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Options for managing early-successional forest and shrubland bird habitats in the northeastern United States

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Abstract

Historically, forests in the northeastern United States were disturbed by fire, wind, Native American agriculture, flooding, and beavers (*Castor canadensis*). Of these, wind and beavers are now the only sources of natural disturbance. Most disturbance-dependent species, especially birds, are declining throughout the region whereas species affiliated with mature forests are generally increasing or maintaining populations. Disturbance must be simulated for conservation of early-successional species, many of which are habitat specialists compared to those associated with mature forests. Both the maintenance of old fields and forest regeneration are needed to conserve brushland species. Regenerating forest habitats are more ephemeral than other woody early-successional habitats. The types and amounts of early-successional habitats created depend on the silvicultural system used, patch size selected, time between regeneration cuts, and rotation age. We recommend that group selection and patch cuts should be at least 0.8 ha, and patches should be generated approximately every 10–15 years depending on site quality. Regeneration of intolerant and mid-tolerant tree species should be increased or maintained in managed stands. Also, frost pockets, unstocked, or poorly-stocked stands can provide opportunities to increase the proportion of early-successional habitats in managed forests.

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1. Introduction

Forests in the northeastern United States were historically subject to several sources of disturbance. In much of the region, early-successional habitats were continuously produced in pre-settlement times by fire, wind, beaver (*Castor canadensis*), flooding, and Native American agriculture and burning (see DeGraaf and Miller, 1996, pp. 6–10 for review). In northern areas, Native American agriculture was

practiced mainly along the coast and major rivers. Natural disturbances were frequently a result of individual tree falls and larger blowdowns. Fire was a minor source of disturbance, but of local importance in areas of glacial outwash sands and gravels, and on shallow soils at higher elevations (Lorimer and White, 2003). In much of the Northeast, many fire-prone areas were occupied upon settlement by Europeans and are not available for management by prescribed fire. Historical levels of disturbance by beavers and flooding were in all likelihood significant and probably the main source of small meadows and shrubland habitats in much of the region (Askins, 2000, p. 12). Beavers were extirpated and most streams and rivers dammed

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before their effects on the landscape were described. Beavers are now increasing in the region but cannot modify the land as in presettlement times, so these sources of disturbance are now greatly diminished from historical levels. Wind still creates small openings in softwood stands, especially balsam fir (Abies balsamea) in mountainous areas, but young hardwood stands, now common across much of southern New England, are fairly resistant to hurricane damage (Leak et al., 1994). Major hurricanes occur at about 150-year intervals (Channing, 1939). Considering all intensities of blowdown, the average interval across the landscape is about 14 years in central New England (Leak et al., 1994). Such events are episodic and cannot be relied upon to create disturbance where and when it is needed. As a result, management is needed to provide habitats for disturbance-dependent species.

Recently, forest managers have been encouraged to consider baseline conditions when selecting a range of forest age distributions. All historical baselines are relative or arbitrary, however. Many different vegetative conditions existed during the last 12,000 years in post-glacial New England: spruce parkland, grasslands and open forest maintained by large browsing ungulates and mastodons (Askins, 2000, p. 17), open areas created by Native American agriculture and burning, dense forests after Native American retreats and declines, the extensively cleared landscape produced by an agrarian society following European settlement, and the present largely forested condition (DeGraaf and Miller, 1996). Choosing the conditions that existed just prior to European settlement is arbitrary and is no more indicative of a "natural" landscape condition than any of the others. Given the wide historical range of vegetative conditions that have existed in the post-glacial era (Lorimer, 2001), managing forested landscapes within the "natural range of variability" has been proposed for maintaining the conditions to which wildlife species have become adopted (Seymour and Hunter, 1999; Thompson and DeGraaf, 2001).

Early-successional wildlife habitats have now become critically uncommon in much of the eastern United States (Trani et al., 2001), especially the Northeast (Brooks, 2003), largely in response to forest maturation. Abandonment of agricultural lands reached a peak in New England in the late 1800s to

mid-1900s (McKinnon et al., 1935; Litvaitis, 1993), and a wave of early-successional habitats followed. Today, such habitats are less common than they were in presettlement times in several regions of the northeastern US, especially southern and south-coastal New England (Litvaitis, 1993; DeGraaf and Miller, 1996) and in the coastal mid-Atlantic region (Lorimer and White, 2003). On the other hand, the proportion of early-successional habitat in northern industrial forests is currently several times that which occurred in presettlement times (Lorimer and White, 2003). The northeastern US landscape is now dominated by human uses, and maintaining early-successional habitats throughout in proportion to presettlement levels is not possible. If the concern is for conservation (i.e. maintenance of viable populations) of early-successional species, management needs to be representative of the "range of historical variation" where feasible. Adherence to presettlement levels is not possible in much of the northeastern US, and proposing management that does not create adequate patches of earlysuccessional habitats, while within the "natural range of variation" locally, will tend to eventually eliminate such habitats and the species associated with them throughout the region.

Most wildlife associated with native shrublands and early-successional habitats were once considered generalist species that flourished at edges and needed no specific management actions. Many early-successional taxa, however, are now either extinct, extirpated, threatened, or species of management concern in the region, largely because of habitat loss (Witham and Hunter, 1992; Litvaitis, 1993). Most early-successional species are not generalist species at all; rather, they are, to a remarkable degree, specialists in vegetation structure or area requirements. Only their former abundance led to their erroneous labeling. For example, New England cottontails (Sylvilagus transitionalis) are obligate users of young stands, occupying habitats when secondary succession has progressed 10-25 years, after which time they decline rapidly when understories thin as trees mature (Litvaitis, 2001; Barbour and Litvaitis, 1993). New England cottontails are also area-sensitive; individuals occupying small (<3 ha) patches of habitat encounter winter food shortages (Villafuerte et al., 1997). Cottontails that forage away from escape cover are killed by predators at about twice the rate as cottontails on large patches (Barbour and Litvaitis, 1993; Villafuerte et al., 1997). Chestnut-sided warblers (*Dendroica pensylvanica*) generally occupy patches of regenerating hardwoods at least 0.2 ha in New England (King et al., 2001), and then only for 3–10 years after harvest. Chestnut-sided warblers build well-concealed nests 0.3–1.2 m above ground in low bushes or saplings (DeGraaf and Yamasaki, 2001, p. 221), and decline steadily in a patch as stand development reduces the availability of nesting habitat.

Grassland and shrubland birds as a group best illustrate the habitat specificity of early-successional species compared to that of mature forest species (Askins, 1993). For example, Henslow's sparrows (Ammodramus henslowii) occur only in fields with a deep litter layer, standing dead forbs and tall, dense grass (Zimmerman, 1988). Yellow-breasted chats (Icteria virens) inhabit brushy old fields only until they begin to be invaded by overtopping trees (Shugart and James, 1973; Thompson, 1977). The decline of agriculture and reversion to forest have essentially eliminated grassland birds from the New England landscape, although many were common a half-century ago (Bagg and Eliot, 1937; Askins, 1993). Shrubland birds that are not adapted to suburbia, such as brown thrashers (Toxostoma rufum), eastern towhees (Pipilo erythrophthalmus), and field sparrows (Spizella pusilla), are now declining across the region (Veit and Petersen, 1993; DeGraaf and Yamasaki, 2001). Mature forest birds, whose habitats are increasing in eastern North America, are as a group quite tolerant of dramatic changes in stand structure (Webb et al., 1977) or patchy disturbance within areas of extensive forest (Maurer et al., 1981; DeGraaf, 1991; Thompson et al., 1992). Grassland and shrubland birds, however, are specialists that quickly disappear from a site as succession proceeds (Litvaitis, 1993).

In New England, approximately 200 vertebrate species occur in shrub/old field habitat and regenerating stands of aspen, paper birch, northern hardwoods, balsam fir, spruce-fir, and oak-pine types in New England (DeGraaf and Yamasaki, 2001). Relatively few species in the region [e.g. northern harrier (Circus cyaneus), savannah sparrow (Passerculus sandwichensis), and vesper sparrow (Pooecetes gramineus)] are limited to non-forest habitat types. There also are relatively few mature forest species that also occur in regenerating forest [e.g. five-lined skink (Eumeces

fasciatus), Swainson's thrush (Catharus ustulatus), magnolia warbler (Dendroica magnolia), Cape May warbler (Dendroica tigrina), black-throated blue warbler (Dendroica caerulescens), and worm-eating warbler (Helmitheros vermivorus)]. The majority of vertebrates in New England are quite plastic in their habitat distributions (DeGraaf et al., 1992; DeGraaf and Yamasaki, 2001). Early-successional habitats are in general decline (Thompson and DeGraaf, 2001). While some species depend on agriculture or frequent burning or mowing (Oehler, 2003), the greatest opportunity to provide habitat for most species lies in evenage forest management (DeGraaf et al., 1992, p. 131).

In this paper, we review the important habitat characteristics of early-successional habitats in the northeastern United States and suggest management options for increasing the amount and quality of these habitats. Although our comments and recommendations are directed toward management of avian habitats, we believe the principles covered will have application to other taxa dependent on early-successional habitats.

2. Natural shrublands and regeneration habitats

Natural shrublands are among the most endangered ecosystems in the United States (Noss et al., 1995). Woody, early-successional communities are dominated by shrubs, young trees, and, to varying degrees, by grasses and forbs. In the northeastern US, nearly all shrub communities are successional. The most stable shrub communities occupy a range of sites, including hydric wetlands (Cowardin et al., 1979), sandy sites (Patterson and Sassaman, 1988), and ledge areas (Kimball et al., 1995). In the Northeast, shrub-dominated communities persist the longest in extremely dry or wet areas, at high elevations, and places exposed to salt spray (Latham, 2003). The character of the woody vegetation that develops on a site varies with type of disturbance. For example, old-field succession that follows agricultural abandonment is a result of the invasion of woody plants from the surrounding landscape. It takes much longer for an old field to be reoccupied by trees than for a regenerating forest stand to become re-established (Tryon, 1945; Stephens and Ward, 1992). Succession is most rapid on forest sites

where tree seedlings and sprouts grow rapidly following a severe canopy disturbance.

In present-day landscapes, more frequent disturbances and large gaps (e.g. due to fires and hurricanes) occur among coastal and valley bottom forests and on mountains and hilltops. Less frequent disturbances and small gaps (e.g. due to blowdown, insect infestation, and ice storms) occur in upland and midslope forests (Lorimer, 2001; Lorimer and White, 2003). Land abandoned by beavers is recolonized by grasses, forbs, sedges, shrubs, and trees, and historically occurred more frequently on lower slopes and along low-gradient streams than on mid- and upper slope positions (Hodgdon and Hunt, 1953; Howard and Larson, 1985). Barrens and other xeric shrublands are maintained in an arrested state of succession by edaphic factors and fire (Tubbs and Verme, 1972; Patterson and Backman, 1988; Whitney, 1994).

Early-successional habitats created by timber harvests are dominated by tree reproduction and differ from other early-successional habitats. A useful distinction between "early-successional habitat," which is dominated by herbs, shrubs, and pioneer tree species such as aspen or pine, and "young forest habitat," which includes young stands of late successional species such as sugar maple (Acer saccharum) has been proposed by Lorimer (2001). Also, some shrubland habitats may be more patchy by nature, and contain more vines and shrubs than do regenerating forest stands, and may have some unique species. Shrublands in the northeastern US also contain high proportions of rare plants. Rich examples exist in the White Mountains of New Hampshire, where 15 of 62 rare plants are shrubs; Maine and New Jersey also contain globally rare shrublands (Latham, 2003). While forest regeneration and shrublands provide

Table 1 Available vegetative characteristics of early-successional habitats in northeastern United States

Vegetative characteristics	Burns ^a	Old fields ^b	Regenerating hardwoods HBEF ^c	Regenerating hardwoods BEF ^{J.e}
Overstory BA m ² >10 cm dbh	Variable ^f	Variable ^f	Nil	<0.93
Trees <10 cm dbh (10 ³ stems/ha)	_	1.4-3.6	_	_
1-year post-treatment (10 ³ stems/ha)	14.8-34.6	_	734	-
5-year post-treatment (10 ³ stems/ha)	27.4-36.3	_	226	6.4-46.4
10-year post-treatment (10 ³ stems/ha)	_	-	231	-
Snag/wildlife tree potential	Variable	Variable	Variable	Variable
			Percent total stems (%biomass)	(10 ³ stems/ha)
Shrub layer (1–3 m tall)				
1-year post-treatment	_	_	8, 19	_
5-year post-treatment	_	_	24, 4	16.6-41
10-year post-treatment	_	-	8, 2	-
			Percent total stems (%biomass)	Percent coverage ^g
Grass/forb layer (<0.5 m tall)				
1-year post-treatment	_	_	11, 3	1-6
5-year post-treatment	_	_	38, 0.1	24-56
10-year post-treatment	-	_	41, 0.1	18-30
Coarse woody debris potential	Variable	Variable	Variable	Variable

^a Mills (1961).

^b Olson (1965).

Martin and Hornbeck (1989).

d Costello et al. (2000).

e DeGraaf and Yamasaki (2002).

f Stephens and Ward (1992).

g Yamasaki (unpublished data).

habitats for many of the same species, both are needed to provide habitats for the full range of disturbance-dependent species (Thompson and DeGraaf, 2001).

Although data are limited, the structure of different types of woody early-successional habitats in New England (e.g. burns, old fields, and regenerating forests) seem to be different at the start (Table 1). Grasses, herbs, and shrubs persist longer on burns and old fields than in regenerating forest habitats. Young forest habitats are therefore more ephemeral. For example, the seedling stage of northern hardwood clearcuts commonly last about a decade (Leak et al., 1987). Among old fields, this stage commonly persists for two to three decades (Stephens and Ward, 1992), and some native shrub communities can persist two to three centuries (Latham, 2003).

The growth of a forest stand after a major disturbance is characterized by four developmental stages: stand initiation, stem exclusion, understory reinitiation, and old growth (Oliver and Larson, 1996). These stages are commonly recognized as seedling/sapling, poletimber, sawtimber, and large-sawtimber stands. Aspen (*Populus* spp.), birch (*Betula* spp.), and northern hardwood forests may remain in the stand-initiation stage for <10 years, depending on site quality. Treatments on poor sites last considerably longer than those on better sites. For example, a 20-year-old aspen stand with a site index of 80 has about 3600 trees/ha and is about 13 m tall, on average. In contrast, a similar stand with a site index of 40 will have about 10,000 trees/ha and be only 6–7 m tall (Perala, 1977).

The stem-exclusion stage begins when the canopy closes and increases in height and the growing space is occupied fully by trees. This stage is the end of early-successional habitat for most wildlife species because the ground vegetation is shaded out and browse, herbage, and soft mast from shrubs are lost. Other species such as ruffed grouse (Bonasa umbellus) and American woodcock (Scolopax minor) prefer this stage because it provides dense overhead cover and lacks dense ground cover (Dessecker and McAuley, 2001).

3. Management of early-successional forests

Resulting early-successional habitats depend on the silvicultural system, size of regeneration cuts, time

Table 2
Species composition 10-15 years after cutting in beech-birch-maple type by tolerance group and cutting method (from Leak and Wilson, 1958)

Tolerance category ^a	Clearcut (%)	Group selection (%)	Individual tree selection (%)
Tolerants	43	62	92
Intermediates	19	34	7
Intolerants	38	4	1

^a Species included in each category. Tolerants: beech (Fagus grandifolia), sugar maple (Acer saccharum), eastern hemlock (Tsuga canadensis), and red spruce (Picea rubens). Intermediates: yellow birch (Betula alleghaniensis), white ash (Fraxinus americana), and red maple (Acer rubrum). Intolerants: aspen (Populus spp.) and paper birch (Betula papyrifera).

between regeneration cuts, and rotation age or re-entry period. Silvicultural prescriptions designed to generate early-successional habitats utilize relatively large regeneration cuts that create favorable environments for dense reproduction of intolerant, intermediate, and tolerant tree species (Leak and Wilson, 1958; Marquis, 1967; Smith et al., 1997).

The extent that the canopy is removed influences the species composition of the developing stand (Table 2). Both clearcuts and large (0.8 ha) group selection cuts produce very dense stands (Marquis, 1967) with a higher stocking of intolerants and intermediate tree species than do small (<0.25 ha) group selection cuts under an uneven-age management system (Leak and Wilson, 1958; McClure et al., 2000). Fleshy fruits are important foods for many species (e.g. Martin et al., 1951), and are abundant in regenerating northern hardwood stands that are open to full sunlight. Wild strawberry (Fragaria sp.), raspberry (Rubus spp.), and blackberry (Rubus spp.) provide soft mast in regenerating stands during the first 10 years post-cut, followed by the rapid development and senescence of pin cherry (Prunus pensylvanica). In the mixed wood stands of southern New England, blackberry and shadbush (Amelanchier spp.) are commonly abundant in the early seral stages.

There is some evidence that generalist foraging guilds (albeit habitat structure specialists) predominate in herb/shrub habitats (May, 1982). Among birds, the relative abundance of fruit-bearing shrubs may be more important than habitat structure in determining habitat use during autumnal migration in the mid-Atlantic region (Suthers et al., 2000).

Also, the movements of post-fledgling juveniles likely reflect foraging optimization; they need abundant food resources to complete the prebasic molt and accumulate fat reserves for migration. For example, juvenile wood thrushes have been shown to leave nearby mature forest habitat and enter early-successional habitat to forage on fruits and invertebrates (Anders et al., 1998; Vega Rivera et al., 1998).

Effect of opening size in forest-dominated landscapes also influences avian species richness (Taylor and Taylor, 1979). Rudnicky and Hunter (1993a) reported that breeding bird species richness increased in regenerating spruce-fir stands and clearcut areas up to 20 ha. Costello et al. (2000) compared songbird response to group selection cuts (0.13-0.65 ha) to clearcuts (8-12 ha) and found that species richness for birds associated with open habitats was higher in clearcut openings than group selection openings, suggesting that smaller group selection cuts do not provide the equivalent habitat for breeding birds that similarly aged larger clearcuts do. King et al. (2001) found that daily nest survival rates for early-successional birds were similar in large group cuts and clearcuts in extensive northern hardwood forests. Early-successional bird species that need large forest gaps, such as olive-sided flycatcher (Contopus cooperi), eastern bluebird (Sialia sialis), and mourning warbler (Oporornis philadelphia), will therefore be habitat-limited where only single-tree and small group selection practices are used. Single-tree selection will not create early-successional habitat under any circumstances.

Forest stand edge effects in forest-dominated landscapes in the northern United States are ephemeral because woody regeneration in cut stands grows quickly (DeGraaf and Yamasaki, 2002). Distinct breeding bird assemblages do not occur at forest interior stand edges; rather, distinct avian assemblages are separated by abrupt interior edges [e.g. seedling/ sapling-sawtimber stand interfaces (DeGraaf, 1992)].

Evidence from studies using artificial nests shows variable effects on edge-related predation depending on location, egg and nest types used, and other factors (see reviews by Paton, 1994; Major and Kendal, 1996). Edge-related increases in nest predation are well documented from both studies using artificial nests (Rudnicky and Hunter, 1993b) and natural nests (King et al., 1996, 1998). Studies in extensive forests in the Northeast show that silvicultural edges do not result in elevated nest predation rates (DeGraaf and Angelstam, 1993; DeGraaf, 1995; VanderHaegen and DeGraaf, 1996; DeGraaf et al., 1999) in contrast to suburban

Table 3

Number of years after clearcutting an eastern deciduous forest that breeding, early-successional birds first appear, become common, and then decline

Bird species	First appear	Become common	Decline
Ruffed grouse (Bonasa umbellus)	10	15	20
Northern flicker (Colaptes auratus)	1	1	7-10
Olive-sided flycatcher (Contopus cooperi)	1	1	3-4
Willow flycatcher (Empidonax traillii)	1	2	5–7
Tree swallow (Tachycineta bicolor)	1	1	7-10
Winter wren (Troglodytes troglodytes)	1	4	7-10
Eastern bluebird (Sialia sialis)	1	1	2
Veery (Catharus fuscescens)	3	10	20
Swainson's thrush (Catharus ustulatus)	2	4	15
Cedar waxwing (Bombycilla cedrorum)	2	4	7-10
Chestnut-sided warbler (Dendroica pensylvanica)	2	4	10
Black-and-white warbler (Mniotilta varia)	3	10	_a
Mourning warbler (Oporornis philadelphia)	2	5	10
Common yellowthroat (Geothlypis trichas)	2	6	10
Canada warbler (Wilsonia canadensis)	5	15	_a
White-throated sparrow (Zonotrichia albicollis)	1	2	_a
Rose-breasted grosbeak (Pheucticus ludovicianus)	3	15	_a

We assumed that some residual stems (snags and live trees) remain (DeGraaf, 1987, Thompson et al., 1992, Thompson et al., 1996).

^a Present until next cutting cycle.

forest edges (Danielson et al., 1997). King et al. (1998) found that forest edge-related nest predation was similar for both clearcut and group selection stands in forest-dominated landscapes in New Hampshire. It would seem that in extensively forested landscapes in northern areas, edges produced by even-age management does not result in an increase in nest predation rates.

Frequency of disturbance also matters because breeding bird composition changes rapidly in the first 10-15 years after complete clearcutting. Many of the earliest arriving birds decline in just a few years as habitat conditions change (Table 3). In the White Mountains of New Hampshire and Maine, regenerating stands 1-5 years old contain about 28 bird species. Of these, five are restricted to that stage. Sapling stands contain about 30 species and pole-timber stands only about half as many (DeGraaf, 1987). Whitethroated sparrows (Zonotrichia albicollis), winter wrens (Troglodytes troglodytes), and willow flycatchers (Empidonax traillii) are generally abundant in the first growing season after complete removal of all live stems. Winter wrens are associated with dense slash. If stubs with old woodpecker holes are left, eastern bluebirds are commonly present. Two years after clearcutting, the number of species doubles. Common vellowthroats (Geothlypis trichas), chestnut-sided warblers, cedar waxwings (Bombycilla cedrorum), American goldfinches (Carduelis tristis), and mourning warblers will invade, along with Swainson's thrushes, eastern towhees, and American redstarts (Setophaga ruticilla). Northern flickers (Colaptes auratus) and white-throated sparrows remain, but eastern bluebirds and sometimes winter wrens are gone. In the third growing season after clearcutting, bird species numbers again double, with about a dozen new species added, including black-and-white warbler (Mniotilta varia), rose-breasted grosbeak (Pheucticus ludovicianus), mostly in low numbers. During the next 12 years, bird species composition changes substantially, as ruffed grouse, red-eyed vireos (Vireo olivaceus), wood thrushes (Hylocichla mustelina), and ovenbirds (Seiurus aurocapillus), among others, arrive but the number of species usually does not change appreciably (DeGraaf, 1991).

The time between periodic regeneration cuts needs to be short enough to maintain the presence of earlysuccessional bird species in a management area. Silvicultural practices that minimize the size of regeneration cuts and the total harvest area or lengthen rotation age and re-entry periods inhibit the creation and maintenance of young forest habitats. Early-successional bird species are capable of locating and using widely dispersed disturbance gaps throughout a northeastern landscape as these habitats become available (Lent and Capen, 1995). It has been suggested that natural disturbance gaps would provide a base level of sufficient habitat. Now that historical sources of disturbance are much reduced, we speculate that small, infrequent, and isolated regeneration cuts in a large watershed, whether created by clearcut, patch, or large group selection methods, would take a long time to be occupied by these species, given the lack of nearby source populations. Avian occupation of isolated patch cuts (1.2-2.4 ha) at the Bartlett Experiment Forest in central New Hampshire, where the percentage of regenerating habitat in the watershed is low (<3%) in any given decade, seems to occur at a slower rate than in larger clearcuts in more actively managed watersheds (Costello, personal communication).

In southern New England, where large openings or clearcuts are socially unacceptable, group selection is the most likely method to create suitable habitat. Groups >0.5 ha need to be cut and clustered closely together to maintain an adequate level of early-successional habitat. Strategies suggested by Hagan et al. (1997) and King et al. (2001) to consolidate both regenerating and mature forest stands into larger blocks would increase the likelihood of systematically and effectively providing habitats for both mature forest and early-successional habitat bird species.

4. Management of shrublands in a forest landscape

Several opportunities exist to provide or maintain shrublands in otherwise forested landscapes. Natural opportunities exist in frost pockets and on poor or depleted sites (Tubbs and Verme, 1972). Old fields, depending on soil conditions, seed bank (Leck and Leck, 1998), density of herbaceous growth and seedling mortality (Gill and Marks, 1991), and densities of rodent herbivores (Manson et al., 2001) and deer (Inouye et al., 1994) can provide early-successional habitat for 30–50 years.

Powerline rights-of-way can contribute significant shrubland habitat area. For example, a 100 m wide corridor provides I ha of shrubland habitat for each 100 m it extends through forest. Powerlines in the Northeast constitute a base on which to build useful core shrubland habitat in human-dominated landscapes where natural disturbance patterns are obviated by landscape fragmentation. The New England cottontail, proposed for listing as an endangered species, does not persist in small patches in human-dominated landscapes. This species would likely benefit most from the provision of 'core habitat' patches at least 10 ha in size, clustered within several kilometers of each other (Litvaitis, 2001) and positioned along adjacent early-successional habitats such as powerline corridors (Askins, 1993). Powerline corridors also provide suitable shrubland bird habitat. For example, nesting and fledging success of chestnut-sided warblers in western Massachusetts powerline corridors were high, and reproductive success and adult survival were sufficient to balance losses from mortality (King and Byers, 2002). Also, nesting success near utility rights-of-way in heavily-forested landscapes in New York, Massachusetts, and Maine was higher than that in the rights-of-way and similar to that in forest, suggesting that negative effects of edge observed in agricultural landscapes are not associated with rightsof-way through forested landscapes (Confer and Pas-

Intensive high-yield silviculture in the industrial forest landscapes of northern New England (Seymour and Hunter, 1992) also can provide an ephemeral

source of shrublands and early-successional forest habitat in the first 10-15 years post-clearcut. The percentage of early-successional woodcock habitat in landscapes (>25%) proposed by McAuley et al. (1996), can most easily be met on industrial forest landscapes. Site preparation and stand culture activities often involve herbicide application, targeting hardwood competition to release conifers to grow quickly (Seymour et al., 1986). Current herbicide formulations temporarily reduce hardwood browse, but re-sprouting and herbicide-resistant hardwoods and untreated 'skip' areas often result in dense shrub patches in which numerous shrub-dwelling birds and browsing mammals can be found (e.g. Hagan et al., 1997; Raymond et al., 1996; Santillo et al., 1989). Precommercial thinning and spacing activities remove the nearest hardwood competition from the desired conifer stems, and still maintain dense hardwood regeneration and shrub zones until the conifer overstory closes, also creating productive woodcock habitat (McAuley, personal communication). These habitat elements, when combined with the extensive alder (Alnus sp.) acreage, can form high value shrubland habitat across the industrial forest landscape during the period prior to overstory crown closure.

5. Practical approaches for providing early-successional habitats

We suggest using habitat composition goals to maintain a balanced and integrated set of forest

Table 4
Structural characteristics commonly found in regenerating hardwood and softwood forests in the northeastern United States

Structural characteristics	Clearcut ^{a,b,c}	Shelterwood ^b	Group selection a,b,d,e,f	Single-tree selection ^{g,h}
Average gap size (ha)	>8.1	Variable	0.2	0.002-0.03
Size range of gaps (ha)	4-30.4	Variable	0.04-0.81	0.002-0.03
Likelihood of regenerating intolerants and mid-tolerant tree species	Moderate-high	Moderate	Low-moderate	None
Time until next stand entry (years)	4060	50-60	15-30	15-30

a Leak (1983, 1999).

coe, 2003).

^b Leak et al. (1987).

^c Marquis (1967).

d McClure and Lee (1993).

e McClure et al. (2000).

^f Lee (personal communication).

g Kimball et al. (1995).

h Seymour et al. (2002).

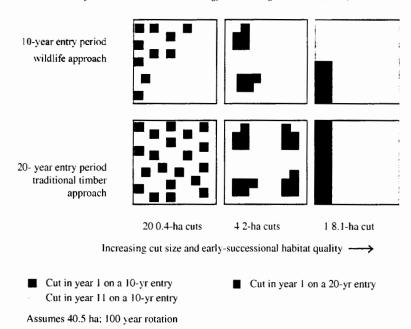


Fig. 1. Comparison of stand entry periods under sustainable, regulated even-age management for providing continuous early-successional wildlife habitat vs. traditional silviculture in the northeastern United States.

conditions that includes early-successional habitats and young forest as well as mature and old forest for a broad diversity of species over time (e.g. DeGraaf et al., 1992). Optimizing early-successional habitats in northeastern landscapes would entail modifying these composition objectives to reflect higher proportions of regenerating forest and perhaps shorter rotational cover-types; the structural composition of the resulting habitats would vary with silvicultural treatment (Table 4). Such management would likely not impact late-successional forest species if disturbance patches were clustered and large blocks set aside for management on long (>125 years) rotations.

Where clearcutting is not an option, managers can use the example in Fig. 1 to modify traditional timber management activities in several ways: (1) maintain even-age management systems in the mix of forest management practices; (2) where using single-tree selection systems exclusively across the landscape, increase the use of group selection and patch cut methods to increase the gap size to at least 0.8 ha; (3) consider splitting a re-entry period by cutting half of the allowable volume in the first 10–15 years; the second half of the allowable volume per re-entry period in years 20–25; (4) maintain or increase the

intolerant and mid-tolerant tree regeneration in managed stands; and (5) consider frost pockets and unstocked or poorly-stocked stands as opportunities to maintain and increase the area of early-successional habitat.

We suggest applying these recommendations at both the landscape and stand level to improve the quality and quantity of early-successional habitats in the northeastern US. Landscape considerations involve the regenerating forest acreage and permanent openings (e.g. powerlines and gas pipeline rights-of-way), brushy post-agricultural set-aside acreage, and scrub-shrub wetlands. Together these habitat types should comprise between 10 and 20 percent of the forest landscape to optimize early-successional species diversity (DeGraaf et al., 1992). Three principles based on the literature review above should guide management where early-successional habitats are needed to arrest or reverse species declines:

 Size of opening affects both woody intolerant species composition in the regenerating stand and breeding bird species richness in the regenerating stand. Small (<0.25 ha) group selection cuts do not provide the equivalent habitat for breeding

- birds that similarly aged larger clearcut units do. Avian reproductive success is similar for species nesting in clearcuts and large group cuts.
- 2. Frequency of disturbance matters; the bird community in young hardwood forest is very ephemeral in the first 10 years after harvest and differs almost completely from those occupying mature stands. Edge effects in extensively forested landscapes are minimal and very different from those in forest-field landscapes. Cowbird occurrence and thus brood parasitism is very low in extensively forested New England landscapes (Yamasaki et al., 2000) compared with forest-field landscapes (Coker and Capen, 2000).
- 3. Spatially and temporally isolated patches of earlysuccessional habitat in extensively forested landscapes likely have lower rates of occupancy for invertebrates such as the Karner blue butterfly (Lycaeides melissa samuelis) as well as nesting turtles [e.g. painted (Chrysemys p. picta), snapping (Chelydra s. serpentina), and Blanding's (Emydoidea blandingii)], snakes [e.g. milk (Lampropeltis t. triangulum), black racer (Coluber c. constrictor), and smooth green (Liochlorophis vernalis)], and passerines [e.g. towhees, brown thrashers, indigo buntings (Passerina cyanea), bluebirds, mourning and chestnut-sided warblers]. Additionally, raptors would benefit from hunting sites [e.g. American kestrels (Falco sparverius), red-tailed hawks (Buteo jamaicensis), and sharpshinned hawks (Accipiter striatus)] and nesting sites [e.g. harriers and Cooper's hawks (Accipiter cooperii)]. A variety of mammals would benefit from additional foraging habitat [e.g. bats, meadow voles (Microtus pennsylvanicus), meadow jumping mice (Zapus hudsonius), red fox (Vulpes vulpes), gray fox (Urocyon cinereoargenteus), bobcat (Lynx rufus), white-tailed deer (Odocoileus virginianus) and moose (Alces alces)]. In other words, there is some critical minimum habitat area required in time and space for each species to be present, and more for them to exist as viable populations. While the actual threshold area for many species is unknown, declining habitat trends are working against their conservation.

Managing these habitats then requires: (a) a significant percent of the landscape in permanent forest

openings, shrub swamp wetlands, the 0-10-year age class and shorter rotation cover-types (intolerants); (b) a variety of opening sizes >0.5 ha; (c) a frequent (i.e. \sim 10 years) re-entry period in places; and (d) clustering these types of activities near existing and maintained permanent openings-old fields, powerlines, frost pockets, old burns, and predictably non-stocked sites. In much of the northeastern United States, especially along the coast and in the major river valleys, human population growth and development continue to increase. These areas were once frequently disturbed by Native American agriculture, fire, and hurricanes and have high potential species richness (Askins, 2000; DeGraaf and Yamasaki, 2001). The continued occurrence of early-successional species depends upon both managing forests to the extent possible in historically-disturbed valley bottoms, and to simulate disturbance to create such habitats in uplands and on lower mountain slopes. Such actions would likely increase the rate of disturbance somewhat from historical levels of natural disturbance in upland forests, but rates would likely not exceed historical levels for the region as a whole. Of one thing we can be sure: continuous management will be needed to conserve and manage these habitats now and into the future or they and the species they support will be lost in much of the region. Management needs to represent, to the extent possible, the historical range of variation in habitat conditions, and not mimic only the forested parts of the historical range in each local area.

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