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# Effects of local and regional landscape characteristics on wildlife distribution across managed forests

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ABSTRACT

Understanding the impacts of local and regional landscape characteristics on spatial distributions of wildlife species is vital for achieving ecological and economic sustainability of forested landscapes. This understanding is important because wildlife species such as white-tailed deer (*Odocoileus virginianus*) have the potential to affect forest dynamics differently across space. Here, we quantify the effects of local and regional landscape characteristics on the spatial distribution of white-tailed deer, produce maps of estimated deer density using these quantified relationships, provide measures of uncertainty for these maps to aid interpretation, and show how this information can be used to guide co-management of deer and forests. Specifically, we use ordinary least squares and Bayesian regression methods to model the spatial distribution of white-tailed deer in northern hardwood stands during the winter in the managed hardwood-conifer forests of the central Upper Peninsula of Michigan, USA. Our results show that deer density is higher nearer lowland conifer stands and in areas where northern hardwood trees have small mean diameter-at-breast-height. Other factors related with deer density include mean northern hardwood basal area (negative relationship), proportion of lowland conifer forest cover (positive relationship), and mean daily snow depth (negative relationship). The modeling methods we present provide a means to identify locations in forest landscapes where wildlife and forest managers may most effectively co-ordinate their actions.



## 1. Introduction

Spatially explicit wildlife population density models, including those that account for the spatial arrangement of local habitat, are essential for forest management (Turner et al., 1995). For example, the spatial arrangement of local forest stands with different composition and size-density characteristics (hereafter referred to as forest structure) may affect ungulate herbivore population density and lead to spatial variation in forest vegetation regeneration success. Landscape pattern has also been shown to influence wildlife species' habitat selection across large regional extents (Kie et al., 2002; Boyce et al., 2003). Forest characteristics and other environmental variables at these larger regional scales may combine with local characteristics to add further spatial variation to herbivore population density and vegetation regeneration success. Understanding wildlife distributions and their relationships to local and regional landscape patterns can aid forest managers in developing harvest strategies that ensure the ecological and economic sustainability of the forests they are entrusted with.

Forest management approaches that mimic natural disturbances have been proposed as a means to achieve this sustainability by maintaining both biological diversity and timber production (e.g., Mitchell et al., 2002). In many managed forests, including the northern hardwood forests of North America, wind disturbance events and tree senescence are predominant natural disturbances that create gaps in the forest canopy. Selection harvesting is a management approach intended to mimic these natural disturbance events by removing single to small groups of trees, creating gaps and maintaining an uneven tree-age distribution in forest stands (Arbogast, 1957; Tubbs, 1977; Tyrrell and Crow, 1994). However, the success of selection harvesting depends on the establishment and survival of desirable shade-tolerant species (such as sugar maple) in the understory at sufficient density to replace overstory trees that are removed by the periodic harvests (Oliver and Larson, 1996). The presence of herbivores that browse these tree species can stunt growth or kill seedlings and saplings, potentially leading to a regeneration failure and threatening forest sustainability (this disturbance pressure is

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likely to be equally important in gaps created by natural disturbances).

White-tailed deer (*Odocoileus virginianus*) is one herbivore that has long been recognized as having the potential to cause regeneration failure and greatly affect vegetation dynamics, stand structure and ecological function in many forest types of North America (Stromayer and Warren, 1997; Waller and Alverson, 1997; Cote et al., 2004). In hardwood-conifer forests in particular, white-tailed deer have been found to drive changes in understory structure and species composition (Augustine and Frelich, 1998; Holmes et al., 2008), cause species composition change of overstory trees (Anderson and Loucks, 1979; Tilghman, 1989; Long et al., 2007) and reduce stand timber value by slowing the recruitment of saplings to canopy positions (Marquis, 1981). These impacts on stand species composition and structure are most severe where deer densities are greatest (Rooney and Waller, 2003). Consequently, understanding the spatial distribution of deer is vital in order to manage for deer browse impacts in forest stands. However, the factors that influence deer density are poorly understood relative to the knowledge about the effects of deer on vegetation (Russell et al., 2001). The ability to estimate deer density from standard forest stand inventory data, forest cover-type data, and other measureable environmental variables at regional scales would be of great benefit to forest managers (e.g., Weisberg and Bugmann, 2003).

Landscape forest cover pattern is likely to be an important determinant of deer density during the winter in mixed hardwood-conifer forests. During winter in these forests, white-tailed deer generally shelter in mature conifer swamps, venturing out to browse in nearby stands, including northern hardwood stands (Verme, 1965; Euler and Thurston, 1980; St-Louis et al., 2000). This behavior is a response to the trade-off between conserving heat and energy in the shelter beneath the closed canopies of the (evergreen) conifer stands versus negotiating deeper snow and colder temperatures in the more open (deciduous) mixed hardwood stands to find adequate forage (Verme, 1968; Armstrong et al., 1983; Schmitz, 1991). Thus, winter habitat for white-tailed deer in hardwood-conifer forests must provide both thermal cover and food, and must do so in close enough proximity for the deer to travel between the two forest types diurnally. In combination with these patterns of forest cover, regional variations in environmental factors associated with winter severity (such as snow depth and low temperatures) are also likely to influence deer activity. For example, Morrison et al. (2003) found that deer movement in forest stands varies with snow depth and the spatial arrangement of shelter in neighboring stands.

Previous studies have considered the spatial distribution of deer at the landscape scale, but these have mainly concerned seasonal migration and home ranges (e.g., Verme, 1973; Tierson et al., 1985; Van Deelen et al., 1998; Brinkman et al., 2005). For example, Kie et al. (2002) examined the relationship of landscape metrics measured over different spatial extents with home range sizes of female mule deer. To the best of our knowledge only one study has examined the influence of local stand-level characteristics on winter deer density. Dumont et al. (1998) found that over a 25 km$^2$ area forest type, proportion of conifer cover, food availability and mean deciduous tree diameter-at-breast-height were the most important predictors of deer density. We are unaware of any previous study that uses estimates of deer density in individual stands to quantify deer-habitat relationships across a large managed forest landscape. Here, we use ordinary least squares and Bayesian regression methods to investigate how local forest structure, with regional-scale variation in snow depth and landscape pattern, can explain the density of white-tailed deer in northern hardwood stands during winter in the managed forests of the central Upper Peninsula of Michigan, USA. Using the quantitative relationships found, we produce spatial estimates of deer density, with uncertainty estimates, and demonstrate how this information can be used to guide co-management of deer and forest regeneration.

## 2. Methods

### 2.1. Study area

The study area comprises approximately 4000 km$^2$ in the Upper Peninsula (U.P.) of Michigan (Fig. 1a). This area was chosen to focus on a predominantly forested region with a minimum of intensive human land uses such as agriculture, urban, suburban, or other settlements. The predominant forest cover types in the study area are lowland coniferous, northern hardwood, aspen and mixed upland. In the central, eastern and southern parts of our study area (Ecoregion Section VIII, Albert, 1995) these forest covers form a relatively regular mosaic of upland hardwood and lowland conifer stands, juxtaposed across the rolling topography of the Menominee drumlin field. Larger patches of hardwood forest cover are found in the north west of the study area (Ecoregion Section IX). Predominant tree species in the study area are *Thuja occidentalis* (northern white cedar) in lowland forests, *Acer saccharum* (sugar maple) in upland forests, and Aspen forest cover is dominated by *Populus tremuloides* (trembling aspen). These forest covers provide habitat for numerous wildlife species and guilds including white-tailed deer and neotropical migrant songbirds (see Laurent et al., 2005 for more details on songbirds and other tree species present).

The primary land use in the study area is forest management for timber products. Northern hardwood stands are managed for a wide-range of wood products including high-value veneer logs, saw logs, and pulpwood. Uneven-aged single-tree selection silviculture dominates northern hardwood management in the study area. Harvest specifications vary with ownership and/or management goals, but stands are typically entered approximately every 10–20 years and 1/4 to 1/3 of the basal area removed to leave 16–18 m$^2$/ha (70–80 ft$^2$/acre) residual basal area (e.g., Schwartz et al., 2005). Land ownership in the study area is divided between State (42%), non-industrial private (38%), and private industrial (20%) owners.

### 2.2. Winter white-tailed deer density data

We surveyed white-tailed deer fecal pellet density to derive an estimate of the number of deer-hours spent in a particular location during the previous winter. We performed all surveys immediately after snow melt between 28th April and 18th May 2008 to represent winter deer density for the time period beginning with leaf-off of the previous autumn (assumed to be November 1st), and ending with counting date. The use of deer fecal pellet counts to estimate deer density has been criticized (e.g., Fuller, 1991). However, experiments have shown that the simple relationship between pellet density and actual deer density is a reasonable approximation (Hill, 2001) and the method has been used since the 1950s by the Michigan Department of Natural Resources (MDNR). In this paper we calculate deer density from our pellet counts by assuming deer produce 13.4 pellet groups/day (consistent with the approach of MDNR). Although this method does not provide a precise estimate of absolute deer densities that can be directly compared with other landscapes, it does provide an internally consistent means to assess spatial variation in deer density across our study area.

At each of 51 study sites we positioned and surveyed ten transects arranged in a "bow tie" configuration established within a 155 m radius of the site center (7.5 ha, Fig. 2). The mean of pellet-group counts for all ten transects was used to calculate deer