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Wildlife Forestry

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1. Introduction

Wildlife forestry is management of forest resources, within sites and across landscapes, to provide sustainable, desirable habitat conditions for all forest-dependent (silvicolous) fauna while concurrently yielding economically viable, quality timber products. In practice, however, management decisions associated with wildlife forestry often reflect a desire to provide suitable habitat for rare species, species with declining populations, and exploitable (i.e., game) species. Collectively, these species are deemed priority species and they are assumed to benefit from habitat conditions that result from prescribed silvicultural management actions.

Early wildlife conservation efforts largely focused on controlling indiscriminate slaughter of wildlife by restricting the season or sex of harvested species (Graham, 1947). Subsequent conservation efforts targeted increased protection of populations through creation of sanctuaries or reserves (Knight, 1999), such as national parks and wildlife refuges, within which harvest of wildlife was prohibited or greatly restricted. Typically parks and wildlife reserves were located in areas with abundant wildlife populations, and therefore, little emphasis was placed on active management to improve or maintain suitable habitat.

In his description of a "land ethic" in which people are members of the natural community, Leopold (1949) indicated the appropriateness of habitat alteration and management to aid the continued existence of wildlife species. His philosophical principles were succinctly stated as "*A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise*."

Anthropogenic alteration of forest habitat for the benefit wildlife species has long been practiced, particularly with regard to intentional use of fire (Bonnicksen, 2000, Ford et al., 2002). Even so, active manipulation of forest structure to purposefully enhance wildlife habitat has been slow to evolve. Most early efforts regarding habitat alteration focused on providing suitable escape cover, foraging habitat, or distinct habitat features (e.g., nest sites) for game species. Within forested landscapes, improving wildlife habitat often meant increasing local heterogeneity and providing more forest edge habitat. However, increased knowledge of the possible negative effects associated with forest edges, such as greater predation and nest parasitism rates, has called into question the practice of providing increased heterogeneity within forested landscapes. At the same time, a desire to provide habitat for specific species that may require specialized habitat conditions, as is the case for some endangered and threatened species as well as other charismatic megafauna with widespread public support, has prompted development of habitat management prescriptions designed to improve forest habitat conditions for specific species (Wilson et al., 2007).

Partly in response to what has been perceived as management for single-species, but also to advocate a desire to prevent future population declines of common species, recent emphases in wildlife conservation have been placed on the development of comprehensive, eco-regional, conservation plans whose scope encompasses multiple species or the entirety of a species-group. This approach gained momentum with the North American Waterfowl Management Plan (1986) which identified conservation actions intended to return waterfowl populations to their former abundance and distribution. Subsequently, this basic concept has been expanded to other species groups such as songbirds (Rich et al., 2004), reptiles and amphibians (Bailey et al., 2006), and shorebirds (Brown et al., 2001), as well as other species groups. Although these conservation plans differ markedly with regard to their recommendations for habitat management, many of these conservation plans advocate use of prophylactic management prescriptions to enhance or maintain suitable habitat conditions for priority wildlife species. Indeed, most conservation plans recognize the need for alteration of habitat and landscapes via management actions so as to attain the desired distribution, abundance, and viability of priority wildlife species.

Before managers can provide appropriate forest habitat for priority wildlife, the landscape and site characteristics that contribute to viable populations of these species must be identified. Preferably, those forest habitat characteristics identified can be quantified via standard measurement protocols. If possible, the desired or acceptable range of values should be determined, and either quantitatively or qualitatively stated, for each of these characteristics. In addition, a threshold value for each characteristic should be determine, that if exceeded would justify prescription of management actions to return site characteristics within the desired range (Fig. 1).

Because wildlife forestry silviculture does not target optimal production of forest products, many forest management practitioners (i.e., foresters) have been reluctant to adopt these alternative silvicultural practices. Indeed, these concerns may be justified, as desired stand conditions may include less then fully stocked stand densities, retention of some economically mature trees, maintaining species diversity which includes less merchantable tree species, and preservation of less vigorous (decadent) trees. However, at present we lack credible, long-term economic data to suggest that development and maintenance of quality forest habitat for priority wildlife species will result in a sacrifice in timber production or quality. Regardless of these overarching financial concerns, silvicultural management actions prescribed to enhance desirable forest habitat conditions for priority wildlife species are expected to be commercially viable. Maintaining the long-term commercial viability of prescribed silviculture is import, because without sufficient financial returns, needed management actions will not be undertaken.

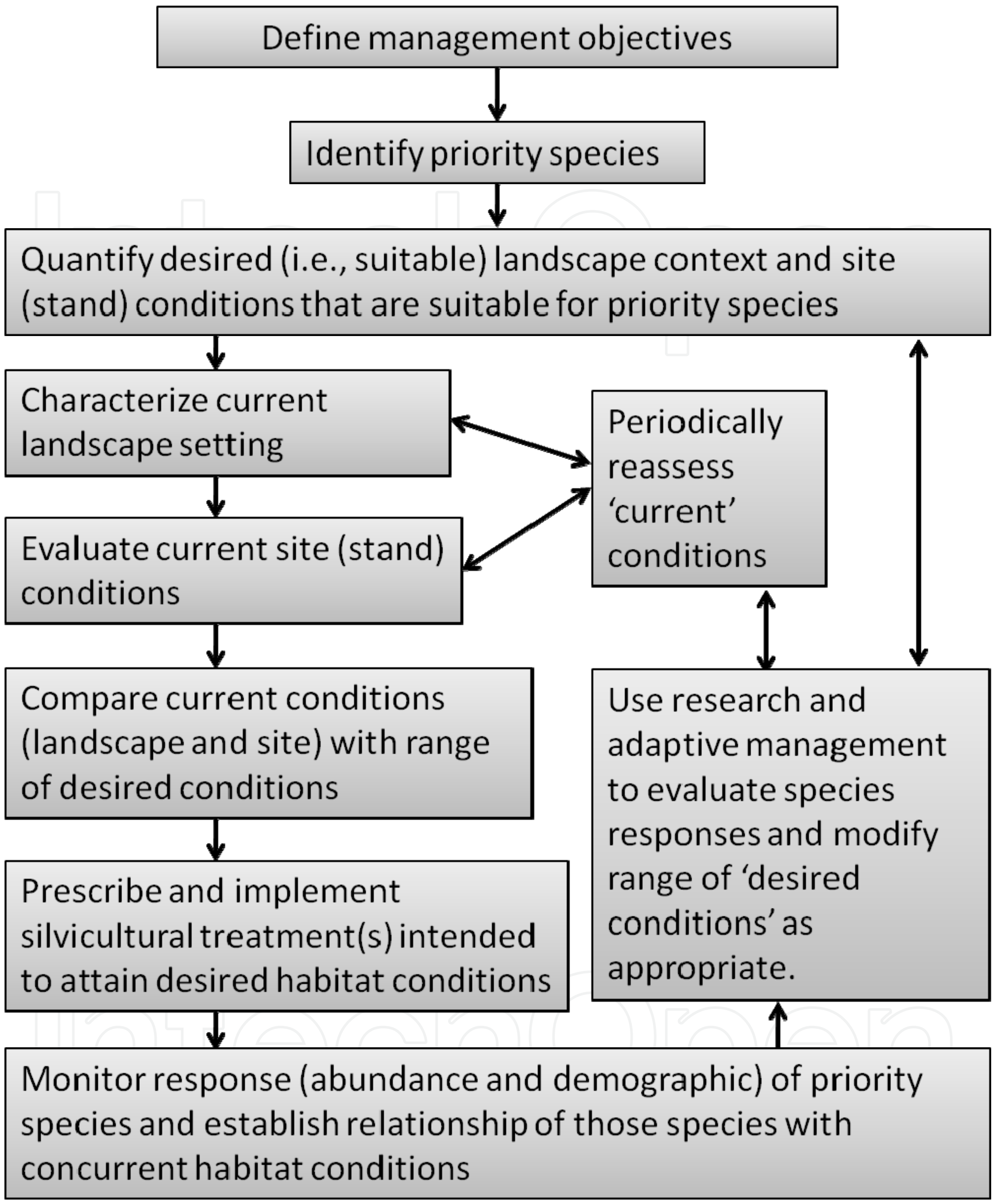

Fig. 1. Characterization of wildlife forestry silvicultural methodology.

2. Forest management

Silviculture is the manipulation of the establishment, growth, composition, and quality of forest vegetation to achieve management objectives. Historically a primary objective on managed forest lands has been to maximize financial returns from production of forest products such as timber and wood pulp. Production-oriented silviculture has focused on reducing the length of production cycles between stand regeneration and harvest while concurrently maximizing wood product yields. Reduction of production cycles (i.e., rotation length) tends to lessen the time regenerating forests are in early seral habitats, and consequently the size and age of shrubs and there their likelihood of persistence within subsequent seral stages is reduced (Hagar, 2004). Often production-forestry objectives favored a limited number of tree species due to their high economic value or growth potential. Concomitantly, to increase growth and yield of desired trees, other species with lesser economic value, as well as congeneric competitors, were culled. These actions result in increased spatial homogeneity within managed stands. The apogee of this trend towards increased spatial regularity is expressed within planted plantation forests. Climate, soils, species, and other factors affect the optimal length of production cycles within production-oriented forests (Lindenmayer et al., 1999). Thus, rotation periods within plantations vary markedly from rotations of up to 150 years to as few as 10 years. Notably, recent developments and increased advocacy of short-rotation woody coppice systems for use in biomass production have further compressed the length of production cycles to <4 years (Tubby and Armstrong, 2002).

Even in non-plantation forest management systems, historical forest management practices, especially those focused on timber or pulpwood production, have often resulted in relatively homogeneous mature forest conditions. This homogeneity has been exacerbated by environmental changes that limit natural disturbances within forest stands (e.g., fire suppression). When these homogenous forests are managed using even-aged silviculture, during which all or most trees are harvested and the entire stand regenerated, successional ‘boom and bust’ conditions are dispersed throughout landscapes. The forest conditions resulting from even-aged management (e.g., clear cuts) are temporarily favorable for some species, specifically benefiting species that exploit early-successional forest habitat (Askins, 2001, Hunter et al., 2001). Even so, these early-successional habitats are transitory and are followed by an extended period of stand development (stem exclusion and understory reinitiation; Oliver and Larson, 1996) during which the homogeneous, closed-canopy forest structure with sparse understory vegetation offers attraction (forage or cover) primarily for common (non-priority) forest wildlife species. Indeed, the abundance of homogeneous, closed canopy forests with sparse understory cover that have resulted from historical silvicultural practices may have contributed to why species for which these habitat conditions are suitable are considered common and are not priority species in need of management actions to increase their abundance. In addition, the altered (often depauperate) species compositions that have resulted from selective harvest and culling during past management practices may amplify the potential for catastrophic damage from outbreaks of insects or diseases or limit the seasonality of mast crops that are exploited by wildlife.

In contrast to the relatively short periodicity of production-oriented silviculture and the periodic boom-bust cycles associated with even-aged silviculture, natural successional processes within forests may require hundreds, or potentially a thousand, years to achieve complete replacement via small-scale disturbance or as the duration between catastrophic stand-replacement events. Owing to differences in their successional development, structural and ecological characteristics within production-oriented managed forests and in forests managed using even-aged silviculture are manifestly different from those same characteristics within natural forests (Seymour and Hunter, 1999). Ecological differences between managed and natural forest stands are exacerbated over time, as natural stands approach climax or 'old-growth' conditions while intensively managed forests are repeatedly regenerated.

To mitigate the detrimental effects of forest management on priority wildlife species, recommendations have been made to increase the length of production cycles, thereby allowing increased time for development of heterogeneous forest structure (Kerr, 1999). Unfortunately, small increases in rotation lengths provide little opportunity for increased complexity of forest structure within these stands – and periodic, complete harvest and stand regeneration thwart retention of forest structure over time. Similarly, forest managers have argued that temporal and spatial dispersion of clear-cuts throughout landscapes will provide continual availability of wildlife habitat – albeit at different locations. Although early-successional habitat may be continuously afforded via such dispersion, few of the other benefits conferred by increased forest structural heterogeneity, such as emergent or senescent legacy trees, are realized.

Increased recognition of the structural and ecological deficiencies within production-oriented forests has spurred interest in and development of alternative silviculture (Franklin, 1989). Alternative silviculture has been especially valuable for stands where management objectives are not solely financial but where stewardship objectives include preservation of regional biodiversity, enhancement of wildlife habitat, maintaining landscape aesthetics, or providing increased recreational opportunities.

Alternative silvicultural methods developed for use in many forest types have been based on identification and quantification of natural disturbance regimes, with subsequent implementation of silvicultural methods intended to emulate these disturbances (Mitchell et al., 2002, 2006; Palik et al., 2002). For many forest types, emulation of natural disturbance regimes includes small-scale disturbances implemented via single-tree and patch-cut harvests (Franklin et al., 2007, North and Keeton, 2008). If successfully implemented, emulation of natural disturbance regimes should promote natural stand development and succession. Unfortunately, natural stand development and concurrent successional changes may conflict with landowner objectives if succession results in changed species composition or reduced financial returns. Moreover, strict adherence to silvicultural regimes that mimic natural disturbance may not be necessary to maintain biodiversity or to provide desired wildlife habitat (Palik et al., 2002).

Another common alternative silviculture has been inspired by the desire to achieve forest structure reminiscent of old-growth forest (Bauhus et al., 2009). Although the structure of old-growth forest varies among forest types (Hayward, 1991), common attributes generally include increased vertical heterogeneity via a multi-layered canopy, increased horizontal heterogeneity associated with canopy gaps and different regeneration cohorts, the presence of large trees that are often in older-age classes, abundant snags (standing dead trees) or senescent trees, and large diameter downed woody debris (Bauhus et al., 2009, Keeton, 2006). Myriad ecological benefits, including increased biodiversity, have been ascribed to old-growth forests (Lindenmayer and Franklin, 2002). As such, forest reserve lands have been designated (e.g., wilderness areas and parks) which afford unfettered, natural development of these characteristics. However, on lands with timber production as an objective, even if not the sole objective, implementation of production cycles that span hundreds of years is not likely to occur. In addition, merely increasing the length of production cycles may provide little enhancement of biodiversity if the forest structure favored by production-oriented silviculture is maintained (Carey, 2006). Furthermore, where forest reserves are small or located within inhospitable landscapes, full ecological benefits of old-growth forests may not be attainable or sustainable (Kneeshaw and Gauthier, 2003).

Fortunately, it is likely that many of the benefits conferred by old-growth forests, or at least specific species associated with old-growth forests, are positively related to the heterogeneous structure (vertical and horizontal) and other structural attributes found within these forests, not necessarily with the prolonged existence of these forests (Beggs, 2004, Carey, 2003b). As such, alternative silvicultural methods have been developed which retain or enhance structural heterogeneity within managed forests, thereby promoting structural attributes of old-growth forests and encouraging greater biodiversity (Bauhus et al., 2009, Garman et al., 2003; McClellan, 2004). Most often, increased heterogeneity and other desired attributes have been achieved via retention of living or dead trees (or other forest elements). These retained structures have been referred to as legacy elements (Franklin et al., 1997).

Based on the concept of retained legacy elements, various alternative silvicultural methods have been advocated to enhance structural complexity within managed forests (Whitman and Hagan, 2003). Some of these methods have being designated as green-tree retention harvests (Zenner, 2000), variable-retention harvests (Aubry et al., 2004. Maguire et al., 2007), dispersed retention harvests (Heithecker and Halpern, 2006), variable density thinning (Aukema and Carey, 2008), and active intentional management (Carey et al., 1999, Carey, 2006). The legacy elements retained under these different silvicultural regimes may differ markedly. Retained elements may differ in quantity (e.g., % canopy cover or % basal area retained; Fig. 2a,b) but they may also differ in their composition, as different canopy species are preferentially harvested or specific regenerating species favored for retention. In addition, the quality of retained elements may differ via selection of retained trees with differing perceived fates – from robust, canopy-emergent trees through decadent, dead or dying trees. Moreover, retained elements may differ in their dispersion (e.g., evenly dispersed or aggregated; Fig. 2c,d) and the spatial juxtaposition of retention (e.g., clumped or linear).

Wildlife forestry silviculture exploits the versatility of legacy retention by combining specific retention and removal of canopy to achieved habitat conditions that are deemed suitable for priority wildlife species. The resultant forest stand may exhibit a mixture of tree species, size classes, and decadence within a heterogeneous distribution of aggregated retention and canopy gaps (Fig. 3).

2.1 Landscape considerations

Although specific silvicultural methods have most often been developed for and are implemented within forest management units (a.k.a. forest stands), a similar ecologically based approach has evolved with regard to maintaining or restoring landscapes surrounding managed forest stands (Lindenmayer et al., 2002, Lindenmayer & Hobbs, 2007). Intact forested landscapes are conducive to maintaining floristic and wildlife diversity, but also provide tangible social and economic benefits (Poudyal et al., 2010).

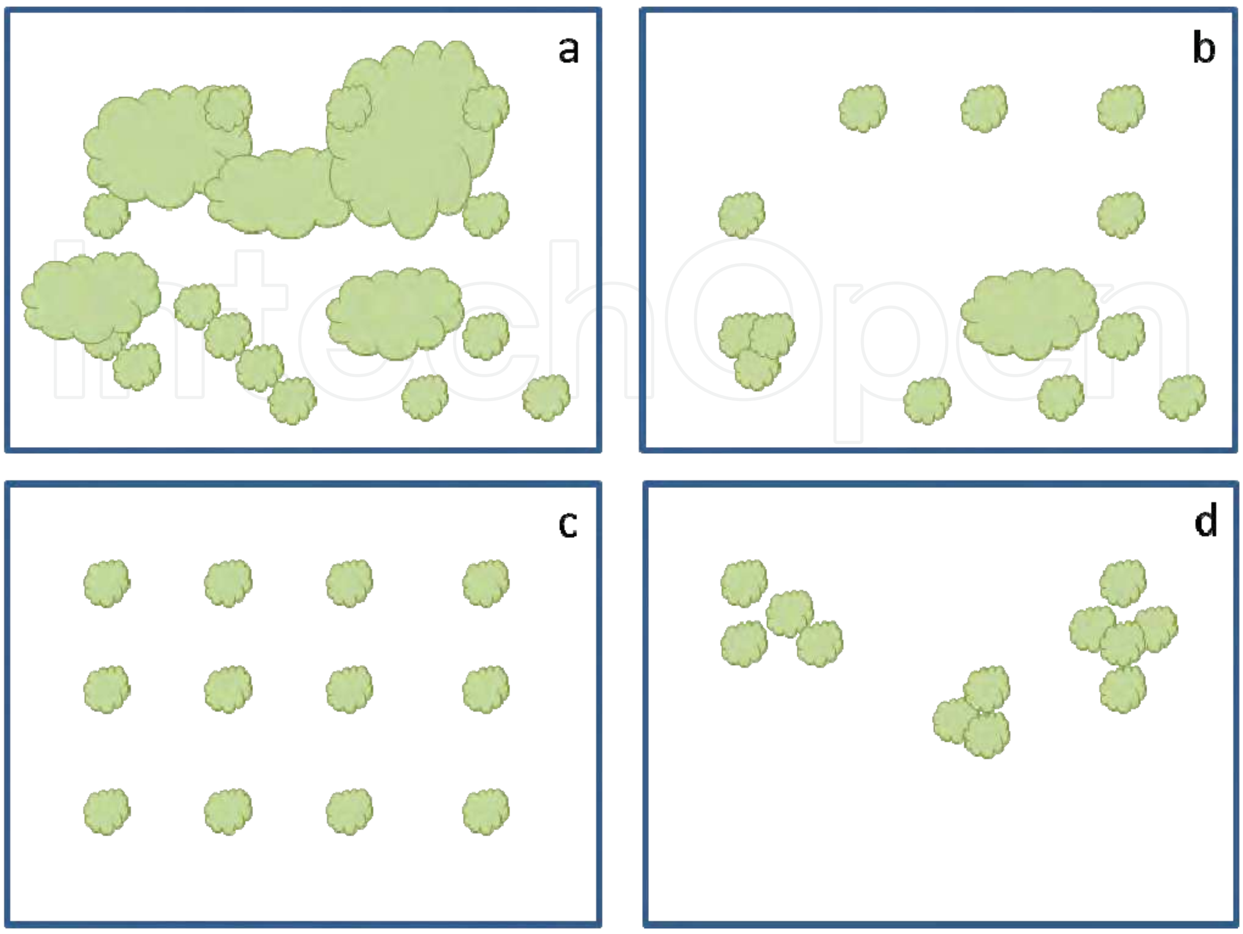

Fig. 2. Potential distribution of legacy elements after application of alternative silviculture, differing in quantity of retained canopy cover (a, b) or dispersion of retained elements (c, d).

Loss of diversity within landscapes is often a reflection of the increased homogeneity within forest stands. Although forest structure within a landscape ranges from regenerating stands to mature merchantable stands, these stands may be monotypic in species composition and physical structure. In addition, ensuring appropriate size of habitat patches and maintaining connectivity among these patches is critical to sustaining viable wildlife populations within landscapes (Franklin and Forman, 1987). Although the appropriate patch size is dependent upon the species under consideration, increased fragmentation tends to disrupt dispersion of fauna and flora and when habitat area is reduced without appropriate connectivity, extirpation of some species can result (MacArthur and Wilson, 1967). Finally, maintaining landscapes capable of sustaining viable wildlife populations requires that evaluation, planning, and management decisions reflect the temporal processes inherent in the ecosystem. Four landscape conditions have been recognized as contributing to ecosystems that support sustainable wildlife populations: 1) diversity within the landscape, 2) connectivity among landscape elements, 3) appropriate habitat patch sizes, and 4) sufficient time to achieve ecological functions (Silva, 1992). The impact of the degradation of forest landscapes was succinctly summarized by Franklin (1989) as: "*In general, we have tended to forget that what is good for wood production is not necessarily good for other organisms or processes in a forest ecosystem. Fully stocked young forests,… are the most simplified stage of forest development in terms of structure and function, and the most impoverished in terms of biological* *diversity.. . . . Simplification--genetic, structural, landscape and temporal—reduces ecosystem resilience…[Thus] the key to retaining resilience must be in maintaining ecological complexity or diversity".*

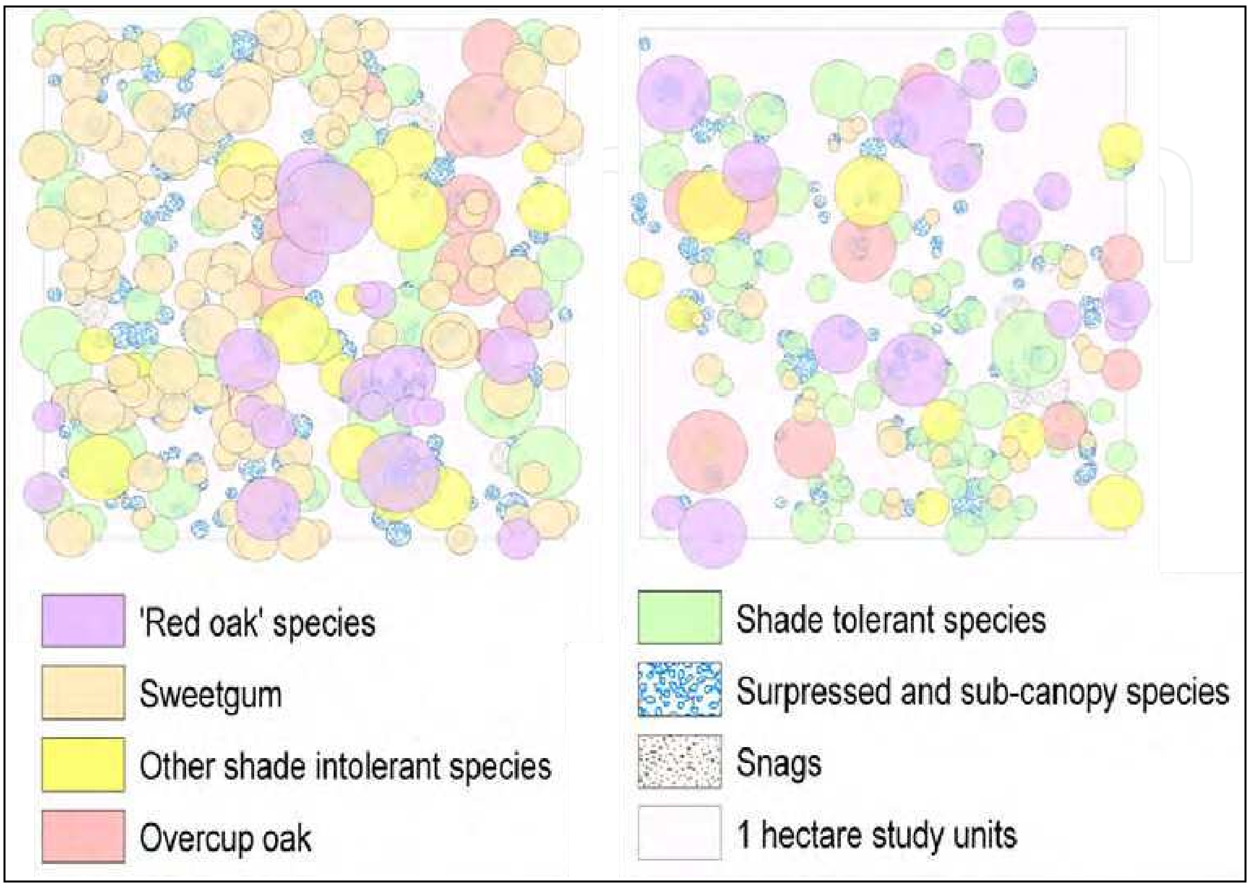

Fig. 3. Canopy cover accounted for by individual tree crowns within bottomland hardwood forests on an untreated control stand (left) and on a stand subjected to wildlife forestry variable-retention silvicultural treatment (right), 6 years after treatment (Twedt & Wilson, 2007).

As when considering disturbance within the context of forest stand development, landscape conditions have often been influenced by large-scale disturbance events, particularly fires (Kaufmann et al., 2003, Van Willgenburg and Hobson, 2008). Forest landscapes that result from management based on historical fire regimes, when compared with landscapes with extensive reserves and traditional silvicultural management, had increased area of late-successional habitat, more overstory structure in young forests, and larger forest patches (Cissel et al., 1999). Similarly, when compared with human altered landscapes, natural landscapes were composed of larger habitat patches which formed the landscape matrix, had greater connectivity among patches, the range of variation in patch size and complexity was greater, as was the likelihood of encountering 'rare' habitat types (Mladenoff et al., 1993).

Despite some understanding of desirable characteristics of forested landscapes, the appropriate landscape area remains nebulous. In part this is because an appropriate landscape area is dependent upon the species being considered, landscape characteristics, desired response, and the management context (Karau and Keane, 2007; Mayer and Cameron, 2003). As an example, the landscape appropriate for a grizzly bear is vastly different from the appropriate landscape for a shrew.

Even with knowledge of the appropriate landscape area and characteristics, manipulation of landscape conditions is usually beyond the purview of individual landowners. This is true even for large industrial or governmental landowners. Nevertheless, landscape conditions influence the ecological benefits conferred by forest stands, including the distribution, abundance, and viability of wildlife species within forest stands. In boreal forests, stand structure accounted for 54% of variability in bird and small mammal communities but landscape characteristics accounted for 29% (St Laurent et al., 2008). Similarly, bird species abundance within coniferous dominated landscapes was positively related to the proportion of broadleaf forest, with landscape thresholds for individual species ranging from 1% to 25% canopy cover. A strong negative relationship was noted between landscape broadleaf forest and avian population trends, such that the species most associated with broadleaf forests had greatest population declines. Therefore, maintaining or restoring broadleaf vegetation is important within coniferous dominated landscapes (Betts et al., 2010).

Because of landscape influences, providing desired forest conditions within forest stands may be insufficient for some priority species if these stands are located within inhospitable landscapes. Moreover, for long-term sustainable populations, most sites, even those with suitable habitat conditions, must have spatial and temporal linkages that facilitate dispersal, colonization, and interchange within metapopulations (Hanski, 1998). Towards that end, desired landscape conditions for priority wildlife species are usually composed of large forest patches as the preponderance of the landscape matrix, have a wide range of variation in patch sizes and complexities, and provide extensive connectivity among forest patches.

2.2 Why wildlife forestry?

The application of wildlife forestry silviculture is in many respects the logical extension of the various alternative silviculture methods whose objectives are to maintain or increase forest biodiversity (Table 1). Although forest management targeting increased biodiversity is a laudable objective in and of itself, managers of public conservation lands (e.g., National Wildlife Refuges and State Wildlife Management Areas) or private lands under conservation easements may have legal, or self-appointed, mandates to manage and conserve priority wildlife species rather than the more general goal of improving biodiversity. On other private lands, the economic and recreational values associated with silvicolous wildlife, including fee hunting, hunt-club memberships, wildlife viewing and other eco-tourism activities, have income potential that may equal or exceed that of extractive timber harvest. Hence, ensuring sustainable populations of wildlife may be essential for maintaining financial revenues from these forest lands.

In addition, land ownership patterns of private forest lands are changing. Changing ownership demographics and associated alteration of management objectives of these forest land owners have resulted in smaller landownership holdings. For owners of small landholdings, maintaining continuous forest cover and the aesthetic considerations associated with forests may be of paramount importance (Kaetzel et al., 2011).

Legacy characteristic	Wildfire	Wind	Insect / disease	Flood	Clearcut	Wildlife forestry
Live trees	Sparse	Variable	Variable	Sparse	Sparse	Variable
Snags	Abundant	Variable	Abundant	Abundant	Sparse	Variable
Downed woody debris	Variable	Abundant	Variable	Variable	Sparse	Variable
Understory development	Abundant	Abundant	Variable	Variable	Abundant	Variable
Spatial heterogeneity	Variable	Variable	High	Variable	Low	High
Duration of alterted state	Variable	Variable	Variable	Variable	Long	Variable

Table 1. State of habitat features following different distubances and prescribed wildife forsetry silviculture (expanded from Swanson et al., 2011).

Even on large land ownerships, such as industrial forest lands or lands managed by timber consortiums, there are increased public expectations to provide sustainable, 'green' forest products (Barneycastle, 2001). Concurrently, corporate efforts to maintain positive environmental images have prompted greater reliance on alternative silviculture, such as wildlife forestry. Finally, even on lands where implementation of traditional silviculture may be the preferred management option, exurban encroachment may constrain traditional forest management practices (Egan and Luloff, 2000).

2.3 Priority species

What are 'priority' species? For some groups of wildlife species, conservation planners have established priority rankings based on objective criteria such as current population abundance, distributions, availability of suitable habitats, perceived threats to habitat, etc. (Mehlman et al., 2004). For example, for North American landbirds, Partners in Flight has established ecoregional priority rankings (Panjabi et al., 2005). For other wildlife groups, priority status may be conferred based on species being listed as threatened or endangered by national or regional governmental agencies (Greenwald et al., 2006) or listed as a species of concern by private conservation organizations (Butcher, 2007). Regardless of the underlying rationale for their selection, priority wildlife species within managed forests differ among regions and forest types. Moreover, the priority species targeted for habitat improvement via prescribed management actions ultimately are determined by the landowner's objectives.

Why favor these species over others? All forest management, including no active management (a.k.a., passive management or benign neglect), influences the abundance and composition of wildlife species. For many priority species, insufficient habitat, or an overabundance of habitat with unsuitable conditions, likely contributed to their designation as a priority species. Therefore, where modification of forest habitat will promote habitat conditions conducive to supporting sustainable populations of these species, it behooves managers to prescribe silvicultural actions that will result in increased habitat for these species.

3. Desired habitat conditions for priority species

Because priority species differ among regions and among forest types, quantification of specific habitat characteristics suitable for all forests and all species is not practical. Even so, empirical evaluations of wildlife species responses to different silvicultural treatments provide insight into the general habitat conditions that benefit different species groups.

Amphibians – Within landscapes, amphibians benefit from protection of existing forest, avoiding further forest fragmentation, and disturbances that mimic natural processes (Kingsburg & Gibson, 2002). Within stands, seasonally available water, especially vernal pools, should be protected from disturbance (e.g., siltation) by retaining forest canopy (≥75%) immediately surrounding pools and maintaining >50% canopy for up to 120 m from seasonal waters (Calhoun & deMaynadier, 2004). Amphibians tend to benefit from retention of sufficient canopy throughout the forest stand to provide a partially shaded forest floor. Their abundance also tends to be positively associated with a deep litter layer and abundant woody debris on the forest floor (Maguire et al., 2005). Within southern pine forests (e.g., longleaf pine [*Pinus palustris*]), thinning and burning are positively related to increased abundance of priority (open-pine adapted) amphibian species (Steen et al., 2010).

Reptiles - The effects of silvicultural treatments on reptiles have been mixed, often exhibiting no discernable effect. Despite inconclusive studies, development of heterogeneous canopies, with numerous gaps enabling light to reach the forest floor, enhances thermoregulation opportunities for reptiles. Herpetofauna (reptiles and amphibians) may exhibit different regional responses to silviculture. Similarly, species-specific response to silviculture may result in species responding positively, negatively, or not at all (Russell et al., 2004). Thus, more research is needed on the effects of thinning and retained structural elements on reptiles and amphibians (Jones et al., 2009; Verschuyl et al., 2011).

Birds: The intensity of harvest, otherwise stated as the magnitude of retention, influences species composition of bird communities. More canopy retention favors retention of mature-forest species, whereas more intense harvest tends to favor early-successional species and forest generalist species (Schieck et al., 2000). In northern hardwood forests, retention of, 20 m^2 ha^{-1} basal area maintained habitat for mature-forest birds yet afforded habitat for birds using early-successional habitat (Homes and Pitt, 2007). Similarly, in South American hardwood forests, combined dispersed and aggregated retention permitted colonization by early successional birds yet retained species characteristic of old-growth forests within retained aggregates (Lencinas et al., 2009). In Tasmanian eucalypt forest, long-term, aggregated retention harvests better sustained mature forest bird communities, post-harvest, compared with clearcut or dispersed retention harvests (Lefort and Grove, 2009). In young, conifer-dominated stands, thinning promotes diversity of breeding birds — a variety of thinning intensities and patterns, ranging from no thinning to widely spaced residual trees, will maximize avian diversity at the landscape scale and provide structural diversity within and among stands (Hagar et al., 2004). In southern pine forests, bird abundance and richness were positively related to volume of coarse woody debris and density of snags (Jones et al., 2009). In Midwestern oak-hickory forests, thinning harvest and prescribed fire increased avian nest survival (Streby and Miles, 2010). However, responses to variable retention harvests are species specific and temporally dynamic: Response of some species is immediate but short-lived, whereas other species exhibit a deferred (maybe several years post-treatment) but long-lasting response (Hagar and Friesen, 2009, Twedt and Somershoe, 2009).

Bats – Many bat species avoid spatial clutter: Thus bats tend to be more abundant in forests with open structure (harvested or old-growth) compared to closed-structured mid-successional forest (Loeb and O'keefe, 2006; Patriquin and Barclay, 2003; Menzel et al., 2005).

Forest structure appears more important than forest composition for foraging bats (Loeb and O'Keefe, 2006). Increased species and structural diversity of woody species, including providing broadleaf trees and shrubs in corridors and surrounding water features, tend to enhance foraging opportunities for bats. Conversely, forest type (or tree species) may be an important determinant of roosting location or behavior (Barclay and Kurta, 2007; Perry et al., 2007). Specifically, roost trees of bats are generally tall with large diameters and are located in stands with open canopies and high snag densities (Kalcounis-Rüppell et al., 2005). Compared to trees used by foliage-roosting bats, cavity-roosting bats use trees within stands that have more open canopies and trees that are closer to water than are random trees (Kalcounis-Rüppell et al., 2005).

Deer – Within landscapes, decreased road density and lessening of associated traffic reduces the negative impacts of disturbance. Silviculture should promote structurally complex, uneven-aged stands, that include forest openings (1 – 20 ha), and provide structural heterogeneity within and among stands (Nelson et al., 2008). Resulting habitat should provide understory forage and cover while retaining species diversity of trees.

Bear – Habitat selection is largely influenced by food abundance (Costello and Sage, 1994). A diversity of tree and shrub species producing hard mast (acorns and nuts) as well as soft mast (berries and fruits) is beneficial. Thinning, group selection, or patch cuts should be used to promote regeneration and recruitment of mast producing species, as well to increase understory food production, escape cover, and bedding areas. Care should be exercised to retain some large trees within each stand and to protect potential den trees during harvest.

Small Mammals – Silviculture that retains legacy structures, variable-density thinning, and management for increased forest decadence combined to support 3 species of squirrel in Douglas-fir forests (Carey, 2000). In southwestern conifer forests, thinning and burning treatments had positive effects on most small mammals. Even so, effects of silviculture on small mammals are species-specific, such that a positive response in abundance of one species may be offset by negative response in abundance of another species.

Effective strategies to achieve habitat for different species across spatial and temporal scales should include developing: 1) measurable objectives, 2) integrated conservation goals and silvicultural prescriptions, 3) clear and practical guidelines, effective training, and communication programs, and 4) a monitoring and an adaptive management process to evaluate and improve results (Munks et al., 2009).

3.1 Desired landscape conditions

Landscape conditions deemed suitable for priority species are highly dependent upon which species have been designated as priority species within the landscape under consideration. Furthermore, even after priority species have been designated, determining the nature and extent of desired landscape conditions have relatively little empirical justification (Moilanen, 1999). Even so, various methods have been employed to evaluate the appropriate landscape area and context for priority species.

A relatively simple, 6-step approach was put forward to identify the appropriate landscapes for forest bird conservation in the Mississippi Alluvial Valley: 1) establish priority species, 2) establish habitat priorities, 3) identify habitat requirements for priority species, 4) determine the extent and location of extant habitat, 5) set site-specific habitat goals, and 6) establish metapopulations goals (Mueller et al., 2000). A variation of this method was used to characterize priority of lands for forest restoration within the Mississippi Alluvial Valley and thereby delineate 107 discrete landscape units that were deemed capable of supporting viable populations (assumed to be ≥500 pairs) of priority silvicolous birds (Twedt et al., 2006; Fig. 4a).

Building upon this model, the Lower Mississippi Valley Joint Venture Forest Resource Conservation Working Group (Wilson et al., 2007) quantified desired forest conditions within these landscapes as:

1. >70% forest habitat, with large contiguous forest areas preferred;
2. 70-95% of forest area actively managed via silviculture intended to encourage desired stand conditions;
3. 35-50% of forest should meet desired forest conditions at any point in time, (Recognizing that habitat conditions are dynamic, silvicultural treatments should target conditions that yield extended temporal duration of desired stand conditions);
4. ≤10% of forest should be in regeneration harvests (where >80% of overstory is removed) that are >3 ha in area;
5. ~5% of area should be in shrub-scrub (thamnic woody vegetation) habitat, but this may including early seral forest stages; and
6. 5-30% of forest area should be passively managed as wilderness, natural areas, or set-aside areas that are not subjected to silvicultural manipulation.

A further refinement of this method has been used within the West Gulf Coastal Plain and Ouachita Mountains Ecoregion to characterize landscape requirements of birds reliant on open-canopy, mature pine forests (Keister et al., 2011). The first steps were again to identify priority species and define suitable habitats for priority species. However, area requirements for each of these priority species were determined by assessing the minimum territory size or home range of breeding pairs. Connectivity among territories of appropriate size was assumed to be related to the likely dispersal distance of each priority species. The minimum viable population size was estimated for each species (Hanski et al., 1996). These species-specific characteristics were used to evaluate existing landscape suitability for priority species. The sum of the total area of all habitats that were capable of supporting a breeding pair (assuming silvicultural management would yield suitable stand conditions) and that were joined by virtue of being within dispersal distance of other suitable habitat was used to evaluate landscapes. Landscapes were deemed suitable when their total areas were sufficient to support a minimum viable population of the species: Non-suitable landscapes were characterized with regard to their suitability based on the proportion of a minimum viable population that could be supported (Fig. 4b-d). Desired landscape conditions for multiple species were then jointly considered (Fig. 4, right).

3.2 Desired site conditions

Desired site conditions are dependent upon which species have been designated as priority species. Even so, as identified above, there are commonalities among stand characteristics that have been found to benefit many species and species groups. Prescribed wildlife forestry silvicultural practices can induce disturbance within forests and thereby stimulate development of desired structural conditions. Specific needs to be addressed when prescribing management actions include: 1) development and maintenance of structural (vertical and horizontal) heterogeneity, 2) achieving and retaining site appropriate tree species diversity, 3) maintaining an appropriate [sufficient yet acceptable] level of decadence, and 4) providing adequate reproduction to ensure sustainable habitat conditions and maintain future management options (Fig. 5).

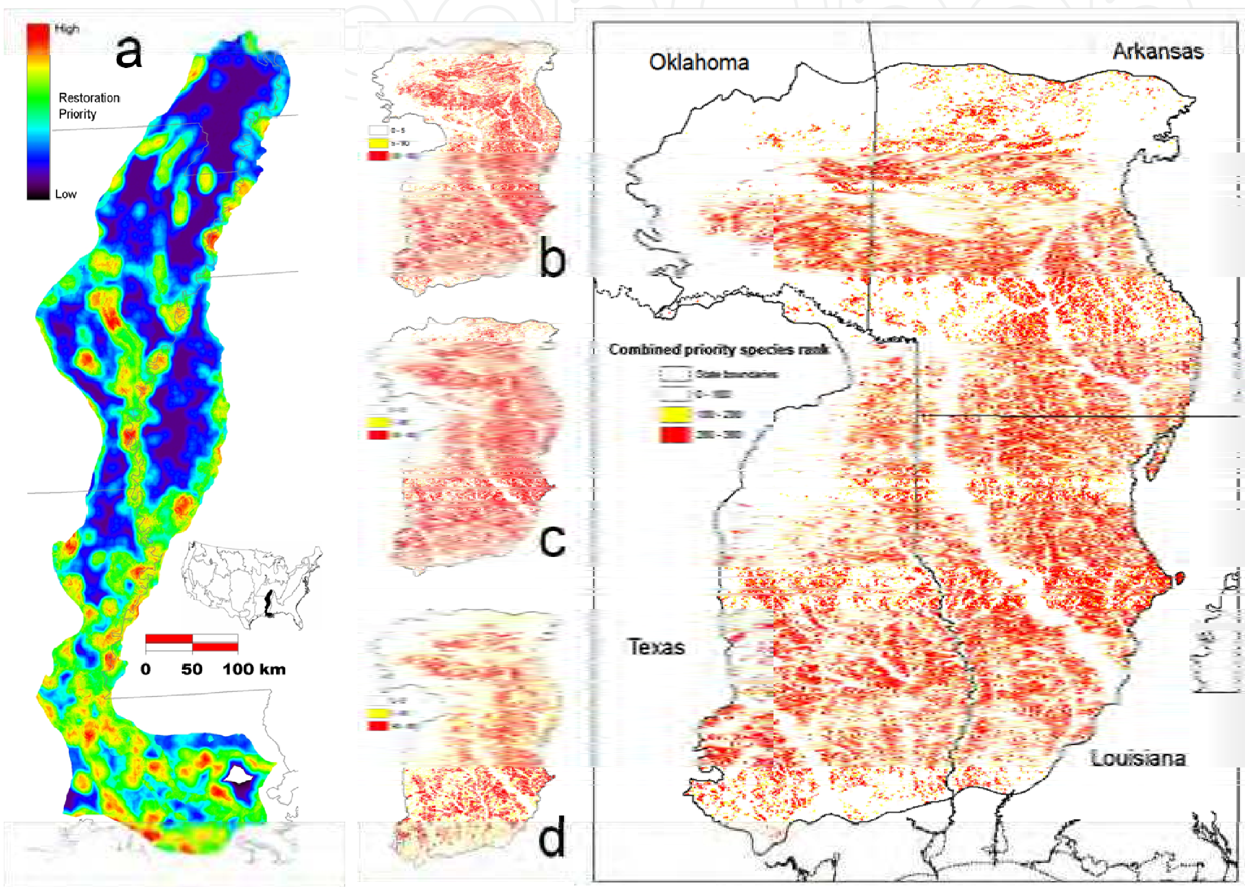

Fig. 4. Landscapes identified for priority birds based on forest restoration (a) in the Mississippi Alluvial Valley (Twedt et al. 2006) and on proportion of minimum viable population supported for Bachman's sparrow (b), brown-headed nuthatch (c), and red-cockaded woodpecker (d) within the West Gulf Coastal Plain (Keister et al. 2011).

Maintaining or enhancing diversity of species – A diversity of flora, in the canopy, mid-story, and understory, buffers fluctuations (annual, seasonal, and temporal) in phenology, productivity, susceptibility, and merchantability of forests, although this is not universally applicable to canopy species (e.g., longleaf pine stand canopies may be predominately one species). Because diversity of fruiting species affords temporal and spatial availability of fruits, and because fruit use by wildlife in temperate forests is substantial, with fruits being consumed primarily during winter (McCarty et al., 2002), maintaining and enhancing diversity of fruit bearing species should be encouraged. Moreover, a variety of fruits provide alternative foods in the event of mast crop failure of other species. Similarly, different plants host different caterpillar (larval Lepidoptera) species, some of which have species-specific relationships. Because butterfly and moth larvae are consumed by many wildlife species, especially birds, maintaining a diversity of trees and other flora within forest stands extends the temporal availability and increases the diversity of these insects (Hagar, 2004, Twedt and Best, 2004). In addition, forests with diverse species compositions are less vulnerable to catastrophic effects of disease and insects. Indeed, recent detrimental oak mortality in the Ozark Mountains Ecoregion has been attributed, in part, to the preponderance of oaks within these forests (Riggins et al. 2009). Similarly, species-specificity of many diseases and insects (e.g. chestnut blight [*Cryphonectria parasitica*] impact on American chestnut [*Castanea dentate*] or emerald ash borer [*Agrilus planipennis*] infestation of ash species [*Fraxinus* spp.]) provides argument for the maintenance of forest diversity to ameliorate the potentially catastrophic effects of regional outbreaks of disease or insect pests.

Fig. 5. Forest structure observed during summer (left) and winter (right) within bottomland hardwood forests circa 4 years after variable-retention, wildlife-forestry based silvicultural treatments (bottom) and on untreated control stands (top).

Finally, our naïve perception of the value of "undesirable species" is likely insufficient to comprehend the value of these species within the ecosystem. Therefore, preferential retention or diminution of native species may have unintended detrimental consequences (Lockhart 2004). For example, although the presence of piñon pine (*Pinus edulis*) is among the most important habitat features for many birds in piñon–juniper forests, the favored (86%) location of nests in juniper (*Juniperus osteosperma*) suggests that managers should avoid preferential thinning of juniper within these forests (Francis et al., 2011).

Increased structural heterogeneity (horizontal and vertical) – More structure generally provides a greater number of habitat niches for occupancy by different wildlife species, thereby increasing species richness, which may include priority species. Managers must, however, be cautious of excessive application of silviculture intended to promote heterogeneity as these excesses may promote what could be viewed as 'homogeneity' of this habitat structure at a more dispersed scale. As different intensity of silvicultural treatment result in different stand complexity, silvicultural decisions made at each stage of stand development affect forest structure (Table 2).

Lower Basal Area – Thinning canopies has a positive or neutral effect on diversity and abundance of most taxa, albeit intensity and biophysical setting influence wildlife response (Verschuyl et al., 2011). In general, lower basal areas are associated with increased density of understory vegetation which adds to structural diversity, provides cover for escape, thermoregulation, and nesting or bedding. Moreover patches of dense understory enhance forage opportunities for species that browse grasses, herbs, or seedlings, species that glean insects from leaves, and frugivores.

Large, old, decadent trees - These features tend to be especially characteristic of old-growth-like forest conditions. As such, these characteristics are difficult to achieve given historical forest management where short rotation lengthen and harvest of economically mature trees limit availability of these features. Large cavity trees are used as den sites by bears, as well as other meso-mammalian (e.g., martens, fishers, raccoons, porcupines, weasels) and larger avian species (e.g., woodpeckers, owls, mergansers, and ducks). Similarly, dominant emergent trees provide perches and nesting platforms for large raptors (e.g., eagles, hawks, and kites). Although avian excavators (e.g., woodpeckers) are the primary cavity producers in North America, producing 77% of nesting cavities, this is not the case globally (≤26%) where most cavity formation results from damage and decay (Cockle et al., 2011). Thus, cavity-using communities are highly dependent upon maintaining decadent trees within forest stands. As such, the presence of large, decadent trees may be essential for occupancy of stands by many of these large fauna.

Abundant standing snags and downed woody debris – Diversity and abundance of birds and biomass of invertebrates are positively associated with the volume of downed coarse woody debris and snags (Riffell et al., 2011). In unmanaged oak and oak-beech forests, 25% of dead wood was standing, whereas 75% was downed (Vanderkerkhove et al., 2009). Snags (and other decadent trees, such as those with heart rot), are characteristically exploited by primary-cavity excavators (e.g., woodpeckers) as well as those species that forage on saprophytic insects. Excavated cavities are subsequently used by myriad secondary-cavity using species. Lack of snags or other decadent trees may restrict this entire suite of cavity using species (Cockle et al. 2011).

Providing sufficient and suitable regeneration – As successional changes in forest species composition are often beyond human life-spans, the need for sufficient and suitable regeneration of canopy trees is often neglected. However, within the concept of wildlife forestry, regeneration of canopy species is ongoing (generally not a single event – as in even-aged forest management). Thus, ensuring sufficient regeneration of marketable trees, and thereby enhancing the long-term merchantability of forest stands, is imperative if desired habitat conditions for priority wildlife species are to be sustained through repeated, prescribed, silvicultural treatments. Notably, where maintaining shade-intolerant species within future generations is deemed desirable for anticipated management options, silviculturally induced gaps (patch cuts or group selections) should be of sufficient area to allow regeneration and development of these shade-intolerant species.

Treatment	Increasing forest diversity, structure, and complexity →		
Regeneration harvest	Clearcut	Legacy retention; dispersed or aggregated	Wildlife forestry; variable retention with canopy gaps
Restoration planting	Monoculture	Monoculture with supplemental natural reproduction	Mixture of species; hard and soft mast; shade tolerant and intolerant
Stand modification (TSI)	Herbicide removal of understory and midstory	Partial removal of competitors	Heterogeneous retention and removal of understory competitors
Thinning	Systematic single species retention	Multi-species retention	Heterogeneous retention and thinning; underrepresented species preferably retained

Table 2. Effects of wildlife forestry and other silviculture on stand structure (expanded from Carey, 2003b).

Although not specially referring to wildlife forestry, Carey (2006) succinctly encapsulated the holistic approach of wildlife forestry as - *"Management … of forest development and landscape dynamics is more likely to be successful in maintaining ecosystem and landscape function than just providing select structural elements in stands and select structural stages in landscapes, as is often suggested for conservation."*

3.3 Regional examples of desired stand conditions

Bottomland hardwood forests - A preponderance of closed canopy, second-growth forests with relatively homogeneous structure prompted recommendations for increased area of open canopied forests with greater structural diversity and more understory vegetation development (Wilson et al., 2007). Basal area should be reduced to 14-16 m^2 ha^{-1} with ≥25% of the basal area approaching biological maturity (i.e., in older age classes). Forest canopy cover should be 60%-70% with at least 5 stems ha^{-1} being canopy dominant trees - emergent canopies preferred. Understory vegetation should be robust yet patchily distributed with 25%-40% cover. Density of snags ≥25 cm diameter at breast height (dbh) should be >15 snags ha^{-1} or have a basal area >0.9 m^2 ha^{-1}. Volume of coarse woody debris should exceed 14 m^3 ha^{-1} and advanced reproduction should be present on 30%-40% of the stand (Table 3).

Northwestern U.S. coniferous forests - Bird species richness and abundance are positively related to proportion of broadleaf forest, from 1% to 25% canopy cover, within coniferous dominated landscapes. Thus, it is import to maintain or restore broadleaf vegetation in these coniferous dominated stands (Betts et al., 2010). Desired stand conditions reflect a structure similar to that of old-growth forest conditions (Cissel et al., 2006). Multiple tree species, representing multiple age cohorts, should occupy stands and this mix should include at least 1 shade tolerant species. Large diameter (>125 cm dbh) conifers should be present at densities of 5-15 stems ha^{-1}. At least half of the 20-30 snags ha^{-1} should be >60 cm dbh and a third of coarse woody debris should be of large (>60 cm) diameter (Table 3).

Southeastern U.S. pines **-** Historically open-canopied pine forests were found throughout the southeastern United States. These open forests were maintained by frequent fires. Prescribed burning, complimented with thinning of pine canopies and herbicide treatments of encroaching hardwoods can restore these historic conditions. Open canopy conditions with an abundant and floristically diverse understory increase species richness of priority open pine associated amphibians (Guyer, and Bailey, 1993, Steen et al., 2010). Similarly, abundance of endangered gopher tortoises (*Gopherus polyphemus*) and red-cockaded woodpecker (*Picoides borealis*) respond positively to prescribed fire within open pine stands. Desired stand conditions include open (40-60%) canopies that are dominated by large (≥35 cm dbh) pines. These large pines should account for ≥ 4.5 m^2 ha^{-1} of a total basal area of 11 – 16 m^2 ha^{-1}. Mid-story should be sparse (<15%) with very limited hardwoods (<5%). Ground cover and understory should be lush (>80% cover) and comprised predominately of grasses and forbs. At least 7 snags ha^{-1} should be present. Relatively frequent fire (≤3 year interval) is likely required to maintain these desired conditions (Table 3).

4. Economic considerations

Wildlife forestry's primary intent is to provide suitable habitat conditions for priority wildlife. Even so, silvicultural practices that require long-term commitments or repeated expenditures may not be undertaken and thus, may not provide desired results. Indeed, silvicultural prescriptions intended to enhance wildlife habitat must be cognizant of their expense and their long-term effect on future merchantability of the stand. With that caveat, wildlife forestry silviculture may have both positive and negative economic effects.

A positive impact of most wildlife forestry practices is a reduction in wildfire hazards. Indeed, managing tree density and species composition with prophylactic silvicultural treatments that include thinning, surface fuel treatments, and prescribed fire reduce the risk of wildfire (Graham et al., 1999).

Negative economic factors include wounding of potentially merchantable trees that remain within stands after silvicultural treatments, as these wounds may result in future economic loss due to mortality or reduction in quality of timber (Hennon and DeMars, 1997). Thus, harvest prescriptions should account for this possibility and provide recommendations to reduce unintended damage to residual trees. On the other hand, from a wildlife use perspective, basal wounds to large retained trees have the potential to increase the number of decant large trees within a stand.

Another negative economic impact of wildlife silviculture may be successional changes in species composition. As noted for ensuring adequate tree regeneration within stands, managers should be aware of unintended shifts in species composition as a consequence of prescribed wildlife silviculture, usually due to an increased presence of shade-tolerant species. Therefore, if shade-intolerant species are intended to be a part of future forest canopies, silvicultural treatments must ensure their regeneration and development (Twedt and Somershoe, in press).

All forests are subject to windthrow (toppling of live standing trees due to wind), although its severity is influenced by wind speed, climate, topography, hydrology, and soils (Ruel, 1995): Toppled trees are present in mature unharvested forests as well as along the edges of clearcuts. Even so, windthrow may increase after partial harvest silvicultural treatments. More retention within a stand, however, tends to lessen the severity of windthrow (Franklin et al., 1997). Windthrow can also be mitigated through judicious silviculture, as some species are more susceptible to windthrow, possibly due to differences in form. Trees with more extensive crown structure or shallow, poorly developed roots are more likely to be toppled by wind (Beese, 2001). Retained, sound, dominant trees are less subject to windthrow than decadent or subdominant trees. The dispersion, orientation, and shape of retention also influences susceptibility to windthrow, with tear-drop shaped, aggregated clumps, oriented with prevailing winds better able to withstand wind damage (Franklin et al., 1997). Even so, small (1.5 ha) patch cuts may be least vulnerable to wind (Beese, 2001).

Stand feature	Bottomland hardwood (Wilson et al., 2007)	Longleaf pine (Bragg, 2004; East Gulf Coastal Plain Joint Venture, unpublished)	Pacific northwest conifers (Cissel et al. 2006)	Young conifers in northern pacific rainforest Altman and Hagar, 2007)
Basal area	14 – 16 m² ha⁻¹	11 – 16 m² ha⁻¹	9 – 27 m² ha⁻¹	
Size class	≥25% of BA approaching biological maturity	>4 m² ha⁻¹, ≥35 cm dbh	several tree species of varying size and age; large emergent trees	large conifer trees
Density	>5 dominant ha⁻¹	12 – 30 pines ha⁻¹, >76 cm dbh	5 – 15 ha⁻¹, >125 cm dbh conifers; 60 – 85 ha⁻¹, 38-76 cm dbh; 250 – 500 ha⁻¹ <38 cm dbh	<500 ha⁻¹; thin to promote growth
Canopy cover	60 – 70%	40 – 60% (≤5% hardwood) Patchy	multi-layered canopies	variation in overstory achieved via silviculture, low % canopy cover to encourage understory
Midstory	25 – 40%	≤15% (≤5% hardwood) Open	open space among the lower branches of canopy	retain and protect old shrubs and shrub patches
Ground cover	25 – 40%	>80%		variation in understory associated with variable canopy
Snags & stressed trees	>15 ha⁻¹, ≥25 cm dbh; or ≥5 ha⁻¹, ≥ 51 cm dbh; or >0.9 m2 ha⁻¹, >25 cm dbh	≥7 (12-25) ha⁻¹, red heart; 10 – 50% cull in retained trees	20 – 30 ha⁻¹ >25 cm dbh; 50% > 60 cm dbh; cavities in standing trees	large
Coarse woody debris	≥14 m3 ha⁻¹	21 – 54 m3 ha⁻¹ (includes snags)	275 linear m >25 cm diameter; 33% > 60 cm dbh	retain, protect, and recruit large diameter CWD
Reproduction	30 – 40% of area with advanced reproduction	10% of area with advanced reproduction		encourage regeneration and retention of a diversity of species
Other	>10 visible cavities ha⁻¹; 1 den tree (4 ha)⁻¹	fire return ≤3 year	≥2 species (≥1 shade-tolerant); ≥2 age cohorts; >150 years old	retain and promote deciduous trees and shrubs

Table 3. Described and quantified desired site (stand) conditions that are deemed to provide enhanced habitat for priority wildlife species in different forest types and seral stages.

There is little basis for economic comparisons of wildlife forestry and other, traditional, silvicultural systems. Wildlife forestry may provide sustained revenues from exploitive use of wildlife, as well as from periodic harvest of forest products. But even without income from wildlife, little economic loss was reported from variable retention silviculture compared to even-aged, shelterwood cuts in *Nothofagus pumilio* forests (Pastur et al., 2009). Similarly, simulation models spanning 300 years that compared economic returns and ecological benefits within Pacific northwest forests being managed for biodiversity with forests being managed for timber production, and incorporating narrow riparian reserves (i.e., set asides), found significantly greater ecological benefits associated with biodiversity management (Carey et al.,1999). Concurrently, the economic cost of achieving those benefits was relatively modest, with 18% loss in net present value (NPV), only 4% loss if riparian protection was similar to that afforded within the biodiversity management model, and fully a 13% gain in NPV when newly enacted state laws for riparian protection were enforced (Carey, 2003a). More notably, under management for biodiversity, tree quality improved, decadal revenues increased by 150%, forest-based employment quadrupled, and manufacturing diversified and became more reliant on high quality products and value added manufacturing (Carey, 2003a, Carey et al., 1999, Lippke et al., 1996).

5. Restoration

If successfully implemented, wildlife forestry is self-sustaining, such that reforestation (e.g., artificial regeneration or stand regeneration) is rare. Even so, appropriate practices are increasingly being sought in conjunction with forest restoration that better enable attainment of desired forest conditions. For example, decades of bottomland afforestation, wherein agricultural lands are being restored to forested wetlands, has provided valuable insight regarding appropriate species and planting densities (Wilson et al., 2007). Management practices similar to those employed for wildlife forestry have also been used to restore longleaf pine forests on sites converted to forests dominated by other species. Similarly, within production-oriented plantation forests management alternatives are sought that will enhance biodiversity and improve wildlife habitat, yet minimally compromise product output.

Recommendations for restoration and mid-rotation management have included planting or maintaining species mixtures to ensure stand diversity and improve forest product quality (Twedt and Best, 2004, Lockhart et al. 2008). Mixed species planting of native species are favored over monocultures of exotic species. Some legacy trees (live or snags) and understory vegetation should be retained at harvest through a second rotation. Site-preparation should reflect natural disturbances and conserve coarse woody debris. Thinning earlier in the rotation and increasing rotation length also increase structural diversity (Hartley, 2002; Kerr, 1999). Finally, for some forest types, maintaining herbaceous or early succession habitat for a longer period provides benefits to priority bird species (Altman and Hagar, 2007).

6. Evaluating results of management actions

Quantitatively defined landscape conditions and desired stand conditions have been identified for only a few ecoregional landscapes and only a few forest types within these landscapes. Wildlife biologists, foresters, and conservation planners must develop a shared vision regarding what each perceives as the desired habitat condition within forests. In the landscape context, these conditions need not be the same for all forests, nor will they be identical for all priority species. Research and monitoring will be required to evaluate species responses to different ranges of habitat conditions perceived as desirable. Judgments may be needed when priority species exhibit conflicting responses to what are perceived as desired conditions.

At present we have little empirical data regarding the range of economic returns from wildlife silviculture relative to traditional production-oriented silviculture. Appropriate measures of economic returns, including an evaluation of the long-term sustainably of different management options, are needed. In addition, we have assessed the faunal responses of relatively few species to wildlife forestry silviculture. Future efforts must assess comparable responses of less-studied priority species and species groups as well as evaluate appropriate demographic responses of all species.

To determine if prescribed management actions elicit intended responses from priority species, monitoring is required. Monitoring should target specific management actions and evaluate spatial and temporal responses. Silvicultural prescriptions should consider incorporation of the principles of adaptive management during their development, implementation, and evaluation (Fig. 1). Feedback from such efforts can provide an assessment of the adequacy and sustainability of wildlife forestry silviculture. Science based knowledge of the results of these management practices is crucial to their long-term success, as "*Conservation is paved with good intentions which prove to be futile, or even dangerous, because they are devoid of critical understanding either of the land, or of economic land use*" (Leopold, 1953).

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