

Decline of Oak Forests and Implications for Forest Wildlife Conservation

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ABSTRACT: Despite dominating many forests in eastern North America for over 10,000 years, oaks (*Quercus* spp. L.) are steadily being replaced by shade-tolerant species, such as red maple (*Acer rubrum* L.). This shift in forest composition may affect forest wildlife by (1) reducing the availability of hard mast resources, (2) altering the composition and abundance of phytophagous arthropods, and (3) impairing the foraging ability of birds due to differences in leaf and tree physiognomy. Indeed, population dynamics of numerous birds and mammals, ranging from red-headed woodpeckers (*Melanerpes erythrocephalus*) to black bears (*Ursus americanus*), have been linked to annual fluctuations in oak acorn crops. Moreover, preliminary research with forest bird communities suggests that abundance and diversity of resident and long-distance migratory birds, woodpeckers, and bark-gleaning species are lower in forests dominated by maple rather than oak. Changing forest composition is an emerging issue in natural resource management and one that can profoundly affect wildlife communities within natural areas and preserves. Given that few empirical data exist to inform management, and that impacts to ecological communities are likely to be profound, more comprehensive research is needed to predict and ameliorate potential outcomes.

Disminución de Bosques de Robles e Implicaciones para la Conservación de Fauna en Bosques

RESUMEN: Aunque hayan dominado la mayoría de los bosques del este de Norteamérica por más de 10.000 años, los robles (*Quercus* spp. L.) están siendo reemplazados por especies tolerantes, tales como *Acer rubrum* L. El cambio en la composición del bosque puede afectar su fauna por (1) reducción de la disponibilidad de recursos de troncos duros, (2) alteración de la composición y abundancia de artrópodos fitófagos, y (3) perjudicar la habilidad predadora de aves debido a diferencias en la fisonomía de hojas y árboles. De hecho, la dinámica poblacional de muchas aves y mamíferos, desde el pájaro carpintero de cabeza roja (*Melanerpes erythrocephalus*) al oso negro (*Ursus americanus*), han sido ligadas a fluctuaciones en plantaciones de roble. Más aun, investigaciones preliminares con comunidades de aves de bosques sugieren que la abundancia y la diversidad de aves residentes y migratoria de largas distancias, pájaros carpinteros, y las insectívoras son menores en bosques dominados por arce que en los de roble. El cambio de composición del bosque es un problema reciente en el manejo de los recursos naturales y uno que puede profundamente afectar las comunidades de animales silvestres en las áreas naturales y las reservas. Dado que pocos datos empíricos existen para informar a quienes deciden, y que los impactos sobre las comunidades ecológicas podrían ser profundos, se necesitan más investigaciones comprensivas para poder predecir y disminuir los potenciales resultados.

Index terms: forest composition, forest birds, maple, oak, wildlife

INTRODUCTION

Oaks (*Quercus* spp. L.) have dominated many eastern North American forests for at least the last 10,000 y (Abrams 1992) and still cover over 63.7 million ha, or 43% of eastern forests (McShea and Healy 2002). Historical accounts describe the composition of presettlement forests as oak-chestnut, white oak (*Q. alba* L.), white oak-red oak (*Q. rubra* L.), or white oak-white pine (*Pinus strobus* L.), especially in the mid-Atlantic region (Abrams 1992). For example, pollen records from New Jersey and southeastern New York indicate that oak, American chestnut (*Castanea dentata* [Marsh.] Borkh.), and hickory (*Carya* spp. Nutt.) dominated most upland forests prior to 1900 (Loeb 1989). Similarly, an analysis of witness trees in the Ridge and Valley Province of central Penn-

sylvania indicated that presettlement forests consisted largely of oak, American chestnut, hickory, and pine (*Pinus* spp. L.) (Abrams and Ruffner 1995).

The historic dominance of oaks is best explained by a combination of factors including a dry and warm climate during the Holocene, periodic fires, Native American land use practices (including burning), and repeated cutting followed by fire after European settlement (Abrams 1992, Abrams and Nowacki 1992). In the late 1800s and early 1900s, many eastern forests were clearcut at 20- to 30-y intervals to fuel charcoal iron furnaces, and large wildfires frequently moved across the landscape (Abrams and Ruffner 1995). In addition, populations of white-tailed deer (*Odocoileus virginianus*) were low, allowing oak regeneration to proceed without

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heavy browsing from deer.

Eastern deciduous forests are now facing a major change in tree species composition due to human-induced changes in disturbance regimes (Orwing and Abrams, 1994, McShea and Healy 2002). Many ecologists and foresters forecast that shade-tolerant species, such as tulip poplar (*Liriodendron tulipifera* L.), red maple (*Acer rubrum* L.), and sugar maple (*A. saccharum* Marsh.), will replace oaks in forests throughout the region. Three important changes in disturbance regimes during the 1900s have facilitated the growth of shade-tolerant tree species in oak forests: the practice of fire suppression, the reduction of even-aged forest management practices, and heavy deer browsing (Lorimer 1984). As a result, shade-tolerant species now dominate the understory and midstory layers of many oak-pine, mixed-oak, and northern hardwood forests and are expected to further increase in importance (Abrams 1992). Red maple, in particular, has dramatically increased in dominance compared to presettlement forests, where it probably represented less than 5% of overstory trees (Abrams 1992, Palik and Pregitzer 1992). For example, red maples are believed to be 3–35 times more abundant in the understory and subcanopy layers of current as compared to presettlement oak-hickory forests of North Carolina (Christensen 1977), Pennsylvania (Abrams and Ruffner 1995), and Virginia (Ross et al. 1982).

IMPACTS ON RESOURCES FOR WILDLIFE

Changing forest composition is an emerging natural resource management issue that can profoundly influence wildlife communities within natural areas and preserves. Although vegetation structure is an important component of habitat suitability for animals (e.g., MacArthur and MacArthur 1961, Roth 1976), plant species composition also can substantially affect habitat quality. Widespread replacement of oak by maple should impact foraging abilities and diets of certain animals in a few respects.

Mast

Maples and oaks offer different food resources (in terms of both mast and arthropods) to animals. Oak acorns are generally high in both energy content and digestibility, making them a valuable food resource for a wide variety of animals (Kirkpatrick and Pekins 2002). Furthermore, the hard outer seed coat of acorns allows them to be stored for long periods, thereby providing a high quality food source during periods of low food availability (e.g., winter). Thus, it is not surprising to find citations for the use of acorns in over 90 North American vertebrate species (VanDersal 1940, Martin et al. 1951). Comparatively few animal species heavily consume maple seeds (Martin et al. 1951), perhaps in part because the soft-tissued seeds of maples decompose more quickly than the longer-lasting acorns of oaks.

Leaves

Differences in the physiognomy (e.g., foliage and bark structure) between oaks and maples also should influence the abilities of insectivorous birds to detect and access prey (Robinson and Holmes 1984, Whelan 2001). Maples have larger leaves and longer petioles than oaks, and this can prevent small foliage-gleaning passerines that move along twigs from easily reaching arthropods on leaves (Holmes and Robinson 1981, Holmes and Schultz 1988, Whelan 2001). In addition, because maple leaves decompose more quickly than the tannin-rich oak leaves, leaf litter in maple stands may be comparatively less developed, which can affect arthropod resources for group foraging animals like the red-bellied salamander (*Plethodon cinereus*) or ovenbird (*Seiurus aurocapillus*).

Bark

Some maple species (especially red maple) have smoother bark than similar-sized oaks, particularly at young ages. Several bird species, such as chickadees (*Poecile* spp.), tufted titmouse (*Baeolophus bicolor*), and white-breasted nuthatch (*Sitta carolinensis*), probe for insects and cache seeds under loose, furrowed, cracked, or rough bark (Kilham 1974, Petit et al. 1989,

Woodrey 1991). Rough bark, in comparison to smooth bark, provides greater surface area for foraging and greater numbers of arthropods (Jackson 1970), and some resident birds in northern North America avoid using smooth-barked trees during winter months (Brawn et al. 1982, Morrison et al. 1985, Rollfinke and Yahner 1991).

Arthropods

Lepidopteran larvae, an important food resource for insectivorous birds in temperate forests, may be less abundant on maple leaves than on other hardwood species during the breeding season (Holmes and Schultz 1988). Similarly, a study of tree-dwelling arthropods in central Appalachian forests documented that maples had fewer species and lower abundances of lepidopteran larvae than white, red, and chestnut oaks and hickories (Butler and Strazanac 2000). However, we lack a detailed understanding of how oaks and maples influence the invertebrate communities that provide a food base for wildlife in forest stands.

IMPACTS ON WILDLIFE POPULATIONS

In eastern forests, many birds and mammals, such as red-bellied woodpecker (*Melanerpes carolinus*), tufted titmouse, blue jay (*Cyanocitta cristata*), wild turkey (*Meleagris gallopavo*), white-tailed deer, mice (*Peromyscus* spp.), chipmunks (*Tamias* spp.), squirrels (*Sciurus* spp.), and black bears (*Ursus americanus*), rely heavily on acorns for fall or winter diets, or both (Smith 1986, Smith and Scarlett 1987, McShea and Schwede 1993, McShea and Healy 2002). Acorn yield has been shown to influence population dynamics of small mammals, such as white-footed mouse (*Peromyscus leucopus*), deer mouse (*Peromyscus maniculatus*), eastern chipmunk (*Tamias striatus*), and gray squirrel (*Sciurus carolinensis*; McShea 2000, McShea and Healy 2002, Schnurr et al. 2002). Distribution and population fluctuations in acorn woodpecker (*Melanerpes formicivorus*; Hannon et al. 1987, Koenig and Mumme 1987), red-headed woodpecker (*Melanerpes erythrocephalus*; Smith and Scarlett 1987), and blue jay (Smith and

Scarlett 1987) are similarly affected by mast production. Abundance, survival, and reproduction of large mammals, such as white-tailed deer and black bear, also are closely linked to annual variation in acorn crops (McShea and Healy 2002).

IMPACTS ON WILDLIFE COMMUNITIES

Ecologists have few empirical data with which to evaluate the potential consequences of such a shift in forest composition for forest bird communities. Recently, Rodewald and Abrams (2002) studied bird communities in structurally similar woodlots that were dominated either by oak or maple in central Pennsylvania. They found that total abundance and species richness of birds was 50–200% greater within oak-dominated stands than in maple-dominated stands in at least one season. In particular, resident species, long-distance migrants, woodpeckers, bark-gleaners, and eleven individual bird species (such as blue jay, red-bellied woodpecker, northern flicker [*Colaptes auratus*], white-breasted nuthatch, tufted titmouse, and wood thrush [*Hylocichla mustelina*]) were more abundant within oak stands than within maple stands in at least one season. To my knowledge, this is the first published evidence that a shift in forest composition from oak-dominated to maple-dominated forests may alter avian community structure.

Recent research also suggests that multitrophic interactions can be mediated by oak mast. For example, densities of small mammals, particularly mice, are correlated with acorn production (Wolff 1996, McShea 2000). By influencing populations of nest predators (e.g., small mammals and blue jays), acorn crops may indirectly influence rates of nest predation on forest songbirds (McShea 2000). Similar interactions may exist between acorn crops, deer densities, and forest understory structure that can ultimately influence forest-nesting birds (McShea and Rappole 1997). In addition, mast production can regulate interactions among small mammals, deer, Lyme disease, and gypsy moth (*Lymnatria dispar*) outbreaks (Elkinton et al. 1996, Ostfeld et al. 1996).

IMPLICATIONS FOR FOREST MANAGEMENT

From both wildlife and human perspectives, oaks represent a critically important resource in North America. In terms of silviculture, oaks currently comprise 23% of the eastern forest resource and profoundly influence timber economies (McShea and Healy 2002). Moreover, the distribution, abundance, and behavior of numerous wildlife species, ranging from bears to warblers, are linked to oaks (reviewed in McShea and Healy 2002). So when faced with compelling evidence that oaks will be less abundant in many forests within the next several decades, biologists and land managers need to carefully consider how current management approaches will affect the persistence of oak forests and their associated biota. In particular, many managers of natural areas and preserves avoid intense manipulation of habitat and these areas, therefore, lack the large disturbances that would favor oak regeneration. This is especially true given public resistance to even-aged management and prescribed burning in many areas. Current disturbance regimes (e.g., fire suppression and uneven-aged forest management) discriminate against oak recruitment on all but the driest sites (Dey 2002). High deer densities in many forested parks and natural areas further compound the problem and contribute substantially to oak regeneration failure. Ultimately, management scenarios that discourage oak regeneration may negatively impact some wildlife species and, at the very least, are expected to influence wildlife community structure and interactions among species. Predicting both the extent and ultimate consequences of a shift in forest composition is admittedly premature. More comprehensive and long-term studies are needed to understand how such a regional change in forest composition might affect biodiversity and economic viability of eastern deciduous forests.

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LITERATURE CITED

Abrams, M.D. 1992. Fire and the development of oak forests. *BioScience* 42:346–353.

Abrams, M.D., and G.J. Nowacki. 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. *Bulletin of the Torrey Botanical Club* 119:19–25.

Abrams, M.D., and C.M. Ruffner. 1995. Physiographic analysis of witness-tree distribution (1765–1798) and present forest cover through north central Pennsylvania. *Canadian Journal of Forest Research* 25: 659–668.

Brown, J.D., W.H. Elder, and K.E. Evans. 1982. Winter foraging by cavity nesting birds in an oak-hickory forest. *Wildlife Society Bulletin* 10:271–275.

Butler, L., and J. Strazanac. 2000. Occurrence of Lepidoptera on selected host trees in two central Appalachian National Forests. *Annals of the Entomological Society of America* 93:500–511.

Christensen, N.S. 1977. Changes in structure, patterns, and diversity associated with climax forest maturation in Piedmont, North Carolina. *American Midland Naturalist* 97:176–188.

Dey, D. 2002. The ecological basis for oak silviculture in eastern North America. Pp. 60–79 in W.J. McShea and W.M. Healy, eds., *Oak Forest Ecosystems: Ecology and Management for Wildlife*. John Hopkins University Press, Baltimore, Md.

Elkinton, J.S., W.M. Healy, J.P. Buonaccorsi, G.H. Boettner, A.M. Hazzard, H.R. Smith, and A.M. Leobhold. 1996. Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* 77:2332–2334.

Hannon, S.J., R.L. Mumme, W.D. Koenig, S. Spon, and F.A. Pitelka. 1987. Poor acorn crop, dominance, and decline in numbers of acorn woodpeckers. *Journal of Animal Ecology* 56:197–207.

Holmes, R.T., and S.K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. *Oecologia* 48:31-35.

Holmes, R.T., and J.C. Schultz. 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. *Canadian Journal of Zoology* 66: 720-728.

Jackson, J.A. 1970. A quantitative study of the foraging ecology of downy woodpeckers. *Ecology* 51:318-323.

Kilham, L. 1974. Covering of stores by white-breasted nuthatches. *Condor* 76:108-109.

Kirkpatrick, R.L., and P.J. Pekins. 2002. Nutritional value of acorns for wildlife. Pp. 173-181 in W.J. McShea and W.M. Healy, eds., *Oak Forest Ecosystems: Ecology and Management for Wildlife*. Johns Hopkins University Press, Baltimore, Md.

Koenig, W.D., and R.L. Mumme. 1987. *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*. Monographs of Population Biology 24, Princeton University Press, Princeton, N.J.

Loeb, R.E. 1989. Lake pollen records of the past century in northern New Jersey and southeastern New York, USA. *Palynology* 13:3-19.

Lorimer, C.G. 1984. Development of the red maple understory in northeastern oak forests. *Forest Science* 30:3-22.

MacArthur, R.H., and J.W. MacArthur. 1961. On bird species diversity. *Ecology* 42: 594-598.

Martin, A.C., H.S. Zim, and A.L. Nelson. 1951. *American Wildlife and Plants: A Guide to Wildlife Food Habits*. Dover Publications, New York.

McShea, W.J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. *Ecology* 81:228-238.

McShea, W.J., and W.M. Healy (eds.). 2002. *Oak Forest Ecosystems: Ecology and Management for Wildlife*. Johns Hopkins University Press, Baltimore, Md.

McShea, W.J., and J.H. Rappole. 1997. Herbivores and the ecology of forest understory birds. Pp. 298-309 in W.J. McShea, H.B. Underwood, and J.H. Rappole, eds., *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institution Press, Washington, D.C.

McShea, W.J., and G. Schwede. 1993. Variable acorn crops: responses of white-tailed deer and other mast consumers. *Journal of Mammalogy* 74:999-1006.

Morrison, M.L., I.C. Timossi, K.A. With, and P.N. Manley. 1985. Use of tree species by forest birds during winter and summer. *Journal of Wildlife Management* 49:1098-1102.

Orwing, D.A., and M.D. Abrams. 1994. Land-use history (1720-1992), composition, and dynamics of oak-pine forests within the Piedmont and Coastal Plain of northern Virginia. *Canadian Journal of Forest Research* 24:1216-1225.

Ostfeld, R.S., C.G. Jones, and J.O. Wolff. 1996. Of mice and mast: ecological connections in eastern deciduous forests. *BioScience* 46:323-330.

Palik, B.J., and K.S. Pregitzer. 1992. A comparison of presettlement and present-day forests on two bigtooth aspen-dominated landscapes in northern lower Michigan. *American Midland Naturalist* 127:327-338.

Petit, D.A., L.J. Petit, and K.E. Petit. 1989. Winter caching ecology of deciduous woodland birds and adaptations for protection of stored food. *Condor* 91:766-776.

Robinson, S.K., and R.T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. *Auk* 101:672-684.

Rodewald, A.D., and M. Abrams. 2002. **Floristics and avian community structure: implications for regional changes in eastern forest composition.** *Forest Science* 48:267-272.

Rollfinke, B.F., and R.H. Yahner. 1991. Microhabitat use by wintering birds in an irrigated mixed-oak forest in central Pennsylvania. *Journal of the Pennsylvania Academy of Science* 65:59-64.

Ross, M.S., T.L. Sharik, and D.W. Smith. 1982. Age-structure relationships of tree species in an Appalachian oak forest in southwestern Virginia. *Bulletin of the Torrey Botanical Club* 109:287-298.

Roth, R.R. 1976. Spatial heterogeneity and bird species diversity. *Ecology* 57:773-782.

Schnurr, J.L., R.S. Ostfeld, and C.D. Canham. 2002. Direct and indirect effects of masting on rodent populations and tree seed survival. *Oikos* 96: 402-410.

Smith, K.G. 1986. Winter population dynamics of three species of mast-eating birds in the eastern United States. *Wilson Bulletin* 98:407-418.

Smith, K.G., and T. Scarlett. 1987. Mast production and winter populations of red-headed woodpeckers and blue jays. *Journal of Wildlife Management* 51: 459-467.

VanDersal, W.R. 1940. Utilization of oaks by birds and mammals. *Journal of Wildlife Management* 4:404-428.

Whelan, C.J. 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. *Ecology* 82:219-231.

Wolff, J.O. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. *Journal of Mammalogy* 77:850-856.

Woodrey, M.S. 1991. Caching behavior in free-ranging white-breasted nuthatches: the effects of social dominance. *Ornis Scandinavica* 22:160-166.