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Barro Colorado Island Forest Dynamics Plot, Panama

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Site Location, Administration, and Scientific Infrastructure

Barro Colorado Island (BCI) is a 1500-ha island in the Panama Canal (fig. 24.1). The island and surrounding mainland peninsulas comprise the Barro Colorado Nature Monument (BCNM), a fully protected national biological reserve since 1923. Both the BCNM and the Barro Colorado Island Forest Dynamics Plot are managed by the Smithsonian Tropical Research Institute. A permanent scientific station located on the island has well-equipped laboratories, computer facilities, housing accommodations, dining facilities, a conference room, and a canopy tower.

A roughly 6-ha Forest Dynamics Plot has been established in wetter but less diverse forest within the limits of Fort Sherman, near the Caribbean end of the Panama Canal, and a 4-ha plot has been established in dry forest at Cocoli, near the Canal's Pacific terminus. In these two plots all individuals $\geq$1cm dbh of free-standing woody tree species have been marked, measured, and identified. In addition, trees $\geq$10 cm dbh have been censused on a number of plots to document the impact of soil type and the effect of the rainfall gradient from the drier Pacific to the wetter Caribbean shore. These plots include twenty-five 1-ha plots scattered throughout the Panama Canal area, two 0.25-ha plots about 50 km west of Cocoli, and seven 1-ha plots in diverse, wet forest between 25 and 75 km east of Ft. Sherman (Pyke et al. 2001).

Climate

From 1972 to 1989, the annual rainfall recorded in BCI's upper laboratory clearing averaged 2551 mm/year, with a maximum of 4469 mm in 1981 and a minimum of 1815 mm in 1976 (Windsor 1990; table 24.1). The dry season is severe, lasting from sometime in December into April or May. In the open, the average diurnal temperature maximum (ADTMx) is 31.1°C, the average diurnal temperature minimum (ADTMn) is 23.2°C, and the average (1984–89) solar radiation (Q) is 181 W/m^2 (Windsor 1990).

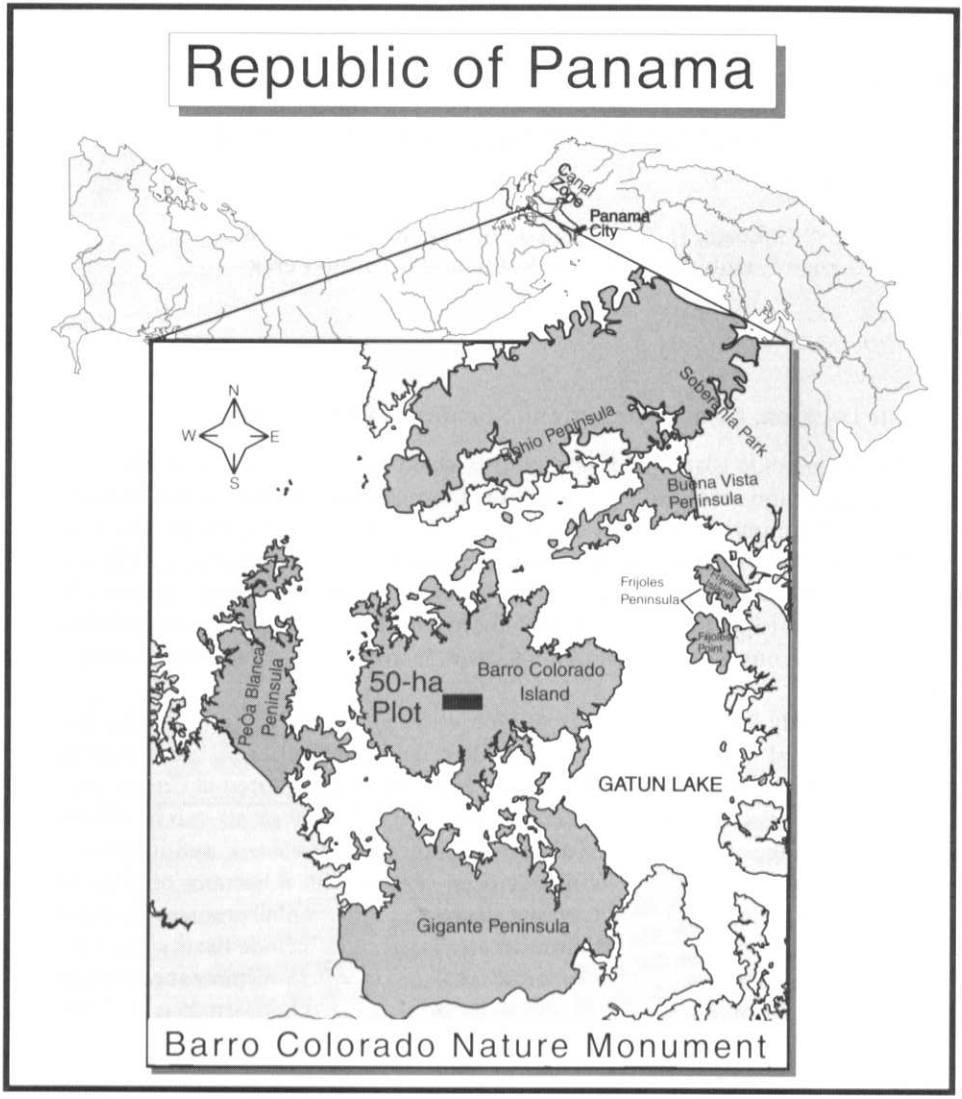

Fig. 24.1. Location of the 50-ha Barro Colorado Island Forest Dynamics Plot.

Topography and Soil

The 50-ha Forest Dynamics Plot is located on Barro Colorado Island, mostly on a level plateau at 140 m above sea level (ranging from 120 to 160 m above sea level). The fringes of the plot, however, include gentle slopes falling away from the plateau, generally 7°–20° in inclination (figs. 24.2 and 24.3.)

Table 24.1. BCI Climate Data

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total/ Averages
Rain (mm)	71	37	23	106	245	275	237	322	309	364	360	202	2551
ADTMx (°C)	31.0	31.3	31.9	32.3	31.8	30.9	30.7	30.7	30.9	30.7	30.5	30.7	31.1
ADTMn (°C)	22.8	22.9	23.1	23.5	23.7	23.5	23.4	23.2	23.1	22.8	23	22.9	23.2
Q (W/m^2)	209	218	242	220	185	154	157	158	167	137	153	174	181.2

Note: Climate data were measured from 1972–1989 at BCI's upper laboratory clearing, 1.3 km northeast of the 50-ha plot's NE corner.

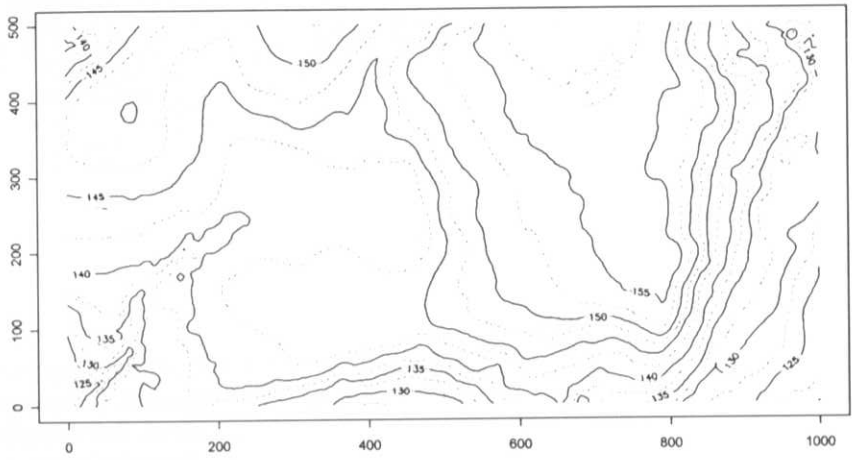

Fig. 24.2. Topographic map of the 50-ha Barro Colorado Island Forest Dynamics Plot with 5-m contour intervals (solid line) and intermediate 2.5 m intervals (dotted lines).

The parent rock beneath the plateau is an andesitic cap. This cap accumulates water and produces springs along the slopes around the plot, where the cap reaches the soil surface. Thus, particularly toward the end of the dry season, soils of slopes contain more moisture available to plants than those of the plateau (Becker et al. 1988). The soils under most of the plot are well-weathered kaolinitic Oxisols with low cation exchange capacity, although the plot also contains a 2-ha seasonal swamp. The 40-ha Conrad catchment, which largely overlaps the 50-ha plot, exports an average of about 110 kg of suspended solids and 110 kg of solutes per hectare per year, representing an average erosion rate of 0.01 mm/year (R. Stallard personal communication). The 50-ha plot supports a vegetation characteristic of fertile soil (Foster and Brokaw 1982).

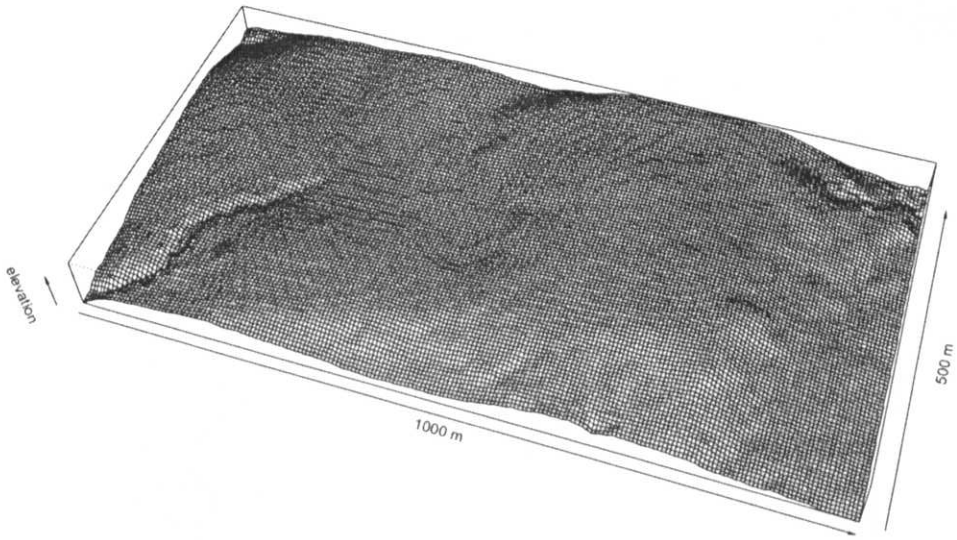

Fig. 24.3. Perspective map of the 50-ha Forest Dynamics Plot.

Forest Type and Characteristics

Barro Colorado Island is covered by semideciduous lowland moist forest, approximately half of which is mature. The canopy is generally 20–40 m tall, with some emergent trees reaching 50 m (Bohlman personal communication). The forest is estimated to hold 281 ± 20 Mg/ha of aboveground biomass, lianas included. A third of this biomass is stored in trees larger than 70 cm dbh (Chave et al. 2003). Leaf-area index is approximately 7 (Leigh 1999). Over one quarter of the canopy tree species are deciduous for part of the dry season. However, normally only 10% of the canopy is deciduous at the peak of leaf loss in March (Condit et al. 2000), although this figure varies according to the severity of the dry season. The understory is evergreen (Croat 1978). From August 1969 through July 1971, the total dry weight of fine litter falling on and near the plot (as measured in over one hundred 1/12-m^2 tubs) was 1151 g/m^2/year, of which 611 g was leaves; from 1988 through 1991, the total fall of fine litter on Poacher's Peninsula, 1.4 km south of the southeast corner of the plot, as measured in sixty 0.25-m^2 litter traps, averaged 1181 g/m^2/year, of which 743 g was leaves.

Tree species composition is relatively homogeneous across the plot. The most common canopy trees are *Quararibea asterolepis* (Bombacaceae) and *Trichilia tuberculata* (Meliaceae), which together account for only one eighth of the plot's

Table 24.2. BCI Plot Census History

Census	Dates	Number of Trees (≥1 cm dbh)	Number of Species (≥1 cm dbh)	Number of Trees (≥10 cm dbh)	Number of Species (≥10 cm dbh)
First	March 1981–July 1983	235,341	305	20,881	238
Second	January 1985–October 1985	242,088	306	20,719	237
Third	February 1990–February 1991	244,059	303	21,233	229
Fourth	January 1995–February 1996	229,049	301	21,455	227
Fifth	January 2000–October 2000	213,802	300	21,205	226

Note: Five censuses have been completed, the next census is expected to begin in January 2005.

Table 24.3. BCI Summary Tally

Size Class (cm dbh)	Average per Hectare							50-ha Plot				
	BA	*N*	*S*	*G*	*F*	*H′*	α	*S*	*G*	*F*	*H′*	α
≥1	32.1	4581	169	120	48	1.62	34.6	301	180	58	1.71	34.2
≥10	27.8	429	91	74	36	1.66	35.6	227	149	52	1.86	35.4
≥30	19.7	82	35	33	23	1.38	23.9	142	101	43	1.72	28.5
≥60	10.8	17	11	11	8	0.95	17.8*	67	56	28	1.54	17.2

*Based on 46 hectares.

Notes: *BA* represents basal area in m^2, *N* is the number of individual trees, *S* is number of species, *G* is number of genera, *F* is number of families, *H′* is Shannon–Wiener diversity index using $\log_{10}$, and α is Fisher's α. Basal area includes all multiple stems for each individual. All individuals were identified. Data are from the fourth census.

basal area. *Hybanthus prunifolius* (Violaceae), an understory shrub, and saplings of the understory tree *Faramea occidentalis* (Rubiaceae), together make up nearly one third of the trees on the plot between 2 and 5 m tall. Species diversity tends to be lower on flat areas than on slopes, which are wetter at the end of the dry season (Becker et al. 1988). Some species, such as *Calophyllum longifolium* (Guttiferae), *Virola surinamensis* (Myristicaceae), *Guatteria dumetorum* (Annonaceae), *Drypetes standleyi* (Euphorbiaceae), and *Piper* spp. (Piperaceae) are more common on or are restricted to slopes. Other species, such as the oil palm *Elaeis oleifera* (Palmae), are restricted to the seasonal swamp, and *Gustavia superba* (Lecythidaceae) dominates the 2 ha of secondary forest, an area of unusually low diversity. For census data and rankings, see tables 24.2–24.7.

Flowering peaks just after the onset of the rains in May (Foster and Brokaw 1982). Fruit fall peaks around the beginning of the rainy season, with a lesser peak in September (Foster and Brokaw 1982). Seed germination peaks shortly after the onset of the rainy season (Garwood 1983). Leaf fall peaks at the end of the rainy season and well into the dry season. Leaves flush around the beginning of the rainy season and evergreens flush at the turn of the year (Leigh and Windsor 1982).

Table 24.4. BCI Rankings by Family

Rank	Family	Basal Area (m^2)	% BA	% Trees	Family	Trees	% Trees	Family	Species
1	Bombacaceae	183.4	11.4	1.0	Rubiaceae	46,715	20.4	Leguminosae	37
2	Leguminosae	159.0	9.9	7.5	Violaceae	38,489	16.8	Rubiaceae	31
3	Rubiaceae	145.8	9.1	20.4	Leguminosae	17,185	7.5	Moraceae	21
4	Meliaceae	122.7	7.6	7.3	Annonaceae	16,690	7.3	Flacourtiaceae	15
5	Euphorbiaceae	107.4	6.7	1.8	Meliaceae	16,611	7.3	Euphorbiaceae	12
6	Moraceae	97.4	6.1	3.6	Burseraceae	10,974	4.8	Melastomataceae	12
7	Lauraceae	62.9	3.9	1.9	Melastomataceae	8,825	3.9	Lauraceae	10
8	Palmae	62.6	3.9	1.3	Moraceae	8,167	3.6	Palmae	10
9	Burseraceae	59.1	3.7	4.8	Guttiferae	6,340	2.8	Annonaceae	9
10	Bignoniaceae	53.2	3.3	0.3	Chrysobalanaceae	5,529	2.4	Guttiferae	9

Notes: The top 10 families for trees ≥1 cm dbh are ranked in terms of basal area, number of individual trees, and number of species, with the percentage of trees in the plot. Data are from the fourth census.

Table 24.5. BCI Rankings by Genus

Rank	Genus	Basal Area (m^2)	% BA	% Trees	Genus	Trees	% Trees	Genus	Species
1	*Trichilia* (Meliaceae)	101.9	6.3	5.8	*Hybanthus* (Violaceae)	36,064	15.7	*Inga* (Leguminosae)	15
2	*Quararibea* (Bombacaceae)	99.0	6.2	1.0	*Faramea* (Rubiaceae)	27,136	11.8	*Ficus* (Moraceae)	12
3	*Alseis* (Rubiaceae)	67.6	4.2	3.6	*Trichilia* (Meliaceae)	13,386	5.8	*Psychotria* (Rubiaceae)	11
4	*Hura* (Euphorbiaceae)	63.7	4.0	0.0	*Desmopsis* (Annonaceae)	11,761	5.1	*Piper* (Piperaceae)	8
5	*Prioria* (Leguminosae)	61.9	3.9	0.6	*Alseis* (Rubiaceae)	8,171	3.6	*Miconia* (Melastomataceae)	7
6	*Faramea* (Rubiaceae)	59.8	3.7	11.8	*Mouriri* (Melastomataceae)	7,130	3.1	*Casearia* (Flacourtiaceae)	5
7	*Ceiba* (Bombacaceae)	53.8	3.3	0.0	*Protium* (Burseraceae)	6,767	3.0	*Bactris* (Palmae)	4
8	*Virola* (Myristicaceae)	48.0	3.0	0.9	*Psychotria* (Rubiaceae)	5,692	2.5	*Cupania* (Sapindaceae)	4
9	*Oenocarpus* (Palmae)	47.9	3.0	0.8	*Swartzia* (Leguminosae)	5,481	2.4	*Eugenia* (Myrtaceae)	4
10	*Jacaranda* (Bignoniaceae)	38.7	2.4	0.1	*Hirtella* (Chrysobalanaceae)	5,084	2.2	*Nectandra* (Lauraceae)	4
								Ocotea (Lauraceae)	4
								Protium (Burseraceae)	4
								Zanthoxylum (Rutaceae)	4

Notes: The top 10 tree genera for trees ≥1 cm dbh are ranked by basal area, number of individual trees, and number of species with the percentage of trees in the plot. Data are from the fourth census.

Table 24.6. BCI Ranking by Species

Rank	Species	Number Trees	% Trees	Species	Basal Area (m^2)	% BA	% Trees
1	*Hybanthus prunifolius* (Violaceae)	36,064	15.8	*Trichilia tuberculata* (Meliaceae)	99.4	6.2	5.6
2	*Faramea occidentalis* (Rubiaceae)	27,136	11.9	*Quararibea asterolepis* (Bombacaceae)	99.0	6.2	1.0
3	*Trichilia tuberculata* (Meliaceae)	12,818	5.6	*Alseis blackiana* (Rubiaceae)	67.6	4.2	3.6
4	*Desmopsis panamensis* (Annonaceae)	11,761	5.1	*Hura crepitans* (Euphorbiaceae)	63.7	4.0	0.1
5	*Alseis blackiana* (Rubiaceae)	8,171	3.6	*Prioria copaifera* (Leguminosae)	61.9	3.9	0.6
6	*Mouriri myrtilloides* (Melastomataceae)	7,130	3.1	*Faramea occidentalis* (Rubiaceae)	59.8	3.7	11.9
7	*Hirtella triandra* (Chrysobalanaceae)	5,044	2.2	*Ceiba pentandra* (Bombacaceae)	53.8	3.4	0.0
8	*Psychotria horizontalis* (Rubiaceae)	4,860	2.1	*Oenocarpus mapora* (Palmae)	47.9	3.0	0.8
9	*Garcinia intermedia* (Clusiaceae)	4,299	1.9	*Jacaranda copaia* (Bignoniaceae)	38.7	2.4	0.1
10	*Tetragastris panamensis* (Burseraceae)	4,139	1.8	*Anacardium excelsum* (Anacardiaceae)	34.1	2.1	0.0

Notes: The top 10 tree species for trees ≥ 1 cm dbh are ranked by number of trees and basal area. The percentage of the total population is also shown. Data are from the fourth census.

Fauna

The 15 km^2 of Barro Colorado Island maintain 40 species and about 5 tons/km^2 of nonflying mammals. The largest carnivores include one resident puma (*Puma concolor*) and more than 20 ocelots (*Leopardus pardalis*). The island's largest herbivores are the tapir (*Tapirus bairdii*), deer (*Mazama americana*), and collared peccary (*Tayassu tajacu*). Barro Colorado Island also has 1300 howler monkeys (*Alouatta palliata*), about 300 white-faced monkeys (*Cebus capucinus*), 1500 agoutis (*Dasyprocta punctata*), and several thousand sloths, mostly three-toed sloths (*Bradypus variegatus*), but with at least 1000 two-toed sloths (*Choloepus hoffmanni*) (Glanz 1982; Leigh 1999). It also has 73 species of bats. Excluding sloths, which comprise some 2.5 tons/km^2 (Glanz 1982), Barro Colorado Island has 2.3 tons/km^2 of nonflying mammals, which annually eat over 40 tons dry weight of food, mostly fruit, per hectare (Leigh 1999). BCI also has about 100 kg/km^2 of birds (about 1300 pairs/km^2) eating about 5.5 tons/km^2/year of food. About half of these pairs are arboreal insectivores, and another quarter are omnivores. Together, they eat 2.4 tons/km^2/year of folivorous insects, an amount that is enough to play a dominant role in limiting insect damage (Leigh 1999).

Table 24.7. BCI Tree Demographic Dynamics

Size Class (cm dbh)	Growth Rate (mm/yr)			Mortality Rate (%/yr)			Recruitment Rate (%/yr)			BA Losses (m^2/ha/yr)			BA Gains (m^2/ha/yr)		
	82–85	85–90	90–95	82–85	85–90	90–95	82–85	85–90	90–95	82–85	85–90	90–95	82–85	85–90	90–95
1–9.9	1.02	0.82	0.58	2.65	2.25	2.56	4.70	3.43	2.14	0.10	0.08	0.10	0.27	0.35	0.18
10–29.9	3.26	2.32	2.14	2.60	1.96	1.88	3.74	3.42	2.93	0.21	0.14	0.14	0.42	0.44	0.32
≥30	6.47	6.07	3.88	3.38	2.07	1.90	3.71	2.37	2.33	0.82	0.35	0.33	0.54	0.50	0.35

Natural Disturbances

Most canopy disturbances are small treefall gaps created when one or a few trees fall (Brokaw 1990; Hubbell et al. 1999). The return time for any particular point in old forest being included in a treefall gap is 126 years (Brokaw 1990). Barro Colorado Island is outside the hurricane belt, although local wind storms sometimes fell a hectare or more of forest. The return time of such wind storms for any particular site is 1000–5000 years (Leigh 1999).

Roughly once every decade or two, an El Niño decreases rainfall during the rainy season, and the following dry season is unusually severe. Mortality was elevated substantially during the 1982–85 census interval due to an unusually severe 1983 dry season associated with the powerful El Niño event that year (Condit et al. 1995). But growth and recruitment were also high during the drought, apparently enhanced by the extra light that entered the forest as a result of the higher mortality (Condit et al. 1992a, 1999). While such events sometimes increase tree mortality, especially among moisture-loving species, to date, El Niño droughts have not had a significant effect on the structure of the canopy (Condit et al. 1992a).

Human Disturbance

About half of Barro Colorado Island, including almost all the 50-ha Forest Dynamics Plot, has been continuously forested for at least 1000 years. In pre-Columbian times, there were two small camps—both over 600 years old—on the site of the 50-ha plot, but there is no evidence of agriculture or forest clearing (Piperno 1990). Most mahogany trees (*Swietenia macrophylla*, Meliaceae) were removed over a century ago. Most of the remaining half of BCI, including 2 ha of the 50-ha plot was cleared by settlers for farms during the 19th century. These camps were abandoned around the turn of the 20th century. No logging or extraction of forest products has occurred since 1923.

Around 1910, the Chagres River was dammed for the Panama Canal. Barro Colorado Island, cut off from the mainland by the rising Lake Gatun, became an island. Afterward, the number of bird and mammal species present on BCI declined. Since the 1920s, several large mammals and birds, and a few small forest birds have gone extinct either due to early hunting or to isolation from the mainland (Enders 1939; Willis 1974; Karr 1982; Leigh 1999; Robinson 1999). White-lip peccaries disappeared from Barro Colorado Island around 1930. Poaching pressure on Barro Colorado Island accelerated greatly in 1932. Pumas were still common there just after World War II, but no puma was sighted on BCI after 1958 until they began to recolonize in 1998. The first jaguar sighting on BCI was in 1983; they are rare visitors. Two harpy eagles were introduced to Barro Colorado Island in 1999 though neither stayed longer than a year. Barro Colorado Island

was effectively protected from hunters from about 1980 onward. At present, the faunal community is largely intact.

The closest forest edge, Wetmore's Cove, is approximately 1 km south of the Forest Dynamics Plot's southern boundary. As an island, the forest is completely surrounded by water.

Plot Size and Location

BCI is a 50-ha, 1000 × 500 m plot; the long axis lies east-west. Northwest corner is at 9°9′20.7″ N, 79°51′18.6″ W; southwest corner is at 9°9′4.5″ N, 79°51′19.1″ W.

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