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The effect of human activity on the structure and composition of a tropical forest in Puerto Rico

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Abstract

From European settlement to the 1940s, the Bisley watersheds of the Luquillo Experimental Forest, Puerto Rico, were used for agroforestry, selective logging, charcoal production, and timber management. Each of these activities affected different parts of the landscape in different ways and at different times. After nearly 50 years of unhindered regeneration, six impacts remain apparent: (1) shifts in the dominance and age structure of canopy species; (2) immigration of subcanopy crop species and the establishment of banana as a riparian dominant; (3) increases in the importance of canopy species used for coffee shade; (4) the impoverishment of certain commercial timber species; (5) an increase in the density of palms around abandoned charcoal kilns; (6) a reduction in the regeneration of canopy species around abandoned charcoal kilns. Changes in the above-ground nutrient pool may also have occurred. Human disturbances in the study site were progressive rather than discrete events, had adverse impacts on forest regeneration, and increased the spatial heterogeneity of the forest.

Introduction

The importance and complexity of human modifications to humid tropical forests are widely recognized. Agriculture (Padoch and Vayda, 1983), selective tree harvesting (Lanly, 1981), indigenous agroforestry practices (Gómez-Pompa, 1987), and other human activities can 'leave a distinct imprint on plant communities' (Hamburg and Sanford, 1986). Although the importance of these practices is acknowledged, their long-term impacts on forest structure and composition are less certain. Nevertheless, traditional uses associated with the gathering of fuelwood alone account for approximately 65% of the wood removed each year from tropical forests (Food and Agriculture Organization (FAO), 1991).

The objective of this study was to reconstruct the land use history of the

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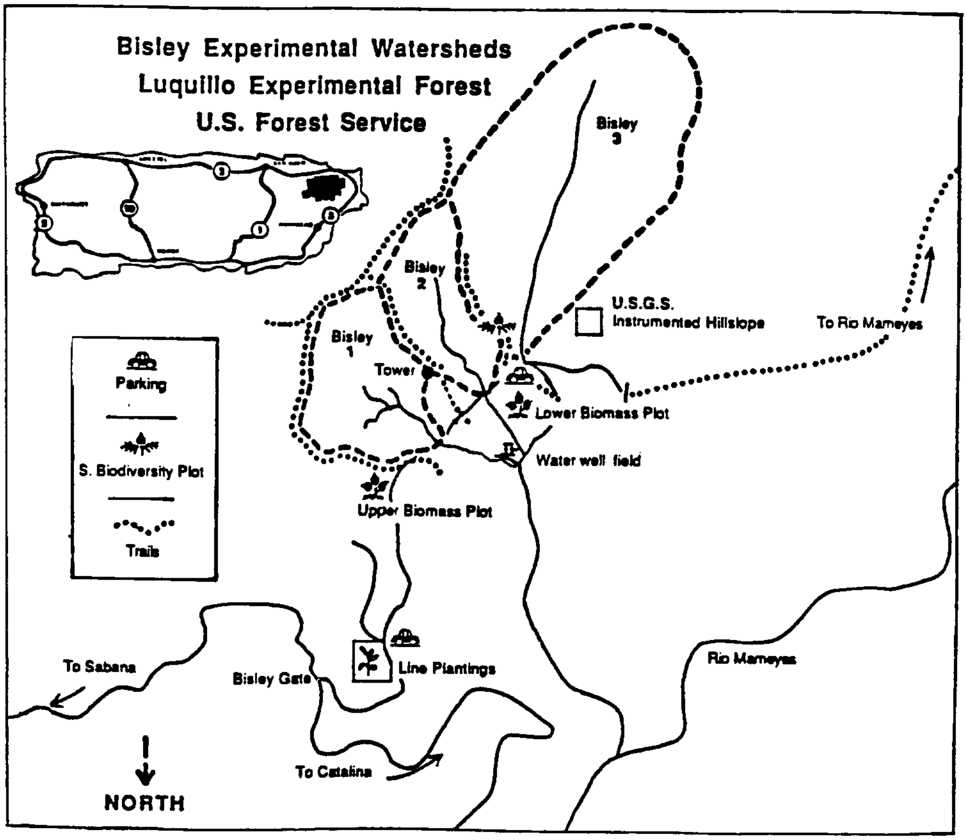


Fig. 1. Location of Bisley watersheds, Luquillo Experimental Forest, Puerto Rico (inset).

forest that covers the Bisley experimental watersheds, Luquillo Experimental Forest (LEF) (18°18′N, 65°44′W), Puerto Rico (Figs. 1 and 2), and to assess how historical human activities are reflected in the present structure and composition of this forest. These impacts were assessed by comparing the structure and composition of plant communities on sites with similar topographic and geomorphic conditions and known land use histories (García-Montiel, 1991).

Study area

Bisley Watersheds 1 and 2 drain 13 ha of tabonuco (*Dacryodes excelsa* Vahl) forest. These watersheds occur in a windward, subtropical wet forest life zone (Ewel and Whitmore, 1973) and have a mean annual precipitation of approximately 3500 mm. The forest is part of the *Dacryodes–Sloanea* association of Puerto Rico and the Lesser Antilles.

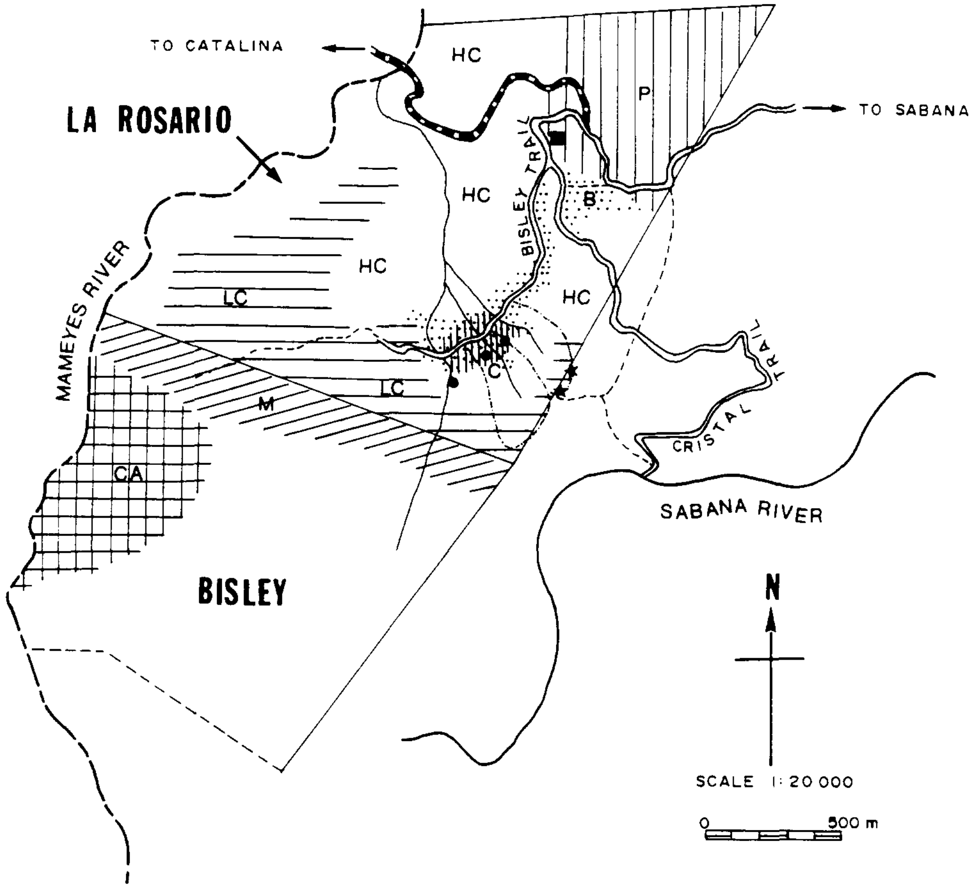
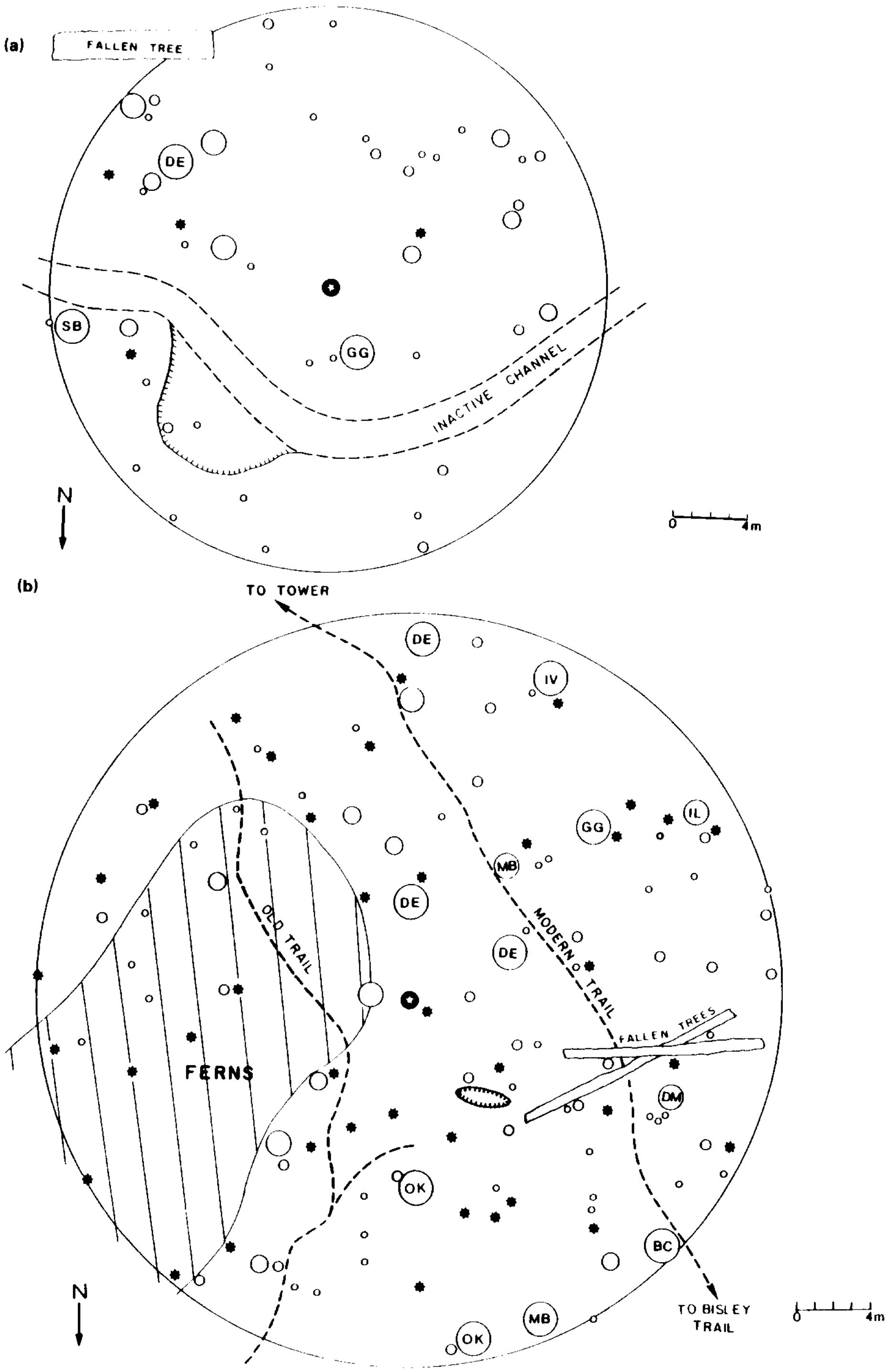


Fig. 2. Map of Bisley area showing the distribution of land use until the 1950s. The entire area now referred to as Bisley was originally divided into 'Hacienda La Rosario' and 'Hacienda Bisley'. The study area was located in the area previously known as 'Hacienda La Rosario'. Legend for 'Hacienda La Rosario': –·–·–·, boundaries of Watersheds 1 and 2; ●, charcoal pit Plots; ★, harvest plots; - - -, old trails; ■, old house; P, pasture land; HC, heavily culled area; LC, lightly culled area (only mature *Manilkara bidentata* were removed); ||C||, coffee plantations before 1936; ::B::, banana plantations before 1936. Legend for 'Hacienda Bisley': M, virgin stand of *M. bidentata*; CA, cultivated area (bananas, sweet potatoes, and others).

Both watersheds are underlain by volcanoclastic sandstones which have weathered into clayey Ultisols. The terrain is steep, highly dissected, and characterized by steep-gradient streams, amphitheater-shaped first-order basins, and narrow drainage divides. Slopes constitute approximately 65% of the landscape, and ridges and valleys each make up about 17%. On the basis of geomorphology and vegetation, the valleys can be divided into two types—riparian and upland (Scatena, 1989, 1990). Riparian valleys have permanent streams whereas upland valleys are drained by intermittent channels.


(a)
FALLEN TREE
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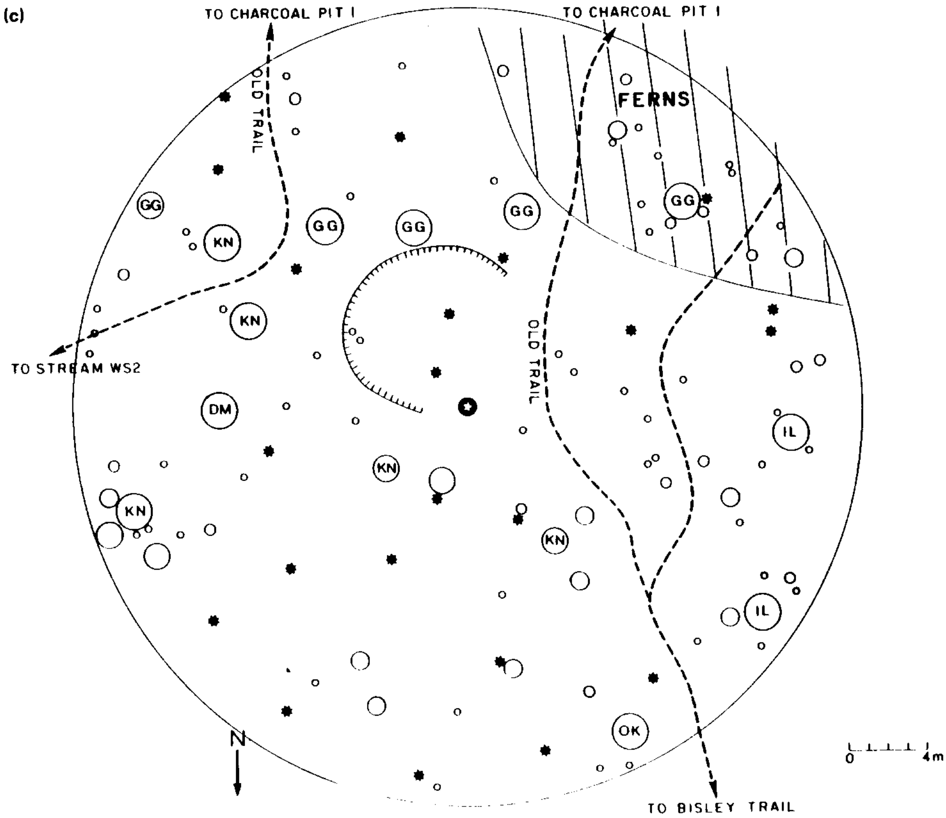


Fig. 3. Site maps of (a) Charcoal Pit 1, (b) Charcoal Pit 2, and (c) Charcoal Pit 3. ✪, Charcoal pit; ┬┬┬, soil depression; —, trail; ✱ *Prestoea montana* (palm); DE, *Dacryodes excelsa* (tabonuco); GG, *Guarea guidonia*; SB, *Sloanea berteriana*; BC, *Buchenavia capitata*; DM, *Didymopanax morototoni*; IL, *Inga laurina*; IV, *Inga vera*; MB, *Manilkara bidentata* (ausubo); OK, *Ormosia krugii*; KN, *Khaya nyasica*.

Previous studies of the vegetation within the watersheds have revealed that topographic setting and slope were significant factors in explaining the spatial pattern of tree species (Basnet, 1990). Hurricanes also play an integral role in the development of these forests (Crow, 1980; Weaver, 1986; Lugo and Rivera-Batlle, 1987). Additional descriptions of the site and surrounding forest can be found elsewhere (Odum and Pigeon, 1970; Brown et al., 1983; Scatena, 1989; García-Montiel, 1991).

Methods

Site history

The history of the study sites was determined from three independent sources—interviews with local residents, historical documents, and artifacts.

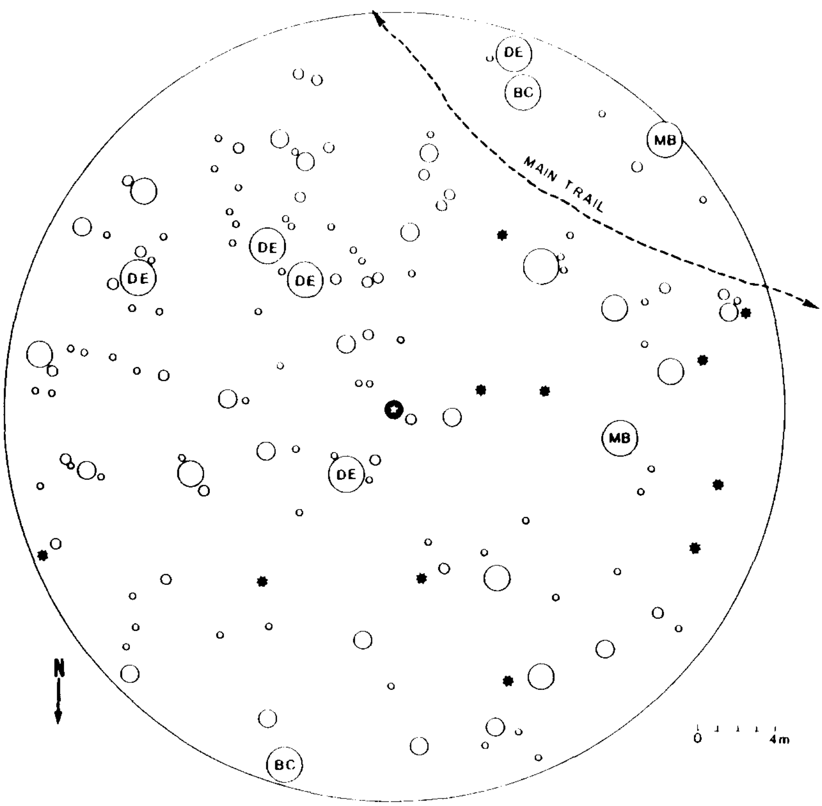
Interviews with two brothers who had lived in the area for 74 and 85 years were particularly useful. The brothers had produced charcoal in the study area during their youth and were able to relocate sites of abandoned kilns that were later used as study plots (see below).

Additional historical documentation was obtained from the US Department of Agriculture (USDA) Forest Service archives at the Institute of Tropical Forestry and from archives at the Institute of Puerto Rican Culture, San Juan, Puerto Rico. These documents included descriptions, inventories, and aerial photographs of the area. Fabrication codes on bottles found around the abandoned charcoal kilns and harvested tree stumps were also used to estimate the age of abandonment (L. Rivera, personal communication, 1989).

Plot establishment

Vegetation was measured and mapped in 1989 (Figs. 3 and 4) around three sites of past charcoal production and two sites of selective harvesting. The three charcoal sites were identified by the presence of charcoal, soil depres-

(a)



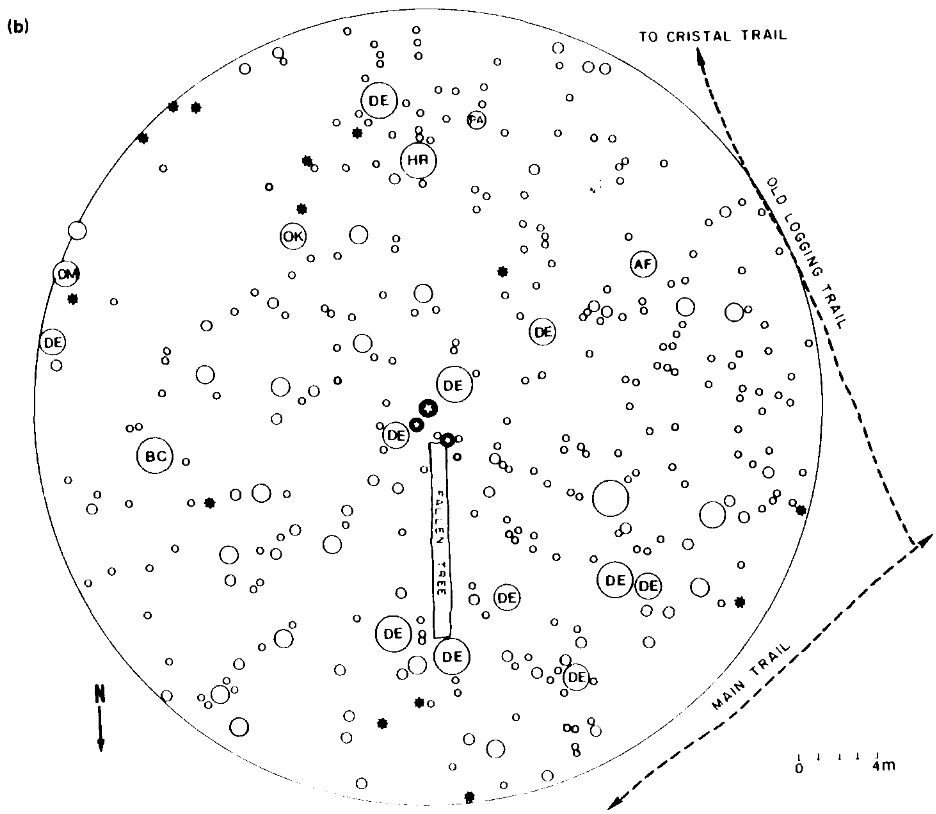


Fig. 4. Site maps of (a) Harvest Plot 1 and (b) Harvest Plot 2. ✪, Stump; —, trail; ✱, *Prestoea montana* (palm); DE, *Dacryodes excelsa* (tabonuco); AF, *Alchorneopsis floribunda*; BC, *Buchenavia capitata*; DM, *Didymopanax morototoni*; MB, *Manilkara bidentata* (ausubo); HR, *Homalium racemosum* Jacq.; PA, *Persea americana* (avocado); OK, *Ormosia krugii*.

sions, and artifacts. These sites were the only well-defined charcoal sites within or adjacent to the watersheds. The two sites of previous tree harvesting were identified by the presence of sawn tabonuco stumps.

The first plot, centered around Charcoal Pit 1, was 30 m in diameter (707 m^2). The remaining four plots were 40 m in diameter (1257 m^2). Charcoal Pit 1 was located in an upland valley around an intermittent stream channel, whereas Charcoal Pits 2 and 3 were located on gentle slopes that provided easy access to permanent stream channels and the road that passes the base of the watersheds. Harvest Plots 1 and 2 were located on ridges.

All stems within the plots with diameters at breast height (DBH; 1.3 m) greater than or equal to 2.5 cm were permanently tagged, mapped, and identified to species level. Tree ferns were identified only to genus level. Species names generally follow Liogier and Martorell (1982).

Stand data from the charcoal and harvest disturbance plots were compared with the vegetation in the surrounding forests. Between 1988 and 1989, the USDA Forest Service established 82 circular plots 10 m in diameter (79 m^2) on a 40 m×40 m grid that covers the 13 ha of Bisley Watersheds 1 and 2 (Scatena and Lugo, 1993). These plots did not contain charcoal kilns or harvested tree stumps and were censused in an identical manner to the disturbance plots.

A transect consisting of 14 rectangular plots (79 m^2 area per plot) in a nearby area was also established to compare the vegetation in the watersheds with an area that had been culled but that was undisturbed by the planting of coffee, bananas, and other trees (see Site History in the Results section). These plots were located at the same elevation as the watersheds and approximately 300 m from their southern boundaries. Unfortunately, Hurricane Hugo (18 September 1989) severely modified this transect before the fieldwork was completed (Walker et al., 1991). Therefore, censusing and data analysis were completed only for tabonuco (*D. excelsa*), ausubo (*Manilkara bidentata* (A. DC.) A. Chev.), *Sloanea berteriana* Choisy, and palm (*Prestoea montana* (R. Graham) Nichols).

Data analysis

Previous studies within the tabonuco forest of the LEF have revealed strong phytosociological relationships between canopy dominants and topography (Wadsworth, 1949; Basnet, 1990; Johnston, 1990). A one-way analysis of variance (ANOVA) on the data collected in the grid plots also indicated a significant effect of topographic position on both basal area ($P<0.01$) and density ($P<0.01$) (García-Montiel, 1991). A pairwise comparison for density between subplots on ridges and those in riparian valleys was also significant ($P<0.01$). Therefore, each disturbance plot was classified by its topographic position and compared with other stands in similar topographic settings. Charcoal Pit 1 was compared with plots in upland valleys, Charcoal Pits 2 and 3 with slope plots, and Harvest Plots 1 and 2 were compared with the subset of grid plots established on ridges.

To quantify internal variability of the disturbance plots, each circular plot was divided into wedge-shaped subplots of 79 m^2. The importance value (Mueller-Dombois and Ellenberg, 1974) of species in each of the disturbance plots was then calculated as the sum of relative basal area, relative density, and relative frequency of the subplots.

Statistical analyses used SYSTAT procedures (Wilkinson, 1990). Comparison of basal area and density between sites was done with one- or two-way ANOVA. Significant one-way ANOVA was followed by Tukey's highest significant difference (HSD) tests. The data were transformed when Bartlett's test indicated no homogeneity of variance. When the transformation did not result in homogeneous variances, a Mann–Whitney *U*-test was used (Sokal and Rohlf, 1981). Frequency distributions were compared using a Kolmogorov–Smirnov test. Statistical significance was accepted at $P<0.05$ unless otherwise stated.

Age and diameter distributions

Because there are no annual rings, ages are difficult to determine for most tropical tree species (Lang and Knight, 1983). However, models based on both diameter classes and periodic annual growth rates have proven useful in understanding the population structures of Luquillo forests (Doyle, 1981; Weaver, 1986).

To compare stand structure with the occurrence of historical events, stand ages were calculated using average annual growth rates of 10 specific tree species of the LEF (Crow and Weaver, 1977). These growth rates are from trees in stands that surround the study site and have similar environmental histories and site conditions (Table 1). Although this approach may overestimate age, as growth rates were based on trees with diameters greater than 10 cm, and must be used with caution (Knight, 1975; Hubbell and Foster, 1987), it has provided useful insights into the dynamics in the LEF (see Doyle, 1981; Weaver, 1986; Scatena and Lugo, 1993).

Table 1
Periodic annual increment (PAI) in diameter for 10 canopy species

Species	Annual diameter increment ($cm\ year^{-1}$)	Range
Alchornea latifolia	0.38	0.00–1.45
Buchenavia capitata	0.69	0.00–1.83
Dacryodes excelsa	0.33	0.00–1.32
Guarea guidonia	0.81	0.13–1.35
Inga laurina	0.46	0.00–1.17
Manilkara bidentata	0.55	0.02–1.14
Matayba domingensis	0.44	0.00–1.17
Ocotea leucoxylon	0.35	0.00–1.27
Ormosia krugii	0.48	0.00–1.32
Sloanea berteriana	0.46	0.01–1.35

The values reported are the weighted average of the PAI estimated at three sites in the Luquillo Experimental Forest by Crow and Weaver (1977). The three sites included: two sites of secondary forest that were culled and cultivated (40 ha between 180 and 360 m above sea-level and 40 ha between 420 and 600 m above sea-level), and one site of mature forest that has never been cultivated or used as a pasture land (129 ha between 210 and 600 m above sea-level). The diameter increments are for the period between 1957 and 1975 for trees with DBH of 10 cm or more.

Results

Site history

The LEF was incorporated into the US Forest System in 1903. Before this, the upper-elevation forests had been under the protection of the Spanish Crown government since 1878 (Wadsworth, 1949). The lower-elevation portions of the present LEF, which include the study site, had been under both government and private ownership before being annexed into the LEF in the early 1930s.

The greatest human-induced transformation to the Bisley forests probably began in the early 1800s, when the land distribution programs of the Spanish government encouraged settlement in the area (Wadsworth, 1949, 1951; Scatena, 1989; García-Montiel, 1991). Although pre-Columbian agriculturists cleared land in Puerto Rico and left rock carvings in the LEF, their activities are believed to have had minor impact on the study site (Wadsworth, 1949; Scatena, 1989). Low population densities and the relatively inaccessible nature of the area also limited utilization during the first three centuries of European colonization.

The amount of managed and cultivated land in and around the watersheds increased steadily from 1800 to 1900. Most of the area was owned by absentee landlords who allowed tenant families to live and work coffee plantations and subsistence farms in the area. The first impacts on the forest probably began with the selective felling of trees for commercial timber and the establishment of coffee (*Coffea arabica* L.), banana (*Musa* spp.), yautía (*Xanthosoma* spp.), and other subcanopy crop species. Although coffee was introduced to Puerto Rico in 1736 (Saldaña, 1935), low population densities, poor economic conditions, and inaccessibility probably limited its establishment in the study area until the 1800s (see Coll y Toste (1922) for O'Reilly's memoir of 1765).

The management of these coffee and crop plantations was not intensive. A common practice was to remove valuable tree species from the forest and then plant coffee under a moderately shaded canopy. Because most primary forest species such as *D. excelsa* and *M. bidentata* produce heavy shade and have economically valuable timber, they were thinned from the forest when the coffee plantations were established. At the same time, the forest was enriched in species with moderate canopies, such as *Inga vera* Willd., *Inga laurina* (L.) Willd., and *Guarea guidonia* (L.) Sleumer. These particular species also have litter that is relatively rich in both nitrogen and phosphorus (Scatena et al., 1993). The resulting canopy that covered the coffee plantations apparently enhanced productivity and eliminated the need for intensive weeding and fertilization (Vicente-Chandler et al., 1968).

Historical documents (Gerhart, 1934, 1936) and interviews indicate that in 1900 the slopes and valleys of the watersheds had an understory of coffee (Fig. 2). During this period, the production of charcoal was limited to that needed for local consumption and was a relatively minor activity. However, deforestation for agriculture and timber resources is believed to have reached its maximum level at this time (García-Montiel, 1991).

By 1934, when the Forest Service annexed the study area into the LEF, most of the area had been exploited 'recklessly' (Gerhart, 1934, 1936). However, Forest Service reports and interviews with local residents indicated that two zones had not been affected to the same extent (García-Montiel, 1991). In one of these areas, all the mature ausubo had been removed and a stand composed of mature and over-mature tabonuco was left. This area was located near the southwest boundary of the watersheds and was the site of the transect used to compare mature culled stands with culled stands with plantings of coffee (Tables 2–4). The other area was located in the extreme southeastern corner of the tract and was not considered in this study.

After incorporating the Bisley area into the LEF, the Forest Service began a silvicultural improvement program (F. Wadsworth, personal communication, 1989). This program included a combination of selective thinning, selective plantings, and charcoal production, and had four goals: (1) to improve the productivity and stock of impoverished forests; (2) to provide reliable energy in the form of charcoal; (3) to provide rural employment; (4) to eliminate harvest waste generated by the silvicultural treatments. According to interviews with local residents and the ages of bottles found near the

Table 2
Density (trees ha^{-1}; DBH of 2.5 cm or more) of dominant tree species by land category, Bisley watersheds, Luquillo Experimental Forest, PR

Land category	Species							
	Dacryodes excelsa	*Guarea guidonia*	*Manilkara bidentata*	*Sloanea berteriana*	*Inga laurina*	*Inga vera*	*Prestoea montana*	Site total
Bisley ridges	289(68)	21(5)	17(4)	441(104)	68(16)	0	72(17)	1685
Harvest Plot 1	366(46)	9(1)	48(6)	175(22)	9(1)	0	104(13)	1114
Harvest Plot 2	485(61)	0	0	80(10)	8(1)	0	119(15)	2658
Bisley slopes	127(33)	23(6)	31(8)	482(125)	50(13)	23(6)	135(35)	1493
Charcoal Pit 2	24(3)	24(3)	24(3)	32(4)	48(6)	24(3)	286(37)	891
Charcoal Pit 3	32(4)	56(7)	0	0	72(9)	32(4)	183(27)	963
Bisley upland valleys	35(3)	58(5)	0	278(24)	58(5)	0	174(15)	1157
Charcoal Pit 1	28(4)	85(6)	14(1)	85(6)	0	14(1)	57(4)	679
Riparian valleys	0	64(4)	0	16(1)	80(6)	0	493(5)	923
Bisley—coffee	214(104)	(20)	24(12)	382(254)	(40)	(6)	123(72)	1480
Bisley—no coffee	136(15)	NA	73(8)	218(24)	NA	NA	382(16)	955

NA, Not applicable.

Table 3
Basal area (m^2 ha^{-1}; DBH of 2.5 cm or more) of dominant tree species by land category, Bisley watersheds, Luquillo Experimental Forest, PR

Land category	Species							
	Dacryodes excelsa	*Guarea guidonia*	*Manilkara bidentata*	*Sloanea berteriana*	*Inga laurina*	*Inga vera*	*Prestoea montana*	Site total
Bisley ridges	23.0	1.3	0.1	5.5	0.3	0	2.4	56.5
Harvest Plot 1	17.8	0.01	4.0	2.3	0.2	0	1.8	49.3
Harvest Plot 2	21.8	0	0	0.4	0.2	0	2.0	52.0
Bisley slopes	9.4	5.4	0.3	3.7	0.7	0.6	2.3	30.6
Charcoal Pit 2	4.6	2.4	2.5	0.4	0.9	1.4	4.5	31.8
Charcoal Pit 3	0.5	8.7	0	0	2.4	1.4	3.3	33.0
Bisley upland valleys	0.6	6.4	0	1.1	1.8	0	2.5	21.6
Charcoal Pit 1	4.8	7.5	2.3	3.6	0	0.3	0.9	25.2
Riparian valleys	0	15.6	0	0.1	1.7	0	1.6	22.6
Bisley—coffee	12.6	NA	0.6	4.0	NA	NA	2.3	36.7
Bisley—no coffee	23.1	NA	4.3	2.1	NA	NA	2.5	38.5

Table 4
Importance value (DBH of 2.5 cm or more) of dominant tree species by land category, Bisley watersheds, Luquillo Experimental Forest, PR

Land category	Species							
	Dacryodes excelsa	*Guarea guidonia*	*Manilkara bidentata*	*Sloanea berteriana*	*Inga laurina*	*Inga vera*	*Prestoea montana*	Site total
Bisley ridges	23.6	1.5	1.1	15.8	3.0	0	5.2	30.8
Harvest Plot 1	28.6	0.7	6.2	11.4	0.8	0	8.1	44.4
Harvest Plot 2	22.4	0	0	3.0	0.5	0	5.4	28.3
Bisley slopes	15.3	7.3	1.9	19.4	3.8	2.0	9.2	40.2
Charcoal Pit 2	6.6	0.5	4.8	3.4	4.9	3.7	22.0	41.5
Charcoal Pit 3	3.1	13.3	0	0	6.7	1.4	14.6	28.3
Bisley upland valleys	3.6	14.3	0	14.6	7.3	0	13.2	38.4
Charcoal Pit 1	9.5	16.7	4.5	12.4	0	2.0	7.5	40.2
Riparian valleys	0	28.7	0	1.8	8.8	0	8.7	64.7
Bisley—coffee	21.5	NA	0.9	18.4	NA	NA	6.9	
Bisley—no coffee	37.1	NA	9.4	14.2	NA	NA	10.9	

Importance value for Bisley with and without coffee is the sum of relative basal area and relative density, and can range up to 200 in each site. For the other sites, importance value is the sum of relative basal area, relative density, and relative frequency, and can range up to 300.

sites, the kiln and harvest plots used in this study were active during this period of silvicultural management.

The silvicultural thinning associated with the improvement program consisted of the removal of 'weed trees' that had been identified and marked by the Forest Service. These trees consisted of individuals that could affect the growth of valuable neighbors, or trees of timber species with poor commercial form. After the selective thinning, saw-logs were prepared in the forest and removed by oxen on skid trails that are still recognizable (Figs. 3 and 4). Any remaining wood was transformed into charcoal. The production of this charcoal was in the range of $(6–8) \times 10^6$ bags year^{-1} (Teesdale and Girard, 1945), and was the major industry in the Luquillo forest throughout the 1940s (Wadsworth, 1949). By 1949, other types of energy became affordable and the charcoal industry declined (F. Wadsworth, personal communication, 1989).

During the silvicultural improvement program, the species used to make charcoal were determined and controlled by the Forest Service. Although nearly all types of wood were used to produce charcoal, *I. vera*, *I. laurina* and *G. guidonia*, which had been planted for coffee shade, were preferred by the charcoal makers (Gerhart, 1936; local residents and F. Wadsworth, personal communications, 1989). In contrast, *Cecropia peltata* L., *Didymopanax morototoni* (Aubl.) Decne. & Planch., and *P. montana* were not harvested because they produce poor charcoal.

The charcoal was produced in kilns that were constructed by piling the wood in a small depression in the ground. While burning, the piled wood was covered with soil obtained from a pit adjacent to the kiln. Water was used to control and extinguish the burning pile, and was typically collected and stored in depressions, some of which can still be found in our study plots (Fig. 3).

Because of better access to water and markets, flat areas adjacent to streams and roads were the preferred sites for the establishment of kilns. Once a kiln site was chosen, wood from the surrounding forest was brought to the kiln area and charcoal was produced over a extended period. When ready, the charcoal was manually transported out of the forest in bags and sold in the nearest town.

Plot descriptions

Interviews with local residents, combined with information on the existing species composition, indicate that the areas surrounding Charcoal Pit 1 and Harvest Plots 1 and 2 had not been extensively planted with coffee, bananas, or other crops (Fig. 2). In contrast, the areas surrounding Charcoal Pits 2 and 3 had been covered by an understory of coffee. Both of these plots also had areas that were covered with ferns (Figs. 3 and 4). Associated with the ferns were successional type species, including *C. peltata*, *Cordia boringuensis* Urban, *Palicourea crocea* var. *riparia* (Benth.) Griseb., *P. montana*, and tree ferns (*Cyathea* spp.).

The uniform spacing of even-sized *G. guidonia* and *Khaya nyasica* Stapf. ex Baker around Charcoal Pit 3 (Fig. 4) suggests that they were transplanted. Interviews with local residents and a report from the USDA Forest Service

(Marrero, 1957) confirm that saplings of these species were planted around kiln sites in the area.

A total of 36 species of woody plants was found in the charcoal kiln plots. Only 16.7% of the species were common to all three plots. In the area surrounding the harvested trees, 39 species were found, of which 37.3% were common to both plots.

In the upland valley of Charcoal Pit 1, *G. guidonia*, *Cyathea* spp., and *S. berteriana* were the most important species (Table 4). In upland valleys where no charcoal production occurred, *S. berteriana* and *G. guidonia* were also the most important species (Table 4). In Charcoal Pits 2 and 3, *P. montana* (palm) was the most important species (Table 4).

A two-way ANOVA using palm density revealed a significant interaction between disturbance by charcoal production and topographic characteristics (df=1, F=8.51, P<0.005). On slopes not affected by charcoal production, *S. berteriana* and *D. excelsa* had the highest abundance. On slopes affected by charcoal production, *P. montana* was the most abundant.

In Charcoal Pit 2, the high importance of *D. excelsa*, *Buchenavia capitata* (Vahl) Eichl., and *Ormosia krugii* Urban resulted from the presence of a few large-diameter individuals. *C. arabica* and *K. nyasica* were found only around Charcoal Pit 3. The two *Inga* species (*I. laurina* and *I. vera*) used to shade coffee plants were abundant in Charcoal Pits 2 and 3 (Tables 2–4). However, the importance values of both *Inga* species were low in Charcoal Pit 1, Harvest Plots 1 and 2, Bisley valleys, and ridges.

In Harvest Plots 1 and 2 and in the grid plots on ridges, *D. excelsa* was the most important species (Table 4). *S. berteriana*, *P. montana*, *M. bidentata*, *Ocotea leucoxylon* (Sw.) Mez, *P. crocea* var. *riparia*, and *B. capitata* were also important in Harvest Plots 1 and 2 (García-Montiel, 1991). *P. crocea* var. *riparia* and *Psychotria berteriana* DC. are understory shrubs that colonize habitats opened by disturbance (Lebron, 1979; Crow, 1980). Trees of avocado (*Persea americana* Miller) were also found in Harvest Plots 1 and 2 and may have been introduced by workers at the time of the harvest. *Byrsonima wadsworthii* Little, a relatively rare species (Weaver, 1989) which can be common in the lower mountain moist forest areas degraded by farming (Little et al., 1974), was also found around Harvest Plot 2.

Comparisons between stands in the watersheds (Bisley grid points) and in the adjacent area that was culled but not planted with coffee (transect plots), indicated that *D. excelsa* and *M. bidentata* were less prominent in areas that had been planted with coffee (Tables 2–4).

Structural composition

Comparison of sample means using a one-way ANOVA did not indicate significant differences (P> 0.1) in basal area or stem density of trees around the three charcoal kilns. Two-way ANOVA comparing mean basal area and density between sites indicated there were no differences in basal area but large differences in density between areas with and without charcoal production (Tables 5 and 6). No effect of use or the interaction of use and topography was found for basal area ($P>0.05$). However, the charcoal production sites had significantly lower densities than sites not affected by this activity ($P<0.001$).

The densities of trees with diameters less than 10 cm were significantly lower

Table 5
Mean basal area ($\pm$SD) ($m^2\ ha^{-1}$) of trees at sites with and without charcoal production in two topographic locations of the Bisley watersheds

Topography	Land use	
	Charcoal pits	Non-charcoal pits
Upland valley	25.20 ± 19.25 (n=9)	21.58 ± 13.58 (n=11)
Slope	32.37 ± 20.88 (n=32)	30.61 ± 23.79 (n=33)

Two-way ANOVA for mean basal area

Source	Sum of squares	df	Mean square	F	P
Use history	0.241	1	0.241	0.30	0.59
Topography	2.776	1	2.776	3.45	0.07
Use × topography	0.028	1	0.028	0.03	0.85
Error	65.178	81	0.805		

Table 6
Mean density ($\pm$SD) (trees ha^{-1}) of sites with and without charcoal production in two topographic locations, Bisley watersheds, Luquillo Experimental Forest, PR

Topography	Land use	
	Charcoal pits	Non-charcoal pits
Upland valley	679 ± 382 (n=9)	1157 ± 408 (n=11)
Slope	927 ± 359 (n=32)	1493 ± 663 (n=33)

Two-way ANOVA for mean density

Source	Sum of squares	df	Mean square	F	P
Use history	4139.307×10^3	1	413.931×10^4	16.03	0.00
Topography	1292.590×10^3	1	129.259×10^4	5.01	0.03
Use × topography	29151.449	1	29151.44	0.11	0.74
Error	209.114×10^5	81	258.166×10^3		

in areas affected by charcoal production than in areas where no charcoal production occurred (Mann–Whitney, $P<0.01$ for upland valleys and $P<0.001$ on slopes (García-Montiel, 1991)). When palms and ferns were excluded from the analysis, the densities in areas previously used to make charcoal were still significantly lower. Whereas the densities of saplings and pole-sized trees were lower in areas used for charcoal production, the density of stems with DBH greater than 10 cm was not significantly different.

As stems less than 10 cm DBH did not contribute greatly to the total basal area of the plots, there was no difference in basal area of sites with dissimilar histories.

Differences in basal area between the harvest plots and grid ridge plots were not significant. The harvest plots did have significantly higher stem densities than other ridge areas ($P<0.001$). However, differences in the density of trees with DBH equal to or less than 10 cm were less striking than for the plots around charcoal kilns.

DBH distribution and stand age

Age and diameter distributions indicate that the densities of the youngest age classes were lower in areas previously used for charcoal production and single-tree harvesting than in similar areas without those disturbances (Figs.

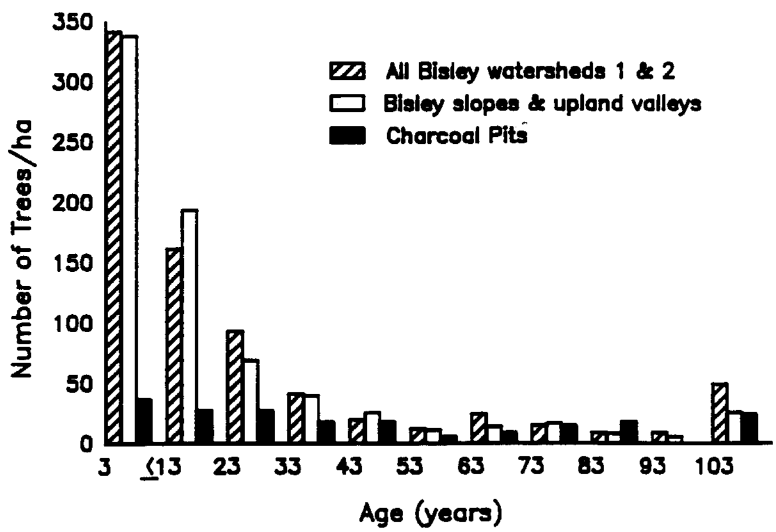


Fig. 5. Density (trees ha^{-1}) of age classes in Bisley Watersheds 1 and 2, Bisley slopes and valleys, and areas affected by charcoal production. Species included are *Alchornea latifolia, Buchenavia capitata, Dacryodes excelsa, Guarea guidonia, Inga laurina, Manilkara bidentata, Matayba dominguensis, Ocotea leucoxylon, Ormosia krugii*, and *Sloanea berteriana.*

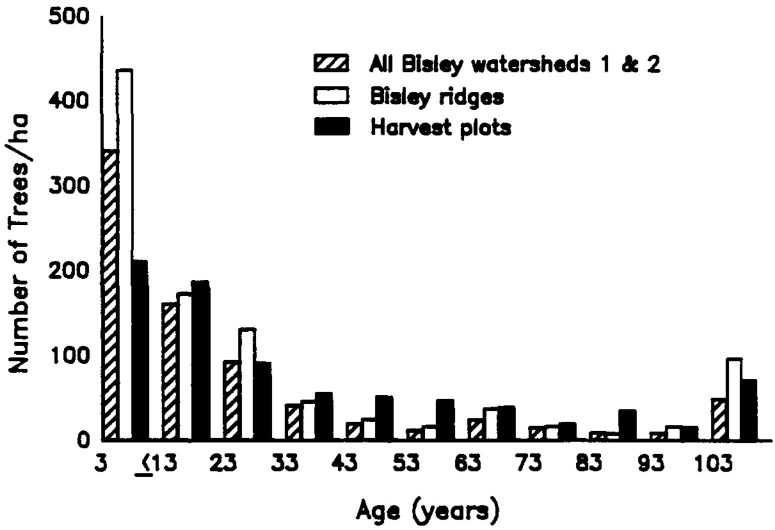


Fig. 6. Density (trees ha^{-1}) of age classes in Bisley Watersheds 1 and 2, Bisley ridges, and areas affected by log harvesting. Species included are *Alchornea latifolia, Buchenavia capitata, Dacryodes excelsa, Guarea guidonia, Inga laurina, Manilkara bidentata, Matayba dominguensis, Ocotea leucoxylon, Ormosia krugii,* and *Sloanea berteriana.*

5 and 6). Age distribution around the charcoal kilns was significantly different from the distribution on slopes and upland valleys, and from that of the entire watersheds (Kolmogorov–Smirnov, $P<0.001$). The age distribution in the harvest plots was also different from that on ridges and from that of the entire drainage (Kolmogorov–Smirnov, $P<0.005$), but this difference was only found for trees with ages estimated to be less than 13 years.

Discussion

Charcoal production

The greatest impacts associated with charcoal making occurred adjacent to the kilns used to produce charcoal (Fig. 5), not in the forest where the harvesting of fuelwood occurred. Although these kiln areas occupy less than 5% of the landscape, 50 years after abandonment they still had marked irregularities in the age and diameter distributions, and significantly lower densities of saplings and pole-sized individuals. The most pronounced effects on species composition around these kiln sites appear to be increases in *G. guidonia* from transplanted saplings, increases in *P. montana* from natural regeneration, and the development of a dense understory of ferns.

Apparently, the canopy dominants that were left around the kilns maintained a closed canopy that did not increase forest floor light to levels that are typical for large gaps (Chazdon and Fetcher, 1984). Instead, the small canopy openings that were created enhanced the heterogeneity of light on the forest floor and were rapidly closed by extensions of the remaining crowns. The trampling and heating of the soils around the kilns also must have modified the local soil, seedbank, drainage, and understory vegetation.

The site conditions of the abandoned kilns were apparently favorable to the establishment of palms, probably because of palm's resistance to periodic flooding and poor drainage (Frangi and Lugo, 1985), its ability to survive in the light regime created by small canopy openings (Lugo and Rivera-Batlle, 1987), and its resistance to trampling (Liddle, 1991). Nutrients released to the soil from burned wood (Uhl et al., 1982) and the low levels of competition from light-demanding species may also have promoted the establishment of palms.

Although the conditions around these kilns may have favored palms, they also caused a reduction in the regeneration of canopy dominants that persisted for at least 50 years. Some of the reduction could be mitigated in the future by restricting charcoal production and other intrusive activities to a minimum number of locations within a management area. Site preparation at the time of abandonment that includes transplanting saplings, or opens the canopy and promotes regeneration, can also be used to mitigate local impacts on regeneration. The effectiveness of the traditional practice of transplanting saplings around abandoned kilns attests to the landscape's resilience and the potential for mitigating the effects of charcoal production in these forests.

Single-tree harvesting

After nearly 50 years, local impacts of single-tree harvesting were still discernible, but less so than those associated with charcoal kilns. Locally, selective harvesting did not result in irregular age- and size-class distributions or marked reductions in regeneration. However, harvesting did lower the forest's basal area, decrease the abundance of tabonuco (*D. excelsa*), and almost completely eliminate ausubo (*M. bidentata*) and *Magnolia splendens* Urban from the watersheds. Harvesting also may have increased the importance of *P. crocea* var. *riparia, P. berteriana*, and *B. wadsworthii.*

Although single-tree harvesting had discernible effects (Fig. 6), the impacts appear to be less than those associated with the charcoal kilns because single-tree harvesting has similar attributes to natural tree falls (Bazzaz, 1983). However, these harvested trees do not create the pits and mounds which can facilitate regeneration (Putz, 1983), nor do they provide biomass for decomposition and recycling (Bormann and Likens, 1979) as do natural tree falls. Furthermore, on-site preparation of saw-logs can severely damage the understory and hinder regeneration of canopy species.

Agroforestry

The most apparent long-term impacts associated with the agroforestry that was practiced in the Bisley watersheds are the shifts in the importance of canopy dominants and the immigration (sensu Bazzaz, 1983) of subcanopy crop species, particularly *Musa* spp. (bananas), *Xanthosoma* spp. (yautías), and *C. arabica* (coffee). The magnitude of these changes varied across the watersheds as coffee was planted on slopes, whereas bananas, plantains, and yautías became established in wet and open riparian sites. The vegetative propagation of banana plants has been so prolific that it is now a dominant species of the riparian plant community.

The shifts in species abundance caused by historical agroforestry and charcoal production may have resulted in a change in the above-ground nutrient pools within the forest. Specifically, the increases in *Inga* spp., *P. montana* and *G. guidonia*, and the decreases in *D. excelsa, M. bidentata* and *M. splendens*, may have influenced the above-ground nitrogen content in the forest, as *Inga* spp. (a legume), palm, and *G. guidonia* all have relatively high concentrations of nitrogen in their tissues (Scatena et al., 1993). Although the magnitude of this change is uncertain, the mass-weighted concentration of N in above-ground plant tissue could have increased from 2.5 mg g^{-1} in the undisturbed forest to the 3.0 mg g^{-1} of nitrogen observed in the modified forest (Scatena et al., 1993).

Conclusions

Since European colonization, the Bisley forest has been affected by agriculture, selective logging, charcoal production, and timber management. Each of these activities has affected different parts of the landscape in different ways. Most likely, only the most inaccessible slopes in the watersheds were not directly affected by human activities.

Unlike many natural disturbances, human disturbances observed in the study area were not discrete events but were cumulative and progressive in nature. Selective harvesting and canopy manipulation led to the planting and naturalization of coffee and other understory crops. After the coffee plantations were abandoned, these areas were preferentially used to supply wood for the production of charcoal because many of the species used to shade coffee also were preferred for charcoal.

The magnitude of human impacts also varied with topographic setting. The major human activities on ridges appear to have been those associated with selective logging and silvicultural management. In contrast, valleys and slopes were affected by logging, agriculture, and charcoal production. The silvicultural improvement program may also have had more impact on slopes and valleys, as these areas presumably contained a larger percentage of 'weed trees' from previous periods of logging and agriculture.

After nearly 50 years of unhindered regeneration, previous human activities have caused long-lasting shifts in the structure and composition of the Bisley forest. The interaction of these human disturbances with natural processes and the intrinsic properties of the landscape have combined to create the existing forest mosaic. The historical approach used to decipher this forest mosaic is applicable to understanding the dynamics of other forests, and is essential in developing appropriate management guidelines and restoration plans.

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