

Potential Effects of Passenger Pigeon Flocks on the Structure and Composition of Presettlement Forests of Eastern North America

JOSHUA W. ELLSWORTH* AND BRENDA C. McCOMB†

Department of Natural Resources Conservation, University of Massachusetts, Amherst, MA 01003, U.S.A.

Abstract: *We considered the possible effects Passenger Pigeon (*Ectopistes migratorius*) flocks may have had on the disturbance regime and species composition of presettlement forests in eastern North America. We suggest that the activities of roosting and nesting Passenger Pigeons caused widespread, frequent disturbances in presettlement eastern forests through tree limb and stem breakage and nutrient deposition from pigeon excrement. We suspect that the deposition of fine fuels resulting from such disturbances may have influenced fire intensity and frequency in presettlement forests. Further, we propose that consumption of vast quantities of acorns by pigeons during the spring breeding season may partially explain the dominance of white oak (*Quercus alba*) throughout much of the presettlement north-central hardwoods region. Consequently, the pigeon's extinction may have facilitated the increase and expansion of northern red oak (*Quercus rubra*) during the twentieth century. Although it is difficult to accurately quantify how physical and chemical disturbances and mast consumption by Passenger Pigeon flocks affected forest ecology, we suspect they shaped landscape structure and species composition in eastern forests prior to the twentieth century. We believe their impact should be accounted for in estimates of the range of natural variability of conditions in eastern hardwood forests.*

Efectos Potenciales de Parvadas de Palomas Migratorias sobre la Estructura y Composición de Bosques en Norte América Oriental antes de la Colonización

Resumen: *Consideramos los posibles efectos que pudieron haber tenido parvadas de Palomas Migratorias (*Ectopistes migratorius*) sobre el régimen de perturbación y la composición de especies de bosques en Norte América oriental antes de la colonización. Sugerimos que las actividades de perchado y anidación de las palomas causaron perturbaciones frecuentes y extensas en los bosques orientales antes de la colonización por medio de la ruptura de ramas y tallos de árboles y la deposición de nutrientes del excremento de las palomas. Sospechamos que la deposición de combustibles resultantes de tales perturbaciones pudo haber influido en la intensidad y frecuencia de incendios forestales. Más aún, proponemos que el consumo de grandes cantidades de bellotas por las palomas en la primavera puede parcialmente explicar la dominancia de roble blanco (*Quercus alba*) en muchos de los bosques nor-orientales. En consecuencia, la extinción de la paloma pudo haber facilitado el incremento y expansión del roble rojo (*Quercus rubra*) durante el siglo veinte. Aunque es difícil cuantificar con precisión como las perturbaciones físicas y químicas y el consumo masivo por parvadas de palomas migratorias afectaron a la ecología forestal, sospechamos que modelaron la estructura del paisaje y la composición de especies en los bosques orientales antes del siglo veinte. Creemos que su impacto debería ser considerado cuando se hacen estimaciones del rango de variabilidad natural de las condiciones en bosques orientales de maderas duras.*

*Current address: 142 Lake Street, Arlington, MA 02474, U.S.A., email vinecontrol@aol.com

†Current address: Watershed Ecology Branch, Western Ecology Division, National Health and Environmental Effects Research Laboratory, U. S. Environmental Protection Agency, 200 SW 35th Street, Corvallis, OR 97333, U.S.A., email mccomb.brenda@epa.gov
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Introduction

The size, severity, and frequency of disturbances affecting forests are major mechanisms influencing the species composition and structure of individual forest stands, and the heterogeneity of the forested landscape mosaic (Oliver & Larson 1990; Spies & Turner 1999). Interest in the mechanisms influencing contemporary forest composition in the eastern United States and the restoration of forests to pre-European-settlement conditions have prompted researchers to examine historical disturbance regimes (Seischab & Orwig 1991; Abrams 1992; Lorimer & Frelich 1994). Shifting trends in the frequency and severity of disturbances such as fire, wind, ice storms, and human-resource use are all considered important influences on the changing structure and composition of eastern forest landscapes (Crow 1988; Seischab & Orwig 1991; Abrams & Nowacki 1992; Lorimer & Frelich 1994). Here we discuss how physical and chemical disturbances and mast consumption by flocks of the now extinct Passenger Pigeon (*Ectopistes migratorius*) may have contributed to the disturbances that shaped landscape structure and species composition in eastern forests prior to the twentieth century.

Until the latter half of the nineteenth century, flocks of Passenger Pigeons occurred throughout eastern North America. The total population was estimated to have been 3–5 billion individuals, roughly equal to the current number of birds of all species that overwinter in the United States (Schorger 1955; Webb 1986). Flocks forming columns over 1 km wide and 400–450 km long were commonly observed (King 1866 as cited in Schorger 1955). Flocks consumed vast quantities of oak (*Quercus* spp.), American beech (*Fagus grandifolia*), and American chestnut (*Castanea dentata*) mast and other plant foods daily (Schorger 1955). They also damaged forests in which they roosted or nested. The ground beneath roosting and nesting sites was often covered with several centimeters of feces, thereby killing grasses, forbs, and understory vegetation (Audubon 1831; Schorger 1955; Savage 1970). Further, the weight of the clustered birds commonly toppled trees and broke branches. Many hectares of forest were affected and few plants grew at roost sites for several years following their use (Wilson 1814; Audubon 1831; Schorger 1955).

Researchers recognize the impact of Passenger Pigeons' roosting and nesting on forests at a local level (Schorger 1955; Savage 1970; Blockstein & Tordoff 1985; Oliver & Larson 1990), but there has been little discussion of their potential of their impact on broader forest landscapes in eastern North America. Employing a preliminary literature review to develop hypothetical flock movements and densities, we speculate on the amount of land affected by physical destruction of vegetation and by fecal deposition. We also discuss how these factors may have interacted with fire and other distur-

bances to cause more intense forest disturbances. Furthermore, although Passenger Pigeons have been cited as a possible dispersal vector explaining the northward migration of nut-producing tree species in the Holocene (Webb 1986), the effect of seed predation by Passenger Pigeons on post-Holocene forest composition has not been examined. We suggest that mast consumption by Passenger Pigeons in the northern portion of the eastern forest during the spring breeding season may have facilitated dominance by fall-germinating white oak (*Quercus alba*) and possibly other species in the white oak group (*Leucobalanus*). We also suggest that the reduction in spring mast consumption after the pigeon's extinction may have been one of the mechanisms behind the shift in oak species composition toward an increase and expansion of northern red oak (*Quercus rubra*) in the twentieth century. We hope our speculations will initiate a more thorough examination of the role that Passenger Pigeons may have played in presettlement forest ecology.

Passenger Pigeon Distribution

Passenger Pigeons ranged over more than 7.25 million km² from north Florida, west to eastern Texas, north and west to Alberta, east to Nova Scotia, and south along the Eastern seaboard (Fig. 1). The primary breeding range covered 1.2 million km² from southern New York, west-southwest across Pennsylvania, northern West Virginia, and Kentucky, north and west to southern Wisconsin, and east through southern Michigan and northern New York to southern Maine (Fig. 1) (Schorger 1955). The breeding range covered the northern part of the central hardwood region (dominated by oaks, hickories [*Carya* spp.], and American chestnut) and the northern hardwood region (dominated by American beech, maples [*Acer* spp.], and birches [*Betula* spp.]) (Braun 1950).

Pigeons formed large flocks during the late winter/early spring migration from their winter range, south of lat. 36° N, to their breeding grounds in the north-central hardwoods and northern hardwoods regions (Fig. 1) (Schorger 1955; Blockstein & Tordoff 1985). During migration, pigeons roosted in trees or shrubs at night or during storms. Once large quantities of mast were located, preserved from the previous fall by the snowpack and exposed during snowmelt, nesting would begin (Bucher 1992). Nesting normally occurred between early April and late June, with a peak between mid-April and mid-May. The pigeons would complete a breeding cycle within approximately 30 days (Bucher 1992). During years with favorable weather or abundant mast, a second or third nesting may have been attempted (Bucher 1992). At the end of the breeding season, the adults dispersed into smaller flocks to search for food, often to the

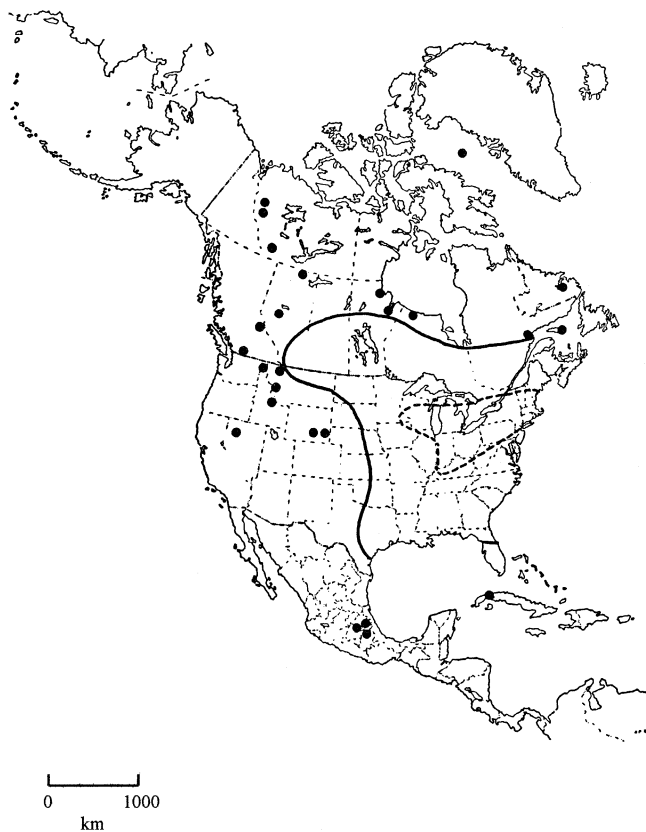


Figure 1. Passenger Pigeon distribution in North America. East of the solid line indicates the normal range, dotted line indicates the principal nesting area, and points signify accidental occurrences. Map from Schorger (1955). Reprinted with the permission of the University of Wisconsin Press, Madison.

northern limits of their range (Fig. 1). By the end of August and through September, the adults and young migrated south (Schorger 1955) to feed in the south-central hardwoods and southern hardwoods regions.

Feeding Habits

Pigeons ate fruits, insects, earthworms, and buds, but when available their diet consisted primarily of mast of American beech, oaks, and American chestnut (Mershon 1907; Schorger 1955), reportedly preferred in that order (Schorger 1955; Bucher 1992). Due to the spatial and temporal variability in mast production (Rogers 1990; Sander 1990; Tubbs & Houston 1990; Healy et al. 1999), pigeon flocks moved across the landscape searching for food in variable-sized flocks. Some years they were reported to have exploited mast in parts of Pennsylvania, Michigan, and New York, and other years they were apparently more abundant in Wisconsin and Minnesota (Schorger 1937). Although movements were not random, they likely were variable from year to year. Nesting success was particularly dependent on a high concentration of mast because

breeding colonies of hundreds of millions of pigeons were confined to one area for a 30-day period (Bucher 1992).

The area over which flocks foraged was large. Bucher (1992) estimated that pigeon colonies would have been able to search the area within an 80- to 160-km radius of their roosting or nesting site (20,000–80,000 km²). The amount of food consumed by flocks was enormous. Pigeons consumed approximately 0.07 L of food/day (Schorger 1955). Therefore, a total population of 3 billion pigeons would have consumed 210 million L/day (0.07 L/bird/day × 3 billion birds). Although acorns made up only a portion of the pigeon's diet during breeding, an examination of acorn production per area helps illustrate the potential impacts of food consumption. There is an average of 80–370 viable red oak (*Quercus rubra*) acorns/L (Olson 1974). In a 3-year study, Healy (1997) observed that unthinned, second-growth red oak stands produced approximately 30,000–155,000 acorns/ha. Based on a median figure of 225 acorns/L, we estimate that the oak stands probably produced from 133 to 689 L/ha. Therefore the entire Passenger Pigeon population could have consumed the total red oak acorn production from roughly 304,789 to 1,578,947 ha of red oak forest per day (210 million L/689 L/ha, or 210 million L/133 L/ha).

Roost Distribution and Size

Pigeons roosted at night and during storms. Roosting was observed in forests, shrublands, and shrub-dominated wetlands (Schorger 1955). Some roosts were used only for a few hours, whereas others were used for several months. Many roosts were revisited annually (Schorger 1955). Roosts were also variable in size, commonly ranging from 0.02 to 10 km², although some may have been as large as 130 km² (Schorger 1955). The density of roosting pigeons is unclear. Although Schorger (1955) provided estimates of the density of pigeons in nesting areas, he did not attempt to estimate pigeon density in roosts. With observers citing every centimeter of medium to large tree branches occupied by roosting pigeons, with some roosting on the backs of others (Kalm 1911; Schorger 1955), 10 pigeons/m² of ground, or approximately 105,000 pigeons/ha, would seem a reasonable estimate. Passenger Pigeons weighed between 255 and 341 g (Schorger 1955; Bucher 1992). Consequently, it is possible that pigeon biomass in roosts may have ranged between 27,000 and 36,000 kg/ha.

Given the variability in roosting-site fidelity, size, and duration, and lack of data concerning the density of roosting pigeons, it is difficult to estimate the land area that was affected by roosts. Nonetheless, to illustrate the possible landscape-level effects of pigeon roosts, we created a hypothetical roosting schedule for a flock of 500,000 adult pigeons for a given year, and using the density estimate

of 105,000 pigeons/ha, we calculated the land area they would have affected.

In estimating the duration of long-term roosts and the number of temporary roosts, we considered the time of year and the related abundance of food. For example, we assumed that during the breeding season pigeons would have roosted in the nesting area, so that roosting during April, May, and June would have been limited to temporary day roosts when pigeons were not foraging. In addition, we assumed that after nesting ended in late June, the pigeons needed to move often, in search of insects, worms, and fruits, and therefore the number of roosts increased and the reuse of roosts decreased. By contrast, in November, pigeons would be in the mast-rich southern hardwoods (Schorger 1955), most likely reducing the need to move roosts in the search for food. Furthermore, we took into account the population fluctuation that would have occurred with breeding and annual mortality. For the sake of simplicity, we assumed a stable year-to-year population for the flock of 500,000 adults at the beginning of the breeding season. By using data for the band-tailed pigeon (*Columba fasciata*), the closest living species to the Passenger Pigeon in breeding biology and size, Bucher (1992) estimated first-year Passenger Pigeon survival at between 45% and 70%. If the middle value of 67% for survivorship is used, the pigeon population in the hypothetical flock rises to 750,000 after breeding. By assuming a constant mortality rate, we subtracted 25,000 individuals per month over the next 10 months, returning the population to 500,000 (Table 1).

From our hypothetical schedule of total annual roosting area, we estimated that a flock of 500,000 pigeons would have affected approximately 633 ha, or 6.3 km², of their range through roosting alone. By expanding the hypothetical schedule to the total population estimate of 3–5 billion pigeons, we estimated that 3,800,000–6,330,000 ha (38,000–63,300 km²), or 0.5–0.8%, of their total range would have been affected annually by both temporary and long-term roosts, with the majority of the affected area located in or near the pigeon's winter range.

Nesting Distribution and Size

Although isolated nesting occurred, most Passenger Pigeons bred in colonies in the north-central hardwoods and northern hardwoods regions (Fig. 1). Successful nesting areas had to be close enough to spring mast reserves to supply the colony for a 1-month breeding cycle. Bucher (1992) suggested that Passenger Pigeons would have needed to nest twice a year on average to maintain a stable population, and if the mast supplies were not sufficient for two sequential nestings they would have moved to a new nesting area. Due to their dependence on shifting mast sources, pigeons seemed to exhibit little

Table 1. Estimated size and location of sites affected by a hypothetical flock of 500,000 Passenger Pigeons (at a roosting density of 105,000 pigeons/ha).

	January	February	March	April	May	June	July	August	September	October	November	December
Population	575,000	550,000	525,000	500,000	625,000	750,000	725,000	700,000	675,000	650,000	625,000	600,000
general location	south of lat. 36° N	near lat. 36° N ^a	north of 36° N ^a	breeding range ^b	breeding range ^b	north of lat. 36° N	north of lat. 36° N	north of lat. 36° N	near lat. 36° N ^c	south of lat. 36° N ^c	south of lat. 36° N	south of lat. 36° N
No. of long-term roosts	1	2	6	nesting	nesting	6	4	4	2	1	1 roost	(for 2 months)
Area (ha) affected by long-term roosts	5	10	29	(617 birds/ha)	n/a	41	28	26	12	6	6	
No. of temporary roosts	4	8	8	8	8	8	8	8	8	4	4	4
Area (ha) affected by temporary roosts	21	40	40	37	45	55	55	52	49	24	23	23
Total area (ha) affected/month	26	50	69	37	45	96	83	78	61	30	29	29
Total area (ha) affected/year												633 ha = 6.3 km ² /year

^aSpring migration.
^bNorth-central hardwood and northern hardwood region.
^cFall migration.

site fidelity to nesting locations (Schorger 1955). Therefore, we assumed that the nesting areas and the resulting disturbance moved within and among years throughout the breeding region.

Nesting areas tended to be much larger and less densely populated than roosts. The typical size of a nesting area, as averaged from 47 literature accounts (Schorger 1955), was 80 km². Much larger nesting areas occurred where large mast supplies were located, some forming a long band measuring 500–800 km² in area, with one that covered more than 2200 km² and contained 135 million adults (an average of 617 adults/ha) (Schorger 1937). Using this estimate, we propose that pigeon biomass densities in nestings may have ranged between 157 and 210 kg/ha (mean = 183.5 kg/ha). Within nesting sites, however, the density of birds was spatially variable. Because of the variability in density within sites, the ecological effects of nesting pigeons should be viewed as proportionally variable.

Employing Schorger's (1937) estimates of adult bird density in nesting sites (617/ha) and a conservative estimate of the number of adult birds (3 billion Passenger Pigeons), we estimate that 97,250 km² of the north-central and northern hardwoods region were affected by nesting disturbances in a given year (3 billion birds/617 birds/ha × 2 nesting attempts = 9,725,000 ha = 97,250 km²). Our calculation is based on the assumption that the pigeon flocks nested twice a year in two different locations.

This area represents approximately 8% of the pigeon's 1.2 million-km² breeding range. Because the selection of nesting areas was variable because of changing mast crops, nesting disturbance may have approached randomness. Therefore, it is reasonable to estimate that there was a return interval for nesting disturbance of 12–13 years.

Possible Ecological Impacts of Roosting and Nesting

Because of the high density of pigeons that roosted communally, roosts were probably the most intense disturbance caused by pigeons. While searching for space, the birds would often alight on top of one another, adding so much weight that small trees would be toppled and the branches of large trees would break (Audubon 1831; Kalm 1911; Schorger 1955). The pigeons also deposited large amounts of excrement on the forest floor (Audubon 1831; Kalm 1911; Schorger 1955). Roosting sites that were used for long periods would have experienced large chemical fluxes because the accumulated feces would have added uric acids and ureates to the soils (Schorger 1955; Blockstein & Tordoff 1985). The disturbances caused by short-term roosts, used for a night or the duration of a storm, would also have resulted in severe physical damage to trees in the form of limb and stem breakage, but

would have created lower nutrient inputs from pigeon feces than long-term roosts.

Because the density of pigeons in nesting areas was lower and spatially more variable than in roosting areas, the physical damage to the local forests may have been less severe but more widespread and more patchy. Schorger (1937) noted that some areas had few nests, whereas some trees had so many nests that they were toppled. Other accounts of nesting density in New York and Vermont report there were 15–25 nests per tree (Wright 1911), adding considerable weight to limbs.

Physical Damage

One effect of pigeon disturbance on forest processes would have been the increase in light at the forest floor following physical damage to the canopy. The breakage of smaller tree limbs and small trees occurring in nesting sites would have led to a patchy increase in light under thinned crowns and in small gaps. From our estimates of the amount of land used annually for nesting, such disturbances would have occurred frequently (every 12–13 years), affecting 8% of the breeding area annually. Other low-intensity, frequent disturbances common to eastern forests are ice storms and moderate windstorms that topple scattered trees and thin surviving trees through limb breakage (Runkle 1985). These disturbances currently affect a slightly smaller area than our estimate of low-intensity pigeon disturbance. Small gaps formed by the loss of a few trees in mesophytic hardwoods annually occur over 0.4–2.0% of the land area (Barden 1981; Runkle 1985), although when crown thinning is included the area affected is most likely greater. The light environment resulting from fine-scale disturbance by ice storms and small windstorms favors shade-tolerant tree species such as American beech, eastern hemlock (*Tsuga canadensis*), and sugar maple (*Acer saccharum*) (Runkle 1985) and may enable the establishment of moderately shade-tolerant oaks in larger gaps (Crow 1988). We suspect that low-intensity disturbance by nesting pigeons may have had a similar effect on forest composition.

The severe physical damage in roosts would have resulted in much higher light levels reaching the forest floor. The overall effects were probably similar to large releasing disturbances caused by high winds, in which most of the canopy is removed and the understory is released from overhead competition (Runkle 1985; Smith 1986). Effects of long-term roosts experiencing high nutrient inputs may have resembled severe disturbances (e.g., hot fires) in which almost all plants are killed (Runkle 1985; Smith 1986). High light levels would have allowed shade-intolerant species to become established (Oliver & Larson 1990) and would have also released previously established moderately shade-tolerant species, such as oaks (Crow 1988) and eastern white pine (*Pinus strobus*) (Kelty & Entcheva 1993).

Presettlement return intervals for catastrophic windthrow events in the northern hardwoods region is estimated to have been in excess of 1000 years (Lorimer & Frelich 1994), a rate considerably lower than our estimate of the land area annually affected by roosts. Much of the information used to develop historical disturbance data comes from historical surveys that record tree species composition and disturbance (Seischab & Orwig 1991; Whitney 1991). These surveys may also reflect roosting disturbances that resulted in dead trees, grasslands, and forest glades. Such surveys could be revisited in researching the possible effects of Passenger Pigeons. Seischab and Orwig (1991) reported that 0.2% of presettlement northern hardwood forest land in western New York was recorded as grassland and 0.006% had standing dead trees. These figures are lower than our estimates, suggesting that either roost disturbances were not intense enough to produce grasslands and large areas of standing dead trees or that our model overestimated the percentage of forest affected by roosts. An overestimate could have resulted from the use of swamps for roosting or from the re-use of roosting sites. Surveys of other regions, including the pigeon's more intensively used winter range, would help refine our model.

Chemical Deposition

Accumulated pigeon excrement deposited in long-term roosts is reported to have caused the death of many understory and overstory plants (Schorger 1955; Blockstein & Tordoff 1985). Wilson (1814) reported seeing dung-covered roosts comprising thousands of hectares in which there was no living vegetation, and all trees either were standing dead or had fallen. In some roosts that were reused annually, dung deposits exceeded 50 cm deep (Schorger 1955). Short-term roosts would have resulted in less deposition. Even though pigeon density in nesting areas was much lower than in roosts, it is likely that considerable nutrient deposition occurred on the sites because breeding pigeons were located in one place for 1 month.

The amount of nutrients deposited by other bird species provides an approximation of the nutrient inputs caused by pigeon congregations. Nightly deposition from wild-trapped Red-winged Blackbirds (*Agelaius phoeniceus*) in New York averaged 1.43, 0.22, and 0.21 mg/g of body weight for nitrogen, phosphorous, and potassium, respectively (Hayes & Caslick 1984). Based on these figures, pigeon nesting at a mean biomass of 183.5 kg/ha would have deposited 0.26 kg N, 0.04 kg P, and 0.038 g K per hectare nightly. Deposition over the 30-day breeding period would have been 7.8 kg N, 1.2 kg P, and 1.14 kg K/ha. Pigeons roosting at a mean biomass of 31,500 kg/ha (our estimate) would have deposited 45 kg N, 6.9 kg P, and 6.6 kg K/ha nightly.

The input of bird guano into an ecosystem can result in a decreasing ratio of carbon to nitrogen through the influx of nitrates, increases in P and K, and can also detrimentally affect vegetation through a change in the osmotic balance due to salt accumulation (Weseloh & Brown 1971). Whereas minor nutrient inputs may benefit existing vegetation, a decrease in plant species richness and density has been observed in response to high levels of fecal deposition in seabird colonies (Gillham 1960) and in a Minnesota heron rookery (Weseloh & Brown 1971). Virginia-creeper (*Parthenocissus quinquefolia*), wood sage (*Teucrium canadense*), and maple-leaved goosefoot (*Cbenopodium hybridum*) were among the species that were tolerant of fecal deposition under heron nests in the Minnesota study.

As a result of the range of nutrient inputs that would have resulted from pigeon flocks, the effects on forest composition could be studied in before-after control-impact (BACI) experiments by adding to treatment sites levels of nutrients representing the range of nutrients estimated to have been deposited at nesting and roosting sites. In this way, the severity of the disturbances as indexed through effects on vegetation dynamics could be more thoroughly assessed.

Potential Interactions among Disturbances by Pigeon Flocks and Other Disturbance Agents

Forest disturbance by pigeons would have spatially and temporally overlapped with other disturbance forces common to eastern forests, such as fires, ice storms, and windfalls. Multiple disturbance events acting on a specific site can interact to affect forest processes, and the results are often dependent upon the order in which the disturbances occur (Platt et al. 2002). For example, if nesting on a given site occurred within several years of ice or windstorms that toppled weakened trees and branches, the nesting pigeons would have confronted a recently thinned stand and the damage might have been less severe. Conversely, if a windstorm occurred after a forest stand had been weakened by nutrient inputs by roosting pigeons, the damage might have been more intense. The severity of windthrow damage to pine (*Pinus* spp.) stands in Florida was positively associated with the severity of past fires (Platt et al. 2002).

We also suspect that disturbance by pigeons may have exacerbated the effects of wildfire. It is widely believed that periodic fires set by Native Americans and lightning strikes were frequent and widespread in the presettlement central hardwood forests (Crow 1988; Lorimer 1993; Whitney 1994). Fire scars on an old oak in a New Jersey forest revealed that, on average, the stand burned every 14 years (6 times between 1641 and 1711) (Buell et al. 1954). It is likely that branches, twigs, and stems that were broken and deposited on the ground as a result of

roosting and nesting pigeons would have provided fuel for wildfires. Dead herbaceous and understory woody plants, killed by high nutrient loads and physical burying, would have increased the availability of fine, easily combustible fuels. Furthermore, increased light conditions at the forest floor caused by the death of and damage to trees would have led to more rapid and thorough drying of accumulated fuel. Similarly, fuel loading following wind damage by hurricanes is thought to increase the intensity of post-hurricane fires in forests of the southeastern United States (Myers & van Lear 1998; Platt et al. 2000).

Increased fire frequency as a result of disturbance by pigeons may have influenced species composition. The frequency of wildfires in the central hardwoods region is one of the main mechanisms used to explain the presettlement-era dominance of oaks and the occurrence of oak savanna ecotypes in the western boundary of the region (Crow 1988; Abrams 1992; Lorimer 1993; Whitney 1994). Oaks are more fire-resistant than maples (*Acer* spp.), eastern hemlock, and American beech and are therefore more common in areas that are burned periodically. Likewise, the absence of fire in postsettlement times is thought to explain why many forests that were previously dominated by oaks are now dominated by less fire-tolerant species (Abrams 1992; Lorimer 1993). Furthermore, fire tolerance among oak species differs as a result of bark thickness. Common oak species ranked in terms of decreasing bark thickness and fire resistance are bur oak (*Quercus macrocarpa*), black oak (*Quercus velutina*), white oak (*Quercus alba*), and northern red oak (*Quercus rubra*) (Crow 1988). Therefore, the high frequency of fires has been cited as an explanation for the predominance of white oak, bur oak, and black oak in presettlement forests (Lorimer 1993; Whitney 1994).

Possible Effects of Mast Consumption by Passenger Pigeons on the Species Composition of Presettlement Forests

Mast consumption by pigeons was most intense during spring nesting. A large Wisconsin nesting area was estimated to contain approximately 135,000,000 adults (Schorger 1937). Therefore, a figure of 100,000,000 adults in a hypothetical nesting area seems plausible. With a total breeding population of 3 billion pigeons, 30 nesting areas of this size could have been located throughout the breeding range. Because large areas were searched by pigeon flocks (20,000–80,000 km²), it is reasonable to assume that from one-half to two times the total breeding range was searched for food. This suggests that the ranges for different colonies often overlapped and that the pigeons in the colonies on the edges of the range may have had to search in areas outside the breeding range.

In conjunction with the possible effects of fire on oak dominance, tree species composition may have been influenced by the enormous quantity of nuts and fruits consumed by Passenger Pigeons. Webb (1986) proposed that seed predation by Passenger Pigeons may have been an important selective force acting upon its food plants. Mast consumption by pigeons in the northern portion of the eastern forest during the spring breeding season may have been an additional factor in the presettlement dominance of white oak and other species in the white oak group (*Leucobalanus*).

Mershon (1907) and Kalm (1911) described pigeons migrating north as the snowpack melted, and Schorger (1955) indicated that nesting sometimes began before all the snow had disappeared. Bucher (1992) theorized that the pigeons' need for abundant mast near their spring nesting areas required them to breed in areas where the winter snowpack prevented a considerable portion of the previous year's mast from being consumed by resident mast consumers. As the snow melted, Passenger Pigeons would have been able to find beechnuts, chestnuts, and acorns of the red oak species group (*Erythrobalanus*) (e.g., red oak, black oak, and scarlet oak [*Quercus coccinea*]). Acorns of the white oak group germinate in the fall, however, and would have been almost useless as a food source by spring (Schorger 1955). In addition, the migration of pigeons to the south in August and September likely means that they were not feeding on many acorns of any oak species in the breeding range during the fall because many of the acorns would have matured after the pigeons left (Rogers 1990).

White oak was the dominant oak species across much of the breeding range of Passenger Pigeons prior to European settlement. Oak forests, particularly white oak, occurred across southern New England, north through New York's Hudson River valley, south and west across southern Pennsylvania, to western Pennsylvania and southeastern Ohio. In many areas, white oak was so dominant that a near monoculture was formed (Whitney 1994). White oak was also commonly found on the drier, more rugged terrain of southern Indiana and the Ozark Plateau. F. A. Michaux (1818–1819) reported that western Pennsylvania had "large forests, nine tenths of which consisted of White Oaks." Others have reported that many parts of the presettlement forests of the north-central hardwoods region were dominated by white oak (Braun 1950; Spurr 1951; Loeb 1987; Abrams & Downs 1990; Abrams & Nowacki 1992; Abrams et al. 1995). Other species in the white oak group were dominant in smaller areas of the pigeon's breeding range. Bur oak was abundant in the western portions of the midwest, primarily in the fire-dependent savanna ecosystems bordering the Great Plains (Lorimer 1993; Whitney 1994). Chestnut oak (*Q. prinus*) was locally abundant on dry ridge tops (Abrams & Ruffner 1995; Mikan et al. 1994; Whitney 1994).

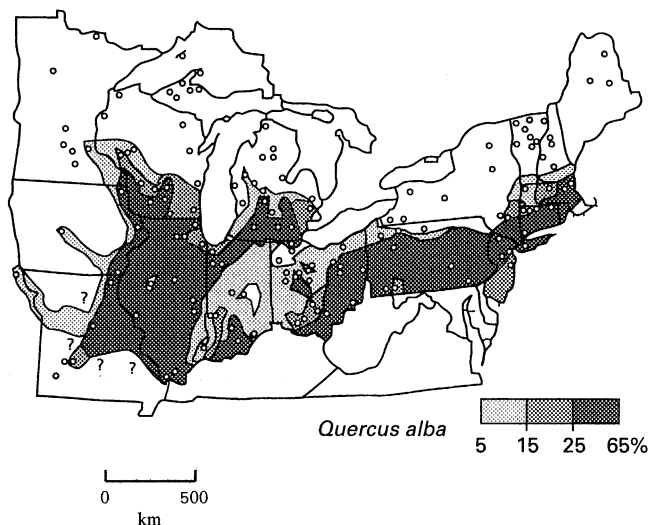


Figure 2. Relative abundance of white oak (*Quercus alba*) in the presettlement north-central hardwood forests. Data gathered from early land surveys. Map from Whitney (1994). Reprinted with the permission of Cambridge University Press, New York.

The proposed relationship between mast consumption by pigeons in their spring breeding ranges and the dominance of white oak is perhaps best illustrated by comparing the map of the Passenger Pigeon breeding range (Fig. 1) and the map showing the presettlement dominance of white oak in the north-central hardwoods region (Fig. 2). A map showing the dominance of American beech (Fig. 3) explains the gaps within the map of

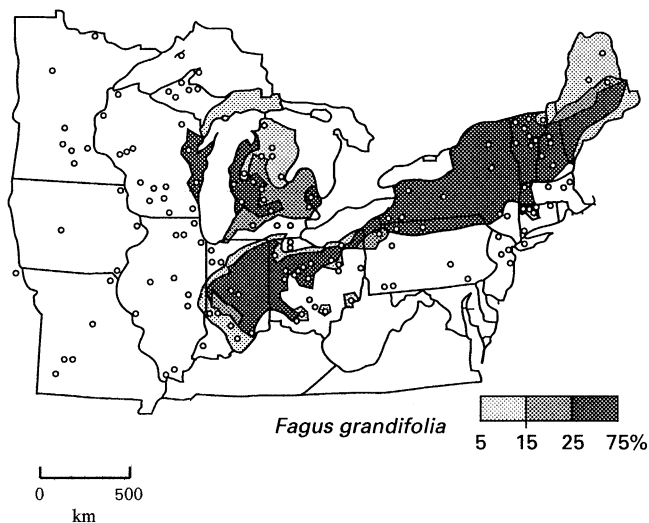


Figure 3. Relative abundance of American beech (*Fagus grandifolia*) in the presettlement northern hardwood forests. Data gathered from early land surveys. Map from Whitney (1994). Reprinted with the permission of Cambridge University Press, New York.

white oak dominance. Even though enormous quantities of beechnuts were eaten by pigeon flocks, it is not surprising that beech would have attained, or maintained, dominance in parts of the breeding range in spite of seed predation. Beech can reproduce vegetatively through root sprouting, which is the primary mode of reproduction, especially in the northern and western portions of its range (Ward 1961; Houston 1975; Tubbs & Houston 1990). Unlike oaks, which are not reported to spread vegetatively through root sprouts (Rogers 1990; Sander 1990), beech is not totally reliant on successful seed germination and establishment for reproduction. Therefore, its population would probably not have been as severely affected by spring seed predation by pigeons as species in the red oak group.

It is important to note that white oak was the dominant oak species in southern Illinois and northeastern Missouri (Fig. 2). Although these areas were outside their main breeding range, the pigeons may have fed on acorns from the red oak group en route to the breeding grounds farther north and east. Most of Illinois and Missouri are north of 36° N and therefore were north of the wintering areas used by pigeons. Schorger's (1955) review of regional newspapers reveals that a considerable number of flocks were reported from those areas in late winter and early spring, just before breeding season. Given the long distances traveled by breeding pigeons to obtain food (80–160 km), it is also possible that flocks searched these regions of Illinois and Missouri from nesting colonies in southern Indiana.

A similar dynamic may explain the dominance of white oak in areas of southern West Virginia. In a study of the presettlement origin of the white pine (*Pinus strobus*)-mixed oak forest in Greenbrier County, West Virginia, Abrams et al. (1995) reported continued recruitment of white oak from 1700 to 1900, whereas red and black oak were not present in the stand until after 1850. Although the pigeons' primary breeding range did not normally include southern West Virginia, nesting was reported to have occurred along the Greenbrier River on occasion, as well as at other sites in central West Virginia (Schorger 1955). Furthermore, this area is roughly 150 km from the southern boundary of the primary breeding range in northern West Virginia, and it is likely that pigeons could have flown to Greenbrier County to feed away from nesting colonies farther north. More comprehensive data on the presettlement abundance of white oak across the southern central hardwoods region is needed to determine whether there was a difference in species composition below the southern edge of the breeding area.

The potential effects of Passenger Pigeons on oak species composition and the effects of fire as cited by others would not have been mutually exclusive. Predation on the acorns of the red oak group and higher fire frequency may have worked together to tilt forest composition in favor of the fire-tolerant white and bur oak. Furthermore,

Table 2. Percent composition of oaks by species in presettlement (pre) versus present-day (PD) forests for four physiographic regions in northern and central Pennsylvania.^a

Species	Allegheny High Plateau			Allegheny Mountains			Allegheny Front			Ridge and valley		
	pre	PD	% change	pre	PD	% change	pre	PD	% change	pre	PD	% change
<i>Quercus alba</i> ^b	1.3	2.5 (±0.4)	+92	18.9	19.1 (±1.7)	0	29.6	17.7 (±1.8)	-40	21.0	12.7 (±1.6)	-40
<i>Quercus prinus</i> ^b	2.1	2.2 (±0.3)	0	2.9	9.4 (±0.8)	+224	13.6	13.0 (±0.8)	0	7.9	27.7 (±3.1)	+250
<i>Quercus velutina</i> ^c	0.9	1.1 (±0.2)	0	7.0	2.0 (±0.3)	-71	7.0	5.5 (±0.3)	-21	8.5	7.5 (±1.2)	0
<i>Quercus rubra</i> ^c	—	9.5 (±1.1)	n/a	2.6	11.2 (±1.8)	+331	0.8	12.0 (±1.2)	+1400	2.0	13.6 (±1.8)	+580
<i>Quercus coccinea</i> ^c	—	0.3 ^d	n/a	—	1.3 (±0.1)	n/a	—	1.5 (±0.1)	n/a	1.7	2.9 (±1.7)	0

^aData from Abrams and Ruffner (1995). Other species are omitted from table, but not discounted. Standard deviations in parentheses; n/a, not available.

^bWhite oak group (*Leucobalanus*).

^cRed oak group (*Erythrobalanus*).

^dStandard error value <0.05.

the effects of fire in some regions may have outweighed mast consumption. Spring-germinating black oak was as common as white oak in some presettlement oak savannas (Crow 1988; Lorimer 1993) and was a smaller but significant component in portions of the north-central hardwood forests (Abrams & Ruffner 1995; Abrams & McCay 1996). The relatively high fire resistance of black oak explains why it was common (Crow 1988; Lorimer 1993), perhaps in spite of acorn predation by breeding pigeons.

Possible Role of Passenger Pigeon Extinction in the Postsettlement Shift in Oak Species Composition

Beginning in the late nineteenth century, white oak recruitment declined in portions of the north-central hardwoods region (Abrams & Nowacki 1992). A broad geographic perspective on the relative importance of oak species over time may be gained by comparing the witness tree surveys that show presettlement species composition with forest inventories from the twentieth century. We compared data from north-central Pennsylvania (Abrams & Ruffner 1995) (Table 2) and northeastern West Virginia (Abrams & McCay 1996) (Table 3). Both Abrams and Ruffner (1995) and Abrams

and McCay (1996) reported a general postsettlement decrease in white oak relative to other oak species in stands where white oak had been dominant. Fall-germinating chestnut oak (*Quercus prinus*) increased in importance in postsettlement forests of the ridge and valley provinces in West Virginia and Pennsylvania and in Pennsylvania's Allegheny Mountains. The authors attributed the increases to the mortality of American chestnut by blight in the early 1900s, which provided growing space for oaks. Chestnut oak was often present on the ridges with American chestnut and would have been well poised to capitalize on newly available growing space. The slight increases in the importance of white oak in the Allegheny Mountains of West Virginia and the Allegheny High Plateau of Pennsylvania is not surprising given that these areas were originally dominated by American beech and Eastern hemlock (*Tsuga canadensis*). Because these two species declined as a result of logging and a short period of increased fire frequency and intensity during early settlement (Abrams & Ruffner 1995), white oak and red oak were able to expand.

In addition to the decrease in white oak, Abrams and Ruffner (1995) reported an increase in red oak recruitment in forests where it had been only a minor component prior to European settlement. A similar shift was observed in other parts of the northeastern and

Table 3. Percent composition of oaks by species in presettlement (pre) versus present-day (PD) forests for two physiographic regions in eastern West Virginia.^a

Species	Ridge and Valley			Allegheny Mountains		
	pre	PD	% change	pre	PD	% change
<i>Quercus alba</i> ^b	32.7	8.6 (±1.3)	-74	1.1	0.3 (±0.2)	-73
<i>Quercus prinus</i> ^b	8.0	14.6 (±1.6)	+83	1.9	0.3 (±0.2)	-84
<i>Quercus velutina</i> ^c	5.3	2.5 (±0.7)	-53	1.5	0.3 (±0.2)	-80
<i>Quercus rubra</i> ^c	3.4	13.8 (±1.6)	+305	0.8	4.3 (±0.8)	+438
<i>Quercus coccinea</i> ^c	—	6.6 (±1.1)	n/a	—	0.3 (±0.2)	n/a

^aData from Abrams and McCay (1996). Other species are omitted from table but not discounted. Standard deviations in parentheses; n/a, not available.

^bWhite oak group (*Leucobalanus*).

^cRed oak group (*Erythrobalanus*).

north-central regions. In the early twentieth century, northern red oak increased in importance across portions of the north-central hardwoods forest (Whitney & Davis 1986; Abrams & Downs 1990) and expanded its range to include sites in the northern hardwoods region, where it had previously been absent (Crow 1988; Nowacki et al. 1990).

The decline in white oak has been explained by a reduction in fire frequency that previously favored the more fire-resistant oaks (Abrams & Nowacki 1992; Abrams & Ruffner 1995; Abrams & McCay 1996). Similarly, the increase and expansion of red oak has been attributed to a reduction in fire occurrence and to the widespread logging of white pine in the early twentieth century that released established red oak seedlings (Whitney & Davis 1986; Crow 1988; Abrams 1992). Abrams and Ruffner (1995), however, reasoned that these explanations alone may not account for the dramatic expansion of red oak. We propose that the elimination of Passenger Pigeons as a spring predator on acorns of the red oak group may have been an additional factor in favor of a shift in oak species composition in the two general forest types used by breeding pigeons.

Conclusions

From our review of available literature, we believe there is sufficient evidence to indicate that the roosting and nesting of Passenger Pigeon flocks caused disturbances to the presettlement forests of eastern North America. Disturbance intensity and frequency would have ranged from frequent, low-intensity crown thinning, which would have released established, shade-tolerant vegetation, to severe, stand-initiating disturbances caused by widespread limb and stem breakage and heavy nutrient loading characteristic of long-term pigeon roosts. Given the birds' extensive migrations and general lack of site fidelity, it is reasonable to assume that the disturbance was widespread. Although it is difficult to accurately quantify the extent, intensity, location, and return interval of these events, we believe that forest disturbance by Passenger Pigeon flocks should be considered in estimates of the range of natural variability of conditions in eastern hardwood forests.

We also suspect that Passenger Pigeons may have influenced oak species composition in three—not mutually exclusive—ways: (1) roosts created mid-sized and large gaps in the canopy that may have favored moderately shade-tolerant tree species such as oak; (2) pigeon disturbance caused fuel accumulation that could have increased the intensity and frequency of fires, thus favoring fire-resistant white oak, bur oak, and black oak; and (3) in the north-central hardwood forests, the consumption of vast quantities of acorns from the red oak group during the pigeon's spring breeding season would have reduced the recruitment of those species but not the recruitment

of the white oak group. In addition, we suspect that the reduction in spring mast consumption following the decline of the Passenger Pigeon in the late nineteenth century may have combined with changes in fire frequency and land use to cause the increased importance of the red oak group across the breeding range.

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