# Forest Wildlife Management

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3.1 Introduction

Just like a collection of buildings devoid of human inhabitants does not make a city, a framework of trees alone does not make a forest ecosystem. Whereas the plant world is mostly sedentary, silent, and full of utilitarian hues of green for photosynthesis, wildlife enliven forests with movement, sound, and color. Wildlife heavily influence forests via behaviors, including pollination, seed dispersal, and herbivory. Importantly, proper management of forest wildlife is contingent on a sound understanding of forest wildlife ecology. In this chapter, we focus on the underlying relationships between plants and animals in forested systems and describe approaches to forest wildlife management.

3.2 Primer in Forest Wildlife–Habitat Relationships

Forests provide habitat for many wildlife species and consequently are among the most biologically diverse terrestrial ecosystems. Habitat can be defined as the set of resources—food, cover, and water—necessary to support an animal population through space and time (Hall et al. 1997). By this definition, habitat must meet the needs of not only individuals but also entire populations of wildlife species.

An animal’s fitness—the ability to survive and reproduce—is influenced by its ability to exploit habitat components to gain and maintain energy. Food—Energy flow through a forest begins with solar energy from the sun, which is photosynthesized by plants to form a major component of the bottom of the forest food pyramid. Some plant species and parts are more digestible, and thus higher-quality food, than others. In fact, forests mostly contain lignin and cellulose, both of which are indigestible to most wildlife species. After herbivores consume digestible plant material or predators consume herbivores, some energy is lost through metabolism and in their urine and feces; the remainder is considered net energy. Cover—Once wildlife gain net energy from food, they must exploit cover to conserve it. Specifically, net energy from food is lost as heat, and the remainder is considered available energy—the true currency of physiological condition. Endotherms (e.g., bird and mammals) generate their own body heat and require relatively constant body temperatures for favorable metabolic function. Heat loss in endotherms thus can be equated to the energy spent maintaining a constant body temperature. Individual survival and successful reproduction is predominantly driven by energy gains from food and exploitation of cover for energy conservation (i.e., reduction of heat loss), but access to water and nutrients also plays a role (McComb 2008). Ectotherms (e.g., reptiles and amphibians) absorb their body heat from the surrounding environment. Ectotherms’ fitness is mainly driven by energy gains from food, exploitation of cover to adjust ambient temperature and exposure, and in some cases, availability of water for thermoregulation and reproduction (Forsman 2000). Other than energy conservation, wildlife also use cover for nesting, raising young, and evading predators (Figure 3.1).

The spectrum of habitat conditions in which a species occurs depends on the range of food and cover resources it can exploit. Habitat generalists are able to exploit a wide range of habitat conditions and use a broad suite of food and cover resources.
These species typically occur over large geographic ranges and inhabit a variety of forest types. For example, the white-tailed deer (*Odocoileus virginianus*) is a generalist species that occurs in boreal, temperate, and tropical forests throughout the western hemisphere (Branan et al. 1985; Russell et al. 2001). On the other hand, habitat specialists are adapted to a narrow range of food and cover resources, selecting unique conditions and specific vegetation types. As such, these species often have a small geographic range and may be restricted to a single community type. For example, the red-cockaded woodpecker (*Picoides borealis*) is a habitat specialist that requires live conifer trees and reduced hard-wood under- and midstories for foraging and nesting (Walters 1991), conditions historically characteristic of fire-mediated pine (*Pinus* spp.) ecosystems of the southeastern United States (Figure 3.2).

Wildlife select habitat hierarchically based on its apparent ability to meet their food and cover requirements (Johnson 1980). The first-order selection is conceptualized on a regional scale and is represented by the overall distribution of a species. For example, wildlife species adapted to tropical forest are unlikely to occur simultaneously in boreal forests. However, the first-order selection can vary seasonally, as is the case for neotropical migrant birds that occur in temperate or boreal forests during the breeding season and tropical forests during winter (Rappole 1995). The second-order selection is represented by home range establishment—the area an animal typically uses throughout the year. Larger species have larger energy demands and thus require larger home ranges for food gathering relative to smaller species (McNab 1963). Additionally, home range size often varies with habitat quality (e.g., a superabundance of food may equate to a smaller home range). The third-order selection refers to the core-use area within an animal’s home range, often centered on a nesting or denning site. Finally, the fourth-order selection includes specific habitat elements within an animal’s core-use area (e.g., shrub for a bird’s nest, a particular log harboring a salamander).
3.3 Basic Principles of Forest Wildlife Ecology

Forest wildlife management involves consideration for five, often interrelated, basic principles: (1) disturbance, (2) succession, (3) structure (vegetation and deadwood), (4) composition, and (5) landscape ecology. In the following section, we describe how each of these ecological principles shapes forest wildlife communities. Forest wildlife typically respond to these factors in the same manner among boreal, temperate, and tropical forests. As such, the concepts we describe in this section can be applied to forests around the globe.

3.3.1 Disturbances

An undisturbed forest reaches a climax state, and the trees comprising it eventually senesc and die naturally. However, nature is chaos; forests historically were shaped by natural disturbances (e.g., windthrows, disease, insect outbreaks, hurricanes, floods, fires; White 1979; Pickett et al. 1989). Indeed, natural disturbance is the primary driver of the development of forest structure and function (Attiwill 1994). Importantly, disturbance triggers the process of forest succession. Succession influences plant community composition and structure and thereby has profound effects on wildlife habitat (see Section 3.3.2).

Plants and wildlife have evolved with disturbance types endemic to the forest ecosystems they inhabit and are adapted to the size and shape, severity, and frequency at which
they occur. **Size**—The size of a disturbance can influence which wildlife species remain or recolonize after a disturbance (Rosenberg and Raphael 1986). Large-scale disturbances create large swaths of early-successional vegetation rich in newly available food and cover resources. For example, following large-scale, severe forest fires in the western United States, woodpeckers and ungulates can be attracted by the influx of snags for nesting and increase in new vegetation growth as forage, respectively (Pearson et al. 1995). In many forest landscapes, there are far more small, natural disturbances (e.g., resulting from wind, fire, treefall gaps) than large ones. As such, a matrix of openings created through natural disturbance and undisturbed areas are often present.

Wildlife respond to variations in the size of openings and resultant habitat conditions created by disturbances. For instance, white-footed mice (*Peromyscus leucopus*) increased in abundance in small openings, while deer mice (*Peromyscus maniculatus*) only occurred in larger openings (Buckner and Shure 1985). Similarly, breeding bird habitat use in bottomland forests increased with increasing size of forest openings for some bird species (Moorman and Guynn 2001). The shape of an area created by disturbance may also have implications on wildlife use of openings, particularly in reference to edge effects (see Section 3.3.6). **Severity**—The severity of a disturbance directly impacts the amount of organic material (alive or dead) remaining following a disturbance. Disturbances such as crown fires or volcanoes can completely replace a stand and destroy most legacy material, resulting in the onset of primary succession. Conversely, removal of only a few trees from the canopy results in a relative influx of legacy material (e.g., downed wood in a treefall gap). Legacy material such as deadwood provides important food and cover resources for some wildlife species immediately following a disturbance (see Section 3.3.4). **Frequency**—The frequency of disturbance—(i.e., return interval)—influences the floral and faunal composition of forests as well as the amount of organic material present over time. The frequency of disturbance varies among forest types and by the type of disturbance. For example, fire return intervals may range from 2 to 5 years in some savanna systems (Harrell et al. 2001) to 300 to 400 years in northern coniferous forests (Wimberly et al. 2000). More frequent, severe disturbances may delay or preclude forest development, whereas less frequent and severe disturbances may facilitate the establishment of more complex vertical vegetation structure in a stand (Franklin et al. 2002). In turn, the vegetative structure created by short and long return intervals, respectively, impacts the types of wildlife that remain or recolonize a stand following disturbance (see Section 3.3.3).

### 3.3.2 Succession

Ecological succession describes the gradual and orderly replacement of plant communities in forest ecosystems over time. The somewhat predictable changes in vegetation following a disturbance form the basis for the concept of ecological succession (Palmer et al. 1997). Conceptually, the age of a forest stand is a reasonable index of its successional stage. In a hypothetical forest system, early-successional stages (i.e., young forests) consist of a lush herbaceous layer, some developing shrub/scrub understory vegetation, and little canopy cover. Plants in early-successional stages are typically shade-intolerant species that require full sun to grow. As the stand ages, vegetation on the forest floor (e.g., herbs, shrubs) is outcompeted (shaded out) by fast-growing, shade-intolerant overstory trees, eventually resulting in relatively sparse understory vegetation cover. As time goes on, shade-tolerant tree species continue to grow beneath the canopy of shade-intolerant trees, eventually outcompeting them to become the
dominant trees in the overstory of old forests (i.e., climax forest; Bazzaz 1975). Another way of conceptualizing forest succession is to break the process down into four general physiognomic stages: (1) stand initiation, (2) stem exclusion, (3) understory reinitiation, and (4) old growth (Oliver 1980). Wildlife diversity and composition differ among successional stages. Traditionally, wildlife diversity was thought to increase through succession and reach its peak in climax forests because this terminal successional stage provides the greatest accumulation of biomass and thus prevalence of niches (Odum 1969). On the other hand, Thomas et al. (1979) demonstrated that wildlife diversity was high in early- and late-successional stands and lowest in the stem exclusion stage. Indeed, more recent theory suggests that early-successional stages can support high species diversity comprising opportunists and early-successional specialists, which often use abundant organic legacy material and post-disturbance plant communities (Swanson et al. 2010). Wildlife responses to succession may be thought of as coinciding with the cycle in which a series of plants and thus wildlife resources appear and disappear in between disturbances (Hunter 1990). In other words, the wildlife species present during a particular successional stage depends on the structural resources (i.e., vegetation, deadwood) at that stage (also see Sections 3.3.3 and 3.3.4). Early-successional stages typically are characterized by bare ground, abundant downed wood, and lack of canopy cover immediately following disturbance, followed by the onset of lush herbaceous cover. At this early stage, early-successional wildlife species dependent on bare ground (e.g., mourning dove—granivory) or herbaceous vegetation (e.g., small mammals—granivory and cover) are most abundant. Conversely, canopy-dwelling species are absent during the early-successional stages because the mature trees upon which they rely have yet to grow. During mid-successional stages, deadwood (i.e., snags, downed wood) is scarce (see U-shaped chronosequence in Section 3.3.4). As such, cavity-nesting wildlife (e.g., woodpeckers) are far rarer in mid-successional stages relative to early- and late-successional stages, which have more exploitable deadwood due to disturbance and senescence of old trees, respectively. Adequate resources may be available to some wildlife species, particularly habitat generalists, through multiple successional stages. On the other hand, habitat specialists including early- or late-successional specialist species tend to be more polarized in their association with particular successional stages.

3.3.3 Structure: Vegetation

Vegetation structure in a forest can be characterized on both the vertical and horizontal plane and is tightly linked to wildlife habitat use. Vertical structure is a measure of the stratification of forest layers starting with ground cover, spanning through the shrub and midstory layers, up to the canopy layer. Ground and shrub cover are especially important to wildlife that cannot fly or climb, because these are the layers in forests that are most accessible to them. Wildlife that can fly (e.g., birds, insects) or climb (e.g., primates, some herpetofauna) can access all forest layers and demonstrate differentiation of niches—the roles or habitats species occupy in the function and structure of ecosystems—among these layers. Niche differentiation can be achieved by vertical segregation of species among forest layers, which reduces spatially explicit competition for resources. For instance, birds are well known to segregate vertically while feeding to reduce competition for food (Cody 1974). In general, more complex vertical structure (i.e., more layers) in forests leads to more niches available to wildlife (MacArthur and MacArthur 1961; Hunter 1990). However, some wildlife species thrive in forests with little vertical stratification, and many fire-regulated forest ecosystems maintain relatively high species diversity despite the reduction or absence of shrub and midstory layers (Figure 3.3).
Horizontal patchiness refers to the distribution of vegetation along the horizontal plane of a forest. Whereas a forest stand with complex vertical structure may contain every forest layer along the vertical plane, within-stand horizontal patchiness pertains to forest layers independently existing along the horizontal plane (e.g., ground cover without canopy cover). Within-stand patchiness naturally occurs after canopy closure when forest openings are created (e.g., treefall gaps) and can be created or enhanced through forest management practices such as thinning and group selection (see Sections 3.4.3 and 3.4.1.2, respectively). At the landscape level, horizontal patchiness can be achieved by interspersing even-aged stands of various ages and structural conditions with more lightly managed stands and riparian corridors (see Section 3.3.6).

3.3.4 Structure: Deadwood

When trees die due to competition, disease, insect outbreaks, lighting strikes, or senescence, they become snags (i.e., standing deadwood) and ultimately fall to the ground to become downed wood (Figure 3.4). Snags and downed wood provide valuable food and cover for a plethora of wildlife (Harmon et al. 1986). Wildlife, including primary cavity users (wildlife capable of excavating cavities in trees) like woodpeckers and secondary cavity users (wildlife reliant on primary cavity users for cavity production) like flying squirrels, use snags for nesting, roosting, and feeding. Downed wood is predominantly used by ground-dwelling wildlife for cover, escape from predators, travel corridors, and in the case of amphibians, its presumably favorable microclimate (Lanham and Guynn 1996; Loeb 1996; Whiles and Grubaugh 1996). Additionally, vertebrate and invertebrate predators alike feed on abundant arthropods harbored by downed wood (Lohr et al. 2002; Ulyshen and Hanula 2009; Castro and Wise 2010). In general, the volume of downed wood on the forest floor of a stand follows a U-shaped chronosequence (Harmon et al. 1986, Figure 3.5).
FIGURE 3.4
(See color insert.) Downed wood is an important habitat component for many ground-dwelling, forest wildlife species. (Photo by Chris Moorman, used with permission.)

FIGURE 3.5
An interpretation of the U-shaped chronosequence (Harmon et al. 1986) illustrating downed wood dynamics in forests. Volume of downed wood (represented by the “U-shaped” line) is high immediately following a disturbance, decreases with stand age as it decays, and slowly increases as mature trees senesce and die. (Schematic by Steve Grodsky.)
Immediately following a disturbance, the volume of downed wood is great. Over time, the downed wood decays, leading to a decrease in its volume. A slight but steady increase in downed wood volume then follows as mature trees senesce and die. Both the role and dynamics of downed wood vary regionally. For example, downed wood in the southeastern United States historically was consumed by frequent fires and decays rapidly due to damp, hot climactic conditions (Moorman et al. 1999). As such, many wildlife species in the southeastern United States have adapted to forest floors with little available downed wood. On the other hand, wildlife in cooler, less disturbed areas of the United States like the Pacific Northwest are adapted to historically high volumes of downed wood on the forest floor (Bunnell et al. 1999).

### 3.3.5 Composition

Plant species composition influences the availability of resources to wildlife. Wildlife diversity generally increases with increasing plant diversity within a stand (also see Section 3.3.6). A mixture of plant species leads to more complex vertical structure, which in turn has positive implications for niche partitioning among wildlife (MacArthur and MacArthur 1961). High plant diversity specifically increases the availability of food and cover. For example, in temperate forests, a mixture of coniferous (e.g., *Pinus* spp.) and deciduous (e.g., *Quercus* spp.) trees may help balance winter cover and food availability to wildlife throughout the year. Conifers are particularly important as winter cover for ungulates (Moen 1973) and as winter roosting sites for eastern wild turkey (Kilpatrick et al. 1988) in colder climates. Additionally, high plant diversity helps to ensure that food resources are available to wildlife year-round, especially in the absence of primary food sources.

Coniferous and deciduous forests differ in the wildlife species they support. The foliage of coniferous trees is less palatable than that of deciduous trees because it is rich in distasteful compounds like terpenes (Longhurst et al. 1968). The decreased palatability of coniferous foliage has ecological implications beginning at the bottom of the food chain, with fewer invertebrates and herbivores eating conifer litter and foliage, respectively, and consequently fewer predators that eat herbivores (Kennedy and Southwood 1984). Deciduous forests tend to have more complex vertical structure than those that are coniferous because the growth form of coniferous trees (i.e., dense foliage) shades out understory plants. For the reasons described earlier, deciduous forests are often considered to be more biologically diverse than coniferous forests. However, many coniferous forests support unique communities (Wiens 1975) and contribute to diversity at larger spatial scales.

### 3.3.6 Landscape Considerations

**Spatial heterogeneity**—Wildlife diversity at the landscape level is affected by the arrangement (i.e., interspersion and juxtaposition) of vegetation types and ages on the landscape. In general, dispersal of many successional stages, forest types, and stand sizes across the landscape helps to maximize landscape-level wildlife diversity. Many wildlife species require multiple forest types or seral stages. Although more mobile species (e.g., birds) can easily access different forest types or stand ages, less mobile species may require some level of connectivity to exploit varied habitat conditions across the landscape (see Connectivity).

**Edges and fragmentation**—An edge is where two land cover types (e.g., ages, land uses) meet. Aldo Leopold (1933) described the “edge effect” after noticing wildlife, particularly game animals, increased in diversity and abundance near edges. Along edges, wildlife have simultaneous access to two or more vegetation types or successional stages. Additionally,
vegetation structure along edges is often more complex because of the reduced canopy cover. An ecotone is the transition zone where environmental conditions of two adjacent land cover types overlap to create a unique set of habitat conditions. Abrupt edges describe narrow ecotones, whereas soft edges describe broad ecotones. Wildlife generally respond more favorably to soft edges than abrupt edges because the transition zone between the two land cover types is wider and thus likely to have greater structural and compositional diversity. Additionally, small and irregularly shaped stands have more edge than larger and more uniformly shaped stands. Importantly, edges between forest and nonforested land uses (e.g., urban, agriculture) differ from edges between different forest types or ages. With the former, true forest fragmentation occurs, which more often leads to negative edge effects (Wade et al. 2003). For instance, edges between forests and nonforested land uses may attract avian nest predators and brood parasites (e.g., brown-headed cowbirds \( \textit{Molothrus ater} \)), thereby lowering nest success of songbirds in forest patches (Patton 1994).

**Connectivity**—Animals may need to move among habitat patches in search of food and cover, to access seasonal life history requirements such as breeding or overwintering sites, to disperse and establish territories, and to maintain genetic connections with adjacent populations. In landscapes where habitat patches are fragmented, connectivity that facilitates the movement of less mobile wildlife from one patch to others may be important (Haddad et al. 2003). For example, linear rain forest remnants have been shown to be particularly important for providing habitat connectivity for arboreal mammals in tropical forests (Laurence and Laurence 1999). However, corridors designed to increase connectivity have also been shown not to facilitate movement between habitat patches for some wildlife (e.g., salamanders—Rosenberg et al. 1998). Instead, less mobile species may be conserved by increasing landscape permeability, which is a measure of how easily an animal can move through a landscape. Permeability varies with a species’ dispersal ability, the degree of habitat specialization the species exhibits, and the arrangement of habitat across the landscape. At the landscape scale, permeability can be increased simply by increasing the percent cover of habitat. Understanding the ecology of target species for which connectivity is a concern is important when considering corridor design (e.g., width, length, connectivity—Lindenmayer and Nix 1993) and permeability (i.e., what is habitat for the target species, what habitat characteristics facilitate movement).

### 3.3.7 Wetlands

Wetlands typically are characterized by presence of hydric soils and plant species adapted to those soils. Wetlands can have high plant diversity, complex vegetative structure, and a diversity of wildlife foods, including arthropods, fruits, and nuts. Examples of wetlands in forested environments include river bottoms, stream corridors, and depressional ponds. Wetlands are especially important for amphibians, insects, and reptiles that rely on water for one or more parts of their life cycles (Batzer and Wissinger 1996; Semlitsch and Bodie 2003). Specifically, many forest amphibians rely on ephemeral pools to breed because they hold water only temporarily and thus do not harbor fish predators that typically consume their eggs (DiMauro and Hunter 2002). Waterfowl and wading birds also rely on wetlands for food and cover, often year-round (Isola et al. 2000). In drier regions, wetlands may provide important sources of drinking water for wildlife.

Given their high value to wildlife, wetland management is an important consideration during forest harvest activities. Buffers parallel to rivers and streams or surrounding small, isolated wetlands established prior to timber harvest typically are effective means by which to reduce potentially negative impacts on wetlands during timber harvest (Semlitsch and
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Bodie 2003). These forested buffers provide shade to maintain water temperatures and help prevent sediment deposition during timber harvest. On the other hand, buffers also may reduce the potential for disturbances emulating those that occurred naturally (e.g., fires, hurricanes). Buffer specifications vary based on target wildlife species, stream width, harvest intensity, slope, forest ecosystem, and the type of natural and anthropogenic disturbances (Russell et al. 2002, 2005). In the United States, each state has developed Best Management Practices (BMPs) for forest management that center on protecting water quality during forest harvest activities. BMPs are tailored for each states’ local conditions and, when implemented properly, are effective means by which to manage and protect forest wetlands.

3.4 Forest Wildlife Management

The central thesis of game management is this: game can be restored by the creative use of the same tools which have heretofore destroyed it—axe, plow, cow, fire, and gun.

Aldo Leopold, Game Management (1933)

Aldo Leopold, a forester and wildlife conservationist, postulated that people have a right to use and manage forests wisely and the responsibility of doing so in a way that recognizes the intrinsic value people share with other species and the ecosystems that contain them (Leopold 1933). By this definition, Leopold captured the true essence of forest wildlife management; he identified that the conservation of forest products and wildlife could be simultaneously achieved. Indeed, forest management, when appropriately implemented, often provides the most practical means by which to manage forest wildlife habitat.

Forest management, especially timber harvest, alters succession and changes plant structure and composition, which in turn affects wildlife habitat. The ecological changes that accompany forest management in some part simulate the effects of natural disturbance on forest ecosystems, and therefore may affect wildlife similarly. Importantly, long-standing natural disturbance regimes have been altered by humans through means such as wildfire suppression and urbanization. As such, the natural disturbance regimes to which many wildlife species adapted to over millennia are far less common in today’s modern world.

As described earlier, different wildlife species associate with different successional stages. Hence, successional changes brought upon by timber harvest create or enhance habitat for some species while simultaneously diminishing habitat suitability for others. In other words, there are always “winners” and “losers.” For example, large-scale removal of trees in a mature stand via clearcutting shifts the vegetation community from late successional to early successional, in turn benefitting wildlife adapted to the conditions therein. Concurrently, late-successional wildlife, especially canopy dwellers, largely will be eliminated in the stand until the canopy redevelops. Because habitat requirements vary among wildlife species, providing habitat for all wildlife species at small spatial and temporal scales is implausible. Therefore, forest wildlife managers should identify focal wildlife species or communities before initiating forest management practices and account for local variations in wildlife–habitat relationships or habitat planning for wildlife must be conducted at large spatial scales (i.e., thousands of hectares). Table 3.1 includes responses of selected wildlife to changes in habitat structure that may occur following forest management practices described in the following sections.

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<table>
<thead>
<tr>
<th>Management Practice</th>
<th>Postmanagement Vegetation Structure</th>
<th>Availability of Deadwood</th>
<th>Percent of Stand Influenced</th>
<th>“Winners”</th>
<th>“Losers”</th>
<th>Citations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Even-aged harvest (clearcut)</td>
<td>Dense herbaceous and shrub/scrub cover; canopy cover absent</td>
<td>High (downed wood); low (snags)</td>
<td>High</td>
<td>Early-successional species requiring large disturbances; downed wood-assOCIated species; granivores; herbivores</td>
<td>Canopy-dwelling species; species requiring a cool, moist microclimate; leaf-litter obligates</td>
<td>Kirkland (1990), deMaynadier and Hunter (1995), Annand and Thompson (1997), Niemelä (1997), Moorman et al. (2011)</td>
</tr>
<tr>
<td>Even-aged harvest (shelterwood/seed tree)</td>
<td>Dense herbaceous cover; moderately dense shrub/scrub cover; low canopy cover</td>
<td>High</td>
<td>High</td>
<td>Similar to clearcut, although retained canopy benefits overstory species and hard-mast consumers</td>
<td>Similar to clearcut, although retained canopy lessens effect on canopy-dwelling species and leaf-litter obligates</td>
<td>Rosenvald and Löhmus (2008)</td>
</tr>
<tr>
<td>Uneven-aged harvest</td>
<td>Patchy herbaceous and shrub/scrub cover; high canopy cover</td>
<td>Moderate (especially if burned)</td>
<td>Low–moderate</td>
<td>Gap specialists; hard-mast consumers; species using both mature and young forest</td>
<td>Early-successional species requiring large disturbances</td>
<td>Lempckert (1999), Moorman and Guynn (2001), Bouget and Duelli (2004)</td>
</tr>
<tr>
<td>Herbicide site prep (after clearcut)</td>
<td>Low to moderate herbaceous cover; low shrub/scrub cover; canopy cover absent</td>
<td>High</td>
<td>High</td>
<td>Downed wood-associated species; early-successional species requiring large disturbances</td>
<td>Herbivores and granivores if reduced herbaceous cover; leaf-litter obligates; shrub-nesting birds if reduced shrub cover; species requiring a cool, moist microclimate</td>
<td>Guynn et al. (2004), Miller and Miller (2004), Miller and Wigley (2004)</td>
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<tr>
<td>Mechanical site prep (after clearcut)</td>
<td>Moderate herbaceous cover; low shrub/scrub cover; canopy cover absent</td>
<td>Low</td>
<td>High</td>
<td>Early-successional species requiring large disturbances; granivores and herbivores (relative to herbicide site prep)</td>
<td>Downed wood-associated species; fossorial species (e.g., invertebrates, snakes); leaf-litter obligates; species requiring a cool, moist microclimate; shrub-nesting birds</td>
<td>O’Connell and Miller (1994)</td>
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<tr>
<th>Management Practice</th>
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<th>Availability of Deadwood</th>
<th>Percent of Stand Influenced</th>
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<th>Citations&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thinning</td>
<td>Moderately dense herbaceous and shrub/scrub cover; moderate canopy cover</td>
<td>Moderate</td>
<td>High</td>
<td>Species benefiting from increased vertical structure (e.g., birds) and understory cover (e.g., shrub-nesting birds, some small mammals)</td>
<td>Species requiring a cool, moist microclimate</td>
<td>Verschuyl et al. (2011)</td>
</tr>
<tr>
<td>Prescribed burning (high intensity)</td>
<td>Dense herbaceous cover; moderately dense shrub/scrub cover; moderate canopy cover due to some overstory mortality</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Cavity nesters (if overstory mortality occurs); grazing herbivores; species associated with herbaceous cover; species requiring hot, dry microclimate (e.g., lizards); understory species</td>
<td>Species requiring a cool, moist microclimate; leaf-litter obligates</td>
<td>deMaynadier and Hunter (1995), Russell et al. (1999), Moorman et al. (2011), Schowalter (2012)</td>
</tr>
<tr>
<td>Prescribed burning (low intensity)</td>
<td>Moderately dense herbaceous, shrub/scrub, and canopy cover</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Browsing herbivores; shrub-nesting birds</td>
<td>Leaf-litter obligates</td>
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</tbody>
</table>

<sup>a</sup> There are always exceptions to the “winners” and “losers” wildlife groups following management. Furthermore, generalist species may be present following most management practices, whereas specialist species may show more unique responses to management practices or variations within a management practice.

<sup>b</sup> Refers to vegetation conditions within the first 5 years after management practice is implemented. Vegetation structure changes over time through succession; see Section 3.3.2.

<sup>c</sup> This list of citations is not exhaustive.

<sup>d</sup> Effects on vegetation and deadwood are for scenarios with no site preparation. For the effects of site preparation, see herbicide site preparation and mechanical site preparation.

<sup>e</sup> Effects of site preparation, especially with herbicides, on wildlife are relatively short-lived (e.g., <3 years posttreatment; Guynn et al. 2004). Mechanical and herbicide site preparation often are concurrently implemented. “Winners” and “losers” include clearcut effects.
3.4.1 Final Harvest

Forest harvest and regeneration are achieved using one of two silvicultural systems—
even aged or uneven aged. Even-aged systems regenerate an entire stand at once and con-
tain trees of either one or two age classes. Single-aged stands are created by clearcutting,
while two-aged stands are created when some overstory trees are retained during harvest
(i.e., shelterwood or seed tree regeneration harvests). Uneven-aged systems create stands
with three or more age classes of trees using frequent, repeated harvests of scattered
individual trees (single-tree selection harvests) or small patches of trees (group selection
harvests). Even-aged stands of timber usually are dominated by shade-intolerant plant
species. Meanwhile, uneven-aged stands commonly promote the regeneration of shade-
tolerant and intermediate shade-tolerant plants.

Habitat conditions created by even- and uneven-aged systems vary both spatially and
temporally. Even-aged harvests typically yield large areas of early-successional vegeta-
tion that persist for several years. Once even-aged stands of timber mature, they offer
large areas of homogeneous (i.e., relatively consistent within-stand vegetative structure)
late-successional vegetation (i.e., mature trees). Dispersed even-aged harvests may lead to
increased habitat diversity at the landscape level because a variety of successional stages
may be present among stands. Meanwhile, uneven-aged harvests often yield heteroge-
neous within-stand habitat conditions, particularly by promoting complex vertical vegeta-
tion structure within and adjacent to harvest openings, mimicking small-scale natural
 canopy disturbance created by treefall.

3.4.1.1 Even-Aged Systems and Wildlife

Wildlife response to implementation of even-aged systems largely is influenced
by the reduction of forest canopy cover and the release of understory vegetation.
Following clearcutting, commercial overstory typically is removed, and canopy-
dwelling wildlife are reduced or eliminated. For example, clearcutting may result
in nearly complete replacement of mature forest bird species with early-successional
bird species (Conner and Adkisson 1977; King and DeGraaf 2000). However, individ-
ual canopy trees may be retained in some managed clearcuts (i.e., clearcut with
reserves), particularly as unharvested stringers and streamside management zones.
Reductions in late-successional bird species can be short-lived, especially where
forest regeneration is rapid following harvest. Additionally, mature forest birds,
including some canopy dwellers, use young forest (i.e., 5–10 years following even-
aged harvests) during the postfledging period (Champlin et al. 2009; Chandler et al.
2012; Porneluzi et al. 2014). Whereas clearcutting removes most of the canopy, seed
tree and shelterwood regeneration harvests maintain some live overstory inde-
dependent of BMPs, thereby retaining denser canopy structure and, in some cases,
continued overstory mast production (e.g., acorns). Seed tree and shelterwood cuts
provide vegetative structure in both the understory and canopy. Hence, they provide
food and cover for wildlife that use these forest layers, including disturbance-phase
insects and birds (Rosenvald and Lõhmus 2008). Even-aged timber harvests main-
tain lush herbaceous layers for several years postharvest, providing habitat for a
plethora of early-successional wildlife species. The herbaceous vegetation provides
abundant forage and seeds. Indeed, many herbivorous and granivorous wildlife
are associated with early-successional vegetation, whereas most insectivores are
associated with late-successional stages (Constantine et al. 2004). Dense understory
in young even-aged stands provides nesting and brooding cover for gallinaceous birds, such as wild turkey (Meleagris gallopavo; Dickson 2001) and northern bobwhite (Colinus virginianus; Burger 2001). Herbaceous groundcover also provides important escape cover for small animals, including sparrows (family Emberizidae) (Lima 1993) and small mammals, among a myriad of other wildlife species. As woody shrubs and sprouting hardwoods develop, other wildlife species colonize recently harvested even-aged stands. For instance, shrub-nesting birds are especially adapted to nesting in harvested timber stands several years after harvest (Brawn et al. 2001). Even-aged stands are also characterized by a hotter, drier environment on the forest floor because of the greatly reduced canopy cover, which may be unfavorable for some amphibians prone to desiccation, such as salamanders, but favorable for ectothermic wildlife (e.g., reptiles) because hotter conditions facilitate thermoregulation (Moorman et al. 2011).

### 3.4.1.2 Uneven-Aged Systems and Wildlife

Uneven-aged regeneration harvests promote a mosaic of small openings within stands of older trees. Given the generally small size of openings, wildlife species adapted to large-scale disturbances typically are excluded. For example, some early-successional bird species (e.g., prairie warbler [Dendroica discolor]) did not colonize small, experimental gaps created via group and single-tree selection (Robinson and Robinson 1999; Moorman and Guynn 2001). However, creating larger group selection openings (>0.5 ha) may increase use by early-successional wildlife species, as has been seen with birds in the southeastern United States (Moorman and Guynn 2001). Lemckert (1999) found that selective logging had little impact on forest-dwelling frogs, which may be related to the relatively low impact of small disturbances brought upon by uneven-aged management. Within-stand forage (e.g., hard mast) and cover (e.g., early-successional herbaceous layer) are interspersed in uneven-aged stands. For example, white-tailed deer may bed and forage in openings and eat acorns in mature forest adjacent to openings all within the same stand.

### 3.4.2 Regeneration and Site Preparation

Stand regeneration following forest harvest can be accomplished either through planting or naturally via stump sprouts or seed from residual trees or the seed bank. Shelterwood and seed tree regeneration harvests in even-aged systems and single-tree selection and group selection regeneration harvests in uneven-aged systems usually depend on natural regeneration. Planting typically follows clearcutting. Prior to planting, sites may be prepared with heavy machinery, prescribed burning, herbicides, or a combination of these practices (the latter two are covered in Sections 3.4.4 and 3.4.5, respectively). Specifically, site preparation is implemented to help control vegetation that may suppress planted crop tree seedlings and is categorized as either mechanical (e.g., shearing, burning, disking, bedding) or chemical (i.e., herbicides). O’Connell and Miller (1994) found that small mammal capture rates were greater in mechanically than in chemically prepared sites, indicating that mechanical site preparation alone may be less detrimental to small mammal populations in some cases. However, soils may be disturbed during mechanical site preparation, which may in turn impact fossorial (underground-dwelling) wildlife species (Moorman et al. 2011). The intensity of site preparation (e.g., chemical only, mechanical only, chemical and mechanical) may influence wildlife response.
However, Lane et al. (2011a) showed that the addition of chemical site preparation had little effect on birds beyond planted pine spacing, indicating that avian abundance was not proportional to site preparation intensity. Winter bird abundance has been shown to decrease with increased mechanical site preparation intensity (Hanberry et al. 2013a), but site preparation intensity had no effect on small mammal abundance (Hanberry et al. 2013b). Planting seedlings at high stocking rates with little spacing facilitates rapid canopy closure, reducing the time early-successional vegetation is available to wildlife. However, wider spacing between planted trees allows sunlight to the forest floor and extends early-successional stages, thus increasing early-successional vegetation available as wildlife forage and cover (e.g., for white-tailed deer—Halls 1973).

3.4.3 Thinning

Once canopy closure occurs in midsuccession, understory vegetation is shaded out, and vertical vegetation structure declines (Figure 3.6a). Thinning reduces the number of overstory trees, which can simultaneously improve growing conditions for residual crop trees through decreased intraspecific competition (Barbour et al. 1997) and increase sunlight penetration to the forest floor, promoting understory development (Bailey and Tappenier 1998). Thinning during early stand development (i.e., precommercial thinning) helps maintain forest herbaceous layers and extends early-successional stages. Intensified thinning typically results in increased understory vegetation cover as light reaching the forest floor increases with greater reductions in canopy cover (Thomas et al. 1999, Figure 3.6b).

Thinning increases structural complexity in forests and may improve habitat for many wildlife species (Hayes et al. 1997). Indeed, a recent meta-analysis on the effects of forest thinning found that forest thinning treatments had generally positive or neutral effects on biodiversity (Verschuyl et al. 2011). As described earlier, wildlife diversity tends to increase with vertical vegetation structure because the presence of multiple layers in the vertical plane of forests provides a high number of niches (MacArthur and MacArthur 1961). Indeed, short-term increases in species richness and densities of songbirds have been recorded following experimental thinning (DeGraaf et al. 1991; Hagar et al. 2004). Similarly, some small mammal populations positively respond to forest thinning (Converse et al. 2006a, b). Effects of thinning may become immeasurable as time passes since initial thinning, as has been seen with bird communities in temperate rain forests 20 years after thinning (Matsuoka et al. 2012) and insect communities in plantations 3 years after thinning (Taki et al. 2010). Thinning is often most effective as forest wildlife management tool when used in conjunction with prescribed burning and herbicides (see Iglay et al. 2010, 2014; also see Section 3.4.4).

3.4.4 Prescribed Burning

Plant and thereby animal communities around the globe have been shaped by fire as a natural or anthropogenic disturbance, making prescribed burning a valuable forest wildlife management tool in historically fire-mediated systems. Historical fire frequencies have helped form the plant communities in traditionally fire-mediated systems present today (Frost 1998). In turn, many plant species within these communities are dependent on fire for reproduction. For example, several pine (Pinus) species exhibit serotiny—the ability to retain seeds in the plant canopy (Lamont et al. 1991)—and their cones remain closed until exposed to high temperatures such as those resulting from fire (Gauthier et al. 1996).
Fire also promotes understory plant communities by removing leaf litter, exposing mineral soil, and releasing nutrients for seedbed preparation (Russell et al. 1999).

As a management tool, prescribed burning typically reduces forest fuels and diminishes the potential for uncharacteristic wildfire (Agee and Skinner 2005), suppresses competing vegetation, encourages regeneration of certain plant species on the forest floor, reverts

FIGURE 3.6
(See color insert.) (a) An unthinned forest stand with a closed canopy and shaded understory that lacks a vertical vegetation structure and (b) a thinned stand with a more diverse vertical vegetative structure due to increased light penetration to the forest floor. (Photos by Chris Moorman, used with permission.)
successional growth, and, in many cases, ultimately improves wildlife habitat (Pyne et al. 1996, Figure 3.7). Effects of prescribed burning on plant communities vary with frequency, intensity, and seasonality (i.e., growing season versus dormant season). For example, intense, hot fires reduce leaf litter and kill overstory trees, whereas lower-intensity fires have minimal effects on overstory trees but may reduce leaf litter and shrub and midstory vegetation in the short term. In general, more frequent fires during the growing season promote herbaceous plant communities, whereas less frequent fires during the dormant season promote woody plant communities. Wildlife species shift concomitantly with vegetative response to fire seasonality, frequency, and intensity. For example, reptile abundance increases following hot fires that result in canopy mortality and more open, hot conditions on the forest floor (Matthews et al. 2010). Moreover, fire may consume snags and downed wood, thereby reducing these habitat elements for some wildlife; however, new snags resulting from fire reduce net snag loss and are in turn used by cavity-nesting birds (Bagne et al. 2008). Similarly, Hanula et al. (2012) found that frequent fires had little effect on the availability of downed wood and consequently abundance of termites. Prescribed burning can result in direct mortality of wildlife, especially when fires are intense as in the case of many wildfires. Yet, given the coevolution of wildlife species and fire, wildlife are well adapted to its occurrence on the landscape. Although some wildlife may perish during fires, most species exhibit behavioral adaptations that allow them to survive. Larger animals and birds may escape fire by running and flying away, respectively, whereas amphibians, reptiles, and small mammals often remain underground or seek cover under rocks or downed wood (Russell et al. 1999).

Following prescribed burning, wildlife forage may be more prolific, nutritious, and palatable (Harris and Covington 1983; Masters et al. 1993). For example, post-fire nutrition in the diets of ungulates has been shown to be elevated for bighorn sheep and mule deer (Hobbs and Spowart 1984) and white-tailed deer (Lashley et al. 2011). Similarly, prescribed
burning may promote fruit production (Penman and Penman 2010) and encourage the growth of seed-producing herbaceous plants, which in turn may increase wildlife forage availability. However, effects on fruit and seed production vary depending on the season and frequency of prescribed fire. For example, fire return intervals less than 3 years may greatly limit the production of understory soft mast (Lashley 2014). Many insects that provide important forage for vertebrate and invertebrate wildlife alike are favored by the flush of understory plant growth following fire, especially in open forest (Schowalter 2012).

Twentieth century fire suppression practices have significantly modified historic fire regimes throughout the world (Ryan et al. 2013). Aversion to fire management mainly stems from sociopolitical constraints including public acceptance and risk aversion. Excluding fire from historically fire-mediated systems changes ecosystem structure, composition, and integrity across multiple scales (Varner et al. 2005). The fate of prescribed fire as a management tool largely relies on increasing public awareness of its positive benefits through education and public involvement (Ryan et al. 2013).

### 3.4.5 Herbicide Application

Technological advancements in the chemical industry coupled with some managers’ inability to use prescribed fire have led to the widespread use of herbicides in forest management, especially in plantations. Herbicides are often used to release crop trees from competing vegetation in young plantations and may also be used later in the rotation to suppress understory or midstory competitors. Forest herbicides typically target biochemical pathways unique to plants and thus have few acute toxic effects on wildlife (Tatum 2004). Rather, herbicides most often directly affect wildlife by changing vegetation structure and composition (Miller and Wigley 2004). Most research studies suggest that the impact of herbicides on plant communities is relatively short-lived (e.g., <3 years; Miller and Miller 2004). Similarly, most negative effects of herbicide application on wildlife are temporary (Guynn et al. 2004). Herbicide application to recent clearcuts has been shown to reduce vegetation complexity, resulting in the temporary decline of some species of songbirds, for instance (Santillo et al. 1989). However, some studies have shown that herbicide use has no appreciable effect on wildlife species or communities or, in some cases, positive effects via shifted successional trajectories and plant communities (Guynn et al. 2004). Indeed, many currently available herbicides are selective and, when applied, can favor plants beneficial to wildlife (e.g., fruit producers) while eliminating undesirable plant species (e.g., nonnative, invasive plants—Miller 2003). In forests where snags and downed wood are lacking, herbicides can be injected into live trees to artificially create snags (McComb and Rumsey 1983), which in turn increases structural complexity and habitat suitability for cavity-associated wildlife species.

Herbicides are useful for restoring potentially desirable open-habitat conditions and early-successional plant communities, especially when used in conjunction with prescribed fire or thinning. For example, herbicides have been used to remove the hardwood midstory in pine–grassland communities to enhance red-cockaded woodpecker habitat (Conner 1989). Maintenance of early-successional vegetation through herbicide applications may also improve forage availability for herbivores like white-tailed deer (Edwards et al. 2003) and vegetative structure for northern bobwhite (Jones and Chamberlain 2004).

Until recently, most studies pertained to the effects of single herbicides applied one time and focused on a relatively small window of time (Guynn et al. 2004; Iglay et al. 2010). Indeed, few studies have addressed long-term changes in successional trajectories following herbicide application (Mackinnon and Freedman 1993). Forest management may also
entail multiple applications of herbicides and simultaneous use of several herbicides (i.e., tank mixes—Miller and Miller 2004). Recent studies involving combinations of herbicides applied to regenerating clearcuts showed that these tank mixes had little effect on small mammal abundance (Hanberry et al. 2013b) or breeding birds (Lane et al. 2011a). In a concurrent study, Lane et al. (2011b) also found that tank mixes had short-lived (i.e., <4 year) effects on herbaceous vegetation but long-term effects on woody vegetation. Additionally, Tatum et al. (2012) documented no synergistic toxicity to aquatic forest wildlife from commonly used forestry herbicide tank mixes.

### 3.5 Case Studies

The following section consists of case studies that reinforce and apply principles of forest wildlife management covered in this chapter. These case studies also illustrate the pivotal role wildlife play as indicators to inform ecological forest management.

#### 3.5.1 Boreal Forests

**3.5.1.1 Palm Warblers as Indicators of Peatland Composition and Structure within Boreal Forests**

Palm warblers (*Dendroica palmarum*) are short-distance migratory birds that breed primarily in boreal forests of North America and winter in the southeastern United States and Caribbean region (Wilson 1996). Most palm warblers breed in Canada’s boreal peatlands (Calmé and Desrochers 1999), but the southern limit of the species’ breeding range includes scattered populations in the northern Great Lakes and New England regions of the United States (Wilson 1996; Cutright et al. 2006). Palm warblers are among the bird species most strongly and perhaps exclusively associated with boreal peatlands during the breeding season (Wilson 1996; Calmé et al. 2002; Lachance et al. 2005, Figure 3.8). Within these boreal forest landscapes, the peatlands used by palm warblers are often distributed as “islands” that are clearly distinguished from the surrounding upland forests in which they are embedded (Calmé and Desrochers 2000).

Specifically, breeding sites of this species are associated with muskegs or open bogs containing deep beds of sphagnum moss (*Sphagnum* spp.) and small copse of black spruce (*Picea mariana*) surrounded by open areas, a situation intermediate between open and closed canopy (Lachance et al. 2005; Cutright et al. 2006). Palm warblers typically nest on the ground but use trees within the copse for singing and surveillance (Welsh 1971). Zolkowski (2008) showed that palm warblers were more frequently encountered and more abundant in peatlands containing primarily conifer trees but with low amounts of overall overhead canopy, consistent with dense but scattered copse of conifers within otherwise open sites (Calmé and Desrochers 2000). Palm warblers were also associated with peatlands containing abundant moss cover and larger numbers of snags (Zolkowski 2008). Snags may provide additional singing perches and may also reflect the mature, open-canopy bogs used by palm warblers. Overall, palm warblers appear particularly sensitive to changes in the vegetative structure of peatlands that increase forest cover at the expense of open patches (Lachance et al. 2005). In addition, palm warbler presence appears to be strongly influenced by peatland area, and individuals may actively avoid small, isolated, or fragmented peatlands (Zolkowski 2008).
Accordingly, palm warblers may be an important indicator of avian habitat conditions within boreal forest peatlands (Calmé and Desrochers 2000; Lachance et al. 2005; Cutright et al. 2006). Afforestation is among the primary vegetative changes recently observed in North American peatlands, most likely in response to wetland drainage (Lachance et al. 2005). Because saturated conditions inhibit the production of commercially important tree species, large areas of peatlands within boreal forests have been drained to support commercial forestry operations (Turetsky and St. Louis 2006). In addition to direct alteration for commercial forestry, peatland ecosystems may be at risk of changes or loss from climate change (Weltzin et al. 2003). The actual effects of climate change on peatlands are unknown but potentially include increased densities of shrub and tree cover and decreased amounts of graminoid species (Weltzin et al. 2003). The frequency of large-scale wildfires has increased across the boreal forests of North America during the last 50 years, and fires are occurring later in the growing season (Kasischke and Turetsky 2006; Flannigan et al. 2009). These changes in fire frequency appear to be climate influenced (Flannigan et al. 2009) and are expected to significantly alter vegetation dynamics within boreal peatlands.

These or other changes in the vegetative composition and structure of peatlands certainly could be expected to significantly alter the distributions and habitat relationships of peatland-associated birds within boreal forests (Lachance et al. 2005). Because of their unique composition and structure, peatlands at lower latitudes often form “refugia” of boreal habitat surrounded by more temperate communities, thus supporting distinct avifaunas (Calmé et al. 2002). This is particularly true for peatlands at the southern extent of their distribution, where they support plant and animal species commonly found at more northern latitudes (Lachance et al. 2005). Populations of species that are currently at the low-latitude edge of their distributional ranges (e.g., Great Lakes and New England populations of palm warblers) may be among the first species to exhibit changes as a result of anthropomorphic alternations to boreal forest peatlands (Hampe and Petit 2005).
3.5.1.2 Invertebrate Biodiversity within Fennoscandian Boreal Forests

Boreal coniferous forest is the dominant biome in Finland and the Scandinavian Peninsula (Esseen et al. 1997). Fennoscandian forests are among the most intensively managed forests in the world, with less than 5% virgin forest remaining (Linnell et al. 2000). Most of these forests are clearcut on a 70–80-year rotation using mechanized harvesting and dense road networks (Linnell et al. 2000). Increasingly, postharvest woody debris and stumps are removed and used for bioenergy production (see Section 3.5.4.1; Siira-Pietikäinen and Haimi 2009). Regeneration is achieved either through artificial planting or through natural regeneration. According to Esseen et al. (1997), the most important ecosystem change in Fennoscandian boreal forests has been the replacement of natural fires with timber harvesting as the predominant disturbance regime. As a result of more than 100 years of fire suppression, early post-fire successional stands have become extremely rare (Esseen et al. 1997). In addition, fire suppression is contributing to the increasing dominance of spruce in previously mixed stands of pine, birch, and aspen (Esseen et al. 1997).

The combined effects of intensive timber harvest, removal of postharvest residue, and fire suppression have had substantial effects on the biodiversity of Fennoscandian boreal forests, including forest invertebrates. Modern forest management practices are considered a major force influencing the landscape-level composition of boreal forest invertebrate communities (Väisänen and Heliövaara 1994). Accordingly, numerous studies have evaluated the impacts of forest management practices on Fennoscandian boreal invertebrates (Esseen et al. 1997; Niemelä 1997; Niemelä et al. 2007; Paillet et al. 2010). For example, most studies of European forest-dwelling Coleoptera have been conducted in boreal forests (Paillet et al. 2010). Traditional methods of clear-cutting that do not incorporate structural retention (i.e., on-site retention of live and dead vegetation after harvest) have influenced the distribution and abundance of a large proportion of red-listed Fennoscandian forest invertebrates (Esseen et al. 1997; Niemelä 1997). Changes in forest microclimates after clearcutting can cause significant shifts in boreal invertebrate richness and abundance. The drier, warmer conditions on clearcut sites have been linked to the declines of several specialist species associated with spruce-dominated mires or swamp forests in late-successional, unmanaged forests, including carabid beetles, mollusks, and noctuid moths (Esseen et al. 1997; Niemelä 1997; Niemelä et al. 2007). Wood-inhabiting species associated with late-successional boreal forests in particular have experienced marked declines (Heliövaara and Väisänen 1984; Esseen et al. 1997). In contrast, several studies have documented greater richness and abundance of generalist, open-habitat, and disturbance-tolerant species carabid beetles, spiders, ants, and butterflies in logged stands when compared to unlogged forests (Niemelä 1997; Niemelä et al. 2007). Although invertebrate species diversity may increase after logging, these communities typically are different from those present in late-successional Fennoscandian forests (Niemelä 1997).

Invertebrate species dependent on snags and downed woody debris also have experienced significant declines in Fennoscandian boreal forests. For example, several studies have reported declines of saproxylic beetles in managed boreal forests when compared to unmanaged forests (Esseen et al. 1997; Niemelä et al. 2007; Paillet et al. 2010). Large logs and snags in different stages of decay are key habitat elements for these taxa (Paillet et al. 2010). However, these structures are almost completely lacking in Fennoscandian managed forests as a result of successive rotations of intensive fiber
removal and fire suppression (Hyvärinen et al. 2009). Additionally, some tree- and
snag-living species of beetles require open and dry conditions in early-successional
stages (Muona and Rutanen 1994). Historically, these early-successional conditions
were created by wildfires. Although clearcutting approximates some early-successional
conditions created by natural burning, residual live and dead trees traditionally are
removed during harvesting. Additionally, fire suppression has resulted in the declines
of many Fennoscandian invertebrates that depend on burned substrates (Muona and
Rutanen 1994; Niemelä et al. 1997; Hyvärinen et al. 2009). For example, in Swedish
boreal forests, Ahnlund and Lindhé (1992) detected 26 species of red-listed insects in
recently burned stands, 14 of which occurred only in these areas. Furthermore, the
burned sites exhibited unique insect faunas when compared to unburned clearcuts

Because of the significant reduction of late-successional forests on one hand and the
virtual disappearance of early-successional forests regenerated by fire on the other,
many specialist Fennoscandian invertebrates have experienced significant population
decrees and in some cases local extinctions (Esseen et al. 1997; Niemelä 1997;
Niemelä et al. 2007). To mitigate this situation, forest reserves have been advocated
and established across Fennoscandia with the purpose of maintaining invertebrates
and other taxa dependent on undisturbed late-successional forests (Esseen et al. 1997;
Niemelä 1997; Lundström et al. 2011). According to Niemelä (1997), sufficient unman-
aged forest must be reserved to protect specialist species and to provide sources for
recolonization of regenerating, managed forests. For example, some saproxylic beetles
require snags decayed by specific polypore fungi that occur only in late-successional
forests (Kaila et al. 1994; Niemelä 1997). However, forest reserves in Fennoscandia
are considered too small and unrepresentative of the range of forest conditions to
adequately maintain the biodiversity of boreal forests (Esseen et al. 1997; Niemelä
1997; Lundström et al. 2011). Forest reserves constitute only about 1% of the productive
forests of Norway and Sweden and approximately 2% of Finnish forests (Esseen et al.
1997; Lundström et al. 2011). Accordingly, the incorporation of silvicultural techniques
that more closely mimic natural disturbances into production forest management
is considered critical for the conservation of Fennoscandian invertebrate diversity
(Niemelä 1997; Hyvärinen et al. 2009; Siira-Pietikäinen and Haimi 2009; Lundström
et al. 2011). Specifically, the use of green-tree retention and prescribed burning in man-
aged forests have been suggested as means of more closely approximating structural
conditions associated with natural disturbances and providing habitat for specialist
invertebrate taxa in boreal forests (Hyvärinen et al. 2006, 2009; Siira-Pietikäinen and
Haimi 2009; Lundström et al. 2011). Although the results of some studies are equivocal
e.g., Siira-Pietikäinen and Haimi 2009), other studies indicate that the retention
of green trees within clearcuts, pre- and postharvest prescribed burning, and combi-
nations thereof can provide habitats for declining and specialist boreal invertebrates
(Hyvärinen et al. 2006, 2009). Important structural features that are almost completely
lacking in the managed boreal forests in Fennoscandia, such as deadwood or live
overstory trees within early-successional stands, are produced by green-tree retention
and the burning of harvested sites with retention trees (Hyvärinen et al. 2009). In the
short term, prescribed burning may temporarily decrease suitability for herbivore
invertebrates and those associated with leaf litter (Hyvärinen et al. 2009). However,
saproxylic and pyrophilous species that have declined the most from successive short
rotations in Fennoscandian forests appear to significantly benefit from these mea-
3.5.2 Temperate Forests

3.5.2.1 Multiscale Conservation Strategies and Bachman’s Sparrows

The flora and fauna associated with longleaf pine (*Pinus palustris*) forests comprise one of the most diverse communities in North America (Van Lear et al. 2005). Currently, this ecosystem occupies a mere 3%–5% of its historical range (Landers et al. 1995; Frost 2006), although it has increased in extent recently due to proactive conservation efforts. A historical longleaf pine forest experienced frequent low-intensity fire and was characterized by widely spaced overstory longleaf pine trees, scattered hardwood patches, and diverse understory vegetation (Frost 2006). Longleaf pine forests once dominated the Atlantic and Gulf Coastal Plains in the southeastern United States, interrupted only by rivers and scattered swamps, whereas today, these forests persist as isolated patches within a matrix of pasture, row crop agriculture, fire-suppressed pine plantations, and urban development. This fundamental shift in landscape context has important implications for the many plant and animal species that evolved in a landscape comprising vast, contiguous tracts of open-canopy longleaf pine forest, including Bachman’s Sparrow (*P. aestivalis*; Figure 3.9).

Bachman’s Sparrows select specific vegetation conditions that reflect fire-maintained forest stands, particularly the presence of a diverse herbaceous groundcover that results from an open overstory and frequent low-intensity fire. In fact, Bachman’s Sparrow is one of six surrogate species used by the U.S. Fish and Wildlife Service for strategic habitat conservation of longleaf pine forest at the landscape scale (Shelton 2014). The range of preferred conditions of Bachman’s Sparrows is so narrow that they abandon habitat patches after as little as 3 years without fire when grasses begin to form a dense thatch that can restrict movement along the ground (Brooks and Stouffer 2010; Jones et al. 2013), and less

![Bachman’s Sparrow](image-url)
fire-tolerant woody species begin to replace existing herbaceous vegetation (Engstrom et al. 1984; Dunning and Watts 1990; Rutledge and Conner 2002; Tucker et al. 2004).

Although local vegetation conditions, particularly the herbaceous groundcover, often are emphasized as the most critical aspects of the Bachman’s Sparrow habitat (Dunning and Watts 1990; Haggerty 1998), sparrow occurrence is also strongly influenced by the percent habitat in the surrounding landscape (Taillie et al. 2015). Patch isolation affects colonization of habitat patches by Bachman’s Sparrows, possibly due to poor dispersal through the matrix of non–longleaf pine land cover types (Dunning et al. 1995; Dunning and Kilgo 2000). Individual sparrows will abandon a patch either because it burned recently (Seaman and Krementz 2001) or because the lack of fire permitted unsuitable vegetation conditions to develop (Engstrom et al. 1984; Tucker et al. 2004), requiring potentially multiple dispersal events in a lifetime (Cox and Jones 2010). Isolation of a habitat patch may amplify the challenges associated with each of these dispersal events (Lampila et al. 2005). Hence, increased landscape connectivity will facilitate successful dispersal to previously unoccupied habitat (Dunning et al. 1995).

For these reasons, restoration of the longleaf pine ecosystem should involve both efforts to establish and maintain vegetation conditions that once characterized fire-maintained upland forest and larger-scale coordinated efforts focused on landscapes comprised of at least 20% habitat (i.e., open-canopy pine forest, including longleaf pine and other pine species, with a diverse herbaceous plant community). This is particularly important as restoration efforts continue to shift to private lands that typically are more fragmented than public lands in the eastern United States (Riitters et al. 2012). Specifically, private lands adjacent to large patches of forest managed for longleaf pine, such as those on many public lands, may serve to more efficiently conserve some species as such properties could still be functionally connected from the prospective of dispersing wildlife. Additionally, frequent burning is necessary to maintain a diverse groundcover layer and prevent the encroachment of woody vegetation (Glitzenstein and Streng 2003; Heuberger and Putz 2003). Unfortunately, the logistical and financial resources associated with prescribed fire currently restrict the widespread and frequent use of prescribed fire by private landowners across the historical range of the longleaf pine ecosystem (Moorman et al. 2002). Overcoming these logistical hurdles will be essential for conserving biodiversity dependent on functional longleaf pine ecosystems.

3.5.3 Tropical Forests

3.5.3.1 Neotropical Migrant Birds and Coffee Agroecosystems

In tropical forests around the globe, agricultural development is in direct conflict with the conservation of forests and the wildlife therein (Gliessman 1992). Agroecosystems define agricultural systems as ecosystems, enabling a framework for the examination of the complex interactions between overlapping ecological, environmental, and cultural components of tropical agriculture (Conway 1985; Francis 1986). Traditional agroecosystems in the tropics focused on long-term sustainability of the system rather than maximizing profits and yield (Gliessman 1992). Yet, increased economic and political pressures for the export of cash crops have led many modern tropical agroecosystems to become production driven and thereby potentially less sustainable (Conway 1985).

Coffee (Coffea spp.) farming is the dominant agroecosystem in the tropics of Latin America, second only to oil in value in many parts of the region (Rice and Ward 1997). Coffee production is particularly prevalent in the biodiversity hotspots of Latin America (e.g., Brazil, Columbia, Mexico) and often occurs in areas with few remaining forests (Mittermeier et al. 1998;
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Hardner and Rice 2002; Philpott et al. 2007). In its native form, coffee is a shade-tolerant understory tree. As such, traditional (i.e., primitive) coffee plantations were established and maintained by placing young coffee plants under canopy provided by one or more native tree species ("shade coffee"; Rappole et al. 2003, Figure 3.10). Efforts in the Latin American tropics to increase coffee production and combat devastating coffee diseases (e.g., coffee leaf rust \([Hemileia vastatrix]\)) have led to the development of coffee varieties tolerant to direct sunlight ("sun coffee"; Rappole et al. 2003). Compared to shade coffee, sun-grown coffee produces greater yields, is amenable to mechanized agricultural practices, and exhibits greater resistance to disease, making it an attractive agroindustry throughout much of modern-day Latin America (Rice and Ward 1997). Despite the cultural and economic benefits of sun coffee, the system is typically far less biologically diverse than shade coffee (Rappole et al. 2003). Indeed, the ecological and economic trade-offs of these competing agroecosystems define the true challenge of implementing conservation-minded coffee production throughout Latin America.

Neotropical migrant birds (herein birds) have become ecological indicators informing the sustainability of coffee production in the Latin American tropics. Birds are especially useful for assessing the conservation value of shade versus sun-grown coffee production because they serve many ecological functions (e.g., seed dispersal, secondary consumers), span across both temperate and tropical forests of the western hemisphere, and respond to changes in habitat structure (MacArthur and MacArthur 1961). Researchers have noted a high diversity and abundance of bird species in both primitive and modern (i.e., emulating primitive production) shade coffee plantations (Griscom 1932; Greenberg et al. 1997). Shade coffee inherently maintains more structurally complex vegetation in comparison to sun coffee, where the coffee plants themselves or coffee and a single-tree species provide vertical structure (Perfecto et al. 1996). The vertical complexity of shade coffee supports more diverse fauna as a whole (MacArthur and MacArthur 1961), and increased prevalence of tall, taxonomically and structurally diverse canopies are especially important for

**FIGURE 3.10**
(See color insert.) Shade-grown coffee plantations are characterized by a more complex vegetation structure than sun-grown coffee, and as such, typically maintain higher levels of biodiversity. (Photo by Chris Moorman, used with permission.)

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supporting bird diversity (Greenberg et al. 1997). The importance of shade coffee as habitat and/or corridors for wildlife has also been demonstrated for ants (Perfecto and Snelling 1995), butterflies (Mas and Dietsch 2004), and monkeys (Williams-Guillén et al. 2006), among other wildlife groups. In general, shade coffee often provides important refugia for biodiversity, especially birds, in the increasingly deforested landscape throughout much of Latin America (Mas and Dietsch 2004).

Coffee certification programs in Latin America exemplify the complex series of trade-offs between economic and ecological forest management inherent to forest certification programs in boreal, temperate, and tropical forests alike. Coffee certification programs operate on the basic premise of branding ecologically beneficial coffee production practices as sustainable (e.g., "green consumerism"—Albertin and Nair 2004), passing some of the economic burden of such production onto the consumer and, in turn, providing economic incentives to coffee growers (Rain forest Alliance 2000). Coffee certification programs may offer a way in which to protect biodiversity while simultaneously maintaining the economic livelihood of coffee farmers (Philpott et al. 2007). However, there is significant contention among ecologists and economists regarding the ability of coffee certification programs to achieve these goals, and variation among the viability of specific certification programs (e.g., organic, fair trade, shade grown) is thought to be high (Philpott et al. 2007). For example, the premium offered to shade coffee growers may not always compensate for the low yields of the most shaded (i.e., most biologically diverse) plantations (Perfecto et al. 2005). Importantly, maintaining the economic viability of shade coffee is paramount to keeping coffee farmers interested in sustainable coffee production.

Cultural and societal inputs in the framework of coffee certification programs illustrate the value of land manager involvement (e.g., coffee farmers). In the early 2000s, coffee prices were comparatively low (Food and Agricultural Organization 2002), in part due to global economic policies and coffee overproduction, putting extreme economic pressure on predominantly small, rural coffee farmers willing to participate in coffee certification programs. During this time, a philosophical disconnect occurred between conservation coffee certification programs and economic stability of rural farmers. In response to this situation, Philpott and Dietsch (1993) suggested the unification of historically independent coffee certification programs linked to price premiums for coffee producers could provide an all-inclusive, long-term solution to meet conservation and economic goals. Importantly, coffee farmers’ perception of the role of shade trees in coffee plantations often overlaps with the conservation objectives of coffee certification programs. For example, farmers in Costa Rica considered tree height an important characteristic of their plantations for coffee production (Albertin and Nair 2004). Meanwhile, Greenberg et al. (1997) found tree height as a significant contributing factor to increased biodiversity in coffee plantations. Most of those same Costa Rican coffee farmers (88%) also expressed interest in adding more trees to their plantations, especially via intercropping fruit trees (Albertin and Nair 2004). In turn, intercropping could increase vegetation structure and potentially improve wildlife habitat. Given the connection between coffee farmers and the agroecosystems they manage in tropical Latin America, a sound understanding of their perception of conservation goals in addition to their financial needs is vital to conserving coffee agroecosystems into the future. This message can be extended to a suite of agroforest systems and the land managers therein (e.g., forests for timber production).

Coffee is just one of a number of cash crops in Latin America. Yet, many of the same land use, forest management, and conservation concerns and strategies (e.g., certification programs) apply to most Latin American cash crops. In the case of agroforests, conservation issues surrounding cacao (Schroth and Harvey 2007) and banana/plantain...
(Harvey et al. 2006) production are especially similar to that of coffee. Oil palm (*Elaeis guineensis*; see Section 3.5.4.2) production also invokes similar global tropical conservation (Fitzherbert et al. 2008) and societal (Rist et al. 2010) concerns as monocultures of sun coffee, although oil palm plantations may have even more severe impacts on land cover.

### 3.5.4 Contemporary Issues in Forest Wildlife Management: Forest Bioenergy

The interface between forest-based renewable energy development and wildlife conservation is an increasingly relevant research area deserving of independent treatment. Forests are capable of producing vast amounts of woody biomass (i.e., dead and live trees), which in turn can be used to produce traditional wood products or generate forest bioenergy in the form of heat, electricity, and liquid fuels (Parikka 2004). While high-value wood products (e.g., timber) from forests remain the primary driver of decisions regarding forest management, by-products of timber production such as woody biomass are important feedstock for rapidly emerging forest bioenergy markets. In an effort to expose readers to the potential effects of forest bioenergy development on wildlife, we briefly cover some primary, regional forest-based energy technologies in the succeeding text.

#### 3.5.4.1 Woody Biomass Harvest in Boreal and Temperate Forests

##### 3.5.4.1.1 Harvest Residues

Forest harvest operations (e.g., clearcutting for timber harvest) typically yield large amounts of harvest residues collectively referred to as fine (foliage, small limbs, and trees) and coarse (downed logs) woody debris (Riffell et al. 2011a). Harvest residues, particularly coarse woody debris, may be gleaned following harvest (i.e., woody biomass harvest; Figure 3.11) and used as a feedstock for the following forest bioenergy technologies: (1) wood pellets (Sikkema et al. 2001), (2) woody biomass and cofired coal power

![Figure 3.11](See color insert.) Following clearcutting, harvest residues may be chipped on-site and transported to forest bioenergy facilities to be converted to renewable energy. (Photo by North Carolina State University Forestry Extension, used with permission.)
production (Annamalai and Wooldridge 2001), and (3) liquid biofuels (USDA 2007). While coarse woody debris may be a prospective feedstock for forest bioenergy, it also provides important food and cover resources to many wildlife species (Harmon et al. 1986; see Section 3.3.4). Some ecologists are concerned that the increasing market viability of woody biomass may lead to intensified harvest, potentially resulting in negative impacts on wildlife species directly and indirectly associated with woody debris (Riffell et al. 2011a). Indeed, wood pellet production in the United States is growing vigorously (Forisk Consulting 2013), especially in response to European Union renewable energy mandates that heavily rely on imported wood pellets as feedstock (Goh et al. 2013). In response to conservation concerns regarding intensified woody biomass harvest, voluntary Biomass Harvesting Guidelines have been developed (e.g., Perschel et al. 2012), yet these guidelines do not yet incorporate results from empirical studies.

Only recently have empirical studies on the explicit effects of woody biomass harvests on wildlife been published. A recent study in the southeastern United States indicated that shrews were associated more with vegetation characteristics than the availability of downed woody debris in young, regenerating clearcuts (Fritts et al. 2015). We anticipate an influx of research and resultant scientific literature on this topic to emerge in the near future. Although not technically a wood-based renewable energy technology, switchgrass (*Panicum virgatum*) is a bioenergy feedstock that has been intercropped within existing pine plantations in the southeastern United States, at times in stands also sustaining woody biomass harvests. Intercropping switchgrass during woody biomass harvest in pine plantations in North Carolina, United States, had no short-term negative effects on herpetofauna relative to traditional pine management (Homyack et al. 2013). Loman et al. (2014) found that birds used intercropped plots less frequently than control plots (i.e., no intercropping) in pine plantations, yet differences in bird use between intercropped and control plots diminished after 3 years. In general, more manipulative studies on the effects of woody biomass harvest on wildlife are needed at more extensive geographic and temporal scales (Riffell et al. 2011a).

### 3.5.4.1.2 Thinning

Forest thinning is a well-established silvicultural practice that generates downed wood, which in turn can be used in all of the same forest bioenergy technologies outlined for the aforementioned harvest residues. Thinning increases structural complexity, understory vegetation, and consequently habitat for a variety of wildlife species (see Section 3.4.3). A review by Verschuyl et al. (2011) reported that forest thinning treatments (precommercial, commercial, and fuels reduction) generally had positive or neutral effects on wildlife, although the magnitude of wildlife response varied with thinning intensity and type, and the review did not include any thinning treatments explicitly meant for woody biomass harvest. To the best of our knowledge, no empirical studies exist on the effects of forest thinning specifically for woody biomass on wildlife. In general, the effects of thinning for forest bioenergy on wildlife likely coincide with the well-known effects of traditional thinning on wildlife. Indeed, the vast database of literature on this subject may be one reason for the paucity of studies focusing on thinning specifically for forest bioenergy.

### 3.5.4.1.3 Short-Rotation Woody Cropping

While forest bioenergy from harvest residues and thinning generally originates as a by-product of traditional forest management, short-rotation woody cropping (SRWC) involves specific cultivation of high-yielding, fast-growing woody crops (e.g., cottonwood and poplars [*Populus* spp.], eucalyptus) using intensive silvicultural techniques to produce woody biomass across short harvest cycles (e.g., 1–15 years; Dickman 2006). Short-rotation
woody crops typically are burned as feedstock for electricity production (Parikka 2004). Riffell et al. (2011b) reviewed the effects of cottonwood SRWC on birds and mammals relative to reference woodlands. Their results indicated that overall bird and mammal abundance was lower on SRWC plantations relative to reference woodlands, but shrub-associated birds were more abundant. Potentially significant habitat conversion from agricultural to SRWC may lead to landscape-level effects on some wildlife populations, such as birds typically found in agricultural landscapes (Dhondt et al. 2004). Similarly, extensive conversion of intensively managed forests to SRWC likely would decrease wildlife populations on plantations, especially if high-conservation value habitats are replaced (Riffell et al. 2011b).

3.5.4.2 Oil Palm Plantations in Tropical Forests

Oil palm plantations for forest bioenergy pose one of the most large-scale and imminent threats to tropical biodiversity, specifically in Indonesia and Malaysia. Palm oil is one of the world’s most rapidly increasing crops and may be used to produce biodegradable and nontoxic biofuel with significantly fewer emissions than petroleum-based diesel (Sumathi et al. 2008). The development of oil palm monocultures typically replaces native forest types. Oil palm plantations already have supplanted large tracts of forests in Southeast Asia, a region historically rich in endemic wildlife species and biological diversity (Fitzherbert et al. 2008). Given the reduced structural complexity of oil palm plantations relative to lowland tropical forests, many wildlife species are displaced when conversions occur. For example, conversion of lowland tropical forests to oil plantations in Thailand reduced species richness of insectivorous and frugivorous birds by 60%, indicating that reduced structural diversity in oil palm plantations resulted in a decrease in available niches (Sirirak et al. 2006). Conversion of preexisting cropland (e.g., rubber) may have far fewer negative ecological repercussions (Koh and Wilcove 2008).

3.6 Conclusion

Proper forest management is contingent on a sound understanding of forest wildlife ecology. Forests provide habitat—food, cover, and water—for many wildlife species and consequentially are among the most biologically diverse terrestrial ecosystems. Wildlife–habitat relationships form the foundation for understanding ecological interactions between forest wildlife and their environment. Specifically, forest wildlife management involves five interrelated ecological principles with implications on wildlife habitat: (1) disturbance, (2) succession, (3) structure (vegetation and deadwood), (4) composition, and (5) landscape ecology. Following Aldo Leopold (1933), the true essence of forest wildlife management is captured by the idea that conservation of forest products for human consumption and forest wildlife can be simultaneously achieved. Forest management practices, including final harvest, regeneration and site preparation, thinning, prescribed burning, and herbicide application, have direct effects on the five ecological principles outlined earlier and consequentially influence forest wildlife habitat. Successful forest wildlife management is often achieved by implementing forest management practices that facilitate habitat conditions for target wildlife species. The fundamental concepts presented in this chapter generally apply to all forests. However, we presented case studies illustrating the application of forest wildlife management in boreal, temperate, and tropical forests and the use of forest wildlife as ecological indicators.
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