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Think globally, manage locally: The importance of steady-state forest features for a declining songbird

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ABSTRACT

Changes in historical forest composition and structure may have cascading effects throughout the forest community. Perhaps nowhere is there a better example of current forests that carry a legacy from their past than in eastern North America. The Cerulean Warbler (*Dendroica cerulea*), a declining Neotropical migratory bird of high conservation concern, is one excellent example of a species that seems to be sensitive to both landscape configuration and subtle features of eastern forests of North America. We used the Cerulean Warbler as a model species to demonstrate how an appreciation of fine-scale structural attributes of forests may improve our ability to conserve late-successional forest species. To do this we evaluated the extent to which multiscale habitat features were associated with density, spatial distribution, and nesting success of Cerulean Warblers in 12 mature forest sites in southeast Ohio, 2004–2006. Results suggest that adjacency of regenerating clear-cuts did not influence density or nesting success of Cerulean Warblers in adjacent mature forest. Instead, variation in demographic parameters was best explained by local habitat features. Density and nesting success were positively associated with canopy openness, numbers of large-diameter trees, and number of grapevines—all of which are typical of heterogeneous steady-state phase forests. Thus, improved management for Cerulean Warblers may require creating features (e.g., large canopy gaps) that mimic old-growth forests. Although fragmentation and habitat loss remain important contributors to population declines of many mature forest species, our work provides evidence that subtle changes in forest structure, particularly to features associated with old forests, warrant additional attention from the conservation community.

1. Introduction

As land cover changes around the world continue to transform our planet, forests are imperiled due to a variety of anthropogenic causes, including resource extraction, development, and degradation. Although conservation efforts generally focus on regions where habitat loss and fragmentation are rampant, forests within regions experiencing regeneration and maturation still may face threats from altered disturbance regimes, invasive species, and other subtle changes in ecological processes. Perhaps nowhere is there a better example of these insidious threats than in eastern North America. Despite the near-complete clearing of forests for agriculture and logging by the early 20th century (Whitney, 1994) and widespread disease (Ellison et al., 2005), many eastern landscapes have returned to forested conditions. Nevertheless, today's forests carry a legacy from their past and they now lack many of the structural and floristic features that characterized presettlement forests (Steyaert and Knox, 2008). Research shows that regenerated forests typically have lower floristic diversity and structural complexity than pre-Euro-American forests (Schulte et al., 2007). For example, insect, mammal, and bird community density and richness were found to be greatest in old-growth forests (Davis, 1996; Haney and Schaadt, 1996; Jeffries et al., 2006). Some of these changes result from altered disturbance regimes (e.g., fire suppression) that support gap phase dynamics operating within older forests (Bormann and Likens, 1979). Older or steady-state forest may be important for wildlife due to its structural and floristic complexity including standing dead trees, widely-spaced large trees, treefall gaps, continuous vertical foliage, rich leaf litter, undisturbed soils, thick herbaceous layer, and downed trees (Davis, 1996; Oliver and Larson, 1996).

The absence of gap dynamics within forests may explain, in part, the apparent paradox of certain declining mature forest birds in the face of decades-long increases in forest cover in eastern North America (Steyaert and Knox, 2008). One species in particular, the Cerulean Warbler (*Dendroica cerulea*), was once a common breeding bird of eastern forests, but populations are estimated to have declined approximately 70% since 1966 (Sauer et al., 2008). In fact, Cerulean Warblers are experiencing the

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greatest declines of any North American warbler (Sauer et al., 2008), are designated a globally vulnerable (to risk of extinction) species by the International Union for the Conservation of Nature and Natural Resources (IUCN, 2008), and were selected as one of the top nine focal species for conservation action by U.S. Fish and Wildlife Service (USFWS, 2005).

Anthropogenic land use changes on breeding and wintering grounds have been implicated as the most likely cause of population declines for Cerulean Warblers. At landscape scales, fragmentation of mature, deciduous forest on breeding grounds is frequently cited as an important contributing factor, particularly given that Cerulean Warblers are usually considered area-sensitive (Hamel et al., 1998, 2004; Hamel, 2000). At smaller spatial scales, changes in forest structure as a consequence of even-aged forest management and loss of key tree species also may, in part, drive population declines (Robbins et al., 1992; Hamel, 2000).

Unfortunately, a paucity of specific information on the responses of Cerulean Warblers to habitat alteration and management at local and landscape scales seriously constrains conservation efforts (Hamel et al., 2006; Hamel and Rosenberg, 2007). Because Cerulean Warblers nest and forage high in the canopy of mature forests, the majority of data on breeding biology comes from habitat associations. Cerulean Warblers are considered area-sensitive, however, area requirements vary widely across the breeding range, probably due to the surrounding land use (Hamel, 2000). That is to say, in highly forested landscapes Cerulean Warblers are more likely to settle in small patches of forest compared to areas with very little forest cover where they nest only in large forest patches. Cerulean Warblers also use edges of timber harvests, roads, and ridgetops within heavily forested areas (Rodewald and Yahner, 2000; Weakland and Wood, 2005; Wood et al., 2006). Cerulean Warblers are most likely to breed in forests with a broken canopy, such as riparian bottomland forest and upland forests (Rosenberg et al., 2000). Local habitat characteristics often associated with Cerulean Warblers include (1) dense, heterogeneous canopies, (2) large, well-spaced trees, and (3) open understories (Hamel, 2000; Jones and Robertson, 2001; Roth and Islam, 2008). Although Cerulean Warblers are known to prefer large tracts of mature forest, numerous studies suggest that canopy gaps, or openings, may be an important aspect of nest-site selection (Bent, 1953; Oliarnyk, 1996; Oliarnyk and Robertson, 1996), while others believe canopy gaps to be of little relevance (Barg et al., 2006). Forest management practices, then, may hold promise for Cerulean Warbler conservation because it may create the heterogeneous canopy structure apparently preferred by the species (Harrison, 1984; Oliarnyk, 1996; Oliarnyk and Robertson, 1996).

We used the Cerulean Warbler as a model species to demonstrate how an appreciation of fine-scale structural attributes of forests may improve our ability to conserve late-successional forest species. In the broadest conceptual terms, we sought to elucidate the relative importance of forest quantity versus forest quality as potential causative agents in the decline of Cerulean Warbler. More specifically, we hypothesized that variation in density and nesting success was explained by: (1) canopy structure (i.e., tall canopies with multiple gaps), (2) tree size, (3) light gaps (i.e., canopy openness and understory vegetation that has been released in light gaps), (4) forest structure (i.e., understory vegetation, large trees, canopy openness and height), and (5) adjacency to clear-cut harvest.

2. Methods

2.1. Study system

Our study area was located in southern Ohio (United States) within the Ohio Hills Physiographic Province, which represents the core breeding range of Cerulean Warblers and supports nearly 50% of the global population during the breeding season (Rosenberg and Dettmers, 2004). Land uses within the ecoregion are diverse, but are primarily in agriculture, silviculture, and exurban development (Rosenberg and Dettmers, 2004). Common tree species in mature forests included white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. montana*), tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), black gum (*Nyssa sylvatica*), black cherry (*Prunus serotina*), and hickory (*Carya* sp.; Brawn, 1989). Regenerating clear-cuts were dominated by shrub communities of woody plants generally <5 m tall and were comprised of tree saplings (see above), *Rubus* sp., greenbrier (*Smilax* sp.), and sumac (*Rhus* sp.). Twelve mature forest sites (stands aged 80–120 years), at least 16 ha each, were selected from Perry, Athens, Vinton and Jackson Counties in southeast Ohio (Table 1). The majority of these study sites had little to no apparent habitat manipulation since clearing of forests. However, two study sites had selection silviculture applied within the site in the 1980s (see Table 1). Stocking levels for our forest stands range from 60% to 85% with 10–12 quadratic mean diameter and 110–190 trees per acre as reported by Hamel et al. (2006). Stands varied in canopy gap size extending up to approximately 25 m in diameter. Study sites were selected such that six sites were adjacent to a regenerating clear-cut stand (treatment = adjacent to harvest) and six were completely surrounded by mature forest (treatment = unharvested). All harvests were <10 years old and ranged from 5.7 to 15.6 ha in size (Table 1). With the exception of recent clear-cuts, 1-km-raduis landscapes surrounding study sites were similar and ranged from 72.1% to 100.0% forest cover (Table 1). Other land uses included small areas of pasture or agriculture, scattered residences and farms, campgrounds and park areas, and two-lane roadways. Adjacency to harvest was the primary factor influencing percent forest cover within the landscape and was, therefore, considered to be a meaningful descriptor of landscape.

2.2. Sampling of Cerulean Warblers

In order to estimate density of Cerulean Warblers and to examine territory placement relative to regenerating clear-cut edges, an intensive spot-mapping approach was used on the 12 sites. Spot-mapping allows estimation of the density of birds within a specified area, and is based on the territorial behavior of birds (Ralph et al., 1993). By marking locations of birds on a detailed map of the study area, we were able to count the number of territories in an area (i.e., density). At each site, a 16–20 ha grid was marked with flagging at 50-m intervals to determine bird locations. We spot-mapped territorial Cerulean Warblers eight times during May–July 2004–2006 at each study site. On each compiled spot-map, we estimated the center of each territory (the intersection of the two longest axes bisecting the territory polygon; Weakland and Wood, 2005) to calculate a distance of the territory center to the nearest harvest edge. For the six sites adjacent to harvests, we split each site's spot-map in half to represent distance categories (i.e., edge versus interior) from the clear-cut edge. Territory centers located in the 'interior' were >200 m from the regenerating clear-cut edge; a distance where most edge effects are no longer detected in forested landscapes (Patton, 1994; Flaspohler et al., 2001). Because number of territories did not significantly differ among years ($P > 0.50$), we first averaged number of territories across years in each distance category and then examined if number of territories was related to distance category.

An information-theoretic approach was used to evaluate and rank 6 *a priori* models explaining variation in Cerulean Warbler density among sites. The following hypotheses were constructed: (1) canopy structure – Cerulean Warblers respond primarily to the