

Timber, Tourists, and Temples

Conservation and Development
in the Maya Forest of Belize,
Guatemala, and Mexico

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Chapter 17

Dynamics and Ecology of Natural and Managed Forests in Quintana Roo, Mexico

Dennis F. Whigham, James F. Lynch, and Matthew B. Dickinson

Shaped by both natural and anthropogenic disturbances, the Maya Forest of Belize, Guatemala, and Mexico has changed dramatically over the millennia. The region's floristic composition has become relatively well known to scientists, but many of its ecological processes are still only partially understood. Studying these processes is a long-term project; accordingly, when we first undertook the investigation of the relationship between forest dynamics and migratory bird populations in this region, we intended our research to span many years. An unintended benefit of this strategy was the good fortune of witnessing the effects on the forest of a major natural disturbance: Hurricane Gilbert. As chance would have it, this powerful hurricane struck our study site after we had completed four years of study, offering a rare opportunity to compare the forest's circumstances before and after a massive natural disturbance. Results of this decade-long project provide insights into processes (e.g., annual patterns of precipitation and disturbance, human activities) that influence the structure and function of forests, and how these in turn influence utilization of forest habitats by birds, especially migratory species such as the hooded warbler (*Wilsonia citrina*), wood thrush (*Hylocichla mustelina*), and ovenbird (*Seiurus aurocapillus*), which forage primarily in the forest understory.

Forest Dynamics and Ecology at Rancho San Felipe: Phosphorus Addition, Precipitation, and Hurricane Impacts

In 1984, we initiated an experiment in the northeastern Yucatán Peninsula of Mexico to test Vitousek's (1984) hypothesis that phosphorus limits tree

growth and litterfall production in most tropical forests. Little ecological research had been conducted in dry tropical forests (Murphy and Lugo 1986) prior to the development of Vitousek's hypothesis, but based on soil characteristics in the northeastern Yucatán (e.g., pH approximately 7.0 and a high calcium content) we predicted that phosphorus would limit tree growth and control patterns of nutrient cycling. We also wished to determine whether or not experimental manipulations of the forest (e.g., removal of leaf litter, addition of phosphorus, etc.) would influence the abundance of resident and Neotropical migratory birds, especially species that forage in the forest understory.

Our experiments were conducted at Rancho San Felipe, a privately owned property approximately 10 km south of the village of Puerto Morelos, Quintana Roo. There was no evidence of recent forest disturbance at Rancho San Felipe, except for a small area that had been cleared for use in agricultural research. The latter studies revealed that phosphorus was the nutrient that most limited crop production following clearing of the forest (Felipe Sánchez Román and Patricia Zugasty Towle, pers. comm.). Details of characteristics of the dry tropical forest at Rancho San Felipe and the experimental design are given in Table 17.1 and Table 17.2 and in Whigham et al. (1990).

Table 17.1. Characteristics of dry tropical forests at Rancho San Felipe and Noh-Bec research sites.

Characteristic	Rancho San Felipe	Noh-Bec
Annual precipitation	~1200 mm with a distinct dry season	~1100–1300 mm with a distinct dry season
Temperature	22–8 degrees C	24–26 degrees C
Soil pH	~7.0	~7.0
Depth	>20 cm	varies w/topography
Soil content	High calcium and high organic matter (~50%)	Organic matter varies from low to >50%
Canopy height	10–20 m	10–30 m
Tree diameter distribution		
10–20 cm	65.6%	66%
20–30 cm	25.6%	17.6%
30–40 cm	5.1%	9.9%
> 40 cm	3.7%	6.6%
Tree density (mean & SE)	768 ± 23 trees/ha	605 ± 5 trees/ha
Tree basal area (mean & SE)	26.9 ± 1.0 m ² /ha	25.1 ± 0.2 m ² /ha

Growth rates of approximately 1,500 tagged trees were measured yearly from 1984 to 1992. Tagged trees were located in 12 40 x 40 m permanent plots that served either as controls or as sites where one of three manipulations were performed twice each year: (1) all leaf litter was removed, (2) leaf litter was removed and superphosphate fertilizer added, or (3) superphosphate fertilizer was added without removing litter. Monthly collections of litterfall were made from five randomly located 1 x 1 m litter traps in each plot. Litterfall collections were separated into leaves and reproductive parts, then

Table 17.2. Dominant tree species at Noh Bec and Rancho San Felipe. For Noh-Bec, the 13 species listed each have > 50 tagged individuals and they account for 73% of all tagged trees in the 82 permanent plots. Seventy-seven species occur in the 82 plots. For Rancho San Felipe, the ten species listed account for 76% of all tagged trees in 1984 in the 12 permanent plots. Seventy-seven species occur in the 12 plots.

Species	Family	% Total tagged trees
Rancho San Felipe		
<i>Manilkara zapota</i>	Sapotaceae	26.9
<i>Brosimum alicastrum</i>	Moraceae	9.5
<i>Drypetes lateriflora</i>	Euphorbiaceae	9.3
<i>Talisia olivaeformis</i>	Sapindaceae	9.2
<i>Gymnanthes lucida</i>	Euphorbiaceae	7.2
<i>Blomia cupanioides</i>	Sapindaceae	3.9
<i>Beaucarnea plicabilis</i>	Liliaceae	3.7
<i>Myrcianthes fragrans</i>	Myrtaceae	2.4
<i>Coccoloba diversifolia</i>	Polygonaceae	2.3
<i>Bursera simaruba</i>	Burseraceae	1.9
<i>Pouteria unilocularis</i>	Sapotaceae	15.1
<i>Alseis yucatanensis</i>	Rubiaceae	10.2
<i>Sabal mauritiiiformis</i>	Arecaceae	8.4
<i>Manilkara zapota</i>	Sapotaceae	7.1
Noh-Bec		
<i>Cosmocalyx spectabilis</i>	Rubiaceae	5.8
<i>Brosimum alicastrum</i>	Moraceae	5.4
<i>Blomia cupanioides</i>	Sapindaceae	4.5
<i>Bursera simaruba</i>	Simarubaceae	3.0
<i>Pouteria campechiana</i>	Sapotaceae	2.8
<i>Drypetes lateriflora</i>	Euphorbiaceae	2.3
<i>Protium copal</i>	Burseraceae	2.2
<i>Simarouba glauca</i>	Simaroubaceae	2.2
<i>Swietenia macrophylla</i>	Meliaceae	2.1

dried, weighed, and analyzed for their phosphorus content. Phosphorus content was also analyzed for litter removed from experimental plots in treatments (1) and (2) described above. Birds were sampled in the 12 plots using two 12 x 2 m nylon mist-nets per plot, operated for three successive mornings in late November 1984 and in February and March during the years 1985 to 1995. Data from the mist-nets in the 12 plots were supplemented by capture data from 15 to 24 mist-nets placed in the same tract of forest but outside of the experimental plots. All captured birds were identified, weighed, sexed, and marked with individually coded plastic leg bands before being released.

Neither litter removal nor phosphorus addition had any detectable influence on tree growth, leaf litterfall, litterfall of reproductive materials, or total nutrients or concentrations of nutrients in litterfall after the first four years of the study (Whigham and Lynch in press), nor were effects observed on the activity of Neotropical migrants or resident bird species (Lynch and Whigham 1995). The most informative results of the first four years of the study were the lack of response to phosphorus additions, the large annual variations in tree growth (Figure 17.1) and leaf litterfall (Figure 17.2), and the relationships of these patterns to annual precipitation (Whigham et al. 1990; Whigham and Lynch in press).

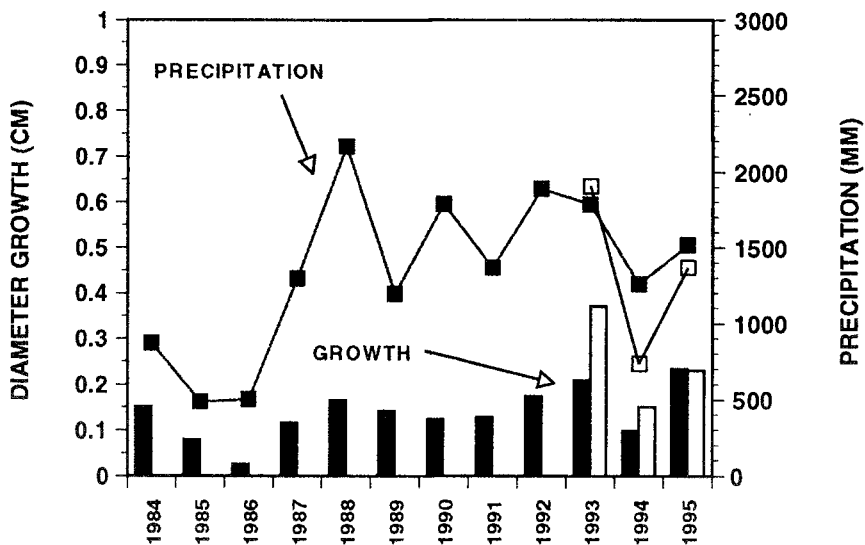


Figure 17.1

Average annual growth (cm) of trees in permanent plots at Rancho San Felipe and Noh-Bec. Rainfall data (mm) are also plotted for both sites. Solid rectangles and columns are data for Rancho San Felipe. Open rectangles and columns are data for Noh-Bec.

In 1988, we decided to modify the original experimental design to simulate the long-term average weekly pattern of precipitation by adding water to half of each of the 12 study plots. Our objective was to continue to test the phosphorus limitation hypothesis, while minimizing the impacts of annual variations in the amount and timing of precipitation. Before we could begin the experimental modifications, however, on September 14, 1988, the site was severely disturbed by Hurricane Gilbert. The emphasis of our project then shifted to an assessment of hurricane impacts (Lynch 1991; Whigham et al. 1991), and we initiated studies to determine how the system responded to the disturbance. All ecological aspects of the initial phase of the study continued, but it was not possible to remove leaf litter from the plots due to the large amount of woody debris generated by the hurricane. We also initiated phenological studies and studies of coarse woody debris (Harmon et al. 1995).

Tree mortality had averaged 0.5% of the tagged trees per year during the four-year pre-hurricane period. The forest was completely defoliated by the hurricane and about 2.5% of the marked trees were killed directly or died over the next five months. By 1993, tree mortality rates had decreased to pre-hurricane levels (Whigham and Lynch in press). The only tree species to experi-

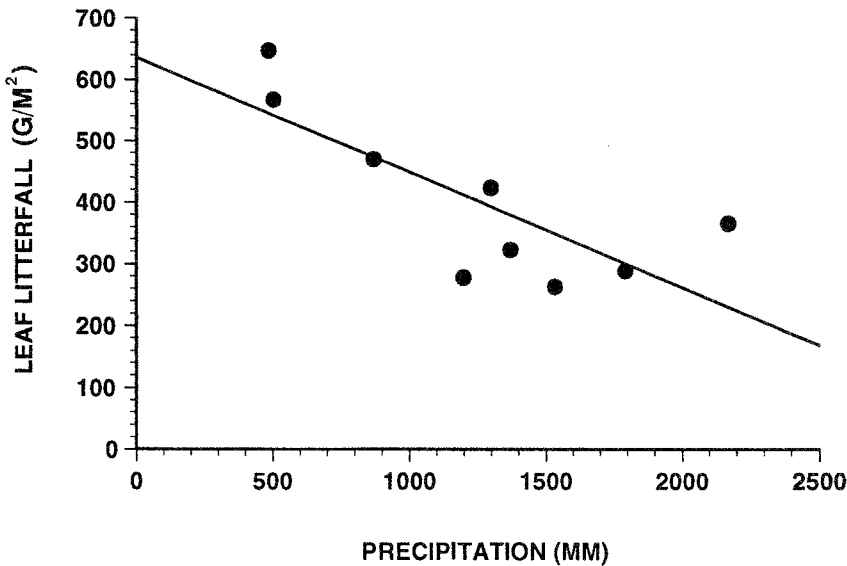


Figure 17.2

Relationship between leaf litterfall (g/m^2) and annual precipitation (mm) at Rancho San Felipe between 1984 and 1991. Data for 1988 are included, but the amount of litterfall and precipitation from Hurricane Gilbert has been removed from the annual total. Litterfall associated with Hurricane Gilbert is compared to other years in Figure 17.3.

ence a major long-term detrimental impact due to the hurricane was ramón (*Brosimum alicastrum*), a canopy co-dominant that decreased in the plots from 143 marked trees in 1984 to 4 trees that were barely alive in 1996. In post-hurricane years, absolute and relative tree growth rates of all species but ramón continued to be controlled by annual precipitation patterns rather than any response to hurricane damage (Figure 17.1).

Defoliation of the forest by Hurricane Gilbert resulted in an enormous increase in leaf litterfall (Figure 17.3) and more than a threefold increase in the amount of phosphorus in leaf litterfall, from a mean of $0.25 \pm 0.1 \text{ g/m}^2$ for the four pre-hurricane years to $0.7 \pm 0.1 \text{ g/m}^2$ generated by the storm (Whigham et al. 1991). The hurricane also had a large impact on the amount of coarse woody debris (downed wood > 10 cm diameter) on the forest floor, which increased from roughly 31 Mg/ha to 47 Mg/ha (Whigham et al. 1991). We estimated that it will take 30 to 150 years for the wood downed by the hurricane to disappear, depending on species-specific differences in decomposition rates (Harmon et al. 1995).

The first post-hurricane mist-netting of birds occurred about five months after the storm. The number of species captured per mist-netting bout increased by approximately 70% and the capture rate (capture rate = $100 \times [\text{individuals/net/hr}]$) doubled (Lynch 1991; Whigham and Lynch in press). Many birds captured following the hurricane were field-associated species such as

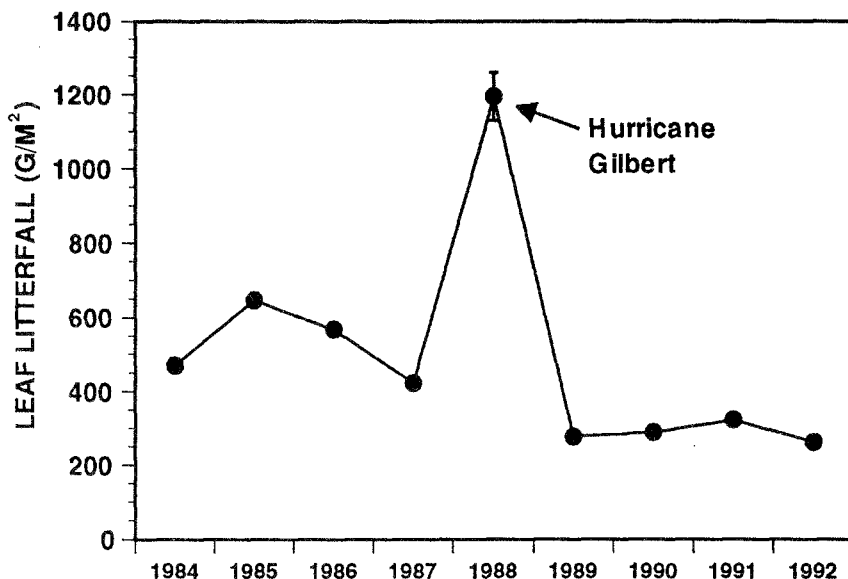


Figure 17.3

Annual leaf litterfall (g/m^2) at Rancho San Felipe between 1984 and 1991.

the indigo bunting (*Passerina cyanea*) and painted bunting (*Passerina ciris*) (Lynch 1992). The species that increased most dramatically was the white-eyed vireo (*Vireo griseus*), a migratory habitat generalist that occurs both in brushy fields and in the forest canopy, but was rarely captured in the understory mist-nets before the hurricane. Its capture rate increased from 0.1 before the hurricane to 3.2 during the first post-hurricane mist-netting bout. The capture rate for the white-eyed vireo began to decline in the second year following the hurricane, but remained higher than the pre-hurricane level through the end of the study in 1995. Other migratory species that typically forage in the forest canopy (e.g., magnolia warbler [*Dendroica magnolia*], black-and-white warbler [*Mniotilta varia*], and American redstart [*Setophaga ruticilla*]) also became more abundant in the dense understory following the hurricane, presumably because the upper canopy was completely defoliated.

The wood thrush (*Hylocichla mustelina*) was the only previously common understory Neotropical migrant that completely disappeared from the forest study plots following the hurricane. This species was not netted in 1989 or 1990, but its capture rate exceeded the mean pre-hurricane capture rate (0.6) in three of the four subsequent years (range = 3.8 in 1991 to 0.2 in 1994). Capture rates were unaffected by the hurricane for the other common understory Neotropical migrants (e.g., hooded warbler [*Wilsonia citrina*], ovenbird [*Seiurus aurocapillus*], Kentucky warbler [*Oporornis formosus*]).

Dynamics and Ecology of a Selectively Logged Forest at Noh-Bec

During the years that we were working at Rancho San Felipe in northeastern Quintana Roo, the Plan Piloto Forestal (PPF), a regional plan for community management of natural forests, was initiated in southern Quintana Roo (Galletti and Argüelles 1987). Most of the PPF's efforts are concentrated on forest-owning ejidos, rural cooperatives established after the Mexican Revolution, roughly 50 to 60 years ago. Two assumptions in the initial forest growth models for the PPF were that the average annual diameter increment of trees varied between 0.5 and 1.0 cm per year, depending on species group, and that natural regeneration was sufficient to sustain economically important species. These assumptions were not based on data for natural forests in the region, however, and it was intended that the management plan would be modified as relevant local data were gathered (Ramírez Segura and Sánchez Román 1992). Our growth data from Puerto Morelos (Figure 17.1) clearly showed that the average annual diameter growth there was much less than 1.0 cm. In addition, little information was available on the regeneration characteristics of either commercial or noncommercial tree species in forests similar to those at Noh-Bec or on their responses to logging disturbance (Negreros 1991; Snook 1993).

In 1993, we extended our research to the ejido of Noh-Bec with three objectives. First, we wished to determine whether or not tree growth rates at Noh-Bec were similar to those that we had been measuring at Rancho San Felipe. We anticipated that growth rates would be higher at Noh-Bec, where the average annual precipitation is slightly higher than at Puerto Morelos (Table 17.1) and soils generally are deeper. Our second objective was to determine what effects, if any, selective logging had on birds. Based on the generally minor responses of birds to Hurricane Gilbert at Rancho San Felipe, we predicted that selective logging at Noh-Bec would have little impact. Our third objective at Noh-Bec was to characterize the natural disturbance regime within the forest and assess regeneration in the intact forest, in natural treefalls, and in gaps created by selective logging.

Noh-Bec is located roughly 50 km south of the city of Felipe Carillo Puerto in southeastern Quintana Roo. Forests at Noh-Bec are generally taller than the forest at Rancho San Felipe (Table 17.1), but forests in both areas were considered to be similar in stature and composition according to Miranda's (1958) classification. Information on the forests that we are studying at Noh-Bec can be found in Table 17.1. In 1993, we tagged all trees > 10 cm dbh in 82 circular 0.1 ha plots. The plots were randomly chosen from a set of several hundred 0.1 ha inventory plots that had been established at 100 m intervals along surveyed N-S lines spaced at 250 m intervals from each other.

Regeneration was studied by sampling seedlings and saplings in closed canopy forest, natural treefall gaps, and logging gaps. We used 40 m wide belt transects and 10 ha plots to sample the distribution, size, and rate of occurrence of natural tree gaps and logging gaps. Sample areas included forest logged about 18 years previously, forest burned 20 years previously, and unlogged forest that had not been burned within the memory of a number of elderly ejidatarios. We predicted that gap size and disturbance type (natural versus logging gaps) would affect the species composition and performance of regenerating trees.

We sampled birds at Noh-Bec using the same protocol that was applied at Rancho San Felipe. Between 1993 and 1995 we sampled birds during three winters (February through March) and two summers (June and July). Mist-netting, supplemented with point counts (Lynch 1992), was conducted at four forested sites that had been disturbed by selective logging at various times in the past, and at one control site that had never been logged.

Tree growth rates of all species combined (Figure 17.1) varied over the first three years of the project and, as we found in the forest at Rancho San Felipe, annual differences appeared to be related to variations in annual precipitation. Annual growth of commercially important species, such as mahogany (*Suietenia macrophylla*), varied in the same pattern as was observed for all tree species combined. Between 1993 and 1996, diameter growth of mahogany, one of the fastest-growing commercial species, was 0.65 ± 0.08 cm in the

wettest year (1993) and 0.20 ± 0.06 in the driest year (1994). At the other extreme, one of the slowest-growing commercially valuable species, siricote (*Cordia dodecandra* [Boraginaceae]), showed no measurable growth over the four-year period.

Along with adequate growth rates, sufficient regeneration of logged species is necessary if timber harvesting is to be sustainable over the long term. In this forest, canopy openings formed by natural treefall and logging are important sites for regeneration, as are the more intense disturbances caused by fire and hurricanes (Snook 1993). The rates of natural treefall disturbance in Noh-Bec are lower than any reported in the literature for tropical forests (Whigham et al., in press). In wet, lowland tropical forests in the Americas, the natural treefall rate is usually about 1 gap/ha per year, the area opened by treefalls each year is about 1.5% of the forest, and the gap turnover time is around 100 years (Denslow 1987; Yavitt et al. 1995). Gap turnover time, an estimate of the number of years required for the equivalent of 100% of the forest to be opened to gaps, is calculated from the area opened to gaps each year. Over three years, the natural rate of treefall at Noh-Bec was about 0.2 gaps/ha per year, and most gaps were smaller than the minimum size reported for other forests. The area opened to gaps each year was about 0.07% per year, and the gap turnover time was $> 6,000$ years. Standing gap area (gaps of all ages) is extremely low, at about 0.27% of the forest area. These results hold for even the oldest undisturbed stands we sampled and are consistent among three methods of estimation.

Two nonexclusive explanations for the exceedingly low rate of natural disturbance at Noh-Bec seem promising: first, low rates of treefall disturbance are typical of tropical dry forests generally (Whigham et al., in press), and second, low rates of treefall disturbance are typical of forests that are periodically burned or disturbed by hurricanes. Noh-Bec is by far the driest forest (1,100 to 1,300 mm rainfall per year) for which disturbance rates have been reported. Closest is the forest of Tai National Park in the Ivory Coast (Jans et al. 1993), which receives about 1,800 mm of rainfall per year. In the Tai National Park, the natural treefall rate was approximately 0.7 gaps/ha per year, the area opened to gaps each year was approximately 0.41% per year, and the gap turnover time was 244 years. The rate of disturbance there is lower than that reported for wet lowland forests in the American tropics, but much higher than the drier forest at Noh-Bec, supporting the hypothesis that dry forests are inherently less dynamic than wet forests.

Hurricanes and fires have been an integral part of the disturbance regime at Noh-Bec (Snook 1993), and the low rates of disturbance we measured in Noh-Bec may be explained in large part by the fact that no hurricanes or fires occurred during our four- to five-year study. Because treefall mortality is pulsed in time, long-term monitoring that included major disturbance episodes would likely yield an average rate of disturbance more comparable to

the year-to-year rates measured in forests not subjected to major disturbance events. In support of this notion, major disturbance by agricultural clearing (Yavitt et al. 1995), wind storms (Veblen 1985), and fire (Lorimer 1989) have been shown to reduce rates of treefall disturbance many years after the event. Periodic major disturbances thus appear to be of great importance for stand dynamics and regeneration in much of the Maya Forest. These disturbances appear to alternate with long intervals of unusually low rates of treefall disturbance and few opportunities for gap-phase regeneration.

One objective of our regeneration studies at Noh-Bec has been to characterize species in terms of their response to the gradient in canopy openness, which in turn is positively correlated with gap size. Seedlings and saplings growing in closed forest, natural gaps, and felling gap plots were sampled and categorized as either "gap specialists" or "generalists." Gap specialist species occupy only the more open-canopy sites, and large individuals of these species (stem height > 50 m) do not occur below a closed canopy. Conversely, seedlings and saplings of generalist species are distributed broadly across the canopy openness gradient. Using this conservative classification, 32% of the 65 species for which sufficient data are available are gap specialists. This proportion of gap specialists is much higher than occurs in wetter forests at Barro Colorado Island, Panama (6%; Welden et al. 1991) and La Selva, Costa Rica (9%; Lieberman et al. 1995). The majority (68%) of the tree species at Noh-Bec are generalists. It is unclear if drier forests generally have a larger proportion of gap specialists, or whether the higher proportion of gap specialists at Noh-Bec reflects the region's history of major periodic disturbance (Whitmore 1974).

Established understory vegetation appears to inhibit the colonization of gaps by gap specialist species. At Noh-Bec the rubber-tired skidders that are used to remove logs from felling gaps kill or damage small trees and understory vegetation and disturb the litter layer. This disturbance induces an increase in root-sprouting, particularly from a handful of gap specialist species. Physical damage associated with log extraction also results in an increase in the establishment of gap specialists from seed. For these reasons, a typical logging gap has a higher density and proportion of gap specialist individuals than does a natural gap of the same size.

A total of 70 bird species were netted between 1993 and 1994 at Noh-Bec, and 148 species occurred in point counts over the same period. Preliminary analysis of the mist-netting and point count data indicates little impact of selective logging on the occurrence of either migrant or resident bird species. For the ten most commonly netted species (Table 17.3), numbers of individuals and species composition were similar at the unlogged control site and four sites that were logged in 1993, 1992, 1987, and approximately 1950. The only Neotropical migrant among the ten most abundant species was the wood thrush (*Hylocichla mustelina*). It was also the only common species that

showed major differences in capture rates among the five sites: it had an anomalously high capture rate at the unlogged control site in the 1993 winter sample (Table 17.3). However, wood thrush capture rates at this site fell dramatically in the winters of 1994 and 1995, suggesting that the high density in 1993 was only transitory. This species has occasionally been captured in unusually high numbers at other sites in Quintana Roo (J. Lynch, unpublished data), perhaps reflecting local population movements during the overwintering period.

None of the bird species characteristic of heavily disturbed vegetation were encountered in net samples from either the logged sites or the control site at Noh-Bec, although these species were common in nearby fields and regrow-

Table 17.3. Abundance of the ten most commonly netted bird species at five sites at Noh-Bec. Entries are the number of individuals captured in 20 mist-nets over a three-day period. Sites are ordered from most recently disturbed to undisturbed. The wood thrush is a Neotropical migrant. Other species are permanent residents.

Species	Year when site was logged				Control	Total
	1993	1992	1987	1950		
Red-throated ant-tanager <i>Habia fuscicauda</i>	41	44	21	31	16	153
Wood thrush <i>Hylocichla mustelina</i>	21	14	27	19	58	139
Ruddy woodcreeper <i>Dendrocincla homochroa</i>	32	15	27	13	28	115
Tawny-crowned greenlet <i>Hylophilus ochraceiceps</i>	24	12	26	25	9	96
Stub-tailed spadebill <i>Platyrinchus cancrominus</i>	12	10	21	21	16	80
Red-crowned ant-tanager <i>Habia rubica</i>	10	14	19	15	16	74
Thrushlike manakin <i>Schiffornis turdinus</i>	12	17	10	12	18	69
White-bellied wood wren <i>Henicorhina leucosticta</i>	9	17	20	12	5	63
Tawny-winged woodcreeper <i>Dendrocincla anabatina</i>	9	17	11	11	15	63
Olivaceous woodcreeper <i>Sittasomus griseicapillus</i>	11	12	11	17	11	62

ing fields. These same species are known to invade forest disturbed by hurricane or wildfire (Lynch 1989, 1991, 1992; Lynch and Whigham 1995). These observations suggest that selective logging as practiced at Noh-Bec causes much less severe disruption of bird populations than do major natural disturbances.

Conclusions

Ten years of data from the Yucatán Peninsula demonstrate that the local dry tropical forests are very dynamic and that they differ in several ways from more humid tropical forests. Annual variations in tree growth are substantial and seem to be driven by annual variation in the total amount and seasonal distribution of precipitation, factors that also appear to control the annual rate of leaf litterfall in both shallow and deep soils (Whigham et al. 1990). The amount of coarse woody debris in Quintana Roo forests appears to be higher than in more humid forests, but this factor is quite dynamic, increasing dramatically after hurricanes while decreasing just as dramatically in areas that burn (Harmon et al. 1995). Rates of natural treefall disturbance in the intervals between major disturbance events are much lower than in wetter forests, suggesting that local forest dynamics may be controlled mostly by periodic disturbances such as hurricanes and wildfire.

Almost all of the habitats that we have examined are important for Neotropical migrant birds. The species that utilize forest habitats appear to be common in both mature and successional forest habitats (Lynch 1989, 1992). Furthermore, the type of selective logging done throughout most of the region appears to have no discernable influence on Neotropical migrant birds or on most resident species. Large-scale disturbances can temporarily influence the dynamics of some bird and plant populations, but recovery tends to be rapid at both the population and ecosystem level. The most lasting damage to dry tropical forest is caused by large-scale conversion to permanent pasture, a land use that displaces most forest-associated birds and slows the rate of recovery of the forest community following pasture abandonment (Lynch 1992).

We are encouraged by the possibility of developing methods for sustainable forestry in portions of the region. Tree growth rates at Noh-Bec may be high enough to sustain timber harvests over the long term even though they are lower than rates assumed in the original management plan. However, observed low regeneration rates of commercially important species may present future problems. Information on natural disturbance and regeneration can be used as a basis for modeling silviculture, but not all types of natural disturbances are equally relevant. At Noh-Bec the majority of commercial timber species (9 out of 13), including mahogany, are gap specialists. Our data suggest that a lack of adequate seed sources and the small size of canopy openings that

result from selective logging are leading to commercial elimination of the most important gap specialist species. For regeneration of these gap specialists large-scale natural disturbances such as hurricanes and fires are better silvicultural models than are natural treefalls.

If management for gap specialist tree species is to succeed, larger canopy openings need to be created and colonization rates by desired species must be increased. One proposed solution to the canopy opening problem is to harvest more species and relax the diameter-limit restrictions (Argüelles 1991; Snook 1993). This approach would potentially create larger openings by encouraging the cutting of more trees, assuming that large numbers of smaller-sized commercial trees grow close together. A potential pitfall of this increased harvesting intensity would be an increase in the impact of logging on wildlife and other nontarget species. To overcome the problem of limited seed availability, widespread enrichment planting of mahogany and Spanish cedar (*Cedrela odorata*) has been done, along with casual trials with other species. Although enrichment planting has not been uniformly successful, the potential exists to improve this and other techniques that might make the PPF logging system more sustainable. We are currently working with foresters and the ejidatarios of Noh-Bec to test experimentally enrichment planting techniques, and we will continue to test silvicultural techniques designed to promote natural regeneration of logged species.

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