coati	abundant	1, 2, 3, 4, 5, 6
Potos flavus	Kinkajou	common	1, 2, 3, 4, 5, 6
Procyon lotor	Raccoon	common	1, 2, 3, 5, 6

Felidae	Cats		
Leopardus pardalis	Ocelot	uncommon	1, 2, 3, 4, 5, 6
Leopardus tigrinus	Little Spotted Cat	uncertain	1, 3, 4, 6
Leopardus wiedii	Margay	uncommon	2, 3, 4, 5, 6
Panthera onca	Jaguar	rare	3, 4, 5, 6
Puma concolor	Puma, Mountain Lion, Cougar	uncommon	1, 2, 3, 4, 5, 6
Puma yagouaroundi	Jaguarundi	uncommon	1, 2, 3, 4, 5, 6
Artiodactyla	**Deer and Peccaries**		
Tayassuidae	Peccaries		
Tayassu pecari	White-lipped Peccary	originally widespread, but now extirpated	
Pecari tajacu	Collared Peccary	common	2, 3, 4, 5, 6
Cervidae	Deer		
Mazama temama [20]	Central American Brocket Deer	uncommon	1, 2, 3, 4, 5, 6
Odocoileus virginianus	White-tailed Deer	uncommon	1, 2
Perissodactyla	**Tapirs and Horses**		
Tapiridae	Tapirs		
Tapirus bairdii	Baird's Tapir	uncommon	3, 4, 5, 6
Species introduced into the area by humans			
Mus musculus	House Mouse	common	1, 2, 6
Rattus rattus	Black, Roof Rat	uncommon	1, 2, 6

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[1] Abundance categories: abundant = often observed and/or captured in appropriate habitats; common = frequently observed in appropriate habitats; uncommon = only occasionally observed in appropriate habitats; rare = very few records for Monteverde; extirpated = previously known from the area, but no longer in the region due to overhunting and habitat destruction; uncertain = of unknown abundance.

[2] Life Zone: These correspond to the 6 Holdridge life zones in Monteverde area. Brief descriptions and elevational ranges of each zone are found in Table 1 below.
[3] A species new to science described by N. Woodman and R. M. Timm.
[4] Name recently changed from *P. parnellii*.
[5] Name recently changed from *C. brevicauda*.
[6] Name recently changed from *S. lilium*.
[7] Name recently changed from *S. ludovici*.
[8] Recently recorded from Costa Rica for the first time.
[9] Name recently changed from *M. keaysi*.
[10] This genus is currently being revised and the authors state that this is probably an undescribed species. For now we provisionally use the name *R. io* to provide consistency with the published literature.
[11] Some anthropologist suggest the name for the Central American capuchins should be *C. imitator*.
[12] Name recently changed from *S. brasiliensis*.
[13] A species recently described from Monteverde by Anderson and Timm (2006).
[14] The correct name for the species of *Melanomys* at Monteverde may be *M*. *chrysomelas.* It is likely that at least two species of *Melanomys* occur in Costa Rica.
[15] Name recently changed from *Oryzomys albigularis*.
[16] Bradley et al. (2016) suggested that the *Peromyscus* at Monteverde should be considered as conspecific with those of Nicaragua and as such *P*. *nicaraguae*. Reed treats all *Peromyscus* in Costa Rica, Nicaragua, and adjacent countries as belonging to the widespread species *P*. *mexicanus*. We suspect that eventually two or perhaps three species of *Peromyscus* will ultimately be recognized in Costa Rica and continue to treat the species at Monteverde as *P. nudipes* until the systematic relationships among these species are better understood.
[17] A new species being described by R. M. Timm and M Soley.
[18] Name recently changed from *Oryzomys bolivaris*.
[19] Name recently changed from *Oryzomys aphrastus*.
[20] Name recently changed from *Mazama americana*.

Table 2. Characteristics of the Holdridge life zones in the Monteverde area and Life Zone code numbers associated with mammal distributions. Life zones are arranged in sequence along a transect across the mountains from the Pacific to the Atlantic slope.

Life Zone	Elevation (m)	Annual Rainfall (range in mm)	Dry Season Duration (months)	Canopy Height (m)	Life Zone
Premontane Moist Forest	700–1300	2000–2500	5.5	ca. 25	1
Premontane Wet Forest	1300–1500	2500–3500	5	30—40	2
Lower Montane Wet Forest	1500–1650	3000–5000	3	25—35	3
Lower Montane Rain Forest	1650–1850	5000–8000	2	20—30	4
Premontane Rain Forest	700–1600	4000–7000	1	30—40	5
Tropical Wet Forest	500–700	3500–4500	1	30—50	6

Modified from Haber (2000).

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8

Plant-Animal Interactions — Update 2014

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Plant-pollinator Interactions

The suites of morphological, phenological, and behavioral characteristics of plants and pollinators that comprise "pollination syndromes" remain useful for predicting the players in pollination mutualisms. For example, red tubular flowers are likely to be visited by hummingbirds, and short-tongued bees are more likely to visit flowers with a more open morphology that doesn't restrict their access to nectar and pollen. However, the frequent finding that floral visitors aren't restricted just to those usually associated with a particular syndrome has increasingly led to criticism of the utility of the syndrome idea itself (e.g., Ollerton 2009, but see Rosas-Guerrero 2014), as has the realization that many animals feed at flowers usually associated with different types of pollinators. {Muchhala, 2003, Exploring the boundary between pollination syndromes: bats and hummingbirds as pollinators of Burmeistera cyclostigmata and B-tenuiflora (Campanulaceae)} work with *Burmeistera tenuiflora* and *B. cyclostigmata* at Monteverde demonstrates some of the ambiguity of pollination syndromes. He found that both birds and bats visited flowers of both plant species, but that only bats effectively pollinated both. Hummingbirds effectively pollinated *B. tenuiflora*, but because the reproductive parts of *B. cyclostigmata* extend further from the nectaries, birds can access nectar without contacting the anthers and stigma. This work nicely demonstrates the need for caution in assuming too much about the identity of pollinators merely on the basis of floral morphology and timing of nectar secretion. Muchhala suggests that these species of *Burmeistera* demonstrate generalization for pollination by both bats and hummingbirds.

Work at Monteverde since 2000 has added detailed information on the basic reproductive biology of local plants as well. {Cascante-Marin, 2005, Reproductive biology of the epiphytic bromeliad Werauhia gladioliflora in a premontane tropical forest}, for example, studied the flowering phenology and breeding system of the bat-pollinated bromeliad *Werauhia* (formerly *Vriesia*) *gladiolifolia*, and {Bush, 2009, Early autonomous selfing in the hummingbird-pollinated epiphyte Pitcairnia brittoniana (Bromeliaceae)} elucidated the breeding system of the hummingbird-pollinated bromeliad *Pitcairnia brittoniana*. Both species were capable of self-pollination, and both fruit- and seed set were equivalent in plants limited to self-pollination as in those available to pollinators. Self-pollination is common among epiphytes, which may suffer unpredictable visitation due to their isolation and limited floral displays {Bush, 1995, Breeding systems of epiphytes in a tropical montane wet forest}, but Bush and Guilbeau found that pollen loads deposited by hummingbirds were also sufficient to ensure nearly full seed set in *P. brittoniana*. As they noted for *P. brittoniana*, it seems likely that many epiphytes cross-pollinate when pollinators are available, but self-pollinate when they are scarce.

Another contribution from Monteverde is Judy Stone's work with colleagues on pollination ecology and breeding system evolution in *Witheringia solanacea*. Self-compatibility has evolved independently many times, but the conditions that favor it remain somewhat controversial because theory predicts that they must outweigh the costs of self-fertilization (primarily lowered fitness via the production of offspring with two copies of deleterious alleles). Most investigations of the evolution of self-compatibility rely on comparisons of different but closely related species, but {Stone, 2006, Variation in the self-incompatibility response within and among populations of the tropical shrub Witheringia solanacea (Solanaceae)} found populations of *W. solanacea* with both self-incompatible (SI) and self-compatible (SC) genotypes at Monteverde and Varablanca. SI genotypes of *W. solanacea* suffered nearly complete embryonic lethality when experimentally self-pollinated ({Stone, 2010, Embryonic inbreeding depression varies among populations and by mating system in Witheringia solanacea (Solanaceae)}, but SC genotypes did not, and Stone et al. concluded that deleterious alleles had already been largely purged from the SC genotypes. Such purging is most likely to occur when plants are severely pollen-limited, and *W. solanacea* populations near the MCFP did indeed have lower pollinator (bee) visitation rates and appear to be more pollen-limited than those at lower elevations (e.g., San Luis) or those further south in Costa Rica (i.e., Las Cruces and Las Alturas; {Stone, 2008, Pollinator abundance and pollen limitation of a solanaceous shrub at premontane and lower montane sites}. However, when {Stone, 2014, Transmission advantage favors selfing allele in experimental populations of self-incompatible Witheringia solanacea (Solanaceae)} created experimental gardens with both genotypes and allowed them to be pollinated naturally, SC and SI plants had roughly equivalent fruit- and seed set but less than 10% of SC seeds resulted from self-fertilization. They concluded that embryonic inbreeding depression was still substantial in SC plants, but suggested that these genotypes will continue to spread because the transmission advantage of selfing through male function effectively outweighs even severe inbreeding depression.

Plant-Frugivore Interactions

Much of the work on plant-frugivore interactions in Monteverde since the book's publication has focused on the post-dispersal fates of seeds. To a large degree this emphasis mirrors that in the field of plant-frugivore interactions in general. It is motivated by the understanding that the evolutionary consequences of seed dispersal for plants (including coevolution with frugivores) are mediated by the effects of dispersal on seed fate and plant demography. Some of Wenny's work on dispersal of large-seeded species also deals explicitly with dispersal *per se*, however. Wenny (1999) showed that seeds of *Beilschmiedia pendula*, one of the largest seeds dispersed by birds at Monteverde, are rarely deposited more than 10 m beyond the crowns of fruiting trees, but that seeds dispersed even short distances from the parent suffer less predation (from rodents and beetle larvae) than those deposited directly beneath the crown. His work demonstrates that dispersal is indeed beneficial for *B. pendula*, and that the effect occurs on quite a small spatial scale. In contrast, seeds of *Ocotea endresiana* suffered nearly complete removal by predators regardless of dispersal distance from the parent tree {Wenny, 2000, Seed dispersal of a high quality fruit by specialized frugivores: High quality dispersal?}. Most birds moved seeds less than 25 m, but male Three-wattled Bellbirds (*Procnias tricarunculata*) often deposited them beneath courtship display perches, many of which overhang treefall gaps. Wenny's experiments failed to show any difference in gap vs. understory seed removal rates, but seedlings in gaps grew more rapidly and suffered less mortality from pathogenic fungi than did those in understory. Thus, male Bellbirds provide a good example of directed dispersal (*sensu* Howe and Smallwood 1982), and may be disproportionately important for recruitment of *O. endresiana*. Determining the strength of the effect relative to that of other dispersers will require more detailed study, however.

Another example of directed dispersal at Monteverde is provided by {Sheldon, 2013, Spatial and Temporal Variation of Seed Rain in the Canopy and on the Ground of a Tropical Cloud Forest} study, which compared the "seed rain" deposited on the forest floor with that deposited in the forest canopy in part of the MCFP. Their study employed seed traps, with those in the canopy estimating seeds that are deposited and that accumulate in epiphyte mats and the soil associated with them. Despite broad overlap, the species composition of the seed rain was statistically distinct in each habitat: epiphyte seeds dominated in the canopy, while those of large trees were most common on the forest floor, suggesting that dispersers do move epiphyte seeds to especially appropriate establishment sites more often than would be expected by chance. Seeds dispersed by birds (rather than by mammals or wind) dominated in both habitats and over all seasons, highlighting the importance of animal dispersers – especially birds – in maintaining the ecological integrity of the Monteverde forest.

{Wenny, 1999, Two-stage dispersal of Guarea glabra and G-kunthiana (Meliaceae) in Monteverde`, Costa Rica} studied the effects of primary (by birds and non-flying mammals) and secondary (by scatter hoarding rodents, e.g., agoutis) dispersal on survival and germination in two species of *Guarea*. Seeds were moved up to 65 m beyond parent tree crowns by primary dispersers, but median distances were within 15 m for both *G. glabra* and *G. kunthiana*. Although secondary dispersers increased median distances only slightly, they did have a profound effect on seed fate by burying seeds 1-3 cm deep in the soil. Buried seeds were far more likely to survive than those that remained on the soil surface, which were killed mostly by rodents and insects (*G. glabra*) or by Collared Peccaries (*G. kunthiana*). Wenny's work on seed fate at Monteverde also included comparisons among ten additional species with different seed sizes, and although highly variable within size categories, seed survival tended to be higher for the largest seeds. Because these seeds continued to suffer rodent attack after germination, however, the relationship between seed size and seedling recruitment was complex. {Wenny, 2005, Post-dispersal seed fate of some cloud forest tree species in Costa Rica} estimated that five species of small rodents were responsible for about 70% of seed predation. Insect infestation was also common in some species, but mostly occurred before dispersal. Secondary movement of seeds (by rodents) for short distances was common, but only *Guarea* was commonly cached and often buried; most seed movement thus resulted in predation.

Given the importance of mammalian seed predators as mediators of plant population dynamics, how forest fragmentation and distributional changes driven by climate change will affect mammal populations is of great importance in montane habitats like those in Monteverde {Gibson, 2013, Near-Complete Extinction of Native Small Mammal Fauna 25 Years After Forest Fragmentation;Meserve, 2011, Global climate change and small mammal populations in north-central Chile;Sheldon, 2011, Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure}. {Chinchilla, 2009, Seed predation by mammals in forest fragments in Monteverde`, Costa Rica} compared mammalian seed predator populations and seed removal rates in a large tract of continuous forest (including the MCFR) and in two nearby forest fragments of 350 and 20 ha. As expected, the fragments were missing some of the larger species of seed predators (e.g., peccaries and pacas), but experienced seed removal rates that were only marginally lower than those in intact forest. Chinchilla attributed much of the compensatory predation in the fragments to the higher abundance of the specialist seed predator *Heteromys desmarestianus* there, compared to intact forest, where it was uncommon.

Murray and Garcia-C. (2002) reported on a long-term study of the roles played by seed dispersal and seed survival in facilitating coexistence of a large guild of pioneer plant species that depend upon a limited resource: space in recently formed treefall gaps. They found that the top 10 cm of Monteverde soils contains 3000 to 6500 viable but dormant pioneer seeds per square meter - seeds that germinate rapidly in response to gap formation. And because species richness is high even on very small spatial scales (ca. 20-25 species per 625 cm^2 sample), both intra- and interspecific competition for space in recent treefall gaps is intense. Murray and Garcia-C's work showed that spatial heterogeneity of the soil "seed bank" was extremely high, however, so that competitively inferior pioneer species were likely sometimes to germinate in gaps without any superior competitors nearby. This phenomenon, termed "recruitment limitation," can facilitate coexistence by reducing the intensity of competition on ecologically relevant spatial scales. Part of the spatial patchiness in the seed bank resulted from patchiness in the seed rain, but site-to-site differences in density and species composition were also magnified by survival probabilities in the soil that varied by species.

Despite the fact that the life histories of most pioneers include a soil seed bank, Murray and Garcia-C. found a wide range in the ability of seeds to survive for long periods in the soil. Some, like *Phytolacca rivinoides*, *Bocconia frutescens*, and *Guettarda poasana,* maintain soil seed banks with densities several orders of magnitude higher than the annual seed rain, suggesting that seeds survive in Monteverde's soil for tens to hundreds of years. In contrast, other species of pioneers, like *Cecropia polyphlebia* and *Urera elata*, maintain soil seed banks with only a year's worth of seed rain, suggesting high mortality rates. Only *Hampea appendiculata* and *Piper umbellatum* among the 23 species studied in detail did not maintain a seed bank at all. Results of replicated field experiments were consistent with the comparisons between seed bank and annual seed rain densities outlined above: seeds of the same species with high seed bank : annual seed rain ratios also survived well in the field since 1993 (Murray and Garcia-C 2002). {Veldman, 2007, Chemical defense and the persistence of pioneer plant seeds in the soil of a tropical cloud forest} investigated the chemical basis for the patterns of mortality among six of the pioneer species in Murray and Garcia-C's (2002) study (*P. rivinoides*, *C. polyphlebia*, *G. poasana*, *U. elata*, *B. frutescens*, and *Witheringia meiantha*), and found that seed extracts from species that survive for long periods in the soil were indeed more toxic to arthropods and fungi in the laboratory. The responsible chemicals in *B. frutescens* were identified as three related alkaloids, all of which were much more concentrated in seeds than in leaf tissue. *P. rivinoides* and *G. poasana* contain chemicals toxic to fungi as well, but they remain as yet unidentified (Veldman et al. 2007, K. G. Murray, *unpublished data*). Chemical defense of pioneer plant seeds is thus clearly important, and much work remains to be done.

{Nadkarni, 2009, Canopy Seed Banks as Time Capsules of Biodiversity in Pasture-Remnant Tree Crowns} found that the soils and epiphyte mats that accumulate in tree canopies also accumulate seed banks, just as do soils on the forest floor. Moreover, they surveyed such seed banks in the canopies of remnant pasture trees to determine whether such seed banks might augment other effects that render remnant trees effective "regeneration foci." They found that these seed banks contained dense and diverse assemblages of seeds, including many woody species characteristic of primary forest, and concluded that pasture canopy seed banks could function as "time capsules" of forest biodiversity that could speed forest regeneration recovery on pastures. Nadkarni and Haber also compared the seed banks in remnant tree canopies with those in primary forest tree canopies and in soils from the forest floor. Seed densities and species richness in forest floor soils, but those from pasture and primary forest tree canopies did not differ from one another

Earlier work on plant-frugivore interactions at Monteverde demonstrated that some of the most important fruit-eating birds migrated altitudinally, and suggested that these movements were driven by seasonal patterns in fruit availability at different elevations. Since the publication of Nadkarni and Wheelwright (2000), these patterns have been further investigated by Chaves-Campos et al. (2003), Chaves-Campos (2004), Powell and Bjork (2004), and Papes et al. (2012). {Powell, 2004, Habitat linkages and the conservation of tropical Biodiversity as indicated by seasonal migrations of three-wattled bellbirds} elucidated the migratory patterns of Three-wattled Bellbirds in detail using radiotelemetry, and found that birds breeding on the Atlantic slope of the Cordillera de Tilaran crossed over to highly fragmented forest on the Pacific slope just 5-15 km away after the breeding season. In September and October, they migrate to the lowlands of northeastern Costa Rica and southeastern Nicaragua, and in November and December they migrate to southwestern Costa Rica, where they remain until returning in March to the Atlantic slope near Monteverde to breed. Powell and Bjork suggested that the birds are following the availability of their primary food sources (fruits in the family Lauraceae) as the fruiting seasons of species in different parts of the bellbird's range wax and wane, rather than following an invariant migratory route. Whatever the reason, the four areas used over the annual cycle were separated by as much as 280 km, and much of the land in three of the four areas (lowlands of northeastern and southwestern Costa Rica, and middle elevations on the Pacific slope of Costa Rica near Monteverde) is highly fragmented and poorly protected. Powell and Bjork concluded that the bellbird population (and hence the forests in which they perform important seed dispersal services) are thus vulnerable, despite adequate protection of the forests used during the breeding season. In part as a result of their work, the Costa Rican government and several private-sector organizations are cooperating to create the Bellbird Biological Corridor, which will protect a migratory corridor on the Pacific slope by promoting habitat restoration and protection, largely on privately held lands.

Similarly, {Chaves-Campos, 2003, Altitudinal movements and conservation of bare-necked Umbrellabird Cephalopterus glabricollis of the Tilaran Mountains`, Costa Rica} studied the occurrence of Bare-necked Umbrella birds at different elevations in the Monteverde-Arenal-San Ramon region of the Cordillera de Tilaran, and found that their movements over an elevation range from 400-1400 m correlated to seasonal patterns in fruit availability. And as with Bellbirds, elevations used for breeding were fairly well-protected, while those used outside the breeding season were not. Like {Powell, 2004, Habitat linkages and the conservation of tropical Biodiversity as indicated by seasonal migrations of three-wattled bellbirds}, Chaves-Campos concluded that the inadequacy of protected lands used during the non-breeding season constituted a significant threat to the species in the region.

{Chaves-Campos, 2004, Elevational movements of large frugivorous birds and temporal variation in abundance of fruits along an elevational gradient} studied changes in the abundances of large fruit-eating birds between 400 and 1400 meters elevation in the Cordillera de Tilaran in relation to the availability of fruits, and found mixed evidence that the migratory movements of these birds are driven in large part by fruit availability. Although small sample sizes and high variation among replicates made statistical comparisons difficult, Chaves-Campos suggested that migratory movements of these birds were driven by fruit availability in the non-breeding season, but not during the breeding season.

Most recently, {Papeş, 2012, - Vegetation dynamics and avian seasonal migration: clues from remotely sensed vegetation indices and ecological niche modelling} investigated the possibility of explaining bellbird movements on the basis of remote sensing data that could serve as a proxy for forest canopy characteristics. They generated ecological niche models based on several remotely sensed vegetation indices that reflect seasonal changes in canopy structure and productivity, but these did not explain seasonal bellbird movements in the Monteverde region reliably. Rather, these models suggested that much of the Atlantic slope is suitable for breeding, but that factors other than vegetation seasonality, e.g., lower rates of nest predation at middle elevations, may attract bellbirds to middle elevations for breeding.

Animal-mediated seed dispersal and cattle pasture regeneration

Since Groom's (2000) study of woody plant regeneration in abandoned pastures, much of the work on seed dispersal at Monteverde has concerned the role that such dispersal by animals plays in pasture regeneration. Cattle production now occupies over 27% of rural land area in Latin America ({Murgueitio, 2011, Native trees and shrubs for the productive rehabilitation of tropical cattle ranching lands}, yet the ultimate fate of most pasture lands is abandonment or conversion to some other use, often via regeneration to forest. Much of the work on pasture regeneration concerns the physical and biological barriers that limit the rate and constrain the trajectory of regeneration (e.g., {Holl, 2000, Tropical Montane Forest Restoration in Costa Rica: Overcoming Barriers to Dispersal and Establishment}, and since limited seed availability is one of the more obvious factors, many have concentratd on the roles that seed dispersing animals play in transporting seeds from surrounding forest into pastures.

{Murray, 2008, The roles of disperser behavior and physical habitat structure in regeneration of post-agricultural fields} reported on a long-term study of regeneration in two pastures near the MCFP, and found that nearly all early colonization by woody plants with animal-dispersed seeds was beneath the crowns of bordering trees and "forest remnant" trees that were left standing in the pasture when it was created. In contrast, wind-dispersed species colonized areas without overhanging vegetation just as frequently as areas beneath remnant trees. Concentration of early colonists beneath remnant trees or planted "tree islands" has been found in many other studies as well (e.g., {Sandor, 2014, Remnant Trees Affect Species Composition but Not Structure of Tropical Second-Growth Forest} and references cited therein; {Zahawi, 2006, Tropical forest restoration: Tree islands as recruitment foci in degraded lands of Honduras} – a pattern that results in part from the attraction of forest birds to habitats with greater structural complexity and in part to the tendency of birds to defecate and regurgitate seeds while perched rather than in flight. The attraction of birds to isolated pasture trees at Monteverde was demonstrated directly by {Sheldon, 2013, The use of pasture trees by birds in a tropical montane landscape in Monteverde`, Costa Rica}, who documented over 900 visits by 52 species in 20 different families to just one common pasture tree species (*Sapium glandulosum*). They also found that the size of the tree, its degree of isolation from other trees, and the size of its epiphyte load increased bird visitation. Surprisingly, Murray et al. (2008) found that wind-dispersed remnant trees were just as effective as recruitment foci for animal-dispersed colonists as were trees that themselves produced fleshy fruits sought by animals, presumably because seed dispersers are also attracted to the elevated perch sites, cover, and perhaps insect food resources that such trees provide.

Murray and colleagues also tracked the progress of regeneration to determine how the spatial and compositional patterns of regrowth that were initiated by seed dispersers changed over time. As has been found elsewhere (e.g., {Schlawin, 2008, 'Nucleating' succession in recovering neotropical wet forests: The legacy of remnant trees}, the concentration of pasture colonists beneath remnant trees formed "recruitment foci" or "nucleation sites" for forest plant species. Subsequent censuses of the same and similar plots 14 and 30 years post-abandonment showed that the initial strong effect of remnant trees on the density and species richness of regeneration became weaker over time – by 30 years post-abandonment, both density and species richness of pasture colonists was just as high in parts of the original pasture that had lacked overhanging tree crowns as in areas beneath remnant trees. The reason, of course, was that as the pasture colonists grew and formed expanding islands of regenerating forest centered on the original remnant trees, the colonists themselves served as perch sites for animals carrying seeds and the land area without overhanging tree crowns decreased to zero.

The work of {Harvey, 2000, COLONIZATION OF AGRICULTURAL WINDBREAKS BY FOREST TREES: EFFECTS OF CONNECTIVITY AND REMNANT TREES;Harvey, 2000, WINDBREAKS ENHANCE SEED DISPERSAL INTO AGRICULTURAL

LANDSCAPES IN MONTEVERDE`, COSTA RICA} in planted windbreaks between active pastures in the Monteverde region also demonstrates the importance of animal seed dispersers in forest regeneration in agricultural landscapes. As was the case for remnant trees, the seed rain of woody species beneath windbreaks was orders of magnitude more dense and far more diverse than in pasture just 5 meters away (Harvey 2000a). Bird-dispersed species predominated, but pastures received almost as many bat-dispersed seeds as windbreaks, perhaps because bats defecate in flight as well as when perched. Harvey (2000b) also studied colonization of windbreaks and adjacent pastures by surveying seedlings of forest plants recruited into them, and in many ways her findings parallel those of Harvey (2000a): forest plants readily recruited into windbreaks, especially those forest plants dispersed by birds. Moreover, both density and diversity of colonists was significantly higher in windbreaks connected to adjacent forest patches than in those not so connected.

Neither Harvey (2000a,b), Murray et al. (2008), nor Sheldon and Nadkarni (2013b) found any correlation between seed input, recruit density or bird visitation with distance to the nearest forest edge, perhaps because the pastures typical of the region are relatively small – rarely more than a few hundreds of meters across. Neither did {Aide, 1996, Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico}) in Puerto Rico, where pastures are also relatively small. In regions like Amazonia, however, where pastures can be kilometers across, distance effects may be common. {DaSilva, 1996, Plant succession`, landscape management`, and the ecology of frugivorous birds in abandoned Amazonian pastures}), for example, found that even tanagers that frequent the forest/pasture boundary rarely travel more than 150 meters into pasture.

Nadkarni and Haber (2009) elucidated another way in which remnant pasture trees may act as effective regeneration foci and thereby facilitate forest regeneration on abandoned pastures: via the seed banks that accumulate in soils and epiphyte mats in the canopies of remnant pasture trees. They found dense and diverse assemblages of seeds, including many woody species characteristic of primary forest and concluded that pasture canopy seed banks could function as “time capsules” of forest biodiversity that could speed forest regeneration on abandoned pastures.

Clearly, both remnant trees and windbreaks facilitate forest regeneration in agricultural landscapes at Monteverde and elsewhere, largely because of the interaction of their physical structure with the behavior of dispersers – especially birds. These patterns highlight both the importance of maintaining healthy disperser populations as well as managing landscape features such as pasture size and composition, so as to maintain the interactions that facilitate forest regeneration.

Fig biology

Figs remain a subject of fascination to biologists, especially those who work in the tropics. Our understanding of figs’ complex interactions with other species has been reviewed most recently by Herre et al. 2008, but new information continues to accumulate at a rapid pace. Yet, in spite of growing worldwide interest in figs, no publications have appeared over the past fifteen years describing research carried out at Monteverde. *Ficus pertusa*, which has attracted the great majority of attention in Monteverde, has been studied a little more elsewhere in Costa Rica as well as in Mexico and Brazil, mostly in the context of its flowering phenology and seed dispersal. *Ficus yoponensis* remains a species of great interest to researchers at Barro Colorado, Panama, where it is consumed heavily by bats that act as highly effective seed dispersers (Heer et al. 2010). *Ficus tuerckheimii, F. crassiuscula,* and *F. velutina* remain little-studied from the pollination and seed dispersal perspective.

It is particularly unfortunate that *F. tuerckheimii* has not attracted more attention, because it offers one of the clearest exceptions to a major piece of conventional wisdom about figs: that every one of the >750 fig species has a unique pollinator. As Ramirez (1970) first showed and several unpublished undergraduate course projects in Monteverde have followed up on, *F. tuerckheimii* has two pollinators (not “no” as the original text of this chapter erroneously states), often cohabiting a single fig inflorescence. They are easily distinguished by color: *Pegoscapus carlosi* is black and *P. mariae* yellow. New molecular data that allow fig wasps that appear identical to the human eye to be discriminated have made it clear that *F. tuerckheimii* may not be that unusual in hosting multiple pollinators (Marussich and Machado 2007). Conversely, certain pairs of fig species are now known to share a single pollinator (Moe et al. 2011). Overturning a related assumption - that figs and fig wasps must usually speciate together, given that there are hundreds of mostly one-to-one interactions - reconstruction of evolutionary relationships using molecular data reveals a much messier picture (Machado et al. 2005, Lopez-Vaamonde et al. 2009). However, how speciation occurs and how associations between particular pairs of fig and pollinator species arise remain unresolved (Cook et al. 2010).

The most surprising change in our ecological understanding of the fig pollination mutualism is that developing fig wasps do not, as was believed for over a century, consume fig seeds. Rather, before laying an egg, a female fig wasp deposits a secretion that transforms an ovule into a gall; her offspring feeds upon sterile tissue (Jousselin and Kjellberg 2001, Martinson et al. 2013). This leads to the obvious question of why these wasps transfer pollen at all, given that their offspring don't eat seeds! There is some evidence that in seedless figs, wasp larvae develop very poorly (Jousselin et al. 2003). Thus, regardless of their diet, active pollination by the mother does appear to increase the success of her offspring. Even though fig wasp larvae don't consume seeds, each one still develops within an ovule that would otherwise produce a seed. It remains unresolved why fig wasps don't lay eggs in every ovule, which would appear to benefit fig wasps in the short run but which could lead to the demise of fig reproduction and the extinction of both partners in the long run. New ideas for how this uneasy relationship can persist over evolutionary time appear regularly (e.g., Herre et al. 2008, Jandér et al. 2012).

Work has accelerated in recent years documenting seed dispersal and the dominant role fig fruits play in the diets of tropical vertebrates. A comprehensive review of fig consumers worldwide is now available (Shanahan et al. 2001), as is a detailed investigation of how fig fruit characteristics have evolved in suites or "syndromes" (Lomascolo et al. 2010). Intriguing geographical differences within individual fig species continue to appear and still remain to be explored. For example, new work finds *F. pertusa* seeds to be abundant in bat droppings in Brazil (Teixiera et al. 2009), suggesting a primary role for bats as seed dispersers there. This is consistent with observations from Panama, but distinctly different from Monteverde, where bats reject the red-ripe fruits.

Ecologists increasingly identify figs as keystone resources for fruit consumers. The health of fig populations worldwide is, however, threatened by habitat loss, habitat fragmentation, and selective harvest for wood (e.g., Felton et al. 2013). Furthermore, invasive frugivores deplete fruits essential to the well-being of native vertebrates, while at the same time failing to disperse fig seeds in a germinable condition (Staddon et al. 2010). There is a pressing need to treat figs as key targets for tropical conservation. They may also hold promising roles for forest restoration.

These and earlier studies at Monteverde highlight both the complexity of the interactions among mutualists and their role in the maintenance of whole ecological communities. As important, they demonstrate how important it is to base conservation planning on sound knowledge about the natural history of the organisms involved. Going forward, we hope that biologists will continue to be drawn to Monteverde both for the opportunity to understand the natural world better and to satisfy their own need to preserve a particularly worthy corner of it.

Literature Cited

9

Ecosystem Ecology and Forest Dynamics — Update 2014

Kenneth Clark

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, Hagel 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^{-1}, and basal area from 33 to 99 m^2 ha^{-1} (Hager and Dohrenbusch 2011). Estimated aboveground biomass ranged from 84 t ha^{-1} in the wettest, most wind-exposed site, to 431 t ha^{-1} in a lower elevation stand (assuming a wood density of 0.56 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 individuals ha^{-1}, with large (>30 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 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 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 and 39 t ha^{-1}. Nadkarni *et al.* (2004) reported an epiphyte mass value of 33.1 t ha^{-1} for an intensively-studied leeward cloud forest. Approximately 60% of the epiphyte mass was dead organic matter (DOM; 20.7 t ha^{-1}), and mass of epiphytic bryophytes, roots, stems and foliage was 4.1, 5.2, 2.1 and 0.7 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 and 32 t ha^{-1} for epiphyte mass, and 6 and 7 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 t ha^{-1} (Kohler *et al.* 2007), with epiphytic bryophytes, vascular epiphytes, and DOM estimated at 11.5, 3.9 and 2.1 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 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 of $\delta^{18}O$ isotope signals in tree stems. Seasonal isotopic signals of $\delta^{18}O$ 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 δ^{13}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}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 δ^{15}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 δ^{15}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 δ^{15}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 ± 0.1 mm day^{-1}. Cloud water measured directly averaged 5% of precipitation during the dry season, while use of a canopy hydrology model based on $\delta^{18}O$ 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 NO_3^-, NH_4^+ and 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 NO_3^- was strongly retained by epiphytic bryophytes, but not by vascular plant foliage. Net retention of NH_4^+ by epiphytic bryophytes and epiphyte assemblages was somewhat lower, and reflected the internal cycling of 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^{-1}, approx. 50% of the inorganic N in atmospheric deposition (6.8 kg N ha yr^{-1}). 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 NO_3^-) to less mobile (exchangeable 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_2 flux followed the same trend as soil carbon; mature forest soils exhibit slightly higher CO_2 flux, but greater spatial variability, and secondary forest soils have a higher flux than pasture soils. They suggested that differences in soil CO_2 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_2 exchange (NEE_c) 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_2 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_c 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_2 exchange and florescence 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_3 and NO_x 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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10

Conservation in the Monteverde zone: contributions of conservation organizations — Update 2014

Leslie J. Burlingame

The Monteverde conservation organizations documented in 2000 have matured and evolved, joined by additional organizations that developed in new niches. Their primary focus has moved beyond talking about sustainability to practicing it, though there is not yet consensus on how to define sustainability and what measures to take (Gora 2013).

More publications and theses/dissertations related to the chapter topic are now available, but most sources are still "gray literature," though much has been posted on the Internet. I have carried out interviews in annual two-week visits to Monteverde, with frequent follow-up e-mail contacts. Updates to essays that were at the end of the chapter are included in the text below as (essay).

10.1 Socio-Economic Developments in the Monteverde Zone

A. General Developments

Population in the Monteverde zone has increased in the last 15 years to about 6000; at least 150,000 tourists visit each year (www.monteverdefund.org). This rapid growth put pressure on local institutions and resources and increased socio-economic problems. Years of effort led to the emergence of a local district government in 2003; it works with national and local organizations to confront environmental problems, especially those related to water and solid waste (Ewing 2007). The Santa Elena office of the Instituto Costarricence de Acueductos y Alcantarillado, AyA (Costa Rican Institute of Water and Drainage), joins with local organizations to protect springs, treat drinking water, and clean and monitor streams and rivers, but there is not enough clean water in the dry season and treatment of gray and black water remains inadequate. In 2010, conservation organizations joined the local government to create a commission (COMIRES) to develop plans to deal with the area's solid waste to comply with a nation-wide 2010 law (Ley No. 8839). The local government now runs regular garbage pick-ups, has built a recycling collection center, involves volunteers in monthly recycling pick-ups, and has started building mini-recycling receptacles around the region (M. Díaz, pers. comm.).

The Coope Santa Elena (Coope), which dominated so many aspects of life in Monteverde from the 1970s to the 1990s, faced bankruptcy in 2001. It closed or sold its credit union, grocery store, hardware, and agricultural supply store; private businesses replaced these entities (Guindon 2001, McCandless 2008). Two Coope-affiliated organizations survived in altered form: Comité de Artesanías Santa Elena-Monteverde (CASEM) and Finca La Bella. The coffee coop producing Cafe Monteverde is in the process of closing or being transferred to a different organization in 2014 (Q. Newcomer and G. Vargas, pers. comm.).

CASEM (essay), like La Campesinita (essay), has empowered women and opened educational and economic opportunities for them since the 1980s (Stocker 2013). It became a completely independent cooperative in 2001 (Cooperativa de Comercialización de Artesanías de Santa Elena de Monteverde or CASEMCOOP R.L.). They currently have more than 85 members producing handmade crafts. In 2010, they added a restaurant that serves "typical" Costa Rican food. They face two main challenges: recruiting younger members and competing with more than a half dozen other art and craft stores that have grown up, many run by former CASEM members (P. Jiménez, pers. comm.).

Finca La Bella's (essay) trusteeship was "transferred to the Institute in 2003 when there was concern that the bank might take it when [the Coope] ... could not pay their debt" (K. VanDusen, pers. comm.). In 2013, representatives from La Bella, MVI, the San Luis Development Association, and the Monteverde Monthly [Quaker] Meeting agreed to transfer land ownership to the farmers of La Bella but to place certain "forested areas ... in ecological easements in the name of the Asociación Finca La Bella with the University of Georgia as the partner organization responsible for assuring that these areas are being conserved in forest" (K. VanDusen and Q. Newcomer, pers. comm., Cresson 2013).

El Buen Amigo (essay) was a second experimental coop located in San Luis (update by E. Vargas):

"…Around 2004 the remaining five families stopped individually managing the dairy operation of the farm. ... They sold the 10+ ha of pastureland that had been bought through the work and effort of the ... members of the group and other support (MCL). ... With the sale income, the families were able to buy or construct another home in San Luis (two families moved to another community). The original farm (131 ha) was not sold; it continued to be a property under the care of one of the Leitón brothers and his family. I still see many reasons to think that this project had a positive impact on the lives of the participants. When I talk with the young people, now adults, that were the small children during the BA farm years I can clearly see how they were proud of themselves and empowered to pursue different or new life projects."

B. Growth of Tourism

Tourism has grown rapidly in Costa Rica since the 1990s. In 2013, the government's Costa Rican Tourism Institute (ICT), which has been promoting tourism aggressively, reported a record 2.4 million international arrivals (Madrigal 2014). Many of these arrivals were tourists who headed to the beaches and non-sustainable mega-developments primarily owned by foreign investors, but many visited more sustainable smaller scale ecotourism venues with local owners in less accessible places such as Monteverde (Honey 2008). Guide books and on-line sources continue to cite Monteverde as a must-visit location; Monteverde and Santa Elena rank number 1 of 25 "Top Experiences" in Costa Rica in *Lonely Planet* (2012). No accurate data on the number of visitors each year exist, but estimates range from 150,000 to 250,000. When the road to Monteverde is paved in 2016, there will certainly be more visitors, though they may not stay as long. Tourism has become Monteverde's primary source of income, replacing the agricultural sector (the iconic Cheese Factory was sold in 2013 to a large Mexican company).

Facilities for tourism have expanded, especially those linked to adventure tourism, including numerous canopy tours with zip lines, hanging bridges, "sky trams," "Tarzan" swings, and bungee jumps. One hotel owner estimated that about half of his guests booked both an adventure tour and a visit to a reserve, with a quarter each on just one type of tour (P. Belmar, pers. comm.).

There are more than 20 larger hotels and many smaller types of lodging, including inns, pensions, cabins, and even one small hotel with rooms built up in trees. Restaurants, cafes, art and craft shops, and souvenir stores have proliferated. Many new educational exhibits have developed, including the Bat Jungle, the Ranario (Frog Pond), Butterfly Gardens (essay), Serpentario (Serpentarium), hummingbird gardens, and orchid gardens. Several private farms offer tours, and almost everyone runs a night tour. Chocolate, sugar cane (the Trapiche), and coffee tours include tastes and the option to buy these goods (R. LaVal, pers. comm.).

ICT developed a Certification for Sustainable Tourism (CST) in 1997; hotels have to meet extensive criteria in four different categories to receive ratings (www.visitcostarica.com/ict/paginas/sostenibilidad, Honey 2008). One hotel in Monteverde now has the highest rating. Its owner said "Our hotel was always developed in a sustainable way...CST was a way to show the world what we did in a way that could be measured... Our guests do very much appreciate the fact that we run an eco operation" (P. Belmar pers. comm., www.hotelbelmar.net, agrees with Gora 2013). Several other rated hotels emphasize their strong sustainability philosophy and practices (H. Smith, pers. comm.). Some tour agencies highlight CST certified facilities. ICT developed a separate certification system, the Blue Flag (Bandera Azul) for beach communities, nature reserves, and ecologically managed land (Honey 2008; www.visitcostarica.com/ict, www.turismo-sostenible.co.cr); the two largest Monteverde Reserves (MCFP and CER) and some sustainable farms and schools fly the Bandera Azul.

The Center for Responsible Travel (CREST) stresses another international approach to ethical tourism, which encourages tourists to support sustainable environmental, economic, and social development of the area they visit. CREST and MVI sponsored an International Travelers' Philanthropy Conference in 2011, which led to a 3-year pilot project (funded by the Inter-American Foundation) that became the independent non-profit Monteverde Community Fund (MCF, Fondo Comunitario Monteverde, FCM) in 2013 (Wilkins 2011; www.monteverdefund.org):

"The Monteverde Community Fund ... is dedicated to mobilizing resources that bolster the work of our engaged citizenry and community organizations around themes of sustainability. Among its varied fundraising strategies is the Monteverde Traveler’s Philanthropy Program, which seeks to more effectively capture resources from the influential tourism sector and equitably channel them into priority initiatives identified by the community. MCF currently provides small grants for projects related to environmental conservation, social and cultural development, as well as sustainable economic practices. Other service offerings include training and technical assistance with project proposal development and facilitating spaces where residents, businesses and non-profit organizations can benefit from peer exchanges. The organization ... operates as an independent entity with 2 staff members, approximately 30 associates and a growing network of local and national business collaborators" (J. Welch, pers. comm.).

Although tourism has brought many benefits to the Monteverde area, it also has negative effects (Chamberlain essay) beyond the obvious water and waste issues. Social and health problems include poorer nutrition and obesity (junk food replacing home grown food), drug use, and thefts. Although natural history guiding has provided many well-paying jobs and financial opportunities, economic inequality has increased; many jobs are in the low-paying service sector, and the cost of living has increased (R. LaVal, pers. comm.). Land prices have skyrocketed, and adequate near-by housing is unaffordable for most. Tourism has become a sort of monocrop vulnerable to environmental and economic changes. The worldwide recession that started in 2008 had serious negative impacts as tourism and international donations dropped. Effects rippled through the Monteverde economy; several businesses went bankrupt (P. Belmar and R. LaVal, pers. comm.). A hotel owner stated: "For the moment, the market is keeping new development at bay, but if we were to experience another boom, the risk of overdevelopment is high" (P. Belmar, pers. comm.). There is still no zoning (H. Smith, pers. comm.). However, numerous groups are aware of these problems and are trying to do something to solve them (Honey 2008, Koens et al. 2009, Burlingame 2013, Stocker 2013).

10.2 The Quakers and Bosqueterno, SA (BESA)

In 2001, Quakers in Monteverde and other community members celebrated the 50th anniversary of the Quaker's arrival in Monteverde. They published an illustrated collection of original documents and essays on life in Monteverde over the 50 years, including material on the history of many of the organizations discussed in this chapter (Guindon 2001).

BESA, the organization that they established in 1974 to protect 554 ha of their watershed, continues to be managed by BESA's Board and protected by the Monteverde Cloud Forest Preserve (MCFP), owned by the Tropical Science Center (TSC) in San José. In 2006, negotiations with TSC produced a new rental agreement for use of Bosqueterno's trails (by ever more visitors) and for leases on telecommunication towers on its Cerro Amigo. These funds, plus new income from Costa Rica's Environmental Service Payments, allowed BESA to start a small grants program in 2008 to support "projects having to do with protection of springs, including reforestation; education focused on water quality and river ecology; prevention, elimination, or treatment of contaminated waters; general education regarding freshwater conservation; education regarding climate change" (bosqueternosa.wordpress.com). They have funded projects for local conservation organizations and schools, and Santa Elena's AyA. They made grants for biodigestors for wastewater treatment on some San Luis farms, for reforestation of springs and riparian buffer zones (CRCF), and for research on bird populations in cloud forests and biological corridors (Bosqueterno poster 2014).

10.3 The Monteverde Cloud Forest Preserve (MCFP)

The MCFP remains the most visited private reserve in the area, welcoming almost 70,000 visitors per year to its cloud forests (TSC 2006). It has 40 employees and creates about 600 jobs directly and indirectly in the area (www.reservamonteverde.com). The Preserve's size is 4025 ha, less than previously because of the 2007 settlement of the dispute with the Monteverde Conservation League (MCL) involving land purchased in the initial Peñas Blancas campaign (1986-1989). MCL kept the 5300 ha from its campaign, and some horse-trading of land parcels smoothed out the border between the CER and the MCFP (B. Law, pers. comm.).

The Management Plan of 2005 reaffirmed land use zoning: 97% of the Preserve has absolute protection; 1% is zoned for special use; and 2% is for public use in the "Triangle," (13 K of trails for tourists). In the last 15 years, several new trails have been built and most existing ones have been widened and re-hardened. A hanging bridge was added; viewing platforms at La Ventana, the waterfall, and restaurant and signs, bridges, benches, and trail edges were rebuilt with recycled plastic boards. Visitation reached a high of 80,270 in 2008 and declined afterwards (with the global recession), then increased to 67,950 in 2013 (www.reservamonteverde.com; R.W. Carlson and C. Hernández, pers. comm.). Most buildings have been remodeled with a focus on sustainable construction and practice, most notably the Casona's "rustic" lodge that can sleep 43 and the restaurant, which were certified in 2009 by the CST Program. The Reserve's web page features a tab for "Sustainability" that lists the practices the Preserve has instituted.

MCFP also received (2012) the ecological Blue Flag award for the protection of natural areas including water and waste management (M. Díaz, pers. comm.).

The Environmental Education Program (EEP) has two staff members who work with 1-6th grade students and teachers in 12 local schools; students also visit the Preserve. EEP has broadened its focus on the Preserve's forest to deal with global climate change, endangered animal species, and water and waste (Blum 2012). The Preserve continues to work with students from all Costa Rican high schools that have ecotourism programs and universities with biology and applied science programs (M. Díaz, pers. comm.). EEP's important role in the Comisión de Educadores Ambientales de Monteverde (CEAM) is discussed in section 10.8.

There have been significant developments in MCFP's support for scientific research and its applications. The new Alexander Skutch Laboratory opened in 1999 as the Monteverde book went to press. The 200 m^2 building has two labs, offices, and a classroom. Some basic lab equipment is provided, but researchers are expected to bring most of their own equipment. The Research Program has a Director and two assistants; its goal is to “generate information and technical and scientific knowledge that will help make management decisions relevant to the protected resources in the area..." (www.reservamonteverde.com/research.html). The 2009 Plan Estratégico de Investigación contains data from 1979 - 2009 showing that 20% of the studies were done by Costa Rican researchers and students. Chapter 1 of *Monteverde: Ecology and Conservation of a Tropical Cloud Forest* had shown a decline in the number of researchers as tourism increased; however, there was a jump in the number of MCFP projects in 2000 and 2001, followed by a decline until 2006, increasing to a high point in 2009, when there were 31 studies; a subsequent document shows the 2009 level continuing and even increasing in 2012 (Programa investigación, RBNBM, CCT 2014). The subject matter of studies from 1979-2009 was on: plants (41%), arthropods (21%), birds (18%), and the remaining 20% on other animals. The Register of Research projects for 2013 shows more individual researchers investigating the effects of climate change on various organisms. Alan Pounds was hired as "Resident Scientist" in 1999 to study climate change in the Reserve. Canopy researcher Sybil Gotsch (Franklin and Marshall College) began a study of the vulnerability of epiphyte communities to changes in climate by examining the ecophysiological responses of selected common epiphytes to water loss (S. Gotsch, pers. comm.). Costa Rican researcher L. Moreno continued her 17-year investigation on the effect of climate change on the abundance and composition of bird species in the MCFP (Y. Mendez, pers. comm.).

The Preserve has also established its own projects in cooperation with Costa Rican Universities and Instituto Nacional de Biodiversidad (INBio). In 2007, they established "Permanent Monitoring Plots" (1 ha each) in seven locations. This work built on previous projects by B. Haber, who "established long-term phenology plots around the community, with a few trees marked in the reserve." Starting in 1987, N. Nadkarni "was the first to put in hectare plots that have been continually re-measured every 5 years, with marked and measured trees (about 2500 in 5 ha, 4 in the primary forest, 1 in the secondary forest within the Research Area of the Reserve" (N. Nadkarni, pers. comm.) In 2010, MCFP set up a network of meteorological stations, and they began an Amphibian Monitoring project under the direction of A. Pounds.

The idea of a corridor to connect the conserved areas in Monteverde to the Gulf of Nicoya had been discussed for years. TSC had taken the lead with the purchase of the largest remaining forest patch on the Pacific side, a 240 ha farm subsequently called the San Luis Biological Reserve, and developed a Management Plan (Méndez 2009). MCFP has played an important role in planning the new Bellbird Biological Corridor (BBC) (Section 10.6. D.)

10.4 The Monteverde Conservation League and the Children's Eternal Rainforest (MCL/CER)

By 2014, MCL's CER grew to 22,600 ha, the largest private reserve in Costa Rica.

MCL has continued to pursue its mission "to conserve, preserve, and rehabilitate tropical ecosystems and their biodiversity" through forest protection, environmental education, reforestation, sustainable development and eco-tourism, and scientific research. MCL has been recognized nationally and internationally for its successful conservation efforts, most recently including the Costa Rican Blue Flag award (Bandera Azul) for protected natural areas. CER has been supported for many years by sister organizations in Sweden, the United States, the United Kingdom, Japan, and Germany (acmcr.org, Burlingame 2013).

The League's financial difficulties in the 1990s made additional land purchases a low priority until 2002, when Rachel Crandell, a teacher, founded the MCLUS in Missouri. In consultation with MCL's leadership, in 2004 Crandell launched a new Land Purchase and Protection Campaign, using 50% of each donation for Land Purchase, 40% for protection (which includes the operation of MCL and MCLUS), and 10% for endowment. MCL established a prioritized list of properties to buy, focusing on filling out the borders of CER to natural boundaries and blocking points of easy entrance, buying land to connect pieces of CER, and buying inholdings. In a return to the original vision for the MCL, they also wanted to extend CER on the Pacific slope to help create a corridor for altitudinally migrating animals. MCL sister organizations in the U.K. and Germany and others also contributed to the land purchases. After Crandell's death in 2009, U.S. supporters continued MCLUS, renamed Friends of Children's Eternal Rainforest (FCER) in 2012 (MCLUS/FCER Annual Reports at friendsoftherainforest.org).

Following the 2007 Peñas agreement between MCL and TSC, MCL had an additional 5300 ha to protect in CER. Squatters are no longer a problem, but MCL's forest guards face serious challenges from illegal poaching, logging, capture of live animals, and removal of plants. Guards monitor endangered species; there was great excitement in 2013 when motion-sensing cameras photographed a jaguar and tapirs. MCL personnel also help researchers. The important Land Ordering Project, which began in 2006, uses GIS and GPS to produce surveys of CER's borders that can be used in legal defenses of those borders and in pursuit of legal titles (MCL Annual Reports, Burlingame 2013).

Major improvements to CER's infrastructure have been made over the last 15 years with attention to environmental sustainability. Trails and signage, road and Internet access have been improved. The two biological stations (San Gerardo and Poco Sol) are powered by renewable energy and have gray water treatment plants; the Poco Sol station was completely rebuilt by 2010. The offices of the MCL on the Monteverde and Atlantic sides of CER and structures at Bajo del Tigre have all been remodeled. The Bajo del Tigre sector is the only part of CER that is easily accessible from the Monteverde area; it receives 75% of the visits to CER (MCL Annual Report 2013). Night walks started at Bajo Tigre in 2003 have become a significant source of funds for MCL. A native plant greenhouse was constructed in 2005, and a labeled demonstration garden was replanted around the Visitors' Center. In 2012, an observation platform overlooking a regenerated forest, a meeting/picnic area, and gray water treatment system were added; the following year, a state-of-the-art classroom was built (MCL Annual Reports, B. Law and W. Zuchowski, pers. comm.).

Although MCL's economic difficulties ended the Environmental Education (EE) Program in 1995, most of MCL's personnel continue involvement with some EE activities, including leadership roles in community recycling and roadside and stream clean-up. In 2007, MCLUS/FCER increased funding for EE. Local children visit Bajo del Tigre for EE activities, with transportation funded since 2010 by BESA, and the Finca Steller Education Center on the Atlantic side of CER. In 2012, a five-year grant provided for an environmental educator to work with schools on the Atlantic side of CER on such topics as recycling, biodiversity, animal welfare and abuse, water resources and the importance of wetlands (www.friendsofthe rainforest.org/annual-report-2012).

The League's tree nurseries have produced 1.6 million trees (B. Law, pers. comm.). Most of these were planted in MCL's windbreak project and persist, as do others planted under special projects. Finca Steller has a small native tree nursery that produces a few thousand native tree species per year. The Fundación Conservacionista Costarricense (FCC) is raising native tree species on the Pacific slope that MCL has used for reforestation of degraded pastureland. Zuchowski's ProNativa organization promoting the use of native plants that began with the greenhouse and demonstration project at Bajo Tigre has expanded (Burlingame 2013).

MCL's financial deficit, incurred when the Debt-for-Nature-Swaps and grants ran out in the mid-1990s and contributions were still earmarked for land purchase, was at its worst in 2001. Gradually, the MCL's finances began to improve. The most important new source of income was payment for environmental services (ESP) by the government program FONAFIFO (Fondo Nacional de Financiamiento Forestal) and two private hydroelectric companies. MVI's Annual Reports document the dramatic increase in the areas of CER included in ESP and an equally dramatic increase in income for the MCL, going from no income in 1996 to an average of 62% of MCL's operation's income from 2009 to 2011 (MCL Annual Report 2013). Other income is from fees for entry to trails, mainly at Bajo del Tigre; unrestricted donations for operations; the sale of merchandise in MCL facilities; and net income from the biological stations. Donations for specific projects, including land purchase, are an important source of income. Another source of funds is interest on investment, including a growing endowment fund; Rachel Crandell had made MCL the beneficiary of her substantial life insurance policy.

Unfortunately, in 2012, the Costa Rican government changed its policies on ESP, deciding to help small landholders with 50 ha or less. MCL and several other conservation organizations in Monteverde saw their incomes drop dramatically as land under ESP phased out. By 2013, inflation and increased expenses (including legal costs) had raised the estimated amount needed to run the organization to a half million dollars per year (MCL Annual Report 2013). MCL is exploring ways to increase the number of visitors to CER from the 2013 level of 7000 and find new funding, especially carbon offset payments for forest protection and reforestation, but first they have to get legal title to all the land in CER, which will require a special legislative bill. The League's case was helped by its successful 25th Anniversary, in recognition of which the Costa Rican postal service issued four commemorative stamps on National Parks Day, August 24, 2011 (Burlingame 2013).

10.5 Santa Elena Cloud Forest Reserve (SECFR)

SECFR is achieving its goals to share "the benefits of tourism and using them as a tool for [sustainable] development where entrance fees are employed for the protection and management of the Reserve and to provide a better quality of education in the Colegio [Sta. Elena high school] and some schools of the zone" (Y.M. Arias, pers. comm.). Since 2009, there have been about 30,000 visitors per year, more than double the highest number in the 1990s. These visitors provide indirect economic benefits to tourism businesses in the community and employment as Reserve staff and guides most of whom are graduates of the Colegio, thus fulfilling another goal of SECFR (W. Bello, pers. comm.). There are new programs in environmental education, reforestation, and species monitoring.

The road to the 310 ha Reserve is now improved, thanks to adventure tourism sites just below. In 2012, the Visitor's Center was rebuilt; it and a new half k of hardened trail are handicapped accessible, making the SECFR the first in the area to meet the requirements of Law 7600 for equal access. An orchid garden whose plants were rescued from the forest floor, a small medicinal plant garden, and other native plants attract butterflies and hummingbirds. The 12 k of the four original trails and their signage have been improved. If the weather is clear, spectacular views of Arenal Volcano and Lake, the Gulf of Nicoya, and the Lake of Nicaragua await those who scale the new 12 m high metal observation tower on the Youth Challenge trail (reservasantaelena.org).

SECFR's environmental education coordinator worked closely with the Colegio students and teachers in the Ecological Tourism degree program. Blum (2012) stressed the broader definition of EE, including environmental ethics and values, used by SECFR and the national high school curriculum compared to MCFP's more biological approach to EE. However, Blum's research was conducted in 2003 just as EE approaches in the two organizations started to converge. Both include more attention to water and waste problems in the area, endangered species, and global climate change. The Commission on Environmental Education of Monteverde (CEAM; see 10.8 below) began in 2003 under the leadership of the heads of EE at SECFR and MCFP. Also in 2003, SECFR started working with 5 primary schools around the Reserve in ways similar to MCFP, providing programs at the schools, workshops for teachers, and engaging students and teachers in activities. SECFR's EE program also works with the Grupo Amigos del Ambiente (Friends of the Environment), a group of Colegio students that that formed in 2011. The group, which had grown to 32 volunteer students by 2012, set up a recycling program in the Colegio and at SECFR and became involved in fieldwork with researchers from four Costa Rican universities monitoring amphibians, birds, and water and air quality (Y.M. Arias, pers. comm.). They also monitor mammals with 8 donated motion detecting cameras and post photos of pumas and ocelots on their website (reservasantaelena.org/proyectos [and] /Boletines). The group joins visitors and other students in a reforestation project in areas bordering the Reserve using donated tree seedlings; since 2011, about 5000 trees have been planted per year (Y.M. Arias, pers. comm.).

The Administrative Board of the Colegio continues to manage SECFR and has signed new leases every 5 years with ACAT-MINAE (Area de Conservación Arenal-Tempisque or Arenal-Tempisque Conservation Area and the Ministerio del Ambiente y Energía or Ministry of the Environment and Energy). The Conservation Area (one of 10 administrative divisions of the country) had been called ACA (Area de Conservación Arenal) and included Arenal National Park. In 2007, the Conservation Area was reorganized to include territory down to the Tempisque River (adding protected areas as Palo Verde and Lomas Barbudal previously part of ACT or the Tempisque Conservation Area). Arenal National Park was put in a new 11th conservation area, Huetar Norte (ACAHN). Although all of SECFR is in ACAT, whose main office is in Tileran, parts of CER are now in three Conservation Areas (Y. Rodríguez, pers. comm., acarenaltempisque.org).

SECFR is a member of other environmental groups in the area such as COMIRES, CEAM, and the Bellbird Biological Corridor. They also have special international agreements with Rocky Mountain National Park in Colorado: a 2012 one through ACAT for exchange visits of department heads, and an exchange of students in 2014 from SECFR and the Park to study scientific monitoring (Y.M. Arias, pers. comm.).

10.6 New Conservation Organizations:

A. Costa Rican Conservation Foundation (CRCF)

In 2002, local residents, including biologists, established the CRCF to protect, connect, and restore "tropical habitats with a special emphasis on the deforested Pacific slope of Costa Rica ... [in] areas critical for the survival of the Three-wattled Bellbird (*Procnias tricarunculata*)" (fccmonteverde.org). CRCF grew out of George Powell's 1990s discovery that the endangered Bellbirds rely on the wild avocado fruit trees that grow in Pacific slope forests, during their post-reproductive period. Although the breeding grounds of the Bellbird and Resplendent Quetzal are well protected on the Caribbean slope of Monteverde, the decline in Bellbird numbers after 1998 was traced to habitat loss in the Pacific Rain Shadow Forest.

CRCF planned to create a 7 k biological corridor to link the protected Monteverde Reserve Complex with a lower protected zone, Cuenca Abangares, creating the Bosque para Siempre (The Forest Forever). They developed strategies to create the corridor: land purchases, conservation easements, cooperation with landowners, and pasture restoration. As of 2014, CRCF owns four wildlife reserves and has two other privately owned areas under conservation easements, providing successful protection to 77.5 ha (D. Hamilton, pers. comm.). Working with farmers and other landowners, conservation organizations, students, and volunteers, they reforested CRCF properties and many others. Their main tree nursery is at La Calandria, a private reserve and biological station in Los Llanos. Research projects include experiments with seedling propagation, survival, and growth rates, and the most effective and cost-efficient restoration practices (fccmonteverde.org, monteverde-institute-blog.org/environmental/2013/9/18/poster...). CRCF has produced and distributed 173,000 free native tree seedlings of 93 species (D. Hamilton, pers. comm.).

CRCF continues its annual Bellbird census. Since 2009, the decline appears to have slowed; the numbers of bellbirds have held steady (D. Hamilton, pers. comm.). Many other birds depend on the corridor, including neotropical migrants, such as scarlet tanagers, rose breasted grosbeaks, wood thrushes, Baltimore orioles, and several migrant warblers. The U.S. Fish and Wildlife Services' Neotropical Migratory Bird Conservation Program has provided several grants to the CRCF. BESA and FCER (see above), along with the British Embassy, GEF from the UN Small Grants Program, and several U.S. zoos also supported CRCF with grants. Many donations and work efforts have come through a student organization, The Change the World Kids (a US non-profit), and researchers, interns, and students (fccmonteverde.org). The CRCF has recently joined other conservation organizations in the creation of two larger projects, the Bellbird Biological Corridor and the Monteverde-Arenal Bioregion Initiative (see D and E).

B. ProNativas-Monteverde (ProNativas)

Reforestation with native rather than fast-growing introduced tree species had gradually become accepted as the norm, but it took a new organization to convince people in Monteverde of the many environmental advantages of planting native ornamental plants and the environmental threats from invasive exotic plants. Willow Zuchowski, author of *Tropical Plants of Costa Rica*, founded the non-profit organization ProNativas in 2004 with the support of local conservation organizations and outside funding. She had to collect seeds and cuttings, have greenhouses built (at MCL, CFS, and MVI), and then plant gardens with help from volunteers and one half-time employee. She created demonstration gardens with signage around these organizations and at the Biological Station, Monteverde Centro, local businesses, and private yards. At CFS, she helped establish gardens featuring specific plants to attract bats, birds, butterflies and bees. In 2007, she developed an illustrated Electronic Field Guide to Native Ornamental Plants of Monteverde (http://efg.cs.umb.edu/efg2/TypePage.jsp) with the Electronic Field Guide Project at U. Mass. Boston. These activities led to the formation of a ProNativas Network in 2008 with workshops, conferences, and a website (pronativas.com, W. Zuchowski, pers. comm.).

C. Curi-Cancha Reserve (Curi-Cancha)

The 83 ha Curi-Cancha opened in 2011 on property owned by the Lowther family, which they purchased in 1970 from Hubert Mendenhall, one of the original Quaker settlers. It forms a corridor linking BESA on the north and east down to land owned by MVI and CRCF and has a "mix of virgin forest, secondary growth of varying ages and some pasture" (J. Lowther, pers. comm.). CRCF has planted many native trees bearing fruits favored by bellbirds and quetzals. Curi-Cancha is legally recognized as a Refugio de Vida Silvestre Privado by MINAE and aims to be an "economically and environmentally sustainable business" (reservacuricancha.com, J. Lowther, pers. comm.). It has become popular with guides and tourists because it is less crowded than MCFP (limit of 50 visitors per day), has more open areas for animal viewing, and a lower admission cost. In 2013, 10,000 people visited the reserve, providing economic benefits for more than 25 guides and for taxi drivers (M. Ramírez, pers. comm.).

D. Bellbird Biological Corridor (BBC)

The Three-wattled Bellbird Biological Corridor (66,000 ha) aims to connect the Monteverde Reserve Complex through four watersheds and 11 life zones down the Pacific slope to the Gulf of Nicoya. In 2008, building on earlier corridor proposals to protect such altitudinal migrants as the Bellbird and the Quetzal, a local Council formed to make the corridor a reality. The seven founding members of the BBC were: the Arenal-Tempisque Conservation Area (ACAT-MINAE), CRCF, MCFP, MCL, MVI, SECFR, and UGACR). In 2009, these groups agreed to pay for a part-time Co-ordinator for the Project. With funding from the GEF-Small Grants Program of the United Nations, they elaborated and are implementing a Strategic Plan with a mission to reestablish and maintain: biological connectivity, conservation of natural resources, and the well being of local communities (Corredor Biológica Pájaro Campana, Plan Estratégico 2011-2016).

By 2014, the Project created maps using satellite images and GIS of the physical, biological, and land-use features of the proposed corridor. They monitored bird populations, documented water abundance and quality, and produced thousands of trees for reforestation. BBC members are requesting funding for native tree reforestation around existing springs. They meet and facilitate workshops with civic and community organizations in the corridor to educate them about the BBC and learn about their concerns. By 2013, 26 organizations were affiliated with the BBC (Welch 2007, cbpc.org, N. Vargas and R. Guindon, pers. comm.).

E. Monteverde-Arenal Bioregion Initiative (MABI)

MABI, the newest cooperative conservation, research, education, and sustainable development project, was launched at a Feb. 2014 conference at the Monteverde Institute. P. Raven, in his welcoming remarks, framed the focus of the conference: "How can the talents and activities of the many organizations who have permanent facilities in this region or visit it repeatedly become a conceptual entity with more facilities, educational opportunities, more extensive conserved and restored areas, an enhanced contribution to sustainable tourism, and lasting value...[that is] fully integrated with the welfare of all the people who inhabit the region"? (iniciativamonteverdearenal.blogspot.com/2014/02/welcoming-remarks-peter).

The Initiative grew out of a symposium organized by N. Nadkarni at the joint 50th anniversary meeting of the Association for Tropical Biology and Conservation (ATBC) and the Organization for Tropical Studies (OTS) held in San José, Costa Rica in June 2013. Entitled, "The Perfect Storm: Educational, Conservation, and Community Synergisms for Tropical Ecology Research in Monteverde, Costa Rica," the session included presentations by six Monteverdans with different institutional perspectives (ATBC Online Web program for S-11, 25 June 2013). They examined the special interactions in Monteverde of "conservation, education, ecotourism, civic awareness, and spirituality" that made Monteverde such a productive location for scientific research even though it had no major biological research station (N. Nadkarni, pers. comm., see Nadkarni and Wheelwright 2000). How could Monteverde's success be improved and how could it serve as a model for nearby and other tropical areas?

MABI drew 55 participants including representatives from all the organizations discussed in this update and more from the larger bioregion and beyond such as MINAE-SINAC; AyA Santa Elena; the Universities of Georgia, Texas A&M, Brown, California, Stanford, Utah, and Vermont in the States and the Universidad Nacional in Costa Rica; The School for Field Studies; FCER; Conservation International and the Nature Conservancy (iniciativamonteverdearenal.blogspot.com/2014/02/instituciones-invitadas-invited.html). The conference began with poster presentations by the different organizations so that everyone knew the focus, priorities, and activities of the other organizations. Emphasis was on forging "communication links between existing groups" (N. Nadkarni, pers. comm.).

Participants worked to develop a common vision. Further discussion and planning took place in committees: Education, Conservation, Research, Maps, Communication, and Funding. The leaders of each committee constituted a Coordinating Committee. The Conference blog outlines the challenges, possible solutions, and committee proposals (iniciativamonteverdearenal.blogspot.com/2014.02....). The Research Committee is developing a website where scientists will be able to post research projects and data sets. A key next step is finding funding to hire a part-time coordinator; a follow-up conference is planned for 2015 (N. Nadkarni, pers. comm.).

10.7 Environmental Education and Sustainability at the University/College Level Primarily for Students from North America

Costa Rica has become the leading Latin American study abroad destination (Dyer 2014, Institute of International Education 2014). Monteverde has been a magnet for college/university courses, starting with the OTS graduate Fundamentals course in 1971 (Burlingame 2002). The Monteverde Institute has offered programs for international students since 1987; in the last 15 years, three other institutions have established centers in the area.

A. The Monteverde Institute (MVI)

MVI has built on its mission of "education for a sustainable future," providing a broad range of courses supported through many institutional partnerships. It puts sustainability and conservation into practice on its campus and through its courses and community interactions. MVI has encouraged students, researchers, interns, and volunteers to develop applied research projects that generate information and options to help local communities deal with pressing issues. In addition, MVI has brought substantial educational, cultural, and economic benefits to local communities (Burlingame 2013, MVI Annual Reports, monteverde-institute.org).

By the end of 2013, MVI had provided nearly 480 courses (long and short) for about 8900 students; there are now about 25 courses each year (F. Lindau, pers. comm.). Tropical Biology and Conservation, the University of California Education Abroad Program (UCEAP) given two semesters per year since 1987, has consistently had the largest number of students. In the continuing long course, "Sustainable Futures" (SF), upper level undergraduate and graduate students in architecture, landscape architecture and planning, engage in “service learning” to develop their knowledge and skills by working (gratis) on planning and designing projects that help local communities and institutions. Projects have ranged from designs for specific facilities (including those of MVI) to large scale “scenario planning," development plotting and tracking in the area, and scenarios for the future. In 2001, a partnership with the University of South Florida produced an annual course on "Globalization and Community Health." A semester-long interdisciplinary place-based program, "Globalization, Development, and Environment," began in 2009 as a joint venture between Mount Holyoke and Goucher Colleges. The Living Routes Program: Tropical Ecology, Development, and Social Justice (2011-2013), focused on the impact of national and international policies on local sustainability, conservation and social justice. MVI also collaborates with partner institutions to offer customized services (F. Lindau, pers. comm., Burlingame 2013).

By 2009, MVI's campus occupied 24 ha; two years later, MVI and CRCF began joint management of the newly created 14 ha Dwight and Rachel Crandell Memorial Reserve adjacent to MVI's campus (D. Hamilton, pers. comm.). This Reserve completes a corridor in the 62,000 ha of privately protected forest reserves known as the Monteverde Reserve Complex.

A new wing was added to the main building in 2002 to house the John and Doris Campbell Library. Behind it is a small classroom building, constructed in 2002 by the Fox Maple School of Traditional Building (Maine) using non-native trees. Construction of a new outside timber-framed, multi-functional, glass-enclosed classroom in 2012 was a collaborative project among local artisans, volunteers, and MVI courses (Burlingame 2013, monteverde-institute.org/facilities-at-mvi). Sustainable construction has been joined by sustainable practice at MVI, as detailed on MVI's web site. MVI has worked with homestay host families to help them improve energy efficiency in their homes, and to promote recycling and composting.

In 2013, students and volunteers developed demonstration organic "Carbon Gardens" around the new classroom, including a vegetable and herb garden, a keyhole garden, rain gardens (to use rain runoff from the Fox Maple roof), a greenhouse for raising native plants, and a native tree nursery producing saplings for reforestation. Native plants and tree saplings are planted on MVI's campus and donated to local people for their use. Volunteers tagged trees behind the main MVI building to establish an arboretum. The gardens will also be used for experiments with sustainable agricultural techniques and will provide educational opportunities and nutritional information for MVI students, staff, and local communities (D. Hamilton, pers. comm.; monteverde-institute-blog.org).

From the beginning, MVI was interested in fostering, facilitating, and applying research in the region. Research done by international students and faculty working with MVI staff and resource people from the area continues to be made available to other researchers and the community through presentations of research findings and the collection of research papers in the library; many are now digitized. In 2008, MVI began its Integrated Water Resources Program, which builds on concerns over use of water resources and public health. The program also carries out education and community outreach, particularly through its Adopt-a-Stream Program that supervises monthly stream monitoring data collection and annual reports by students from the three high schools. "The Impact of Economic Change on Food Habits and Nutritional Health in Monteverde, Costa Rica: Mixing Agriculture and Tourism," began in 2008 with funding from the National Science Foundation and collaboration from the University of South Florida. Data indicated that as families increased their involvement in tourism, food insecurity and health problems increased. In 2012, MVI decided to promote better nutrition through demonstration gardens and to encourage more physical exercise with a "Monteverde in Motion" program (Burlingame 2013).

MVI has used proceeds from its international courses to support programs that enhance education, well being, and sustainable development and culturally enriching activities in Monteverde and surrounding communities (monteverde-institute.org/current-projects for link to PDF: Community Initiatives and Programs 2013). They collaborated with the local district council to make safe walkways along the main road a reality. In 2012, MVI reached out to a new group, local 12-15 year olds, with a camp experience. Counselors aged 16-20 and adult volunteers from seven area communities helped the younger kids have fun, engage in community service, and "develop healthy and educational links between Monteverde's youth and its community members." It is now an annual event (monteverde-institute.org/summer-camp).

MVI has provided direct financial benefits for staff, teachers, taxi drivers, cooks, guides, and for families offering homestays for MVI students, as well as owners and employees of tourism establishments and other businesses. In 2010, MVI paid out more than $350,000 to community service providers (Wilkins 2011). These payments, in turn, flow back into the community, as does money spent by MVI's international faculty, students, and researchers. Some in the community have received individualized financial benefits such as scholarships to attend MVI courses or aid (for MVI employees) to continue their education.

MVI developed serious financial problems by 2005 as its financial debt burden grew (from the construction of its new building and library addition and from land acquisition) while income from courses decreased. Beginning in 2006, MVI's Director, working closely with the Board, instituted drastic reductions in expenses through major personnel cuts, sale or divestment of some properties, and expanded efforts to increase income and find new partnerships for offering courses on a regular basis. The leaner, more focused MVI paid off its debts by 2008 and successfully began expansion of its financial base (more courses and students) and extension of its community outreach. The Director reactivated the U.S. non-profit Alliance for the Monteverde Institute (AMVI) in 2009.

B. Council on International Educational exchange (CIEE)

CIEE is a U.S. based non-profit organization that has provided international exchanges in many countries since 1947 (ciee.org). In Costa Rica, CIEE is based in Monteverde, where it started offering a summer Tropical Ecology and Conservation Program with MVI in 1989. Alan Masters became the Director in 1993 and oversaw expansion into semester programs in 1996. MVI provided Spanish language instruction until 1999, when CIEE became a freestanding program. In 2007, CIEE added Sustainability and the Environment, with Karen Masters as Director. CIEE then moved to its own Study Center in Cerro Plano where there are classrooms, meeting areas, a library, and computer facilities with eco-friendly construction and native plant landscaping; students live with homestay families. The

Ecology Program has courses and lives at the Biological Station (ciee.org/study-abroad/costa-rica/monteverde/sustainability-environment). Both Programs take extensive field trips on the Pacific and Altlantic slopes (A. and K. Masters, pers. comm.).

The Tropical Ecology and Conservation Program is designed for biology majors, with courses in biology, conservation, and Spanish, and one that explores the historical impact of humans on tropical ecosystems, including indigenous cultures, European settlement, ranchers and farmers, ecotourists, and conservationists (A. Masters, pers. comm.; course details and reports on the website). The full texts of all research papers since 2004 are available in MVI's library digital collection; each one has an abstract in English and Spanish and the collection is key-word searchable (M. Leitón, pers. comm.; monteverde-institute.org/mv-digital-collections-Tropical Ecology).

The Sustainability Program includes courses in conservation biology, policy, natural history, Spanish, and sustainability (K. Masters, pers. comm.). Students have completed internship projects ranging from construction of a biodigestor and composting toilet for a coffee farm to designing native plant gardens and greenhouses. They built artificial wetlands to treat gray water, created a website and produced GIS maps of reforestation plots for CRCF, and worked with Hydroponics of Monteverde on "alternative, renewable fertilizers" (K. Masters, pers. comm.).

C. University of Georgia, Costa Rica (UGACR)

In 2001, the University of Georgia Foundation purchased the 63 ha Ecolodge San Luis and Biological Station in San Luis to develop a satellite campus for UGA. The property, which adjoins both the MCFP and CER, is 60% forest, 30% sustainable farm, and 10% built space (Q. Newcomer, pers. comm.). UGACR's Mission "is to advance our understanding, through instruction, research and outreach, of the interconnected nature of human and environmental systems, particularly the concepts of socio-cultural, ecological, and economic sustainability" (dar.uga.edu/costa_rica).

Over the next ten years, UGACR built campus facilities with an emphasis on sustainability. Climate is controlled in: a wet lab furnished with basic equipment, an insect collection, GIS lab, and herbarium, which includes William Haber's donation of his extensive herbarium. Indoor and open-air classrooms are equipped with the state of the art electronic equipment. There are three weather stations, one of which posts real time data on the website; fiber optics and WiFi connect campus sites to the Internet. Four bungalows house students; faculty, researchers, and interns have their own residences. The sustainable capacity is 60 people per night (Q. Newcomer, pers. comm.). The cafeteria, a computer lab, library, and offices are located in the student union. A recreation center, fields and courts for various sports, and 3 k of trails provide activity options. UGA landscape architecture students designed a 1.5 ha botanical garden, which includes medicinal plants and an arboretum. UGA rebuilt the 12-room Ecolodge San Luis, and in 2012, was awarded 4 leaves under ICT's Certification for Sustainable Tourism (CST). (UGA Sustainability Report 2010 & 2013, Q. Newcomer and A. Cruz, pers. comm.).

UGACR began tracking goals and improvements in campus sustainability in 2010 (dar.uga.edu/costa_rica). The campus has an organic farm that produces 15% of food consumption. Livestock waste is processed by a biodigestor, set up as a demonstration project for local farmers. In 2013, a large biodigestor was built on campus to process all human waste; it produces methane to power the kitchen stove, and 97% of the water used is returned clean to the forest (A. Cruz, pers. comm.). A native tree nursery (started by CRCF and taken over by UGACR) produces 4000-5000 seedlings of 50 species of native trees to donate for reforestation projects each year. Over 30,000 trees have been planted on San Luis farms and lower elevations, some by students seeking to decrease their carbon footprint incurred by their travel to the Campus. (dar.uga.edu/costa_rica/index.php/site/sustainability_initiatives, Q. Newcomer and L. Ramírez, pers. comm.).

UGACR runs about 25 UGA programs (semester and short-term) per year, representing

40 disciplines and 11 Colleges with about 250-275 students and 75 faculty and teaching assistants. Programs include Tropical Biology, Landscape Architecture, Tropical Reforestation Service-Learning, Veterinary Medicine, Sustainability of Tropical Agro-Ecosystems, Environmental Anthropology, Latin American and Caribbean Studies, and Theater and Film (dar.uga.edu/costa_rica). About 40-45 short programs (average 5 days) for institutions other than UGA, including OTS, bring ca. 1200 students and faculty a year. More than 700 tourists are staying an average of 4 days at the Ecolodge in 2013-2014; they eat in the cafeteria and participate in campus activities. (Q. Newcomer, pers. comm., dar.uga.edu/costa_rica). UGACR actively promotes research on campus and in the area, offering information on facilities, logistical support, institutional partnerships, and research sites; research project are listed at dar.uga.edu/costa_rica.

Community involvement and outreach are part of UGACR's mission. They purchase 25% of their food and many services from local providers. UGACR joined MVI to raise funds for 12 small-farm sized biodigestors in the San Luis community; their students and other volunteers provided installation labor and aid to San Luis schools (UGACR Strategic Plan 2013, Q. Newcomer, pers. comm.). UGACR is an active partner in the BBC; they conduct water quality research at 5 sites on each of the 3 rivers in the corridor and have contributed to GIS maps of the corridor (A. Cruz, pers. comm.).

D. Texas A&M-Soltis Center (TAMU-Soltis)

Texas A&M opened its 117 ha Soltis Center for Research and Education in 2009. It is located in San Isidro de Peñas Blancas, San Ramon, adjacent to the eastern border of CER (soltiscentercostarica.tamu.edu). TAMU-Soltis seeks to: “train succeeding generations of Texas A&M students with the aid of experiential, field-based learning; catalyze and facilitate critical and innovative research in the biological, physical, and social sciences; [and] serve as a major international location for research and education in sustainability issues and wise stewardship of natural resources" (soltiscentercostarica.tamu.edu/content/mission-vision-and-objectives).

The land and facilities of the new center were donated to the TAMU System by Bill and Wanda Soltis. Bill Soltis, a TAMU graduate, had traveled to Costa Rica on business and started buying forested land next to CER to preserve it. He donated 16 ha that had been deforested for a farm and reforested it for the campus, provided a 100 year free lease for ca. 100 ha of primary and secondary forest that he and partners own on the border of CER (E. Gonzalez, per. comm.), and underwrote construction costs for the Center, using designs by TAMU architecture students. An academic building has a wet and dry lab, 3 classrooms, library, computer facilities and WiFi, offices, and cafeteria, with 8 dormitories that sleep up to 56. All of the facilities are handicap accessible (soltiscentercostarica.tamu.edu).

The Center hosts courses run by TAMU faculty focused on Environmental Design, Water Management, Field Studies in Tropical Biology, and Geography Mapping. They also facilitate service-learning programs; in 2010, TAMU's chapter of Engineers Without Borders built a computer lab at the School of San Juan de Peñas Blancas. Students from TAMU's College of Education established an English as a Second Language Program for local children and donated English books to the school (soltiscentercostarica.tamu.edu). Non-TAMU schools and organizations, such as OTS, have brought courses, workshops, and tour groups to the Center (soltiscentercostarica.tamu.edu).

Since 2007, geographers and other researchers have been mapping and establishing benchmarks in the 100 ha of forest, gathering baseline data on biota, making species lists, and collecting data at a meteorological station that posts real time on-line information (soltiscentercostarica.tamu.edu). Monteverde scientists have contributed to baseline research; D. Hamilton and R. LaVal have collected vertebrates, and B. Haber has collected insects for his Electronic Field Guide Project (D. Hamilton, pers. comm.). Most of the current researchers come from TAMU. The Director encourages more researchers to use the site, as the site provides a unique and rich setting for research and education activities (E. Gonzalez, pers. comm.).

10.8 Environmental Education in the Public and Private Schools

A. EE in Schools of the Monteverde Area-Overview

EE in local primary and secondary schools include more attention to water and waste issues, climate change, endangered species, and sustainable living (Blum 2012). Primary schools (grades 1-6) supported by the government include two in Santa Elena and Cerro Plano and ca. 20 other in surrounding towns. The Colegio Técnico Professional de Santa Elena offers specialized programs or majors in agriculture, ecological tourism, and food services in addition to traditional academic subjects (See Section 10.5). Their web page states: "The protection of nature and its resources are our principal objective in teaching" [colegiosanta elena.org; author's translation]. There are also 3 private bilingual schools in the area: Monteverde Friends School (MFS), The Cloud Forest School (CFS), and the Adventist School that are now accredited by the Ministerio de Educación Pública (MEP: Ministry of Public Education). All area schools have basic curricula, including Environmental Education, shaped by MEP. Teachers in the primary schools still lack sufficient training and resources for EE and depend upon the EE Programs at the two cloud forest reserves (Blum 2012). CEAM (see below) helps coordinate EE activities.

A new initiative in sustainable development involving Colegio majors comes from a Monteverde Community Fund grant to the Colegio in 2014 to help build a biodigestor to process animal waste from the agricultural program, which will keep the waste out of regional streams and produce methane gas for cooking in the Food Services Program (monteverdefund.org/mcf-newsletter-January - 2014). Students from the 3 high schools are involved in the Adopt-a-Stream program offered by MVI for monthly monitoring of the health of local streams.

B. Monteverde Friends School (MFS)

MFS had 115 students in pre-K through 12th grade in 2013-2014 (C. Evans, pers. comm.). The school is committed to Quaker values, including "Stewardship: The school promotes an appreciation of and connection to the natural world. By increasing our awareness of our interdependence with all life on earth, we strive to use water, land, and other resources mindfully and wisely. Our resolve is enhanced by the natural beauty and biodiversity that surrounds us" (mfsschool.org/about-us). Students go on field trips to local reserves and educational nature exhibits. They carry out an independent project in their last year; e.g., following a stream from its origin to the sea, investigating the local recycling program. High school students have organized recycling at the school.

C. Cloud Forest School (CFS)

The CFS, established in 1991, has 200 students and is the only school in the area dedicated to "learning the language of a sustainable future" through environmental education and on-campus land stewardship. (cloudforestschool.org, Burlingame 2013). CFS acquired its 46 ha campus through a loan from the U.S.-based Nature Conservancy, to establish legal precedents for conservation easements in Costa Rica. The easement put the farm (72% forested) under strict protection. "Green Building" standards for new buildings were developed in 2003 and used that year in construction of the Gazebo or Kiosco (with Monteverde's first solar panel) and all subsequent construction (Burlingame 2013**).**

Once CFS owned the land, they hired a steward to monitor land-use plans and work with the EE Coordinator, staff, and volunteers to integrate the curriculum with stewardship activities. By 2013, more than 14,000 native trees had been planted (M. Brenes, pers. comm.). Volunteers have constructed and maintained trails and mapped all the reforestation areas (CFS Rainbow Spring 2014). An organic vegetable garden and farm, worm composting facilities, 2 greenhouses, and native plant gardens featuring a medicinal plant garden and thematic gardens to attract bats, butterflies, bees, hummingbirds, and birds provide additional EE resources.

Environmental Education has always had a central role in CFS's curriculum. Recently, the EE Coordinator introduced grade level themes based on the National Education for

Sustainability, K-12 Student Learning Standards (L. Grenholm, pers. comm.; s3.amazonaws.com/usp_site_uploads/resources/ 123/USP_EFS_standards_V3_10_09.pdf). This is part of a "spiraling curriculum [that] allows for an interdisciplinary approach to learning about the environment, society, and economy for CFS students beginning at the age of 3" (CFS Rainbow Fall 2013). Land stewardship is an integral part of EE, and students care for their own campus daily; they have established a campus-wide recycling program. They also take field trips to local reserves and educational nature exhibits.

CFS is enrolled in the ICT Blue Flag Program (L. Grenholm, pers. comm.). In 2013, CFS formed a new alliance with UNION VARSAN S.A., owner of a local sustainable farm, to offer students opportunities for internships, hands-on farm activities, and educational tours. The business is committed "to offer young people a career alternative to tourism" (CFS Rainbow Spring 2013, G. Vargas, pers. comm.).

D. CEAM

The Commission on Environmental Education of Monteverde (Comisión de Educación Ambiental de Monteverde; CEAM) is a cooperative group of environmental educators formed in 2003 by the MCFP, SECFR, CER, ACAT, the local government, and local office of AyA (ceamonteverde.weebly.com). They coordinate environmental activities, raise local environmental consciousness, and contribute to sustainability. From 2005-2009, they sponsored an annual prize contest for ecological stories by students from 14 schools. The 15 best stories from all these years were published in 2014 with funding from the local government and BESA (M. Díaz, pers. comm.).

CEAM, under the leadership of M. Díaz from MCFP and Y.M. Arias of SECFR, organized a 3-year training program for those concerned with environmental issues and education. Funded by ACAT and the US Fish and Wildlife Service, workshops involved 103 people from conservation organizations, local government, and agencies in the region (Menacho 2010). ACAT's CREA (Comisión Regional de Educación Ambiental or Regional Environmental Education Commission) has more than 40 active organizations in its network (ceammonteverde.weebly.com/integrantes.html).

10.9 Conclusion: Lessons from Monteverde and Topics for Future Research

A. Recommendations for Future Work

Environmental organizations and conservation activities are rich areas for historical analysis and documentation. Many of the organizations discussed in this Update are more than 20 years old; their early records are deteriorating in quality. This history should be preserved in digital form, preferably in a central location. It would be ideal to have a single electronic database with up-to-date-records and live web-site links for all these organizations.

AyA Santa Elena and ACAT based in Tileran have become important players in conservation, EE, and sustainable development; they are both involved in MABI. The developments of these and emerging regional organizations (e.g., BBC and MABI) should be followed. EE programs started at MCL in 1986, at MCFP in 1992, and at CFS in the early 1990s. Those early students are now adults; the impacts of EE on their lives should be assessed.

Recommendations for special projects are: a) a history of the Finca La Bella community; b) analysis of the evolution of issues and players related to water in the Monteverde area; c) sustainable and organic agricultural experiments in the zone; d) the developments of personal networks linking conservation organizations and their impact on building a base for consensus decision-making.

There are many topics to explore in the growth of Monteverde area tourism, beginning with an accurate estimate of the number of tourists in Monteverde to assess environmental impacts, including water and waste. This is also critical to understand the impact of paving the road up the mountain. A study on the growth of the area’s adventure tourism industry, and the effects of the commission system, will show the sector's economic contribution to the Zone. How sustainable are tourism businesses, and how do they define, value, measure, and implement sustainability? The answers to these questions will come from carefully designed social science surveys and questionnaires, which brings up another issue. MABI is in the process of setting up a database of researchers and research in the sciences; social scientists should be included in this. Finally, this Update has shown that large changes have occurred in the last 15 years; there needs to be a mechanism to add current information to this online Update at least every five years.

B. Failures or Problems of Conservation Organizations

"There are multiple visions and practices of environmentalism operating in a scene of complicated regional social, economic, political, and ecological change" (Vivanco 2006). Conservation organizations have not made sufficient efforts to understand the differing visions and practices. "The fact that many residents see the now-protected forests as off-limits to their recreation and use reinforces the authority of the environmental organizations that police those lands, but fuels quiet talk by some people of future land invasions" (Vivanco 2006). Another anthropologist discusses conflicts between the values of conservationists and more urban Costa Ricans in Sta Elena and Cerro Plano with their development associations and their understanding of sustainability in more social and economic terms (Blum 2012). Some Costa Ricans have resented a lack of access to scientific research information generated in Monteverde but available only in English and in locally inaccessible specialized journals (Blum 2012).

Some think that the rapid development of tourism, especially adventure tourism, is destroying what was special about Monteverde. Crowds of tourists in MCFP and other tourist destinations, billboards, and heavier traffic are associated problems. In addition, tourists and the population increase they caused have strained water supplies, increased amounts of waste, and burdened infrastructure.

Financial stability remains a persistent problem for many of the conservation organizations in Monteverde. Problems were magnified with the global economic downturn by 2009; for Monteverde, this involved decreases in tourism and international donations. Organizations are aware that they need to develop endowments and more stable sources of funding.

C. Successes of Conservation Organizations

1. A traditional measure of conservation success is the amount of forest that has been acquired. By 2014, BESA, MCFP, CER, SECFR, Curi-Cancha, and CRCF had acquired 27,650 ha; these reserves are part of the Arenal-Monteverde Protected Zone of 70,000 ha. Most of them are included in ACAT's 395,046 ha which have some measure of protection.

2. Local residents are employed by the reserves as unarmed guards; they try to build good relations with people living around the reserves while protecting wildlife and plants from poachers.

3. The practice of linking forest patches to protected areas via corridors has expanded beyond buying land. CRCF has been establishing a corridor linking two protected areas, and BBC is establishing a corridor from the continental divide in Monteverde to the Gulf of Nicoya that includes people living in the area.

4. Reforestation in rural and more settled areas has continued through the efforts of many organizations and projects.

5. Environmental Education is part of the curriculum for primary and high schools. Numerous groups have provided EE for local schools and for the broader community. For example, in June 2014, CEAM, the University of Costa Rica (UCR), and the National University of Costa Rica (UNA) organized an all-day Water Fair (Feria del Agua) in Sta Elena. Almost all the conservation organizations discussed in this update had multiple representatives with tables full of literature, posters, and small give-aways. Water was the central focus of lectures, workshops, demonstrations, and lots of fun educational activities for children, who packed the place. Other forms of EE have expanded in the institutions for foreign university students, in guided tours of reserves, and in educational businesses with animals and orchids.

6. Organizations have continued to emerge: a local government, a cooperative group to solve garbage and recycling problems (COMIRES), a Community Fund, the CRCF, ProNativas, the BBC, and MABI. Volunteers serving on committees and on each other's Boards link these organizations to each other and to

continuing organizations. Monteverde's conservation organizations occupy different niches and do not compete with each other.

The successes of conservation organizations in these areas have been possible because of the following factors (Burlingame 2000):

1. Resident and visiting scientists provided basic and applied knowledge that led to the formation and growth of conservation organizations and their programs.

2. Economic prosperity and a diversified economy supported the development of conservation organizations and made an educated middle class a reality. Since 2000, tourism has surpassed agriculture as the main economic driver.

3. Successive immigrants brought new perspectives, skills and knowledge, starting with the Costa Rican settlers, followed by the Quakers, then the biologists, the tourists and business people, civic leaders, educators, and artists to create what the 2013 session at the ATBC called "The Perfect Storm: Educational, Conservation, and Community Synergisms for Tropical Ecology Research in Monteverde, Costa Rica."

4. Monteverde's conservation organizations and the people who support them have been able to change as conservation thinking evolved from a focus on preserving particular endangered species to concern about threats to biodiversity to today's more general challenge of climate change and need for ways to implement sustainable development. They learned how to tap into outside sources of funding and steer benefits of tourism to conservation and sustainable development ends. The organizations have shown resiliency and resourcefulness; their success has been possible because of dedicated, hard-working, and creative people.

5. Information access has been improving. Having the Monteverde book and Updates available on the Internet in English and Spanish with free access will be a major contribution. The proposed online MABI database will also be important. MVI's library has been building a digital collection and has created an electronic list of MCFP's library holdings. MVI has an offprint collection, but they are missing many articles; researchers need to be encouraged to submit copies of their articles or opt for open access to their publications (L. Kutner, pers. comm.).

D. The Monteverde Zone and its Conservation Organizations as Models

Simply copying Monteverde and its conservation organizations and applying these activities elsewhere is problematic because of the unique elements in Monteverde and in Costa Rica. However, some of the conservation and educational organizations can serve as models. Monteverde's successes with ecotourism as a way to support conservation organizations and the development of ecotourism businesses can serve as a model for certain locations.

The Monteverde-Arenal Bioregion Initiative, launched in 2014, proposes to extend the synergisms of the Monteverde area that have contributed to its successes in research, conservation, and education to the larger bioregion around it.

E. "Human Voices Around the Forest"

E. Vargas' update to his (essay), "Human Voices Around the Forest" offers a concluding vision of promises and challenges to conservation successes:

“As neighbors living around the protected areas, we enjoy the beauty of landscape, the pureness of water and air, the peace of the bird’s songs; but it also implies a responsibility: to care for this natural richness, as the source of life and admiration for all creatures, among them, human beings. For this purpose, it is essential that our short and medium term actions be framed by an integral, long-term vision.

"The conservation organizations and the government highlight the extension of protected forest as proof of conservation success in Monteverde and Costa Rica. However, we do not know if in a few decades, these organizations will have the capacity and the necessary resources to ensure the protection of such a large area. Will they be able to do it without the participation and support of the people living around these forest reserves? What will be the future pressures on these areas? Other actor’s voices are being heard, from the inhabitants of nearby communities (e.g. Guacimal, Chachagua) defending their water sources for human consumption from the agro-industry and tourism developments pushing for water concessions. Furthermore, public and private hydroenergy companies are creating more pressures as they construct dams on various rivers whose main water sources are in the Monteverde Reserve Complex.

"These cases offer an idea of the big challenges for the conservation organizations, governments, educational institutions, community leaders, farmers and enterprises of the region. Enduring sustainability will depend on the will among all organizations and actors involved to maintain and improve the collaborative work relationships that have distinguished our communities."

Key to Acronyms

ACAT: Area de conservación Arenal-Tempisque [Arenal-Tempisque Conservation Area; previously ACA]
ATBC: Association for Tropical Biology and Conservation
AyA: Acueductos y Alcantarillados [Costa Rican Water and Drainage Institute]
BBC: Bellbird Biological Corridor
BESA: Bosqueterno, S.A. [Eternal Forest, Inc.]
CASEM: Cooperativa de Artesanías de Santa Elena-Monteverde [Crafts Cooperative of Santa Elena and Monteverde]
CEAM: Comisión de educación ambiental de Monteverde [Commission on Environmental Education of Monteverde]
CER: Children's Eternal Rainforest [previously BEN in English]
CFS: Cloud Forest School [previously CEC in English]
CFSF: Cloud Forest School Foundation
CIEE: Council on International Educational Exchange
COMIRES: Comité de manejo integral de residuos sólidos [Solid Waste Management Committee]
CRCF: Costa Rican Conservation Foundation
CST: Certification for Sustainable Tourism [from ICT]
EE: Environmental Education
ESP: Environmental Service Payments
FCER: Friends of the Children's Eternal Rainforest [previously MCLUS]
ICT: Instituto Costarricense de Turismo [Costa Rican Tourism Board]
MABI: Monteverde-Arenal Bioregion Initiative
MCF: Monteverde Community Fund
MCFP: Monteverde Cloud Forest Preserve
MCL: Monteverde Conservation League
MEP: Ministerio de Educación Pública [Ministry of Public Education]
MFS: Monteverde Friends School
MINAE: Ministerio del ambiente y energía [Ministry of the Environment and Energy]
MVI: Monteverde Institute
OTS: Organization for Tropical Studies
SECFR: Santa Elena Cloud Forest Reserve
SINAC: Sistema nacional de areas de conservación [National System of Conservation Areas]
TAMU-Soltis: Texas A&M University Soltis Center for Research and Education
TSC: Tropical Science Center
UGACR: University of Georgia, San Luis Costa Rica

Sources

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NOTE: Most of the sources for this Update are “gray literature,” unpublished computer generated reports, newsletters, and documents available from the organizations that produced them. Also, most all of the organizations discussed in this

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11

Agriculture in Monteverde, Moving Toward Sustainability — Update 2014

Joseph D. Stuckey, Fabricio Camacho C., Guillermo Vargas L.,
Sarah A. Stuckey, and José Vargas L.

1. Introduction

The agricultural systems and sustainability issues described in the late 1990s remain relevant 15 years later. However, because land use patterns respond to dynamic social and economic conditions, change is taking place on the margins of Monteverde's land use economy. This 2014 Addendum to Chapter 11, "Agriculture in Monteverde, Moving Toward Sustainability" outlines the direction of these changes, and identifies key global and local trends that appear to drive this change. We comment on: economic trends (J. Stuckey), climate change (F. Camacho), dairy (J. Stuckey), coffee (G. Vargas), and integrated farms (F. Camacho). Table 11.1 presents a list of people interviewed.[1]

2. Summary

Climate in the Monteverde bioregion is changing, and Monteverde's economy is becoming increasingly integrated with global commerce. The climate is becoming warmer and (generally) drier, and in recent years, weather events (rain, drought, and wind) have become more severe and their timing less predictable.[2] Monteverde's production and consumption patterns are increasingly dependent on global markets, prices, and international regulations. Small but growing numbers of landowners are implementing more ecologically, socially, and economically sustainable practices. Dairy

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[1] Each of the authors is a long-term Monteverde resident. Where possible, the information reported in this addendum is based on peer-reviewed literature. However, most of the observations about the local economy are based on interviews with local farmers and community leaders.

[2] Trade winds are a hallmark of dry season; they produce generally drier conditions on the Pacific slope and wetter conditions near the continental divide. As cloud water is intercepted at the peaks, the winds flow down the Pacific slope drying out the landscape, and preventing Pacific moisture – the source of the region's heavy rains – from ascending. Shifts in trade wind patterns, whether linked to ocean temperature cycles, changes in the jet stream or other phenomena, can produce dramatic local effects. When trade winds occur in rainy season, as has happened with some frequency in recent years and notably in 2013 and 2014, we see extreme local variations: more moisture on the Atlantic slope; and on the Pacific slope, wetter highlands and more drought in the lowlands. Generally we see more days of drought, but more intense rainy days, where in a very short amount of time it may rain most of the water of the month, as happened in May 2014 (F. Camacho and J. Stuckey, pers. comm.).

farmers have adopted some new technologies; their economic future remains uncertain as they face global competition, rising land prices, and demographic shifts. Coffee production patterns may shift as climate warms; many small producers have developed synergies with eco- and educational tourism as a survival strategy.

3. Economic Trends

Two key forces are shaping the Monteverde region's economy.[3] First, international free trade agreements are opening Costa Rica to global competition, which puts small producers and businesses at a disadvantage relative to large scale, capital intensive ones. Second, the local grafting of a tourist economy into an agrarian economy has created population growth, with accompanying pressures and opportunities that influence land use. Monteverde's tourist economy grew at a phenomenal, although undocumented, rate until the 2008 global economic downturn. As the population and tax base have grown, infrastructure and access to public services have expanded. This, and increased use of digital and other technologies, has increased quality of life, in the sense that producers and consumers have more choices than before.[4] The use of cell phones, internet banking, and credit and debit cards is prevalent. Three banks, three milk processors, two supermarket chains, and several national food and beverage distributors operate in the area. With the exception of eggs, most of the food and fresh produce consumed locally comes from outside the area.

Countering this increased commercialism, some Monteverde residents seek to produce and consume food that is grown with environmentally and socially sustainable practices. A small but growing number of integrated farms and gardens provide produce for local markets. Several farmers have linked their farming activities to eco-tourism; some coffee farmers are marketing farm-branded products directly to clients.

3.1 Demographic Trends

A population estimate based on extrapolation of potable water connections administered by local community water associations, (*Acueductos y Alcantarillados*, popularly known as AyA) indicates that Monteverde and surrounding communities comprise on the order of 5,000 to 8,000 inhabitants, not including "floating" tourist populations (V. Molina, pers. comm.) See Table 11.2.

The area has experienced immigration of people from diverse socio-economic and cultural backgrounds. Youth are increasingly mobile. The area is undergoing cultural blending, which is associated with the value of English as an economic language, the effect of local private schools, and educational tourism.

The social and economic effervescence surrounding land use decisions contributes to five trends:

1) Tourism has created economic opportunities that drive increased population through immigration and retention of local youth who stay in the area. This increases urbanization pressure, which drives up land prices first in communities closest to urban centers, and then, more gradually, in outlying communities.
2) Squeezed by the economics of global trade, some farmers have ceased commercial farming, while others are increasing the scale of their businesses, adopting new technologies or market niches to remain economically viable.
3) Youth increasingly pursue secondary and university education, which increases their mobility. Although some leave the area, the growing economy has provided jobs or business opportunities that attract others to stay.
4) Youth are leaving the farms. Older farmers may remain tied to the land by culture or by necessity, or may sell their land. This raises a central question: *in the future, who will own the land, and how they will use it?* Land

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[3] We use the term "Monteverde" as defined in Chapter 1, section 1.1, and in Chapter 11, p. 390 of the 2000 publication.

[4] The area's growing commercial activity has contributed to changing lifestyles. As a simple function of access to services and opportunities, quality of life has generally (but not uniformly) increased. It would be interesting to study perceived changes in quality of life if "quality of life" were to be measured by other indicators, for example "happiness".

subdivision for residential or commercial purposes is occurring in some communities, whereas in some cases, new landowners develop integrated, diversified farming systems.

5) The wealth generated during tourism's boom years has led to changes in the lifestyles of many residents and in the values of voluntary cooperation for the common good. This change is evident in the growth of consumerism, which, with the advent of lean years in the economy has led to unsustainable debt levels for many entities, and can lead to more social problems, in addition to the existing cases of bankruptcies, foreclosures and unemployment. Financial institutions have facilitated this trend through their lending policies, and by aggressively popularizing the use of credit cards.

3.2 Commercial Trends

Local farm production costs are closely tied to international petroleum and basic grains prices, but due to the particular dynamics of Costa Rica's small economy, input prices tend to rise quickly and fall slowly in response to international price fluctuations. Dramatic fluctuations in international dairy prices have destabilized production and marketing plans (González 2008, Montero 2013, J. Vargas, pers. comm.).

Implementation of free trade agreements, principally with the United States and the European Union will end protective tariffs on imported dairy and other goods, and obligate Costa Rican producers and exporters to conform to rigorous international standards. The Costa Rican government has increased its enforcement of environmental and sanitary regulations. Trade agreements have paved the way for transnational companies to buy local businesses that decide to sell rather than compete. Since the early 2000s, having tied Costa Rica's economic aspirations to international commerce, government administrations have relied on information technology and tourism as economic centerpieces, and have not articulated strong agricultural development and food security policies. (Vargas 2009, and J. Monge, pers. comm.).

3.3 Tourism

Commercial tourism in Monteverde has generated substantial wealth and jobs, and has created important local synergies for economic opportunity. Some land-owners have abandoned farming to establish tourist businesses; others have integrated some tourism activities into their farms. But tourism has not been a stable economic model: it is vulnerable to world events, and to boom-bust cycles. Monteverde's tourism is characterized by seasonal fluctuations in visitation rates, and by intense competition among local businesses. This results in the payment of high commissions to booking agents, which drives up prices and reduces Monteverde's competitiveness as a destination. Availability of jobs in the tourist sector tends to reduce the number of people available for farm work.

Educational tourism seems to be a stabilizing feature of Monteverde's tourism, and a growing market segment. Several universities have campus facilities, staff, and/or programs operating in the area **(see Chapter 10's addendum for more details on "Environmental Education and Sustainability at the University/College Level Primarily for Students from North America"**. Beyond providing jobs and markets for farm products university people and programs have shared information and provided assistance that influence local attitudes and practices linked to land use.

3.4 Institutional Evolution

Monteverde's first District Municipal government was elected in 2002. It and subsequent administrations failed to adopt land use planning, but did increase the amount of revenue for local development. National institutions continue to expand services, tax collection, and enforcement of health, environmental, and other regulations.

By 2014, the Ministry of Agriculture (MAG) plays three roles for Monteverde agricultural producers. Nationally, it monitors compliance with international trade standards, e.g., by certifying that herds are brucellosis-free, and issuing the Veterinary Operating Certificate (CVO), which is required to commercialize farm products (J. Monge and J. Álvarez, pers.

comm.). Monteverde's local MAG officials help farmer organizations gain access to government funds for special projects, and offer technical assistance in dairy, coffee, horticulture, aquaculture, and agro tourism. MAG's assistance responds to demand rather than to national planning priorities, and is constrained by a limited budget (J. Álvarez and J. Martín, pers. comm.).

SENARA (*Servicio Nacional de Aguas Subterráneas, Riego, y Avenamiento* – the government agency that supervises subterranean water, irrigation, and drainage) and MAG promote agricultural irrigation schemes in several communities in the Monteverde region. MAG and INEC, Costa Rica's National Institute for Statistics and Census, are conducting a national agricultural census, which may signal increased government commitment to develop a national agricultural sector plan (Martín 2014).

Locally, the Monteverde Milk Producers' Association (APLM) has gradually expanded sale of farm supplies and technical assistance provision. Productores de Monteverde, S.A., the cheese plant that was founded by the Quakers in 1953, supported the National Milk Producers Chamber's efforts to influence national dairy policies and free trade agreement negotiations. In 2013, Productores de Monteverde S.A. was sold to the Mexican transnational conglomerate Sigma Foods, and continues to operate locally. After decades of having been the only company buying milk in the area, it now competes for local milk with Dos Pinos, Costa Rica's large dairy cooperative, and Coopeleche, a regional dairy cooperative that sells its milk to Florida Farm and Ice, a transnational beverage company. In 2013, CoopeSanta Elena failed, and in 2014 Coopeldos struggles to survive.

4. Agricultural Production in the Face of Climate Change in Monteverde

By Fabricio Camacho C.

4.1 Trends

Critical signs of climate change in the Monteverde area are trends toward an increasing number of dry days, and the gradual increase in minimum temperatures (Pounds *et al.* 2006) and of precipitation in the highlands (IMN 2008). These and other non-documented trends have caused important changes in ecosystem dynamics. These variations are expressed through the emergence of new disease vectors that have appeared to contribute to the extinction of species such as the golden toad *(Incilius periglenes)* and the harlequin frog *(Atelopus sp.*, Pounds *et al.* 2006), and through the decline of other amphibians and the presence of invasive species representative of warmer lowland climates in the cloud forest.

One would expect that just as changes have occurred in the dynamics of natural ecosystems in Monteverde, changes would also have occurred in the production patterns of agricultural processes. However, no specific analyses of the impact of climate variability on local production exist, so it is imperative document this information.

Global and regional projections indicate that change in the main climatic variables is imminent even under the most drastic scenarios for mitigation and reduction of emissions of carbon dioxide and other greenhouse gases (IPCC 2007, 2013, Anderson *et al.* 2008), therefore it may be concluded that Costa Rica's climate will be subjected to dry and rainy extremes (IMN 2008). Locally, when comparing the average rainfall between 1961 and 1990 with the average projected under the A2 scenario (according to the IPCC nomenclature) between 2071 and 2100 for the mountainous region of the Tilarán mountain chain, that variable will decrease by 17% (IMN 2008). Maximum temperature will rise an average of 6.39 ° C while the minimum temperature will also suffer an increase of 2.88 ° C (IMN 2008).

This new climate scenario may be perceived as a threat or an opportunity for agricultural production in the Monteverde area, as the future distribution of the climatic conditions of the region can reduce or increase the productive capacity of the currently installed systems. For example, coffee production in the region is shifting towards higher altitude areas such as Cañitas and Las Nubes. This could represent a better business opportunity for producers in these communities but also could mean direct competition or displacement for producers in lower areas such as San Luis, where plantations might be more prone to disease and to receiving lower market prices because of lower quality coffee.

4.2 Adapting to Climate Change

The future success of Monteverde's agricultural production will depend on the capacity and speed of local producers to adapt to new climatic conditions. For example, coffee producers in warmer areas could incorporate agroforestry techniques, combining production of shade grown coffee interspersed with food crops and high value forest trees that allow producers to generate food for the household and ensure a more resilient system that could compensate for the lower yield of coffee. Some producers in San Luis have established agroforestry systems for shade grown coffee, although these are motivated by cultural and economic reasons, rather than as a climate change adaption. However, these systems are more natural, less dependent on external inputs, and resemble traditional plantations and home gardens, which make them more attractive to rural tourism and better adapted to climate change.

Other important factors that influence the level of success of future agricultural production include: 1) the level of producer innovation to acquire technology that allows them to be competitive without exceeding the land's carrying capacity; 2) access to information and technical support from government and private organizations to help producers develop balanced systems; and 3) the ability to develop new market opportunities that recognize the real value of local production.

Demand for food by Monteverde's tourism sector, and by the local population, represent two opportunities to capitalize agriculture. Except for a few small distributors of foods such as eggs, chicken meat, and vegetables, Monteverde currently has no direct, robust connection linking agricultural producers, residents, and tourists, so the majority of its foodstuffs come from other regions, even though the area has adequate conditions to produce fresh food that could be absorbed by the local market.

Monteverde has the potential to increase local produce consumption, but this will require a cultural change by households and commercial consumers (supermarkets, grocery stores, hotels and restaurants) to consume local products. This change, which would differentiate Monteverde's economy, may be a selling point for tourism. It would generate important links in the local production chain that might be organized through the creation of an entity that coordinates logistics so that producers can connect directly with consumers. In any case, it is important to begin adapting agricultural activity to a model of clean and sustainable production that is closely linked to the market and that guarantees the sound management of natural resources, ensuring a balanced development of production systems that meets but does not exceed the carrying capacity of the land and the needs and aspirations of producers and consumers.[5]

5. Dairy

By Joseph Stuckey

5.1 Economic Trends

Dairy farmers are being squeezed by rising costs. They face the threat of stagnant or falling milk prices as protective tariffs on dairy imports are eliminated, even as the amount of capital needed to stay in business rises. These trends favor large producers over small ones.

5.1.1 Climate Change

Between 1999-2014, water production of 14 springs supplying the Santa Elena *Acueductos y Alcantarillados* (AyA) potable water system fluctuated in 2-3 year cycles that seem responsive to the El Niño and La Niña warming and cooling events, which produce drier and wetter conditions locally (A. Sandí: unpubl.

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[5] "Clean" production refers to a world- wide movement for "cleaner production" based on producing services and goods in an environmentally responsible way, by mitigating and minimizing negative impacts such as water pollution and GHC emissions. One definition for *cleaner production*: "*Manufacturing process minimizing waste and applying continuous prevention practices. These method[s] include (1) raw materials and energy conservation, (2) toxic inputs elimination or reduction, and (3) toxic outputs reduction or elimination*" (http://thelawdictionary.org/cleaner-production/).

data, Santa Elena AyA, pers. comm.).[6] Although most do not keep weather records, farmers comment that in drier years, higher elevation clouds reduce the beneficial effect of dry season mist, making dry seasons more intense and slowing pasture growth for upland farms that normally receive this precipitation. However, in the drier years (e.g., 2013), farmers report that an increased number of dry sunny days in rainy season favor pasture growth. The drier years are associated with strong, un-seasonal, easterly winds. When such winds occur in rainy season, they prevent the Pacific moisture that normally produces heavy rains from reaching Monteverde, and exert chilling and mechanical effects that slow pasture growth. In recent years, rainfall has tended to be concentrated in fewer, but larger events, so that although total annual rainfall may decline only modestly, more water runs off, causing increased erosion and aquifer depletion. (F. Donato and J. Monge, pers. comm.).

5.1.2 Dependence on Supplemental Feed Grains

Farmers and local agricultural professionals report that the amount of supplemental feed grain being used to produce a kilo of milk may have increased in recent years. Although we found no local studies to test this perception, if true, it would suggest that the profitability of dairy farming may have declined, both because it is more expensive to produce milk using imported feed grains than using farm-grown forages, and because the cost of grain has risen relative to the price of milk (Montero 2008 and Vargas 2009).

5.1.3 Impact of Free Trade Agreements

Costa Rica’s milk prices have exceeded world milk prices in recent years (Montero 2013), and its dairy industry has been protected by tariffs amounting to 65% of the value of imported dairy products. The Central American Free Trade Agreement (CAFTA) requires elimination of dairy import tariffs over nine years, starting in 2016. Falling tariffs will affect milk prices to farmers. To comply with international norms, farmers are also required to invest in new technology and management practices.

5.1.4 Land Ownership Succession

The trend of youth leaving the farm is especially significant for dairying because: a) more people in Monteverde directly or indirectly depend upon dairying than on other types of farming, and b) the success of dairy farms depends on the quality of daily management, which is more difficult to achieve when delegated to hired labor.

5.2 Farm Production Trends

By 2014, the number of small farms producing milk had declined significantly. In the 1990s 17 farms in San Luis sold milk to the dairy plant; by 2014, only four remained (J. Fuentes, pers. comm.). Factors that contributed to this trend include: requirements to install on-farm refrigeration and other technologies, rising production and transportation costs, rising land values, opportunities for on-farm diversification or for off-farm employment, and demographic shifts. During the same period, herds on some of the more specialized farms grew in an effort to become more efficient.

In both lowland and highland dairies, all farms use refrigeration equipment and nearly all use milking machines. About 95% of the milk is transported in tank trucks. Many farms have installed concrete cow paths to reduce erosion. Many farmers have improved their barns and pasture irrigation systems in response to waste regulations. Nearly a dozen farmers use bio digesters and/or earthworm composting systems to process animal waste. Electric fences are increasingly used to manage grazing. Farmers use motorized backpack sprayers to apply herbicides, pesticides, and foliar fertilizer; weed-eaters have mostly supplanted the machete for cutting weeds. Some use harvesting machines to cut forage. Larger farmers keep computerized financial and reproductive health records. (J. Monge and A. Murillo, pers. comm.).

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[6] Santa Elena draws water from 26 springs, and new sources are constantly being sought; long term production data only exist for the 14 older springs.

5.3 Highland Dairy Production Trends

Between the late 1990s and 2014, average highland milk production increased by 60% to about 16 kg per cow per day. Over the same period, the amount of land in production declined, while stocking rates increased slightly. Jerseys became the predominant highland breed, significant because Jersey milk contains more solids than other breeds, and the milk price is linked to milk solids content. These trends seem to result from increased use of supplemental feed grains, supplemental forage feeding in dry season, and genetic improvement through artificial insemination (J. Monge and A. Murillo, pers. comm.).

5.4 Lowland Dual Purpose Dairy-beef Production Trends

Over the same period, lowland milk production increased about 142%, rising from ca. 4.5 kg to 10.9 kg per cow per day, an increase associated with fundamental changes that were made in the production system: planting improved grass varieties; increased cross breeding of beef breeds with higher production, heat resistant dairy breeds; increased use of feed grain supplements; transition from once-a-day to twice-a day-milking; expanded use of parasite controls; increased use of electric fences; and on some farms, installation of irrigation systems to improve pasture growth. By 2014, lowland farmers had not adopted the practice of applying fertilizer to pastures (J. Monge and A. Murillo, pers. comm.).

5.5 Efficiency

Increased production per cow per day in both highland and lowland areas is associated with better management and increased use of various energy inputs. However, it seems probable that the per-cow production average rose, in part, because the number of the smallest farms declined at the same time that the remaining farms were becoming more specialized. Further study is needed to know whether the increased average per-cow production resulted in a net increase of milk coming from these communities to the dairy plant and to assess the relative profitability and environmental sustainability of lowland and highland dairy production systems on the Pacific slope.

6. Coffee in the Local Economy

By Guillermo Vargas L.

As with other agricultural products and processes, the region's coffee economy is changing. With the disintegration of CoopeSanta Elena and the proliferation of brands and marketing channels for Monteverde's coffee, there are no data available to quantify coffee production in 2014, but an outline of the history and current patterns of coffee production can provide insights on its future.

6.1 Before 1950

The families who settled in the Monteverde region in the first quarter of the twentieth century came mostly from the western part of Costa Rica's Central Valley. These families brought with them the culture of coffee production and consumption.

In the 1940s, several families in San Luis and Los Cerros produced enough coffee to sell part of the harvest in Las Juntas, and to the roaster Café La Moderna in Puntarenas. Coffee berries were dried on farms and then peeled by hand in a wooden pestle. Transportation by horse to Las Juntas, and by oxcart and boat to Puntarenas, was slow and arduous. Coffee was not a viable economic option for local residents until the early 1950s, when one of the settlers, Ramón Brenes, commercially developed the cultivation and processing of coffee on his own farm. The abundant water and better sun in the lower part of San Luis created the opportunity to set up a mill at the confluence of the San Luis and Guacimal rivers.

6.2 From 1950 Through the Mid '80s

From 1950 to 1980, coffee became the main economy of small communities of San Luis and Los Cerros, and during harvest, generated employment for residents of Santa Elena, Cerro Plano and Guacimal. The coffee was partially processed (wet processing) in San Luis, and then transported to the Central Valley for drying and classification before being exported. The producers had no direct involvement in or control of those stages. At that time, growers achieved good yields because the soils sustained much of their original fertility. However, the price received for their labors did not correspond to the export value of the beans, due to ignorance of small farmers of their legal rights, and the existence of multiple intermediaries.

The development of Monteverde's dairy economy presented an opportunity for economic diversification, giving farmers the possibility of obtaining steady incomes and selling to a local company in which they could participate as co-owners. Another opportunity presented itself at the early 1970s, when Coopeldos R.L., a regional coffee cooperative serving producers, was founded. However, poor roads limited the ability of San Luis producers to take advantage of this cooperative marketing opportunity.

6.3 Cooperativization of Coffee (1985-2000)

In the early 1980's, the main coffee producer and owner of the coffee processing plant in San Luis shifted from coffee to beef cattle production. When the San Luis coffee processing plant stopped operating regularly, farmers chose to take their coffee to Coopeldos R.L. or to the Nicoya Peninsula to Coopepilangosta R.L., but both options incurred high transport costs. In response, in 1988 CoopeSanta Elena R.L. started processing and marketing coffee, having leased the San Luis processing plant.

During the 1990s coffee production and marketing in Monteverde expanded significantly. CoopeSanta Elena managed to sell about half of its members' harvest to Montana Coffee Traders, in Montana USA, at prices superior to international prices. Based on an agreement with Productores de Monteverde, S.A. the co-op created "Monteverde Coffee", a brand sold regionally as "Coffee Produced in Harmony with Nature". It also received "Fair Trade" certification, which allowed Monteverde Coffee to be sold at higher prices in international markets. With a ready market and good prices, the area's production increased. However, the cooperative later faced economic problems and weakened. This caused a loss of confidence by farmers, a slight decline in the area's coffee production, and encouraged the search for alternative marketing channels.

6.4 Proliferation of Local Coffee Companies and Weakening of the Cooperative Economy

With the cooperative's weakening, and the rapid growth of tourism, some farmers moved into tourism, as employees, entrepreneurs, or by diversifying their farms to appeal to tourists. For example, agro-tourism has created economic opportunities for several Monteverde families, and has become the third most popular attraction for visitors (after eco and adventure tourism). An estimated 20,000 tourists each year participate in tours of coffee, sugar cane, cocoa and other farms developing more sustainable agro-ecological practice (Holland 2010; G. Vargas, pers. comm.).

Private coffee processing and roasting initiatives began in the early 2000s. By 2014, there were 12 local coffee brands in the Monteverde. Micro-processing and roasting plants proliferated along with the brands. **Café Florencia**, one of several small family-farm initiated brands, illustrates this tendency (see Table 11.7).

6.5 Looking to the Future

In 2014, the coffee economy is diverse: dozens of brands from outside the area compete with Monteverde's own brands. Some local entrepreneurs are seeking strategies for joint marketing of the region's coffee. There is general support for collectively promoting Monteverde as a region that produces high quality coffee. For example, in 2012 producers co-sponsored a Regional Coffee Fair. However, local entrepreneurs who have successfully developed niche markets have a strong incentive to strengthen their own brands, rather than to subsume them under a collective identity.

In a region apt for both coffee production and tourism, one producer reflected on the past and future. "Our region has a special combination of opportunities for producing, processing, and marketing coffee. Our product is known for its high quality, and for sustainable environmental and social practices; however we face marketing constraints related to scale and capital. What can we learn from our previous successes and failures?"

7. Examples of Entrepreneurship and Sustainable Farming in Monteverde

By Fabricio Camacho C.

Thanks to the leadership and vision of organizations and community members in the Monteverde area, as well as favorable climate, soil and market conditions, several agricultural projects have integrated the concept of sustainable production in farming operations. Here, we summarize progress being made with integrated farms, agro-ecotourism, local production and consumption, and farmers' markets.

7.1 Integrated Farms

Integrated farms respect the carrying capacity of the land and incorporate management practices that minimize the negative impacts of agriculture, while maximizing the use of available resources without degrading them to generate direct and indirect benefits for farmers and for the environment and society in a sustainable manner over time (MAG 2008, Navarro 2012). See Table 11.8 for a more technical summary of the concept of integrated farms, and Table 11.9 for a map of several integrated farms in the Montverde region.

(INSERT: Table 11.8, Integrated Farms Technical Summary

INSERT: Table 11.9, Integrated Farms in Monteverde, 2014

7.2 Agro-ecotourism

Although agro-ecotourism has been more predominant on coffee plantations in the Monteverde area (e.g., Café Monteverde, Café San Luis, Café La Bella Tica, Café Don Juan), other farms have also taken advantage of tourism to diversify their productive activities. They often offer guided farm tours, and educational activities linked to the region's natural history and culture; some offer lodging and entertainment for visitors.

The Terra Viva and Rancho Makena projects, in the San Bosco-Las Nubes area, are dairy farms that have incorporated farm production and environmental impact mitigation processes with ecotourism. Both dairies offer lodging in cabins, and opportunities for tourists to engage in farm activities.

Cabinas Capulín and Farm, between Santa Elena and Las Nubes, is a project that produces food (mainly vegetables) with low environmental impact, for home consumption and for sale to the community. The project provides lodging to visitors and the opportunity to participate in farm activities. Other models have been developed which also demonstrate, for tourists, artisan food production mainly for family consumption and local sales, e.g., the Brenes Family Model Farm (La Cruz), Finca La Bella (San Luis) and Finca el Trapiche (Cañitas). These farms do not provide lodging, but charge visitors a fee that helps offset the farm's operating costs. The products of the Brenes Family Farm are sold at the Farmers Market in Santa Elena.

7.3 Production for Home Consumption and Local Market

Although not necessarily motivated by the objective of low impact farming, the Monteverde area is beginning to develop a Farm-to-Table movement led by some hotels and restaurants to produce, on their own land or in partnership with local farmers, some of the food for their own operations. The two most consolidated examples of this model are the Hotel Belmar and the Restaurant and Pizzeria Johnny. Meanwhile, the Monteverde Hydroponic Garden, located at Cabinas Los Pinos in Cerro Plano, produces vegetables and spices for area restaurants and hotels and for direct sale to the public at the garden or at the Monteverde Farmers Market.

Another interesting process is the use of traditional home gardens, small semi-urban gardens, and livestock propagation systems for home consumption, which produce vegetables, fruits and root crops, eggs, poultry, and pork. This type of production requires little space, uses local inputs, and increases family food security. Some families sell their surplus production, or exchange it with neighbors, helping the domestic economy and reducing dependence on external food markets.

Finally, the production of eggs for local consumption is significant in Monteverde. This production process has evolved around small family businesses that produce enough to meet the needs of the local market, a minimum of

5000 eggs per day (C. Santamaría, pers. Comm.). The eggs are distributed directly to local businesses and the Monteverde Farmers Market.

7.4 The Monteverde Farmers Market

In 2014, the Monteverde Farmers Market celebrated its sixth anniversary. This weekly event provides a venue for local producers and producers elsewhere in the country, to sell their products to local consumers. It also functions as an opportunity to strengthen and enrich the cultural ties of friendship and unity among the residents of the community. The mix of producers, consumers, and visitors, as well as the generational diversity, is an example of the cultural richness that characterizes the Monteverde area.

8. Topics for Future Research

A fundamental challenge that applies to all farms is to develop a management culture involving record keeping and analysis. Other pressing questions meriting quantitative and qualitative study include the following.

8.1 Climate Change

1. What impacts has climate change had on agricultural production in the area?
2. What are possible scenarios for the impact of climate change on future agricultural production?
3. What adaptation mechanisms can area farmers undertake?

8.2 Economy

1. How are demographic, economic, and social trends affecting land use options? What outcomes are desired? What policies, incentives, and institutional arrangements are needed to move toward the desired outcomes?
2. What role does indebtedness play in household livelihoods and land use decisions?
3. To what degree does the economic viability of dairy and coffee farms depend upon specialized versus diversified income sources? How might the results of this analysis change if the unit of analysis were "households" dependent upon dairy or coffee farms, as opposed to "viable farms?"
4. How have educational opportunities expanded options for youth? What are current trends related to youth education, employment, and mobility? For example: how many youth pursue higher education or technical studies? How many are graduating? How many drop out to work locally or in other regions? How many return to live, work or share their knowledge locally? How many have graduated, but work in other parts of the country? How many have studied abroad? How many receive scholarships or support from local organizations, businesses, or private individuals for primary, secondary, or university education? Such a study could involve participation by the students themselves, with support of local organizations.

8.3 Dairy

What can be done to reduce supplemental feed grain use, and to increase production of quality forages? This should be linked to technical assistance on soil fertility management. Artificial insemination programs might consider the use of sires that have been bred to maximize milk production in high forage/low supplemental grain ration contexts. Further study could also be done to measure the relative profitability and environmental sustainability of lowland and highland dairy production systems on the Pacific slope.

8.4 Coffee

1. What climate change adaptation measures are available for local coffee farmers? For example: coffee varieties with greater resistance to Coffee Rust *(Hemilieia vastatrix)* and "*Ojo de Gallo*" *(Mycenia citricolor)*; alternatives for natural control of fungus and insects (Coffee Borer Beetle, *Hypothenemus hampei*).
2. What opportunities exist for the development of an umbrella brand for all the local coffee that meets certain quality standards?

8.5 Integrated Farms

What is the current and potential demand for, and capacity to produce local food? With this information it would be useful to design a plan to activate farm production. The study should consider aspects such as funding opportunities (development banks, the Monteverde Community Fund, microcredits), stratification and production coordination, farm product collection systems, storage, distribution, marketing, online ordering platform, technical assistance, local production of inputs, linkages, financial analysis, ecosystem services, carbon neutrality, and rural tourism, among others.

9. Conclusions

Land use in Monteverde is dynamic. The original chapter, written in the late 1990s, focused on agricultural production, stating that *"(a)n agrarian society requires healthy land and adequate incomes for farmers"*. In the intervening years, we have seen rapid development of tourism, coupled with biodiversity conservation and various environmental and educational programs. Tourism immediately affects the communities closest to the forest preserves, but its ripples influence job opportunities, immigration patterns, land prices, access to information, and cultural diversity throughout the region. Interaction between the area's three economic pillars – tourism, dairy and coffee – has created trends that shape opportunities and influence land use decisions. In short, moving the economy towards more sustainable land use goes beyond farming: larger social, economic, and demographic trends shape the opportunities to which farmers respond.

Farmers walk a fine line between profit and loss. Sustainable technologies take capital, and increased managerial effort and labor. We do not observe a trend toward increased managerial capacity of most farmers despite the promotional efforts of various institutions, but we do increasingly see cases of engaged, innovative, committed people who are developing more sustainable production systems. This trend is promising. It is a gradual process that requires cultural change, especially when the cost and the "work" of making the change is "now", and the benefits are long term, diffuse, or uncertain. Momentum is growing, in part because tourism provides opportunities for local farmers to diversify, develop market niches, and to gain increased access to information.

Climate change as well as globalization and dependence on external markets represent unprecedented challenges for agricultural producers in the Monteverde area. However, in Monteverde, there exists capacity and leadership to meet these challenges with courage, intelligence, unity, and hard work. The mystique of agriculture, and love for the land have not been eroded and are still alive in people who have learned to work hand in hand with nature. The great challenge that remains in the short term is to transmit knowledge to new generations so that they will be motivated to return to the farms and make the job of feeding society a way of life that gives them an opportunity for employment and personal fulfillment. It is imperative to work with the local market – households as well as hotels and restaurants – to develop strategic alliances so that it can absorb local food production as a distinguishing feature of the economy and tourism.

10. Tables and Figures

10.1 Table 11.1 People Interviewed

The trends identified in this addendum are based on interviews with professionals working for farm support organizations, including the cheese plant, the Monteverde milk producers' association, the local office of the Ministry of Agriculture, and the AyA, plus farmers, and others.

Resident	**Community Activities**
Francisco Donato	Director, Monteverde Milk Producer’s Association (APLM)
Ronald Briceño	Agronomist, APLM
Jose Aníbal Murillo M.	Cattle Producer Relations Analyst, Productores de Monteverde, S.A.
Juan José Monge M.	Veterinarian, Farm Affairs Manager, Productores de Monteverde, S.A.
Javier Marín	Agronomist, MAG, Santa Elena
Aníbal Álvarez M.	Agronomist, MAG, Director of the Santa Elena office
José Luis Vargas L.	Business consultant, former General Manager, Productores de Monteverde, S.A.
Manuel Torres O.	Forestry Engineer, Monteverde resident
Claudia Rocha M.	Community Outreach Program Coordinator, Monteverde Institute
Juan Ramón Fuentes R.	Dairy herdsman and longtime resident of San Luis and Monteverde
Victorino Molina R.	President, AyA Santa Elena[7]
Aura Sandí S.	Administrator, AyA Santa Elena
Virgilio Brenes	President, AyA San Luis
Fray González N.	Treasurer, AyA La Guaria
Marvin Ramírez	Administrator, AyA Monteverde
José Vargas G.	Coffee producer in the Monteverde area prior to 1960
Eugenio Vargas L.	Co-owner, Vargas Leitón Family Farm, San Luis
Guillermo Vargas L.	Forestry Engineer, co-owner of Varsan, S.A. Farm, Cañitas
Fabricio Camacho C.	Forestry Engineer, General Manager, University of Georgia San Luis campus
Joseph Stuckey	Dairy farmer, economic and community development specialist
Sarah Stuckey	Co-owner, Costa Rica Study Tours, S.A., Monteverde
Oldemar Salazar	Owner, organic coffee farm, San Luis

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[7] Community Water and Drainage Administrative Association, (Asociación Administradora de los Sistemas de Acueducto y Alcantarillado Comunal, ASADA, also known as AyA).

10.2 Table 11.2 Indicative Population Monteverde and Surrounding Areas

Indicative Population – Monteverde and Surrounding Areas

Community	AyA Connections	Est. Population
Cabeceras	**234**	**936**
Cebadilla (estimate)	**15**	**60**
Guacimal, Fernández, Santa Rosa, & Sardinal	**270**	**1,080**
La Cruz (estimate)	**15**	**60**
La Guaria	**42**	**168**
Las Nubes	**36**	**144**
Los Tornos (estimate)	**25**	**100**
Monteverde	**94**	**376**
San Luis	**80**	**320**
Santa Elena, Cerro Plano, Lindora, los Cerros, Cañitas	**1,400**	**5,600**
Turín	**22**	**88**
Total	**2,233**	**8,932**

Notes:

1) Local AyA leaders estimate 4 people per connection. However, some connections serve no households; others serve multiple households; some households are served by non-AyA sources. For example San Luis reports 80 connections, but a 2012 community census identifies 103 households with a population of ~400-420 people.
2) Sardinal is not usually considered to be part of the Monteverde region.

Source: V. Molina, V. Brenes, and other ASADA leaders (pers. comm.).

10.3 Table 11.3 The “Homestay” Industry

Educational tourism, which has been operating in Monteverde since the late 1980s, has been a vehicle for cultural integration. An evidence of this is the “homestay” industry in which local families are paid to host visiting students in their homes. For example, in June 2014, the Monteverde Institute, one of the larger organizations that organize homestays, lists 176 active homestay families in their database. These are distributed among the communities of Santa Elena, Cerro Plano, Monteverde, Cañitas, Los Llanos, San Luis, and La Cruz (Claudia Rocha, pers. comm.). Hosting homestay students is a popular strategy to augment household income, but often, personal relationships resulting from homestays open doors of opportunity for both nationals and visitors, including occasional marriages, as well as opportunities for travel and education.

10.5 Table 11.5 Dairy Production Indicators

This replicates information from the 2000 chapter to give a comparative snapshot of a typical upland dairy farm in 2014. Information for the update was compiled by: Juan José Monge, José Aníbal Murillo, Francisco Donato, Ronald Briceño, Javier Marín, and Joseph Stuckey.

Indicator	**1990s**	**2014**
Herd size	**16 cows, 67% of herd in production**	**16 cows, 80% of herd in production**
Cow breeds	**In order of importance: Holstein, Jersey, Brown Swiss, Guernsey**	**In order of importance: Jersey, Holstein, Brown Swiss, Guernsey**
Feed	**Rotational grazing on Star Grass pasture; 0.5-2.5 kg/day grain; Elephant or King Grass; salt, minerals, urea, molasses**	**Rotational grazing continues, but with greater dependency on use of supplemental grain; some silage bales, hay, and cut feed in dry season, as well as salt, minerals, urea, and molasses.**
Stocking rate	**1.8 cows/ha**	**2 cows/ha**
Milking	**Twice per day**	**Same**
Farm size	**18 ha total, 14 ha in pasture (CATIE 1983)**	**10 ha total, 8 ha in pasture**
Milk production	**10 kg per cow per day**	**16 kilos per cow per day**
Pasture management	**Manual fertilization and liming, herbicides (CATIE 1983, Stuckey 1989)**	**Same**
Fertility	**Artificial insemination; birth rate 58%; calf mortality rate 8% (CATIE 1983)**	**Artificial insemination; no data on calving and mortality rates.**
Mechanization	**In 1995, 60% of farmers used milking machines (up from less than 5% in1979). Some farms had electric fencing and/or a tractor. No farms had refrigeration (cold water was used to cool milk)**	**In 2014, almost 100% use milking machines; all have refrigeration, and hot water tanks; 95% transport milk using bulk tank trucks. The use of motorized backpack sprayers and "weed eaters" is common.**
Labor	**Mostly family labor supplemented by part-time hired help.**	**Family labor remains important, but the amount of contracted labor is increasing; tendency for youth to study and leave the farms.**
Family size	**4.5 dependents per farm**	**3 dependents per farm.**

10.6 Table 11.6. Highland/lowland Dairy Indicators, 2013-2014

Data from Farms that Deliver Milk to Productores de Monteverde, S.A. (May 2013 through April 2014)		
Indicator	**Highland**	**Lowland**
No. of producers	**107**	**32**
Gross milk received at the cheese plant, daily average	**27,271.79 kg.**	**5,238.6 kg.**
Farm production, daily average, kg	**254.87 kg.**	**136.96 kg.**
No. milking cows per farm, average	**16**	**15**
Production, kg per cow per day, average	**15.9 kg.**	**10.9 kg.**
Area, ha per farm, average	**10 ha**	**30 ha**
Cattle breeds	**Jersey, Holstein and crosses between the two**	**Brown Swiss, Simmental, Gir, and crosses of these with Brahman**
Artificial insemination	**50% of producers use AI**	**No AI, use natural mounting**
Refrigerated bulk tank	**95,0%**	**100%**
Pasture fertilization	**Yes. Soils are acidifying, pH<~5.5; require lime, magnesium; high in iron/aluminum; limited phosphate availability.**	**No.**
Forages	**African Star grass predominates *(Cynodon nlemfuensis)*, King Grass/maralfalfa *(Pennisetum sp)*, sugar cane, imperial *(Axonopus spp.)*, mulberry *(Morus* spp*)*, and natural grass. In dry season some use cut feed and hay: transvala *(digitaría decumbes)*, and rice straw.**	**Improved pastures: *Brachiaria brizantha*, guinea/mombasa grass *(Panicum máximum)*, sugar cane maralfalfa, natural grass.**
Supplemental grain (kg per cow per day)	**No data.**	**1-2 kg**
Farm labor (Full time equivalent – FTE)	**2 people per farm**	**3 people per farm**
Family labor (FTE)	**About 70% of the farms rely on family labor. ~10% milk with hired labor. Most contract occasional labor to build fences and clean pastures.**	**About 80% of the farms use family labor.**

Source: Juan José Monge and José Aníbal Murillo Méndez

10.7 Table 11.7 The Café Florencia Case

Café Florencia is a coffee brand originating on a farm owned by the Vargas Leitón family in San Luis. It has been certified organic since 2009 by Eco-LOGICA, an organic products certifier, through a Costa Rican producers association called Organic Agriculture Movement of the Central Pacific (MAOPAC).

Approximately 25% of the crop is consumed by the Vargas Leitón family (*"a rather large clan!"*). The excess is marketed to:

- International student groups and professors that visit the farm as part of their educational programs,
- The Monteverde Institute,
- One of the local hotels, as part of its Certification for Sustainable Tourism program (CST)[8],
- A small group of clients in Portland Maine, members of a Community Support Agriculture (CSA) group,
- Other contacts in San José.

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[8] A program of the Costa Rican Institute of Tourism (ICT), http://www.turismo-sostenible.co.cr/index.php?lang=es.

10.8 Table 11.8 Integrated Farms Technical Summary

By Fabricio Camacho C.

The technical principles underlying the management of integrated farms are: 1) increased productivity, 2) increased ground cover and water protection, 3) increased water infiltration into the soil profile and decreased runoff, 4) the proper management of soil fertility and maintenance of organic matter, 5) neutralization and / or abatement of contamination and 6) the efficient use of energy (MAG 2008).

On integrated farms, every aspect is planned and linked together blending traditional production methods with modern technologies that enhance the natural productivity of the land through a system that operates on planning and efficient use of space, resources (water, soil, biomass, waste) and energy available to generate fresh, clean, varied and healthy food, and to constantly boost agricultural employment, income, learning, innovation, mystique, belonging, identity and culture as a result of assimilation of, and immersion in, the environment experienced by people who are involved in the production process (Palomino 2004, Navarro 2012).

It is also estimated that integrated farms are suitable models to combat the aftermath of the Green Revolution as the management system helps to mitigate carbon emissions, to adapt to climate change, and to achieve food security, which impact positively on poverty reduction, promoting more equitable rural development and a better quality of life in rural communities (UNDP SINAC 2013, INTA 2012, Gomez 2011, Palomino 2004).

10.9 Table 11.9 Integrated Farms in Monteverde, 2014

Farm Name	Products	Market	Organic Fertilizer Production	Waste Management	Value added Foods	Educational Activities
University of Georgia, San Luis (1)	Pigs Cow milk Garden produce Fruit	On-campus consumption	Compost Earthworm compost Bio-foliar fertilizer	Tube bio digester	Cheese Sour cream	Students Local residents
La Querencia, San Luis (2)	Vegetables and other garden produce Cow milk Pigs Sheep	Household consumption Local market sales	Compost Bio-foliar fertilizer	Tube bio digester	Dried beef Beverages	Students Local residents
Olivier Garro and Family, San Luis	Chickens Eggs Pigs	Household consumption Local market sales	Compost Chicken manure Bio-foliar fertilizer	Tube bio digester	Chicken and pork processed in pieces	NA
Rancho de Lelo, San Luis (3)	Tilapia Pigs Chickens Eggs Vegetables Coffee	Household consumption Sale in own restaurant Local market sales	Chicken manure Bio-foliar fertilizer	Tube bio digester	Tilapia and pork sold in restaurant	NA
Finca Florencia, San Luis	Coffee Garden produce Fruit Sugar cane	Household consumption Local and international market sales	Compost	NA	Farm branded coffee Certified organic farm(5)	Students
Gregory Paradise Café, San Luis (4)	Coffee Medicinal plants	Household consumption Local and international market sales	Compost Bio-foliar fertilizer	NA	Farm branded coffee Certified organic farm(5) biodynamic	Tourism
La Bella Tica, San Luis (4)	Coffee Pigs Fruit Vegetables	Household consumption Local and international market sales	Compost Bio-foliar fertilizer	Tube bio digester	Farm branded coffee Certified organic farm (5)	Students Tourism
Café San	Coffee	Household	Compost	Tube bio	Farm	Students

Farm Name	Products	Market	Organic Fertilizer Production	Waste Management	Value added Foods	Educational Activities
Luis, San Luis (4)	Fruit Vegetables	consumption Local and international market sales		digester	branded coffee	Tourism
Benito Guindon, Monteverde	Goat milk Cow milk Sheep Vegetables Fruit Garden produce	Household consumption Local market sales	Compost	NA	Goat cheese Marmalades	NA
Life Monteverde, Cañitas (3)	Goat milk Coffee Eggs Garden produce Fruit	Household consumption Local market sales	Compost Earthworm compost Bio-foliar fertilizer	Tube bio digester	Farm branded coffee Goat cheese	Students Local residents

(1) Functions as an integrated demonstration and experimental farm; engages in technology transfer including, for example, the installation of biodigesters in neighboring farms in the Monteverde area. To date, 15 biodigesters have been installed.

(2) Functions as a membership model in which clients pay for farm products in advance and periodically receive harvested products.

(3) Has been awarded the Ecological Blue Flag.

(4) Processes coffee on site. In the case of La Bella Tica and Café San Luis, they buy coffee from other local producers to process and sell under their own specific brand.

(5) Internationally certified as organic coffee through Movimiento de Agricultura Orgánica del Pacífico Central (MAOPAC) (Central Pacific Organic Agriculture Movement), in affiliation with Certificadora de Productos Orgánicos y Sostenibles Eco-LOGICA, (Eco-LOGIC Organic Products Certifier) http://www.eco-logica.com/.

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12

Conservation Biology — Update 2014

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In the 14 years since *Monteverde: Ecology and Conservation of a Tropical Cloud Forest* was published (Nadkarni and Wheelwright 2000), vast tracts of land have been newly protected in the Monteverde-Arenal Bioregion, thanks to the work of the Monteverde Conservation League, Costa Rican and international conservation groups, and numerous generous donors. The Children's Eternal Rainforest is now the largest private reserve in Costa Rica, with an area of 22,500 ha, more than twice the size of the Monteverde Cloud Forest Reserve (see Chapter 10 Update by Burlingame). A new generation of young scientists and policy makers, many of them students on courses offered by the Organization for Tropical Studies, the Council on International Educational Exchange, and the University of California Education Abroad Program, has visited Monteverde's forests. Building upon what was known about the region's flora and fauna a decade and a half ago, they and others have worked with local organizations to connect knowledge to conservation action.

The first step in protecting biodiversity is conducting thorough inventories of species. In this regard, Monteverde has been a leader among neotropical sites. Documentation of the region's stunning biological diversity continues to be expanded by the observations of visiting biologists and ecotourists, as well as local farmers and citizen scientists (e.g., Rowe and Pringle 2005, Yanoviak et al. 2003a). A team from the Monteverde Cloud Forest Reserve, led by Yoryineth Méndez, has been conducting regular censuses of frogs and toads from the Peñas Blancas Valley to the Reserve to the San Luis Valley. Preliminary results indicate recovery of species that had been missing for more than a decade. Another team, led by Mark Wainwright, documented the recovery of the Green-eyed Frog (*Lithobates vibicaria*). However, there remains much to do in Monteverde with regard to several key areas of conservation biology highlighted by Wheelwright (2000). As of 2014, no one has yet published a study of the impact on cloud forest plant or animal communities of invasive species or native lowland species that have expanded their range upslope (e.g., Keel-billed Toucan, *Ramphastos sulfuratus*; Bronzed Cowbird, *Molothrus aeneus*). We still can only guess which plants or animals in Monteverde are keystone species (species whose loss would have disproportionate negative effects on biodiversity; *Ficus tuerkheimii* and *Acnistus arborescens*, trees whose fruits are eaten by numerous bird species, are good candidates), and the population genetic structure and demographics are known for virtually no Monteverde species (although see Soare et al. 2014). Gathering such information is critical because it will help us prioritize conservation efforts and effect management plans that target particularly vulnerable or ecologically important populations.

Monteverde's arthropods have been well-catalogued (Yanoviak et al. 2003b, 2007; Schonberg et al. 2004, Hanson 2014) but knowledge of most herbivorous insect species' host plants is lacking (see Hanson 2014). Soil fauna—bacteria, protists, fungi—remain a mystery, although Nadkarni and colleagues (Nadkarni et al. 2002, Rains et al. 2003) continue to make progress understanding the biology of soils in cloud forest canopies. Monitoring species that are easy to count and are ecologically (or economically) important or that indicate the health of Monteverde's communities and ecosystems ("indicator species") is essential. Populations of vocal animals such as frogs, insects, mammals and birds can be monitored using new technologies such as real-time bioacoustics monitoring (Aide et al. 2013). Three-wattled Bellbirds (*Procnias tricarunculata*) and Resplendent Quetzals (*Pharomachrus moccino*) are two obvious species to begin with. For monitoring plant responses to environmental changes, much could be learned by recording the annual timing and magnitude of flowering and fruiting of a taxonomically diverse set of common, easily recognized tree species (Wheelwright 1986); transects could be set up along readily accessible roads in Monteverde with observations made by "citizen scientists" and entered into on-going phenological databases (c.f. U.S. National Phenology Network). These studies need to be designed and implemented quickly, with the goal of pursuing them over the long-term.

Understanding the causes and consequences of rarity is also crucial for protecting biodiversity. Jankowski and Rabenold (2007) found that endemic species in neotropical montane rainforests such as Monteverde tend to be locally rare: there is a positive correlation between distribution and abundance at several spatial scales. There is also a correlation between regions of high species richness and high endemism, at least for taxa such as bromeliads, palms, aroids and scarab beetles, according to Kohlmann et al. (2010), who single out premontane wet forests in the Cordillera de Tilarán as among the most important conservation priority areas in Costa Rica because of their biological diversity and uniqueness.

The main focus of conservation biology at Monteverde since 2000 has been on the role of landscape features in preserving biodiversity, particularly connectedness between habitats at different spatial scales. Since the late 1970's, not only has the size of protected areas in the Monteverde-Arenal Bioregion (MAB) been greatly expanded, but forest regeneration has also occurred throughout the region, thanks in large part to ecotourism, changes in local attitudes, and abandonment of pastures and coffee parcels (see Chapter 11 Update by Stuckey et al.). As a direct result, population declines in numerous species have been reversed. For example, there was little or no change in the number of bats (individuals and species) captured per unit time per net length over a 27-year period (LaVal 2004). Twenty-four new bat species, most of them from the lowlands, colonized the area over the same time, presumably in response to warming climates and a 19% increase in forest area between 1973 and 1998 (based on aerial photographs; LaVal 2004). Agricultural windbreaks, increasingly planted in open pastures throughout the zone, have had numerous beneficial effects for biodiversity. For one thing, they provide habitat for forest tree species and facilitate forest regeneration within agricultural areas: 91 tree species representing primary and secondary forests occur in Monteverde windbreaks, with tree seedling densities highest in windbreaks connected to forest patches (Harvey 2000a). Dispersal of the seeds of trees and shrubs was greater in windbreaks planted on dairy farms than in nearby pastures, with 199 species recorded in seed traps during a single year; the presence of remnant forest trees in pastures increased the number of tree species (Harvey 2000b). One encouraging discovery is that, in addition to attracting seed dispersers, relict pasture trees can serve as "regeneration foci"—increasing ecological connectedness on a temporal scale—by ameliorating soil microclimates and supporting diverse canopy seed banks in their decomposing epiphyte masses (Nadkarni and Haber 2009).

O'Donnell and colleagues have studied the effect of forest fragmentation in Monteverde on army ants (Formicidae: Ecitoninae) and the birds that facultatively take advantage of them to flush insect prey. In one study, they found that, compared to forest fragments, continuous forest supported greater bird species richness, larger flocks and great total body mass of birds attending army ant swarms (Kumar and O'Donnell 2007). In another study, microsatellites were used to reconstruct genotypes and determine population genetic structure and found "isolation by landscape resistance": forest clearing impedes dispersal and gene flow between colonies of the keystone ant species *Eciton burchellii* (Soare et al. 2014). The increase in road-building and traffic in Monteverde over the last several decades is likely to have created new barriers to gene flow for numerous species (including, surprisingly, certain understory bird species: Develey and Stouffer 2001). Dust from traffic, as well as noise and light pollution, are other unstudied factors that could negatively affect species near developed areas in Monteverde.

For more mobile species, such as birds that migrate altitudinally, the importance of habitat connectedness is evident at much larger scales. In the last 14 years, radio transmitters and other tracking devices have revealed details of the altitudinal migrations of species such as Bare-necked Umbrellabirds (*Cephalopterus glabricollis*) and Three-wattled Bellbirds (Chaves-Campos et al. 2003, Powell and Bjork 2004, Papeş et al. 2012). These studies confirm the importance of safeguarding natural habitats within parks, reserves, and protected private lands across a broad altitudinal range—essentially, from the Continental Divide to sea level—and across international boundaries.

Climate change has surged to the fore as the central concern in conservation biology. Making headlines in the popular press in ways that tropical deforestation and the extinction crisis never succeeded in doing, fears about climate change have awoken the public to take action to mitigate the worst effects of global warming on crop production, rising sea levels, disease outbreaks, etc. It was apparent in 2000 that Monteverde had already begun to feel the effects of climate change. In future decades, the flora and fauna of cloud forests throughout Latin America will suffer from climate changes more than those of lowland habitats. Montane landscapes support distinctly high beta diversity (the accumulation of increasing diversity as one moves between sites; Jankowski et al. 2009). Moreover, refuges to escape the rises in temperature and alterations in rainfall and seasonality that are already upon us are limited on mountaintops, and they diminish even further as species are forced upslope. At least half of the 77 cloud forest bird species included in the modeling study of Gasner et al. (2010) are predicted to decline in the next century, with eight species restricted to Central America projected to become locally extinct. Species that are particularly threatened include the Mountain Robin (*Turdus plebejus*)—one of the commonest and most important seed dispersers in the 1980s— and Collared Redstart (*Myioborus torquatus*), a familiar and unwary denizen of the cloud forest known as "amigo del hombre." Gasner et al. (2010) recommend improving protection of cloud forests in larger mountain ranges, such as the Cordillera Central and Talamanca, as a way of safeguarding threatened species from the Cordillera de Tilarán. Epiphytes will be negatively affected as well by shifts in microclimate, as demonstrated by greenhouse studies and experiments by Nadkarni and Solano (2002). Epiphytes that were transplanted along with their arboreal soil from upper cloud forests to lower elevation trees exposed to less cloud water had higher leaf mortality, lower leaf production, and shorter lives. The death of epiphytes resulted in radical changes in the composition of canopy communities (Nadkarni and Solano 2002).

Still, some biologists, myself included, wonder whether today's focus on climate change has diverted attention from urgent and long-standing—but still unsolved—threats to biodiversity (Tingley et al. 2013). It is critical for Costa Rican decision-makers—in fact, people interested in protecting cloud forests worldwide—to understand that species are declining right now in Monteverde and elsewhere primarily not so much because of climate change but because of familiar factors such as habitat fragmentation, environmental contaminants, and introduced species. Armed with a better understanding of the present causes of rarity and extinction, conservationists, teachers, taxpayers, and voters can be make more informed decisions about where to invest scarce resources for protecting biodiversity. For example, *Ocotea monteverdensis*, a tree species in the Lauraceae restricted to premontane wet forest on the Pacific slope of the Cordillera de Tilarán between 1200 and 1450 m, has recently been red-listed by the International Union for the Conservation of Nature as "critically endangered." Why? Because of "habitat loss and degradation as forest areas have been cleared for agriculture and housing, business and tourist developments" (Joslin et al. 2013). (Note that this formerly common species was called *Nectandra hypoglauca* in earlier publications [e.g., Wheelwright et al. 1984, Mazer and Wheelwright 1993].) Although there is almost certainly more forest cover today in Monteverde than 35 years ago (LaVal 2004; F. Joyce, pers. comm.), the main point is that many species are in decline quite independent of climate change.

Debate continues about whether altered climate caused the demise of the Golden Toad (*Incilius [Bufo] periglenes*) in Monteverde. Using stable isotope measurements of tree cores to reconstruct a century of hydroclimatology in Monteverde, Anchukaitis and Evans (2010) found annual variation in dry season moisture associated with El Niño Southern Oscillation (ENSO) events and argue that the extinction was likely due to a severe drought caused by the 1986-1987 El Niño, rather than a long-term trend in global warming. Research by Cheng et al. (2011) implicates an "epidemic wave" of the chytrid fungal pathogen *Batrachochytrium dendrobatidis* (Bd), which moved south through Central America and apparently reached Monteverde by 1987, with disastrous consequences for the Golden Toad. It is worth noting, however, that Richards-Hrdlicka (2013) failed to find Bd in preserved Golden Toad specimens. Pounds et al. (2006) envision an interaction between global warming and Bd, with warming climates creating the conditions for Bd outbreaks in the highlands of Costa Rica.

There is much to be optimistic about in terms of conservation in Monteverde (Wheelwright 2007). Forest regeneration, habitat connectedness, population rebounds of certain high profile species (e.g., danta, *Tapirus bairdii*), increasing awareness of other environmental issues, engagement of concerned citizens—all of these are promising signs. We hope that the next generation of Latin American researchers will find in this book specific ideas for their own research projects, and inspiration to advance and apply what we know about conservation biology to protect biodiversity in the cloud forests of Monteverde and throughout Latin America.

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