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Fire and forest in the highlands of the Cordillera Central, Dominican Republic : modern dynamics and long-term history

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To the Graduate Council:

I am submitting herewith a dissertation written by Lisa Marie Kennedy entitled "Fire and forest in the highlands of the Cordillera Central, Dominican Republic : modern dynamics and long-term history." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Geography.

Sally P. Horn, Major Professor

We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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We have read this dissertation
and recommend its acceptance:

Kenneth H. Orvis

Henri Grissino-Mayer

Arthur C. Echternacht

Accepted for the Council:

Vice Provost and Dean of Graduate Studies

FIRE AND FOREST IN THE HIGHLANDS OF THE CORDILLERA CENTRAL, DOMINICAN REPUBLIC: MODERN DYNAMICS AND LONG-TERM HISTORY

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Lisa Marie Kennedy
December 2003

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Fund for the Study of World Affairs, and a grant to Sally Horn and me from the Stewart K. McCroskey Memorial Fund in the Department of Geography.

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ABSTRACT

This dissertation investigates past and present environments of the highlands of the Dominican Republic using paleoecological and modern ecological techniques. The relatively unstudied highlands (>2000 m) of the Cordillera Central are blanketed by a mosaic of pine forests, open pine woodlands, and grasslands, with broadleaf trees joining the canopy in sheltered locations. My research on modern vegetation and fire ecology, and on long-term fire and vegetation history, helps fill gaps in the knowledge of Caribbean environments, and may assist land managers in conservation efforts in the Dominican highlands.

A study of the relationship between modern pollen rain and vegetation cover in the highlands provided a basis for interpreting pollen assemblages in sediment profiles. As expected, pine pollen dominated most samples. Detrended Correspondence Analysis indicated that the modern pollen spectra of forested uplands and open wetland sites are clearly distinct, while a variety of other site types that are intermediate in terms of vegetation are also intermediate in terms of modern pollen spectra. Forested sites were widely dispersed, while intermediate sites and wetlands were more tightly clustered, indicating greater similarity in pollen spectra of those sites. Lack of pine stomata was an excellent indicator of treelessness. The distinction between forested and non-forested sites may be useful in interpreting highland fossil records that may reach back into the last glacial period.

Analysis of a 126.5 cm sediment core from a bog in Valle de Bao on the windward slope of the Cordillera Central indicated that disturbances by fire, tropical storms, and climatic fluctuations have been part of the highland ecosystem for millennia.

The bog formed during a relatively moist period around 4000 yr BP. The record includes strong signals of dry periods during the late Holocene, and matches some trends in a sediment record from Lake Miragoane, Haiti, near sea level.

A study of postfire regeneration of pines and shrubs at five recently burned sites provided evidence that the woody vegetation of the pine-forested highlands is well adapted to fire. Most shrubs at all sites resprouted from their bases, and in one site, shrubs regained prefire stem heights within seven years. Recovery of shrub stem diameters lagged behind. Large pines can survive fire, but in this study, no trees <13 cm in diameter survived. Repeated fires may create and maintain a shrub-dominated landscape.

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CHAPTER 1

Introduction and Environmental Setting

The Dominican Republic (17°36'–19°58' N, 68°19'–72°01' W) occupies the eastern two-thirds of Hispaniola, the second largest island (after Cuba) in the Antilles. The island contains a great diversity of habitats that range in elevation from sea level to over 3000 m, and which support a flora that is the richest in the Antilles (Hartshorn et al. 1981). More than one-third of the plant species (~5600) are endemic to the island (Hartshorn et al. 1981). The principal mountain chain on the island, the Cordillera Central, contains the highest peaks east of the western American mountain chains, with several approaching or exceeding 3000 m. This high mountain range situated in the interior of the island essentially constitutes an "island" within an island, harboring unique plant communities that exist under climatic conditions and disturbance regimes that are only beginning to be studied (Orvis et al. 1997, Horn et al. 2000, Horn et al. 2001, Clark et al. 2002).

Mountain environments have sometimes been conceptualized as supporting only "simple" ecosystems (e.g., Chapin and Körner 1995). This view was based mainly on studies of mountain ecosystems at broad scales, and on the general trend toward decreasing species richness with altitude (Haslett 1997). However, recent analyses aimed at interpreting biological and physical landscapes at different spatial scales have fostered recognition of the spatial variability and complexity of mountain environments (Boggs and Murphy 1997, Haslett 1997, Peterson et al. 1997). Plant communities of the Dominican highlands include humid montane broadleaf forest, mixed pine/broadleaf forest, pure pine stands, and treeless grasslands arranged in a mosaic that reflects complex environmental gradients and the history of natural and human disturbances.

These highland landscapes of the Dominican Cordillera Central are important to many people and for many reasons. They contain large numbers of endemic species and most of the forested land remaining in the country. They also encompass the headwaters of important river systems that affect the lives of many Dominicans. The mountain forests stabilize soils, moderate water storage, provide timber and fuelwood to inhabitants, and can play an important role in the conservation of biodiversity as lower elevations are increasingly deforested. Like many mountainous areas in the world (Messerli and Ives 1997), the Cordillera Central is little studied, scarcely managed, and under increasing pressure from human activities.

The ecology and environmental history of the highlands are still little known, especially in the pine-forested landscapes that exist above 2000 m elevation. Though naturalists and scientists have been collecting and observing plants (and animals) in the Cordillera Central sporadically over much of the last century, new species are still being discovered (Mejía et al. 1994, Liogier and Mejía 1997). Vegetation patterns have received little attention, and existing studies are at the broadest scale. Paleoecological records are rare on Hispaniola as throughout the Caribbean region, leaving major gaps in the documentation of past vegetation, climates, and disturbances such as fire. The study of the environmental history of Hispaniola has until recently been limited to analyses of a sediment core from Lake Miragoane, near sea level in Haiti (Brenner and Binford 1988, Hodell et al. 1991, Curtis and Hodell 1993, Higuera-Gundy et al. 1999). This study, and the related work of the larger project of which it is a part (Orvis et al. 1997, Horn et al. 2000, Clark et al. 2002), are the first to document landscape history at high elevations.

It is becoming clear that fire plays an important role in shaping vegetation patterns in the pine-forested highland landscapes of the Cordillera Central (Horn et al. 2000, Horn et al. 2001, this dissertation). Pines with multiple fire scars provide evidence of recent fires (Speer et al. in press), and charcoal in sediments and soils indicate highland fires during the late Pleistocene and at intervals throughout the Holocene (Horn et al. 2000). Questions remain, however, on temporal and spatial patterns of fire, and on fire-vegetation dynamics (Horn et al. 2001). We know that fires burned highland forests in the distant past (Horn et al. 2000), but were fires a consistent disturbance in highland ecosystems before Spanish colonization of Hispaniola? Most highland residents consider fires to be extremely detrimental to montane pine forests, and believe that most, if not all, fires are ignited by people. Is there evidence of prehistoric human influence on fire regimes? Have pines long dominated montane forests, and how do fires affect these forests?

Documentation of past human activities in the Cordillera Central is sparse and even less is known about the prehistory of the area. Even for recent fires, causes and extents are not well known. Fortunately, a very few high elevation bogs and ponds exist in the Cordillera Central that contain sediment records that can help us begin to answer questions about how the montane environments have changed through time; one of them, a bog in Valle de Bao, is the focus of Chapter 3 of this dissertation. Knowledge of the relationships between pollen spectra from modern surface samples and present vegetation can improve understanding of stratigraphic pollen records from these bogs and ponds, and is the subject of Chapter 2. The regeneration of vegetation after fire is considered in Chapter 4, which presents a study of five sites that have burned in the last decade.

This work was part of a larger study, funded by grants to S. Horn, K. Orvis, and M. Clark from the National Science Foundation (SBR-9809798) and the National Geographic Society, which was aimed at documenting the Pleistocene to Holocene environmental history of the larger Cordillera Central region. The specific goals of this dissertation are:

1. To characterize the relationship between modern pollen deposition and vegetation from the study of surface samples, which will inform interpretations of sedimentary pollen records from the highlands (Chapter 2).
2. To characterize the long-term history of forests and fire from evidence contained in a 4000-year-old sediment record from a bog on the windward slope of the Cordillera Central (Chapter 3).
3. To present a body of data on the effects of fire on pines and shrubs that can add to the sparse existing scientific knowledge and improve our understanding of fire-vegetation relationships in the highlands (Chapter 4).

Secondary goals are to draw attention to the uniqueness and importance of the Dominican highlands, and to contribute information on the ecology of these landscapes, especially on the role of fire, that may assist land managers who aim to preserve them.

Dissertation Organization

This dissertation contains five chapters. This Chapter (1) presents a brief introduction to my dissertation work, and a description of the environmental setting of the study area. Chapters 2, 3, and 4 are presented as stand-alone manuscripts in preparation for publication. The study area descriptions in those chapters are brief to reduce redundancy in this document; additional details may be added before submission.

Chapter 2 is an analysis of modern pollen deposition in the Cordillera Central, from sample sites on both sides of the mountain range, especially at elevations above 1800 m. In this study, I examine the relationships between surface pollen and spore spectra and the highland plant communities that they represent. The results have been, and will be, used to inform the studies of sedimentary pollen and spore records from ponds and bogs in the Cordillera Central (e.g., Chapter 3). Chapter 3 presents a paleoecological study of a bog in Valle de Bao on the windward flank of the Cordillera Central. In this chapter, I examine sedimentary evidence of forest history, and of fire and climatic fluctuations over the last 4000 years.

In Chapter 4, I present a study of postfire recovery of trees and shrubs in sites at over 2000 m elevation in the Cordillera Central. In this work, I investigated regeneration strategies and rates of regrowth of woody plants in five sites that burned between about two and seven years before the data collection. Finally, Chapter 5 is a brief statement of the major conclusions of this dissertation work.

Environmental Setting

The northwest-southeast trending Cordillera Central cuts through the central part of Hispaniola extending from northwest Haiti nearly to the capital city of the Dominican Republic, Santo Domingo. It is the island's oldest mountain range, consisting of a Cretaceous plutonic core with accreted sedimentary and metamorphic rocks, and characterized by high relief and poor, shallow soils (Bolay 1997). Containing the highest peaks in the Caribbean, Pico Duarte and La Pelona (3098 m and 3094 m respectively;

Orvis in press) and 23 others over 2000 m in height, the Cordillera Central blocks the northeasterly trade winds, setting up a major division in rainfall distribution on the island. This mountain chain is also the source of most major rivers in the country. It is flanked by the valleys of Cibao and San Juan de la Maguana, which are major agricultural regions.

Three highland parks in the Cordillera Central (Figure 1.1) protect most of the pine forest left in the Dominican Republic, along with patches of humid montane broadleaf forest in sheltered areas. These parks contain the study areas for this dissertation work. Armando Bermúdez National Park (ABNP) encompasses 766 km^2 of rugged terrain on the windward (northern) flank of the Cordillera Central. At the crest of the mountain range, ABNP adjoins another national park of nearly the same size, José del Carmen Ramírez (JCRNP), which includes the leeward (southern) slopes. To do the fieldwork for Chapters 2 and 3 of this dissertation, my colleagues and I entered these two remote parks through trails originating in the village of La Cienega on the windward slope. From there, we followed park regulations by hiring guides to accompany us to our field sites, all of which must be reached by trail, as no passable roads exist beyond La Cienega.

About 60 km to the south of those two remote mountain parks, the Juan B. Peréz Rancier National Park (JPRNP, formerly the Valle Nuevo Scientific Reserve) occupies a high plateau, which is separated from the main part of the Cordillera by a lowland area. Alto de la Bandera (2842 m), the highest point in JPRNP, contains communication towers and a Dominican military installation. JPRNP can be accessed by vehicle on an unpaved road, Carreterra Hector B. Trujillo Molina, which traverses the entire park north

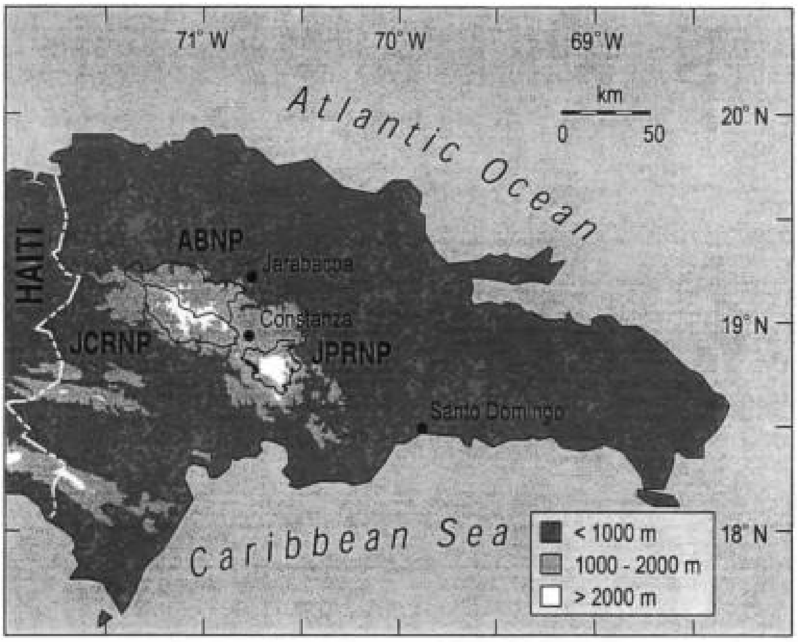


Figure 1.1. Locations of the three national parks of the Cordillera Central, Dominican Republic. JPRNP=Juan B. Peréz Rancier National Park, ABNP=Armando Bermúdez National Park, and JCRNP=José del Carmen Ramírez National Park. The cities of Jarabacoa, Constanza, and Santo Domingo are also shown. Modified from Clark et al. (2002).

to south. Other old logging roads in the park are still passable by 4-wheel drive vehicles in some places. In 1998, however, Hurricane Georges did considerable damage to all of these roads.

Climate

High elevations, mountainous terrain, and a location at the northern limit of modern movement of the Intertropical Convergence Zone (ITCZ) are the primary controls of climate in the highlands. The Cordillera, with elevations exceeding 2000 m along a 60 km front, forms an effective topographic barrier to the northeasterly trade winds that leads to strong contrasts in precipitation on the opposing flanks. Rainfall on windward slope locations (north and east) can be more than double that on leeward slope locations (south and west), which experience a more distinct dry season (Horst 1992).

The trade wind regime dominates in the highlands for most of the year, but weakens with ITCZ proximity in summer, while midlatitude cyclonic storms sometimes reach Hispaniola in winter (Horst 1992). Conditions are typically dry and stable between January and March. Maximum rainfall occurs at elevations below the trade wind inversion, which caps the moisture-laden marine boundary layer at around 2150 m (Schubert et al. 1995). Rainfall weakens above 2500 m and fog becomes an important moisture source for plants (Liogier 1981).

Long-term climate data are entirely lacking for the upper Cordillera Central, with general information deriving from stations at lower elevations, such as Jarabacoa and Constanza (Figure 1.1). Other information, such as temperature minima and frost events, comes from personal observations of park visitors and researchers (including our research team) rather than from sustained monitoring. Horst (1992) estimated that windward slopes receive 1750–2500 mm of rain annually, while leeward slopes receive 625–825 mm. Bolay (1997) estimated 900–4000 mm of precipitation for the highest relief areas around Pico Duarte. In locations above 2100 m elevation, mean annual rainfall was estimated by Hartshorn et al. (1981) to be about 1000–2000 mm.

Records for Jarabacoa, at 529 m on the lower windward slope, indicate an annual average rainfall of ~1500 mm, and at Constanza (1164 m elevation) of <1000 mm (Horst 1992). Tropical storms and hurricanes can, however, produce large quantities of rainfall on both windward and lee slopes in some years, and may skew annual averages. Hurricanes are especially frequent between August and mid-October; records compiled for 1871–1991 indicate that hurricanes can be expected to strike the Dominican Republic every 3.6 years on average (Horst 1992).

Annual mean temperature is 21.5°C at Jarabacoa and 18°C at the higher Constanza station (Horst 1992). Temperatures in the highlands are strongly influenced by topography; annual variation is negligible, but diurnally temperatures oscillate from below 0°C to over 30°C (Bolay 1997). Subzero temperatures occur everywhere in the highlands at elevations above 2100 m (Hudson 1991), especially under clear skies in winter. Snowfall has never been documented, but highland locals report occasional hailstorms, and our research team traveled through driving hail high on the northern flank of La Pelona in 1996. Radiational surface cooling on clear nights produces katabatic cold-air drainage and frequent frosts, especially in cold air traps such as Valle de Bao (~1800 m, Chapter 3). Temperatures as low as –8°C have been recorded in the highlands (Bolay 1997).

Vegetation

The vegetation of the highlands and of other areas of the Dominican Republic has been classified in a variety of ways including the Holdridge Life Zone System (Holdridge 1947; used by OAS (1967)), and other classifications used by the FAO (1973), Liogier (1981), and Tolentino and Peña (1998). Below, I briefly describe the basic vegetation types that occur in the Cordillera Central based on published information (as cited) and field observations. The classification of types is modified from Liogier (1981), and is the same one used in the modern pollen study presented in Chapter 2 of this dissertation.

Humid montane broadleaf forests (HMBF) and mixed pine/broadleaf forests: In many windward sites below 2000 m, and above that elevation in some canyons and other protected locations, a diverse array of broadleaf evergreen species dominates the canopy or shares it with pine (*Pinus occidentalis* Swartz), depending on precipitation, exposure, and substrate (Zanoni 1990), and on disturbance history and successional status. With increasing elevation, the more tropical elements drop out while other broadleaf species are reduced to understory shrubs as the canopy changes (gradually or sometimes abruptly) to one dominated by pine above 2000 m. Humid montane broadleaf forests of the Cordillera Central have received some study (García et al. 1994, Guerrero et al. 1997, May 1997, Mejía and Jiménez 1998), mainly at more accessible sites outside our study area.

Common broadleaf tree taxa include *Dendropanax arboreus* (L.) Decne. & Planch. (Araliaceae), *Oreopanax capitatus* Decne. & Planch. (Araliaceae), *Prestoea montana* (Graham) G. Nicholson (Arecaceae), *Brunellia comocladifolia* Bonpl. (Brunelliaceae), *Clusia rosea* Jaqu. (Clusiaceae), *Weinmannia pinnata* L. (Cunoniaceae), *Alchornea latifolia* Swartz (Euphorbiaceae), *Pithecellobium arboreum* (L.) Urban (Fabaceae), *Garrya fadyenii* Hook. (Garryaceae), and *Myrsine coriacea* (Swartz) R.Br. (Mysinaceae) (Liogier 1981, 1989). The shrub layer in these humid forests includes species in the Myrtaceae, Melastomataceae, Piperaceae, Rubiaceae, and Solanaceae families. Herbs include members of the Cyperaceae, Orchidaceae, Poaceae, and Urticaceae families (Liogier 1981). Pteridophytes are locally abundant on windward slopes. *Pteridium aquilinum* (L.) Kuhn (bracken fern) and *Lophosoria quadripinnata* (J.F. Gmel.) C. Chr. often occur in disturbed areas, and tree ferns (e.g., species of *Cyathea* Sm.) are sometimes prominent on landslides, where they are among successional species (Tryon and Tryon 1982). Diverse epiphytic orchids and bromeliads, together with dense tangles of lianas, give humid montane broadleaf forests the expected tropical appearance.

Liogier (1981), Bolay (1997), and Tolentino and Peña (1998) recognized "cloud forests" as a special type of humid montane forest with permanent high humidity and clouds, and high annual rainfall (approaching or exceeding 4000 mm) that occurs in a few trade wind-exposed sites between ~900–2300 m elevation in the Cordillera Central. Cloud forest vegetation represents ~8% of Dominican forests (Tolentino and Peña 1998), but this forest type is rare in the Cordillera Central, possibly covering only 36 km^2 (Hartshorn et al. 1981). Typical cloud forest tree genera include *Alchornea*, *Brunellia*, *Byrsonima* Rich. ex Kunth, *Magnolia* L., *Ocotea* Aubl., *Persea* Mill., and *Trema* Lour. (Liogier 1981, May 1998). According to Bolay (1997), an abundance of epiphytes (including bromeliads, orchids, and cryptogams), palms (*Prestoea montana*), and tree ferns are good indicators of this very high rainfall zone.

Montane pine forests: Montane pine forests and open or semi-open pine woodlands blanket most of the highlands in the Cordillera Central, especially above 2000 m (Zanoni 1990). Above the broadleaf forests, which reach their upper limits at ~2000 (except in some protected sites), *Pinus occidentalis* is the only species that reaches canopy height. Broadleaf species grow mainly as shrubs or small trees (usually lower than 3 m in height, e.g., *Myrsine* and *Weinmannia*) in the pine forests. Occasional freezing temperatures at most elevations above 2100 m (Hudson 1991) probably play an important role in the shift from broadleaf forests to pinelands at around that elevation. Cold air drainage, even at lower elevations (~1800 m at Valle de Bao, Chapter 3), helps to explain the treeless condition in many topographic depressions in the highlands (Clark et al. 2002).

The structure and composition of the forest understory vary considerably in response to local site factors (e.g., climate, topographic position, substrate) and disturbance history. The forest understory is often dominated by broadleaf evergreen shrubs, many of which occur as canopy trees at lower elevations or in protected areas. Recently burned sites may be dominated by fire-resistant shrubs (rather than pines) and tussock grasses, and are taxonomically and structurally similar to the fire-prone shrub páramos of the neotropical mainland (Horn et al. 2001, and Chapter 4).

Typical shrub taxa include *Garrya fadyenii* (Garryaceae), *Myrica picardae* Krug & Urban (Myricaceae), *Myrsine coriacea* (Myrsinaceae), *Baccharis myrsinites* (Lam) Pers. (Asteraceae), *Weinmannia pinnata* (Cunoniaceae), *Ilex tuerkheimii* Loes. (Aquifoliaceae), and species of *Lyonia* Nutt. (Ericaceae), *Senecio* L. (Asteraceae), *Miconia* Ruiz and Pav. (Melastomataceae), *Cestrum* L. (Solanaceae), and *Fuchsia* L.

(Onagraceae). Ferns such as *Botrychium* Swartz , *Elaphoglossum* Schott ex J. Sm., *Hypolepis* Bernh., *Pellaea* Link, and *Polypodium* L. are also common understory elements (Liogier 1981). *Pteridium aquilinum* and *Lophosoria quadapinnata* are especially abundant in recently disturbed forests.

In some pine stands, the shrub layer is sparse and herbs become more prominent, especially in high-light situations such as in canopy gaps, along streams, and in open woodlands. The endemic tussock grass *Danthonia domingensis* Hack. & Pilger often dominates the herb layer. Other grasses and sedges (especially *Carex* L.) are common along with *Gnaphalium* L. (Asteraceae), *Hieracium* L. (Asteraceae), *Scrophularia* L. (Scrophulariaceae), *Siphocampylus* Pohl (Campanulaceae), *Paepalanthus* Mart. (Eriocaulaceae), *Chamaesyce* Gray (Euphorbiaceae), and *Pilea* Lindl. (Urticaceae) (Liogier 1981, Bolay 1997). Mosses and lichens are common as epiphytes and on the ground, and *Selaginella* P. Beauv. and several species of *Lycopodium* L. are locally abundant. The hemiparasitic shrubs *Dendropemon* (Blume) Rchb. (Loranthaceae) and *Arceuthobium* M. Bieb. (Viscaceae) are common, mainly on pines (Liogier 1981).

On the lee side of the Cordillera Central, semi-open pine forests and open pine woodlands are more extensive. The shrub layer is often sparse, less species-rich, and shorter in height than in windward sites. Many of the same broadleaf taxa occur on both sides of the Cordillera, but on the lee side these taxa rarely attain canopy status.

Mountain peak vegetation: Treeline is not presently reached in the Dominican highlands; pine trees occupy even the highest peaks though they are shorter in stature in the most exposed areas. Thin soils, aridity, strong winds, low temperatures, frost, and high diurnal temperature contrasts result in an extreme environment on the high peaks that limits recruitment and survival of both pines and broadleaf shrubs. These conditions also favor relatively frequent fires (ignited by lightning or humans), and may further restrict survival of young pines. Open woodlands and elfin forest predominate above 2500 m elevation, with a sparse and depauperate shrub layer in most sites. Vegetation in this zone above the trade wind inversion is mainly watered by fog drip and is similar on both the windward and leeward sides of the high peaks. Common shrub species include *Garrya fadyenii* (Garryaceae), *Satureja alpestris* (Urb.) Jiménez (Lamiaceae), *Baccharis myrsinites* (Asteraceae), *Lyonia heptamera* Urban (Ericaceae), and species of *Hypericum* L. (Hypericaceae) (Zanoni 1990). The bunchgrass *Danthonia domingensis* (Poaceae) is abundant.

Non-forested sites: grasslands, bogs, and ponds: Grasslands ("sabanas") in the highlands generally occur on flat to rolling terrain where cold air pooling and/or poor drainage, and possibly a long history of fire (Clark et al. 2002), restrict pine recruitment and survival. The tussock grass *Danthonia* dominates in drier sites, and sedges and other grasses and herbs are more abundant in wet places. Scattered pines are sometimes present in better drained grasslands.

Small bogs are common in poorly drained areas of large grasslands and sometimes in smaller forest openings, and two ponds were located during earlier fieldwork (1996) for the larger project. Bogs and ponds in the highlands support a variety of aquatic species including *Drosera intermedia* Hayne (Droseraceae), *Xyris caroliniana* Walter (Xyridaceae), *Ranunculus flagelliformis* Sm. (Ranunculaceae), *Polygonum hydropiperoides* Michx. (Polygonaceae), *Callitriche heterophylla* Pursh

(Callitrichaceae), and species of *Utricularia* L. (Utriculariaceae), along with sedges and grasses (Liogier 1981).

Natural Disturbance

Highland ecosystems are commonly disturbed by fire, landslides, and tropical storms. Evidence of past fires is abundant in pine-forested areas of the Cordillera, especially in leeward sites. Much of JCRNP burned in an extensive fire in 1997 and much of the isolated plateau encompassed by JPRNP, which is a southeastern extension of the main mountain chain, burned in 1983 (Martínez and Hernández 1984, Martínez 1990).

Slope failures are widespread on the windward slopes due to steep topography paired with high rainfall. They are especially common after storm events and fires. During January 1999 fieldwork in the highlands, we observed ubiquitous evidence of extensive wind damage, slope failures, and flooding related to Hurricane Georges, which struck the Dominican Republic in September 1998. Six other hurricanes have struck Hispaniola since 1955 (K. Orvis, personal communication).

Human History and Societal Issues

The earliest colonists arrived in Hispaniola by about 6000 yr BP, apparently from the Yucatan Peninsula (Wilson 1997a). This first colonization was followed by several migrations from a number of mainland areas and from other parts of the Antilles. The first agricultural society, the Saladoid people, migrated from the north coast of South America through the eastern Caribbean islands into the Greater Antilles around 2500 years ago (Rouse 1992, Haviser 1997). The interactions of these Saladoid peoples with the non-agricultural peoples already present on the islands gave birth to the Taino culture that dominated large areas of the Greater Antilles including Hispaniola at the time of European contact (Wilson 1997b). The early farmers did not begin to move around the rugged interior of Puerto Rico until between 1500 and 1000 yr BP. Their expansion in Hispaniola may have been limited to the eastern tip of the island by the presence of the non-agricultural peoples (Rouse 1992, Wilson 1997b).

The movements of prehistoric people around the island of Hispaniola are still largely unknown. Prehistoric peoples from all periods appear to have depended on some combination of marine resources and on wild and (later) cultivated tropical plants (Petersen 1997). Broad-scale landscape alteration of the highlands by prehistoric people is unlikely due to the lack of game and temperatures too cold to support cultivation of the early staple, manioc. Prehistoric petroglyphs in ABNP (Hoppe 1989), however, attest to at least some human activity in the highlands, possibly for ceremonial purposes. There is some indication that Tainos fled to mountainous areas under the repressive conditions associated with the later Spanish occupation (Bolay 1997).

European settlers arrived in Hispaniola in A.D. 1492, and within a few years had ventured into the central valleys. Though these new inhabitants noticed the mountain slopes covered by thick pine forests, they apparently paid little attention to them for the next several centuries because of the isolation these pine forests (Chardon 1941, Darrow and Zanoni 1990a). Pine forests were essentially preserved, but the island's total forest area has been reduced to less than 10% of its pre-Columbian size (Bolay 1997).

Much of the Cordillera Central apparently remained uninhabited between A.D. 1650 and A.D. 1850 (Kustudia 1998). Historical accounts and photos indicate that clearing of mountain pine forest by slash and burn agriculturalists was occurring in areas around Jarabacoa and Constanza at least by the late 19th and early 20th centuries (Darrow and Zanoni 1990b). Commercial logging began in the early 1900s, but only on small scales due mainly to the inability to transport logs to urban areas (Darrow and Zanoni 1990b). Several sawmills were in operation deep in the pine forests by 1930, and the advent of World War II and the dictatorship of Rafael L. Trujillo Molina brought about massive logging operations in the 1940s (Darrow and Zanoni 1990b, Bolay 1997).

Over the next two decades, Trujillo built access into the mountains and allowed his friends and business associates to cut huge numbers of pines without concern for government regulations or good forestry practice (Darrow and Zanoni 1990b). This poor forest management by the Dominican government drew criticism from the Organization of American States (1967). Trujillo's logging roads opened up the Cordillera Central to exploitation by timber workers and farmers, causing rapid population growth in the highlands (Kustudia 1998). Uncontrolled logging continued after the war, peaked in 1958, then was banned by the government in 1962 (Kustudia 1998). Control of the state forest service, Dirección General Forestal (commonly known as "Foresta"), was transferred to the armed forces in 1967 and enforcement of the law began in earnest (Darrow and Zanoni 1990b). Since that time, cutting of all trees has been illegal throughout the country—even on private land—without government approval (Kustudia 1998).

The two remote mountain parks (ABNP and JCRNP) were established in 1956 and 1958, respectively (Ottenwalder 1989), as pine forest reserves became depleted. The Juan B. Peréz Rancier National Park (JPRNP) was initially protected in 1983 as the "Valle Nuevo Scientific Reserve" and only recently gained status as a national park.

JPRNP is jointly controlled by the military and the national parks directorate. Despite governmental "protection," human disturbances continue in the mountain parks including illegal logging, slash-and-burn agriculture, grazing of livestock, and human-set forest fires, especially at lower elevations near the margins of the parks (Darrow and Zanoni 1990b, Bolay 1997, and personal observation).

The "latifundio-minifudio" system of many small farms and few large estates still predominates in the Dominican Republic (Kustudia 1998), as in many Latin American states. The 1981 agricultural census indicated that 82% of the farms were less than hectares in size, and accounted for only 12% of the agricultural lands (Kustudia 1998). A few wealthy Dominican landlords own the best land and poor peasants are often compelled to cultivate lands with low agricultural potential, such as those in the rugged Cordillera Central. In one important watershed of the Cordillera Central, the Yaque del Norte, which drains much of the eastern and northern portions, some estimates indicate that 80% of the forests (broadleaf, pine, and mixed) have been converted to poor pastures by logging, deliberate burning, and shifting cultivation (Kustudia 1998). According to Kustudia (1998), a number of complex socio-economic issues, not recognized or dealt with by the Dominican government, may underlie a tendency for the rural poor to exhibit animosity toward the mountain forests.

The environmental degradation that has taken place in Haiti is well known in the Dominican Republic, and many Dominicans wish to prevent such a fate on their side of the island. There have been recent efforts to improve management of remaining forests, but recognition of social issues, education, and more integrative management, including community-based conservation, may be needed if these efforts are to succeed (Bolay

1997, Kustudia 1998). The advancement of scientific knowledge, especially in the relatively understudied mountain areas, will also be key to successful conservation.

CHAPTER 2

Modern Pollen Spectra from the Cordillera Central, Dominican Republic

This chapter is in preparation for submission to the journal, *Review of Palaeobotany and Palynology*, by me, Sally P. Horn, and Kenneth H. Orvis. My use of "we" in this chapter refers to my co-authors and myself. The descriptions of the study area presented here are brief and will be augmented with information in Chapter 1 before submission.

Introduction

Paleoecologists working to reconstruct past vegetation and environments from sediment records in previously unstudied areas face the challenge of interpreting "novel" pollen assemblages. The influence of vegetation on pollen assemblages is not straightforward. Because of differences in pollen production and dispersal, some plant taxa are commonly overrepresented in pollen records, while others are underrepresented or not represented at all (Tauber 1965, Prentice 1985, Sugita 1993, Jackson and Lyford 1999). Modern surface pollen and spore spectra can provide key information, and have been widely used to help refine interpretation of fossil pollen samples (Wright 1967, Flenley 1973, Moore and Webb 1978, Birks and Birks 1980, Liu and Lam 1985, Delcourt and Pittillo 1986, Fall 1992a). Surface soils and sediments, and other material such as moss polsters, contain pollen and spores that reflect modern vegetation. The study of these modern pollen spectra can help to identify taxa that are likely to be overrepresented in fossil records, and elucidate other relationships between contemporary pollen deposition and present-day vegetation, in this way strengthening paleoecological and paleoclimatological studies based on sedimentary pollen.

Like most paleoecological research, the vast majority of work on modern pollen spectra has been carried out in temperate regions. In the past decade, however, an increasing interest in modern and past tropical environments has led to expanded work on tropical pollen spectra. Several recent studies have focused on tropical areas of Africa (Vincens et al. 1997, El Ghazali and Moore 1998, Vincens et al. 2000, Elenga et al. 2000), Australia (Kershaw and Strickland 1990, Kershaw and Bulman 1994, Crowley et al. 1994), southeast Asia (Bonnefille et al. 1999, Anupama et al. 2000), and the mainland neotropics (Bush 1991, Islebe and Hoogheimstra 1995, Rodgers and Horn 1996, Bush and Rivera 1998, Bush 2000, Bush et al. 2001, Marchant et al. 2001). In the Caribbean islands, a few studies exist of sedimentary pollen profiles from lowland sites (Hodell et al. 1991, Higuera-Gundy et al. 1999), but modern pollen studies are lacking.

This paper focuses on modern pollen spectra in the Cordillera Central, Dominican Republic. The Dominican Republic occupies the eastern portion of the second largest Caribbean island, Hispaniola. Its central mountain range includes high peaks (two above 3000 m) that exceed any in eastern North America. Our modern pollen samples represent a range of elevations (1200–3000 m) on both the windward and leeward flanks of the Cordillera Central.

Vegetation patterns in the Cordillera Central vary in response to mesoscale climatic factors (e.g., leeward vs. windward position, and elevation). Overlain on these broadly predictable patterns are complex local patterns of community composition, diversity, and structure that reflect the rugged mountain topography and variable disturbance history (e.g., fire history, windthrow due to storm events, human impacts). Forests of the highlands range from humid montane broadleaf forests in frost-free zones, mainly on the windward side, to pure stands of West Indian pine (*Pinus occidentalis* Swartz) in the higher sites, and at lower elevation in poor sites, and in areas that burn frequently or are otherwise successional. In high but protected sites, pines intermingle in the canopy with broadleaf species that in more exposed sites are absent or limited to the understory. Forest understory composition and structure vary locally; understories may be dominated by broadleaf shrubs and ferns, by grasses and regenerating pines, or by something in between. Open pine woodlands are increasingly prominent above 2000 m, and in locations leeward of the crest. Grassy openings, locally referred to as "sabanas," exist mainly in areas prone to cold air pooling and poor drainage. Boggy depressions of variable size (less than 1 ha to several tens of ha) are common features in grasslands.

The dataset of 47 highland surface pollen samples described here was developed to inform interpretation of fossil pollen spectra in highland bog and pond sediments that we are analyzing to reconstruct long-term vegetation and climate history in the Dominican highlands. Sedimentary pollen records from montane regions are often especially useful in climate reconstruction because they are sensitive to short-term and low-magnitude climate shifts that are not represented in lowland records (Gaudreau et al. 1989).

Montane pollen records present special problems for interpretation that necessitate understanding relationships between modern pollen and vegetation. First, steep climatic gradients in mountain environments result in vegetation zones that are packed closely together along elevational gradients. The combination of closely spaced vegetation zones and strong orographic winds results in transport of pollen over long distances, especially upslope (Markgraf 1980), which can make it difficult to recognize vegetation types based on their pollen assemblages (Markgraf 1980, Solomon and Silkworth 1986, Gaudreau et al. 1989, Spear 1989, Jackson and Whitehead 1991, Fall 1992b). Even at a single elevation, extreme variability in local climates in mountainous areas (Barry 1992) brings different vegetation types into close proximity and can further confuse interpretation of pollen records.

Our main objective was to determine whether the modern pollen spectra in the Dominican highlands reflect basic differences in cover type such as those between closed canopy pine forest, broadleaf or mixed pine/broadleaf forest (both including many zoophilous taxa), open pine woodlands, or herb-dominated sabanas and bogs surrounded by pine forest. We expected that the tendency of pine pollen to overwhelm other pollen types (Fall 1992a, Jackson and Smith 1994, Jackson and Wong 1994) would make differentiating the local vegetation mosaic using pollen spectra problematic. Pine produces abundant and well-dispersed pollen that can dominate even other wind-pollinated taxa, and thus may significantly dilute the contributions of pollen of the zoophilous taxa. For this reason, we expected that the abundance of pine pollen might counter any tendency for the pollen of lower montane broadleaf forests to be overrepresented in areas upslope.

If cover types were distinguishable by their pollen spectra, we wanted to establish whether groups of taxa provided “signatures” for vegetation types, or whether particular “indicator” pollen types (Spear 1989) might exist. We also wanted to determine whether differences in the spectra might reflect larger environmental gradients defined by elevation and position in the mountain range.

This study also provided an opportunity to compare samples from different substrates. Ideally, modern pollen samples would come from environments similar to those used in paleoecological studies—in our case, ponds and bogs. Unfortunately, bogs, and especially ponds, are relatively rare in the highlands and do not occur within all cover types for which we wanted to obtain modern pollen data. Along with surface sediments from bogs and ponds, we therefore also included surface soil samples from a range of other site types. About two thirds of our samples were from forested sites, with the rest from grasslands, bogs, a small fen, and two ponds.

Methods

Study Area

Our sample sites are all within the two adjoining national parks, Armando Bermúdez (ABNP; Provincia de Santiago) and José del Carmen Ramírez (JCRNP; Provincia de San Juan) (Figure 2.1, Table 2.1). The parks, with combined areas of ~1500 km^2, are situated in the core of the northwest trending Cordillera Central. They share a boundary along the crest of the mountain range, with ABNP occupying the windward northeastern slopes and JCRNP the drier leeward southwestern slopes. Information on highland climate is included in Chapter 1 of this dissertation.

Fires, landslides, tropical storms, and various human activities disturb highland ecosystems on a variety of spatial and temporal scales. Pines bearing multiple fire scars and patches of regenerating vegetation of different ages provide evidence of recurring fires especially in leeward sites. Slope failures are widespread on the windward flank, and wind damage from tropical storms is a regular source of disturbance. Fieldwork for this study, in January and February of 1999, followed an extensive fire that burned

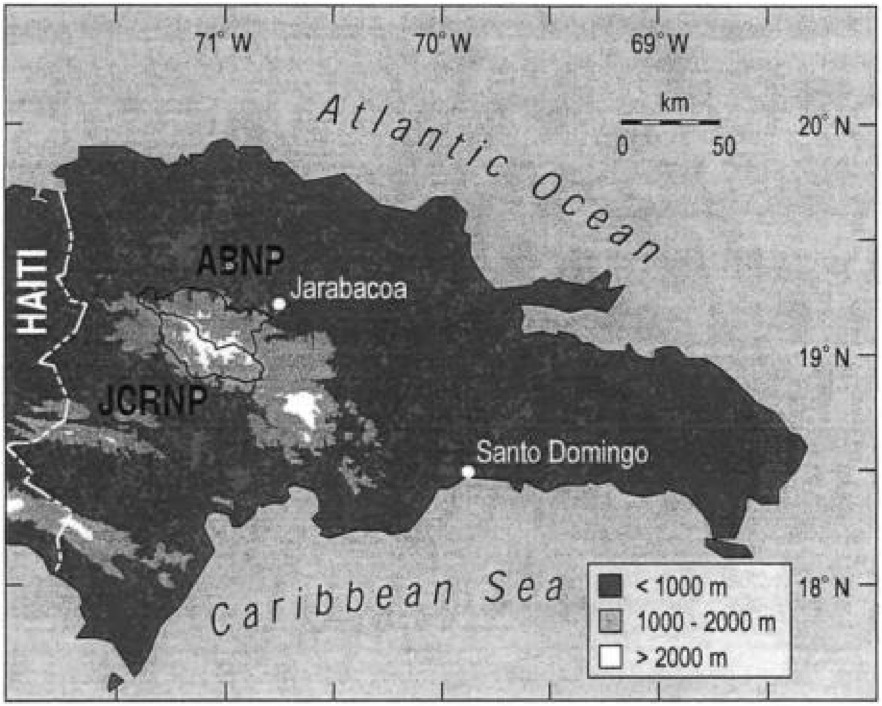


Figure 2.1. Locations of José del Carmen Ramírez National Park (JCRNP) on the southwestern (leeward) side of the crest of the Cordillera Central, and Armando Bermúdez National Park (ABNP) on the northeastern (windward) side of the divide (modified from Clark et al. 2002).

Table 2.1. Provenance of samples used in analysis of modern pollen spectra in the Cordillera Central, Dominican Republic. "Wind" = windward and "Lee" = leeward of the main ridgeline of the Cordillera Central. Vegetation categories are explained in the text. "Sed." = sediment. Latitude and longitude are based on differentially corrected GPS data, with typical one-sigma accuracies of one to five meters. Positions are relative to the 1927 North American datum, Caribbean section, in UTM coordinates, zone 19 north, to match published Dominican Republic 1:50,000 scale topographic maps. Italicized locations were taken directly from topographic maps when GPS data were unavailable. Elevations were estimated from topographic maps. Site order follows the order of samples in the pollen diagrams (Figures 2.3, 2.4, and 2.5). Samples were collected by "random pinch" method except 64 and 65, which were "grab" samples of surface mud under standing water.

Site	**Position**	**Vegetation**	**Sample Type**	**Elev. (m)**	**Northing**	**Easting**
43	Wind	Humid Montane Broadleaf Forest	Soil	1300	*2107330*	*301050*
44	Wind	Humid Montane Broadleaf Forest	Soil	1400	2106942	300839
32	Wind	Mixed Pine/Broadleaf Forest	Soil	1820	2109892	286057
28	Wind	Mixed Pine/Broadleaf Forest	Soil	1825	2107654	286301
29	Wind	Mixed Pine/Broadleaf Forest	Soil	1860	2107638	286525
20	Wind	Mixed Pine/Broadleaf Forest	Soil	1880	2109476	286492
40	Wind	Mixed Pine/Broadleaf Forest	Soil	1980	2107309	287097
19	Wind	Mixed Pine/Broadleaf Forest	Soil	2160	2108792	287237
17	Wind	Mixed Pine/Broadleaf Forest	Soil	2340	2108163	287771
08	Wind	Pine Forest	Soil	1620	2110794	286186
45	Wind	Pine Forest	Soil	1700	2105917	299561
27	Wind	Pine Forest	Soil	1795	2108153	286005
33	Wind	Pine Forest	Soil	1800	2109833	286056

Table 2.1. Continued.

Site	**Position**	**Vegetation**	**Sample Type**	**Elev. (m)**	**Northing**	**Easting**
38	Wind	Pine Forest	Soil	1810	2109822	285909
21	Wind	Pine Forest	Soil	1840	2109649	286283
46	Wind	Pine Forest	Soil	2260	2104777	298077
16	Wind	Pine Forest	Soil	2380	2108049	287797
15	Wind	Pine Forest	Soil	2420	2107847	287899
14	Wind	Pine Forest	Soil	2465	2107835	288022
13	Wind	Pine Forest	Soil	2525	2107534	288326
54	Peak	Wet meadow	Soil	2930	*2108950*	*289400*
04	Peak	Open Pine Woodland	Soil	2980	*2105105*	*290138*
48	Peak	Open Pine Woodland	Soil	3050	2105352	288766
53	Peak	Open Pine Woodland	Soil	3080	*2104380*	*289700*
02	Lee	Closed Pine Forest	Soil	2220	2106565	279028
23	Lee	Closed Pine Forest	Soil	2150	2105939	279540
24	Lee	Closed Pine Forest	Soil	2060	*2105700*	*280250*
31	Lee	Open Pine Woodland	Soil	2020	2105336	281385
37	Wind	Transitional grassland-pine	Soil	1800	2109764	285930
03	Wind	Transitional grassland-pine	Soil	1785	2109250	285592
25	Wind	Transitional grassland-pine	Soil	1780	2108933	285896

Table 2.1. Continued.

Site	**Position**	**Vegetation**	**Sample Type**	**Elev. (m)**	**Northing**	**Easting**
51	Lee	Dry Grassland	Soil	2330	2108241	277786
58	Lee	Dry Grassland	Soil	2320	2107769	277721
22	Lee	Dry Grassland	Soil	2150	2106212	279321
60	Lee	Dry Grassland	Soil	2000	*2105750*	*281400*
35	Wind	Bog	Sed.	1775	2109420	285798
63	Wind	Bog	Sed.	1775	*2109650*	*285850*
36	Wind	Bog	Sed.	1775	*2109600*	*285800*
06	Lee	Bog	Sed.	2230	2106620	278852
55	Lee	Bog	Sed.	2230	2106667	278870
49	Lee	Bog	Sed.	2230	2107012	278620
50	Lee	Bog	Sed.	2330	2108177	277811
56	Lee	Bog	Sed.	2210	2106576	279059
57	Lee	Moist area on pond perimeter	Sed.	2040	2105726	279967
05	Lee	Bog	Sed.	2000	2105875	280465
64	Lee	Pond	Sed.	2040	2105843	280803
65	Lee	Pond	Sed.	2010	2105663	279893

thousands of hectares in JCRNP (and some in ABNP) in 1997. During that fieldwork, we observed widespread evidence of wind damage, slope failures, and extensive flooding related to Hurricane Georges, which crossed the Cordillera Central at Category Four (Saffir-Simpson scale) in September 1998. Human influence on vegetation in the two parks is highly skewed toward the lower elevations, especially around the park's perimeter, and toward areas around the few main trails and campsites.

Vegetation Types and Sampling Sites

Below we list the main vegetation types that we recognized in this study and summarize the sampling performed in each type. Chapter 1 contains descriptions of these vegetation types.

Humid montane broadleaf forests and mixed pine/broadleaf forests: Two of our sites (43 and 44, Figure 2.2) are below 1500 m elevation under a mainly broadleaf canopy. Seven sites, mostly from the slopes above Valle de Bao, have a mixed canopy of diverse broadleaf species and pine. Effective drainage of cold air from steep slopes allows enclaves of humid broadleaf forest taxa to exist as canopy trees at higher than usual elevations (up to ~2400 m) in certain restricted locations; these anomalous broadleaf forests are especially diverse in the canyons, where they are protected from reradiation. Some authors (e.g., Liogier 1981, Bolay 1997) delineate "cloud forest" as a special type of humid montane broadleaf forest that occurs in some mid-elevation wind-exposed sites. We did not make this distinction in our study.

Montane pine forests: We collected 15 samples from pine forests with semi-open to closed canopies formed exclusively by pine (not including mountain peaks >2900 m): 11 from windward sites at ~1600–2500 m, and four from leeward sites ~1900–2400 m.

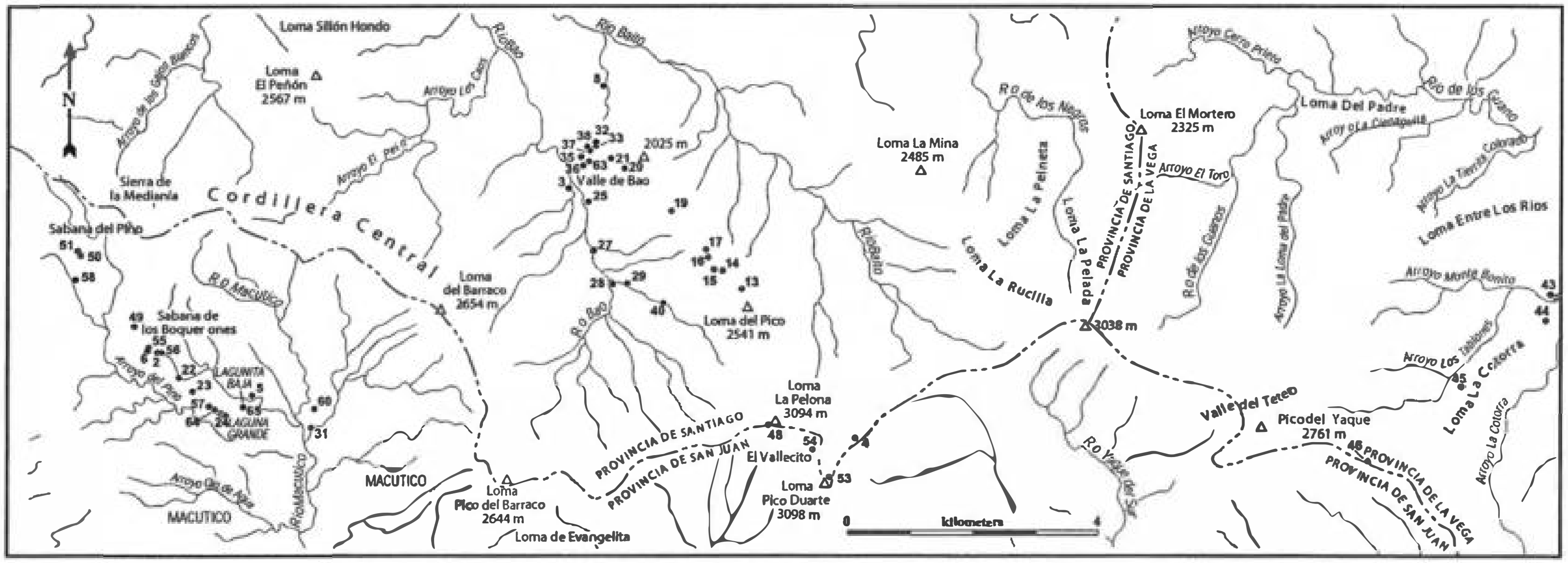


Figure 2.2. Location of modern pollen sampling sites in the Cordillera Central, Dominican Republic.

The 1997 fire burned most of the leeward sites that we sampled. Fire intensity ranged from lower intensity surface fires that reduced the forest understory but spared most canopy trees to intense fires that destroyed the canopy in some sites. Most broadleaved shrubs and *Danthonia domingensis* Hack. & Pilger were resprouting copiously in the burned areas. Dicotyledonous herbs, especially Asteraceae species, were abundant in the high-light conditions produced by loss of the pine and shrub canopy and reduced *Danthonia* stems.

Mountain peaks: Five samples are from above 2900 m near the two highest peaks in the Caribbean, Pico Duarte and La Pelona (3098 m and 3094 m respectively; Orvis in press). One of the five is from a flat, treeless savanna, El Vallecito de Lilis (~2920 m), which occupies the saddle between the neighboring peaks; the others are from forested sites on both sides of the peaks.

Non-forested sites: grasslands, bogs, and ponds: Valle de Bao (~1800 m, Figure 2.1), a 2.5 x 0.3 km trough on the windward slope below Pico Duarte, contains a large grassland likely treeless as a result of cold air pooling and poor drainage. *Danthonia* dominates the valley floor along with patches of *Rubus* L., other grasses, sedges, and herbs. We sampled some of the small peat bogs scattered across the flat-bottomed valley.

Several relatively large named grasslands (e.g., Sabana del Pino and Sabana de los Boquerones) and many smaller unnamed treeless patches are located on the leeward side of the range, in the area labeled on the topographic map as “Macutico” (due west of the ridgeline between Loma Pico del Barraco and Loma del Barraco). We collected samples from both dry grassy areas and bogs within these sabanas. In Macutico, we also sampled two shallow ponds, Laguna Grande and Lagunita Baja, and a small fen, Boquerones. Vegetation in the leeward grasslands appears broadly similar to that of Valle de Bao. In total, four of our samples are from dry open grasslands, 10 are from bogs, and two from ponds.

Transitional grassland-pine vegetation: Three samples are from sites that appeared to be in transition from open grassland to a closed forest situation. These were essentially grassy areas with open stands of young pine.

Field Sampling and Laboratory Techniques

We collected our modern pollen samples using the "random pinch" method of Adam and Mehringer (1975) and following Rodgers and Horn (1996): 10 pinches of the top one to two cm of surface material randomly collected in an area from ~50–100 m^2, and then homogenized in a plastic storage bag. Where the pine duff (or other litter) was deep, we collected material from the litter/soil interface. Surface pollen samples represent a longer (but undetermined, perhaps 5–50 years) period than pollen collected in "traps" (Gosling et al. 2003).

For most sites (wherever possible), our precise locations were acquired using differentially corrected global positioning system (GPS) data, with typical one-sigma accuracies on the order of 2–5 m. We report positions relative to the 1927 North American datum, Caribbean section, in universal transverse Mercator (UTM) coordinates, zone 19 north, in order to match the published Dominican Republic 1:50,000 scale topographic maps. Elevations and positions for which GPS data were unavailable were taken directly from the topographic maps using the UTM overprint grid.

At each sample site, we recorded information on topographic context and position, (e.g., ridgetop), slope and aspect, canopy type, and evidence of disturbance (e.g., windthrow; recent fire; proximity to camps, trails, or human impacts). We also listed prominent plant taxa in each site, and noted particularly abundant taxa in each stratum.

In the laboratory, we first followed a "pretreatment" schedule (Appendix A). The bagged "pinch" samples were mixed thoroughly by massaging the bag. Subsamples of 15–25 cc were removed and soaked in distilled water for 30 minutes, then washed through 250 μm screens to remove coarse organic debris and large mineral grains. The sieved material was centrifuged down and the remaining pollen-rich material stirred well. Two samples (each 1.2 cc in volume) were then removed, one for chemical extraction of pollen, and the other to first determine water content (by drying overnight at 100°C), and then organic content by loss on ignition at 550°C for one hour (Dean 1974). We processed the samples for pollen analysis using standard techniques (HF, HCl, KOH, acetolysis, safranin stain; Faegri and Iverson 1989; Appendix B), adding *Lycopodium* tablets as controls (Stockmarr 1971). Pollen residues were mounted on slides in silicone oil.

We counted at least 500 pollen grains per sample (except for sample 43, which had a pollen sum of 304) exclusive of spores and indeterminate grains. Pollen grains and spores were identified at 400x magnification using pollen reference material from the Dominican highlands and other tropical and temperate sites, and published keys and photographs (Heusser 1971, McAndrews et al. 1973, Markgraf and D'Antoni 1978, Moore and Webb 1978, Hoogheimstra 1984, Moore et al. 1991). Pollen grains representing the order Urticales were classified by pore number, except for *Cecropia* Loefl. In the earliest counts, we did not separate the small tricolporate pollen grains of the broadleaf trees, *Brunellia* Ruiz & Pav. and *Weinmannia* L., so pollen of these two taxa are combined in diagrams.

Unknown pollen grains were sketched and recorded as morphological types. We classified unknown fern spores by morphology. Spores of the native clubmoss, *Lycopodium clavatum* L., were present in many of the surface samples, but we believe that in the vast majority of cases we were able to distinguish it from the control spores that were prepared from the same species. The controls had a slightly shrunken and darker appearance (probably due to effects of processing and age) compared to the native spores, which were brighter, retained true size and shape, and exhibited a broader reticulate pattern. Many samples contained abundant microscopic charcoal but we did not quantify it.

We also tallied pine stomata during our pollen counts. Conifer stomatal guard cells are preserved in surface soil samples and in surface sediment and deep-profile sediment samples long after needles have decayed. They are not destroyed by traditional pollen processing methods, and usually can be identified to genus (e.g., Hansen 1995, Hansen et al. 1996, Parshall 1999, Pisaric et al. 2000). The stomata we found in our surface soil and sediment samples generally matched the morphological description of pine stomata presented by Hansen (1995) for pines in Canada and southern Alaska. For this reason, and because *Pinus occidentalis* is so abundant and is the only conifer that we observed in our sampling sites, we assumed the stomata in our samples to be from that species. Two other conifers, *Podocarpus* L'Hér. ex Pers. and *Juniperus* L., are also present in some highland areas but are rare, and *Pinus caribaea* Morelet is sometimes planted, but we did not observe it in JCRNP and ABNP. Stomata of angiosperms are easily differentiated from conifer stomata by their smaller size and distinctive morphologies (Hansen 1995, Parshall 1999) and are rarely preserved in either stratigraphic sediments (Hansen 1995) or surface soil or sediment samples (Parshall 1999) in temperate areas. We counted only whole, well-preserved stomata.

We plotted the relative percentages of pollen and spores, and stomata to total pollen ratios, using a modified version of CalPalyn (Bauer et al. 1991). We used a modified version of detrended correspondence analysis (DCA) (Hill and Gauch 1980) in PC-ORD 4.14 (McCune and Mefford 1999) to statistically examine the dataset. DCA (Hill and Gouch 1980) is an eigenanalysis ordination technique based on reciprocal averaging (Hill 1973) that ordinates both sites and samples simultaneously. In both modern pollen and vegetation ordinations, the primary axes are often interpreted to represent environmental gradients (Bush 1991, Kent and Coker 1992). The PC-ORD 4.14 software resolves the problem of sensitivity to sample order that was detected by Oksanen and Michin (1997) in earlier versions of DCA. We used a correlation matrix of the pollen and spore taxa and groupings that are represented in our pollen diagrams; all taxa and groupings appeared in at least two sites and had at least one value over 1%. In the case of fern spores, we did not use percentages for "total monolete" and "total trilete" (which are shown in the diagram) because they overlap with other categories of spore data.

Results

Pollen Taxonomy

Relative percentages of the most important pollen and spore taxa are presented in three pollen diagrams (Figures 2.3, 2.4, and 2.5). The samples are arranged in each

Figure 2.3. Percentage diagram for modern pollen and spore spectra of the Cordillera Central, Dominican Republic presenting mainly tree and shrub taxa. Pollen types are expressed as percentages of total pollen excluding indeterminate grains, and pine stomata are expressed as a ratio of stomata to total pollen and spores. Samples are arranged by vegetation type. Leftmost column shows site elevations; windward sites are indicated by bold, italicized site numbers. "Lower Montane Trees and Shrubs" includes pollen of the broadleaf taxa *Alchornea*, *Bocconia*, *Cecropia*, *Cordia*, *Fucshia*, *Hedyosmum*, Melastomataceae, Myrtaceae, *Piper*, Tiliaceae, and *Zanthoxylum*. "HMBF"=Humid Montane Broadleaf forest; "Transitional"= transitional grassland-pine.

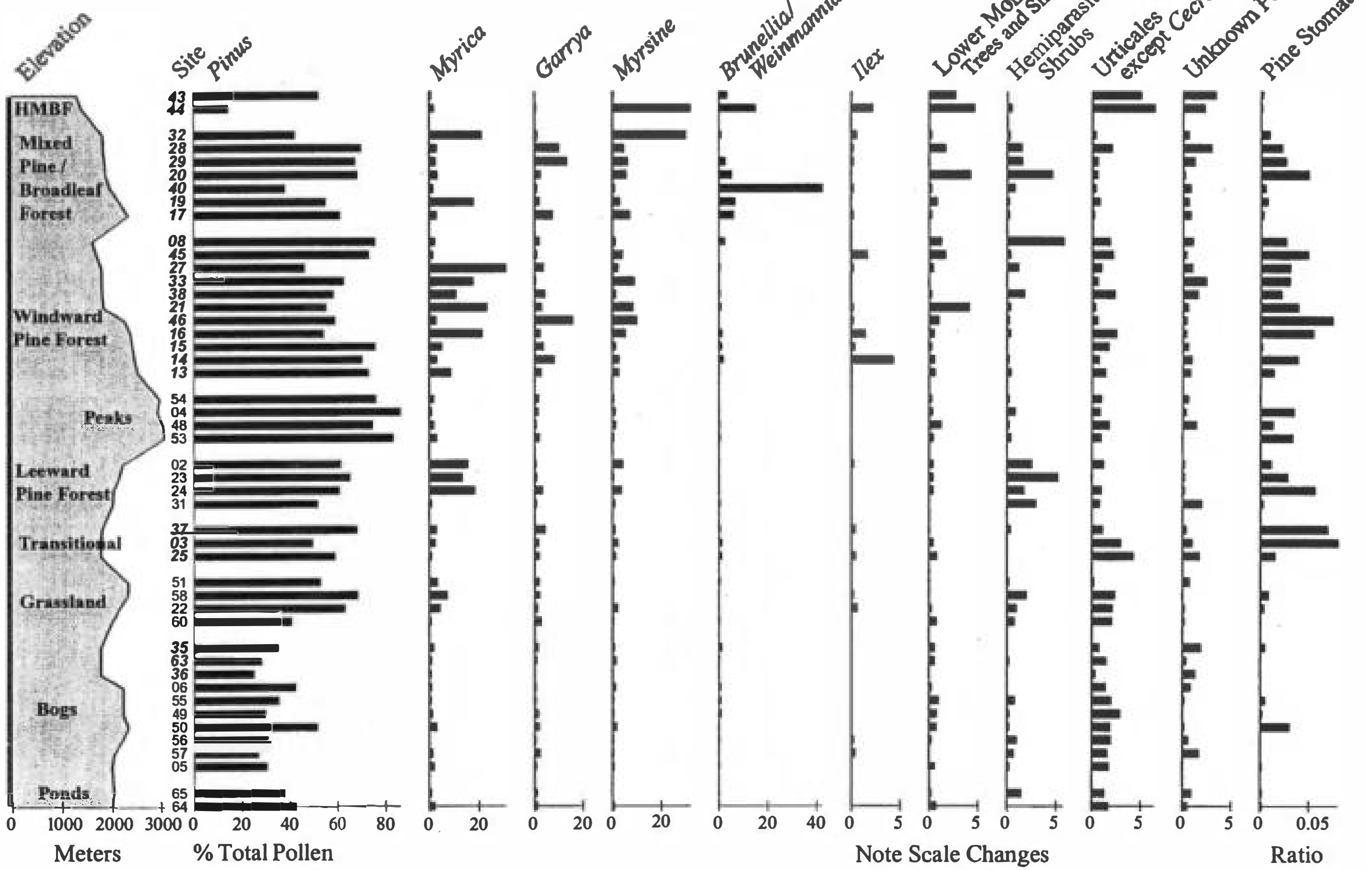

Elevation
Site
Pinus
Myrica
Garrya
Myrsine
Brunellia/ Weinmannia
Ilex
Lower Montane Trees and Shrubs
Hemiparasitic Shrubs
Urticales except Cecropia
Unknown Pollen
Pine Stomata
HMBF
Mixed Pine / Broadleaf Forest
Windward Pine Forest
Peaks
Leeward Pine Forest
Transitional
Grassland
Bogs
Ponds
43
44
32
28
29
20
40
19
17
08
45
27
33
38
21
46
16
15
14
13
54
04
48
53
02
23
24
31
37
03
25
51
58
22
60
35
63
36
06
55
49
50
56
57
05
65
64
0
1000
2000
3000
Meters
0
20
40
60
80
% Total Pollen
0
20
0
20
0
20
0
20
40
0
5
0
5
0
5
0
5
0
5
Note Scale Changes
0
0.05
Ratio

Figure 2.4. Percentage diagram for modern pollen and spore spectra of the Cordillera Central, Dominican Republic presenting mainly herbaceous taxa. Pollen types are expressed as percentages of total pollen excluding indeterminate grains. Samples are arranged by vegetation type. Leftmost column shows site elevations; windward sites are indicated by bold, italicized site numbers. "Rubiaceae herbs" represents three recognized pollen genera: *Galium*, *Mitracarpus*, and *Spermacoce*. "Other herbs" includes *Hydrocotyle*, *Ranunculus*, *Verbena*-type, and *Utricularia*. "Aquatics" includes *Elodea* and *Nuphar*. "HMBF"=Humid Montane Broadleaf forest; "Transitional"= transitional grassland-pine.

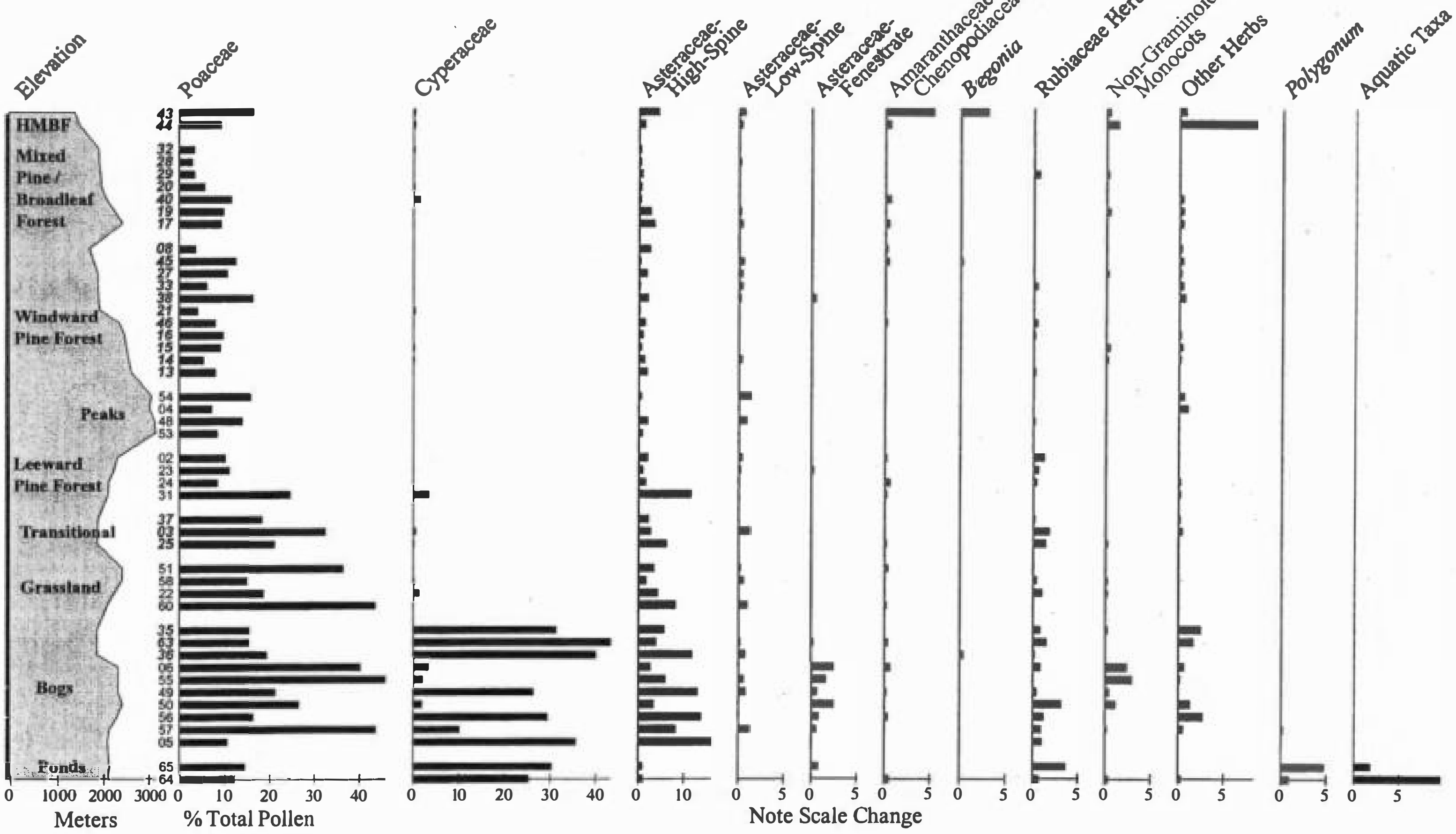

Elevation
Poaceae
Cyperaceae
Asteraceae-High-Spine
Asteraceae-Low-Spine
Asteraceae-Fenestrate
Amaranthaceae/Chenopodiaceae
Begonia
Rubiaceae Herbs
Non-Graminoid Monocots
Other Herbs
Polygonum
Aquatic Taxa
HMBF
Mixed Pine / Broadleaf Forest
Windward Pine Forest
Peaks
Leeward Pine Forest
Transitional
Grassland
Bogs
Ponds
43
44
32
28
29
20
40
19
17
08
45
27
33
38
21
46
16
15
14
13
54
04
48
53
02
23
24
31
37
03
25
51
58
22
60
35
63
36
06
55
49
50
56
57
05
65
64
0
1000
2000
3000
Meters
0
10
20
30
40
% Total Pollen
0
10
20
30
40
0
10
0
5
0
5
0
5
0
5
0
5
0
5
0
5
0
5
0
5
Note Scale Change

Figure 2.5. Percentage diagram for modern pollen and spore spectra of the Cordillera Central, Dominican Republic, presenting pteridophyte taxa, and a fungal spore, *Anthoceros*. Spores are expressed as percentages of total pollen grains and spores (excluding indeterminates). Samples are arranged by vegetation type. Leftmost column shows site elevations; windward sites are indicated by bold, italicized site numbers. "HMBF"=Humid Montane Broadleaf forest; "Transitional"= transitional grassland-pine.

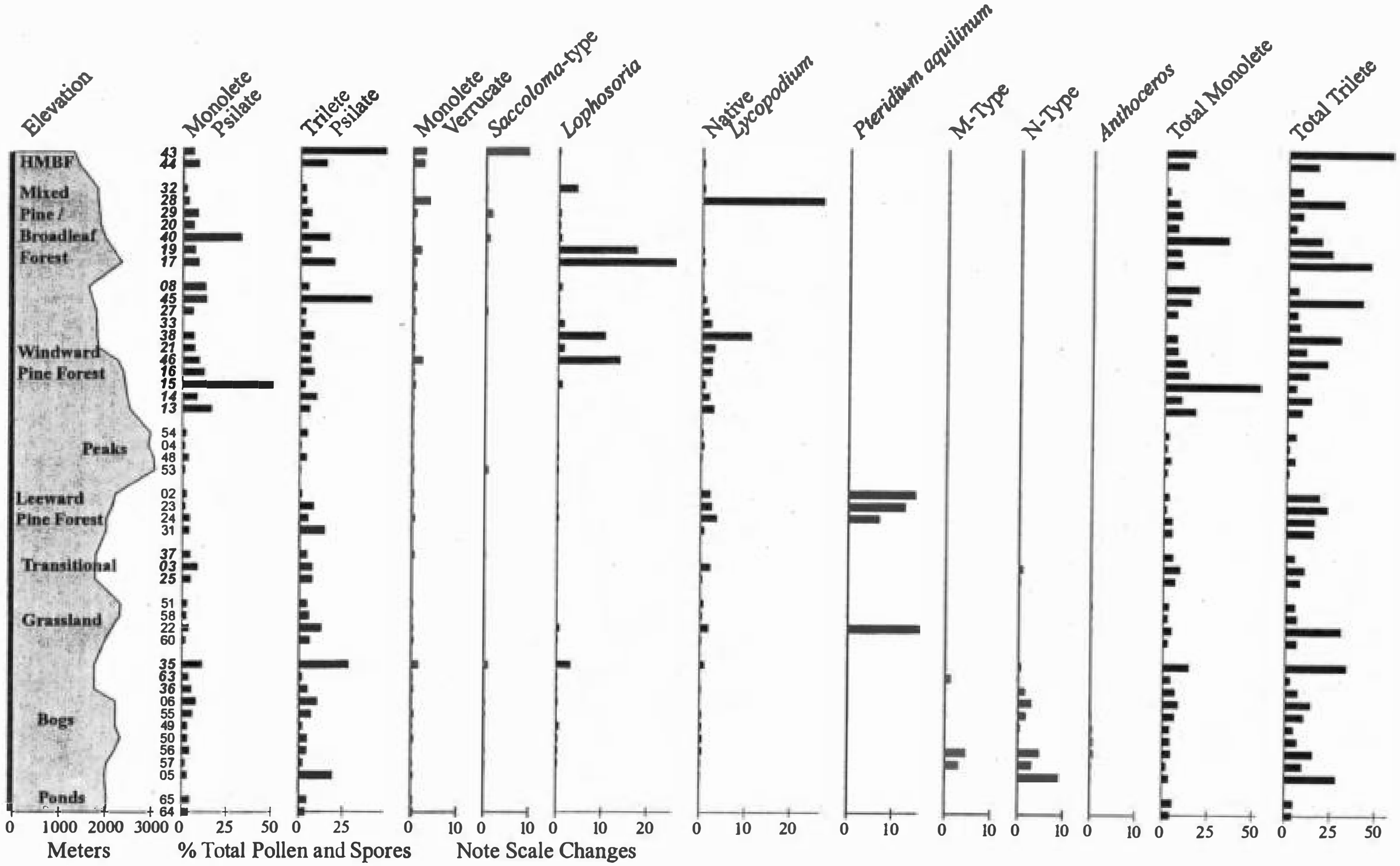

Elevation
Monolete Psilate
Trilete Psilate
Monolete Verrucate
Saccoloma-type
Lophosoria
Native Lycopodium
Pteridium aquilinum
M-Type
N-Type
Anthoceros
Total Monolete
Total Trilete
HMBF
Mixed Pine / Broadleaf Forest
Windward Pine Forest
Peaks
Leeward Pine Forest
Transitional
Grassland
Bogs
Ponds
43
44
32
28
29
20
40
19
17
08
45
27
33
38
21
46
16
15
14
13
54
04
48
53
02
23
24
31
37
03
25
51
58
22
60
35
63
36
06
55
49
50
56
57
05
65
64
0
1000
2000
3000
Meters
0
25
50
0
25
% Total Pollen and Spores
0
10
0
10
0
10
20
Note Scale Changes
0
10
20
0
10
0
10
0
10
0
10
0
25
50
0
25
50

diagram by vegetation type, and within those groups, from lowest elevation to highest. Windward locations are distinguished in the diagram by site numbers in bold, italicized font.

Most samples contained abundant pollen in good condition; indeterminate (damaged) pollen percentages were highest in the wetland sites and in the two sites lowest in elevation (<1500 m; 43 and 44) where they ranged between 10% and 15%. We recognized 54 pollen types, many of which were rare, and recorded about that many unknown morphotypes. Spores were assigned to one of 31 classes, which included five genera, four *Lycopodium* types, and several other morphotypes and morphological classes. Unknown pollen percentages were typically lower than 1% and never higher than 3.3%.

Most of the Urticales pollen was in the diporate class. The order Urticales includes the families Urticaceae, Moraceae, Ulmaceae, and Cecropiaceae, all of which are represented in the Dominican Republic (Bolay 1997). Curves for the Urticales are plotted on the diagram of tree and shrub pollen (Figure 2.3) as many of the diporate grains probably represent the genus *Trema* (Ulmaceae), a common tree of cloud forests in the Dominican highlands (García et al. 1994, Guerrero et al.1997). Pollen of the order may also represent herbaceous taxa, such as *Pilea* (diporate), which grows in cloud forests and other moist forests (García et al. 1994, Guerrero et al.1997).

Pollen Spectra

Pine pollen dominated surface spectra in nearly all forested sites, as well as in grasslands (37–85% in all but site 44). Most angiosperm pollen types were relatively poorly represented in forest samples, swamped by the abundant pine pollen. Pine pollen was also important in wetland samples (24–42%), but pollen of herbs, especially sedges, grasses, and composites (Asteraceae), dominated associations in those sites.

Forested sites (broadleaf, mixed pine/broadleaf, and pine-dominated): Pine-forested sites could generally be distinguished from non-forested and broadleaf forest sites based on the presence of pine stomata. Pine stomata to total pollen ratios were good indicators of the local abundance of pine. Pine forest samples had relatively high ratios of pine stomata to total pollen grains, while ratios in samples from open woodlands characteristic of peaks and transitional grassland-pine sites were low. Very few or no stomata were present in samples from humid montane broadleaf forests and non-forested sites (bogs, grasslands).

Pine and mixed forest samples from sites (~1800–2500 m) on both sides of the mountain range were characterized by relatively high percentages of native *Lycopodium* spores. Pollen percentages for broadleaf shrub and tree taxa were highly variable among forest samples. Pollen of parasitic shrubs was notably higher in lower elevation forests (both mixed and pine-dominated) and especially in leeward forest sites.

Pollen spectra of mixed pine/broadleaf forest sites (all on windward slopes) were not easily distinguishable from those of the windward closed pine forest sites. However, relatively high percentages and diversity of broadleaf tree and shrub pollen, especially *Weinmannia*/*Brunellia*, along with low ratios of pine stomata to pollen, were good indicators of sites in which broadleaf taxa were important constituents of the community.

Samples from the two humid montane broadleaf forest sites (43 and 44) at the lowest elevations contained almost no pine stomata, and displayed the only prominent spikes in Urticales pollen. *Garrya* Douglas ex Lindl. and *Myrica* L. pollen percentages were notably low, and pollen percentages of other broadleaf woody taxa were relatively high. Spikes in the weedy taxa Amaranthaceae/Chenopodiaceae and Asteraceae in sample 43, and "Other Herbs" in sample 44, may represent high levels of both human and natural disturbance. Those samples were collected near heavily used trails and streams.

Mountain peaks: Peak samples were markedly low in pollen and spore diversity. Pine pollen percentages increased in sites above 2400 m elevation, culminating in the highest pine percentages in the mountain peak sites (> 2900 m). Pollen percentages of broadleaf taxa and fern spores were very low, probably due to a combination of upslope pine pollen transport and possibly lower local pollen productivity of non-pine species in these sparsely vegetated sites. Sample 54 (from El Vallecito, a treeless meadow) was not materially different from samples representing forested areas of the peaks, except that it lacked pine stomata.

Transitional grassland-pine sites: Pollen spectra of the transitional sites (37, 03, 25) were remarkably similar to those of the grassland samples (58, 51, 22, 60), despite site locations on opposing flanks of the cordillera. Pine pollen percentages in both site types were comparable to forest samples on both slopes, but like the peak samples, transitional grassland-pine sites had markedly low percentages of woody broadleaf taxa.

Grasslands ("sabanas"), bogs, and ponds: High percentages of grass (Poaceae) and herb pollen characterized pollen spectra of non-forested and open forest sites compared with closed forest sites. Pollen spectra of dry grassland sites (all leeward) were similar to transitional grassland-pine sites, but lacked stomata. Among the grasslands samples, pine pollen percentages were highest in the two smallest grasslands (58, 22).

Pine pollen was abundant in wetland (non-forested) sites as well, ranging from about 25–52%, but these sites on both slopes were dominated by pollen of herbs, especially Poaceae and Cyperaceae, except in site 50. Pine stomata were rare in all but site 50, consistent with the lack of trees. Conspicuously low pollen percentages of woody taxa correctly reflected the general absence of woody vegetation in the bogs. The most notable between-site difference in the bog pollen spectra was whether grass or sedge pollen was most dominant. The abundance and diversity of herb pollen, especially Asteraceae and Rubiaceae, and the presence of certain spores (M-type, N-type) provided a signature for the bog pollen spectra. Pond samples were set apart from bog samples by the presence of pollen of the aquatic taxa *Elodea* Michx. and *Nuphar* Sm., and by a species of *Polygonum* L. that is likely aquatic. Pond samples also displayed low percentages of other herb taxa (Asteraceae, Chenopodiaceae/Amaranthaceae, and "Other Herbs") compared to bog samples. Ponds, and a few bog samples, had very low percentages of total fern spores.

Windward vs. leeward sites: Between-site variability in pollen spectra was highest among forest samples from the windward slopes, especially for pollen of woody taxa and fern spores. Broadleaf woody taxa (*Garrya*, *Myrsine*, *Weinmannia/Brunellia*, *Ilex* L., Lower Montane Trees and Shrubs group), were better represented in pollen spectra of windward forests than leeward. *Lophosoria* C. Presl. spores (sometimes in high percentages) and relatively high percentages of native *Lycopodium* also helped to delineate the windward forests. Total fern spore percentages were widely variable between sites but values among the windward sites were consistently higher, and monolete spores were especially abundant in these samples.

Pollen percentages of *Garrya* and *Myrsine* L. were markedly low in pollen spectra of the four leeward pine forest sites (02, 23, 24, 31). Leeward pine forest samples were also marked by relatively, and consistently, high percentages of pollen of parasitic shrubs (mainly *Arceuthobium*) and the presence of *Pteridium aquilinum* L.-type spores. Monolete spore percentages were conspicuously low in all leeward sites (forested and non-forested). Pollen spectra of bogs on both slopes were similar, but fenestrate Asteraceae pollen percentages were higher in leeward bogs.

Detrended Correspondence Analysis (DCA): Results and Interpretation

The first two axes of the DCA (Figures 2.6, 2.7) explained nearly 70% of the variation (Table 2.2); the third axis (not shown) explained just 3.5%. The DCA shows that the modern pollen spectra of forested uplands and open wetland sites (bogs and ponds) are easily distinguished from each other, while a variety of other site types that are intermediate in terms of vegetation are also intermediate in terms of modern pollen spectra (Figure 2.6). Axis 1 scores separated upland sites from wetland sites. Woody pollen taxa representing upland vegetation received relatively low scores, while herbaceous taxa, dominant in wetlands, received high scores. Intermediate sites (transitional grassland-pine, peaks, and dry grasslands) fell between the closed forest and the open wetland sites on the graph. Forested sites were widely dispersed, while intermediate sites and wetlands were more tightly clustered, indicating greater similarity in pollen spectra of wetland sites. Mixed pine/broadleaf forest sites overlapped with pine forest sites and were not distinguishable in the DCA. The two low-elevation sites (43, 44) in broadleaf forest were dissimilar (distant from each other on the graph) and did not overlap with the other forest sites.

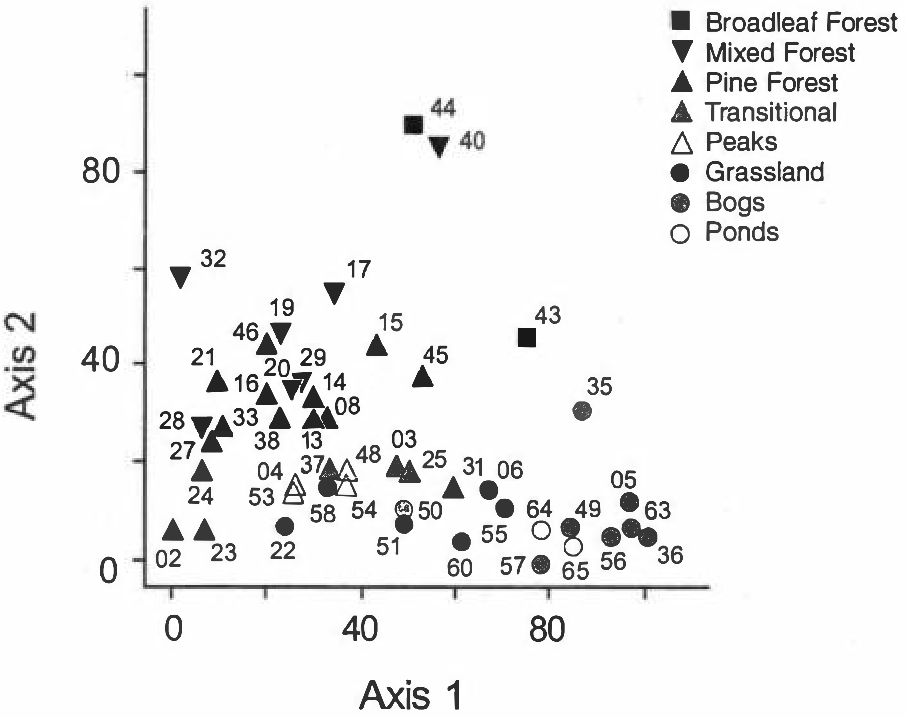


Figure 2.6. Results of DCA ordination of modern pollen data from sample sites within various cover types. Points are sample sites and indicate cover type. Axes are scaled using the "% of Max" method such that Axis 2 is scaled in proportion to Axis 1 (longest), allowing the most accurate portrayal of the similarity relationships among points. The data cloud was rotated by an angle of 30°.

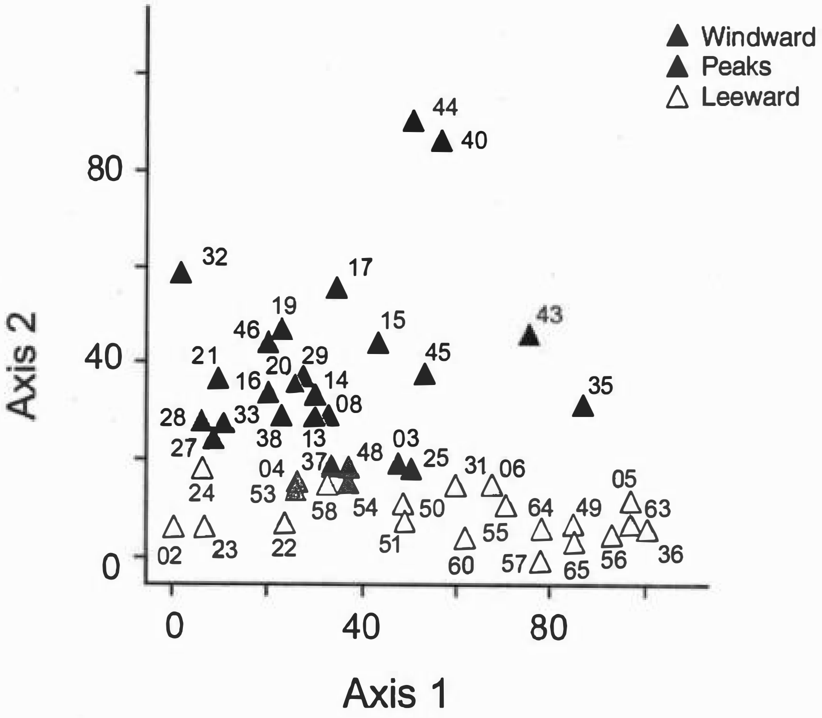


Figure 2.7. Results of DCA ordination of modern pollen data showing sample sites in windward, peak, and leeward locations. Points are sample sites and indicate position with respect to the crest of the Cordillera Central. Axes are scaled using the "% of Max" method such that Axis 2 is scaled in proportion to Axis 1 (longest), allowing the most accurate portrayal of the similarity relationships among points. The data cloud was rotated by an angle of 30°.

Table 2.2. Coefficients of determination for DCA of modern pollen samples. Distance measure was Relative Euclidean.

	R^2	
Axis	Increment	Cumulative
1	0.421	0.421
2	0.277	0.698
3	0.035	0.733

Axis 2 separated windward from leeward sites (Figure 2.7) with broadleaf trees and shrubs, and herbs and spores typical of humid montane forests receiving the highest loadings compared to pollen of herbs and spores representing open areas and wetlands. Samples from mixed pine/broadleaf and humid broadleaf forests received high scores on Axis 2, while the drier leeward pine forests had the lowest Axis 2 scores.

The two humid montane broadleaf forest samples were clearly distinct from all others (except sample 40 from mixed pine/broadleaf forest) in the DCA. However, with only two sites representing that vegetation type, more data are needed to make confident generalizations.

While Axis 1 of the DCA mainly separates upland sites from wetland sites, Axis 2 appears to represent a gradient in moisture availability, and possibly temperature. The more humid or protected forests have high Axis 2 values, and are reflected in the pollen spectra by higher percentages, and greater diversity, of pollen of broadleaf woody taxa such as *Brunellia/Weinmannia*, *Myrsine*, *Ilex*, and the "Lower Montane Trees and Shrubs" (LMTS) group as shown in the pollen diagram (Figure 2.3). *Myrica* pollen, on the other hand, increases at the expense of other broadleaf pollen in higher or less-protected sites. *Myrica* pollen, high pine stomata to total pollen ratios, and the presence of native *Lycopodium* spores (Figure 2.5) together provide a good signature for drier, more exposed pine forests. *Pteridium aquilinum* spores, relatively high pollen percentages for parasitic shrubs, and a lack of broadleaf pollen separated the leeward pine forests from the windward. These differences may reflect the influence of more frequent fires on vegetation in the drier leeward forests.

At coarse resolution, Axis 2 represents a transect over the Cordillera Central, beginning with high values representing humid forests at lower elevations on the windward side, proceeding to elevations above the TWI, then over the peaks and down into the drier leeward pine forests (sites 02, 23, 24, 31). However, complicated mountain topography and climate, among other environmental factors, interfere with such a simplistic "elevational" ordering of the sites. For example, some lower elevation (ca. 2000 m) forests around Valle de Bao have fewer broadleaf elements than sites on the surrounding slopes that are protected by cold air drainage into the valley below.

The variability in pollen spectra of the pine forest-mixed pine/broadleaf forest group is reflected by the relatively wide spread of points in the DCA. There are several reasons to expect that the windward pine forest and mixed pine/broadleaf forest samples would not be clearly distinguished from each other in the DCA. First, while the vegetation structure is different, species composition is often relatively similar because many of the common pollen taxa (e.g., *Myrsine* and *Garrya*) occur as both canopy and sub-canopy elements. Forest canopies in these sites may differ more than would be indicated by the pollen spectra. Secondly, solely pine-dominated stands are often in close proximity with more diverse mixed stands due to heterogeneous topography and climate, and because patchy disturbance patterns can strongly affect local vegetation. Even if two adjacent sites are strongly distinctive in terms of composition, mountain winds may mix the pollen signals.

Intermediate sites (transitional grassland-pine, peaks, grasslands) fell neatly between most forests and wetland sites in the DCA, with only one leeward pine forest sample (31) intruding. The 1997 fire that scorched most of JCRNP affected all the lee sites, but sample 31 was the only one from a site in which the entire pine canopy had been removed by the fire. The relatively low pollen percentages of pine and other woody taxa and the spike in Asteraceae pollen in sample 31 were probably due to heavy canopy reduction by the fire and the accompanying flush of herbaceous growth. This likely caused the pollen spectra of sample 31 to more closely resemble those of open woodlands or grassland sites.

The peaks and transitional grassland-pine samples clustered tightly in the DCA, indicating high similarity, while the grassland samples were scattered, their scores probably influenced by variations in their proximity to forest. The pollen diagrams show that the clearest distinction between grassland samples and samples from open woodlands of peaks and transitional grassland-pine sites is the lack of pine stomata in the former.

Discussion

Despite the over-representation of pine pollen, pine stomata and other pollen and spore taxa provided signals that statistically separated the modern pollen spectra into four mostly distinct groups: 1) humid montane broadleaf forest, 2) pine and mixed pine/broadleaf forest, 3) unforested wetlands (bogs and ponds), and 4) intermediate sites (open woodlands of peaks and transitional grassland-pine sites, and grasslands). Changes in pine pollen percentages alone were less important in distinguishing cover types. When pollen data are expressed as percentages, each value depends not only on the abundance of that particular taxon in the pollen source area, but also on the abundance and productivity of all the other taxa represented by the pollen assemblage. For this reason, pine pollen percentages in our samples may simply rise and fall with changes in other pollen taxa rather than in response to any real difference in pine abundance. Thus, while a background of pine pollen is common in all highland sites, pollen of broadleaf woody plants and herbs, fern spores, and pine stomata were the key indicators of differing vegetation in these sites.

Aside from clear contrasts in the major constituents of the local vegetation, taphonomic differences may also play a role in the separation between pollen spectra of the four groups. Our analysis incorporated samples from several surface types: wet and dry soils and duff under closed or partially closed canopy forest; dry soils in open grasslands; organic sediment from small bogs within the open grasslands; and in two cases, pond sediments. The accumulation and preservation of pollen grains likely differs between sites, complicating the interpretations of their pollen spectra.

All surface samples contained pollen spectra from both local and regional pollen sources. For example, the sheer abundance of pines within or near most of our sites, and throughout the entire highland region, is responsible for the prominence of pine pollen in all samples including open grasslands and bogs. A substantial portion of pollen deposited in small basins, or under a closed canopy, originates from vegetation growing close to the collection site, while pollen from more distant sources often overshadows the local signal in large basins (Tauber 1965, Jacobson and Bradshaw 1981, Prentice 1985, Sugita 1993, Jackson 1994, Jackson and Wong 1994, and Jackson and Kearsley 1998). Even though sedimentation rates (time represented by the sample) and taphonomic processes likely vary between the ponds and bogs, the DCA indicated that the pollen spectra of the ponds and bogs were similar. Within bog sites, dominance by grass or sedge pollen likely reflects local variations in the water table, with sedges dominating sites that are consistently wetter.

Taphonomic differences do make it difficult to interpret differences between the pollen spectra of the bog and pond group and other sites in which the material collected was soil and duff. While anoxic sediments that stay wet usually preserve pollen well, soil and duff impose harsh constraints on preservation. Pollen grains in soils generally present themselves in a range of conditions from fresh to unrecognizable, requiring judgment on the part of the analyst (Orvis 1998). Taphonomic differences between soils and sediments make interpretations of soil pollen spectra less applicable to ancient sedimentary pollen assemblages, which are generally well preserved.

Despite the possibility that some between-sample differences in pollen spectra may reflect taphonomic differences, rather than vegetation differences, the strong patterns within the forest (broadleaf, mixed, and pine) and woodland (peaks, transitional grassland-pine) samples indicate that real differences in vegetation are reflected by pollen spectra of those samples. In the DCA, a clear trend exists along Axis 1 from low values for samples representing less diverse and more open forests and woodlands of the peaks, leeward, and transitional grassland-pine sites, to higher values for denser, more diverse windward forest. What is less clear is to what degree the pollen assemblages are representing local or regional vegetation differences.

In early research on pollen deposition in small forest hollows in temperate regions of the U.S., Bradshaw (1981) and Heide and Bradshaw (1982) estimated that most of the pollen was transported only 20–30 m. Recent studies of closed canopy sites have shown strong representation in assemblages by pollen from non-local (>100 m) and even distant sources, if non-local vegetation includes an abundance of taxa such as pine that produce large quantities of easily dispersed pollen (Jackson and Wong 1994, Sugita 1993, Calcote

1995, Jackson and Kearsley 1998). Some of the pollen of pine and other wind-dispersed taxa in these samples may represent both local and non-local populations.

Fluctuations in pine stomata appear to be the most robust indicators of stand-scale differences in canopy composition. Unlike pollen, which may derive from "extralocal" vegetation, stomata are probably dispersed only short distances (Parshall 1999), and thus are good indicators of the local presence of conifers. Several studies have used conifer stomata to complement pollen studies in detecting local changes in boreal and alpine treeline from lake and bog sediments (Hansen 1995, Hansen et al. 1996, Pisaric et al. 2000, Gervais and MacDonald 2001). Recently, analyses of sediment profiles from closed canopy sites, such as forest hollows, have used macrofossils and conifer stomata to track changes in individual forest stands through time (Parshall 1999). Our results indicate that such studies may be promising in the Dominican highlands where the history of human and natural disturbances, such as forest clearance, landslides, tropical storms, and fire, are little known or understood.

Conclusions and Applications

Despite our expectation that the pine-dominated pollen assemblages in a rugged montane region may not provide signatures of the local vegetation, our analysis showed that at least for some cover types, pollen spectra were distinctive. Pollen spectra of closed forests had high proportions of tree and shrub pollen, while those of the open woodlands of mountain peaks and transitional grassland-pine sites, along with grasslands, were distinguishable by their comparative lack of arboreal pollen. Abundant Cyperaceae and low arboreal pollen characterized the highland bog samples, while pollen of *Polygonum* and aquatic taxa marked pond spectra. Grasslands and open woodlands had similar pollen assemblages, but the absence (or rarity) of pine stomata proved to be an excellent indicator of "treelessness" in grassland sites. The distinction between forested and non-forested sites may be one of the most useful in helping to understand and interpret highland fossil records that may reach back into the last glacial period. For example, we may be able to detect whether landscapes were more open in the past during drier, or cooler periods.

Humid montane broadleaf forest samples had unique pollen spectra, but our sample size was inadequate to fully characterize them. In spite of pine dominance and lack of representation of some prominent broadleaf taxa, relative percentages of broadleaf pollen could be used to make broad inferences about environmental conditions of the sites. In particular, higher percentages and diversity of broadleaf pollen taxa reflected more mesic sites, or sites protected from frost and fire that would harbor more tropical elements of highland vegetation.

While the results of our study suggest trends in the relationship between modern pollen data and vegetation and environmental gradients, it is important to emphasize that these patterns cannot be directly related to fossil pollen assemblages because most of our samples are not equivalent to pond and bog sediments. Our findings will inform studies of sedimentary pollen and should enhance our interpretations, but must be used judiciously.

An interesting application of the results of this study will be to determine whether glacial-age vegetation assemblages have a modern analog in the Dominican highlands. Paleoecological studies from both tropical (Colinvaux 1987) and temperate (Delcourt 1979, Delcourt and Delcourt 1987, Webb 1987) regions have shown that some glacial-age plant communities were quite unlike modern communities; species have assembled and disassembled in novel ways in response to past climatic change. Comparison of the modern pollen spectra with sedimentary pollen spectra representing ancient communities may help to clarify whether glacial plant associations differed significantly from present ones.

In their study of modern pollen in 95 lakes in Oregon and southern Washington, Minckley and Whitlock (2000) suggested that it is not always necessary to use the full suite of pollen taxa present if the goal is to reconstruct vegetation at the level of a vegetation type or zone. In the Dominican highlands, most of the story was told by a dozen or so pollen and spore taxa along with pine stomata. At the stand level, however, careful consideration of the full array of pollen taxa may allow for more precise reconstruction of vegetation and disturbance history. Future studies that combine vegetation analysis with analyses of pollen and spores, stomata, and plant macrofossils in sediment profiles in forest hollows, bogs, and ponds in the Dominican highlands may help to shed light on both tropical mountain ecological processes, and on taphonomic processes, which are still little known in tropical areas.

CHAPTER 3

A 4000-yr Record of Fire and Forest History from Valle de Bao, Cordillera Central, Dominican Republic

This chapter is in preparation for submission to the journal, *Palaeogeography, Palaeoclimatology, and Palaeoecology*. My use of "we" in this chapter refers to my co-authors, Sally P. Horn and Kenneth H. Orvis, and myself. Aspects of the environmental and cultural setting now covered in Chapter 2 of this dissertation will be added to the manuscript before submission.

Introduction

Despite growing interest in tropical climate and environmental history, paleoenvironmental records from lakes and swamps remain sparse in the Caribbean and neighboring subtropical Atlantic region. Published studies of sedimentary records have so far focused on Lake Miragoane, Haiti (18°N, 73°W; ~20 m elevation) (Brenner and Binford 1988, Hodell et al. 1991, Curtis and Hodell 1993, Higuera-Gundy et al. 1999), Wallywash Great Pond, Jamaica (18°N, 78°W, 7 m elevation) (Street-Perrott et al. 1993, Holmes 1998), Laguna Tortuguero, Puerto Rico (18°N, 68°W, ~1 m elevation) (Burney et al. 1994), and Church's Blue Hole, Bahamas (25°N, 78°W, <14 m elevation) (Kjellmark 1996). All of these lakes are near sea level, leaving a gap in understanding of the environmental history of higher elevation sites. This paper presents a 4000-yr sediment record from a high elevation bog (~1800 m elevation) at the ecotone between humid montane broadleaf forest and upslope pine forests in the Cordillera Central, Dominican Republic.

Some prior research has focused on sedimentary evidence of prehistoric human activity on Caribbean islands. Burney et al. (1994) studied sedimentary charcoal from Laguna Tortuguero, in part to refine the date of initial colonization of Puerto Rico. The near absence of charcoal in sediments deposited between ~7000–5300 cal yr BP (likely prior to human colonization) suggested that fire has not always been a major component of the regional ecosystem (Burney et al. 1994). The authors interpreted a charcoal spike at ~5300 cal yr BP to signal anthropogenic burning by the island's earliest inhabitants. In sediments from Church's Blue Hole, Bahamas, Kjellmark (1996) interpreted a peak in charcoal concentrations concurrent with a shift from pollen of hardwoods to pine ~700 cal yr BP to signal human arrival, or an increase in human-set fires. In both the Puerto Rico and Bahamas studies, climatic interpretations for at least parts of the records are complicated by the likely influence of human activity.

Other sediment studies have focused more on evidence of climatic change. At Wallywash Great Pond, Jamaica, physical and geochemical properties of sediments (Street-Perrott et al. 1993, Holmes et al. 1995) and changes in ostracod assemblages (Holmes 1998) revealed three cycles of alternating wetter/drier conditions during the Holocene period, along with a major flooding event at around 1200 cal yr BP. Stable isotopes, geochemistry, and pollen and charcoal assemblages in a sediment profile from Lake Miragoane, Haiti, documented environmental history over the past ~12,000 cal yr (Binford et al. 1987, Brenner and Binford 1988, Hodell et al. 1991, Curtis and Hodell 1993, Higuera-Gundy et al. 1999). Stable isotopes and trace metals in ostracod shells from the lake (Hodell et al. 1991, Curtis and Hodell 1993) yielded a high-resolution record of shifts in relative evaporation/precipitation ratios. The record revealed several shifts in climate during the Holocene, with a recent trend (~3400 cal yr BP to present) toward drier conditions that is also shown by the pollen record from the site (Higuera-Gundy et al. 1999).

This study of a sediment record from a high elevation Caribbean bog was undertaken to provide information on the climate, vegetation, and fire history of a portion of the windward slope of the Cordillera Central, Dominican Republic. This record was developed as part of an ongoing study of the modern and ancient environments of the larger region of the Cordillera Central, Dominican Republic (Orvis et al. 1997, Horn et al. 2000, Horn et al. 2001, Clark et al. 2002, Speer et al. in press, other chapters of this dissertation).

Study Area

The Dominican Republic occupies the eastern portion of Hispaniola, the second largest island (after Cuba) in the Greater Antilles. The island's Cordillera Central is the highest in the Caribbean, reaching elevations of 3100 m on Pico Duarte (Orvis in press). Our core site is in Valle de Bao (19°04' N, 71°02' W, Figure 3.1) on the windward (north) flank of the Cordillera Central in the Armando Bermúdez National Park (ABNP). The vegetation, climate, and other aspects of the physical and cultural environments of the Cordillera Central are discussed in greater detail in Chapter 1 of this dissertation.

The Core Site

Valle de Bao (~1800 m elevation) is a 2.5 x 0.3 km trough located ~6 km northwest of Pico Duarte. The valley floor is treeless, dominated by an endemic tussock grass, *Danthonia domingensis* Hack. & Pilger, and other grasses and sedges, and punctuated by several bog-filled depressions. Scattered colonies of *Rubus* L. (blackberry) are the only woody plants occupying the valley floor. Cold air draining from higher slopes is trapped in the valley and likely inhibits invasion by pine (Clark et al. 2002). The lower slopes around Valle de Bao consist of pure pine stands, but the

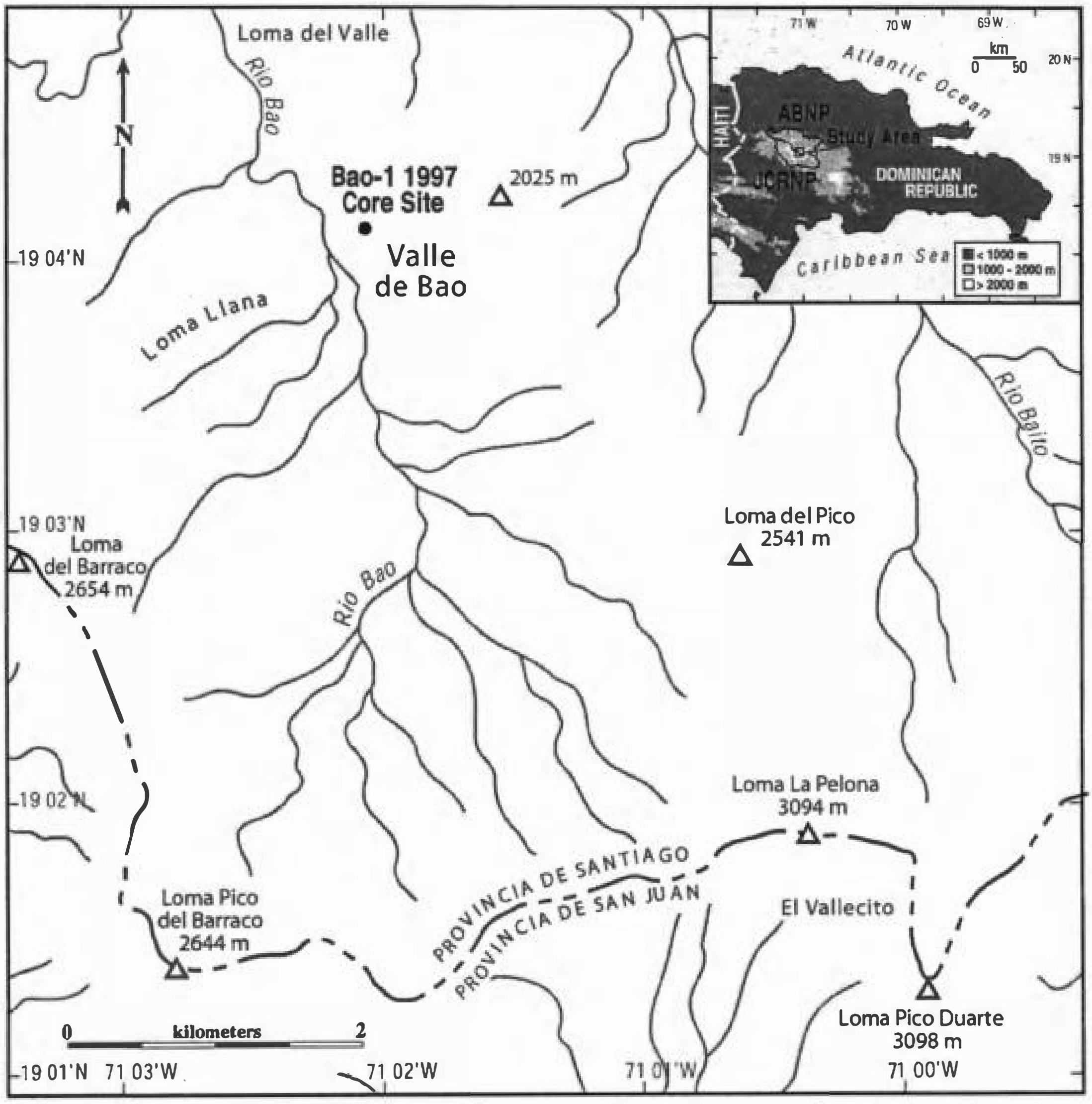


Figure 3.1. Map of study area and Bao-1 1997 core site. Inset shows position of study area in the Cordillera Central, Dominican Republic, and the two national parks, ABNP (Armando Bermúdez) and JCRNP (José del Carmen Ramírez). The core site is in ABNP. The spine of the Cordillera Central divides the parks and is shown on the larger map as a dashed line. The elevations of the peaks of La Pelona and Pico Duarte are based on Orvis (in press).

middle slopes of Loma del Pico and La Pelona (~1900–2500 m) are effectively drained of cold air and presently support a diverse assemblage of tropical broadleaf trees, anomalous at these elevations. The core site (Figure 3.1) was a small peat bog (Bao Bog 1) with a water depth of ~15–20 cm in a topographically low area (~1775 m) of the valley.

Methods

We retrieved a 340 cm sediment core from the bog in February 1997using a Colinvaux-Vohnout (C-V) locking-piston corer (Colinvaux et al. 1999) while standing on wooden planks. We recovered the core in several successive one-meter drives, and returned the core sections to the laboratory in the original sampling tubes (5 cm diameter, aluminum). We obtained near-surface sediments using a PVC tube (5 cm in diameter) with a serrated edge. We twisted the tube into the sediment and then raised it holding the lower end closed with a shovel blade. We extruded and sliced these sediments in 2 cm increments in the field, storing them in plastic bags. The C-V core sections and material from the PVC tube together constitute the Bao-1 1997 sediment core.

Here we report our analysis of the uppermost 126.5 cm of organic-rich, pollen bearing sediments. The upper 40 cm of sediment were sampled with the PVC tube. Samples between 40–103 cm are from Core Section I, and those between 103–126.5 cm are from Core Section II, recovered with the C-V corer. These two core sections and the PVC tube section were each collected from separate holes a short distance (<2 m) apart.

In the laboratory, we opened the C-V core sections with a table-mounted router, photographed them, and described their texture and color (Munsell). We sampled for pollen and charcoal analysis at 4 cm intervals in the sediment matrix avoiding organic clasts composed of peat and soil (see "*Radiocarbon dates and core description*" section).

We dried duplicate samples at 100°C for 8 hours (or longer) to determine water content, and performed loss on ignition (LOI) for one hour at 550°C and 1000°C to estimate organic and carbonate content (Dean 1974). We used sample volumes for pollen and LOI analysis of 1.2 cm^3 for the two uppermost levels (0 and 2 cm depth), 0.6 cm^3 for the next two deeper samples (4 and 6 cm depth), and 0.5 cm^3 for the remaining levels.

We processed the samples using standard pollen preparation techniques (HF, HCl, KOH, acetolysis, safranin stain; Faegri and Iverson 1989; Appendix B) and added *Lycopodium* tablets as controls (Stockmarr 1971). We mounted the pollen residues on microscope slides in silicone oil, and counted a minimum of 400 pollen grains per sample exclusive of indeterminate pollen and spores. Pollen and spores were identified at 400x magnification using pollen reference material from the Dominican highlands and elsewhere, and published keys and photographs (Heusser 1971, McAndrews et al. 1973, Markgraf and D'Antoni 1978, Moore and Webb 1978, Hoogheimstra 1984, Moore et al. 1991). Pollen grains of the Urticales were classified by pore number, except for *Cecropia* and *Trema*.

We sketched unknown pollen grains and recorded them as morphological types. Unknown fern spores were classified by morphology. Although the same *Lycopodium* species used for the control tablets, *L. clavatum* L. grows in the Cordillera Central, the vast majority of *Lycopodium* spores in our samples appear to be the controls we added. Our control spores had a slightly shrunken and darker appearance (probably due to effects of processing and age) in comparison to the native spores, which were brighter, retained truer size and shape (when compared to modern reference samples from the highlands), and exhibited a broader reticulate pattern. We identified fewer than 20 native *Lycopodium* spores in all samples.

We counted charcoal fragments >50 μm in maximum dimension during the standard pollen counts. We tallied only completely black, opaque, angular fragments.

Pollen and spore percentages and charcoal values were plotted using a modified version of CalPalyn (Bauer et al. 1991). For the purpose of discussion, we divided the diagrams into four zones based primarily on physical changes in the sediment profile, and shifts in influx of pollen, spores, and charcoal. To construct the chronology of the core, we submitted 12 samples (mostly charcoal) from the upper organic section of the Bao-1 1997 core for AMS radiocarbon dating.

Results

Radiocarbon Dates and Core Description

Three radiocarbon dates on charcoal fragments were out of order (Table 3.1), older by 1000–3000 or more years than ages extrapolated from the remaining dates (Figure 3.2).

The bottom of the organic portion of the Bao 1-1997 core (at 126.5 cm) abuts a truncated paleo-surface of mottled clay soil (Munsell color 10YR 5/4) with some evidence of desiccation cracks, and poor pollen preservation. The basal unit from 103–126.5 cm is composed of organic-rich sandy silt (10YR 3/1) containing scattered organic clasts and coarse sand. A thin layer of lighter-colored (10YR 4/1) fine-grained mineral silt extends from 100–103 cm. The 94–100 cm unit is similar in color to the basal unit, but is mottled by light-colored material (10YR 4/6), is much more clay-rich, and contains abundant clasts of peat and mineral soil. The uppermost unit (0–94 cm) is dark

Table 3.1. Radiocarbon determinations for Bao-1 1997 core samples. AA samples were dated by the NSF Arizona AMS Facility; β samples were dated by Beta Analytic, Inc. All of the dated samples were charcoal except AA40257, which was seeds, and β-155839, which was seeds and charcoal. Dates were calibrated using the CALIB 4.3 calibration program (Stuiver and Reimer 1993) and the datasets of Stuiver et al. (1998). Errors estimate 68% (1σ) and 95% (2σ) probability. *Samples interpreted as redeposited charcoal (see text). **The radiocarbon date for sample AA43340 does not appear in the pollen diagrams (Figures 3.3, 3.4, 3.5) or age-depth graph (Figure 3.2) because pollen samples were only taken from the PVC core section between 0–40 cm; all lower pollen samples are from Core Sections I and II.

Core Section			Uncalibrated ^{14}C Age	Calibrated Age(s)	Calibrated Age Range (cal. yr BP)	
Depth (cm)	Lab No.	δ^{13}C	(^{14}C yr BP)	(cal yr BP)	±1σ	±2σ
PVC 16–18	AA40257	-25.5	191 ± 34	280, 170, 153	290–3	301–1
PVC 16–18	AA40258	-26.1	167 ± 43	273, 188, 147, 12, 4	285–1	299– 0
PVC 38–40	AA43339	-24.2	*2126 ± 59	2118	2300–2000	2310–1950
PVC 40–42	AA40256	-26.4	553 ± 66	545	640–520	660–500
PVC 58–60	AA43340	-23.9	**1816 ± 57	1723	1820–1630	1880–1570
Section I 47.5–48.5	AA39458	-25.5	*3016 ± 49	3236, 3232, 3211	3081–3322	3064–3356
Section I 75.5–76.5	β-155839	-25.2	1300 ± 40	1261	1285–1170	1293–1155
Section I 86.5–87.5	β-155840	-25.9	2260 ± 50	2312, 2218, 2211	2340–2160	2350– 2120
Section I 99–100	β-13524	-24.9	*5210 ± 50	5933	5990–5920	6170–5900
Section II 105.5–106.5	AA40253	-26.6	3083 ± 38	3334, 3282, 3270	3357–3258	3379–3170
Section II 112.5–113.5	AA40254	-24.8	3348 ± 38	3628, 3620, 3605, 3602, 3576	3636–3481	3688–3470
Section II 125.5–126.5	AA40255	-24.5	3690 ± 86	4070, 4046, 3988	4150–3890	4280–3730

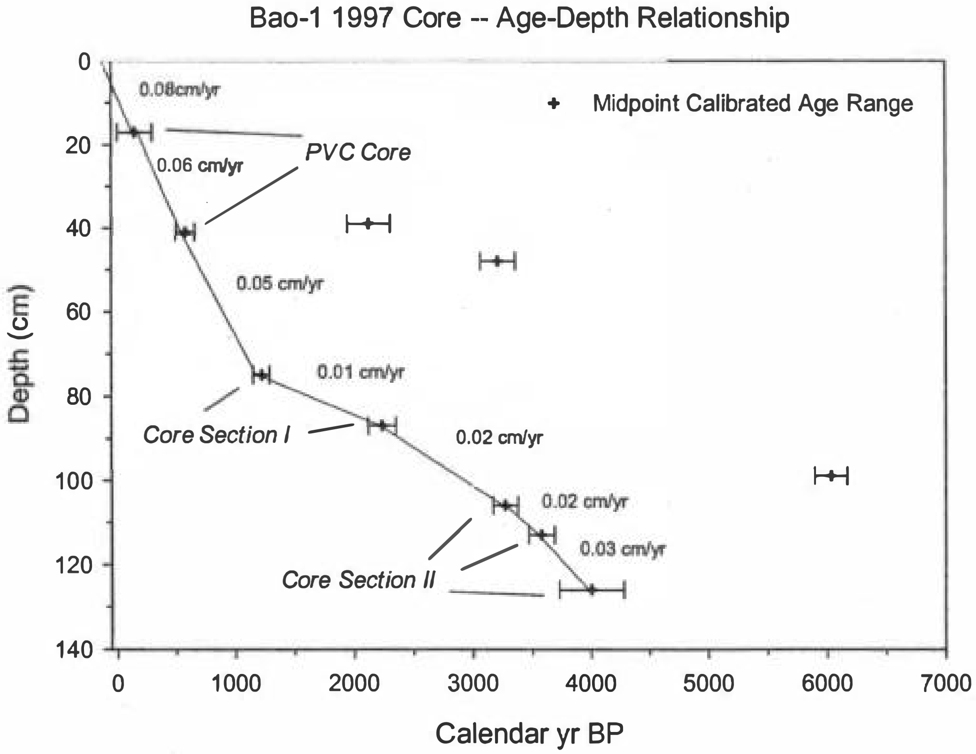


Figure 3.2. Radiocarbon ages plotted against depth for Bao-1 1997 core. Bars indicate the 2σ calibrated age ranges, and crosshair symbols indicate the midpoint of the range. Approximate sedimentation rates (labeled and represented by the lines between dates) are estimated by interpolating between the midpoints. The three bars on the right side of the graph (not connected by lines) represent calibrated age ranges on samples that are interpreted to be redeposited charcoal. The core sections that the dated material was taken from are shown in italics. There are two overlapping samples at 17 cm with nearly identical age ranges.

(10YR 2/2), fine-textured peat, grading downward to material with a higher silt content (10YR 2/1), with some sand and scattered organic clasts, mainly below 40 cm in Core Section I. The uppermost 20 cm of sediment is especially rich in plant roots and undecayed plant material.

Pollen Spectra

We identified 50 pollen types, many of them rare; unknown pollen percentages accounted for less than 1% of the pollen in all levels (Figures 3.3–3.6). Pollen preservation varied downcore with indeterminate grains accounting for 3–16% of the total pollen. Indeterminate percentages were highest in the lower, less organic sediments (below ~85 cm; Figure 3.4). Pollen and spore influx (Figure 3.3) is high in the basal pollen zone (Zone 4), but declines and remains lower in Zone 3. It then dramatically increases remaining generally higher in Zones 2 and 1, except in the uppermost samples of Zone 1, where it decreases again. Pine (*Pinus* L.), grass (Poaceae), and sedge (Cyperaceae) pollen dominate the record, accounting for ~50–90% of the pollen in most samples (Figure 3.3). Fern (pteridophyte) spore percentages show little change over time, except for prominent peaks in *Cyathea* Sm. and *Lophosoria* C. Presl. (Figure 3.6).

Charcoal fragments smaller than 50 μm were not enumerated but were ubiquitous. Microscopic charcoal >50 μm is expressed in four ways: as charcoal to pollen ratios, as concentrations in both wet and dry sediment, and as influx (fragments/cm^2/yr) (Figure 3.4.) The curves for charcoal to pollen ratio and charcoal concentration in dry sediment are generally similar; charcoal is abundant throughout the record with the only dramatic change a decline in the uppermost section representing about the past 50–100 years. Charcoal concentrations in wet sediment are higher in Zones 4 and 3 and gradually

Figure 3.3. Summary pollen and spore percentage diagram of selected taxa for the Bao-1 1997 core. Chronology and stratigraphy are shown on the left, and charcoal, organic content, and pollen and spore influx are shown on the right. The "Selected Broadleaf Trees and Shrubs" group includes *Brunellia*, *Cecropia*, *Myrsine*, *Trema*, and *Weinmannia.*

Bao-1 1997: Summary Diagram

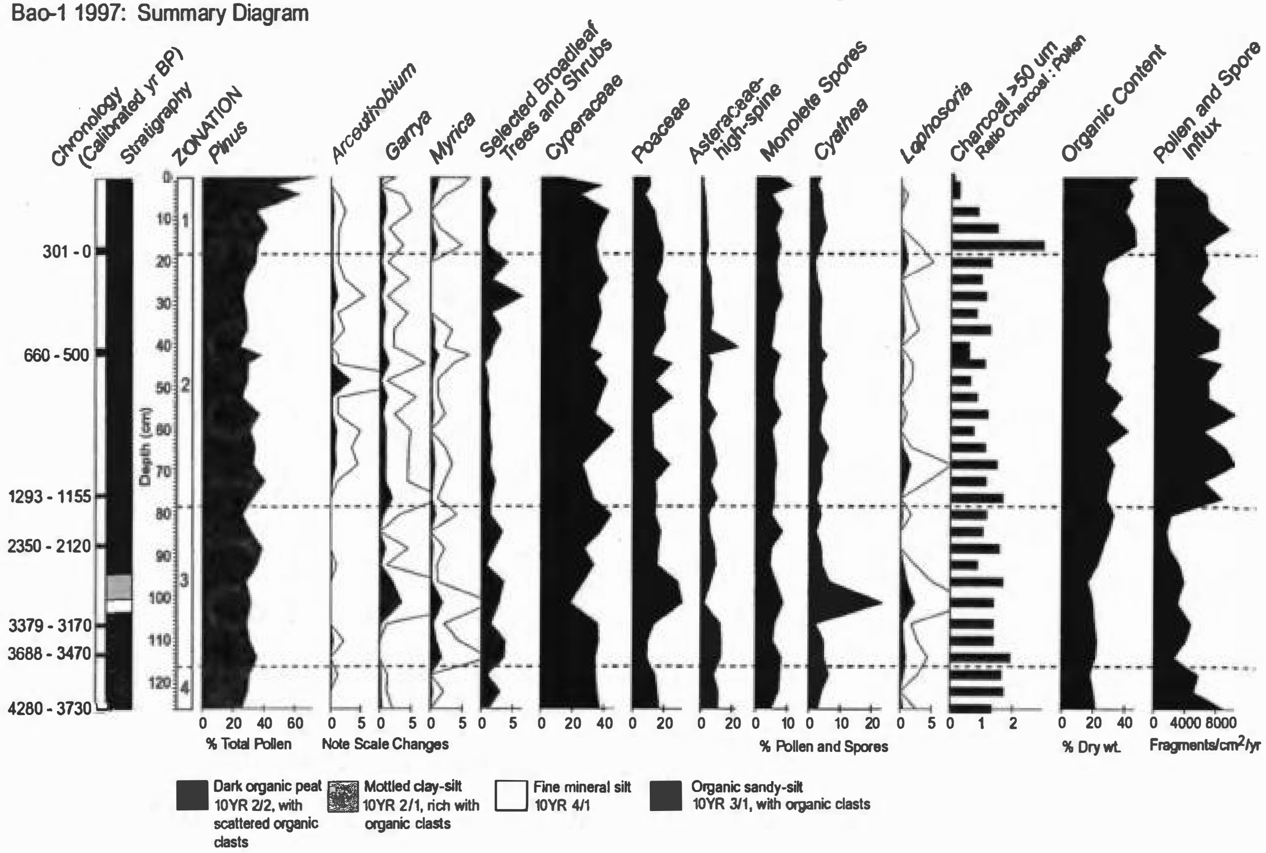


Figure 3.4. Diagram showing chronology and stratigraphy, pollen and spore concentrations and influx, indeterminate pollen percentages, organic content (%), and charcoal fragments (>50 mm) expressed as charcoal:pollen ratios, fragments per g dry sediment, fragments per cc wet sediment, and influx (per cm^2 per year) for the Bao-1 1997 core.

Bao-1 1997

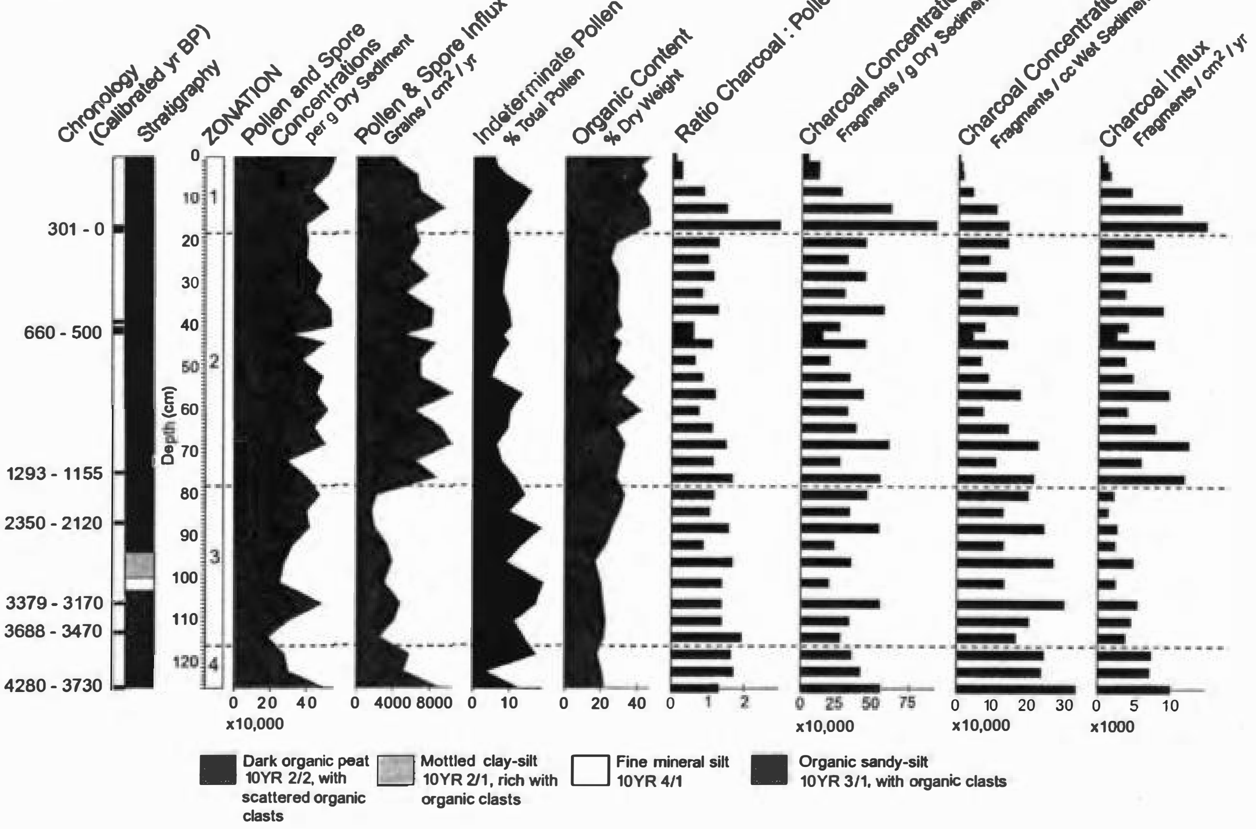

Chronology (Calibrated yr BP)
Stratigraphy
ZONATION
Pollen and Spore Concentrations per g Dry Sediment
Pollen & Spore Influx Grains / cm2 / yr
Indeterminate Pollen % Total Pollen
Organic Content % Dry Weight
Ratio Charcoal : Pollen
Charcoal Concentration Fragments / g Dry Sediment
Charcoal Concentration Fragments / cc Wet Sediment
Charcoal Influx Fragments / cm2 / yr
301 - 0
660 - 500
1293 - 1155
2350 - 2120
3379 - 3170
3688 - 3470
4280 - 3730
Depth (cm)
0
10
20
30
40
50
60
70
80
90
100
110
120
1
2
3
4
0 20 40
x10,000
0 4000 8000
0 10
0 20 40
0 1 2
0 25 50 75
x10,000
0 10 20 30
x10,000
0 5 10
x1000
Dark organic peat 10YR 2/2, with scattered organic clasts
Mottled clay-silt 10YR 2/1, rich with organic clasts
Fine mineral silt 10YR 4/1
Organic sandy-silt 10YR 3/1, with organic clasts

Figure 3.5. Pollen percentage diagram of tree and shrub taxa for the Bao-1 1997 core. The "Other Humid Montane Taxa" group includes *Ilex*, *Hedyosmum*, *Didymopnax*, *Alchornea*, *Juglans*, Melastomataceae, *Bocconia*, *Piper*, *Zanthoxylum*, and Solanaceae (which may include herbaceous taxa). Chronology and stratigraphy are shown at left and organic content and charcoal:pollen ratios at right.

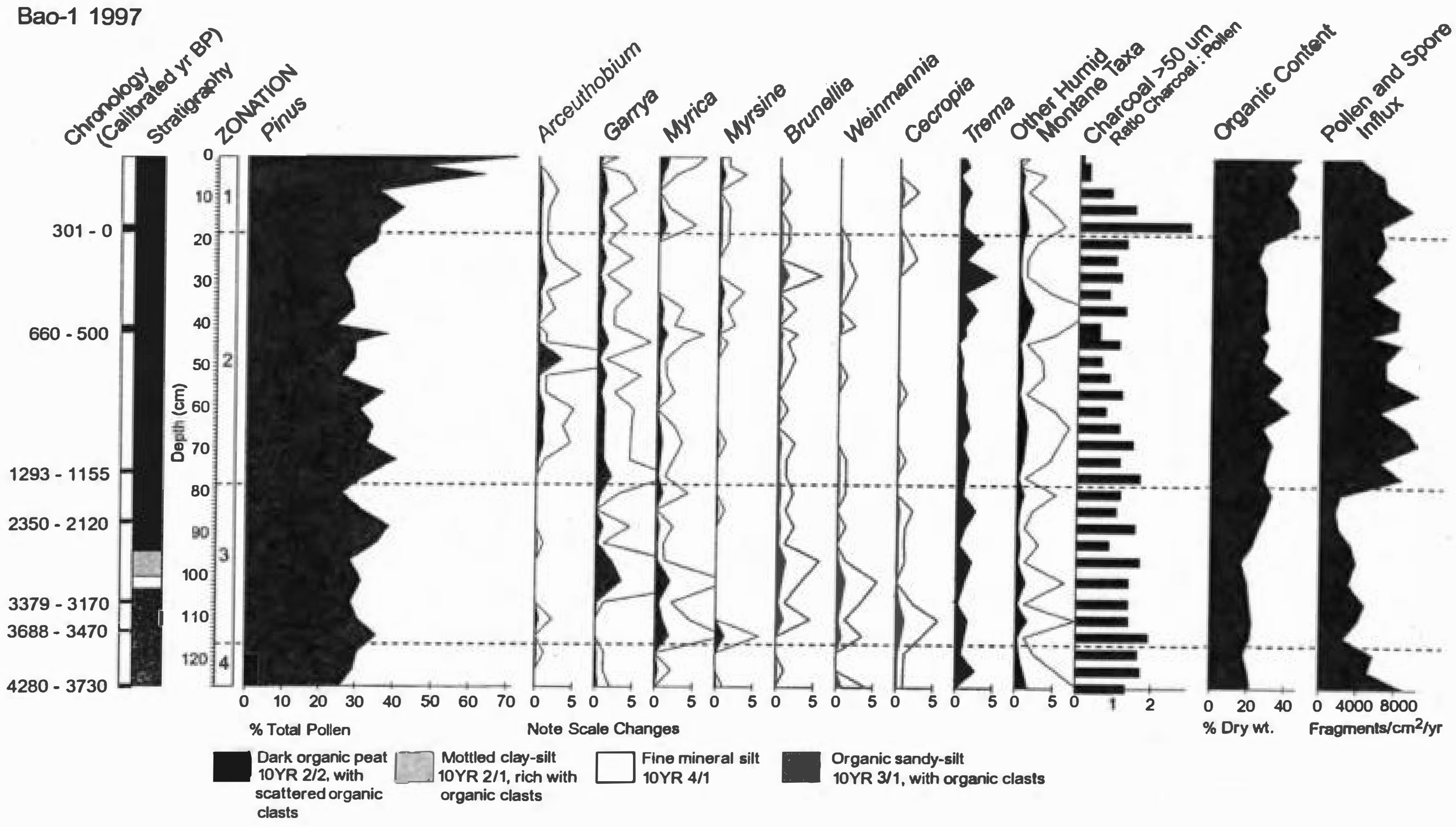
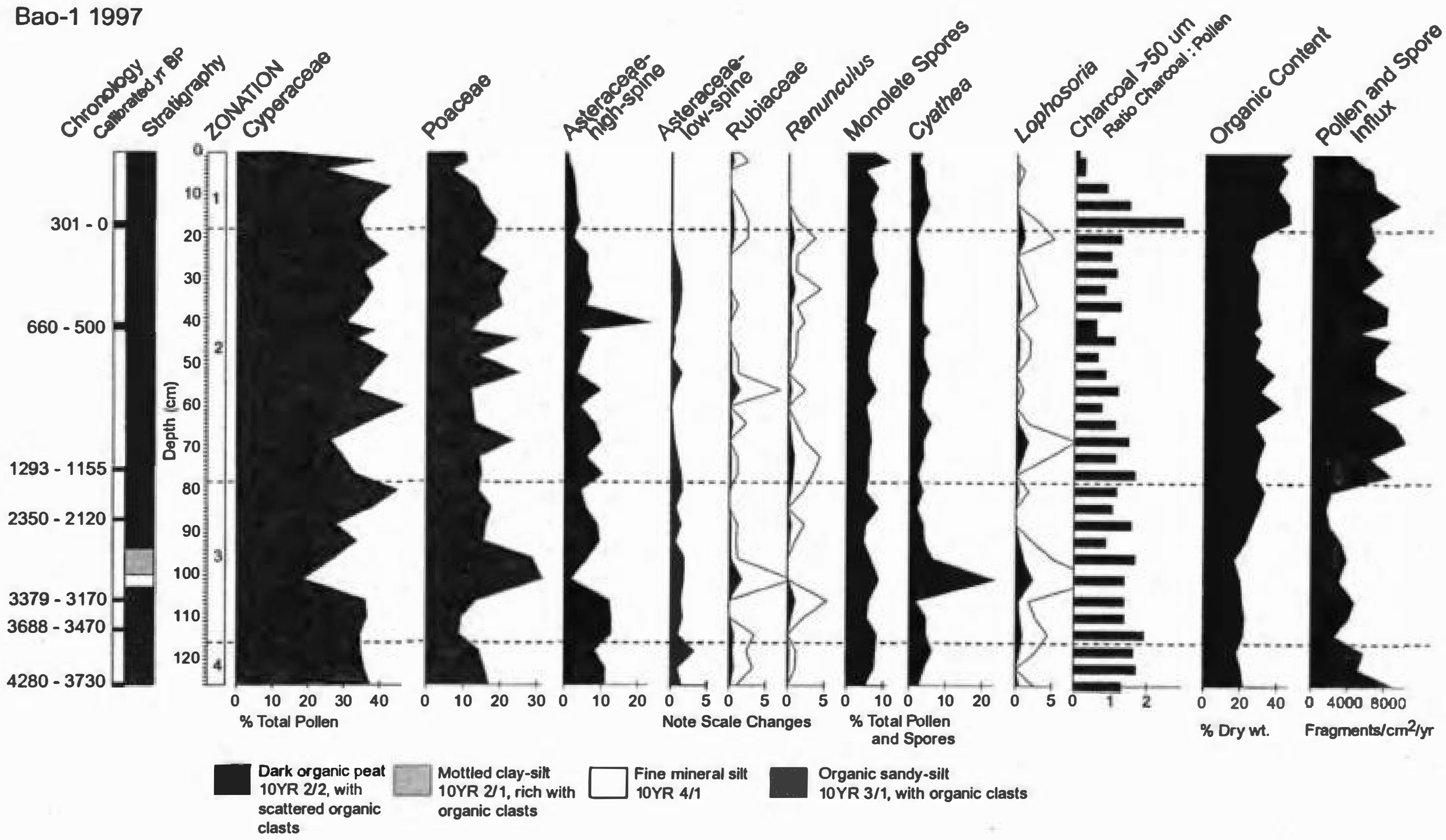

Bao-1 1997
Chronology (Calibrated yr BP)
Stratigraphy
ZONATION
Pinus
Arceuthobium
Garrya
Myrica
Myrsine
Brunellia
Weinmannia
Cecropia
Trema
Other Humid Montane Taxa
Charcoal >50 um
Ratio Charcoal : Pollen
Organic Content
Pollen and Spore Influx
301 - 0
660 - 500
1293 - 1155
2350 - 2120
3379 - 3170
3688 - 3470
4280 - 3730
Depth (cm)
0
10
20
30
40
50
60
70
80
90
100
110
120
1
2
3
4
0 10 20 30 40 50 60 70
% Total Pollen
0 5 0 5 0 5 0 5 0 5 0 5 0 5 0 5 0 5
Note Scale Changes
0 1 2
0 20 40
% Dry wt.
0 4000 8000
Fragments/cm2/yr
Dark organic peat 10YR 2/2, with scattered organic clasts
Mottled clay-silt 10YR 2/1, rich with organic clasts
Fine mineral silt 10YR 4/1
Organic sandy-silt 10YR 3/1, with organic clasts

Figure 3.6. Percentage diagram showing selected mainly herbaceous pollen taxa and pteridophyte spores for the Bao-1 1997 core. The "Rubiaceae" taxon was dominated by pollen of *Galium*, but also included pollen of *Mitracarpus*, and *Spermacoce*. Herbs in the Asteraceae family are common in the highlands and we expect that most pollen in that group represents herbaceous plants, but some may represent woody genera such as *Baccharis* and some *Senecio* species. Chronology and stratigraphy are shown at left and charcoal:pollen ratios at right.


Bao-1 1997
Chronology
Calibrated yr BP
Stratigraphy
ZONATION
Cyperaceae
Poaceae
Asteraceae-high-spine
Asteraceae-low-spine
Rubiaceae
Ranunculus
Monolete Spores
Cyathea
Lophosoria
Charcoal >50 um
Ratio Charcoal : Pollen
Organic Content
Pollen and Spore Influx
301 - 0
660 - 500
1293 - 1155
2350 - 2120
3379 - 3170
3688 - 3470
4280 - 3730
Depth (cm)
0
10
20
30
40
50
60
70
80
90
100
110
120
1
2
3
4
% Total Pollen
Note Scale Changes
% Total Pollen and Spores
% Dry wt.
Fragments/cm2/yr
0 4000 8000
Dark organic peat 10YR 2/2, with scattered organic clasts
Mottled clay-silt 10YR 2/1, rich with organic clasts
Fine mineral silt 10YR 4/1
Organic sandy-silt 10YR 3/1, with organic clasts

decline toward the surface, a pattern that reflects in part the water content of the sediments (wettest near the surface becoming drier with depth). The charcoal influx curve generally mirrors the trends in the pollen and spore influx curve, with a dramatic increase in Zone 2. Both charcoal influx and the charcoal to pollen ratios display a period of slightly lower values between ~300–1000 cal yr BP, which is less clear in the charcoal concentration curves.

Discussion

Radiocarbon Chronology

Field and laboratory evidence of a dynamic land surface history in the Bao-1 1997 bog (explained in a later section) led us to obtain a relatively high number of radiocarbon dates to cover the upper organic section of the Bao-1 1997 profile. Dates on charcoal fragments from depths of 38 cm (2126±59 ^{14}C yr BP), 48 cm (3016±49 ^{14}C yr BP), and 99 cm (5210±50 ^{14}C yr BP) were much older than dates on charcoal from nearby levels. These apparent reversals themselves offered information on environmental history. Our interpretation of these "old" dates is discussed in a later section.

Climate and Fire History

The most prominent and straightforward aspect of the environmental history recorded in the Bao bog sediments is the long and continuous history of pine dominance and fire (Figure 3.3). This history is not surprising given what Agee (1998) has characterized as an "inextricable link" between pines and fire through space and time. The Bao record provides clear evidence that fire has been an important influence on the high elevation landscapes of the Cordillera Central, even on the windward slope, for at least the past 4000 years. This result corroborates our previous findings of ubiquitous charcoal of ages between ~1200–13,000 cal yr BP (and some older) in soils and sediments from various high elevation sites in the Cordillera Central (Horn et al. 2000). The long history of highland fires contrasts sharply with the evidence from lowland sites in Haiti (Higuera-Gundy et al. 1999) and Puerto Rico (Burney et al. 1994).

Again in contrast with the records from Puerto Rico, Haiti, and the Bahamas (Kjellmark 1996), our sediment record from Valle de Bao provides no clear evidence of prehistoric human activity. People colonized the island of Hispaniola around 6000 years ago (Wilson 1997a), before the Bao-1 1997 bog originated, but probably spent little time in mountainous areas where food sources would have been scarce (Wilson 1990). Prehistoric petroglyphs in ABNP (Hoppe 1989) indicate at least some human activity in the highlands, but the archaeology of area remains little studied. Dominicans only began to exploit the highlands as a source of timber and for cattle grazing during the last century (Bolay 1997). It is likely that most of the charcoal in the Bao record was generated in fires ignited by lightning.

A dramatic decrease in charcoal in the uppermost levels of Zone 1 (probably representing ~50 years) follows a steep spike in charcoal (Figure 3.4), which marks a major fire, or a period of high fire frequency, that probably occurred over a century ago. This event or episode may or may not be related to human activity. The recent decrease in charcoal is coupled with a marked increase in pine pollen, which is unprecedented in the earlier record. Pine pollen percentages are more or less complacent throughout the record, generally remaining between 25–35% of the pollen sum, except in the uppermost levels. These percentages are consistent with percentages of pine pollen in modern surface sediments of several bogs in the Cordillera Central (Chapter 2, this document).

Pine is locally dominant, and the genus is known to produce abundant pollen that is widely dispersed (Bradshaw and Webb 1985, Fall 1992b, Jackson and Smith 1994). A portion of the pine pollen in the Bao bog sediments may originate from distant pine forests on the middle and upper slopes of the Cordillera Central, while much of the charcoal we counted (>50 µm) probably derives mainly from fires on nearby slopes (Clark 1988, Pitkänen et al. 1999).

The increase in pine pollen in the uppermost sediments probably reflects a local increase in pine around Valle de Bao and on adjacent lower slopes. The peaks may just signal regeneration after the large fire that generated the charcoal peak, or possibly following clearance of nearby forests (e.g., for grazing purposes). Alternatively, the pine pollen peaks may point to an increase in temperature minima (fewer dry season frost and freeze events) during recent times, which could allow pine to increase on the lower slopes and upper floor of the basin. Aerial photos from 1979 show a disappearance of pine in some of the upper valley reaches between that date and the earlier photo taken in 1958. The treeless upper valley subsequently reforested and remains forested at present, but the reasons for the changes are not known.

Both the pollen and spore, and the charcoal influx curves show dramatic changes that could signal significant local environmental change (Figure 3.4). Both curves show relatively high influx levels just after the formation of the bog at around 4000 cal yr BP (Zone 4), but values decline abruptly upcore and remain low until ~1200 cal yr BP. A decline of such magnitude in influx could reflect a major change in vegetation around the site, but no other sedimentary evidence (e.g., pollen percentages, or different measures of charcoal) supports such a change.

Instead, reduced pollen and spore concentrations and organic content, along with peaks in indeterminate (damaged) pollen (Figure 3.4) appear to reflect poor conditions for pollen preservation and accumulation prior to ~1500 cal yr BP. It appears that extended periods of aridity, or enhanced seasonal drying, desiccated the Bao bog at times between ~3700–1200 cal yr BP, causing deflation of sediments, and degradation of remaining pollen and spores. The lower influx levels and sedimentation rates (Figure 3.2) during that period may be due to missing sediments. Interestingly, even in the uppermost part of Zone 3 (~2500 cal yr BP) when organic content is increasing, influx of pollen and spores, and of charcoal, are at their lowest levels. This may indicate a return to a semi-permanent high water table in the bog, but still with occasional periods of desiccation and deflation. Near the boundary between Zones 3 and 2 (~1500–1200 cal yr BP), charcoal and pollen and spore concentrations and influx rise and more or less stabilize throughout Zone 2 to levels similar to those in Zone 4 around the time of bog formation, possibly suggesting an even more permanent bog.

The isotopic data from Lake Miragoane, near sea level far in the lee of the central mountain ranges of Hispaniola, indicate a relatively dry climate in the region between ~12,000–9700 cal yr BP, becoming increasingly moist until ~7800 cal yr BP, and then remaining moist until about 3400 cal yr BP. At that time, a gradual drying trend commenced lasting through the present with only brief returns to moister conditions (e.g., ~1600–900 cal yr yr BP) (Hodell et al. 1991, Curtis and Hodell 1993, Higuera-Gundy et al. 1999). This recent drying trend has also been documented in sediment records from Church's Blue Hole, Bahamas (timing uncertain due to internal problems with chronology) (Kjellmark 1996); Lake Valencia, Venezuela (Bradbury et al. 1981, Curtis et al. 1999); and Lake Chichancanab, Mexico (Hodell et al. 1995); and in geomorphic investigations of Lago Enriquillo, Dominican Republic (Mann et al. 1984, Taylor et al. 1985). Orbitally-driven increased seasonality has been used to explain these climatic trends at Lake Miragoane (Hodell et al. 1991) and Lake Valencia, Venezuela (Curtis et al. 1999). Moist conditions in the early to middle Holocene at these sites are attributed to enhanced seasonality, and the recent drying trend to decreased seasonality as perihelion shifted into Northern Hemisphere winters (and aphelion into summers) resulting in reduced N–S movement of the Intertropical Convergence Zone (ITCZ) and decreased precipitation in the circum-Caribbean region (Hodell et al. 1991, Curtis et al. 1999).

The basal date on the Bao-1 1997 sediments indicates that the bog originated around 4000 cal yr BP, which matches with the initiation of ponding at Laguna Grande de Macutico at 2048 m elevation on the leeward side of the Cordillera Central (Horn et al. in preparation). The development of bogs and ponds around 4000 cal yr BP indicates an enhancement of moisture availability at high elevations, which fits with the Miragoane record of relatively moist conditions around that time. The highest Miragoane lake levels occurred during the early Holocene (~8900–6800 cal yr BP), but high percentages of moist forest types in the Miragoane pollen record indicated that the wettest episode of the Holocene occurred between ~4400–3400 cal yr BP (Higuera-Gundy et al. 1999), about the same period in which bogs and ponds were forming in the highlands of the Dominican Republic. That the Dominican highland bogs and ponds did not form earlier, when conditions were relatively moist at Lake Miragoane, may indicate differences in the timing and nature of climatic change between the low and high elevation sites.

Peaks in pollen percentages of several broadleaf tree taxa (Figure 3.5) in the older (>~2500 yr BP, Zone 3) Bao sediments suggest that arid phases alternated with moister periods during which broadleaf forest may have expanded on the slopes above or below Valle de Bao. Analysis of modern surface pollen samples (Chapter 2, this dissertation) revealed that *Weinmannia* L. and *Brunellia* Ruiz & Pav. were especially good indicators of broadleaf forest cover. An increase in temperature minima, possibly associated with higher precipitation (cloudy skies), might also be responsible for a local increase in broadleaf species, which are sensitive to frost and cold temperatures. Upslope transport of pollen is likely in mountainous areas (Markgraf 1980, Fall 1992b), and the broadleaf pollen may have been transported from forests downslope. These forests are presently dominated by pine in their upper elevations (>1700 m), but past changes in disturbance or climate regimes might have altered the position of the ecotone between pine and broadleaf forest, and in this way affected broadleaf pollen percentages in the Bao bog sediments. The spiky pattern of the broadleaf pollen percentages may be further evidence that these moist periods were interspersed with drier intervals.

The evidence of periodic drought and a fluctuating water table between ~3700–1200 cal yr BP may relate to the orbitally forced regional drying trend identified by Hodell et al. (1991) and Curtis et al. (1999). A return to a more permanent bog, with higher organic accumulation beginning before ~1500 cal yr BP, fits with the temporary return to moister conditions found at Lake Mirgoane between ~1600–900 cal yr BP, except that the period of high-water table at Bao does not end, but continues to the present. Charcoal accumulation appears to be slightly lower in most of Zone 2 (charcoal to pollen ratio, and concentrations per wet cc sediment, Figure 3.3), which may also support the idea of moister conditions.

Although there is no associated change in pine pollen percentages, the consistent presence of *Arceuthobium* pollen beginning around 1000 cal yr BP may indicate a local increase in pine around Valle de Bao. The pollen represents *Arceuthobium bicarinatum* Urban (Viscaceae), the only known species in Hispaniola, which is an endemic dwarf mistletoe parasitic on *Pinus occidentalis* Swartz (Hawksworth and Wiens 1996). Darrow and Zanoni (1990a) estimated that *Arceuthobium* M. Bieb. had infected 15–85% of pines in the Cordillera Central. The increase in pollen of *Arceuthobium* may also (or instead) signal a change in the local fire regime. The distribution and abundance of dwarf mistletoes have been historically linked to wildfires (Wicker and Leaphart 1974, Alexander and Hawksworth 1975, Hawksworth and Wiens 1996). Frequent crown fires may limit *Arceuthobium* populations because trees can regenerate much faster than the mistletoe (Hawksworth and Wiens 1996). But spotty fires (not affecting all crowns) may actually increase dwarf mistletoe populations by leaving behind live mistletoes that can re-infest forests (Hawksworth and Wiens 1996). The increase in *Arceuthobium* pollen may hint at a shift in fire regime toward few fires overall, or fewer crown fires. The lower charcoal in Zone 2 may provide additional evidence of such a shift.

"Old" Redeposited Charcoal as Evidence of Tropical Storm Events

Though down-mixing of younger carbon is possible, we believe that the most likely explanation for the "too-old" dates in the Bao-1 chronology is the deposition of old charcoal eroded from nearby slopes during storm events. Evidence of landslides is abundant on the rugged windward slope of the Cordillera Central in the form of numerous slope scars that expose bare rock or show regenerating vegetation of various ages. Rugged topography combined with heavy orographic rainfall induces widespread slope failures, especially when high intensity precipitation occurs during tropical storm events (Hartshorn et al. 1981, personal observation). During fieldwork in January–February 1999, about four months after Hurricane Georges (September 22–23, 1998; Class IV) struck Hispaniola, we revisited our Bao-1 1997 core site to find that a debris flow from the mid slopes of Loma del Pico (Figure 3.1) had spilled onto the valley floor, reaching to within a few meters of our 1997 core site.

Hurricane Georges also produced widespread overbank debris deposits along streams in the Valle de Bao, especially in its upper reaches. The flat-bottomed Valle de Bao is drained by numerous small streams, one of which is only a short distance (several meters) from the Bao-1 bog. Having seen the impressive effects of Hurricane Georges on Valle de Bao and surrounding highland landscapes, we find it easy to envision past heavy precipitation events, which could generate substantial gully erosion on nearby slopes. These events could expose older subsurface charcoal, and transport it across the valley floor in streams or debris flows. The presence of distinct clasts (up to 1.0 cm in diameter) composed of peat and soil in the core sections is likely further indication of periodic deposition at the core site of material eroded from the surrounding slopes.

In the 99–100 cm interval, where charcoal fragments dated to between 6170–5900 cal yr BP, synchronous peaks (Figure 3.3) in Poaceae (grass) pollen, and *Cyathea* (tree fern) and *Lophosoria* spores, may be further evidence of a particularly large tropical storm event. *Cyathea arborea* (L.) Sm., a tree fern species primarily of humid montane forests in the Dominican highlands (Bolay 1997), is often a pioneer in landslide areas and slippage sites along streams (Tryon and Tryon 1982, and personal observation). *Lophosoria* is a terrestrial fern also associated with disturbed sites (Tryon and Tryon 1982). The dramatic *Cyathea* spike at 100 cm, and a peak in *Lophosoria*, may indicate a high incidence of slides and flows associated with an extreme precipitation event. The peak in Poaceae pollen may reflect grass colonization of newly deposited sediment on the bog surface. These peaks and others in several tree and shrub taxa in Zone 2 (Figure 3.5) may reflect increased disturbances on a landscape already in adjustment to changing moisture availability.

The other two dates interpreted as representing redeposited charcoal were not associated with unusual patterns in the pollen record, except that a steep spike in Asteraceae (high-spine) pollen accompanied the anomalously old charcoal at 38–40 cm (Figures 3.3, 3.6). Herbs in the Asteraceae family are most common in dry open areas of the highlands and in forests that have been "opened up" by fire (personal observation). In a study of modern pollen deposition (Chapter 2, this dissertation), all Asteraceae pollen types (high and low spine, and fenestrate) were most closely associated with pollen of Poaceae and other herbs (e.g., Rubiaceae, Cyperaceae) that reflect treeless or sparsely forested sites in the highlands. Plants in the Asteraceae could be expected to be among herbs colonizing landslides or newly deposited sediment.

Conclusions and Summary

This pollen record from a high elevation bog on the windward slope of the Cordillera Central provides the first stratigraphic evidence of past climate change and disturbance history in the Caribbean highlands. Clearly, continuous pine dominance and fire are the central themes in the 4000-year environmental history reconstructed from the

Bao-1 1997 sediment core. However, conditions in the Dominican highlands have not been placid; instead, the sediment record indicates that disturbances by fire, tropical storms, and climatic fluctuations have been integral to the highland ecosystem for millennia.

Conditions became moist enough for bog formation at around 4000 cal yr BP. Shortly thereafter, a dramatic decline in influx of pollen and spores, and of charcoal, along with low organic content and other evidence, suggest that sediments were deflated at times between about 3700–1200 cal yr BP due to periods of desiccation. Spikes in pollen of various broadleaf trees and shrubs, mainly before 2500 cal yr BP, may indicate that relatively moist conditions were interspersed with the dry periods. Deposition of "old" charcoal on the bog's surface, along with peaks in Poaceae, *Cyathea*, and *Lophosoria*, indicate the likelihood of a particularly large tropical storm event around 3000 cal yr BP. Numerous clasts of peat and soil in the core are likely signals of other high precipitation events throughout the bog's history. Throughout most of the profile, ubiquitous large charcoal (>50 μm diameter) provides evidence of the continuous influence of fire.

Unlike most other records from the lowland Caribbean and tropical Atlantic, the Bao-1 1997 sediment record provides no clear evidence of prehistoric human activity (although changes in the uppermost sediment may partly reflect historical human activity). The record includes strong signals of dry periods during the late Holocene. The timing and direction of climatic trends parallels some aspects of the Miragoane record. The match is not exact, but an exact match should not be expected given differing modern climate and controls. Further paleoecological studies are needed in the

Caribbean to refine knowledge of the timing and directions of past climatic change, and of other aspects of environmental and human history throughout the region.

CHAPTER 4

Postfire Regeneration of Pines and Shrubs in the Cordillera Central, Dominican Republic

This chapter is in preparation for submission to a vegetation/ecology journal. Aspects of the environmental and cultural setting now covered in Chapter 1 of this dissertation may be added to the manuscript before submission.

Introduction

A growing body of literature points to the importance of fire in shaping high-elevation vegetation on the neotropical mainland, especially in grass- and shrub-dominated communities (Williamson et al. 1986; Horn 1989, 1990, 1998a, 1998b; Balslev and Luteyn 1992; Verweij 1995; Ramsay and Oxley 1996; Luteyn 1999; Safford 2001). These fire-adapted plant communities show considerable overlap in floristic composition at the generic and family level, and many component taxa show consistent responses to fire, such as basal resprouting among shrubs. Rates of vegetation colonization and regrowth following disturbances in these high-elevation ecosystems are slow in comparison to those observed in neotropical lowlands.

The effects of fire and other disturbances on tropical high elevation vegetation have received much less study on Caribbean islands, where highland habitats are of limited extent and are geographically isolated. The Dominican Cordillera Central on the island of Hispaniola has several peaks that reach near to or above 3000 m, but these peaks, unlike the highest mainland peaks, never reach treeline. Above ~2000 m, forests are dominated by a single endemic pine species, *Pinus occidentalis* Swartz (West Indian pine), that may form dense stands or open woodlands that are interspersed with tussock grass savannas. Evergreen broadleaf shrubs, including many species that occur as trees in lower elevation sites, are prominent in the understory, along with the endemic tussock grass *Danthonia domingensis* Hack. & Pilger. This high mountain range is essentially an "island" within an island, harboring numerous endemic species, many of which are still being documented. This paper focuses on the ecological impacts of fire on pines and shrubs in the high elevations of the Cordillera Central.

Radiocarbon-dated charcoal in highland soils and sediments (Horn et al. 2000, Chapter 3 of this dissertation), along with ubiquitous fire-scarred pines (Speer et al. in press), indicate that fires have influenced landscapes of the Dominican highlands in both the recent and distant past, including prior to human colonization of the island. This is not surprising given the strong link between fire and pine forests around the globe (Agee 1998). Some researchers have suggested that the distribution of pine forest in mainland tropical and subtropical sites is primarily the result of a long history of natural and human-set fires (Goldammer 1993). Contemporary fires in the Dominican highlands are often attributed to ignition by people, both intentional and accidental, such as fires that escape upslope when used to clear agricultural areas (Hartshorn et al.1981, Velez 1984, Darrow and Zanoni 1990a, Bolay 1997). Natural ignitions from lightning also occur (Horn et al. 2000, Chapter 3 this dissertation).

Fire management has become a major issue in pine-forested areas of the U.S. and elsewhere, and land managers are beginning to consider the issue in the Dominican highlands. The Cordillera Central encompasses three high elevation national parks (Figure 4.1) with combined areas of ~2000 km^2 (Ottenwalder 1989) that comprise mainly landscapes dominated by pine, and mixed pine/broadleaf forest. A half century ago, Holdridge (1942) suggested the need to develop fire management plans for

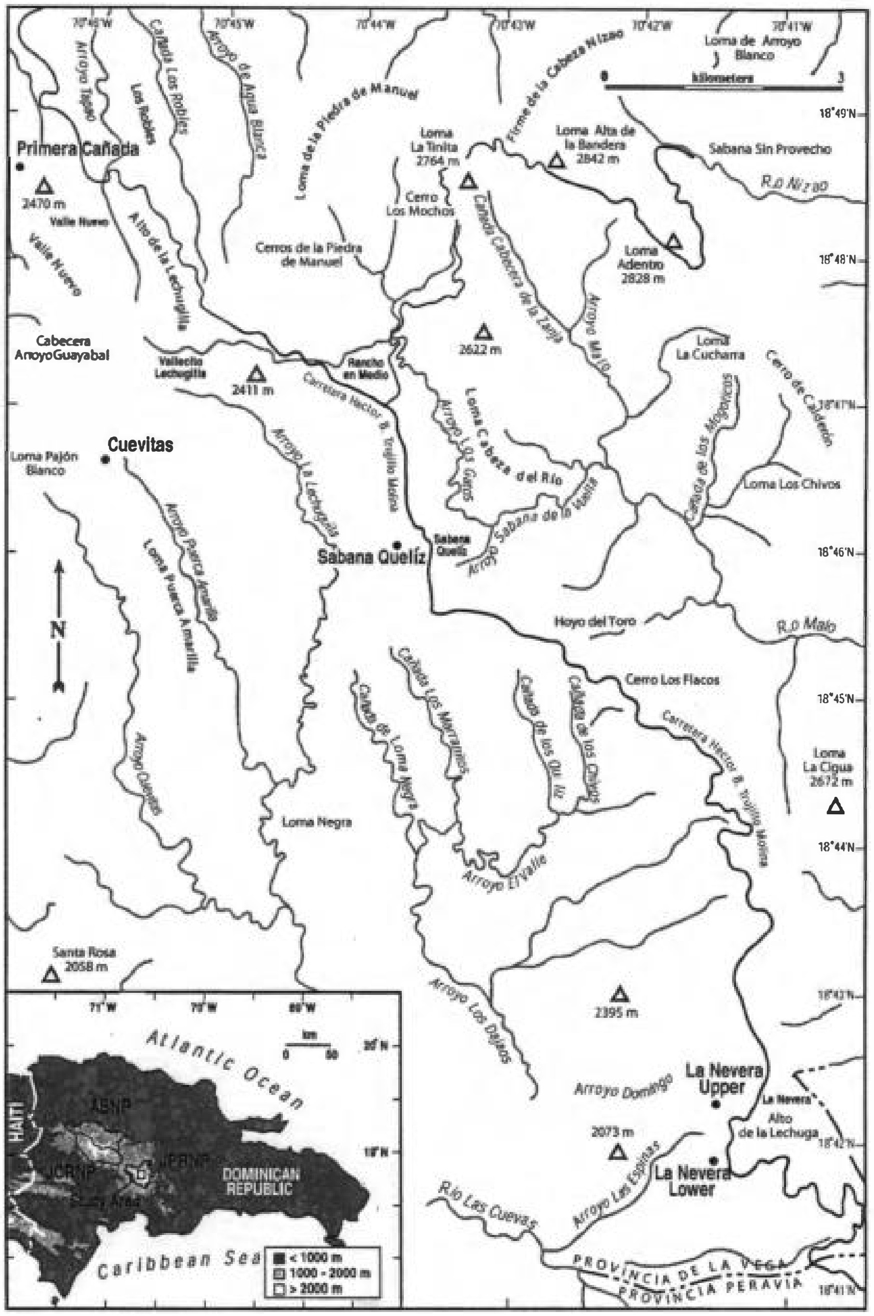


Figure 4.1. Map showing the five postfire regeneration study sites. Sites are indicated by filled circles. Two main roads are shown, Carreterra Hector B. Trujillo Molino, which transverses the entire park, and the road to Alto de la Bandera, the park's highest peak. The unimproved dirt track to the Cuevitas site is not shown. Inset shows the three national parks of the Cordillera Central, Dominican Republic (JPRNP=Juan B. Peréz Rancier National Park, ABNP=Armando Bermúdez National Park, and JCRNP=José del Carmen Ramírez National Park), and the location of the study area within Juan B. Peréz Rancier National Park (JPRNP).

P. occidentalis forests in the mountains of neighboring Haiti. At present, most fire management in the Dominican highlands centers on prevention of accidental fires, and local residents nearly always view fire as destructive. Information on the frequency, spatial distribution, and ecological effects of fire in the highlands is needed for management but is at present mostly anecdotal; detailed historical records and scientific studies are sparse. To date, only one study has looked at the effects of fire on the high elevation pinelands of the Cordillera Central. That study, in which I collaborated, investigated a single 2-year-old burn site in Juan B. Peréz Rancier National Park (JPRNP, formerly the Valle Nuevo Scientific Reserve) (Horn et al. 2001). We found high rates of resprouting by most shrub species, and evidence of pine regeneration two years after the fire. One other study (May 1997) of fire in lower elevations (1240–1300 m) of the Cordillera Central considered the effects of fire on *Magnolia pallescens* cloud forest. May (1997) found that plants resprouting from buds below ground were relatively rare compared to those that had reproduced by seeds.

This study focuses on the effects of fire on pines and shrubs at five high elevation burn sites of different ages within JPRNP (Figure 4.1). The main objective was to build on the earlier work by developing a larger dataset that can provide better understanding of the response of highland shrubs and pine to fire, and of patterns of recovery. This larger study includes older burn sites that offer greater insight on pine regeneration and rates of recovery, and sites with varied environmental characteristics, which may help to explain spatial differences in vegetation recovery.

Methods

Study Sites

JPRNP is located atop a high plateau about 60 km to the southeast of the two adjoining national parks, Armando Bermúdez National Park (ABNP), and José del Carmen Ramírez National Park (JCRNP) (Figure 4.1), which contain Hispaniola's highest peaks (>3000 m). ABNP and JCRNP are remote roadless parks, while JPRNP can be accessed by unpaved road from Constanza. JPRNP was established as the Valle Nuevo Scientific Reserve in 1983 and was recently granted national park status.

JPRNP's highest peak is Alto de la Bandera at 2842 m, and much of its land area exceeds 2000 m. While no long-term climate data exist for the park, an isohyet map for the Dominican Republic as a whole indicates annual precipitation in the park of ~1000–1600 mm (Martinson 1992). Rainfall in the highlands is strongly seasonal; little rain falls between January and March, and subfreezing nighttime temperatures and frost are common during that time. A second shorter, less intense dry season generally occurs in August.

Humid broadleaf montane forests, and mixed pine and broadleaf forests, occur in some of the lower elevations of JPRNP, mainly in its eastern portion, but most of the plateau is covered by pine forest and open pinelands in various stages of regeneration from cutting and fire (FAO 1973). Pine forests throughout the Cordillera Central were logged extensively in the mid-1900s under Dominican president Trujillo (Bolay 1997). In 1967, President Balaguer closed the sawmills and implemented a ban on the cutting of any tree on private or state land without government permission (Kustudia 1998). Even so, small-scale timber removal in the Cordillera Central continues (Kustudia 1998), perhaps preferentially in recently burned sites (Horn et al. 2001, and personal observations). More information on the history and environment of JPRNP is included in Chapter 1 of this dissertation.

I studied postfire regeneration of woody plants in five recently burned sites within the park that were relatively easily accessed; most were visible from roads (Figure 4.1, Table 4.1). All sites were between 2300 and 2440 m elevation and were located on moderate to steep slopes with thin rocky soils, except at La Nevera Upper (LNU), which had a gentle slope and deeper soil (Table 4.1). The Cuevitas (CUE), Sabana Quéliz (SAQ), and LNU sites were on relatively large single slopes that varied little in terms of aspect and gradient, while Primera Cañada (PRC) and La Nevera Lower (LNL) were collections of small hillocks with varied aspects. Primera Cañada was the highest site in the study at ~2440 m, and the subject of the Horn et al. (2001) study. The site in this study of PRC was burned in the same fire described in Horn et al. (2001), but encompasses a group of burned knolls on the crest approximately 100–200 meters to the west and southwest of the site previously examined.

Dense, continuous pine forest surrounded LNU and LNL at the south end of the reserve, while more open pinelands bordered CUE and SAQ. Pines were especially sparse for some distance beyond the recent burn at PRC, giving the appearance of especially poor pine regeneration in that area. The slope at SAQ faced a large grassland (Sabana Quéliz proper) to the south, which has been cultivated in the past and contained a settlement during the time of logging and for some time after. It is now clear of all but one building, but the presence of a number of European weeds attests to its history of human disturbance.

Table 4.1. Summary of study site information. Latitude and longitude, and elevations, are approximate and based on a 1:50,000 topographic map: Sabana Quéliz, Edition 1, Series E733, Sheet 6072 II, assisted by a handheld GPS. The "Average Slope" is the average of all slope measurements taken along all belt transects at each site. "Total Area Surveyed" is the total area of all belt transects combined, and "Total # Individuals" includes all plants measured at each site. The fire dates and ignition sources are based on information from local informants; no historical documentation was available for any of the fires. The "Yrs. Since Fire" column is reported with respect to the time of data collection (1999).

Site	Northing Easting (UTM)	Elevation (m)	Average Slope	Total Area Surveyed Total # Individuals	Approximate Fire Date / Yrs. Since Fire	Probable Ignition Source
Primera Cañada	2080700 N 321700 E	2440	23°	570 m^2 356	1996 / 3	Lightning
Cuevitas	2077000 N 322700 E	2400	34°	612 m^2 351	1992 / 7	Human
La Nevera Upper	2068700 N 330700 E	2380	11°	340 m^2 638	1996 / 3	Human
La Nevera Lower	2068300 N 330400 E	2300	20°	720 m^2 784	1994 / 5	Human
Sabana Quéliz	2075900 N 326600 E	2300	19°	320 m^2 119	1997 / 2	Lightning

I obtained information on the dates and ignition sources of all fires from local informants, but no absolutely reliable information or documentation was available. A major fire, which burned much of JPRNP in 1983 (Martínez and Hernández 1984, Martínez 1990) may have burned some or all of the study sites.

Field Sampling

I sampled vegetation in July 1999, following methods adapted from postfire regeneration studies carried out in the high elevation páramos of Costa Rica (Williamson et al. 1986, Horn 1989), and the previous study in the Dominican highlands (Horn et al. 2001). The vegetation at the sites consisted variously of surviving and regenerating pines and shrubs; the tussock grass, *Danthonia domingensis*; other grasses and sedges; a variety of herbs; and pteridophytes, especially *Pteridium aquilinum* L. (bracken fern) and *Lophosoria quadripinnata* (Gmel) C. Chr. at some sites. I reconstructed prefire woody vegetation stature, composition, and density based on standing, intact dead stems killed in previous fires. Burned woody stems are typically preserved for long periods in cool, high-elevation environments owing to reduced rates of decay (Horn 1989).

I established a baseline along the contour of each slope studied, and placed randomly located 2 m belt transects perpendicular to it. I recorded each transect's slope and aspect using one or more measurements as needed. The length, orientation, and steepness of each belt transect varied with the size and topography of the sites; the total area sampled at each site also varied (Table 4.1). An elevation was assigned to each site based on interpolation of contours from the 1:50,000 Sabana Quéliz topographic map, at locations identified with the assistance of a handheld GPS.

I identified and measured all woody plants (except *Rubus* L. and *Gaultheria domingensis* Urban, see below) within the belt transects and assigned them to a fire response category as follows: "dead" (fire-killed), "resprouter" (experienced complete crown loss but later resprouted from the base), "fire survivor" (scorched, but with some portion of the crown surviving and producing new growth), or "postfire colonist" (juveniles with no sign of charring that established in space not previously occupied by a mature individual). I considered each well-defined clump of stems an individual, except when underground connections were clearly visible. I identified dead shrubs based on stem architecture, and bark and wood characteristics.

I estimated prefire heights for the "dead" individuals and "resprouters" by measuring the tallest dead stem, and established postfire height of "resprouters" and "fire survivors" by measuring the tallest living stem. If the tallest dead stem was broken, it was measured, but omitted from the analysis, so that sample size (n) is typically smaller for calculations based on dead stems than on live stems. Prefire height data underestimate true prefire height, as the fine stem termini are easily burned away by the fire, or destroyed by wind or other disturbances. I also measured the basal diameters of pine boles (standing and downed), and the largest dead and live stems of the shrubs.

I ran correlations on the paired data (including only unbroken prefire stems) to check whether prefire heights and diameter were associated with postfire heights and diameters, respectively. To compare rates of regrowth of shrub taxa across sites, using means derived from different samples sizes, I calculated the standard error of the ratio of means using an estimator formula (Thompson 1992) as follows: I computed the means of paired samples X (postfire measurements) and Y (prefire measurements), denoted X_S (n includes only postfire measurements with a paired prefire measurement) and Y_S, and the mean of larger sample X, denoted X_L (n includes all postfire measurements). Next, I calculated the ratio of means $r = Y_S/X_S$ and $r = Y_S/X_L$, and a predicted Y for every X in the smaller group of paired samples (r*x), and the mean-square of the differences between Y and r*X as $s_r^2 = \frac{\sum_{i=1}^{n}(y_i - rx_i)^2}{n-1}$. Then, I computed the variance of r as $\mathrm{var}(r) = \frac{s_r^2}{n\bar{x}^2}$ (Cochran 1977), and the standard error of r by taking the square root of var(r). Finally, I constructed lower and upper confidence interval endpoints as [r ± *t* stderr(r)] and compared whether the confidence intervals overlapped (no statistical difference), or were distinct.

Rubus spp. (blackberry, Rosaceae) and *Gaultheria domingensis* (Ericaceae) occasionally appeared in the study sites as prostrate, trailing, or erect woody stems typically <50 cm in height. Both taxa can produce numerous similar-sized stems, by underground rhizomes in the case of *Gaultheria*, or by root suckering and tip end rooting in *Rubus*, making it difficult to determine individuality. In this study, I focused on regeneration of pine and the larger shrubs and did not include *Rubus* and *Gaultheria* stems.

Three species of *Lyonia* Nuttall (Ericaceae) are common in JPRNP (Judd 1995), but two were particularly difficult to distinguish in the field from mainly sterile or juvenile specimens. Hybridization occurs between species (Judd 1981), and further complicates field identification. I distinguished the species most common in JPRNP, *Lyonia heptamera* Urban (just those that had cordate leaf bases), but in order to avoid misidentification, grouped the other species, mainly *L. tuerkheimii* Urban and *L. urbaniana* (Sleumer) Jiménez, as "*Lyonia* spp." The group may also include some juvenile *L. heptamera* that did not display the characteristic cordate leaf bases, but these are probably rare instances. Voucher specimens reside at the University of Tennessee herbarium.

Results

Fire Response

Most of the woody individuals enumerated belonged to one of 10 shrub species or the "*Lyonia* spp." group (Table 4.2 lists shrub species and authorities), or were native pines. *Pinus occidentalis*, *Baccharis myrsinites*, *Lyonia heptamera*, *Myrica picardae*, and *Myrsine coriacea* were by far the most abundant species. Only *Ilex*, *Myrica*, and pine appeared in all sites. PRC had the highest woody species richness, containing pine and representatives of all 11 shrub taxa.

All of the shrub taxa are capable of resprouting after fire; most resprouted at high rates (Table 4.2). Only three species exhibited rates below 90% and two of those had very small sample sizes. *Baccharis* had the lowest resprouting rate (56.3%) among common shrubs.

All sites appear to have been nearly completely burned, as very few above-ground stems survived the fires (Table 4.3). Among shrub species, resprouting was by far the most common response; 88.1% (n=957) of the prefire shrubs (all sites combined) resprouted after fire. LNU and LNL had especially high percentages (78.0% and 51.7%

Table 4.2. Resprouting rates for each shrub taxon in all sites combined, listed by rank. Sample size includes all the prefire shrubs with complete canopy loss.

Taxon	Family	Resprouting Rate (%)	Sample Size (n)
Eupatorium illitum Urban	Asteraceae	100.0	30
Weinmannia pinnata L.	Cunoniaceae	100.0	6
Myrsine coriacea (Sw.) R.Br.	Myrsinaceae	99.5	213
Ilex tuerkheimii Loes.	Aquifoliaceae	98.2	54
Lyonia heptamera Urban	Ericaceae	95.8	189
Myrica picardae Krug & Urban	Myricaceae	94.9	215
Senecio picardae Krug & Urban	Asteraceae	94.6	56
Lyonia spp.	Ericaceae	94.4	18
Garrya fadyenii Hook.	Garryaceae	80.0	10
Bocconia frutescens L.	Papaveraceaeae	75.0	4
Baccharis myrsinites (Lam.) Pers.	Asteraceae	56.3	135

Table 4.3. Fire responses of shrubs and pine at each of the 5 study sites.

Site (yrs since fire)	Response Category % (n)							
Taxon	Dead		Resprouter		Fire Survivor		Postfire Colonist	
Primera Cañada (~3)								
Baccharis myrsinites	65.2	(15)	13.0	(3)	0.0	(0)	21.7	(5)
Bocconia frutescens	0.0	(0)	100.0	(1)	0.0	(0)	0.0	(0)
Eupatorium illitum	0.0	(0)	100.0	(1)	0.0	(0)	0.0	(0)
Garrya fadyenii	16.7	(1)	66.7	(4)	0.0	(0)	16.7	(1)
Ilex tuerkheimii	4.0	(1)	72.0	(18)	4.0	(1)	20.0	(5)
Lyonia heptamera.	3.8	(2)	92.5	(49)	1.9	(1)	1.9	(1)
Lyonia spp.	50.0	(1)	50.0	(1)	0.0	(0)	0.0	(0)
Myrica picardae	4.1	(3)	93.2	(68)	2.7	(2)	0.0	(0)
Myrsine coriacea	0.0	(0)	73.5	(100)	0.7	(1)	25.7	(35)
Senecio picardae	9.1	(3)	87.9	(29)	0.0	(0)	3.0	(1)
Weinmannia pinnata	0.0	(0)	66.7	(2)	33.3	(1)	0.0	(0)
% Totals for Shrubs	**7.3**	**(26)**	**77.5**	**(276)**	**1.7**	**(6)**	**13.5**	**(48)**
Pinus occidentalis	100.0	(11)	0.0	(0)	0.0	(0)	0.0	(0)
Cuevitas (~7)								
Baccharis myrsinites	16.7	(2)	0.0	(0)	0.0	(0)	83.3	(10)
Eupatorium illitum	0.0	(0)	64.4	(29)	0.0	(0)	35.6	(16)
Garrya fadyenii	10.0	(1)	40.0	(4)	20.0	(2)	30.0	(3)
Ilex tuerkheimii.	0.0	(0)	20.0	(3)	6.7	(1)	73.3	(11)
Lyonia heptamera	3.8	(4)	90.4	(94)	2.9	(3)	2.9	(3)
Myrica picardae	1.9	(1)	67.3	(35)	1.9	(1)	28.8	(15)
Senecio picardae	0.0	(0)	27.6	(8)	13.8	(4)	58.6	(17)
% Totals for Shrubs	**3.0**	**(8)**	**64.8**	**(173)**	**4.1**	**(11)**	**28.1**	**(75)**
Pinus occidentalis	12.0	(10)	0.0	(0)	8.0	(7)	80.0	(67)
La Nevera Upper (~3)								
Baccharis myrsinites	3.9	(14)	8.4	(30)	0.0	(0)	87.7	(314)
Ilex tuerkheimii	0.0	(0)	70.8	(17)	0.0	(0)	29.2	(7)
Lyonia heptamera	0.0	(0)	71.4	(20)	0.0	(0)	28.6	(8)
Lyonia spp.	0.0	(0)	0.0	(0)	0.0	(0)	100.0	(1)
Myrica picardae	0.0	(0)	69.2	(9)	0.0	(0)	30.8	(4)
Myrsine coriacea	0.0	(0)	22.2	(4)	0.0	(0)	77.8	(14)
Weinmannia pinnata	0.0	(0)	100.0	(4)	0.0	(0)	0.0	(0)
% Totals for Shrubs	**3.1**	**(14)**	**18.8**	**(84)**	**0.0**	**(0)**	**78.0**	**(348)**
Pinus occidentalis	92.2	(177)	0.0	(0)	2.1	(4)	5.7	(11)

Table 4.3. continued.

Site (yrs since fire)	Response Category % (n)							
Taxon	Dead		Resprouter		Fire Survivor		Postfire Colonist	
La Nevera Lower (~5)								
Baccharis myrsinites	18.6	(27)	28.3	(41)	0.0	(0)	53.1	(77)
Bocconia frutescens	25.0	(1)	50.0	(2)	0.0	(0)	25.0	(1)
Garrya fadyenii	0.0	(0)	0.0	(0)	0.0	(0)	100.0	(1)
Ilex tuerkheimii	0.0	(0)	72.2	(13)	0.0	(0)	27.8	(5)
Myrica picardae	6.8	(6)	76.1	(67)	0.0	(0)	17.0	(15)
Myrsine coriacea	0.0	(0)	33.6	(100)	2.7	(8)	63.8	(190)
Senecio picardae	0.0	(0)	85.7	(6)	0.0	(0)	14.3	(1)
% Totals for Shrubs	**6.1**	**(34)**	**40.8**	**(229)**	**1.4**	**(8)**	**51.7**	**(290)**
Pinus occidentalis	89.2	(199)	0.0	(0)	2.7	(6)	8.1	(18)
Sabana Quéliz (~2)								
Baccharis myrsinites	25.0	(1)	50.0	(2)	0.0	(0)	25.0	(1)
Ilex tuerkheimii	0.0	(0)	100.0	(2)	0.0	(0)	0.0	(0)
Lyonia heptamera	6.9	(2)	62.1	(18)	0.0	(0)	31.0	(9)
Lyonia spp.	0.0	(0)	80.0	(16)	0.0	(0)	20.0	(4)
Myrica picardae	3.8	(1)	96.2	(25)	0.0	(0)	0.0	(0)
Myrsine coriacea	4.3	(1)	34.8	(8)	8.7	(2)	52.2	(12)
Senecio picardae	0.0	(0)	90.9	(10)	0.0	(0)	9.1	(1)
% Totals for Shrubs	**4.3**	**(5)**	**70.4**	**(81)**	**1.7**	**(2)**	**23.5**	**(27)**
Pinus occidentalis	100.0	(4)	0.0	(0)	0.0	(0)	0.0	(0)

respectively) of postfire colonists, while the other sites were mainly composed of resprouting stems (Table 4.3).

Pine trees fared poorly overall (Table 4.4), with >50% mortality at all sites. The highest survival rate was at CUE where about 41% (n=17) of the prefire individuals survived. Prefire pine populations were low in all but LNU and LNL, and in those sites pines were nearly extirpated (Tables 4.5–4.9). In PRC and SAQ, all pines were dead, even those with stem diameters larger than 20 cm; however, some individuals at those sites and in CUE appeared to have died in earlier fires and some were cut stumps that had been harvested before or after death.

Prefire heights were significantly associated with postfire heights for seven taxa, and prefire diameters were significantly associated with postfire diameters for five of the seven. However, relationships were not especially strong in most cases (Table 4.10). Comparing by site, shrubs at CUE and PRC exhibited the largest absolute growth rates. Postfire colonists were by far the largest in CUE, while prefire shrubs were shortest and had the smallest stem diameters in LNU and LNL. *Garrya* and *Senecio*, both more upright shrubs with fewer stems than some of the other species, tended to show the fastest growth in height. There was wide between-site variation in species that gained stem diameter size most quickly.

Comparisons of shrub recovery across sites revealed a general trend toward greater recovery in sites with older fire dates (Figure 4.2). Tukey tests revealed differences at the $P<0.20$ level, but not at the $P<0.05$ level. *Lyonia heptamera*, *Myrica*, and *Myrsine* exhibited differences in percent height recovery, and *Myrica* and *Senecio* in percent diameter recovery, in some sites. Shrubs recovered height much more quickly

Table 4.4. Survival rates of *Pinus occidentalis* by size classes. Includes combined data from all sites, but excludes dead trees that appeared to have died in previous fires, and a few for which the cause of mortality was unclear (e.g., rotted stumps). Most of these data were from LNU and LNL, the sites that had large pine populations. (Yates' chi-square, $P<0.01$; Kent and Coker 1992)

Basal Diameter (cm)	Survival Rate (%)	Sample Size (n)
0.0–12.9	0.0	320
≥13.0	22.7	75

Table 4.5. Mean heights (A.) and diameters (B.) ± SD (cm) of dead and living shrubs at the Primera Cañada site an estimated three years after last fire. The letters "nd" (no data) indicate that stems were present but broken, missing, or otherwise not used in the analysis. Sample sizes for prefire heights are lower than for postfire due to exclusion of broken dead stem measurements from calculations. Other discrepancies between samples sizes here and in other tables or figures result from missing values.

A. HEIGHT	Dead	Resprouter		Fire Survivor	Postfire Colonist
Taxon	Prefire (n)	Prefire (n)	Postfire (n)	Postfire (n)	Postfire (n)
B. myrsinites	142.7 ± 32.2 (15)	81.3 ± 26.7 (3)	59.7 ± 9.5 (3)	None	43.0 ± 15.5 (7)
E. illitum	None	10.0 (1)	30.0 (1)	None	None
G. fadyenii	150.0 (1)	167.0 ± 84.9 (2)	140.3 ± 25.0 (4)	None	36.0 (1)
I. tuerkheimii	54.0 (1)	86.6 ± 44.3 (12)	63.9 ± 32.1 (23)	120.0 (1)	48.6 ± 16.3 (6)
L. heptamera	144.5 ± 51.6 (2)	118.2 ± 42.4 (45)	81.2 ± 28.8 (48)	37.0 (1)	10.0 (1)
Lyonia spp.	120.0 (1)	203.0 (1)	144.0 (1)	None	None
M. picardae	82.7 ± 17.8 (3)	106.2 ± 43.4 (62)	55.1 ± 23.7 (68)	88.5 ±54.5 (2)	None
M. coriaceae	None	107.8 ± 49.8 (69)	66.1 ± 24.8 (100)	64.0 (1)	42.7 ± 14.7 (35)
S. picardae	141.3 ± 21.4 (3)	136.8 ± 31.0 (29)	84.2 ± 24.6 (29)	None	90.0 (1)
W. pinnata	None	262.5 ±116.7 (2)	89.0 ± 9.9 (2)	260.0 (1)	None
P. occidentalis	nd	None	None	None	None

B. DIAMETER	Dead	Resprouter		Fire Survivor	Postfire Colonist
Taxon	Prefire (n)	Prefire (n)	Postfire (n)	Postfire (n)	Postfire (n)
B. myrsinites	3.5 ± 1.3 (15)	1.9 ± 0.8 (3)	0.9 ± 0.2 (3)	None	0.4 ± 0.1 (5)
E. illitum	None	0.9 (1)	0.2 (1)	None	None
G. fadyenii	2.2 (1)	3.3 ± 1.4 (4)	1.4 ± 0.7 (4)	None	0.7 (1)
I. tuerkheimii	1.3 (1)	1.5 ± 0.7 (23)	0.9 ± 0.4 (23)	2.1 (1)	0.9 ± 0.3 (5)
L. heptamera	3.0 ± 0.1 (2)	2.6 ± 1.1 (48)	1.6 ± 0.8 (48)	0.7 (1)	0.4 (1)
Lyonia spp.	6.5 (1)	3.4 (1)	1.8 (1)	None	None
M. picardae	1.7 ± 0.4 (3)	2.7 ± 1.2 (67)	1.0 ± 0.4 (68)	2.6 ± 1.0 (2)	None
M. coriaceae	None	1.3 ± 0.8 (99)	0.9 ± 0.4 (100)	4.2 (1)	0.5 ± 0.2 (35)

Table 4.5. Continued.

B. DIAMETER	Dead	Resprouter		Fire Survivor	Postfire Colonist
Taxon	Prefire (n)	Prefire (n)	Postfire (n)	Postfire (n)	Postfire (n)
S. picardae	2.5 ± 0.6 (3)	1.9 ± 0.7 (29)	0.9 ± 0.3 (29)	None	0.5 (1)
W. pinnata	None	2.1 ± 1.5 (2)	0.9 ± 0.2 (2)	4.2 (1)	None
P. occidentalis	23.6 ± 17.9 (11)	None	None	None	None

Table 4.6. Mean heights (A.) and diameters (B.) ± SD (cm) of dead and living shrubs at the Cuevitas site an estimated seven years after last fire. The letters "nd" (no data) indicate that stems were present but broken, missing, or otherwise not used in the analysis. Sample sizes for prefire heights are lower than for postfire due to exclusion of broken dead stem measurements from calculations. Other discrepancies between samples sizes here and in other tables or figures result from missing values.

A. HEIGHT	Dead	Resprouter		Fire Survivor	Postfire Colonist
Taxon	Prefire (n)	Prefire (n)	Postfire (n)	Postfire (n)	Postfire (n)
B. myrsinites	103 ± 18.4 (2)	None	None	None	89.5 ± 29.5 (10)
E. illitum	None	76.5 ± 24.5 (11)	90.1 ± 21.2 (29)	None	102.9 ± 39.7 (16)
G. fadyenii	nd	215.0 (1)	221.3 ± 60.9 (3)	130.5 ± 122.3 (2)	66.1 ± 25.0 (7)
I. tuerkheimii	None	49.0 ± 5.7 (2)	81.0 ± 12.7 (2)	90.0 (1)	80.5 ± 22.9 (11)
L. heptamera	44.5 ± 15.3 (4)	83.6 ± 39.3 (52)	94.3 ± 36.4 (101)	61.7 ± 14.2 (3)	68.0 ± 6.1 (3)
M. picardae	nd	93.8 ± 47.1 (8)	94.1 ± 33.8 (35)	120.0 (1)	71.5 ± 24.1 (15)
S. picardae	None	86.0 ± 68.1(3)	117.0 ± 47.4 (8)	88.0 ± 31.7 (4)	76.6 ± 28.4 (17)
P. occidentalis	nd	None	None	All > 8 m (7)	105.9 ± 66.2 (67)

B. DIAMETER	Dead	Resprouter		Fire Survivor	Postfire Colonist
Taxon	Prefire (n)	Prefire (n)	Postfire (n)	Postfire (n)	Postfire (n)
B. myrsinites	1.7 ± 0.42 (2)	None	None	None	1.0 ± 0.55 (10)
E. illitum	None	0.9 ± 0.4 (29)	0.8 ± 0.2 (29)	None	0.9 ± 0.3 (16)
G. fadyenii	1.4 (1)	5.2 ± 4.5 (2)	3.0 ± 0.5 (3)	3.6 ± 4.8 (2)	0.6 ± 0.2 (7)
I. tuerkheimii	None	2.4 ± 1.3 (3)	1.5 ± 0.7 (3)	1.0 (1)	1.3 ± 0.5 (11)
L. heptamera	2.9 ± 0.7 (4)	2.4 ± 1.1 (101)	1.8 ± 0.7 (101)	1.7 ± 0.7 (3)	1.2 ± 0.6 (3)
M. picardae	1.9 (1)	2.4 ± 1.4 (26)	2.0 ± 0.9 (50)	1.3 ± 0.7 (15)	1.1 (1)
S. picardae	None	1.5 ± 0.6 (8)	1.5 ± 0.6 (8)	1.4 ± 0.6 (4)	0.9 ± 0.6 (17)
P. occidentalis	18.2 ± 14.3 (10)	None	None	20.5 ± 5.4 (7)	1.6 ± 1.1 (67)

Table 4.7. Mean heights (A.) and diameters (B.) ± SD (n) of dead and living shrubs at the La Nevera Upper site an estimated five years after last fire. The letters "nd" (no data) indicate that stems were present but broken, missing, or otherwise not used in the analysis. Sample sizes for prefire heights are lower than for postfire due to exclusion of broken dead stem measurements from calculations. Other discrepancies between samples sizes here and in other tables or figures result from missing values.

A. HEIGHT	Dead	Resprouter		Fire Survivor	Postfire Colonist
Taxon	Prefire (n)	Prefire (n)	Postfire (n)	Postfire (n)	Postfire (n)
B. myrsinites	101.0 ± 79.6 (7)	92.2 ± 28.0 (12)	75.9 ± 27.2 (30)	None	42.5 ± 25.0 (314)
I. tuerkheimii	None	70.4 ± 41.9 (12)	33.2 ± 21.8 (17)	None	22.3 ± 7.7 (7)
L. heptamera	None	72.5 ± 47.8 (17)	49.4 ± 24.6 (20)	None	41.3 ± 9.1 (8)
Lyonia spp.	None	None	None	None	30.0 (1)
M. picardae	None	106.5 ± 30.4 (2)	20.2 ± 9.6 (9)	None	35.5 ± 16.9 (4)
M. coriaceae	None	79.0 ± 60.8 (2)	48.3 ± 35.0 (4)	None	26.9 ±16.7 (14)
W. pinnata	None	147.3 ± 97.6 (3)	53.0 ± 70.4 (3)	None	None
P. occidentalis	nd	None	None	nd	34.5 ± 28.8 (11)

B. DIAMETER	Dead	Resprouter		Fire Survivor	Postfire Colonist
Taxon	Prefire (n)	Prefire (n)	Postfire (n)	Postfire (n)	Postfire (n)
B. myrsinites	3.2 ± 1.6 (14)	1.8 ± 1.0 (29)	1.5 ± 0.6 (30)	None	0.7 ± 0.5 (314)
I. tuerkheimii	None	1.6 ± 1.0 (17)	0.5 ± 0.3 (17)	None	0.5 ± 0.2 (7)
L. heptamera	None	1.8 ± 1.1 (20)	1.2 ± 0.7 (20)	None	0.7 ± 0.3 (8)
Lyonia spp.	None	None	None	None	0.3 (1)
M. picardae	None	1.5 ± 1.2 (8)	0.6 ± 0.4 (9)	None	0.4 ± 0.2 (4)
M. coriaceae	None	1.0 ± 0.5 (4)	0.7 ± 0.4 (4)	None	0.4 ± 0.2 (14)
W. pinnata	None	1.2 ± 0.8 (4)	0.9 ± 0.7 (4)	None	None
P. occidentalis	7.6 ± 17.4 (177)	None	None	13.6 ± 0.3 (4)	0.8 ± 0.5 (11)

Table 4.8. Mean heights (A.) and diameters (B.) ± SD (n) of dead and living shrubs at the La Nevera Lower site an estimated five years after last fire. The letters "nd" (no data) indicate that stems were present but broken, missing, or otherwise not used in the analysis. Sample sizes for prefire heights are lower than for postfire due to exclusion of broken dead stem measurements from calculations. Other discrepancies between samples sizes here and in other tables or figures result from missing values.

A. HEIGHT	Dead	Resprouter		Fire Survivor	Postfire Colonist
Taxon	Prefire (n)	Prefire (n)	Postfire (n)	Postfire (n)	Postfire (n)
B. myrsinites	122 ± 61.7 (13)	74.2 ± 19.3 (21)	72.5 ± 18.9 (41)	None	63.4 ± 24.5 (76)
B. frutescens	64.0 (1)	74.0 ± 36.8 (2)	98.3 ± 32.2 (2)	None	95.0 (1)
G. fadyenii	None	None	None	None	54.0 (1)
I. tuerkheimii	None	74.3 ± 58.0 (10)	56.9 ± 26.8 (13)	None	57.0 ± 21.7 (5)
M. picardae	44.8 ± 21.3 (6)	57.1 ± 34.7 (45)	49.8 ± 18.4 (67)	None	44.1 ± 26.0 (15)
M. coriacea	None	33.0 ± 23.8 (39)	52.0 ± 23.5 (100)	31.1 ± 13.2 (8)	39.9 ± 17.5 (190)
S. picardae	None	83.2 ± 50.4 (6)	93.0 ± 28.8 (6)	None	57.0 (1)
P. occidentalis	nd	None	None	nd	48.1 ± 26.8 (18)

B. DIAMETER	Dead	Resprouter		Fire Survivor	Postfire Colonist
Taxon	Prefire (n)	Prefire (n)	Postfire (n)	Postfire (n)	Postfire (n)
B. myrsinites	3.0 ± 0.9 (27)	2.0 ± 1.0 (38)	1.3 ± 0.6 (41)	None	1.0 ± 0.6 (76)
B. frutescens	6.6 (1)	1.0 ± 0.9 (2)	2.4 ± 0.6 (2)	None	1.6 (1)
G. fadyenii	None	None	None	None	0.5 (1)
I. tuerkheimii	None	2.2 ± 1.5 (13)	1.4 ± 0.7 (13)	None	1.3 ± 0.3 (4)
M. picardae	3.1 ± 1.5 (6)	2.2 ± 1.2 (67)	1.4 ± 0.5 (66)	None	1.1 ± 0.4 (15)
M. coriacea	None	1.1 ± 0.8 (97)	0.8 ± 0.6 (99)	0.7 ± 0.5 (8)	0.6 ± 0.3 (190)
S. picardae	None	2.1 ± 1.3 (6)	1.6 ± 0.4 (6)	None	0.7 (1)
P. occidentalis	10.1 ± 8.3 (199)	None	None	24.4 ± 8.6 (6)	1.0 ± 0.5 (18)

Table 4.9. Mean heights (A.) and diameters (B.) ± SD (n) of dead and living shrubs at the Sabana Quéliz site an estimated two years after last fire. The letters "nd" (no data) indicate that stems present but broken, missing, or otherwise not used in the analysis. Sample sizes for prefire heights are lower than for postfire due to exclusion of broken dead stem measurements from calculations. Other discrepancies between samples sizes here and in other tables or figures result from missing values.

A. HEIGHT	Dead	Resprouter		Fire Survivor	Postfire Colonist
Taxon	Prefire (n)	Prefire (n)	Postfire (n)	Postfire (n)	Postfire (n)
B. myrsinites	160.0 (1)	121.5 (1)	58.0 (1)	None	27.0 (1)
I. tuerkheimii	None	79.0 (1)	73.0 (1)	None	None
L. heptamera	37.5 ± 17.7 (2)	145.2 ± 58.3 (15)	84.0 ± 30.4 (18)	None	50.1 ± 17.5 (9)
Lyonia spp.	None	56.7 ± 43.5 (11)	64.3 ± 32.4 (16)	None	56.0 ± 32.7 (4)
M. picardae	91.0 (1)	100.2 ± 42.9 (18)	47.1 ± 31.3 (25)	None	None
M. coriaceae	131.0 (1)	169.5 ± 43.8 (3)	62.0 ± 15.9 (3)	97.0 ± 38.2 (2)	49.7 ± 22.5 (12)
S. picardae	None	158.6 ± 69.6 (9)	89.8 ± 41.8 (10)	None	72.0 (1)
P. occidentalis	nd	None	None	None	None

B. DIAMETER	Dead	Resprouter		Fire Survivor	Postfire Colonist
Taxon	Prefire (n)	Prefire (n)	Postfire (n)	Postfire (n)	Postfire (n)
B. myrsinites	4.0 (1)	1.6 ± 1.3 (2)	0.3 ± 0.1 (2)	None	0.5 (1)
I. tuerkheimii	None	1.37 ± 1.9 (3)	0.87 ± 0.55 (3)	None	None
L.heptamera	0.5 ± 0.2 (2)	2.9 ± 1.8 (18)	1.5 ± 0.6 (18)	None	0.8 ± 0.3 (9)
Lyonia spp.	None	1.4 ± 1.1 (12)	0.9 ± 0.5 (12)	None	0.9 ± 0.6 (4)
M. picardae	1.5 (1)	2.8 ± 1.2 (25)	1.0 ± 0.6 (25)	None	None
M. coriaceae	2.9 (1)	2.5 ± 0.5 (3)	0.9 ± 0.4 (3)	1.7 ± 1.4 (2)	0.6 ± 0.3 (12)
S. picardae	None	2.2 ± 1.5 (10)	0.9 ± 0.4 (10)	None	0.5 (1)
P. occidentalis	21.8 ± 2.4 (4)	None	None	None	None

Table 4.10. Correlations between prefire and postfire heights (A.) and diameters (B.) by taxon. Data are from all sites combined. Only taxa with statistically significant correlations (P<0.05) are listed.

A. Taxon	R-value
Lyonia spp.	0.82
Eupatorium illitum	0.68
Myrsine coriaceae	0.58
Senecio picardae	0.51
Lyonia heptamera	0.44
Ilex aquifoliaceae	0.42
Myrica picardae	0.32

B. Taxon	R-value
Lyonia spp.	0.67
Ilex aquifoliaceae	0.64
Myrsine coriaceae	0.45
Baccharis myrsinites	0.35
Senecio picardae	0.34

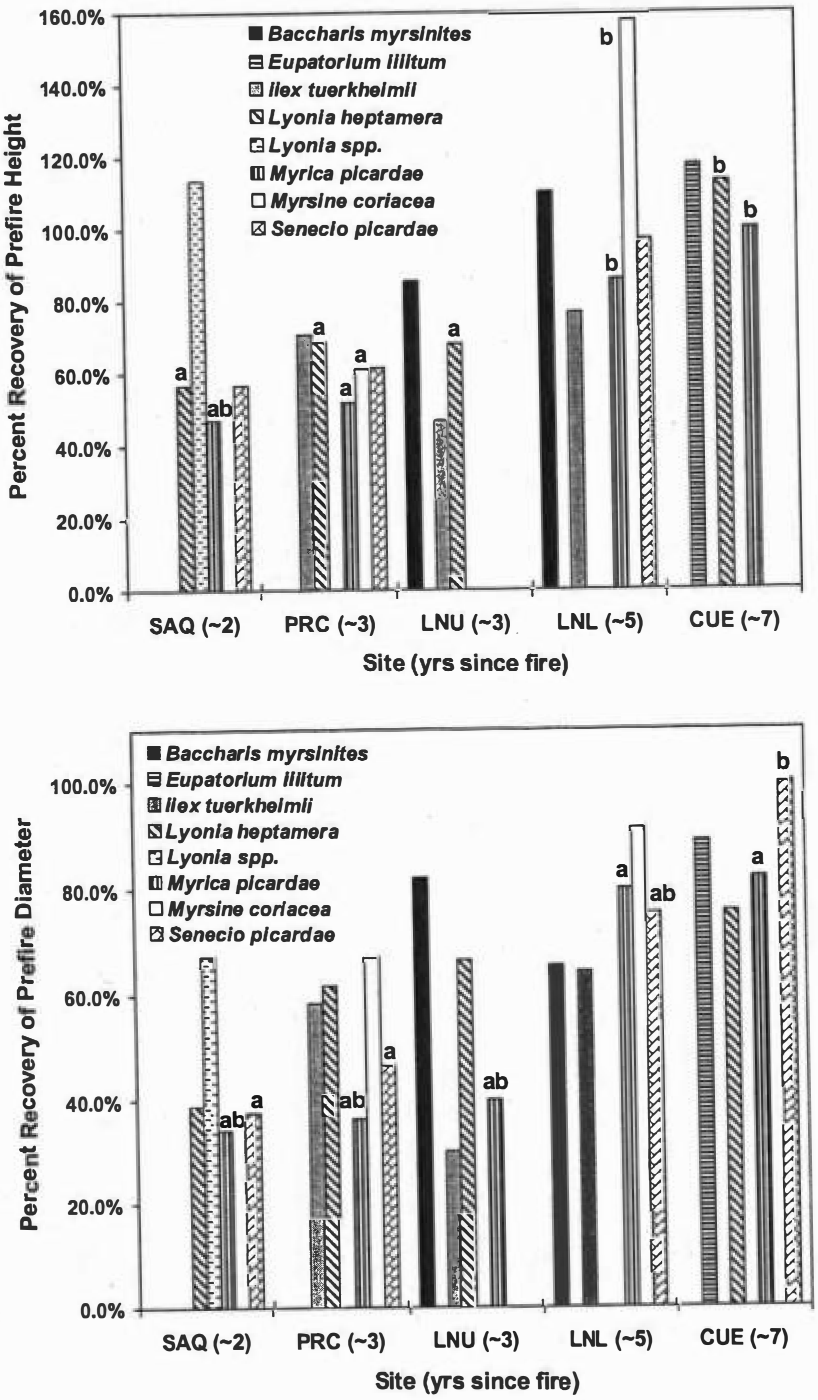


Figure 4.2. Comparisons of percent recovery of prefire height and prefire diameter for resprouting shrubs by site. Sites are ordered by estimated time since fire. Taxa with at least five measurable (not broken) dead stems at the site are shown. Different letters denote values for taxa that are significantly different across sites at P<0.20 (Tukey test). Note the different scales of the Y axes.

than stem diameter. Most species in LNL and CUE had recovered most of, or surpassed, their prefire heights in about 5–7 years since the last fire. In terms of percent recovery of height and diameter, again there was variation between sites, but *Baccharis*, *Myrsine*, *Senecio*, and *Lyonia* spp. (other than *L. heptamera*) tended to show the most rapid recovery.

Pines reached prefire densities only in CUE, the site with the longest time since fire (Figure 4.3). The postfire density of pine at CUE was, in fact, several times higher than the prefire density as reconstructed by counting pines killed by the last fire. In PRC and SAQ, pines had not begun to regenerate. *Baccharis* and *Myrsine* had by far the greatest changes in postfire densities, increasing dramatically in LNU and LNL respectively. Changes in densities of other species were minor, but tended toward slight increases in most species at most sites. In only two cases (*Garrya* at LNL and *Lyonia* spp. at LNU) did species appear in the postfire vegetation that were not sampled in the prefire vegetation. These taxa may have been represented by prefire individuals outside the belt transects.

Discussion

Shrub Regeneration

The high rates of resprouting for shrub species in the Dominican highlands matches well with similar studies in the páramo shrublands of Costa Rica (Janzen 1973, Williamson et al. 1986, Horn 1989, 1998b) and in high elevation shrublands ('campos de altitude') in southeastern Brazil (Safford 2001). Nearly all species resprouted vigorously from protected underground buds after fire, exhibiting the "obligate resprouter" reproductive strategy of Keeley and Zedler (1978). Reproduction by seed appears to be

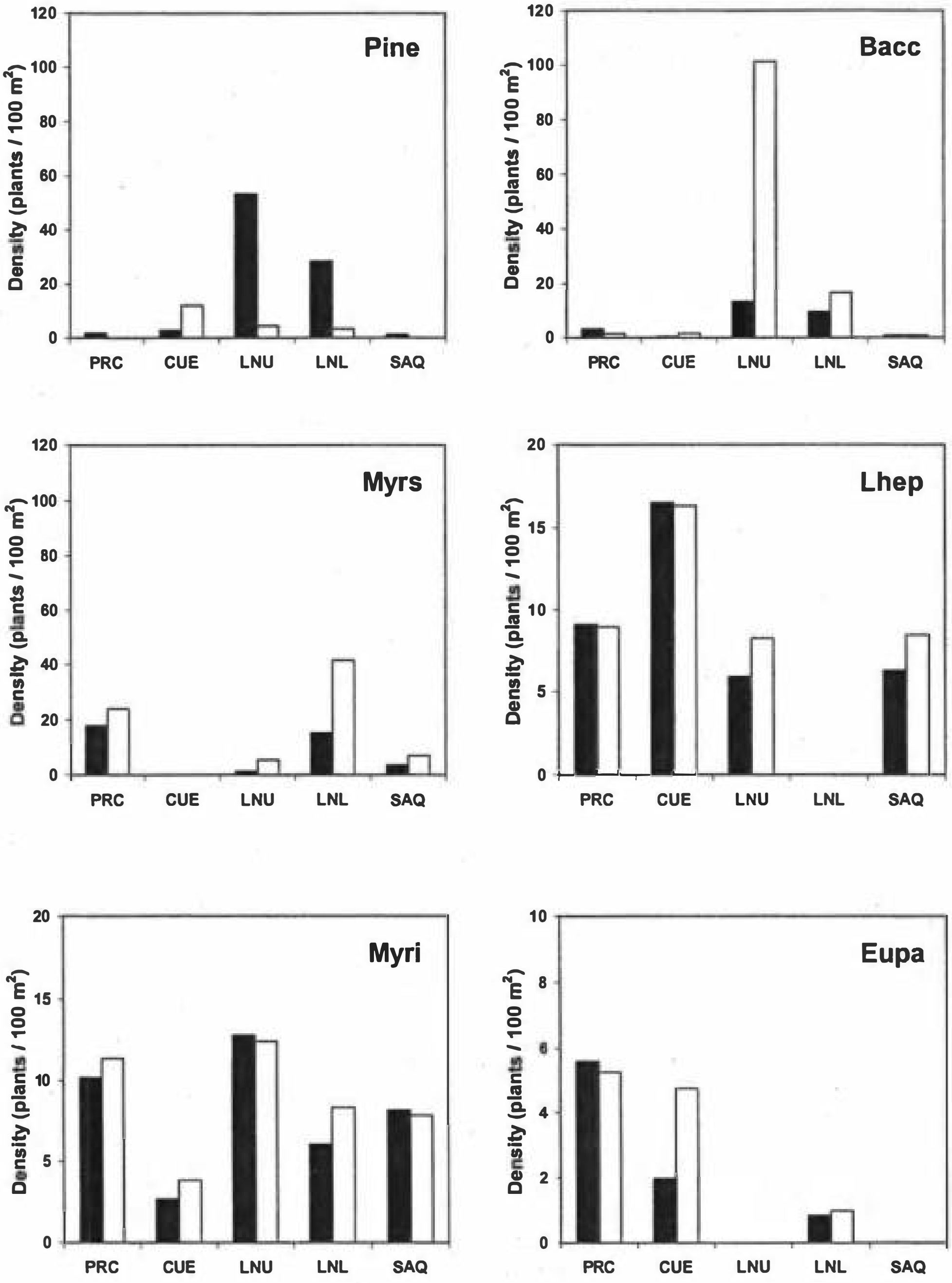


Figure 4.3. Comparisons of pre- (black) and postfire (white) densities of pines and shrub taxa compared across the five study sites. Only taxa with at least five occurrences in any single site are included. Note the scale changes on the Y axes. PRC = Primera Cañada, CUE = Cuevitas, LNU = La Nevera Upper, LNL = La Nevera Lower, SAQ = Sabana Quéliz. Pine = *Pinus occidentalis*, Bacc = *Baccharis myrsinites*, Eupa = *Eupatorium illitum*, Garr = *Garrya fadyenii*, Ilex = *Ilex tuerkheimii*, Lhep = *Lyonia heptamera*, Lspp = *Lyonia* spp., Myri = *Myrica picardae*, Myrs = *Myrsine coriaceae*, Sene = *Senecio picardae*.

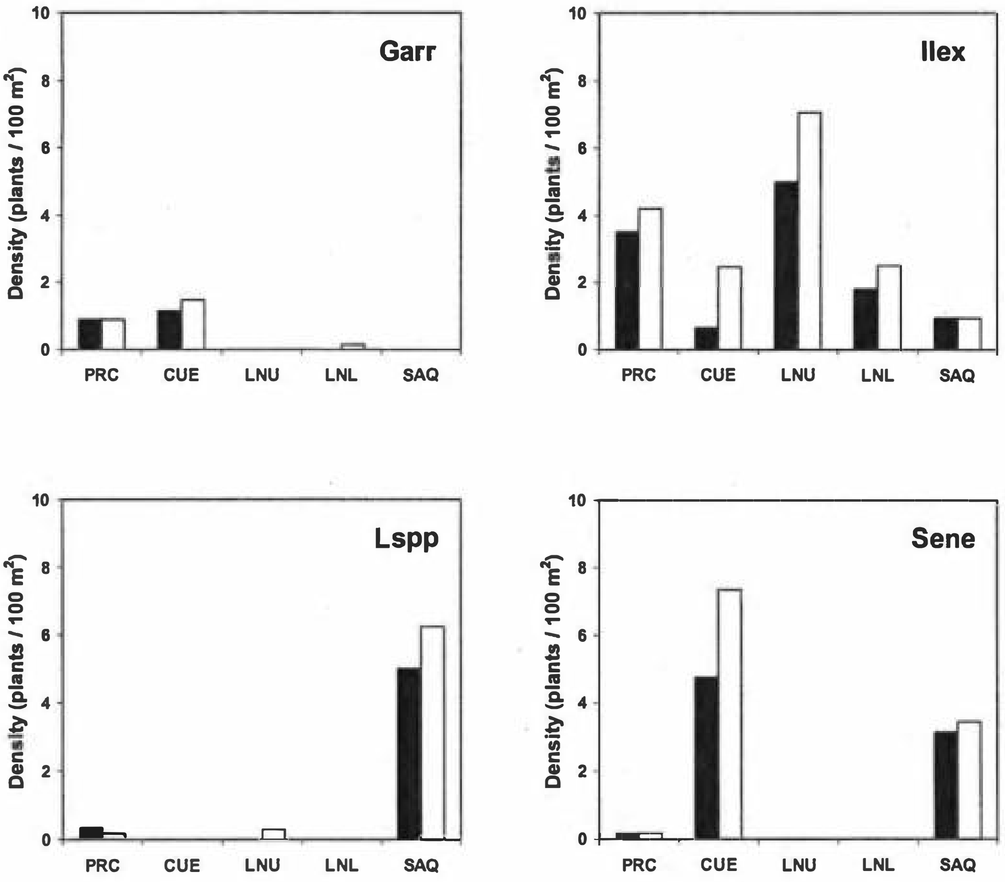


Figure 4.3. Continued.

relatively rare among shrubs in the highlands. The two major exceptions are *Myrsine* and *Baccharis*, which acted as "facultative resprouters" (Keeley and Zedler 1978), both resprouting and producing numerous seedlings in some sites. Representatives of these two genera were the only taxa that behaved as facultative resprouters in the campos de altitude of Brazil, where most shrubs were obligate resprouters, as in the Dominican highlands (Safford 2001; his *Rapanea=Myrsine*). The shrubs *Ilex*, *Senecio*, and *Eupatorium* also increased their populations through seeding in some sites, although not as dramatically as did *Myrsine* and *Baccharis*. Most species, in fact, recorded at least instances of reproduction by seed (Table 4.3), but none were "obligate seeders" (Keeley and Zedler 1978), which recruit primarily through germination of a dormant seed bank. Basal resprouting was clearly the most common reproductive strategy of the shrub taxa.

No shrub or tree species are common between the mainland páramos, the campos de altitude of Brazil, and the Dominican highlands, but generic and family affinities are notable. For example, the Ericaceae and Asteraceae families, and *Myrsine* and *Baccharis*, are represented in all three regions. In the Dominican highlands, *Myrsine* had a 99.5% resprouting rate across all sites, which closely matches the findings of the previous study at PRC (Horn et al. 2001). The 56.3% resprouting rate for *Baccharis* found in the much larger sample population of this study is substantially higher than the 20% rate found in the previous study (Horn et al. 2001). *Baccharis* showed higher rates of resprouting in the campos de altitude of Brazil (Safford 2001) than in the Dominican highlands, and *Myrsine* rates were higher in the Dominican highlands.

Comparisons of postfire heights of Ericaceous shrubs and congenerics from PRC, the Costa Rican páramos, and the Brazilian campos de altitude were presented in Horn et al. (2001). The larger dataset in this study confirms patterns discussed in that paper, and makes possible a comparison of Ericaceous shrubs in older sites. *Lyonia heptamera* at CUE had grown to a height of 94.3 cm (n=101) seven years after fire, while *Vaccinium consanguineum* (Valle Conejos, Costa Rica; elevation ~3500 m) reached only 75.6 cm (n=18) in nine years after fire in the higher Costa Rican páramo site (Horn 1989).

Comparisons of percent recovery (Figure 4.2), which depends in part on the size of the prefire shrubs, of taxa across Dominican highland sites, along with some similar trends in the absolute growth of shrubs at each site, provides some support for the estimated fire dates provided by local informants. Some species in sites with longer time since fire had recovered a significantly greater proportion of their former heights and diameters. In most cases older burn sites also had larger postfire stems and more postfire colonists. One exception was that PRC, which burned only three years ago, had large postfire stems. It also had the largest prefire shrubs of all sites, which may have had more extensive root reserves that enabled faster regrowth.

The composition of the shrub layer varied from site to site, along with species dominance, but changed little after fire (Figure 4.3.). The obligate resprouters came back after a short time, and only the species that also reproduced abundantly by seed (*Baccharis* and *Myrsine*) were able to increase their populations, and then only in some sites. In sites where *Baccharis* and *Myrsine* have produced abundant seedlings, they may gain dominance over other species, if the seedlings are able to persist and mature. The much higher success rate of shrub regeneration by seed in the neighboring LNU and LNL sites may be associated with their local climates, which may make them more favorable environments for seed germination and survival of young shrubs. Though no climate data exist for comparison between sites (or elsewhere in JPRNP), my observations are that the area of La Nevera, in a saddle along the crest of the plateau, is nearly continuously cloaked in fog, which is channeled through the saddle. CUE and PRC in comparison are particularly exposed on steep, rocky slopes, and appeared drier, especially CUE, which is in the lee of the crest.

Pine Regeneration

Like most pines, *Pinus occidentalis* does not resprout, but the ubiquity of live fire-scarred pines in JPRNP and elsewhere in the Cordillera Central attests to its ability to survive fires. Even so, pines declined drastically after fire in these study sites, and strong regeneration was observed only in the site that is about seven years postburn. Darrow and Zanoni (1990a) considered *P. occidentalis* to be well adapted to surviving fire in its mature state, but not particularly fire resistant in younger stages. As the tree matures it begins to put on thick bark (Holdridge 1947, Darrow and Zanoni 1990a), which is one of the common traits of fire-adapted pines (Keeley and Zedler 1998). Holdridge (1942) estimated that *P. occidentalis* in Haiti were not "fire-hardy" until 15 to 20 years of age. This study does not address the age of pines able to resist fire, but can speak to the size at which trees presumably develop bark thick enough to protect the cambial tissue. Pines in these sites showed dramatic differences in survival rates when they reach and exceed diameters of 13 cm (Table 4.4).

If fires burn sites so frequently that trees never reach the age and size at which they become resistant to fire, pines may disappear altogether. The previous study at PRC (Horn et al. 2001) indicated that a shift from pine to shrub dominance might have resulted from frequent fires possibly in combination with illegal harvesting. In LNU and LNL, the prefire vegetation included dense stands of pines mostly <13 cm in diameter. This finding, and the short stature of the prefire shrubs, suggests that these two sites may have burned shortly before the last fire. The most recent fires approached these two sites from adjacent downslope agricultural areas, which may be sources of frequent ignitions. It appears that a cohort of young pines regenerated after the last fire but did not reach fire-resistant size before burning again. A study of pine growth in the Cordillera Central showed that trees at 1400 m grew 8 mm in diameter/year, and at 2400 m, 5 mm/year (Sachtler 1974). Assuming that rates of 5–7 mm/year could be extrapolated to JPRNP, 19–26 years would be required for pines to grow to 13 cm diameter. True growth rates could be higher or lower and would likely vary locally with abiotic and biotic site factors.

Our observations of standing dead pines at PRC (Horn et al. 2001, and this study), LNU, LNL, and other burn sites in the Cordillera Central indicate that pines can and do regenerate abundantly, but the question of timing remains. At PRC, one year after the Horn et al. (2001) study and three years after fire, pine regeneration was still lacking. This may have been due to the same reasons cited in Horn et al. (2001): lack of seed bank, scarcity of seed trees, site factors, changes in soil after fire, or some combination. In many pine habitats, conditions allow germination within a few months of dispersal, so seedbanks are not generally present in soil (Keeley and Zedler 1998). The age at which pines begin to reproduce is highly variable but most bear seed before 20 years of age (Lanner 1998), and in areas of high fire frequency, trees often become reproductive at younger ages (Keeley and Zedler 1998). However, young trees often produce sparse seed crops with poor dispersal (Lanner 1998). Whether the problem in some of the Dominican highland sites is in seed production and dispersal, or in establishment, is not yet clear.

Along with the other reasons already offered for delayed regeneration at PRC, sufficient time for regrowth of burned shrubs may also play a role in pine regeneration because shrubs may provide pine seedlings and saplings protection from frost and desiccation. Pedersen (1953), who observed major damage to young pines in Haiti after an exceptionally cold winter in 1950–51, suggested that pine regeneration would benefit from shelterwood to protect seedlings from frost damage.

SAQ (~2 years postburn) also did not show any signs of pine reproduction, while LNU (~3 yr postburn) and LNL (~5 yr postburn) had small numbers of pine seedlings (11 and 18, respectively). Only the CUE site (~7 years postburn) had produced a large pool of juveniles (67, mean diameter 1.6 ± 1.1 cm), even though it is a highly exposed site, with extremely steep slopes, thin and rocky soils, and a local climate that appears to be drier than the other sites due to CUE's leeward location. CUE's postfire increase in pine density was notable. It is possible, however, that pine seedlings existing prior to the fire were totally consumed by it, erasing any evidence of their prior existence and magnifying the postfire increase in pines.

The LNU and LNL sites in the south end of JPRNP contained large populations of bracken fern and *Lophosoria*, which in Haiti are thought to significantly raise fire hazards, providing highly flammable fuel when killed by frost (Holdridge 1947). It is unclear whether these ferns cause, or result from, a frequent fire cycle, and whether they are more flammable than *Danthonia*, the tussock grass often prominent in forest understory. *Danthonia*, like many other tussock grasses, appears well adapted to fire, generally resprouting quickly after fire (Horn et al. 2001, and personal observations). When forest canopy is opened, bracken fern can form dense cover that can inhibit the establishment of trees (Long and Fenton 1938). Bracken fern is a fierce competitor for light and other resources (Marrs et al. 2000), and can inhibit conifer establishment through phytotoxicity (Dolling 1996, Ferguson 1999). The effects of bracken fern on pine establishment in the Dominican highlands have yet to be elucidated.

Field observations for this study revealed that the practice of illegal timber harvesting discussed in Horn et al. (2001) is occurring in other sites around JPRNP. In PRC in 1998 (Horn et al. 2001), I observed Dominican *campesinos* (rural residents) removing dead pine boles using mules to drag them downslope. In 1999 in LNU and LNL, large numbers of the small fire-killed pines had been cut at knee level by machete. At LNU, much of the wood was stacked in an adjacent wooded area near an old logging road, out of sight of the main road through the park. Some timber removal had also occurred at SAQ, which is the most visible and easily accessible site, and the closest to dwellings. Just as in PRC (Horn et al. 2001), only dead pines were removed at these sites, possibly because this activity would be overlooked by authorities or viewed as "less criminal" than removing live trees, or because locals do not consider this activity harmful to the forest. The basic need for fuelwood may override any fear of consequences or other reasons to not harvest dead wood. Small scale timber removal has been documented elsewhere in the Cordillera Central for similar reasons (Kustudia 1998). As pointed out by Horn et al. (2001), the removal of dead timber may have ecological consequences for plant and animal communities, including effects on plant regeneration.

Successional Patterns

Patterns of recovery of woody vegetation in the Dominican highlands seems to fit well within Egler's (1954) classic successional model of "Initial Floristic Composition," which was later integrated into the "tolerance" pathway of Connell and Slatyer (1977). These models emphasized the importance of the species already present at a site following a disturbance, and deemphasized the role of "facilitation" by species in early successional stages. A third qualitative model by Noble and Slatyer (1980) seems even more applicable in the Dominican highlands. Their model deals mainly with succession in plant communities that are susceptible to recurrent disturbances, such as fire, and emphasizes the properties of individual species. The three key features of the model aim to consider 1) the method of species arrival, or persistence, after a disturbance, 2) the ability of species to establish and grow in the post-disturbance community, and 3) the time taken for species to reach critical life stages. Each of these features seems important for understanding successional patterns in the fire-prone pine forests of the Dominican highlands. Only rarely do shrub species appear to arrive in postfire sites where they were not already present, and all were well suited to recolonize the sites quickly after the fire. Thus, shrub species composition changes little after fire. However, facultative resprouters already present may gain dominance in sites that burn more frequently if site conditions promote germination and survival of juveniles. In the case of pine in JPRNP, large changes in abundance are possible if young trees do not reach the "critical life stage" of reproductive age. Questions remain on the timing of pine regeneration, and the frequency of fire, and how these factors may influence future vegetation change.

May's (1997) research on regeneration after fire in cloud forests of the Ebano Verde reserve, located about 1000 m downslope from the highland burn sites, had only two tree/shrub species (*Myrsine coriacea*, *Baccharis myrsinites*) and genera (*Bocconia*, *Eupatorium*) in common with this study. All of these taxa regenerated by seed, though a few *Myrsine* plants resprouted from above-ground buds. In contrast with the high-elevation sites in this study, two years postfire the cloud forest sites were dominated by herbaceous plants and trees and shrubs that had colonized from seed (91% of all individuals, 77% of species present), rather than by resprouting. Consequently, unlike the high elevation sites in this study, vegetation two years after fire was much different than before the fire, even in terms of trees and shrubs (May 1997). May concluded that the highland cloud forest vegetation was poorly adapted to fire as compared to mechanical disturbances such as tropical storms and landslides, which occur relatively frequently. This contrast in reproductive strategies illustrates clear differences in successional pathways after fire between high elevation pine-dominated landscapes in which fires are frequent and lower elevation cloud forests where fires are likely rare in nature.

Compared to pine forests in the remote parks, JCRNP and ABNP, most forests in JPRNP are more open, and evidence of human disturbance abounds (e.g., cut stumps, exotic weeds, remains of structures, and people and vehicles). Much of the north end of the park, near PRC, appears to be regenerating very slowly from previous fires (probably the 1983 fire) and logging. Pines are sparsely distributed and small even in areas that have not burned recently. Based on fieldwork in the late 1960s, a survey team mapped much of the park along both sides of the main road as "pine forest devastated by logging with trees almost dead, and dead, due to fires" (translated from Spanish) (FAO 1973).

Darrow and Zanoni (1990a, b) reviewed historical documentation of the pine forest areas of the Cordillera Central, including the area of this study, and found that fire has been a part of the ecology of Hispaniolan pine forests since the earliest recorded visits. Around the turn of the 20th century, slash and burn plots were already established in valleys of the Cordillera Central, and fires kept the forests open and easily traveled. Sawmills cutting pine were established in the early 1900s, although lumber production later increased dramatically with the construction of roads. The accessibility of the Valle Nuevo area (now JPRNP) has promoted heavier logging in the past and greater incidence of continuing illegal timber removal than in the remote parks. Fire frequencies in JPRNP may be higher than the natural regime due to ignitions by people. The long history and intensity of human disturbance may be major factors in explaining patterns of poor pine regeneration in many areas of the park.

Conclusions

This second study of postfire recovery in the Dominican highlands has generated larger datasets, which confirm our earlier conception of the highland woody vegetation as well adapted to fire (Horn et al. 2001). More than 88% of the 957 shrubs surveyed resprouted after fire. This paper includes data on the fire response and recovery of three taxa (*Senecio picardae*, *Eupatorium illitum*, *Bocconia frutescens*) not appearing in the earlier study (Horn et al. 2001). It also extends our knowledge to a variety of site types, revealing that there is considerable between-site variation in the shrub community in terms of species composition and dominance.

The variety of fire ages presented here has helped identify patterns through time. Most of the shrub taxa resprouted and grew to prefire height relatively quickly, although regrowth of stem diameters lagged behind. In contrast to the shrub taxa, pines in these sites are regenerating much more slowly through seeding. *Pinus occidentalis* does not resprout and takes several years to attain fire-resistant size. Frequent fires due to human ignitions may cause a decline in pines on the landscape.

Studies of fire history, and the reproductive ecology of *P. occidentalis*, will be key to understanding the recovery of vegetation after fire in the Dominican highlands. Dendrochronological analyses of *P. occidentalis* (Speer et al. *in press*) may provide answers to questions on fire frequencies and spatial patterns of fire, age-size relationships in pine, the age at which pines become reproductive, and other aspects of pine regeneration and ecology that remain undocumented. Research on the role of recovering shrubs, the tussock grass *Danthonia*, ferns, and other plants in the germination and growth of pines may also help explain pine regeneration patterns.

Future monitoring of these study sites will provide longer-term data on successional patterns, particularly on the timing and variability of pine regeneration. Herbaceous vegetation patterns, and the role of site factors, woody debris, and human activities in postfire plant communities deserve further study (Horn et al. 2001), as do the effects of other disturbances on highland vegetation, such as tropical storms and landslides, and their possible interactions with fire. Paleoecological studies (such as in Chapter 3 of this dissertation) in JPRNP may help illuminate the long-term fire and disturbance history and lead to a clearer understanding of factors that influence the generation and maintenance of plant communities in the Dominican highlands. Further research on the ecology of these unique tropical mountain plant communities will assist land managers in making plans for their conservation.

CHAPTER 5

Conclusions and Summary

This study has provided a first look at several aspects of past and present environments of the highlands of the Dominican Republic. My dissertation research includes the first study of modern surface pollen spectra from Hispaniola (Chapter 2), and the first long-term environmental reconstruction from a sediment profile in the highlands (Chapter 3). This dissertation has also expanded on the single prior study (Horn et al. 2001) of postfire vegetation in high-elevation pinelands (Chapter 4). One of the important outcomes of my research on these three themes has been the gathering of a body of evidence that demonstrates that plant communities in the pine forests of the Cordillera Central have developed in a context of disturbance by fires and climatic fluctuations.

A sediment profile from a bog in Valle de Bao (~1800 m) yielded a record of recurring fires over the past 4000 years, along with climatic oscillations, and likely evidence of tropical storm events (Chapter 3). The Bao 1-1997 sediment record indicated that the bog formed around 4000 years ago, which is consistent with the occurrence of ponding in Laguna Grande de Macutico on the leeward slope of the Cordillera Central (S. Horn and K. Orvis, unpublished data). Pine pollen dominated the entire record, indicating little change in the forests around Valle de Bao over the past four millennia. Ubiquitous charcoal in the profile showed periodic fires throughout the record; however, unlike sediment records from the lowland Caribbean and tropical Atlantic (Brenner and Binford 1988, Burney et al. 1994, Kjellmark 1996, Higuera-Gundy et al. 1999), the Bao record showed no clear signs of human impact. Most of the highland fires were probably ignited by lightning.

A dramatic decline in influx of pollen and spores, and of charcoal, along with low organic content, provided evidence that the bog sediments dried and deflated at intervals between about 3700–1200 cal yr BP. Spikes in pollen of broadleaf trees and shrubs, mainly before 2500 cal yr BP, indicate that episodes of relatively moist conditions were interspersed with the dry periods. Peaks in grass pollen and certain fern spores at around 3000 cal yr BP, along with the deposition of old charcoal on the bog's surface, are likely signals of a major hurricane event around that time. Abundant clasts of peat and soil in parts of the profile were probably washed in by heavy rainfall associated with other past tropical storm events. The climatic changes indicated by the Bao record are consistent with those recorded in the sediments of Lake Miragoane, Haiti (Hodell et al. 1991, Curtis and Hodell 1993, Higuera-Gundy et al. 1999).

Our interpretations of the sedimentary pollen and spore record from Valle de Bao were informed by an analysis of modern pollen and spore deposition and its relationship to modern highland vegetation (Chapter 2). Despite dominance by wind-blown pine pollen, DCA analysis showed distinctive pollen and spore spectra for most major cover types. Pine-forested sites had especially high percentages of pollen of non-pine trees and shrubs. High percentages and diversity of broadleaf pollen taxa indicated more mesic sites, or sites protected from frost or fire that harbored more broadleaf elements. Pollen spectra of humid montane broadleaf forests were unique, although this site type requires further sampling. Bogs and ponds were characterized by abundant Cyperaceae pollen and low arboreal pollen percentages, while ponds were distinguished by pollen of

Polygonum and aquatic taxa. Grasslands and open woodlands had similar pollen spectra, but the absence of pine stomata proved to be an excellent indicator of "treelessness." Though pine stomata were extremely rare in the stratigraphic sediments from the Valle de Bao bog, sediment profiles from other highland bogs and ponds in smaller forest openings may contain stomata. Stomate records from forest hollows could help clarify whether the sites were more open during past drier or cooler periods.

My study of postfire regeneration of pines and shrubs in the Dominican highlands (Chapter 4) provided support for our earlier conception (Horn et al. 2001) that woody vegetation of pine-forested highlands is well adapted to fire. This result matches well with studies of pine-forested and high-elevation landscapes around the globe. Not surprisingly, the Dominican highlands had many floristic similarities to the treeless páramos of Central and South America and to shrublands of the campos de altitude of the southeastern Brazilian highlands.

This research also added evidence that frequent fires in the Dominican highlands may cause pines to decline on the landscape. Pines are able to survive fires, but only when they reach a size at which they have adequate bark thickness. Juvenile pines, without the thick bark needed to withstand burning, are likely to perish in fires, and repeated fires may result in a landscape dominated by shrubs.

In contrast to pines, most highland shrubs survive fires and resprout from their bases. More than 88% of all the shrubs in the study survived the fires and resprouted. Most species appeared to be obligate resprouters; only *Mysrine coriacea* and *Baccharis myrsinites* acted as facultative resprouters, reproducing both by seeding and resprouting. With many pines able to survive fires, and so much resprouting and so little seeding by shrubs, site composition changed little after fire. Succession in highland pinelands follows successional models that emphasize the importance of species already at a site (Egler 1954, Connell and Slatyer 1977, Noble and Slatyer 1980).

While pines regenerated more slowly through seeding, most highland shrubs grew relatively quickly to prefire heights. At one site, Cuevitas, shrubs had regained and in some cases surpassed their prefire heights seven years after burning. However, stem diameter recovery lagged behind stem height recovery at this and all other sites; time needed to recover the total site biomass is not yet known. The relatively quick recovery of prefire shrub height does not imply that overall plant diversity or other ecosystem properties (e.g., soil fertility) have returned to prefire levels. These aspects of the postfire environment require further study.

The fires at two of the five study sites started in agricultural areas adjacent to the park and escaped upslope. Compared to the remote parks, JCRNP and ABNP, the area of this study, the Juan B. Peréz Rancier National Park (JPRNP, formerly the Valle Nuevo Scientific Reserve), is smaller and has roads and a military installation. Many private residences are also found in the park. These features probably bring more human activities into and around the edges of the park, and likely cause more frequent fires than in pinelands with less human activity. Preventing high fire frequencies (and possible pine declines) in JPRNP may require that buffer zones be added around the park's edges, or a plan to better control agricultural burning be implemented.

Further research is needed to better understand modern and past fire regimes, and human influence on them. A long history of human activity in some pine-forested areas (especially JPRNP) has resulted in common occurrences of introduced species, mostly

European weeds. How fires and human activities in the highlands will affect the expansion of these exotics is not yet known. Questions also remain on the timing of pine maturity and reproduction, herbaceous vegetation patterns, and the role of abiotic site factors in postfire community development. Additionally, we still have little documentation of the extent and effects of human activities, both past and present, in the highlands.

Information on the long-term history of landscapes is important to understanding modern landscape processes. Large gaps still exist in our knowledge of past environments in tropical areas, especially the Caribbean region. This dissertation has added information on both the modern and past environments of the pine-forested highlands of the Dominican Republic. Future studies of sediments and tree rings in the Dominican highlands will help to resolve and refine recent and long-term patterns of fire and other disturbances, as well as climate history. Further research on both modern and past environments will lead to a better understanding of the factors that influence the creation and maintenance of distinctive highland plant communities.

Many Latin American and Caribbean island nations are only beginning to develop management plans aimed at conservation of their remaining wildlands. Land managers can be sure that the pinelands of the Cordillera Central have long been influenced by disturbances such as fire and tropical storms. Though the effects of fire on herbaceous vegetation and overall biodiversity is still in question, it is clear that highland pines and shrubs are well adapted to fire, provided fire-free intervals are long enough for pines to reach the size at which they can resist fires and reproduce. Any successful management plan for the Dominican highlands will need to consider the needs and viewpoints of the local inhabitants whose activities strongly influence the highlands. It is my hope that the information generated through this research will aid land managers in conservation efforts in the highlands, and draw needed attention to the unique landscapes of the Cordillera Central and other highland areas of the Caribbean.

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APPENDICES

APPENDIX A

PRETREATMENT SCHEDULE FOR MODERN POLLEN SAMPLES FROM HIGHLANDS OF THE DOMINICAN REPUBLIC

(after Rodgers 1994)

Keep track of the steps in a lab book. Set up a chart to record the sample names and the numbers of the corresponding beakers and tubes. All wash water, paper towels, sieve contents, and other contaminated materials resulting from pretreatment of tropical soils and other surface samples require special handling to comply with USDA regulations (see logbook for quarantined soils for instructions). The entire sampling and pretreatment process including cleanup and initial steps of loss-on-ignition analysis takes about 4 hours.

1. Mix the sample well in the bag. This step is very important to get a representative sample. Open the ziplock bag, keep upright, and manipulate the sample thoroughly.
2. Measure 15–25 cc soil using 100 ml glass beaker. Use smaller volume of dense material, more of lighter more organic material. Pack down lighter material to measure.
3. Put soil/sediment sample into 250 ml glass beaker and then add 50 ml distilled water.
4. Stir well mashing the lumps with metal or plastic implement.
5. Let sit 30 minutes or more to help deflocculate clays, then stir again and pour through 250 µm sieve. Wash through the sieve with a strong jet of distilled water from a squeeze bottle, occasionally stirring the material on top of the sieve, and resulting in about 100–200 ml of liquid in the beaker after washing.
6. Centrifuge down beaker contents to concentrate the pollen. Add a few drops ETOH to each tube, if there is a large component of floating material (fresh pollen—most common with drier samples) during centrifuging.
7. After all the material has been concentrated and water poured off, record the volume of the material in each tube, then stir well to homogenize the sample. Vertical sorting of pollen grains may have occurred during centrifuging.
8. Use a metal stirrer and measuring spoon to remove a 0.6 cc sample for pollen analysis to a clean, preweighed test tube. Then, remove a 1.2 cc sample to a preweighed crucible for loss-on-ignition analysis. Use clean stirrers and spoons for each sample.
9. Weigh the tubes containing pollen samples, then add about 10 cc distilled water to each tube and stir. Cover and keep cold until processed.

APPENDIX B

PROCESSING SCHEDULE FOR SURFACE SAMPLES AND SEDIMENTS FROM THE HIGHLANDS OF THE DOMINICAN REPUBLIC

This schedule is based on other soil and sediment processing schedules developed by Dr. Sally Horn and students at the University of Tennessee using standard techniques (Berglund 1986) and has been modified to extract pollen from surface samples and bog sediments from the highlands of the Dominican Republic.

Keep track of steps in a lab book.
Note: Always remove wooden stirring sticks while samples are in hot or boiling water baths. Centrifuge times are 2 minutes at about 2500 rpm unless otherwise specified.

1. Place six pretreated (see pretreatment schedule) (for surface samples use 0.6 cc samples; for sediments use 0.5 cc brass sampler) in preweighed 15 ml polypropylene test tubes and reweigh. If the samples have been stored in distilled water, centrifuge 2 minutes and decant.
2. Add 1 Lycopodium tablet (record the batch number) to each tube.
3. Add a few ml 10% HCl and let reaction proceed; stir with stick and then slowly add more 10% HCl until there is about 10 ml in each tube. Stir well and place in hot water bath for 3 minutes. Remove from bath, centrifuge 2 minutes (at about 2500 rpm, IEC table top centrifuge model MB), and decant. If material is floating, stir in several drops of ETOH and re-centrifuge for 2 minutes. Decant. [Floating material may contain fresh pollen grains buoyed by waxy exine. This commonly occurs when processing surface samples, but may also occur with fossil samples.]
4. Add 10 ml distilled water, stir, and place in hot water bath for 3 minutes. Centrifuge for 2 minutes and decant. Repeat for a total of 2 washes.
5. Add 10 ml 10% KOH, stir, and place in boiling water bath for 5 minutes, stirring after half of the time has elapsed. Remove from bath to seive.
6. Stir samples and pour through 125 µm sieves collecting liquid in a beaker beneath. Wash material through the sieves with squeeze bottle of distilled water.
7. Centrifuge down materials collected in the beakers by repeatedly filling the original test tube with the corresponding beaker contents, centrifuging for 2 minutes, and pouring off decant.
8. Add 10 ml distilled water, stir, centrifuge for 2 minutes and decant for a total of 3 washes.
9. Slowly add a few ml of concentrated (49%–52%) HF and stir gently, watching for a reaction; explosive reactions are rare but possible. Slowly fill to 8 ml and stir. Carefully place tubes in boiling bath for 20 minutes, stirring after half of the time has elapsed.

Note: HF is extremely dangerous. Be familiar with its hazards and trained in its use. Wear rubber gloves, lab coat, eye protection, and a special HF respirator. Contact safety personnel to determine the appropriate level for the hood sash during the hot water bath. You must sign and date the “HF Log Book” each time you use HF.

10. Centrifuge for 2 minutes and check for floating materials. If material is floating, stir in several drops of ETOH and re-centrifuge for 2 minutes. Decant.
11. Add 8 ml 10 % HCl, stir, and place tubes in hot bath for 3 minutes.
12. Centrifuge for 2 minutes and check for floating materials. If material is floating, stir in several drops of ETOH and re-centrifuge for 2 minutes. Decant.

Note: All DR samples need a 2nd HF treatment. Repeat steps 9–12, then proceed to step 13.

9a. Add HF, stir, and place in boiling bath for 20 minutes, stirring halfway.
10a. Centrifuge, check for floating material, decant.
11a. Add 10% HCl, stir, and place in hot bath for 3 minutes.
12a. Centrifuge, check for floating material, decant.

13. Add 8 ml hot Alconox solution (1 tsp. (about 5 g) dry Alconox per 1000 ml distilled water). Add this slowly to prevent foaming over the top of the tubes. Stir, let sit 5 minutes, centrifuge for 2 minutes, and decant.
14. Add 10 ml hot distilled water, stir, centrifuge for 2 minutes, and decant. Repeat for a total of 3 washes.
15. Add 10 ml glacial acetic acid, stir, centrifuge for 2 minutes, and decant.
16. Perform acetolysis by mixing together 9 parts acetic anhydride and 1 part concentrated sulfuric acid and adding 8 ml of this mixture to each tube. Carefully mix the solution immediately before using. For 6 tubes, measure 54 ml acetic anhydride in a 100 ml glass cylinder, then add 6 ml sulfuric acid and stir. Pour any unused solution into the waste container. Place the tubes in a boiling bath for 5 minutes, stirring after half of the time has elapsed. Centrifuge for 2 minutes and decant.
17. Add 10 ml glacial acetic acid, stir, centrifuge for 2 minutes, and decant.
18. Add 10 ml distilled water, stir, centrifuge, and decant.
19. Added 10 ml 5% KOH, stir, and place the tubes in a boiling bath for 5 minutes, stirring after half of the time has elapsed, centrifuge, and decant.
20. Add 10 ml hot distilled water, centrifuge for 2 minutes, and decant, for a total of 3 washes.
21. After decanting the last wash, mix the material in tube using a mechanical vortex mixer for 20 seconds.
22. Add one drop Safranin stain to each tube and mix with vortex mixer for 10 seconds. Add distilled water to make 10 ml / tube, stir, centrifuge, and decant.
23. Add a few ml TBA, mix with vortex mixer for 20 seconds. Fill to 10 ml with TBA, stir, centrifuge, and decant.
24. Add 10 ml TBA, stir, centrifuge, and decant.
25. Mix the residue left in the tube with the vortex mixer for several seconds, then carefully transfer to clean, labeled glass vials. Use a few more drops of TBA to clean out each tube, vibrate with vortex mixer, and add to the corresponding vial. If the vials become too full, centrifuge down midway through the transfer process, decant and continue. Make sure the centrifuge is balanced and use wood spacers in each centrifuge tube to make the glass vials easy to retrieve.
26. Centrifuge down the vials for 3 minutes and decant.

27. Add several drops of silicone oil (2000 centistokes viscosity) to each vial and stir thoroughly with a clean toothpick.
28. Place uncorked vials in a dust-free cabinet to let the TBA evaporate. Stir again after one hour, adding more silicone oil if needed.
29. Check the samples the following day; if there is no alcohol smell, cap the samples. If alcohol smell persists, give them more time to evaporate. It often takes 2 days for TBA to evaporate from large samples. If the samples appear crusty, add more silicone oil.

VITA

Lisa Kennedy was born in Beech Grove, Indiana and raised in Hendricks County, Indiana, where she graduated from Cascade High School. After high school, she worked for several years in family businesses involving growing and marketing produce and bedding plants. She received a Bachelor of Arts degree in Geography from Indiana University–Purdue University, Indianapolis in December 1992. During her B.A. work, she developed strong interests in biogeography while studying with Dr. Tim Brothers. In her final year, Lisa participated in a tropical biology field course in Costa Rica, an experience that helped focus her research interests on tropical environments and paleoecology.

Lisa entered the graduate program in the Department of Geography at the University of Tennessee in August 1993 to work with Dr. Sally Horn. While working on her M.S. degree, Lisa served as a teaching assistant for two years, and then as a research assistant on several research projects led by Dr. Horn. She received the Master of Science degree in 1998, presenting a M.S. thesis entitled, "Prehistoric Agriculture, Fires, and Droughts at the La Selva Biological Station, Costa Rica: Paleoecological Evidence from the Cantarrana Swamp."

During fieldwork with Dr. Horn in the high mountains of the Dominican Republic, Lisa developed ideas for her dissertation research entitled "Fire and Forest in the Highlands of the Dominican Republic: Modern Dynamics and Long-Term History." In total, Lisa visited the Dominican highlands five times during her graduate studies. She also continued to work with Sally as a research assistant on her Costa Rica projects, and was able to travel over most parts of that country on several field trips. Lisa is presently an Assistant Professor in the Department of Geography at Virginia Tech.