Chapter 10 Biodiversity Conservation History and Future in Costa Rica: The Case of Área de Conservación Guanacaste (ACG)

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Prologue

This essay-like chapter is directed to the audience of, in this order of importance, present and future staff of Área de Conservación Guanacaste (ACG), staff of the entire system of conserved wildlands of Costa Rica, and the people of Costa Rica (for all, to be transliterated into Spanish in another document), foreign visitors of all kinds and nations to Costa Rica, the world audience, and the scientific community.

History of Área de Conservación Guanacaste (ACG)

In the Beginning: Geology

Eighty-five million years ago and before, when dinosaurs and their associates wandered and swam the earth, today's 163,000 ha Área de Conservación Guanacaste (ACG, Fig. 10.1) was a big blue patch of a great expanse of ocean between what today we call the Pacific Ocean and the Atlantic Ocean. There was no Central America. Far out to the west there was an island, the terrain that today we call Península Santa Elena, the peninsular portion of ACG that extends to the west. There were other Pacific islands as well, islands that gradually moved eastward through what would become Costa Rica, to become islands in today's Caribbean (see Fig. 10.9–10 in Graham 2003; Fig. 10.4 in Hoernle et al. 2002; and see Alvarado and Cárdenes, chapter 3 of this volume).

Some 65 million years ago, when Central America still had not emerged from the ocean, a 20 km diameter meteor hit where today lies the tip of the Yucatan Peninsula, creating global-encompassing tidal waves that were kilometers in height. The aerial debris blocked out the sun for years. *Adiós* to almost all that depended directly on photosynthesis and the sun's daily dose of heat. *Adiós* to the dinosaurs and most of their associates—though note that not only did some small mammals survive this event, but so did "micro-dinosaurs," the ancestors of the animals that today we call "birds" (Zelenitsky et al. 2012). This perturbation opened the world for a great evolutionary explosion. Who survived this catastrophic event, to become the raw material for this evolutionary explosion? Those species that could live (or stay dormant) for years in nearly continuous darkness and cold, those who could feed on dead and dormant species, and those who in turn ate them. Look to today's ocean depths for some living examples, to creatures of the night for others. From these ragged refugees and their predators and parasites largely evolved the world of macro-organisms that we know today, when the sun shone again on nature's green solar panels.

About 16 million years ago, the island that was to become Península Santa Elena in ACG, the land once walked by dinosaurs and ever since above the sea, crunched into the emerging archipelago of Central America. This Central American land bridge was first an archipelago lying between the southernmost extension of the Rocky Mountains where they end today in southern Honduras, and northern Colombia-Venezuela as the northern end of the Andes. Central America eventually became a solid land bridge between North and South America, finally closing a mere 3 million years ago. With this closing, the Pacific and the Atlantic oceans became two separate puddles, with all the expected

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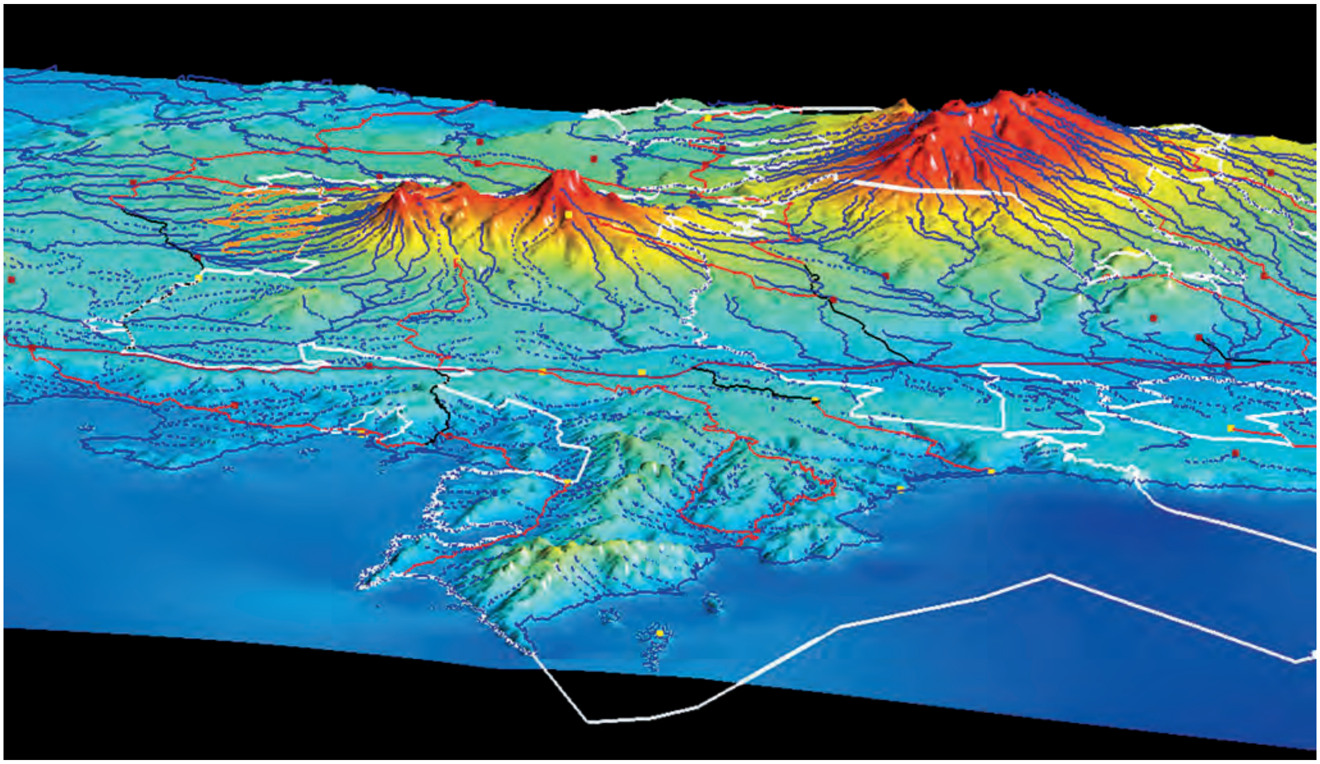

Fig. 10.1 Área de Conservación Guanacaste (ACG), enclosed by a white boundary (orange around Sector Del Oro), as viewed from the west out over the Pacific Ocean; ACG extends from 6 to 18 km into the Pacific Ocean across the dry-forested coastal lowlands up to 1,450–1,650–2,000 m cloud-forested volcano peaks (red) and down to 90 m in the rain-forested Caribbean lowlands (see Figs. 10.2, 10.3, 10.8, and 10.33 for map views).

evolutionary consequences of dividing a population into two parts, each to now live out separate evolutionary trajectories according to the different ecological worlds of the two different oceans (Jackson and D'Croz 1998). And with this closing, the land bridge that allowed extensive blending of North and South American biodiversity was complete (Cody et al. 2010, Marshall et al. 1982, Rich and Rich 1983, Iturralde-Vincent and MacPhee 1999, Jackson and D'Croz 1998, Wallace 1997).

However, for tens of millions of years before the closure there must have been substantial south-north interchange through island-hopping up and down the archipelago of Central America-to-be and between the two continents (and see Johnson and Weckstein 2011). Not only were these islands stepping stones, but also they had their isolated, and thus speciating, populations that were then thrown together after full emergence of the land bridge, to yield part of the high biodiversity encountered in Central America today.

As recently as 1.5 million years ago, there was a large lake perched on this land bridge, extending at least from today's Managua/Granada in central Nicaragua south to Liberia, in northwestern Costa Rica. The trade winds from the east/northeast brought sufficient moisture-laden air from the Caribbean, and perhaps from the lake itself, to foment rain forest all the way from the Caribbean coast to the Pacific coast across the narrow land bridge at this point. Among the emergent volcanic islands in the lake was a 6-million-year-old volcano, today a weathered 617 m hill, Cerro El Hacha, located in north central ACG (Figs. 10.2, 10.13). And on the southeastern shore of this lake was a 2,500 m volcano, roughly centered on what is today the Rincón de la Vieja complex of the Cordillera de Guanacaste that crosses ACG from southeast to northwest (Figs. 10.1 and 10.2). For reference, 2,500 m is nearly as high as the highway over Cerro de la Muerte in the Talamanca mountain range lying between San José and Panama.

And then there was a Krakatoa-scale explosion of this volcano. In 20 minutes, perhaps, the entire content of this volcano was exploded-lifted-and-dropped on most of the Costa Rican portion of Lake Nicaragua, forming what we think of today as the Mesa Santa Rosa, the 200–300 m elevation flat area crossed by the Inter-American Highway (Pan-American Highway of older terminology) as it bisects ACG from south to north (Figs. 10.2, 10.8). The pink area of the geological map of the ACG area (Fig. 10.3) outlines the western portion of this volcanic debris. When drilling for water wells in 2008 in the Área Administrativa of ACG, Sector Santa Rosa, rotting organic matter from the old lake

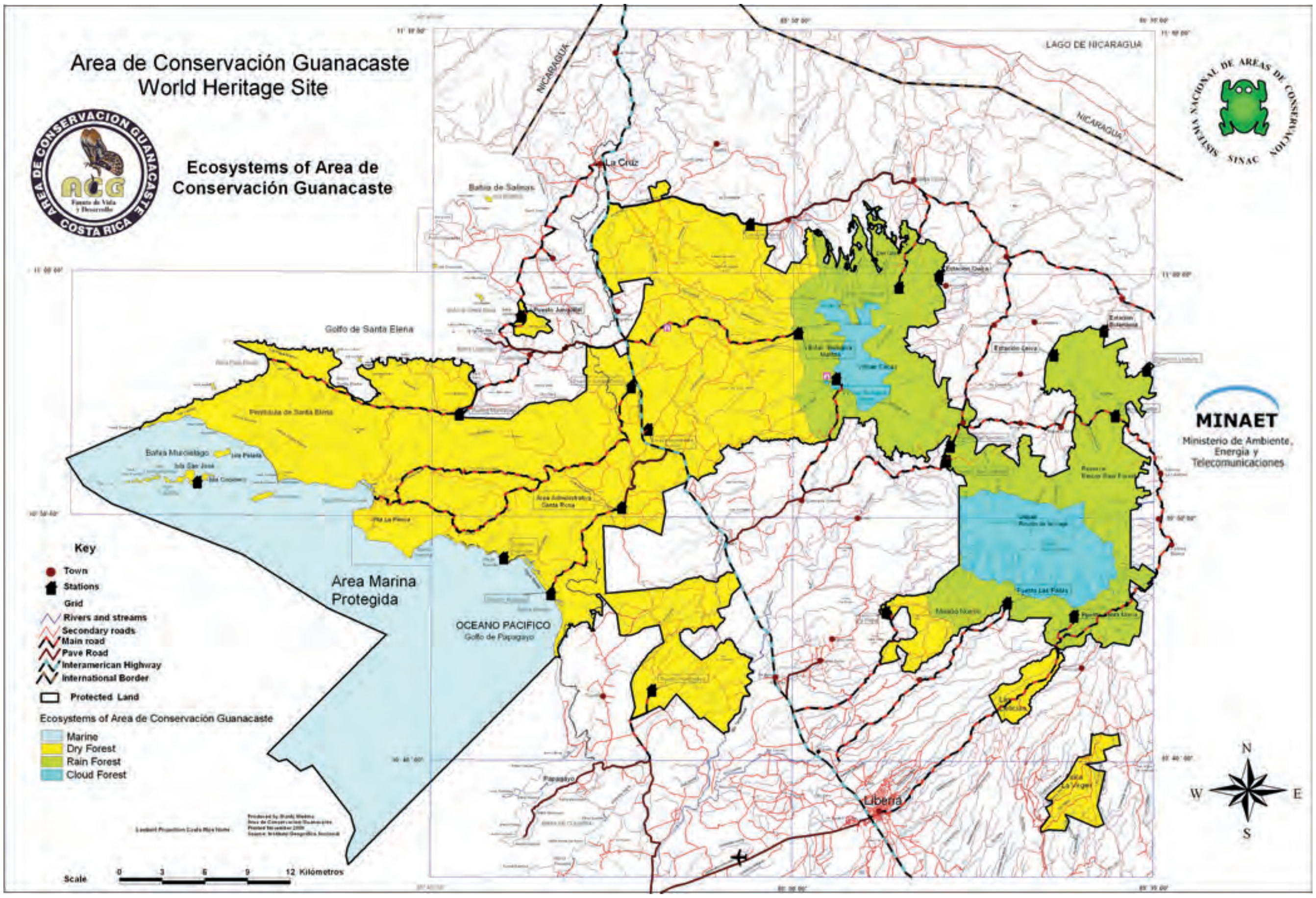

Fig. 10.2 The ACG's four primary ecosystems: light blue, marine, 43,000 ha; yellow, dry forest, ~75,000 ha; green, rain forest, ~38,000 ha; dark blue, cloud forest (above 1,000 m), ~10,000 ha and shrinking.

bed was encountered at about 100 m depth. The exploding volcano splashed its debris all the way out onto the base of Península Santa Elena, as evidenced by the oak-covered white volcanic tuff just west of La Angostura (Figs. 10.3, 10.32). The volcanic deposit stopped at about the steep ocean-facing slopes behind what would at that time have been a large bay, and today is the coastal dry forested alluvial lowlands inland behind Playa Naranjo. And the fossil wood that erodes out of the base of this volcanic deposit, which we found in 1978 at the 15–20 m level of the Ojochal (the *Brosimum* or "ojoche" forest behind Playa Naranjo between Río Poza Salada and Argelia), where the coastal alluvium is overlain by this volcanic deposit, contains rain forest species such as *Calatola costaricensis* (Icacinaceae). *C. costaricensis* is a large tree that today grows in the ACG rain forests on the Caribbean side of the Cordillera de Guanacaste, and on the Osa Peninsula. Both sites are ecologically far distant from ACG dry forest of the Ojochal of Sector Santa Rosa.

In short, after the explosion 1.5 million years ago, ACG looked like a lunar landscape. It would have been raw rock and volcanic tuff in all directions, with scattered remnants of badly damaged forest at the mainland margins, but Nicaraguan dry forest to the north and Nicoya dry forest to the south, Caribbean rain forest to the east and northeast, and cloud forest yet further to the southeast around Lago Arenal. The "natural" history of ACG today is therefore very much one of long-term restoration following that event. This restoration occurred through invasion from adjacent dry forest, cloud forest, and rain forest habitats and ecosystems, a process that continues right up to the present day and will be with ACG for millennia to come, though it has been substantially set back by 400 years of European agricultural and ranching attack both outside and inside ACG. It has been different kinds of restoration at different rates for different organisms with different histories—and today yet further overlain by the impact of climate change and insularization in an every-day more agro-industrialized agroscape. Because of this long-ago perturbation, it is doubtful that much of the biodiversity that we meet today in ACG is the product of on-site local evolution of the species that are there. Rather, this biodiversity has come together through the juxtaposition and ecological fitting together of hundreds of thousands of species arriving with the great bulk of their present-day traits already genetically in place, traits evolved in other places and often in response to other biotic and abiotic partners and circumstances (Janzen 1985a). And once arrived, they and their associations have been frequently repositioned and buffeted by both naturally occurring cycles of glaciation and today's climate change, and 400 years of various assaults by humans. Again, they have survived different kinds of restoration at different rates for different organisms with different partners, and with different histories. And even as of today, the next centuries of ACG will experience the same, but with the difference being that the direct anthropogenic assaults will be minimized through explicit conservation and through allowing natural restoration processes (e.g., Janzen 2000a). However, the indirect assaults of climate change will come on more rapidly than ever and be inflicted on a seriously weakened and insularized mass of habitat.

Beginning some 50,000 years ago, long after the restoration of the post-eruption lunar landscape back to lowland and mid-elevation rain forest, the southern part of the Cordillera de Guanacaste—today the Rincón de la Vieja complex—emerged and filled the huge crater left by that ancient explosion. This crater was 25 km wide. The hills of Cerro Gongora and vicinity are remnants of its western walls. Volcán Cacao (1,659 m elevation) then emerged about 30,000 years ago. The northeastern wall of its crater is what we recognize as Volcán Cacao today, curving around its crater lakebed that has filled in to become the swampy pasture you cross before climbing over a low section of crater wall through forest to cloud-forested Estación Biológica Cacao at 1,150 m. The terrain between Volcán Cacao and Quebrada Grande is the remains of the southwestern wall that exploded outward. Then 20,000 years ago Volcán Orosí emerged—just as Volcán Concepción is being formed today in Nicaragua (Figs. 10.4, 10.5)—to complete the northern end of Cordillera de Guanacaste (Kempter 1997 and pers. comm.).

From a biological viewpoint, Cordillera de Guanacaste is simultaneously the northernmost extension of the Andean highlands and a mountain mass blocking the trade winds, creating a strong rain shadow on its west/southwest side, and therefore creating the ACG dry forests, and their intergrades with cloud forest and rain forest to their east. The moisture-laden trade winds from the east and northeast rise up the slopes of this wall, condense out their moisture into the headwaters of Río Tempisque, and continue west and southwest to dry and create the ACG dry forest. The Cordillera de Guanacaste is also the northernmost end of the Costa Rican archipelago of highlands that extends south through the country to the "mainland" highlands of the Talamancas. Northernmost Volcán Orosí of the Cordillera de Guanacaste (there is another area named Orosí in central Costa Rica) is the smallest highland cloud-forested island of them all (1,440 m elevation, Fig. 10.5). The Cordillera de Guanacaste is also the northernmost end of the Costa Rican archipelago of highlands that extends south to the "mainland" highlands of the Talamancas to the south (with a deep break at the Meseta Central).

The First Humans and Their Impact

Sometime between 25,000 and 11,000 years ago, the first people arrived in the area. Initially they were hunter-gatherers, and then farmers. These peoples probably had a very low population density and were prone to harvest from, and impact, the best concentrations of high-quality food, such as that of marine edges, river mouth deltas and lake edges, acorns from the acorn-producing ACG stands of *Quercus oleoides* (the single species of lowland oak in Costa Rica), the highest quality soils (coastal and river alluvium, some flat eroded shoulders of the volcanoes), and permanent fresh water sources. While their impact would have been quite visible at these points of harvest and farming concentration, the impact zones would have been lightly scattered among large expanses of dry forest and its intergrades with wetter forest of all elevations, impacted largely by light hunting and acorn-gathering forays, just as prehistoric Europeans were intense predators on acorns (Logan 2005).

About 11,000 years ago, specialized big game hunters arrived, continuing the wave of extinction of New World megafauna that rendered Neotropical habitats permanently, strongly, and universally human-impacted—glyptodonts, gomphotheres, ground sloths, horses, and all their associated predators and scavengers, were extinguished (Martin 1973, Ripple and Van Valkenburgh 2010), gone forever, leaving the neotropics with a host of tropical Pleistocene anachronisms (big fruits, big-seeded fruits, anti-mammal leaf chemistry, spines, and branch morphology, etc.) (Janzen and Martin 1982, Janzen 1981a, 1981b, 1982a-c, 1985b, 1986c) (Figs. 10.11 and 10.12). These professional hunters also had help—as they pushed the density of the big, edible and human-naive prey down, the starving carnivores would have eliminated the last ones (Janzen 1983a, Ripple and Van Valkenburgh 2010). And today it appears that this over-hunting extinction process may well have gotten a boost by the meteor impact that generated the 1,000-year cooling of the Younger Dryas period at the same time

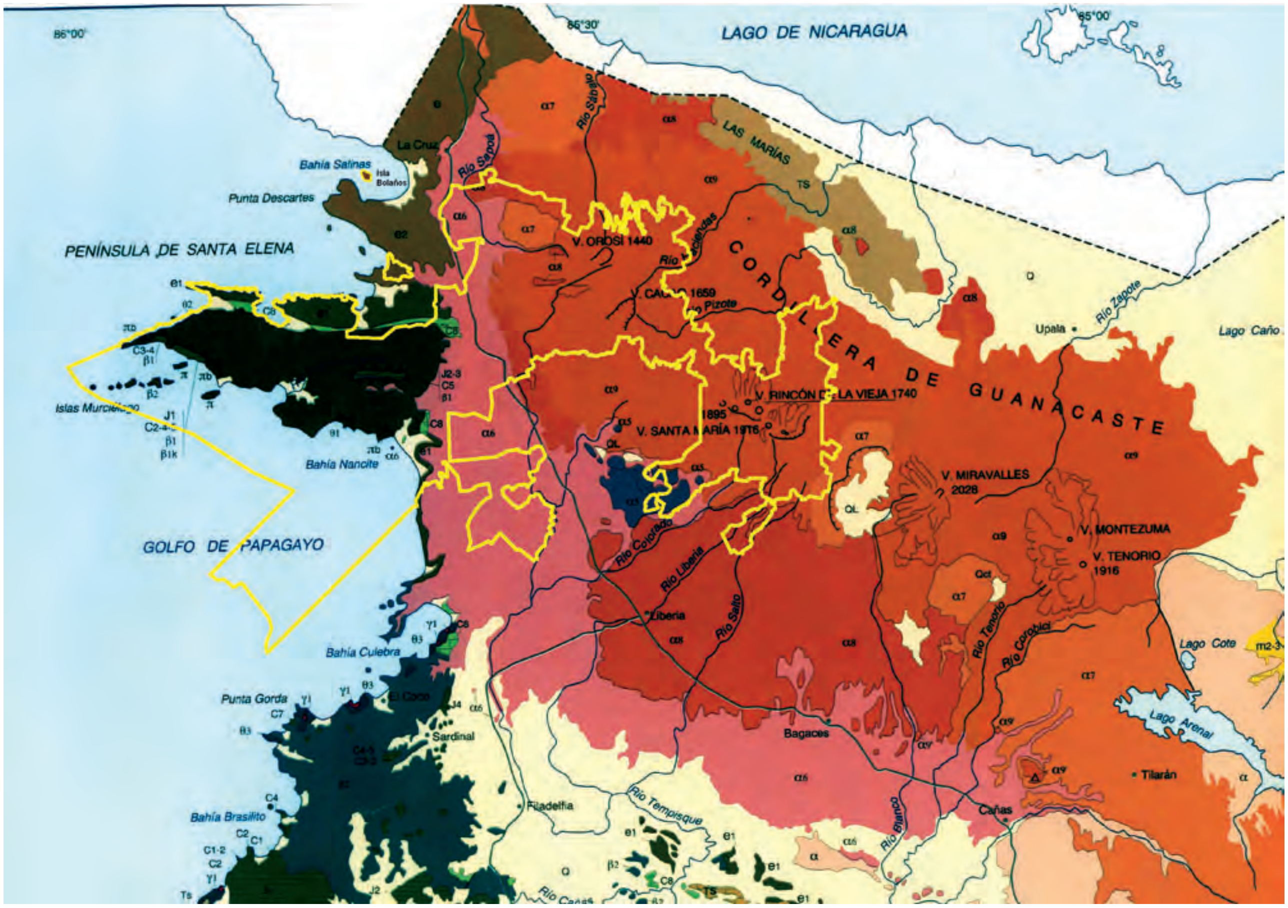

Fig. 10.3 The geological extent of the volcanic cover (pink and red area of the Geological Map of Costa Rica, Tournon and Alvarado 1997) that was generated by the explosion of an ancient volcano that took place 1.5 million-years-ago at the place where today lies the Rincón de la Vieja volcano. Note the tiny pink area splashed onto the base of the dark green 85-million-years-above-the-sea serpentine barrens of the Península Santa Elena just west of La Angostura. Legend on p. 295.

(Kerr 2007). Whatever process or processes extinguished the Neotropical megafauna 10,000–11,000 years ago, it is clear that the agrarian societies that followed would not have been compatible with these giant vegetarians (or the predators that accompanied them), any more than African farming is compatible with a natural density of African megafauna today. The megafauna we did not extinguish at that time would have been extinguished by man in the past 5,000 years, long before medicinal gardens, royal hunting reserves, national parks, and other forms of nature conservation began to become more than a tiny niche activity in human societies.

When the Spaniards first walked through largely megafauna-free ACG about 1523, on their way from Nicaragua to Nicoya, they would have met largely unbroken forest except for perhaps three areas. First, there would have been some farming (accompanied by hunting) on the flatlands to the south of Lake Nicaragua (Lago Cocibolca) and extending south of the lake to Cerro El Hacha (the low hill in north central ACG to the west of Volcán Orosí, Fig. 10.1) and the ceremonial area of the Pedregal Orosí (Figs. 10.6, 10.26) on the slopes of the lower western flanks of Volcán Orosí. Second, there was intense coastal marine gathering, inland hunting, and perhaps scattered shifting cultivation on the very best soils of lowland Sector Santa Rosa as far uphill as the vicinity of the drainages of the Río Centeno, Río Aserradero, and Río Tempisquito at 300–600 m elevation. Near the coast and on the off-shore islands there are stacked shell middens from very large oysters and other mollusks; in the lowlands of Sector Santa Rosa, between the Río Poza Salada and Argelia, there is a patch of forest (Ojochal), the species of which have human-edible seeds and fruits (e.g., *Brosimum*, *Samanea*, *Manilkara*, *Hura*, *Sideroxylon*, *Prosopis*, *Caesalpinia*, *Guazuma*) just as is the case of the so-called "natural" forest around Tikal in the Petén (which is simply a massive naturally restored young forest on long abandoned indigenous farmland). The Ojochal also contains massive amounts of bone-shell

middens, which together with its edible-seeded and edible-fruited forest suggest that it is an ancient coastal village site. Indigenous grave sites, mostly long ago looted, are scattered across the Mesa Santa Rosa (including those in Bosque San Emilio of Sector Santa Rosa and in Sector Mundo Nuevo). Third, there would have been relatively sedentary semi-shifting agriculture on volcanic mid-elevation shoulders such as the flat where today stands Estación Biológica Cacao (1,150 m), the bed of the former crater lake in Volcán Cacao (1,030 m), and the mini-lake next to the road traversing Rancho Harold (950 m); at these sites, pottery fragments, *manos* and *metates* and pieces of flint brought from the lowlands give some hints of an indigenous culture that most likely extended north from the Meseta Central and the Tilarán/Arenal intermediate elevations. Its farming activity could easily be the cause of some of the forest heterogeneity on the upper western slopes of Cordillera de Guanacaste. There is no hint indication this pre-European land use, and its post-megafaunal extinctions (if there were any), had anything more than a superficial and quickly restored impact on the biology of ACG biodiversity at select points. Ruderal species would have been more abundant than they would have been were humans absent, and select prey and select hunter-gatherer foods would have been impacted here and there, but the large expanses of relatively undisturbed forest would have maintained most populations and interactions close to their natural carrying capacity and structures for the various ACG ecosystems.

Fig. 10.4 Volcán Concepción in Nicaragua in full eruption on February 9, 2007. Volcano formations of this nature must have been an integral part of the birth of the volcanoes of Cordillera de Guanacaste.
Photograph by Emanuel Sferios.

Arrival of European Culture and Subsequent Land Use History

Europeans arrived in the ACG in two very different ways. While Pizarro did walk across it on his way south to Nicoya in 1523, all of the subsequent marine traffic up and down the Pacific coast passed close by the shores of ACG, and probably harvested from it. According to rumor, colonial records document that many houses in Lima, Peru, are constructed with wood harvested from the forests behind the ACG beaches, and specifically, from the shores of Península Santa Elena. Timber, dye wood (*Haematoxylum brasiletto*), tannin and medicinal-bearing woods in coastal forest would have been a ready harvest for any boat with space in the hold. Fires that escaped from camping on the beach would have followed, easily invading the lightly logged forests and quickly converting them to mixes of native grasses and secondary succession small woody plants, which are much more inflammable in the dry season than is old-growth forest. For example, the flatland forest rich in mahogany/caoba (*Swietenia macrophylla*) trees immediately northwest of the north end of Playa Potrero Grande (Fig. 10.15) appears to be untouched by "modern" society, but is suspiciously even-aged (Janzen 1998). Yes, perhaps a tsunami in the 1800s leveled it to bare mud, along with the even-aged mangrove forest behind Playa Potrero Grande, but on the other hand it may also be a case of natural restoration following thorough harvest as well. The name "Potrero Grande" (big pasture) dates to at least the 1600s and refers to the enormous long and thoroughly deforested valley bottom (and its stone corrals built with indigenous labor under early Spanish administrations) turned into an ocean-accessible pasture that backs the swamp behind Playa Potrero Grande and is the site of Oliver North's airstrip built during the Contra war orchestrated by the United States of America against the Nicaraguan *Sandinistas* in the 1980s (Fig. 10.7). It will take major biological detective work to puzzle out the details of European impact on the biodiversity of the coastal zone of ACG from the mid-1500s to the time of the World War II in the 1940s (if indeed it is even possible). However, whatever the details, it is clear that none of the ACG lowland coastal forest, including that of its islands, can be regarded as pristine old-growth, even if the loss of the megafauna is disregarded. However, above about 200 m elevation on the outer end of the Península Santa Elena there are about 2,000 ha of highly inaccessible and generally unburned dwarf forest that probably approximates old-growth status. At the uppermost elevations of this forest (about 700 m) there even survives a mossy remnant of a depauperate and very insular cloud forest (Maria Marta Chavarria, pers. comm.) that has probably never seen an axe or chain saw.

Modern Landscape-Level Changes since the 1500s

Each region of Costa Rica has its own peculiar four centuries of history of European colonization. In one sentence, the goal of the colonists and their offspring—no matter in which century—was to harvest and/or remove the natural vegetation and replace it with anthropogenic structures, croplands, plantations, and pastures that produced goods and services for direct use and sale. In the case of the dry northwestern part of Costa Rica, the region of ACG with its Pacific dry forest and wetter Cordillera de Guanacaste, this was a four-century-long and complicated process, and fortunately only variably successful and thorough.

Its nature was determined largely by transportation routes to other places, soil type, climate, and world-level markets/inventions. A brief visit to this past sheds light on some of the larger social processes that led to the region of ACG being, in 1966–1985, still populated by remnants of the wild organisms and ecosystems that could generate

Fig. 10.5 Volcán Orosí viewed from the north, with the Del Oro orange plantations in the foreground (March 7, 2001). The blue cloudless skies of the ACG rain shadow dry forest in the dry season on the right (west) contrast strongly with the heavy rain clouds of the rain forest to the left (northeast), and the tuft of clouds bathing the Volcán Orosí cloud-forested top.

Fig. 10.6 Pedregal Orosí at the western, dry forest base of Volcán Orosi (Fig. 10.5), 500 m elevation, on February 13, 1987, while still under a regime of heavy grazing and annual burning. Many hundreds of the rocks in this *pedregal* have deeply carved petroglyphs (Fig. 10.26) dating from pre-Columbian times, and the site may well have been deforested since then.

the landscape-level restoration process in motion at present. Perhaps the most important trait of this past was the combination of being a long distance from major social centers (Managua-Granada far to the north in Nicaragua, and the Puerto Viejo-Meseta Central-Puntarenas axis to the south in Costa Rica), and having soils bad for agriculture, scarce water, and severe dry seasons, all of which were inhospitable to farming and ranching. There is not a single ever-flowing river on the Mesa Santa Rosa, the Mesa is essentially a volcanic tuff-rock tableland derived from the innards of that volcano that exploded 1.5 m years ago (Fig. 10.3), and the long dry season (December-May) is largely rain-free while the short dry season (July-August) is erratic in length and intensity. These obstacles are what allowed the survival of ACG biodiversity long enough and completely enough to perform the beginnings of landscape-level restoration when allowed (Janzen 1988a, 1988c, 2002), starting with the inauguration of Monumento Nacional Santa Rosa and Parque Nacional Santa Rosa (today Sector Santa Rosa of ACG) in 1966–1971 (Government of Costa Rica 1998) and intensified with the beginning of ACG as the Proyecto Parque Nacional Guanacaste in 1986 (Allen 1988, 2001, Janzen 1988a, 1988c, 2000a, 2002).

During the 1500s and 1600s, a major route from the eastern United States and Europe to California and Chile was for an ocean-going boat to go up the Río San Juan all the way to Lake Nicaragua, sail across it, disembark at Rivas, walk and mule-train the 20 km to the Pacific, and then sail north to Mexico and California, or south to Panama, Peru, and Chile. In the mid-1700s, an earthquake raised the bed of the Río San Juan shortly after it left Lake Nicaragua, forcing large boats from the Atlantic to disembark at that point. From the date when the opening of the Panama Canal in 1914 rendered this transport route obsolete, trains of hundreds of mules carried the cargo to Lake Nicaragua for paddle-wheeler boat transport across to Rivas, or muled all the way from the Río San Juan to Rivas along the southern lake shore.

The 1848 California Gold Rush was largely populated via this route and it was very active at the time of the US

Fig. 10.7 Playa Potrero Grande (background) and Potrero Grande (center) with Oliver North's Contra airstrip remnants in the center, Península Santa Elena (January 9, 1988). The dark green forest near the beach is mangrove forest while the woodland immediately towards the inland is regenerating freshwater swamp forest. The yellow-gray hills are covered with a native (and inedible to livestock) grass, *Trachypogon plumosus*, that has spread from natural disturbance sites (cliffs and rocky ridges) following centuries of annual to semi-annual manmade burning of these serpentine barrens that were originally covered with low-stature and highly deciduous dry forest.

Civil War in 1861; William Walker was ousted from Nicaragua by the US military in 1857 for tampering with US business interests that managed this cross-Nicaraguan transport (Jamison 1909, Doubleday 1886, Wight 1860, Wells 1856). The mules for this massive transport were produced in Hacienda Santa Rosa, which stretched from the coast at Playa Naranjo and Nancite (and probably Potrero Grande) to the mid-elevational, moister slopes of Volcán Cacao (and mules were presumably also produced at other haciendas in its vicinity, such as Hacienda Inocentes and Hacienda Orosí on the drier foothills of Volcán Orosí). The implication is that the original erratic clearing (largely by fire) of the ACG dry forest for native grass pasture, beginning in the late 1500s, was to grow large herds of horses, *burros*, and mules as well as some long-horned red-furred cattle ("*ganado*"). In the 1970s, 80-year-old Santa Rosa employees said that in their youth, large herds of horses produced foals in the pastures near the coast in the early rainy season, and then moved on their own to the still-green pastures on the foothills of the Cordillera de Guanacaste during the long dry season, and then back again to the coast at the beginning of the rainy season in mid-May (see Fig. 10.8 for this transect).

In the 1600s–1800s a major cattle slaughter industry developed at the port of Puntarenas far to the south, where hides and tallow were packed into barrels and shipped around the bottom of South America to Europe. These cattle would have come from all parts of Guanacaste Province but ACG was probably too far north to have contributed heavily. However, when the indigo dye industry in Guatemala and El Salvador emerged in the late 1700s to 1800s, requiring large amounts of field labor to pick and process leaves from plantings of native *Indigofera* (a small shrub in the Fabaceae), herds of cattle were produced in northwestern Costa Rica and driven north as food for this labor. This was not a very lucrative business, at least in part because the cattle lost a lot of weight on the drive north, and because there were no easy pastures to fatten them on in El Salvador (the pastures having been converted to indigo plantations). Furthermore, when the cattle herd arrived, the buyer offered a very low price because there were no other buyers and certainly they were not going to be driven all the way back to Costa Rica if prices were low. At the same time, the growing urbanization of the Meseta Central was becoming a cattle buyer in the same way, and the business was also not lucrative for the same reasons. Hacienda Santa Rosa was very far from everywhere economically, and in combination with its very poor soils and being very far from the political centers of power to the north and south, it was apparently always a low-yield largely extensive (rather than small area intensive) cattle-ranching system. Records in the colonial archives in Granada, Nicaragua, indicate that Santa Rosa had more than 40 different owners between the late 1500s and the 1960s, suggesting repeated ranching and farming failures by a succession of owners. This in turn saved nearly its entire dry forest species from local elimination, though these ranching/burning/hunting activities certainly altered their population, community, and ecosystem biology.

On March 29, 1856, when an exploratory contingent of William Walker's army encountered General Mora and his Costa Rican troops at the Casona Santa Rosa (Wells 1856), the greater Hacienda Santa Rosa extended from the tip of Península Santa Rosa to the forests of Cordillera de Guanacaste and had been an extensive low-productivity mule and cattle ranch for two and a half centuries. Apparently it was the second hacienda to be established in Costa Rica, after Hacienda Inocentes on the northern foothills of Volcán Orosí (with a somewhat moister climate and much closer to Lake Nicaragua). Santa Rosa was paying taxes to Spain by the end of the 1500s. It appears that it was first created as a land grant from the Queen of Spain to one of her captains, who then committed some offense that caused her to take it back. The captain's son then bought it back and the record of this transaction is somewhere in the colonial archives in Granada, Nicaragua (fortunately not burned by one of the marauding pirates of the 1600s–1700s, when there was still big-boat-free access to the lake from the Atlantic to Grenada via the Río San Juan).

The traditional way of clearing land for cattle pasture was still in use in the 1900s–1960s. The "traditional way," probably in operation since the 1500s, was as follows. Wherever a natural (or anthropogenic) break in the forest canopy allowed sunlight down to ground level and therefore a patch of herbaceous vegetation developed, the cowboy encountering it in the dry season simply set a fire in it. The same process was repeated the next year and within a few years flat areas on good soil were largely covered by grasses and herbs, with the rocky (and wetter) ravines and cliffs still largely forested. Such an extensive pasture system was easily maintained relatively free of woody (shading) vegetation by annual or semiannual burning near the end of the long dry season (April-May). The indigenous population would probably not have used fire this way because the last thing that they wanted—except for ceremonial purposes—would have been a large patch of grass (not even the deer are grass-eaters; however, the indigenous people might have hunted *Sigmodon hispidus*, the hispid cotton rat, which can be extremely common in large pasture systems in Guanacaste). The African grass *jaragua* (*Hyparrhenia rufa*) was introduced to Costa Rica in the 1920s and by the 1940s the Hacienda Santa Rosa cowboys were carrying sacks of *jaragua* seed and sprinkling it into the pastures

Fig. 10.8 The transect from the north end of Playa Naranjo (foreground) to the lower slopes of Volcán Orosí (center rear) and Volcán Cacao (right rear) (January 29, 1988). The Mesa Santa Rosa is evident as a flat mosaic of yellow jaragua grass pasture and forest remnants through the center of the image. The Inter-American Highway roughly bisects the Mesa from right to left slightly inland from the dark central line of the cliffs bordering the Cafetal-Rio Cuajiniquil headwaters.

Fig. 10.9 Mosaic of ungrazed and unburned jaragua grass pasture and forest remnants on the western edge of Mesa Santa Rosa between Quebrada Vaca Blanca (to the left) and Portón de los Perros (out of sight to the right) (March 16, 1987). This is the patch of yellow jaragua on the far left in Fig. 10.8. See also Fig. 10.21.

after burning, gradually converting all the pastures to a much higher yield forage (Daubenmire 1972) (Fig. 10.9). Simultaneously, cebu cattle, which are far more resistant to the Guanacaste heat and long dry season than are European breeds (derived from *Bos taurus*), were introduced into these same pastures. Cebu cattle are genetically derived from *Bos indicus*, an Indian-African species of tropical dry forest origin, with part of their resistance prominently displayed as the large fat-containing food reservoir hump over the shoulders. By the 1960s–1970s, during the neoflowering of the ancient Guanacaste cattle industry (Parsons 1983, Shane 1986, Janzen 1988b), the Guanacaste herds still often contained a mix of both cattle breeds (Fig. 10.10).

While many ranchers in southern Guanacaste Province were gradually converting to more intensive cattle ranching, with more thorough elimination of wild biodiversity (and replacement of *jaragua* with other, even more productive species of African grasses), ACG pastures were treated in the old-style extensive and non-intensive ranching that was basically unchanged from the 1700s except for better breeds of cattle and deliberate seeding of *jaragua* (local ranchers were still coming to Parque Nacional Santa Rosa in the 1970s to harvest truck-loads of *jaragua* to seed their pastures). In brief, a herd of several thousand or more cattle (steers, cows, and bulls) were turned loose in many thousands of hectares of brushy pasture (with watercourses) and then harvested at yearly or more intervals.

Pasture "care" consisted of setting fire to it, often in the second or third month of the dry season but later in the year if it was desired that the forest margins be more thoroughly pushed back (by the hotter fire created by the drier soil and fuel). The wind-driven fire did its job. The only pasture management was to "*hacer rondas*," which meant clearing the herbaceous material to nearly bare ground for a long meter back from the barbed-wire fences, in hopes that when the fire swept through, the wooden fence posts would not be incinerated. The fence posts came from trees cut either during the original clearing of the forest, or trees cut from forest patches that had burned less readily. Posts were therefore abundant and cost only cheap labor. By the early 1990s, when these posts needed to be replaced at a much higher cost, the somewhat higher salaries (formerly a

Fig. 10.10 Management of mixed cebu and brown European cattle (Palo Verde, Guanacaste, March 10, 1976). The brown cattle (*Bos taurus*) were being replaced by the much more heat-resistant and productive cebu (*Bos indicus*).

mere pittance) and other costs made extensive cattle ranching marginally economic, if that.

All of this is relevant to conservation today because the large extensive cattle pastures were quite rich in biodiversity that survived on the patchy sites that burned poorly because they were moist or contained low amounts of herbaceous fuel (because of thorough grazing by livestock). As vehicle-based agro-civilization developed, the large holdings were gradually partitioned into small areas of higher yield (rice fields, higher quality [often replanted] African grass, fruit orchards, sugar cane, peanuts, cotton, pineapple, etc.), sometimes irrigated, and polished quite free of their biodiversity. Other areas were abandoned, logged, burned, and used for subsistence-level micro-ranching of a few horses and a small cattle herd. Both treatments resulted in a gradual erosion of dry forest biodiversity, exacerbated by the usual effects of fragmentation and insularization. Even the strips of forest, left by tradition and some laws standing along Guanacaste Province watercourses, had gradually dissolved from their once species-rich community structure to a still-dwindling mix of living dead (Janzen 2001), ruderals, and agrochemical-resistant species. This mess is sprinkled with a few species that "do well" (whatever that means) in the presence of massive human manipulation of the system (boat-tailed grackles, magpie jays, ctenosaurs, *Guazuma ulmifolia*, *Senna pallida*, *Sida* spp., etc.).

Throughout this process, the state of the erratically damaged vegetation suggests that large-scale farming was not a part of the European land-clearing process in the tens of thousands of hectares of Hacienda Santa Rosa, the core area of ACG dry forest, until about the 1940s. At this time some of the flatter and better soil pastures to the west of the Casona Santa Rosa were plowed and seeded to dryland rice. This was a short-lived experiment, due to both the low-quality soil and the erratic rain patterns. Various rocky slopes and hills of the lowland coastal area (e.g., the hillside inland from Argelia behind central Playa Naranjo and the southern sides of the valley containing the Río Poza Salada, Fig. 10.14), and almost all of the flat coastal plain behind Playa Naranjo (5–100 m elevation, Fig. 10.8), were thoroughly cleared of their dry forest to grow corn, yucca (cassava), beans, papaya, banana, fruit trees, and rice planted in the style of colonizing small-scale farmers and squatters. These areas are today covered by secondary forests of varied ages, heights, and characteristics, such as their degree of deciduousness in the long dry season. What distinguishes them and their restoration from that of the Mesa Santa Rosa is that they were never planted with pasture grasses, they were closely surrounded by forest seed-sources, and they were on somewhat good soil. The consequence is that they quickly turned back to young forest when abandoned in the 1960s and 1970s at the time Parque Nacional Santa Rosa was decreed and the colonists relocated outward. While these lowland areas were swept by dry season fires, both set on-site and invading from the fires sweeping the pastures of the Mesa Santa Rosa in the 1940s–1960s, they have for the most part not been burned since their abandonment with the removal of the colonists in 1970. The other small-scale European clearing of ACG dry forest was the subsistence farming (which cleared most of the forest off of the lower slopes of Cerro El Hacha in the 1970s, Fig. 10.13) and rudimentary coffee plantings in a few places on the southwestern intermediate elevation slopes (Sector Pailas and Sector Santa Maria) of the Rincón de la Vieja massif. Coffee planting was one of several clearing activities of Hacienda Santa Maria (today, Sector Santa Maria of ACG) above Liberia, and along the trail from Estación Pailas to the Rincón Crater in Sector Pailas. This

Fig. 10.11 Ripening (browning) newly fallen (i.e., presented to ground-based frugivorous large mammals) *jicaro* fruits (*Crescentia alata*), a botanical anachronism whose seeds were once dispersed by the now-extinct Pleistocene megafauna, and are now dispersed again by that same megafaunal horse returned by the Spanish conquistadores (see Fig. 10.12). Sector Santa Rosa, ACG, 1978.

climate, elevation (800 m), and soil is perfect for coffee, except that it was very far from the Meseta Central coffee industry, which was aimed at Europe. This distance saved this ecotone between dry forest and rain forest from its total elimination for coffee plantings, in contrast to the fate of the forests that once clothed the slopes in the western part of the Meseta Central of central Costa Rica. For example, according to the *1997 IUCN Red List of Threatened Plants* (Walter and Gillett, 1998), an endangered large tree with spectacular cauliflory, *Parmentiera valerii* (Bignoniaceae), of which there are apparently only 1–5 adults remaining in the Meseta Central (and INBio does not even register it as occurring there), occurs by the thousands in this ACG soil and climate of the Pacific slopes of the Cordillera de Guanacaste that is so apt for coffee plantations.

Throughout the four centuries of ranching and farming development of the ACG area, social distance from the centers of power has been critical in saving much of its dry forest biodiversity. In the beginning, the land route from Nicaragua to the farming/indigenous centers in Nicoya apparently went south from Rivas to La Cruz to Puerto Soley to Santa Rosa to the Liberia intersection (the stoplight over the Inter-American Highway), and then turned out into the Nicoya Peninsula. Only a short spur went south to the monastery at Bagaces. Access to central mainland Guanacaste was into the Golfo de Nicoya by boat from Puntarenas and then up the Río Bebedero to Cañas, or by stagecoach from Puntarenas to the gold mines at Abangares. Movement from the Meseta Central to Nicoya crossed the Golfo Nicoya by boat/ferry. Not until World War II (1939–1945) was the major Inter-American Highway built south from Rivas to Liberia to Bagaces to Cañas to turn inland towards San José at Puntarenas (though from the very beginning there were primitive ox-cart roads from San José to Puntarenas). The rain forests and swamps of the San Carlos flatlands of northern Costa Rica apparently blocked the alternate possibility from La Cruz to Santa Cecilia to Upala to Puerto Viejo de Sarapiquí (and then over the mountains from San Miguel to Heredia). The new Inter-American Highway thus cut straight across the very large ranches that had generally extended from more coastal climates to the moister Pacific foothill climates of the Cordillera de Guanacaste bordering the coastal plain south to Esparza. The access provided by the Inter-American Highway changed all of the political economics of Guanacaste Province as a whole, and the ACG region specifically—making it easier to ranch and farm *vis á vis* the Meseta Central and its markets, instead of crossing the Nicaraguan border to go north. This changed again when the tourist “invasion” began with caravans of vacationers in the 1960s–1970s and a steady flow of tourists down this new highway—a spark of early tourism development for the Liberia area. This was, however, abruptly halted by the July 1969 Soccer War in El Salvador (Durham 1979) and later wars in Nicaragua (1970–1987) (Weissberg 2001). In addition, by 1987, the 1960–1980 Costa Rican cattle boom (Janzen 1988) was beginning to die and the cattle industry was formally “killed” by the Costa Rican government in a meeting with the cattle industry in August

Fig. 10.12 A Pleistocene megafauna—the horse was evolved in the New World and survived in the Old World, to be reintroduced by the arriving Spaniards in the 1500s—breaking a native Costa Rican Pleistocene megafauna fruit before scooping out the sweet black insides with its tongue (see Fig. 10.11). Sector Santa Rosa, ACG, 1978.

1994. At that time the Minister of Agriculture and Ranching (Mario Carvajal) and the Minister of the Environment and Energy (René Castro) met with many representatives of the cattle industry at the ACG Horizontes Forest Experiment Station (personal observation); the meeting announced that the government policy would be no more bank loans for the extensive cattle industry (personal observation).

All indications are that by the mid-1900s, the only original dry forest remaining in what is today ACG was a few scattered patches of 1–20 ha on the Mesa Santa Rosa (mostly centered on severe ravines and watercourses), some parts of the lower slopes of Cerro El Hacha, and the 2,000 ha still-forested slopes of the seaward tip of Península Santa Elena (Fig. 10.15). As mentioned earlier, even the magnificent tall tree forest of the Ojochal is obviously regrowth on a very large indigenous village midden (there are many mammal bones, potsherds, and mollusk shells just a few cm below the soil surface). Even the old-growth Bosque Húmedo near the Casona Santa Rosa had its large mahogany trees removed in the early 1940s (the oxen-based log extraction road to the Pacific for transport to the Caribbean boat-building industry via the Panama Canal is today's road to Playa Naranjo). The name of Playa Potrero Grande reflects the enormous alluvial flatland *potrero* (pasture) that had been burned out of the dry forest backing the Playa Potrero Grande mangrove and freshwater swamp. The clearing and farming of the flatlands behind Playa Naranjo and Playa Potrero Grande was well underway by the mid-1960s.

When in 1966 the government of Costa Rica expropriated the Casona Santa Rosa and 1,000 ha around it to be a national monument and recreational area for government workers, the owner, Anastasio Somoza, at that time Nicaragua's dictator, replied that he would happily donate it to Costa Rica. Costa Rica refused the donation and insisted on expropriation and its accompanying payment. The government, in the form of Sr. Walter Hine, in January 1967 invited Dr. Kenton Miller (deceased), a young professor of conservation biology (Miller 1980) from the University of Michigan, to visit Santa Rosa and draw up a plan for its development as a historical and recreational site, much as in the US tradition of incorporating battlefields and other historical events in national parks. At the time, Dr. Miller was teaching at CATIE (the OAS-sponsored Tropical Agricultural Research and Higher Education Center experimental station near Turrialba). His father was visiting him in Costa Rica and they made an excursion of it. They arrived at the Casona Santa Rosa over an "awful 12 km road" off the Inter-American Highway (Kenton Miller, pers. comm.). The Casona was the ancient headquarters of Hacienda Santa Rosa as a working ranch; the cowboys opined that the Millers ought to continue on, down to the coast and see the beach, which they did. In the process they drove down the north face of the Canyon Del Tigre containing the Río Poza Salada, a site from which a local hunter was reputed to be harvesting 5–10 jaguars per year, probably well subsidized by feeding on the thousands of free-ranging cattle and the sea turtles nesting on the beaches. Miller went back to San José to suggest to the nascent national park service that instead of a small monument, they should decree a national park from the Inter-American Highway to the coast and out to sea to the national limit of 12 nautical miles. This decree produced the 9,900 terrestrial hectare Parque Nacional Santa Rosa (PNSR) that was born on March 27, 1971 during the government of President Daniel Oduber. The young Álvaro Ugalde (deceased), who, along with Mario Boza and Pedro León, devoted his life to the development of the Costa Rican national park system (Wallace 1992), was its first director. In 1977 it was increased to a size of 10,800 terrestrial ha through expropriation of a portion of a neighboring ranch that owned the land behind the southern part of Playa Naranjo. This version of PNSR contained 23,000 ha of marine area at that time as well, though this is generally not included in statements about its early size and was essentially ignored at that time.

The decree that created Costa Rica's first dry forest national park was blemished by mistakenly viewing the pastures and old fields populated by introduced grasses (largely *jaragua* or *Hyparrhenia rufa* from East Africa) as "savannas," seemingly and romantically analogous to African grasslands. In this context, the annual anthropomorphic dry season fires seemed almost natural, and besides, the fires were something so large, that a few no-budget "*guardaparques*" could not even dream of eliminating. At best they could prevent the fires from consuming buildings. Restoration was not even a management concept, though of course it began to occur by default on the prior farmland and pastures within the park close to the Casona. The PNSR staff focus was on stopping the hunting, which seemed to be as much an insult to the "King's Garden" as it was biologically undesirable, on removing the colonizing farmers/squatters, stopping further logging, and simply surviving. As these things gradually came under control, the focus shifted to expelling the 2000+ cattle still foraging throughout Parque Nacional Santa Rosa. This expulsion was both because "it is a national park" and because the cattle and horses symbolized people, something that was anathema to national park systems everywhere at that time (and that regularly led to the destruction of buildings, roads, fruit trees, etc., on the farms that were incorporated into lands of the emerging national park system).

A landmark court decision was won by Costa Rica's *Servicio de Parques Nacionales* (SPN) in 1976, telling the owner along the south boundary of Sector Santa Rosa that he had to remove his cattle from the park or they would be shot. About 1,000 cattle were removed, and the Guardia Rural came into Santa Rosa and shot 1,000+ cattle in 1977. Every vulture in Costa Rica appeared to be working

Fig. 10.13 Cerro El Hacha, the core of a 6 million year old volcano that once was an island in Lake Nicaragua, as viewed from the fire tower lookout on Cerro Pedregal on the upper slopes of Volcán Cacao. Its yellow upper portion is covered with a native grass *Trachypogon plumosus*, a population expanded by man-made fire from small populations once occupying natural disturbance sites. The yellow flatland pastures are jaragua grass (*Hyparrhenia rufa*) introduced from East Africa.

Fig. 10.14 Estación Argelia, the administration station for Playa Naranjo in Sector Santa Rosa, and originally the house for the large salt extraction works in the estuary behind it (July 1973). Note the cleared hillside dry forest behind the station, the kind of clearing that characterized all of the slopes near the ocean, slopes that were probably also cleared of their old-growth forest centuries earlier through ocean-access logging.

in Santa Rosa, and this was the only time that nesting vultures have been encountered there. At this time, there was no effective fire control program in Santa Rosa. Removal of the cattle was the removal of the biotic mowing machines. For centuries before this time, there had been a crude equilibrium between the highly fractured patches of dry forest, the closely grazed pastures, and the human-set fires (Janzen 1988c, 2002). Each annual fire burned the closely cropped pastures and trimmed the edges of the forest/secondary woody succession (Figs. 10.16 and 10.17).

Fires in dry years (or later in the dry season) burned further into the forest margin, expanding the pastures. Fires in wet years (or earlier in the dry season) did not kill the woody marginal vegetation, thereby shrinking the pastures. If an area did not burn for several years, the fire was more severe when it did arrive. When the cattle were removed, the result was instantaneous and highly predictable. The African grass grew to dense stands 1–2 m in height (Fig. 10.18), and the fuel for the annual fires was sufficient to create a wall of flame 1–4 m high that gobbled up the forest margins in huge bites (Fig. 10.19 and 10.20). Trees and patches of forest that had coexisted with the cattle-grazed grass-fires were incinerated, and fires burned downwind all the way through the understory of dense forest. By 1984 it was obvious that the multiple-aged stands of variously aged secondary dry forest and even the tiny fragments of "original" forest (old-growth) would be burned to total elimination if something was not done (Janzen 1988d, e). A fire elimination program was initiated by visiting research biologists and Santa Rosa staff. The current Santa Rosa and ACG status of being largely covered with various stages of woody succession vegetation is a direct result (compare Fig. 10.21 and 10.22). There are no natural fires in a "natural" ACG. There are no lightning strikes in the dry season; a rainy season lightning strike may set an individual *veranillo*-dried pasture or dead tree on fire, but that fire does not burn past the limit of the dry spot. The Costa Rican habit of labeling fires as "forest fires" is a misnomer, since intact living ACG forest basically does not burn; what burns is the pasture grasses and low herbs, with the heat killing tree seedlings and other young trees, thereby allowing more sunlight, which in turn generates more dry season fuel for the next fire.

Fig. 10.15 Peninsula Santa Elena as viewed from over its base where it connects with the volcanic mainland (January 9, 1988). The foreground yellow grass is almost entirely *Trachypogon plumosus*, a native (inedible to livestock) grass promoted by centuries of annual fires that have removed the gray-colored low deciduous old-growth forest that still clothes about 2,000 ha of the outermost slopes of the peninsula; the advancing line of grass, where the downwind-moving fires stop, is readily visible as are the remnant bits of forest in rocky ravines where there is little grass for fuel. The freshwater marsh of Punta Respingue is uphill backed by jaragua and *Trachypogon* ancient deforestation, and the Playa Potrero Grande snakes through even-aged but old mangrove forest.

Biology and Conservation of Present-Day Dry Forest in ACG

Defining a Dry Forest in the Costa Rican Tropics

The only "natural" wildland ecosystem likely to survive in northwestern Costa Rica is ACG itself, since all the remainder is destined for conversion (or already is converted) to an intense agroindustry or tourism development (or its forest patches and patchlets that are gradually dying from fragmentation and insularization; Janzen 2001), just as is the case with most of the remainder of non-explicitly protected/conserved wildland Costa Rica. Therefore we focus on the "Area Silvestre Protegido" (ASP) of ACG itself rather than attempt a generalized description of the entire northwest of Guanacaste Province as it might have been when the Spaniards arrived, since that would be a largely conjectural exercise.

"Tropical dry forest" is generally taken to be a natural forest growing in the lowland tropics in places where the climate has a very noticeable and regularly occurring relatively rain-free dry season of 4–8 months duration, but in the other months a total of 0.5 to 3 m of rain falls, which is quite enough to sustain what anyone would call "forest" (also known as lots of woody plants with a closed woody canopy). Dry forest and its variations go by many names in classifications of vegetation and legal documents—seasonal forest, deciduous forest, semi-moist forest, dry forest, dry-forest, etc.—but is usually meant in a contrast to cloud forest, rain forest, marine ecosystems, and desert—the other four major tropical natural ecosystems (ACG lacks a desert, though parts of the serpentine barrens of Península Santa Elena are certainly desert-like in appearance). The ACG dry forest is less than 1% of the dry forest that once extended from the foothills behind Mazatlán, Mexico, south, covering the Pacific coastal plain to the Panama Canal, with a rain-forested interruption around the port of San José (Puerto de Hierra), Guatemala, and the coast from about Carara, Costa Rica, to shortly across the Panamanian border (Janzen 1988a). This dry forest also extended across the Mexican Isthmus of Tehuantepec and from there north to the lowlands of Veracruz to Tampico and south to Yucatán, and then occurred in inland patches in Belize, Guatemala, and Honduras. Other large expanses of tropical dry forest once covered much of Venezuela, Colombia, Bolivia, Paraguay, Brazil, eastern to southern Africa, India, Pakistan, Thailand, Cambodia, Vietnam, Sri Lanka, Burma, and northern Australia (Murphy and Lugo 1986, Pennington et al. 2006, Bullock et al. 1995, Dirzo et al. 2011). We explicitly do not call a tree plantation a "forest" for the obvious reason that it is a crop and exists under quite different biodiversity and socioeconomic rules than does a naturally occurring forest of any age. Creating a tree plantation is not "reforestation."

Nearly all tropical dry forest has been thoroughly converted to pasture, cultivation, urbanity, and secondary succession forest following many kinds of human uses—hunting, farming, burning, irrigation, etc. The remainder is generally hunted, burned, and selectively logged. About a quarter of Costa Rica's forests was what can be generally termed dry forest. Well less than 1% of what originally was tropical dry forest has formal conservation status globally, though at one time more than half of the forested tropics was dry forest (Murphy and Lugo 1986). The basic conservation problem is that overall, dry forest ecosystems are substantially more user-friendly than are rain forests and cloud forests for ancient to modern human occupiers, despite their long dry season. The long dry season depresses pests, facilitates food storage, makes forest easier to remove (by fire), encourages fewer human diseases, makes for easier land transport, etc. The only way to conserve old-growth dry forest blocks of sufficient size to maintain continental-type biodiversity is through their restoration at a landscape scale, such as is occurring throughout in ACG per its original plan (Janzen 1988a, 2000a).

Furthermore, the few dry forests that still have significant populations of most of their species—enough to allow natural large-scale restoration—are those that are either so far from modern human society that they are relatively intact, or if near modern society such as is ACG, they are on such poor soils that they have never been thoroughly cleared of their dry forest biodiversity.

Because its ecosystem is so generally hospitable, and

Fig. 10.16 Closely grazed rainy season pasture (also burned during the previous dry season), Sector Santa Rosa, June 1975. Compare with Figs. 10.17–10.20.

Fig. 10.17 Closely grazed dry season pasture following usual dry season fire, Sector Santa Rosa, March 1976. Compare with Figs. 10.16, 10.18–10.20.

because it has been so thoroughly replaced by agroecosystems, tropical dry forest is poorly known and understood by both the academic scientific community and the conservation community, at least in comparison with tropical rain forests. This means that restoration is not in the direction of attempting to reconstruct something that is visualized or understood in detail so much as it is in "giving" the terrain back to nature and let the extant species fight it out among themselves and reconstruct their own ecosystem. It will be future and distant generations who will see once again what tropical dry forests looked like, more or less, when people first began their intensive assault on them. However, this philosophy has an important *caveat*. The tropical dry forests that are restored back into old-growth status will all be, irrespective of their sizes, ecological islands (and thus to some degree depauperate) in an ocean of agro-scape. Additionally, they will be lacking at least some of the other ecosystems with which they originally interchanged migratory species, and from which they received ecological (and evolutionary) colonists. In effect, the conservation process of Meso-American forest islands takes us back to the archipelagos of 20 million years ago, with the other islands surrounded by agro-scape instead of sea water. Some of those islands will be largely dry forest with contiguous rain forest and even cloud forest (such as occurs in ACG), while others will be made largely of rain forest and contain montane cloud forest at intermediate and high elevations. There is no escape from this inconvenient reality. Finally, the warming, drying, and erratic weather patterns of the current climate change (and during the past 20 years) is altering and creating novel mixtures of survivors with highly unpredictable consequences in all ACG ecosystems.

Because many species of plants respond to strong seasonal availability of rainwater by shedding their leaves in the dry season (Figs. 10.23 and 10.24), tropical dry forests are very visibly and microclimatologically different in the dry season from the various kinds of tropical evergreen forest ecosystems. While the reaction is less visible to the casual observer, the dry forest animal community responds equally strongly to the dry season—often by physically or physiologically escaping from the scarcity and heterogeneity

Fig. 10.18 Jaragua grass development following removal of cattle, Sector Santa Rosa, October 1980. Compare with Fig. 10.16–10.17 and 10.19–10.20. Sr. Roberto Espinoza for scale.

of water, and the subsequent reactions by plants, but sometimes also by finding the dry season to be the "best" time of year. The latter is the case with many species of flower-visiting solitary bees, seed predator mammals and insects, visually orienting predators such as owls, etc. (Janzen 2004). However, detailed ongoing studies of adjacent ACG rain forest biodiversity are uncovering strong seasonality even in the evergreen rain forest and cloud forest, even though they are not necessarily as strikingly synchronized with or by the beginning of a rainy season as are the species of ACG dry forest.

We tend to overlook a striking contrast between dry forest and adjacent rain forest because we are largely diurnal mammals. In the daytime, the difference between the two adjacent ecosystems can be enormous, and especially during the dry season. At night, however, the temperature and moisture differences between the two ecosystems are much less severe. Nocturnal biodiversity displays this well in the prominent movements back and forth between the two ecosystems. Likewise, the omnipresent clearing and other kinds of perturbations to dry forest are comparatively less dramatic in their increased insolation, heating, and drying effects on the forest, than is the case when adjacent rain forest is cleared. A pasture clearing in a rain forest is a "Death Valley" from the viewpoint of many species; a pasture clearing in dry forest is more like an early beginning of the dry season or late arrival of the rains. The clearing is not a happy circumstance, but it is something that the bulk of dry forest species have dealt with before in their annual cycles (Janzen 1967c). In this context, it is striking to hear rain forest colonists, bereft of the weather-mediating gadgetry of urban society, complain strongly about a slight temperature or moisture change that would not even be a topic of conversation to colonists in dry forest.

Dry Forest Climate

ACG was born as two things—a national monument in 1966, and in 1971, a national park for the conservation of tropical dry forest remnants. The latter was despite that the old pastures, fields, and huge blocks of secondary forest are manmade. The dry forest biodiversity and its accompanying climate of "Guanacaste" are quite different from the generally wetter, other 75% of the country. Here we imagine Santa Rosa at 10 degrees North latitude to be the center of the ACG dry forest, and then examine the climate outward into other ecosystems.

Classically, in "pre–Climate Change" days, in early May, near the end of the long dry season, the thermal equator passes overhead on its way north to the Tropic of Cancer. The heat builds up from the daily direct radiation and about May 15 the air mass over Santa Rosa is heated enough from the sun and soil radiation to rise through the overlying air masses, and this also generates a low pressure area that pulls in moist air from the Pacific. The rising moist air is cooled at high altitudes and the condensate from the towering cumulonimbus clouds drops a heavy rain shower between about 2 pm and midnight. The long rainy season has begun (Fig. 10.25). The thermal equator continues north until it gets to the Tropic of Cancer (23.5° N latitude), with its heating influence on Santa Rosa gradually waning during these months. Consequently, the heat-induced rains likewise gradually diminish until late July or early August, and Santa Rosa enters into a short dry season (the *veranillo*, or "little summer"). By the first week of September the returning thermal equator passes overhead on its way south, heating the already heated landscape and again leading to rising hot moist air that is drawn in from the Pacific, and heavy rains. This second part of the long rainy season, September

Fig. 10.19 Dry season fire fueled by non-grazed jaragua, Sector Santa Rosa (March 18, 1987). Compare with Figs. 10.16–10.18 and 10.20.

Fig. 10.20 Result of dry season fire fueled by non-grazed jaragua, Sector Santa Rosa, March 1986. Compare with Fig. 10.16–10.19 and note the woody vegetation killed by heat at the edge of the pasture, the remains of which will be consumed by next year's dry season fire as it eats away vegetation along the forest edge.

into late November, is generally wetter in aspect, cloudiness, and total rainfall than the first two months of the rainy season. By December the thermal equator has long since left on its long journey south to the Tropic of Capricorn and Santa Rosa becomes largely rain free, even though the moist soil and vegetation maintain a rainy season aspect for 1–2 months. There is only a gradual drying out of roads, creeks, ponds, foliage, etc. (in contrast to the abrupt change from dry to wet at the beginning of the rainy season in May). By January, the moisture-free Tradewinds are blowing strongly at ground level from the northeast. The rain shadow effect of the Cordillera de Guanacaste is in full force and the December–mid-May long dry season heats and dries Santa Rosa down to its full extent of largely leafless secondary succession forest, great susceptibility to man-made fires in pastures and early succession, dry and passable dirt roads, herbivore quiescence, strong sun, etc.

The above general scheme has several very noticeable and significant variations for biology, aside from the impact of global climate change (see below later). The "beginning" of the long rainy season, May 15, can be delayed by a few days (commonplace) to as much as two weeks (rarely), and its intensity can be highly variable—from 2–4 days of heavy afternoon deluges to just light rain in the middle of the night. Since these first rains are in the form of heavy rain from towering cumulonimbus clouds, instead of a generally widespread rainstorm, they often fall very heavily on one site and only a few hundreds of meters away very little rain falls. A distinctly different kind of variation is when it gets hot enough in late April or early May to then generate strong cumulonimbus-based rain for 1–2 days (as occurred in 2007 and in 2011). The general temperature is cooled by these "atypical" rains, sometimes causing the real rainy season to begin as much as a week late. This particular variant can cause some species to act as though the rainy season has indeed begun in late April. For example, in 2007 there was no general, massive, and synchronized appearance of Lampyridae ("lightning bugs" or *luciernagas*) with the mid-May beginning of the rainy season, apparently because their annual seasonal emergence occurred when heavy rains fell in late April 2007.

A quite different weather variant is that the length and

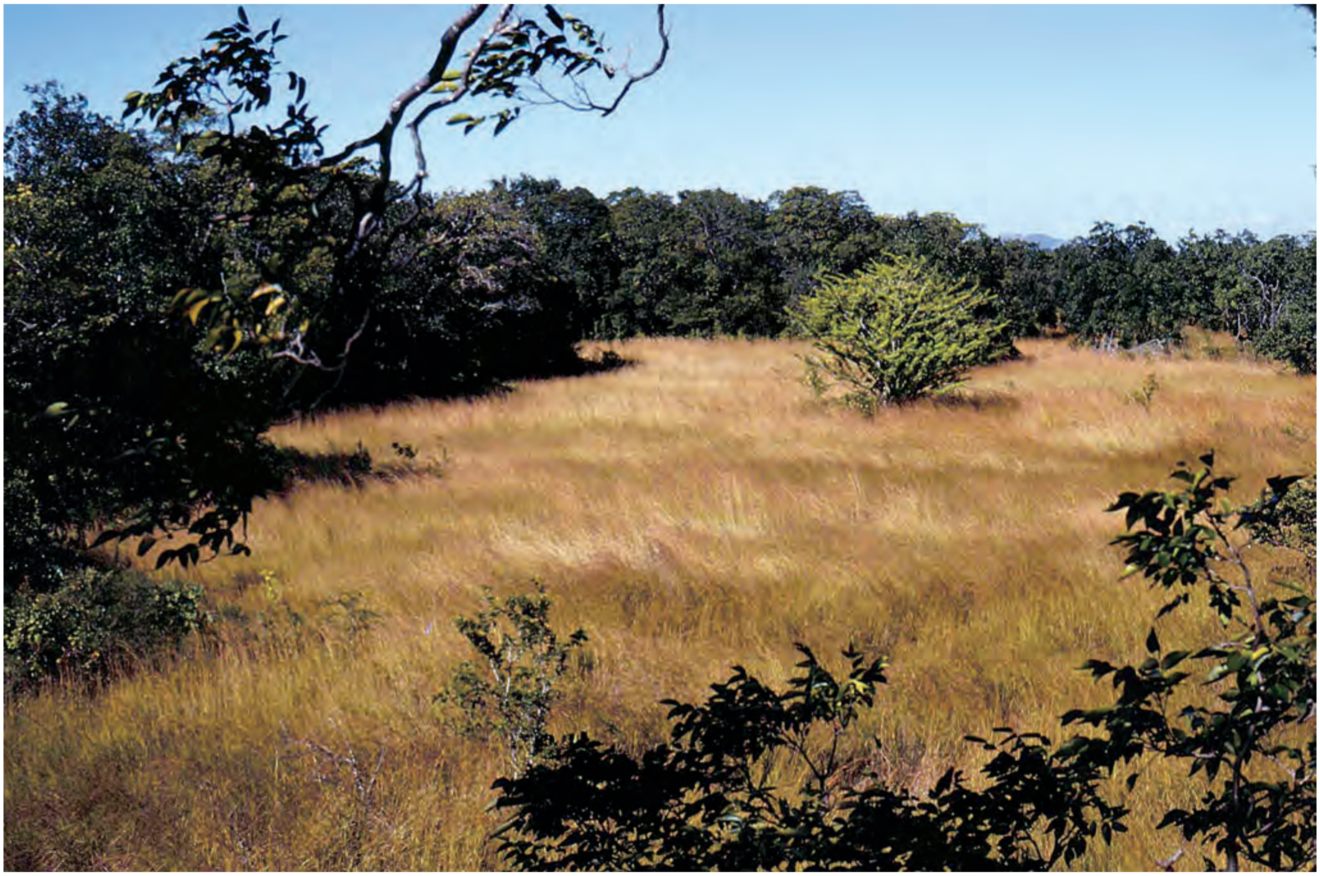

Fig. 10.21 Jaragua-forest edge that was characteristic of tens of thousands of hectares of Mesa Santa Rosa of central ACG dry forest at the beginning of the restoration process (December 30, 1980) and burned every 1–3 years. This pasture is at least 200 years old and was previously populated by native grasses. The forest to the left and background is encino (*Quercus oleoides*) old succession following logging and burning. Compare with Fig. 10.22.

intensity of the late July-August short dry season is highly variable (see Fig. 10.25 for an example of a very poorly developed *veranillo* in 2006). The short dry season is a time of pupal dormancy and adult sexual inactivity among Santa Rosa moths and butterflies, a dormancy that is generally broken by the second peak of heavy rain in early September (Janzen 1987, 1988f, 2004). If the short dry season is exceptionally dry and hot, moth pupae that would normally have remained dormant until the following May may eclose with the arrival of the September rains. For example, adults of the moths *Xylophanes turbata*, *Manduca dilucida*, and *Manduca lanuginosa* (Sphingidae) may be (unusually) caught in a September light trap. They usually remain as dormant underground pupae from June-July all the way through to the following May. This is just one of many small suggestions that the drying and warming of the Sector Santa Rosa dry forest under climate change will change its overall biology.

The tapering off (December-January) of the long rainy season into the beginning of the long dry season is highly variable in intensity, depending on how much rain fell during the total rainy season, and its pattern. The duration of dry season leafiness is also impacted by the intensity of the strong tree-level December-to-mid-March trade winds that blow across Santa Rosa after having passed over the Cordillera de Guanacaste. When they abruptly stop in March, the temperature climbs rapidly to the largely wind-free and intense dry season 33–35°C daily maxima temperatures that last until the long-rainy season begins in May. However, as mentioned above, about mid-March this increase in temperature often brings 1–2 days of early afternoon strong rain showers, a "false beginning" that seems to deceive no species but can soak unwary campers expecting a rain-free dry season.

The semi-orderly seasonality described above, created by the combination of the orderly seasonal passage back and forth of the thermal equator across ACG, the proximity of the Pacific Ocean, and the rain shadow of the Cordillera de Guanacaste, is strongly disrupted by hurricanes in either ocean. A Caribbean hurricane brings 2–5 days of heavy overcast to the Santa Rosa dry forest, and frequent heavy rain intermingled with lighter showers and drizzle. If combined with either the May-June or September-October rainy peaks, the Santa Rosa seasonal watercourses can contain major temporary streams and rivers (Figs. 10.28 and 10.29). A Pacific hurricane can be even more intense, filling almost all seasonal watercourses to their brim and overflowing (Figs. 10.30 and 10.31). However, it is noteworthy that (apparently) owing to their dense and relatively undisturbed forest cover, even during a hurricane the watercourses of the upper slopes of the ACG volcanoes flow strongly but do not rise substantially, with the flooding and major erosion being more noticeable at lower elevations where there is massive lateral surface run-off from pastures and saturated young secondary forest (e.g., Figs. 10.28–10.31).

Moving away from the Santa Rosa "classical" dry forest climate on the Mesa Santa Rosa (at 250–300 m elevation) towards the ocean yields no major climate surprises or disjunctions. Owing to the high soil porosity of Península Santa Elena, the coastal portion of the ACG dry forest ecosystem is conspicuously drier, as expressed by the morphology and species of its biodiversity (see general ecosystem aspect in Fig. 10.32). To the north, the climate gradually moistens; Piedras Blancas on the border with Nicaragua had a tree species composition (prior to deforestation) that was similar to that of Cabo Blanco and Puntarenas to Carara (Fig. 10.33), complete with *Attalea rostrata* (formerly called *Scheelea rostrata*) palms and espavel trees (*Anacardium excelsum*). This great expanse of dry forest to rain forest intergrade between the Pacific and Lake Nicaragua and the La Cruz area, and then eastward towards Santa Cecilia, has been so thoroughly destroyed that it is difficult to imagine what it was originally. To the south, toward Liberia, the current species composition of insects suggests that the climate was somewhat more moist than is Sector Santa Rosa, but it is very hard to distinguish that possibility from the effects of less wind, better soil, and the more moist flood plains that are today occupied by pastures and crops.

Fig. 10.22 Exactly the same view as Fig. 10.21, after 20 years without fire and absence of livestock (November 4, 2000). The canopy of encino is still visible and Winnie Hallwachs' hand (center) is positioned at a height of 2 m. The isolated jicaro (*Crescentia alata*) tree in Fig. 10.21 is completely shaded by this new forest (and therefore dying). The bulk of this young forest is wind-dispersed yayo (*Rehdera trinervis*, Verbenaceae) intermixed with another seventy wind- and vertebrate-dispersed woody species. Such invasion by forest is characteristic of many tens of thousands of unburned hectares of ACG pasture. Though moderate grazing speeds up forest invasion (and reduces the damage by escaped fires), livestock also does considerable damage to watercourses, and cowboys and their dogs cannot resist hunting.

Fig. 10.23 Forty-year-old dry forest in the rainy season (June), Sector Santa Rosa; same view as Fig. 10.24.

Fig. 10.24 Forty-year-old dry forest in the dry season (April), Sector Santa Rosa; same view as Fig. 10.23.

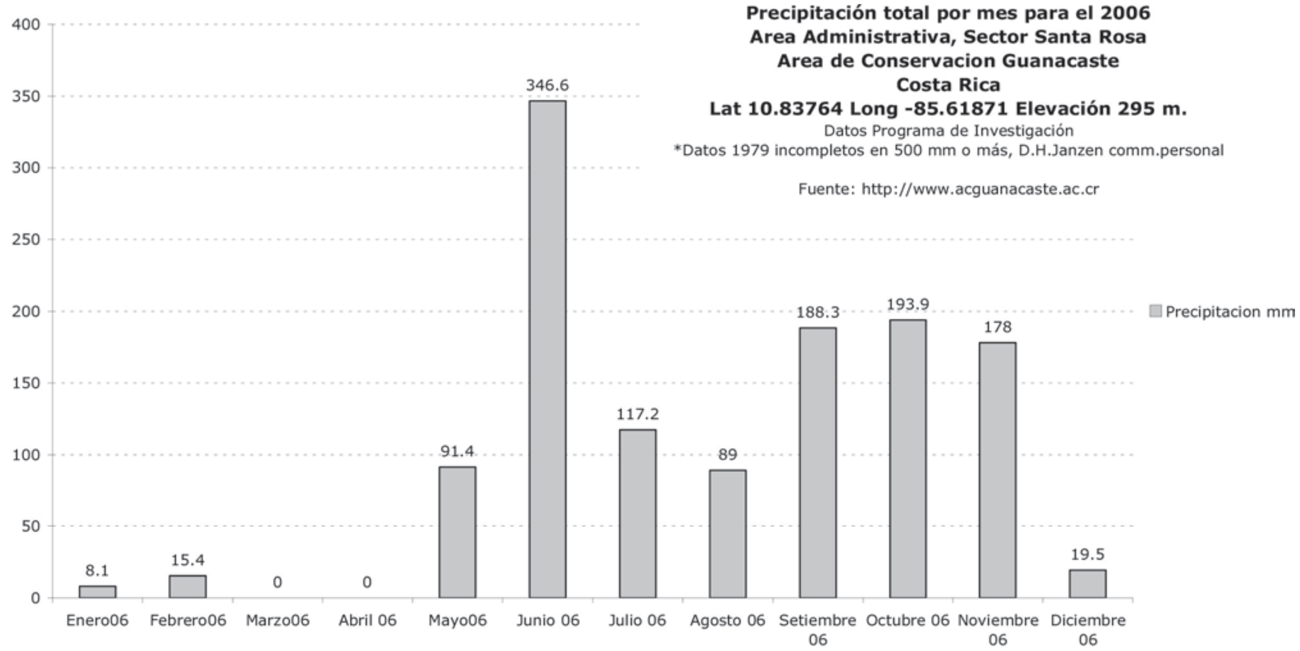

Fig. 10.25 Monthly rainfall in the Administrative Area in Sector Santa Rosa for 2006, in which year the August *veranillo* was almost non-existent, and exceptional rain fell in December–February.
Source: Weather station of Estación Biológica Santa Rosa; credit Maria Marta Chavarría.

Fig. 10.26 Pre-Columbian tapir (*Tapirus bairdii*) petroglyph, Pedregal Orosí on the lower western slopes of Volcán Orosí (Fig. 10.6) (January 6, 2007).
Photograph by Alejandro Masís.

Fig. 10.27 Danta (*Tapirus bairdi*) with juvenile in dry season Península Santa Elena dry forest (March 31, 2007); compare with Fig. 10.26.
Photograph by Luciano Capelli.

Certainly, to the south of ACG, the rainy season arrived a few days earlier as the thermal equator gradually moved north day by day in mid-May.

But moving to the northeast and east from Santa Rosa several major climate disjunctions emerge. First, the beginning of the long rainy season in Santa Rosa's dry forest—an alleviation of the strong rain shadow effect—does not extend far into the Cordillera de Guanacaste and to the Caribbean side. It is commonplace to sit at a still-dry-season Estación Biológica Cacao at 1150 m elevation in late May on Volcán Cacao and watch torrential rain falling on Sector Santa Rosa. Equally, the ACG rain forest stations (Estación Biológica Pitilla, Estación Biológica San Gerardo, Estación Biológica Caribe) can be suffering water shortages while waiting for the May rainy season to become full force, while Sector Santa Rosa is soupy wet. Equally, weeks to months of rainy weather are commonplace on the Caribbean side of the Cordillera de Guanacaste during both Santa Rosa's short and long dry seasons.

Second, as one moves from Sector Santa Rosa toward the volcanoes, the lower to mid-elevation western slopes of the Cordillera de Guanacaste become rapidly evergreen with progressively fewer deciduous tree species, owing to increased total rainfall and the cooling that comes with increased elevation. This effect is exacerbated by the everflowing streams/rivers flowing down these slopes, fed by both cloud condensate and rain.

However, these watercourses do not flow out into the Mesa Santa Rosa (where all watercourses are seasonally intermittent) but rather to the Pacific through the Río Tempisque drainage or to the Caribbean via Lake Nicaragua (through Río Sapoa, Río Animas, Río Mena). While the original (pre-European deforestation) Sector Santa Rosa dry forest intergraded rather abruptly from the flatlands of Mesa Santa Rosa and the coast below, into the more moist, almost rain forest, of the west-facing volcano slopes, it intergrades more gently if followed around the northwestern slope of Volcán Orosí to full low elevation (200–800 m) intergradation with Caribbean rain forest (Fig. 10.5). While this huge intergradation zone of Sector Del Oro, the only low elevation dry-rain intergrade in Costa Rica, has been 90% destroyed by first logging and pasture, and then contemporary agriculture, enough remnants remain near the river channels to dimly perceive what once was.

In short, both the biodiversity of the Pacific dry forest of Costa Rica and the biodiversity of the intermediate to low elevation Caribbean, can be found living in the same hectare in the forests of Sector Del Oro. For example, the large-fruited *Manilkara zapota* (rain forest) and smaller-fruited *Manilkara chicle* (dry forest) grow side by side, and at lower elevations, small-fruited *Enterolobium schomburkgii* (rain forest) and large-fruited *Enterolobium cyclocarpum* (dry forest) can be encountered in the same hectare. Study of the details of this interdigitation/overlap of two major ecosystems is today, however, rendered nearly impossible by the habitat insolation created by pastures, fields, plantations, roads, etc. They render practically everything into "edge effect." The edge effect jumbles many species together into the same mixing pot rather than allowing the fine-scale species-to-species contacts that must have originally occurred when all was old-growth forest and the disturbances were "natural" (Janzen 1986a, b).

The upper elevations of the Cordillera de Guanacaste were very likely to have been lightly glaciated in the last Pleistocene cool period, at its maximum about 20,000 years ago. Volcán Orosí, at 20,000 years of age now, would have been newly formed then, and the other older volcanoes would have been in a state of becoming vegetated. Narrow altitudinal bands of different kinds of tropical forest would have marched up the slopes, from the most cold-intolerant lowland dry forest (Pacific side) and rain forest (Atlantic side) up to the most cold-tolerant evergreen cloud forest at the top. However, at the peak of the last glaciation, sea level was about 100 meters below current levels, so there would have been more linear space over which to spread that gradient at least on the Pacific dry forest side.

As the climate gradually warmed, the continuous (across the Cordillera) mid-elevation bands would have moved upward and become fragmented into upper elevational (and progressively smaller) islands by the mid-elevation valleys between them. For example, one of these valleys is today the Quebrada Grande-Nueva Zelandia-Dos Ríos mountain pass. Today, these upper elevation insular cloud forests (visible as blue area in Fig. 10.2), and their biodiversity, are being literally cooked off the tops of the Cordillera as global warming heats (and dries) this part of Costa Rica (and other tropical mountains as well). Equally threatening to these ecological islands, the upper elevations are being reduced in size and quality as dry season refuges for birds and flying insects of the lowlands that spend parts of the year at cool, upper elevations (e.g., Hunt et al. 1999; Fig. 10.34). Perhaps even more unfortunate, those portions of cloud forest biodiversity that can tolerate the increased temperatures and loss of rain/cloud cover are now being subjected to invasion

Fig. 10.28 Río Tempisque at Potrerillos, Inter-American Highway, ACG margin and collecting all ACG Pacific run-off from the western side of Volcán Cacao and Volcán Orosí; normal rainy season level (July 22, 2003); compare with Fig. 10.29.

Fig. 10.29 Río Tempisque at Potrerillos, Inter-American Highway, ACG margin when collecting all ACG Pacific run-off from the western side of Volcán Cacao and Volcán Orosí; flood level during a hurricane from the Caribbean (October 1999); compare with Fig. 10.28. Photograph by Felipe Chavarría.

of novel competitor and predator/parasite regimes from the lowlands. For example, the army ant *Eciton burchelli* and other species of ants are now foraging all the way to the top of Volcán Cacao (1,650 m) and directly attacking dormant *Polistes* (Hunt et al. 1999) from the lowlands, whereas in 1985 there were no visible ants at all at 1,000 m and above on the same volcano. A particularly dramatic case of this impact is probably taking place now in the small patches of inaccessible remnant cloud forest at 700 m elevation at the mountaintops of Península Santa Elena, and along the upper elevations of the Rincón de la Vieja massif.

The general long-term climate-change trend of increasing rainfall in the tropics is concentrated well to the south of Costa Rica (Adler and Gu 2007) but apparently moving slowly northward to engulf the region ACG to El Salvador (Sachs and Myhrvold 2011). In ACG as a whole, global climate change is warming and drying ACG—all ecosystems—and reducing the total amount of water arriving by rainfall, as well as reducing the amount condensing on the vegetation in the upper parts of the Cordillera de Guanacaste. This is reducing annual and seasonal river flow from the volcanoes, especially in the dry seasons. When the dry forest rainy season is shorter, less intense, and more erratic in start and end dates, there are very visible effects on the biodiversity. At the same time second order consequences are rampant, such as litter decomposition happening less thoroughly in a dry rainy season, presumably affecting all of the organisms that depend on litter recycling, as well as leaving more fuel for a dry season anthropogenic fire.

As the dry season advances, seasonal watercourses flow less and leave temporary pools of shorter duration. This curtails the activity of aquatic species and reduces the capacity (and ranges) of water-dependent species. As ACG dries, there is a reduction in the amount and diversity of the annual rainy season invasion of the dry forest by “rain forest species,” species that generationally move from east to west during the rainy season. There is also a reduction in the number of species that survive multiple years in local small moist habitats as residual fragments of once larger populations. Particular weather events that are used as cues by dry forest biota for reproduction, dormancy, migration, growth, and other periodic events, such as the timing of the beginning of the May rainy season, or cool windy weather in November, may easily be out of phase with other processes or species needed as mutualists or prey/hosts. Particular seasons needed for fat storage, fledgling-friendly learning, growth, migration, dormancy, etc., may not be as long as needed, may be de-synchronized with other events, or may even be too long. The occasional hurricane or other intense tropical storm that dumps 0.5 to 1.5 m of rainfall over a few weeks certainly does not compensate for the general de-synchronizing and drying that is taking place, even if it results in the annual average rainfall staying about the same year by year (e.g., Fig. 10.35).

In theory, and probably in practice, part of the salvation of the ACG dry forest biodiversity in the face of climate change is in having the opportunity to move from west to east, moving up the moisture gradient and to some degree, up to cooler elevations as well. This has been a major part of the rationale for expanding ACG to the wetter east during the past decade (http://janzen.sas.upenn.edu/RR/Rincón_rainforest.htm) and is currently the impetus for further eastward expansion (http://janzen.bio.upenn.edu/saveit.html; http://www.gdfcf.org). However, the warming also means that the species at the uppermost and the easternmost portions of the moisture/elevation gradient have nowhere to flee, since the upper portion is bounded by air, and the eastern section is bounded by cultivation and lower elevations. A part of future management discussion in ACG will be whether to contemplate moving species from the 1400–1600 m elevations on the tops of Volcán Orosí and Volcán Cacao to upper elevations at the Rincón de la Vieja complex (up to 2000 m), a sort of local “Noah’s ark rescue operation” or whether to simply let their Orosí and Cacao populations die out (assuming that these species are already on Rincón de la Vieja), as would happen with the smaller and lower islands in an oceanic archipelago following a rise in sea level. This “*conservation* conversation” will need to be part of the larger discussion (e.g., Thomasa 2011) of what to do when some other more distant conservation area wishes to view the elevated parts of Cordillera de Guanacaste as a refuge, a conversation that belongs in the yet larger discussion of what to do about the species, habitats, and minute ecosystem fragments that will gradually disappear as the entire ACG moves over centuries through its successional stages to become once again old-growth forest—and a new one at that, in view of climate change.

Returning to the question of “what is the impact of climate change on ACG?”, there is no straightforward reply—other than “perturbation.” While the climate is unambiguously changing as perceived by both humans and others living there, and by weather station records, the multiple ACG dry forest biotic changes that are evident even without looking explicitly for them have at least four major causes. All four causes are intertwined and interinfluencing: (1) climate change per se, (2) climate/habitat change from the woody succession/restoration/de-fragmentation taking place throughout all ACG ecosystems (many species become common, many other species become rare or much less ubiquitous), (3) insularization of ACG as a whole (yes, the species richness of its final equilibrium will not be as great as it once was when it was part of an unbroken expanse of natural ecosystems) and occupied many of its Holdridge Life Zones (Fig. 10.33), and finally, (4) the gradual dying out of the “living dead” individuals, populations, and ecosystems (Janzen 2001) that characterize the biodiversity that seems to be surviving in the surrounding agro-scape (and seascape). Additionally, other macroinfluences will arrive (e.g., invasive alien species, overwhelming human desire for targeted resource extraction [especially water and geothermal energy], evolutionary change in the fragments of once-widespread species, sea-level rise, etc.). It is a striking and inconvenient characteristic of ACG that whenever a particular conservation topic—biofuels, introduced species, climate change, fragmentation, territorial expansion, water extraction, whatever—is put in the spotlight, it cannot be discussed and treated in isolation from the other challenges and traits. An integrated solution or action must be sought, yet simultaneously management has to resist the temptation to let all considerations tangle up each other to where there is no action. This means that solutions need to be integral—the so-called “ecosystem approach” (Janzen 2000a, 2000b), both biologically and sociologically—yet also take specific and rapid actions for a specific problem even if, because of the other considerations, the solution is not a perfect solution. When the victim is bleeding to death, you stop the bleeding, even if it leads to scars and amputations down the road.

Dry Forest Seasonality

The most visibly outstanding trait of ACG dry forest is its strong seasonality, briefly alluded to above (and see Fig. 10.23, 10.24, 10.25, 10.30, 10.31, 10.33, and see

Fig. 10.30 Cafetal, headwaters of Río Cuajiniquil, a typical ACG seasonal river bed during the dry season (March 15, 1999). Compare with Fig. 10.31.

Herrera, chapter 2 of this volume). Dry forest seasonality, and its impact on organisms, merits many books full of descriptions, analyses, and discussion on the topic. Here we touch on just a few of what have been some of the more startling seasonal aspects to us as biologists, with an extratropical upbringing, living in ACG in all seasons of the year.

Seasonality of Insect Migration

When the heavy rains begin in mid-May in ACG dry forest (Fig. 10.25), a large number of insects abruptly appear in any census system—moths and beetles in light traps (Fig. 10.36), wasps and flies in Malaise traps, caterpillars on foliage, defoliation by caterpillars and beetles, caterpillars brought to nestling birds, wasp nests being built, etc. These peaks were previously spoken of as the result of "hatching with the rains," but it is much more complex than that. As each species is investigated in detail, each is found to have its own complex relationship to the breaking of the long (and hot) dry season. These sets of relationships become progressively harder to summarize the more that is known.

However, all of them have to a great degree the phenology of their lives tied to the seasonality of the beginning of the end of the long dry season and the beginning of the long rainy season (Janzen 1983b, 1984a, 1987, 1988f). As an example, the large number of moths that appear in a light trap in the period from early May (1–2 weeks before the rainy season) through the end of May (two weeks after the beginning of the rains), have three principal origins. There is a set of species that have been dormant pupae suspended in silk cocoons (a few such as *Rothschildia erycina* and *R. lebeau*, *Automeris zozimanaguana* [formerly *A. zugana*], and *A. tridens*, some Megalopygidae and Limacodidae) on the

Fig. 10.31 Cafetal, headwaters of Río Cuajiniquil, a typical ACG seasonal river bed during the full rainy season strongly enhanced by the edge of Hurricane Mitch (October 30, 1998). Compare with Fig. 10.30.

foliage. There is a set that pass the dry season as dormant pupae in the litter/soil (mostly) since the previous June (e.g., *Manduca dilucida*, *M. lanuginosa*, *Xylophanes turbata*, *X. juanita*, *Schausiella santarosensis*, *Arsenura arianae*, *Eutelia furcata*, *Euscirrhopterus poeyi*, *Neotuerta sabulosa*, *Dysodia speculifera*, *Holochroa ochra*, *Protographium epidaus*, *P. philolaus*, etc.). In entomological terminology many of these species are univoltine, meaning that they have just one generation per year. These species are "migrating" into the rain-soaked dry forest at the beginning of the rains from a dry forest microecosystem—a pupal or prepupal dormancy chamber underground or in the litter. They have been hiding for 11 months, "hoping" not to be found by a predator or parasite. Their cue for eclosion ranges from extreme heat, and perhaps an internal calendar, to the cooling that comes from the first rain. Several of them are conspicuous in emerging as adults days to weeks before the actual rain (Janzen 1988f), indicating the ability of the pupa to "anticipate" the rains. Next, there are many species that have been in the forest as adults in reproductive stasis (in diapause or aestivation in entomological terminology), hiding as inactive adults in crevices in tree bark and other nooks and crannies. When the cool and moist nights of the rains come, or some other associated weather cue arrives, they "turn on" to fly, mate, and search out food plants on which to lay their eggs, thereby beginning a period of 1–2 to 3–4 generations during the rainy season. The last generation of adults to eclose at the end of the long rainy season in December-January again hides to pass the long dry season (or sometimes the adults both hide and search for food in rotting fruit). This group contains many species of small Noctuidae and Erebidae, with many species of *Eulepidotis* and *Letis* being conspicuous examples; but butterflies such as *Eunica monima*, *Myscelia pattenia*, *Eurema daira*, *Urbanus proteus*, *Callicore pitheas*, *Archaeoprepona demophon*, and *Historis acheronta* do the same (Janzen 1983b). Again, many of the species of moths of this ilk appear in a dry forest light trap 1–10 days before the rains actually begin.

And third, there is a set of species that arrive by migration from the wetter side of ACG—from the rain forest, cloud forest, and intergrades (Janzen 1988g). These species left the ACG dry forest at the end of their first generation in late June to July, or in a few cases at the end of the rainy season, apparently flying to the "other side" of Costa Rica to be sexually inactive (but feeding) adults and to return 10 months later, or to have one or more generations in the rain forest to cloud forest before their offspring return to the dry forest at the beginning of the following rainy season (Janzen 1988b, Haber and Stevenson 2004). Some members of some of these populations apparently remain in ACG dry forest feeding at flowers for a while after the caterpillar season has passed, and sometimes have a light second generation during the September- November second heavy peak of rains (e.g., the sphingid moths *Pachylia ficus*, *Xylophanes chiron*, *X. anubus*, *Aellopos fadus*, *Enyo ocypete*). This cycle of seasonal migration is being viewed here as seen from the dry forest–centric viewpoint.

Alternatively, some of these species may be viewed as a rain forest species that, at the beginning of the rainy season, expands into the dry forest to have a large generation at a time of superabundant edible foliage and minimal populations of predators and parasitoids (that are satiated by the very large synchronized peak of prey), and then "retreats" to the rain forest for subsequent generations.

However, the situation is yet more complex than it appeared in the first several decades of study of Santa Rosa dry forest insects. The insect and caterpillar inventory (Janzen 1996, Janzen et al. 2009) of ACG was very pleased to find

Fig. 10.32 On the horizon, the dark evergreen encino (lowland oak: *Quercus oleoides*) forest on the splash of white volcanic tuff (see Fig. 10.3) overlying the Santa Elena Peninsula serpentine vegetation (scattered green to yellow to brown to gray deciduous) at La Angostura (March 25, 2002).

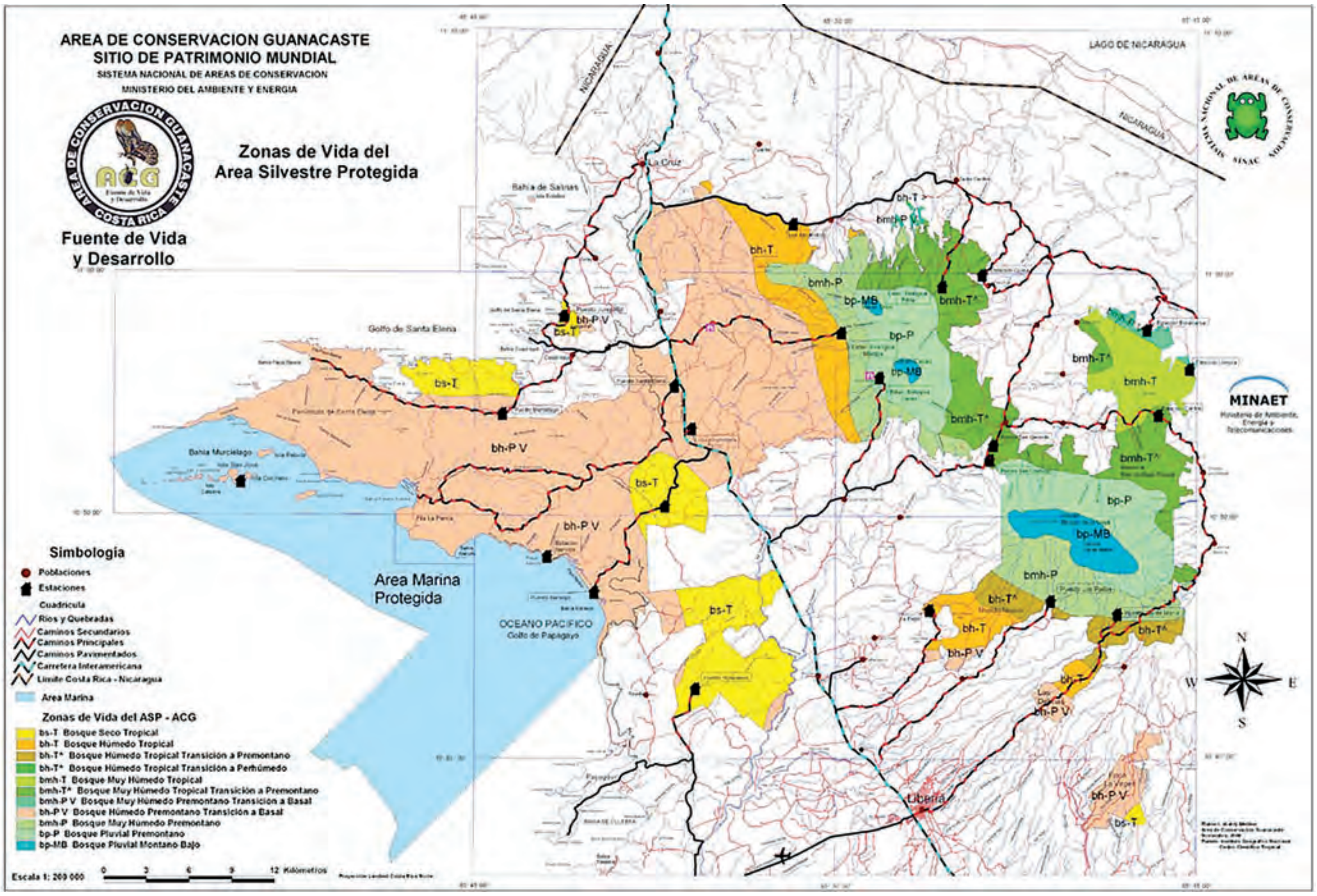

Fig. 10.33 ACG Holdridge Life Zones, demonstrating their wide variety as expressed in the changing transect running westward from the dry Pacific sector to the cloud forest and then on the Atlantic rain forest.
Source: Waldy Medina, September 2007.

many "dry forest species" of Sphingidae caterpillars in the ACG rain forest at the time of year when they have disappeared from the dry forest after their first generation in May-July. However, when adults reared from all of these species were DNA barcoded (Janzen et al. 2005, 2009, Holloway 2006), it was found that *Xylophanes porcus* and *X. libya,* for example, were in fact each two populations (= two species) (other species do appear to be just one population, migrating as previously believed). While *X. porcus* does not seem to have a morphological trait to distinguish the dry forest population from the rain forest population, *X. libya* does. Its dry forest specimens are lighter in color, a trait that would normally have been viewed as an ecophenotype, except that DNA-identified adults of the dry forest population reared from wild-caught rain forest caterpillars are just as light in color as are its conspecifics from the dry side of ACG. This means that when the dry forest *X. libya* caterpillars disappear from the dry forest for 9 months of the year, the population may in fact not be gone but rather, may be simply invisible to our trapping methods (not being attracted to lights, and not generating caterpillars). Alternatively it might be living in the moister interface between dry forest and rain forest at the western base of the volcanoes. Only more inventories will determine what is happening. However, when the adults caught at lights over the years—specimens accumulated by the INBio national biodiversity inventory and of unknown caterpillar origins—were then DNA barcoded (see Janzen et al. 2005), it was found that there are in fact three *X. libya* populations (= species) of free-flying adults—those of Pacific dry forest, those of Atlantic rain forest at intermediate elevations, and those from Atlantic rain forest low elevations. And, adults of all three have been collected from a single light trap at Estación Biológica Pitilla, which is Atlantic rain forest at an intermediate elevation (700 m), but within a few tens of kilometers of both Pacific dry forest and Atlantic lowland rain forest on the northeastern side of Volcán Orosí-Orosilito. There is much more complexity to both the species and migrations of *X. libya* than meets the eye, and this is probably the case with many ACG species of moths and butterflies.

A seasonal migratory phenomenon that is very visible to humans is the annual single generation of a set of species of large yellow and white pierid butterflies. It begins with the arrival in the dry forest of single and unnoticed females (and perhaps males, but they have not been censused) of a group of species during the 1–2 weeks bracketing the beginning of the rains, species that lay their eggs on newly expanded leaves (e.g., *Phoebis philea* and *P. sennae* on *Senna* spp.; *Anteos maerula* and *A. clorinde* on *Senna atomaria*; *Aphrissa statira* on *Callichlamys latifolia* and *Xylophragma seemannianum*). These species of butterflies are also present in low to intermediate elevation rain forest, where their caterpillars have been occasionally encountered by the ACG caterpillar inventory at all times of year (adults reared from these caterpillars have the same DNA barcode as those of the May-June generation in ACG dry forest). The dry forest generation of adults ecloses in large numbers in the last half of June and then both sexes are encountered, flying east in large numbers, back to the rain forest. Many hundreds per hour of 5–8 species may pass a single point on the Sector Santa Rosa entrance road. For the remainder of the rainy season, an occasional caterpillar of one of these species (most commonly, *Phoebis philea*) is encountered in the ACG dry forest, and the occasional adult is seen. During the long dry season, only the very occasional adult is encountered (and if they were not large and yellow, their density is so low that they would not be noticed). To complicate matters, as woody succession—also known as forest restoration—has progressed in ACG dry forest, the density of these species per year has steadily declined with the shrinking populations of their caterpillar food plants, all of which are short, shrubby, and shaded out by the growing trees. In the same dry forest, two bright orange nearly identical cryptic species, *Phoebis argante* and *Phoebis hersilia*, are having nearly year-round continuous generations on their evergreen (and somewhat riparian) food plants—*Inga vera* and *Zygia longifolia* (food plant records in Janzen and Hallwachs 2011, discussion in Janzen et al. 2009).

A conspicuous example of ACG dry forest seasonal migration and reproductive dormancy is displayed by the (previously) common social wasp *Polistes instabilis* (Hunt et al. 1999; Fig. 10.34) that is a predator on lowland caterpillars. This wasp builds open-faced *papier-maché* nests ("lengua de vaca") initiated by single females (or perhaps small groups of females as well) hanging on twigs within dense foliage 1–2 m above the ground in the lowland ACG dry forest at the beginning of the long rainy season (these nests were also commonly built under the eaves of buildings). The wasps actively seek caterpillars, chew them into pieces, and carry the pieces to their larvae. The nest size grows rapidly to where there can be 10–30 wasps at a nest by the end of June. Throughout the remainder of the rainy season, the nest grows more slowly, but may have as many as 100 wasps by December. Sometime in November-January, the nest is abandoned and the wasps fly to the cloud forest at 1,000+ m elevation on Volcán Cacao (Hunt et al. 1999). Thousands of wasps, mostly females with males scattered among them, aggregate in hollow trees (and buildings when available) in the cold foggy climate to inactively pass the long dry season. In effect, they have put themselves in a refrigerator. On hot days, some become active and fly out of the cavities—not to forage but "sunning" on foliage. When the rains begin in Santa Rosa, the wasps abruptly disappear from the cloud forest, and appear in the dry forest in the lowlands below, building their nests. As the clouds have moved up Volcán Cacao during the past 20 years of climate change, wasp-occupied hollow trees are now encountered higher up on the volcano, and with fewer wasps in them. Equally bad for the wasps, *Eciton* army ants (major predators on *Polistes* wasp nests) have now reached the (warming) very top of Volcán Cacao, thereby adding yet another dry season challenge to the wasps' survival. Over the same period, rainy season nests have become noticeably scarcer in the lowland dry forest. Very few *P. instabilis* individuals remain in the dry forest during the long dry season; while active nests have not been located, the adults are encountered drinking water from waterholes.

While this obvious reduction in *P. instabilis* wasp density is likely due to the shrinking size and quality of the volcano-top "refrigerator" in which the wasps hibernate, it may also be caused by the general decline in caterpillar density being experienced by the Santa Rosa dry forest over this same period. It may even be associated with cooler temperatures at the more strongly shaded ground-level dry forest microhabitat occupied by these wasps in the rainy season, as forest succession advances; cooler temperatures lead to slower larval growth and hence smaller population sizes. While this wasp displays unambiguous seasonal migration in ACG, exactly analogous to monarch butterflies *(Danaus plexippus)* in their Canada to Mexico annual seasonal migration, it does have a large neotropical dry forest distribution from Mexico to Panama (http://zipcodezoo.com/Animals/P/Polistes_instabilis.asp). In all of its range it is within a few tens of kilometers of higher elevations where it could be passing the long dry season.

However, it is also the case that a few active nests of *P. instabilis* survived the dry season in Sector Santa Rosa in the 1980–1990s, at a time when the overall rainy season nest density was easily 100-fold greater than at present. These could be the breeding stock for quick selection for a non-migrating population if the volcanic refrigerator disappears, and the lowland caterpillar density remains high enough for

Fig. 10.34 Caterpillar-hunting *Polistes instabilis* (Vespidae) social wasps from Sector Santa Rosa dry forest passing the dry season aestivating/hibernating in a cavity (building) in cloud forest at 1,150 m on Volcán Cacao (Estación Biológica Cacao, January 18, 2007); these wasps are mostly female individuals, which are derived from many hundreds of small nests in the lowlands in the previous rainy season. They will return to the lowlands at the start of the next rainy season to solitarily found new nests.

them to maintain a rainy-season population large enough to have enough nests for some to make it through the largely caterpillar-free long dry season (the dry season also means heavy nest predation by white-faced capuchin monkeys and *Eciton* army ants, and no free-standing drinking water over large areas). Alternatively, these dry season nests may have been aberrant, sick, or otherwise dead-end members of the population, and offer no genetic escape for a species locked into seasonal migration to the volcano cloud forest as a way of escaping the inimical dry time of the year.

Of Plant Reproduction and Plant-Animal Interactions

Reproductive dormancy by adult organisms is most vividly displayed by ACG dry forest trees. Each species flowers, and matures its seeds, at quite specific periods of the year, many in the dry season and some in the rainy season. They display strong within- and between-year synchronies as well. There are three major seasonality-derived arrays of evolutionary drivers behind this phenology: (1) competition among vegetative individuals during the rainy season selectively favors minimal use of product and reserves for flowering and seeding at this time; this is the time when vegetative growth is most feasible and necessary in crown-to-crown and root-to-root competitive interactions (e.g., Janzen 1967a, 1978, 1982d); (2) seasonally influenced (largely) co-evolutionary interactions with pollinators, seed dispersers, and seed predators evolutionarily drives reproductive phenology; and (3) the "best" physical conditions for seedling and flower/fruit growth select for timing of reproduction. These three drivers and their interactions generate an incredibly diverse array of species-specific and ecosystem-specific patterns of reproductive, as well as vegetative, dormancy. When climate change and microclimate change generated by succession is added in, the patterns and the departures from "one size fits all" become even more complex.

The reproductive dormancy of a large ACG dry forest tree, *Hymenaea courbaril* ("guapinol"; Fabaceae, the bean family) offers multiple examples. The flower buds are visible immediately following the January shedding of the 11.5-month-old leaf crop and its replacement with a new set of leaves during 1–2 weeks; in other words, despite it seeming to have leaves year-round, *H. courbaril* is not evergreen as an adult. The visible flower buds are produced in January-February (early dry season). Following massive bud predation by the larvae of three species of *Anthonomus* weevils (Clark 1992; *Anthonomus* is the genus of the cotton boll weevil and in the Curculionidae), the buds open to flowers that are visited and sometimes pollinated by *Glossophaga* bats (see Teixeira de Moraes and Sebbenn 2011) in late February to early April. On most years, no fruits are set from these (perfect) flowers. The trees are essentially acting as males, presumably with their pollen being carried by the far-flying bats (at least up to 7 km), to distant trees that will bear a fruit crop that year. On those "male" years, the tree is not investing in the cost of fruit production. At long intervals a patch of *H. courbaril* has many members that bear a fruit crop of 100–2,000 (large) fruits per individual. The last massive and synchronized *H. courbaril* fruit crop in Bosque Húmedo of Sector Santa Rosa dry forest was in 1983, over 33 years ago. In 2007 a small patch of trees on the Sendero Natural in Sector Santa Rosa had their first large crop in 24 years (and some may well have been pollinated by flowering "males" in the Bosque Húmedo 3–4 km distant). In a fruiting year, the young green fruits gradually accumulate bulk and reserves until the end of the long rainy season. The mature fruits fall from the tree in late December to early February (a full eleven months after flowering). Once on the ground, these hard large megafauna fruits (Janzen and Martin 1982) are today gnawed open by agoutis (*Dasyprocta punctata*) and their seeds both preyed upon and dispersed/cached underground (Hallwachs 1986).

Throughout tens of millions of years (Neotropical commercial amber is the 30–40 million-year-old fossil resin of *H. courbaril*) the dispersal coterie of *H. courbaril* also included animals big enough to molar-crunch the hard fruits and swallow the hard large seeds entirely, which in turn would generate a quite different seed shadow than occurs today with agoutis being the primary dispersal agent (Hallwachs 1986). While the fruits are full-sized but still in the canopy and protected by a thick resin-rich rind (fruit wall), two species of *Rhinochenus* weevils (Curculionidae) oviposit through the fruit wall and the large larvae prey on the seeds (Janzen 1974, 1975).

Each year a few trees produce 1–20 fruits, presumably "physiological accidents," and this steady low dribble of fruits is what sustains the *Rhinochenus* population as well as being one of the many species of seeds and fruits that sustain the agouti population. Throughout this cycle there are seasonal aspects. Fallen fruits (dropped to dispersal agents) are harvested (and their seeds dispersed) at very different

Fig. 10.35 Total rainfall recorded per year by the weather station at Administrative Area of ACG in Sector Santa Rosa dry forest. To appreciate the general dessication of this dry forest rainy season input, one needs to subtract the heavy load (0.5 to 1 m) of rainfall occurring over a few days during the event of a hurricane in the vicinity (e.g., 1988, 1999, 2005), and recognize that after the mid-1980s, the beginning of the rainy season has been characterized by sporadic rains, rather than many consecutive days of soaking rainfall as in the past.

Fig. 10.36 Moths attracted to battery-powered fluorescent lights in ACG dry forest, just four days after the beginning of the rainy season (May 19, 2007). There are at least 300 species of moths captured in this photograph, some of which have migrated into the dry forest from cloud and rain forest. Some of these moths have very recently eclosed from long-dormant pupae, and some have become active after passing the dry season as quiescent adults.

rates by agoutis in the rainy season and the dry season, presumably both because of alternative food availability and because of the loud (and revealing) sound of gnawing into one of the very hard fruits in the dry season (Hallwachs 1986). The tiny *Anthonomus* weevils have just one February-March generation and then immediately emerge as adults from the aborted fallen flower buds. They then have to hide somewhere in a crevice in tree bark or in a dry rolled leaf for the remainder of the dry season and all of the six-month rainy season, and then into the beginning of the following dry season before there is again an oviposition site available in a flower bud. Flowering in the rain-free dry season obviates having physiologically rain-resistant flowers and pollen, and occurs at a time of the year when there are no other known bat-visited flowers in ACG old-growth dry forest. The tree is also investing flowering resources in the dry season, when there is no threat of crown-to-crown vegetative competition with other large trees. Avoidance of inter-crown competition may well be why *H. courbaril* has been selected to dump its old leaf crop and grow a new one in the early dry season (as opposed to some other time of the year) *before* bud expansion and flowering, though it does not explain why it drops a full crop of what appear to be perfectly normal leaves that are demonstrably capable of withstanding all the rigors of the dry season. The tree even grows its woody diameter seasonally, leading to very well defined September-October growth rings that allow a tree's age to be counted from a polished cross section.

The light defoliation by caterpillars of adult, sapling, and seedling *H. courbaril* is also highly seasonal, occurring almost entirely in the May-June first part of the rainy season (and conspicuously not at the time of new leaf production). Even the spectacular total defoliations of *H. courbaril* crowns by the large caterpillars of *Schausiella santarosensis* (Saturniidae), observed during 2003–2008 (and absent during 2010–2012) in Bosque Húmedo in Sector Santa Rosa, is restricted to the first six weeks of the rainy season. The great bulk of the host-specific monophagous *S. santarosensis* caterpillars are univoltine and remain dormant pupae in the leaf litter for 11 months. The defoliated trees gradually and weakly refoliate with smaller leaves during the second half of the rainy season. All of these seasonal events can be, and probably are, interrupted or calendar-shifted by climate change. Now multiply that across 400 species of dry forest trees in the same 10 km^2!

Dry Forest Succession, Restoration, and Conservation

Fragmentation and Restoration of the Dry Forest

Parque Nacional Santa Rosa (PNSR) was established in 1971 as a "right-now" act of conservation of dry forest remnants. Even then they were not understood to be as much remnant as they were, since they were embedded in old fields and pastures that were incorrectly called "savannah" (e.g., Daubenmire 1972). These remnants were also disappearing in the face of advancing local, national, and international agricultural society (Government of Costa Rica 1998).

The Parque Nacional Santa Rosa absorption into "Proyecto Parque Nacional Guanacaste (PPNG)" in 1985, which morphed into ACG over the following two decades (Allen 1988, 2001, Janzen 2000a), was driven by the concept of "restoration of tropical dry forest" (Janzen 1988a, 2002). Had there been some huge portion of Meso-American old-growth dry forest still intact to preserve in 1985, as there was and still are large areas of rain forest in other parts of the world, and had tropical dry forest still been relatively well conserved in other parts of the tropics, there would have been little incentive to invent the concept and strategy of PPNG through its restoration. In the simplistic terminology of those years, "since there is no dry forest conserved, large enough to biologically and sociologically survive, it is necessary to restore one." At that time, the mantra of conservation was "decree it, buy it, and conserve it now before it is cut down, because once cut, it is gone forever." While there was obvious truth in this mantra, it was also obvious from many examples of "accidental", naturally occurring restoration that a forest could be restored if the seed sources (animal and plant) were within dispersal distance (e.g., living in the woody succession in tree falls, landslides, old river courses, abandoned/failed/neglected farms and ranches, etc.). Within a few years, and stimulated by the propaganda being created by PPNG, it became generally accepted that the donor audience, and policy-maker audience, could grasp two messages—yes, save it if it is still there, but grow it back if it is not there. A large amount of farming/ranching/plantation activity is, in fact, dedicated to blocking restoration or succession (burning pastures, shooting elephants, weeding plantation understory, etc.). To quote an old-time rancher neighbor of ACG in 1986, "Of course the forest will come back if you let it. Why do you think we burn the pastures?"

The ACG dry forest landscape, and that of the more wet ecosystems to the east, are restoring themselves (Janzen 2000a, 2002) as hunting, logging, burning, grazing, and farming have been removed and the wild population fragments allowed to re-invade and re-occupy their former terrain. But there was a very human-generated underlying condition. While ACG had suffered more than four centuries of European-style intervention, and in select sites, as mentioned earlier, millennia of indigenous peoples' intervention, it is generally a quite inhospitable place for ranching and subsistence agriculture. Below much of its dry forest were truly poor soils, some of the worst in Costa Rica—both recent and unweathered volcanic soils below the dry forest in general, and mineral-rich serpentine in Santa Elena. ACG was very far from the centers of social and political power, and from markets in both Nicaragua and the Meseta Central of Costa Rica (though the production of beef for the *indigo* farms of El Salvador and mules for the cross-isthmus transport from the Río San Juan or Lago Nicaragua to the Pacific, and the Inter-American Highway in the 1940s did generate major ranching impacts). Its volcano slopes are steep and wet with rain and fog/clouds. It had no big navigable rivers, but instead many small rocky ones, and none at all in the Mesa Santa Rosa. Exploitable indigenous labor appears to have been generally minimal by the time of original European colonization. All of these things, as mentioned earlier, are reflected in the colonial archives in Granada, which indicate that Hacienda Santa Rosa had more than 40 different owners over four centuries, an ownership turnover that is fully congruent with the observation that despite the enormous impact of European uses, they were very far from thorough—far less thorough than the uses experienced by large holdings on good soil and climate, and near social centers, that would be owned by a several-generation family lineage.

As a consequence, until as recently as 1965–1985, the Mesa Santa Rosa, and its surroundings, contained fragments of populations of easily 99% of the species that were present when the Europeans arrived (only the giant anteater, *Myrmecophaga tridactyla*, is known to have been lost). These surviving species were intermingled throughout in an extremely diverse mosaic of different ages and histories of incomplete ecosystem damage (though some of the pastures and former fields were many hundreds of hectares in area and many individuals and populations were "living dead"). The dry forest area of ACG was dotted with single trees, small patches of secondary forest, wooded ravines, and rocky slopes (see Fig. 10.9). The more wet forests on the western volcano slopes were bullet-holed by 1–300 ha pastures or fields, but these were often bordered by equal-sized expanses of forest that were either unlogged, or had been only high-grade logged and then ignored. It was as though a hurricane had passed through. On the eastern and northern rain-forested volcano slopes, the same was true but even larger expanses were covered by old-growth or only high-grade logged forest without subsequent ranching or cultivation.

During the original focus in 1985 on restoring the dry forest of Sector Santa Rosa (well before we understood the importance of incorporating the wetter forests of the Cordillera de Guanacaste and beyond), the most self-evident management decision was to stop/eliminate the man-made fires (Janzen 2000a, 2002). In 1986–1988, minimalist experiments in tree planting in pastures were tried, but it became immediately obvious that when confronted with 60,000 ha of pasture with scattered dry forest remnants, the correct use of budget and administrative resources was not in planting trees, but rather in stopping the fires and letting nature do the reforestation. The policy quickly became "let the plant species mutualize with animals and fight it out among themselves, and thereby they themselves determine what species and community composition will eventually come to occupy what particular soil type, slope, moisture condition, elevation, etc." Naturally occurring woody succession into the pastures began as soon as the fires were stopped. However, it was initially discouraging that 3–5 years were required for the woody plants to be tall enough to be generally visible over the oceans of ungrazed pasture and begin to strongly shade out the introduced 1–2 m tall African grasses (Janzen 2002). After this 3–5 year delay, the ACG staff and planning felt that they were unambiguously on the right course and that all the work of eliminating the fires was worth the effort.

This invasion of dry forest pastures—"ensuciarles" (dirty them)—by fire-free woody succession was unambiguously aided by four biological factors, all four of which were generally understood prior to this very pragmatic application of anthropogenic succession ecology (and all four of which are qualitatively different in ACG rain forest pastures).

First, more than 100 species of common ACG dry forest trees, vines, and shrubs have wind-dispersed seeds. There was a continual downwind rain of these seeds from scattered adults surviving at pasture edges. ACG rain forest is characterized by having very few wind-dispersed species.

Second, dry forest vertebrates, nearly all of which are to some degree frugivorous and therefore walking or flying containers of seeds, about to be defecated, spit out, or buried, are generally exposed to heat/sun/dryness in their life cycles. They are therefore generally willing to (or forced to) cross the sun/heat/wind/exposure of pastures (and perch in or below isolated pasture trees), thereby dispersing hundreds of species of animal-dispersed seeds into pastures. Furthermore, their seed shadows are very different from those created by wind and can extend over distances of many kilometers (Janzen 1988c). In this context, some small bird or bat, or even a larger animal (coyote, coati, ctenosaur, opossum, collared peccary, white-tailed deer) that seems of minor conservation importance because it appears to be not threatened with extinction, can be of enormous importance in the restoration process. The same applies to the importance of individual woody plants—very few dry forest species (e.g., only "caoba" [or *Swietenia macrophylla*] and "cocobolo" [*Dalbergia retusa*] of the original invaders in the Santa Rosa restoration process are considered by Costa Rican legislation to be threatened). Rain forest animals in general avoid the sun and harshness of pastures.

Third, the establishing woody plant seedlings encountered the spores of mycorrhizal fungi for their roots in the treeless dry forest pastures, owing to these fungi annually producing wind-dispersed spores in the dry season. Rain forest mycorrhizal fungus spores are generally dispersed by surface ground water flow and therefore generally rare to absent in treeless pastures.

Fourth, while the dry forest juvenile attempting to establish in the "death valley" habitat of a dry forest pasture does encounter severe climate challenges, they are not nearly as different from those inside its "normal" dry forest as are the challenges encountered by a rain forest woody plant juvenile attempting to survive in the full sun and erratic drought of a rain forest pasture.

In the early years of fire control and elimination in ACG dry forest there were three key methods, each of which had their special importance and place in time. First and foremost was the decision to actually put out the fires, both in ACG and sometimes, before the fire got to ACG. This required: 1) funds for minor equipment, and 2) the willingness to realize that something as simple as a broom (better, water-soaked wet brooms, in quantity) and effort could extinguish many kinds of grass fires. Most of them were burning in litter or pasture grass, and not the forest per se. And it required: 3) team-based individual initiative to be permitted around-the-clock with full-time (specialized) staff, with a fire program both responsible for all fire extinguishing and allowed to receive appropriate applause. In other words, fire control and elimination was a "people problem," rather than a biological problem.

Second, for the first time in ACG history, fire-breaks and back-fires were set and managed, often at night. Using fire to fight fire was a reasonable and familiar tool for Guanacaste resident neighbors hired onto the fire team, and setting fire to a national park was not anathema to them.

Third, for large areas of ACG, cattle were left in the brushy pastures for 1–3 years after land was purchased; in the late 1980s there were as many as 7,000 cattle in ACG at the peak time of using cattle as biotic mowing machines (and they even disperse some seeds). They did eat broad leaf plants to some degree, but they saved far more by grass removal (reducing fuel for fire and reducing competition from grass). By far the fastest way to create young woody vegetation (also known as forest invasion) in an ACG dry forest pasture was to have moderate cattle density coupled with full elimination of fire. However, once the woody vegetation had made a firm start at forest restoration, the cattle were removed because they can also maintain the forest in a state of deflected succession through selective browsing and trampling, and because they perturb streams, ponds, marshes, and other water sources. Horses are more complex, both because they are (a) native animals (the horse was evolutionarily invented in the New World); (b) good seed dispersers (Janzen 1981a, 1981b, 1982b) (the guanacaste tree, *Enterolobium cyclocarpum*, is going extinct in ACG and throughout much of Guanacaste Province because of horse removal); (c) present in much lower numbers than cattle; and (d) less damaging to watercourses. To make this all yet more complex, however, it needs to be noted that pre-human ACG dry forest had a complement of large vegetarian mammals (and their predators and scavengers) that would have done substantial "damage" to the vegetation and watercourses in what we think of as being pristine old-growth today. No East African waterhole remains clear and clean during the dry season. While it is an easy decision to exclude cattle once the woody restoration process is well on its way, there is an argument to be made for having a sector of ACG dry forest with free range horses and some kind of artificial predation to hold their numbers at a reasonable level, just as we would do if someone were to discover a population of ground sloths today.

In general terms, the Santa Rosa dry forest invades (and invaded) the abandoned pastures by creeping in downwind from the upwind side of the pasture. The accidents of what species of what age happens to be growing on the upwind side thereby influences the nature of the succession invasion for centuries to come. The other form of invasion is the gradually enlarging patch of animal-dispersed vegetation that accumulates below and next to a single large tree in a pasture (Janzen 1988c). Again, the accidents of which particular species of dispersal agents happen to be visiting a particular perch or shade tree will determine the structure of the resulting forest for centuries.

These two invasion processes gradually merge as the woody vegetation takes over the pasture. And, as the forest becomes shadier and denser, there is more lateral movement by larger and more ground-bound vertebrates that bring larger seeds, many of which are seeds of seemingly evergreen species of trees (e.g., agoutis as seed dispersers, Hallwachs 1986). This in turn begins the centuries-long process of recovering the largely evergreen to semi-evergreen aspect of the forest that once clothed Mesa Santa Rosa. In short, the initially invading forest is almost entirely deciduous during the long dry season. The exception is when a coyote (*Canis latrans*) goes into the forest and eats fallen fruits of *Manilkara chicle* (a long-lived seemingly evergreen tree), and then defecates their seeds in the shade of an isolated pasture tree. This eventually creates a very shady spot in the regenerating deciduous forest. This secondary forest, made of species with a) fast-growing and light-demanding seedlings, b) annually-produced large crops of small seeds, and c) relatively short-lived trees, is the first owner of the terrain previously occupied by a semi-evergreen forest (removed by logging or simply clearing). The final old-growth forest, almost unknown to the residents of Guanacaste Province but easily accessible in the Bosque Húmedo of Sector Santa Rosa, contains all these species but at much lower density and intermingled with 5–15 species of apparently evergreen canopy trees (they really are not evergreen, but drop and replace their leaves over just a few weeks at a species-idiosyncratic time of year, and therefore seem to be evergreen, as described earlier for *Hymenaea courbaril*).

As a pasture fills in with rapidly growing juvenile woody plants (large numbers of individuals of the same species), there are several very visible consequences. First, these juveniles are largely non-reproductive, which means that the site is very poor in food for the many species of ACG seed predators and fruit feeders—an ocean of young forest can be a desert for them. Second, the growing vegetative parts that are potential food for browsers are literally moved too high for the ground-bound animals to get to them, and rendered much harder for the ground-bound observing human being to see them when they are being eaten. The consequence is that the biologist, tourist, or manager may feel that a species of animal is becoming rare when it may have simply moved up and out of sight (as well as its population becoming "diluted" among the ocean of juvenile plants). Third, many species of herbs, low shrubs, vines, and even stunted larger woody plants are no longer insolated near ground level (as they were before when living on the pasture edge). They either go locally extinct or persist as the few and relatively invisible individuals that make it into the generally rising canopy (where they may continue to reproduce, but be nearly invisible to the ground-based observer). Fourth, for both shade and disease causes that are not understood, the wave of surviving juveniles (which largely later die through competition and herbivory) that appear in the pasture when the fires are halted does not continue to annually appear in the understory of the successful adults now reproducing in the canopy. For example, it is very striking to encounter a large and somewhat widely spaced stand of adult guacimo (*Guazuma ulmifolia*) trees filling an old pasture and now generating billions of viable seeds annually, yet having no juvenile guacimo growing in the mottled shade below or even in the clearings created by adult deaths or other species in between the adult *G. ulmifolia*. It is likely that this is because the soil saturated with germinating seedlings of this species quickly becomes a killing zone due to a population explosion of lethal fungi specific to that species of seedling. This phemenon is very visible below large-seeded guanacaste trees, where no seedling survives past about 50 cm in height, and surviving seedlings require a seed disperser to drop them relatively far from a seeding adult.

The initial ACG fire-control/elimination program was and still is not perfect. While most of ACG dry forest and accompanying pastures/fields has not been burned since 1984–1986, a few areas have been burned at 2–10 year intervals, and yet fewer more frequently.

The relationship of the occasional fire to the succession process is highly variable, but in general the longer the site goes without a fire, the more shade there is and therefore the less herbaceous vegetation there is at ground level to fuel a dry season fire. Very low quality soils (e.g., volcanic tuff, serpentine) restore their forests the slowest of all, with the consequence that they can remain as "open vegetation" when impacted by a fire only every few decades, while high quality and more moist soils can re-vegetate with woody plants so rapidly that now after two decades without a fire they are almost unburnable (and certainly a litter fire can be rapidly extinguished in them). In the management goal of not letting fire deflect the process of woody succession, perhaps the most important strategy is to avoid a second fire in the next year in a burned early succession forest. This is because the first fire opens the canopy enough (by the heat killing woody stems, more than by direct consumption of woody plants) to allow substantial herbaceous development low to the ground, which means that the fire in the next year burns much more intensely because it is drier and has more fuel. Second, the first year fire may wound the base of, but not fell, a large tree. The second-year fire then burns in and through the dead wounded area, felling the tree and creating a large tree fall that fills with herbaceous vegetation. Third, the root reserves of a woody plant are often enough to substantially replace the shade-generating leafy crown after a single fire, but the plant is often not able to do this if burned again the next year (Janzen 2002).

The only natural "grasslands" in ACG are those growing on the old volcanic mud flows on the western slopes of Volcán Rincón de la Vieja, and those in swamps such as Punta Respingue at Península Santa Elena. These open areas will eventually be reinvaded by the same kinds of forest as currently occupy the other slopes of the same volcanic complex, if they are allowed to do so by management and climate change over the centuries. All of the grasslands (actually old pastures, sometimes incorrectly called "savannas") on ACG good soils are anthropogenic (and largely occupied by introduced African grasses) and are rapidly filling with many kinds of secondary forest now that the contemporary assault by fire has ceased (though climate change may cause any given hectare to fill to a different equilibrium state than it bore in pre-European times, for obvious reasons).

Those "pastures" on poor soils—for example, those on Santa Elena serpentine, volcanic tuff from Volcán Cacao to Santa Maria to Liberia, or the volcanic core of Cerro El Hacha (Fig. 10.13)—are largely covered with a single species of native grass (*Trachypogon plumosus*) with hundreds of species of herbaceous plants mixed in. These grasslands are being reoccupied by forest much more slowly than are the pastures on high-quality soil. Even with the elimination of man-made fires they will use centuries to shrink back to their former, small and fractured habitat of cliffs, rocky ridges, landslide scars, ravine margins, etc., embedded in closed-canopy forest. It is worth noting that the only "natural" fires in ACG occur when a rainy season lightning strike hits a tree (lightning does not occur in the long dry season). If that tree is in a pasture (especially an ungrazed one), it may well start a pasture grass fire that burns to the forest edge and stops. This event was occasional in the 1970–1980s in Sector Santa Rosa's abandoned pastures. If the struck tree is dead and in forest, the tree may well burn, leaving a pile of white ash where it lay, but the litter (and surrounding vegetation) is too moist to burn past this point.

The ACG pastures in cloud forest, rain forest, and ecosystem intergrades display forest invasion and restoration very differently than has been the experience in the ACG dry forest. If a well-established and clean rain forest pasture is simply abandoned, it often grows a dense waist-deep stand of whichever of tens of species of introduced Old World grasses occupy it, and decades later it is still largely in that condition. Intense or light grazing, plowing, burning, and seedling planting does little to hasten forest invasion, though it eventually can help. The reasons are the four listed earlier: rain forest pastures have almost no wind-dispersed woody plants in their vicinity, are much disliked by rain forest potential seed dispersers, are sprinkled very little with wind-dispersed mycorrhizal spores, and are an extreme microclimate for rainforest juvenile plants. However, by noticing that a rain forest understory develops in the strong shade of abandoned gmelina plantations (*Gmelina arborea* is a verbenaceous southeast Asian tree grown for cardboard fiber and cheap lumber), ACG has successfully removed well-established rain forest pastures by planting them with gmelina as if for a timber plantation, which effectively shades out the grasses, but "abandoning" the plantation 1–2 years after planting. The plantation dies of old age after 10–20 years, and the juveniles do not survive in the plantation's own shade.

All of the problems with mid-elevation rain forest restoration on old ACG pastures are exacerbated with increasing elevation on the western, drier sides of the Cordillera de Guanacaste, but with a new complication. Because the upper elevations are less species-rich, and becoming even more so with climate change, there are yet fewer species to contribute to the invasion of old pastures. The restoration toolbox has fewer tools.

Additionally, on the western slopes of the Cordillera, as the forests were cleared, their more xeric nature and yet more abundant moisture made them prime habitat for lowland Guanacaste dry forest plants and animals to invade. This invasion gives the wildland-plus-agro-scape mix a drier aspect, a more "dry forest aspect," than the site "should" have. These "weed" species in themselves will also increase the competitive blockage of return by the native rain forest species. On the eastern/northern, and therefore wetter slopes of the Cordillera within ACG, the same process occurs, albeit involving those yet fewer species of dry forest invaders that have moved to the wet side.

For a variety of sociological reasons, the decision to fully protect and restore the marine portion of ACG got a very slow start, and today is approximately where the terrestrial effort was about 1985–1990—there is removal of sport fishing and large commercial fishers, and now only light poaching by artisanal fishers (= marine hunters). Owing to difficult access, the dry forest beaches themselves, at least of the most remote parts of Península Santa Elena, remained about as pristine in their rock formations and contemporary back beach vegetation as any on the Pacific coast of Costa Rica. This became apparent only during the detailed examination (Janzen 1998) associated with the court case for the Hacienda Santa Elena expropriation for inclusion in ACG. Below the surface of the ocean, the exceptionally high biodiversity of Sector Marino survived as fractured and human-hunted populations largely because of the unfriendliness of the area (windy, rocky, current-rich). However, the area was overrun by the desperate fishers pushed south by the wars in Nicaragua in the 1960–1990 period. Since the damage was largely through underwater hunting/poaching, and since marine populations that are only partly impacted seem to display good natural restoration on their own when unmolested, the primary ACG challenge is in continuing the gradual-to-abrupt removal of artisanal hunting from Sector Marino, and letting nature take its course in restoration.

By far the most damaging invasive species in ACG is *Homo sapiens*. For ACG to survive as a conserved wildland (and wild marine area) into the indefinite future it will have to withstand and tolerate a light level of this impact indefinitely (roads, power lines, people presence, trails, buildings, lights, sounds, pesticides, smells, invasive other species, insularization, etc.). This impact is an inevitable cost of ACG being accepted as a full-status social institution within Costa Rica. The next most visible invader, *Hyparrhenia rufa*, or "*jaragua*," the East African pasture grass introduced to Costa Rica in the 1920s, has been found to be a trivial challenge as woody vegetation restores itself throughout ACG dry forest on the "good" soils occupied by *jaragua*. This is simply because *jaragua* is very susceptible to shade. Poor soils are "invaded" by *Trachypogon plumosus*, which is apparently native to natural disturbance sites in ACG dry forest. However, this species also dwindles to trivial presence as woody vegetation reappears (more slowly) on poor soils. The rain forest and cloud forest portions of ACG are strongly invaded by an array of African pasture grasses and several hundred species of Guanacaste dry forest plants and animals, but these also dwindle to zero or very close to it as the forest restores itself or is restored with gmelina, except in roadsides, buildings, and other sites that are deliberately kept open.

The generally observed inability of introduced garden plants and animals to invade undisturbed mainland tropical ecosystems is in full play in ACG, with the dry forest itself showing many examples of human-associates hurtling into local extinction in ACG dry forest wildlands now that their nurturing humans have been removed (e.g., *Musa, Citrus, Cassia grandis, Enterolobium cyclocarpum, Spondias purpurea, Persea americana, Hyparrhenia rufa, Vachellia farnesiana, Crescentia alata*, *Acrocomia aculeata*, etc.).

ACG island habitats are a different matter. The super abundant *Rattus norvegicus* population on Isla San José of the Islas Murciélagos in Sector Marino, yet absent from the mainland as a wild animal, is a conspicuous example. However, the mainland ACG is probably due for multiple invaders that are not so easily removed as was *jaragua*. For the past ten years, ACG staff have noticed a growing population of the introduced African terrestrial orchid *Oeceoclades maculata* in the understory of lightly disturbed vegetation on the dry forest—rain forest intergrade in Sector Orosí at 400–600 m elevation and hence towards the Pacific in the dry forest. This plant could become a major ACG weed since it is a widespread invader, apparently tolerant of many ecological circumstances, not removed by shade, and with no visible herbivory.

The Africanized honeybee (*Apis mellifera*) invasion swept through ACG dry forest in 1984, built up to high density (1986–1988), and has now shrunk to be almost non-existent but persistently present at very low density—it is unknown how many species of native stingless or other bees it has competitively impacted. While this bee is now an established member of the ACG wild fauna, its impact appears to be not much other than that of an equal volume/weight of some single other social bee species.

A very large question mark hangs over the head of the Old World tilapia fish (*Oreochromis* spp.), which has been deliberately and accidentally introduced into Costa Rican wild rivers, ponds, and streams. Tilapia has been found in the Río Tempisquito above the Inter-American Highway but other species of fish and aquatic insects are also still present. While the potential impact of tilapia is huge, the actuality is unknown and not being monitored. Trout (*Onchorhynchus* spp.), widely introduced with disastrous impact on stream biodiversity in other parts of Costa Rica, have (thankfully) not yet appeared in any ACG waters. The most terrifying potential at the moment is the Indian mongoose that has been introduced and established in northern South America (Hays and Conant 2007). Should this animal expand northwards through the agroscape to Costa Rica and points north, it would be a major disaster for the very large number of species of ground-nesting vertebrates everywhere in Costa Rica, with ACG ecosystems being no exception.

ACG, its dry forest, and its adjacent, other three ecosystems are overall challenged, though to different degrees, by the three most important (today's) challenges facing all of Costa Rican wildland biodiversity—conversion of unprotected vegetation into the crop called biofuels, climate change, and apathy (the fragmentation challenge to ACG is somewhat healing itself through massive restoration of the vegetation between the fragments). Apathy can be truly approached only through dissemination of information and experience about ACG wild biodiversity to all social sectors, and encouragement of all of society to make non-damaging use of it both through knowledge and direct hands-on experience (e.g., the invention of cheap personal DNA-based identification devices, Janzen 2005, Janzen and Hallwachs 2011, Janzen et al. 2005, 2009, 2011, Holloway 2006). The ACG Programa de Educación Biológica (PEB) for all 2,500 neighboring school children (and more programs like it for adults) is a very direct, one-on-one, and two-decades-old example, consuming 20% of the ACG annual budget. At the other end of the scale lie general articles (e.g., Miller et al. 2006, 2007) such as this chapter, designed for all kinds of users, including being translated into Spanish for the ACG staff itself. Scientific papers and web-based information (http://www.gdfcf.org; http://www.acguanacaste.ac.cr) are off on a third axis.

Climate change can really be combated by ACG itself only through (a) restoration of its ecosystems, a process that is moving ahead about as fast as nature will perform, (b) the ongoing purchase of more, and more diverse, terrain (especially to the east and the slopes of the volcanoes) for addition to ACG (e.g., http://www.acguanacaste.ac.cr, http://janzen.bio.upenn.edu/caterpillars/RR/Rincón_rainforest.htm, http://janzen.bio.upenn.edu/saveit.html, http://www.gdfcf.org), (c) through minimizing humans' direct impact on the most fragile parts (such as minimizing trail systems through cloud forests and controlling camping in back beach areas), and (d) having an intellectually top-quality staff who are local residents and socio-economically integrated with the neighboring communities.

Noah's Ark functions for species seeking shelter from climate change, through deliberate transfer from elsewhere, will need to be very carefully weighed against the potential damage by these native yet introduced species (Thomasa 2011). Such Noah's Ark operations also must take into account that the warming and drying through climate change also allows lowland species to move into higher elevations and thus contract, build, or disrupt new associations of prey, parasites, mutualists, commensalists, and other forms of symbionts.

Potential conversion of explicitly unprotected wild vegetation into biofuels is the new problem on the horizon of all of Costa Rican, and global, conservation. The agro-scape surrounding ACG is certainly not immune to this social problem. In the absence of the biofuel mania sweeping the globe, ACG had at least a chance to compete with all the more classical uses of the agro-scape when purchasing new lands for inclusion. In the face of general abandonment of the agro-scape surrounding ACG, it is both that large areas have been left in a semi-wild (often regenerating) forested condition, and lands with little classical agronomic yield are happily sold for conservation at reasonable prices (unless they lie on the evermore popular coastal regions favored by tourism and second home development). The ACG complex of interwoven ecosystems has been constructed through such purchases over the past two decades. The semi-abandoned and regenerating portions of this agro-scape also sustain larger wild populations of some species than would be the case if the only habitat available to them were to be the ACG.

Standard agroindustry (oranges, melons, sugar cane, palm heart, pineapple, rice, improved pasture, tuber crops, etc.) is moving in on these lands with noticeable velocity. However, their general agricultural inviability (without major investment) prior to the appearance of biofuels is their true protection, especially in a world where fewer and fewer people chose to live as hard-scrabble subsistence farmers without the benefits of urban and middle-class society. This is largely owing to Costa Rican education, improved communication and transport, and democracy at all levels. Biofuels derived from free-growing wild biomass are now reaching the technical and investment level whereby every patch of wild vegetation is potentially a crop, with ethanol or even gasoline (Wald 2012) being the harvest product and the more than one billion global automobiles being the consumer. This is now raising the cost of land purchase for conservation and will greatly decrease the amount of agroscape left in a semi-wild state. This in turn means that ACG is ever closer to the final size and configuration that it will have in the future, an ecological island surrounded by an ever more biodiversity-unfriendly ocean of high-investment agroindustry for both classical crops and the crop of ethanol/gasoline derived from wild biomass.

Anthropogenic Succession and Distorted Population Dynamics

ACG dry forest vividly displays a problem that has long plagued field ecologists and evolutionary biologists, to say nothing of conservationists, bird watchers, hunters, and all other users of wild biodiversity. Its hundreds of thousands of species interacting in a single place have morphological, physiological, behavioral, etc. traits that evolved through interactions with yet other species, and through interactions with an array of other physical conditions, to say nothing of other geographic places. While the specific partners in that evolutionary history, or their ecological surrogates may or may not be present in a present-day old-growth ecosystem, there is certainly some array of participant demographics and traits that is characteristic of an old-growth ecosystem. There are some relatively intact (also known as "old-growth") tropical forest ecosystems that do exist, or have existed recently, from which an idea of these arrays can be gained. However, the dry forest ecosystem in general, and specifically the dry forests of ACG and other parts of Costa Rica, are not blessed with such a "gold standard" against which to measure and contrast the interactions that we see today. For ACG dry forest, we are looking at the consequences of a massive short-term and man-made random or haphazard perturbation that has been in motion for the past four centuries (to say nothing of the previous perturbation of the extinction of the megafauna, a kind of animal that has always been present to some degree except on islands). There is a very poor match between the demographic and community structure of today's dry forest inter- and intraspecific interactions, and what these interactions would have been during the evolutionary history of these species.

All of ACG is undergoing successional change following human interference. This began with the extinction of the megafauna 9,500 yr before present (BP) (Janzen and Martin 1982), and for Mesoamerica, only Baird's tapir (Figs. 10.26, 10.27) survived. This extinction severely altered many animal-plant interactions that were based on the megafauna and the species and vegetation that they dispersed, crushed, ate, and otherwise "disturbed" (e.g., Hallwachs 1986, Janzen 1985b). We can only lightly infer the successional changes that occurred following this extinction, but it would have involved dramatic shrinkage of many populations, and shrinkage of their microgeographic and ecosystemic coverage, for a wide variety of megafauna-dispersed and megafauna-enhanced plants. These would have ranged from small-seeded herbs (Janzen 1984b) to large-seeded trees (Janzen 1982b,1985b, Janzen and Martin 1982). The opposite would have occurred as well. Heavily browsed species would have taken on increased density and ecosystem occupation once released from this herbivory. All these changes are mirrored in the dramatic changes in community structure and species densities that take place in contemporary African habitats when the modern megafauna is extinguished, and in modern ACG pastures when cattle and horses (and fire) are removed.

The ACG Pleistocene megafauna-free communities were then gradually impacted by indigenous users (e.g., Titiz and Sanford 2007) and very intensively impacted by four centuries of European brutality, before being allowed, beginning around 1985, to begin the multi-century process of succession, back to something. Tropical biology as we know it today is essentially entirely based on our perceptions of the norm as derived from observation of population densities, population distributions, and community structures in this highly perturbed state. Now that the terrain of ACG has been designated as a conserved wildland into perpetuity, succession will generate, and is now generating, very different densities, distributions, and structures.

A portion of this phenomenon is illustrated by the conspicuous changes in the population density (and microgeographic location) of ACG dry forest organisms over the past two decades of succession, roughly beginning with the elimination of man-made fire, further logging, cattle, and hunting in the mid-1980s. Irrespective of location within ACG, there is a general decline in the size of many animal populations throughout ACG dry forest (and perhaps throughout adjacent wetter forests, but densities have always been so low there that a decline is harder to detect). How much is due to climate change, how much is due to introduced diseases, how much is due to successional changes through forest restoration, how much is due to ACG and specific ecosystem insularization, and how much is due to synergism (or the lack of it) among these major forces is unclear. Furthermore, the amount of on-site, detailed and multi-year observations and experiments that it will take to tease out the "why and how" is so large that it will not be done during the lifespan of the major successional changes taking place now.

Perhaps the most easily observed is the conspicuous decline in density and ecosystem occupation of many species of dry forest plants as human impacts are strongly reduced. For example, in the 1960s to 1980s, and presumably for several centuries before this, the ACG dry forest ant-acacia (*Acacia collinsii*, now known as *Vachellia collinsii*) with its three species of obligate mutualistic *Pseudomyrmex* acacia ants ("*hormiga del cornizuelo*") (Belt 1985, Janzen 1983c), were very common plants in pastures, pasture-forest interfaces, roadsides, and "naturally disturbed" sites such as tree falls, landslides, ravines, and cliffs. Today the overall density of this plant (and therefore its ant colonies) in ACG is not more than 5% of what it was 20 years ago. The surviving population of ant-acacias has a very high proportion of senescent old individuals, and juveniles are very rare even in both natural and man-made disturbance sites (many of which were colonized previously by seed flow from anthropogenically disturbed sites; e.g., Janzen 1983d). It will not be surprising for the plant to be extinct within-ACG, or nearly so, fifty years from now. Heavy shade created by the closed and rising canopy severely weakens the few *V. collinsii* that germinate and are fortunate enough to acquire a healthy *Pseudomyrmex* colony (just as was found to be the case with the ant-acacia *Vachellia cornigera* in remnants of Guanacaste-like dry forest and pasture in Veracruz, Mexico; Janzen 1967b). There may also be a major decline in the density of fruit-eating bats (*Corollia perspicillata*, *Glossophaga soricina*) and magpie jays (*Calocitta formosa*), all of which were major seed dispersers for ant-acacias (as well as many other species of plants), when there was a massive community of frequently disturbed sites filled with early succession fruit-bearing herbs, vines, shrubs, and trees in ACG dry forest.

Many other ACG dry forest early successional species are "suffering" the same decline in density as are *Vachellia collinsii*—*Casearia nitida* (known as *Casearia corymbosa* in earlier literature), *Cochlospermum vitifolium*, *Senna pallida* (known as *Cassia biflora* in earlier literature, e.g., Janzen 1980), *Senna atomaria*, *Bauhinia ungulata*, *Malvaviscus arborea*, *Cayaponia racemosa*, *Ipomoea digitata*, *Sida acuminata*, *Byrsonima crassifolia*, *Sida* spp., *Vachellia farnesiana*, and even *Guazuma ulmifolia*. However, guacimo (*G. ulmifolia*) can grow to a tree as much as 20 m in height and persist in at least some pasture-to-forest succession for 100+ years. Some of the disappearing species were very directly dependent on cattle, horses, and people for their maintenance as a "population" in ACG dry forest (e.g., *Enterolobium cyclocarpum* [the introduced national tree of Costa Rica and the namesake for Guanacaste Province], *Crescentia alata*, *Spondias purpurea*, *Cassia grandis*, *Vachellia farnesiana*, and *Vachellia cornigera* [an ant-acacia of wetter areas, such as the margins of Palo Verde swamp in Área de Conservación Tempisque, and even there may have been introduced by cattle brought from Mexico centuries ago]). These pasture associates are/were so omnipresent throughout Costa Rica's dry forest agro-scape that they are thought of as characteristic members of the dry forest of Guanacaste Province. However, they may largely or totally disappear from dry forest in the absence of manmade disturbance (just as they probably did with the initial disturbance of extinction of the megafauna).

Future generations will discover what are the predominant ACG dry forest species after several centuries of succession, and which species drop out entirely or are restricted to a few scattered peculiar and perpetually disturbed sites (probably on steep slopes and ravines). However, it is even now abundantly clear that the density and community structure components of animal-plant interactions will be very different once the ACG dry forest is again a relatively "natural" community. For example, in the 1980s and earlier it was the norm to encounter healthy, large acacia-ant colonies of all three species in any ACG dry forest habitat, though there was a slight bias towards *Pseudomyrmex flavicornis* being more abundant in very insolated sites and *P. nigrocinctus* and *P. spinicola* being more abundant within shady young forest. Each of these three species was probably the competitive dominant in some particular kind of naturally occurring disturbed site (e.g., tree falls, versus cliffs and landslides, versus watercourse margins), but anthropogenic disturbance had leveled the playing field by offering the brushy pasture to all. Today, the distinctive black *P. flavicornis*, the most sun- and heat-tolerant species, is nearly extinct following three decades of succession.

A particularly noticeable aspect of dry forest succession following massive manmade disturbance is the re-emergence of interdigitating tongues or peninsulas of wetter, more evergreen, forest extending out from the evergreen rainforests bordering ACG dry forest on its eastern margins (Janzen 1986a, b). However, this phenomenon is simultaneously being extinguished by the general drying of ACG dry forest as expressed in such things as the post-1980 disappearance of "rain forest and sometimes dry forest species" from the Bosque Húmedo in Sector Santa Rosa. For example, the following animals and plants were there but now appear to be missing or almost so: *Anolis biporcatus*, *Ochroma lagopus*, *Ceiba pentandra*, *Banara guianensis*, *Piper marginatum*, *Piper psilorhachis* [formerly *P. amalago*], *Cecropia obtusifolia*, *Trema micrantha*, *Muntingia calabura*, *Vismia baccifera*, *Phaenostictus mcleannani*, *Herpetotheres cachinnans*, *Chromacris colorata*, *Biblis hyperia*, *Nasutitermes* sp., *Iguana iguana*, *Nyctomys nyctomys*, *Dasypus novemcinctus*, and *Didelphis virginiana*.

Conclusion

On that sad note we end this discourse on some salient features of ACG dry forest and its immediately adjacent wetter and cooler ecosystems. The biology of the ACG dry forest ecosystem deserves a massive book-length treatment, and a massive website of images and description; one has germinated (http://www.acguanacaste.ac.cr, and see also http://www.gdfcf.org). However, in the urgency of taking the conservation steps to ensure that a maximum amount of it is still with us a millennium from now, most of that documentation and analysis has had to wait. If we expend our energy and effort on that more enjoyable and more academic task, we will then turn around one day and find that what we documented is gone. Yet, if we fail to portray it and make it available to all of society, it will likewise be gone.

Acknowledgments

This essay and the information in its contents have been strongly supported by the staff and parataxonomists of Área de Conservación Guanacaste (ACG) and by ideas and information from many hundreds of natural historians, ecologists, and taxonomists, as well as by more than 9,500 private and government donors to ACG, and by 45 years of generous support of our research and these conservation efforts by the US National Science Foundation (NSF), the Wege Foundation, the Government of Canada, the Biodiversity Institute of Ontario, the JRS Biodiversity Foundation, Permian Global, the University of Pennsylvania, and major private donors.

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