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.

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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

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 km² 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 km² 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 m²/ha (70–80 ft²/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
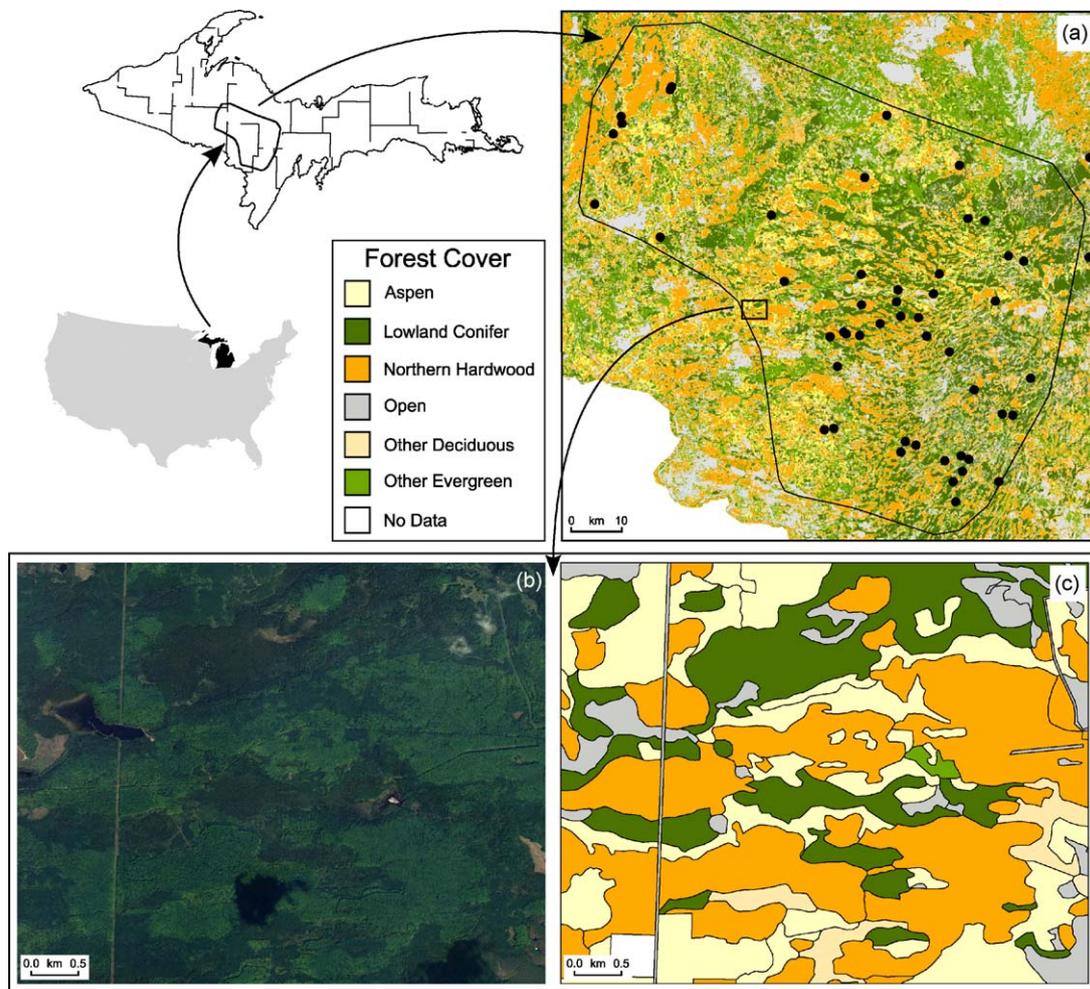
Fig. 1. Michigan Upper Peninsula study area. (a) 51 sites, shown by black dots, were selected from across the study area which is characterized by a mosaic of hardwood and conifer stands. (b) Aerial photography of the section of the study area selected for the production of spatial deer density estimates. (c) Stand data (cover type, stand DBH and stand BA) for the entire study area were available at the spatial precision shown (note presence of areas with no data). Note power lines running north–south in west of study area section in (b) are correspondingly represented as open area in (c).
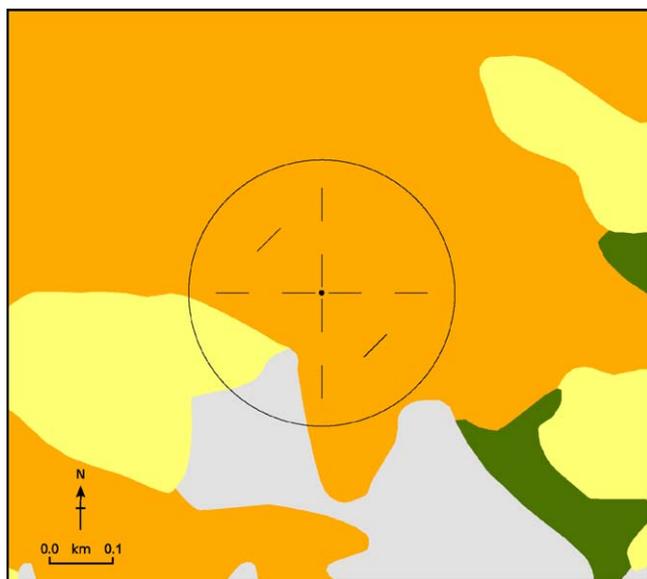
Fig. 2. Plot sampling design for deer-pellet counts. Ten 50 m deer-pellet count transects (straight black lines) were organized in a 'bow-tie' shape around each site center in northern hardwood stands. Transects were 4 m wide and double-counted. The circle shown has radius 200 m corresponding with the LOIs we examined. Colors representing different forest cover types are as for legend in Fig. 1.

density (deer/km^2) at each site. Study plots were centered in northern hardwood stands. Locations of study sites were selected using three different criteria based on time since harvest and locations of previous data collection: 16 sites were northern hardwood stands that underwent selection harvest during 2005–2007; 13 sites were stands that underwent selection harvest during 1994–2003; and 22 sites were used previously by Laurent et al. (2005, description of location selection described therein). Each of the ten transects in the plots had dimensions of 50 m × 4 m (0.02 ha). Pellets within transect areas were counted independently by each of two field crew members walking in opposite directions along transects.

2.3. Local forest structure data

Our forest structure data are from the MDNR Forest Operations Inventory (OI), private industrial forest stand records, and timber stand cruises of private industrial and non-industrial forest stands undertaken during summer 2008 and early spring 2009. The OI classifies stands based on vegetation as well as management objectives and contains information such as stand type (e.g., aspen, northern hardwood, mixed swamp conifer, etc.), stand basal area (BA), and mean stand diameter-at-breast-height (DBH). MDNR update OI data for individual stands on a 10-year rotation, so we adjusted the OI to account for changes in BA and DBH since last data collection for each northern hardwood stand. These stands

were projected to their 2008 state by assuming increments in annual BA (between 0.40 and 0.48 m^2/ha/year dependent on residual stand basal area) and DBH (between 0.32 and 0.50 cm/year, Crow et al., 1981) from the year of data collection to the year of pellet data collection. There are no stands in our data that were harvested since the last year of DNR OI data collection. Private industrial inventories contain stand type only and no tree data. Therefore we measured stand BA (10 BAF prism) and mean stand DBH (diameter tape) on private industrial and non-industrial forest land in the vicinity of our deer density estimates (see below for description of the area measured). Stand characteristics data were linked in a GIS (ESRI, 2006) with stand boundary maps for MDNR and industrial private lands (e.g., Fig. 1c). Stand boundaries for private non-industrial land were digitized using aerial photography with field notes.

We hypothesize, given the literature cited previously, that the density of deer at a location in the landscape will be influenced by stand size-density characteristics and forest cover composition of surrounding areas. For each deer density estimate, we calculate stand-level characteristics for surrounding Landscapes of Influence (LOIs) of radius 200 m (12.5 ha, Fig. 2). We term forest characteristics that are measured only within these LOIs as 'local landscape variables'. In the central Michigan U.P., deer winter home ranges have been found to vary between 730 and 1859 ha (Van Deelen et al., 1998). Here we consider smaller areas because we are concerned with local factors affecting winter deer use and not seasonal range dynamics, and because they minimize data requirements for future management applications of our results.

For each LOI we calculate area-weighted mean northern hardwood stand DBH (termed Hardwood_DBH in the remainder of the paper) and area-weighted mean northern hardwood stand BA (termed Hardwood_BA). We also calculate the range of DBH (termed Hardwood_DBH_Range) and BA (termed Hardwood_-BA_Range) for stands in each LOI containing more than one northern hardwood stand. We examine these variables to investigate the potential effects of local timber management on winter deer density. We calculate the spatial composition (proportion) of each LOI in the three forest cover classes that dominate the study area: northern hardwoods (termed Hardwood_Proportion), lowland conifers (termed LC_Proportion), and aspen (termed Aspen_Proportion). We define lowland conifer stands as those dominated by northern white cedar, black spruce and mixed swamp conifers (from the OI classification). We also calculate the total number of stands with some area within each LOI (termed Number_of_Stands). We examine these measures of local landscape composition as they reflect the literature on the requirements for winter deer habitat outlined above (i.e., deciduous forest cover for food and lowland conifer cover for shelter).

2.4. Regional landscape data

To assess the importance of landscape variation at scales larger than the LOIs we examine, we consider locations of lowland conifer stands, snow depth and ecoregion. We term these variables, regional landscape variables, to contrast our, local, landscape variables. We use our stand-level GIS data to calculate distance to the nearest lowland conifer stand for each deer density estimate (termed Distance_LC). This is a measure of the proximity of winter deer shelter (potentially outside the LOIs we consider). We use data from the Snow Data Assimilation System (SNODAS) produced by National Snow and Ice Data Center (NOHRSC, 2004) to account for potential effects of snow depth on deer density. For more details about the specifics of the SNODAS snow mass and energy balance model and the assumptions it makes, see Barrett (2003)

and references therein. We use the daily snow depth variable from SNODAS to calculate mean daily snow depth (mm) for November 2007 to April 2008 (termed Snow_Depth). Snow depth is believed to be a factor influencing winter deer movement at both local and regional scales (Pauley et al., 1993; Brinkman et al., 2005). Given the broad variation in land cover pattern across our study area described above, we examine whether ecoregion subsections associated with regional vegetation patterns (Albert, 1995, termed Ecoregion) are an important regional driver of winter deer density. Finally, we do not consider regional factors related to deer hunting, as most land in our study area is publicly open to hunting and subject to State game laws. Therefore, we believe there is little potential for these factors to have sufficient variation to drive regional deer distribution.

2.5. Linear regression and model inference

We use ordinary least squares (OLS) regression to examine the effects of our independent variables on deer density. To meet normality assumptions of linear regression, we log$_{10}$ transform deer density estimates for use in these models. Other variables are normally distributed. We do not include a spatial autocorrelation component in our models as Moran's I (globally standardized) indicates no significant autocorrelation in deer density data for lag distances of $\leq$10 km.

With $n = 51$ for our data set we must minimize the number of variables in multiple linear regression models to prevent the possibility of over-fitting. To do this, we first examine univariate models and select most useful predictors from these models for examination in multi-variate models. To further reduce the number of predictors, and to aid inference regarding the most important independent variables, we use Bayesian Model Averaging (BMA). This approach is increasingly being used in ecological species distribution modeling (e.g., Wintle et al., 2003; Thomson et al., 2007), and provides a method to account for model uncertainty by calculating (approximate) posterior probabilities for each possible model that could be constructed from a suite of independent variables (Hoeting et al., 1999). Bayesian model averaging also provides a posterior probability for the inclusion of each variable in the best candidate model. This probability can be used to produce weighted mean values for all variable parameter estimates (i.e., mean parameter estimates are weighted by the probability that they occur in the best model), each with its own confidence interval. We use the package 'BMA' in R (Raftery et al., 2009) to perform these analyses.

We evaluate OLS model performance with both adjusted R^2 and τ, the Kendall rank correlation coefficient, which allows us to evaluate if our deer density data are best modeled as absolute (R^2) or relative (τ) deer density. Furthermore, if P is the probability that observed and modeled deer densities for a randomly chosen site are ranked at the same position in the entire sample of sites, then $\tau = 2P - 1$. We present both τ and P in our results. For OLS models, we also consider model statistical significance and variable parameter estimates as measures of model performance and variable importance, respectively. Because our data set is not large, we do not split it into 'calibration' and 'testing' data sets. Instead, we test our OLS models using fivefold cross-validation, a case of k-fold cross-validation (Hastie et al., 2001). By replicating the cross-validation multiple times we produce central tendency and variance of error estimates (i.e., R^2 and τ). We use $k = 5$ in our cross-validation to compromise between reducing variance of our error estimates and maximizing the use of our sample data for model testing. All OLS methods described above were performed in R (R Development Core Team, 2009), using 'stats', 'bootstrap', and 'spdep' packages.

2.6. Spatial estimates of deer density

We produce spatial estimates of deer density for northern hardwood stands in a section (~20 km²) of our study area (Fig. 1b and c) by applying parameter estimates from the 'best' and averaged Bayesian linear regression models (from BMA) to raster maps (30 m resolution) of the independent variables. Confidence intervals for each variable parameter estimate can be used to produce a model ensemble that provides both a mean estimate of deer density and a standard deviation of that estimate for each map pixel (Araújo and New, 2007). These standard deviations can be used as an indicator of uncertainty in the pixel estimate (larger standard deviation of predicted values across model realizations implies greater uncertainty). The model ensemble is composed of multiple realizations of the Bayesian linear regression models, with parameter values for each realization sampled from the posterior probability distribution for each independent variable. We use 1000 realizations for each model ensemble, performing analyses with a bespoke computer program. We examine a section of our study area because our data are spatially incomplete for the entire study area.

3. Results

For univariate regressions, *Distance_LC* has a significant ($P < 0.05$) negative relationship with deer density and explains more variance than any other variable (Table 1). The relationship indicates that we can expect an average of approximately 19 deer/km² at locations where the nearest lowland conifer stand is 100 m distant, and approximately 6 deer/km² at 800 m. Relationships between deer density and *LC_Proportion* (positive relationship) and *Hardwood_DBH* (negative relationship) were also significant at $P < 0.05$, and *Snow_Depth* (negative relationship) and *Hardwood_BA* (negative relationship) were nearly significant ($P = 0.079$ and $P = 0.081$, respectively) (Fig. 3). All other single variable relations had $P > 0.10$.

To prevent over-fitting we use the five best univariate predictors (all $P < 0.10$) in a 'full' OLS linear regression model (Table 2). This 'full' OLS model is statistically significant ($P = 0.011$) and is able to predict 28% of the variance in deer density estimates (R^2). For this same model, using τ as a measure of model performance indicates a 69% chance that observed and modeled

Table 1

Univariate ordinary least squares regression models of (log) deer density for three LOI data sets. Variables statistically significant at $P < 0.05$ are shown in bold and at $P < 0.10$ in italics. Models use data with $n = 51$ except *range* variables which use data for LOIs with *Number_of_Stands* > 1 (resulting in $n = 20$).

	β	P	R^2	τ[a]
Regional				
Distance_LC (km)	**−0.726**	**0.007**	**0.14**	**0.21**
Snow_Depth (mm)	*−0.002*	*0.079*	*0.06*	*0.11*
Ecoregion	−0.015	0.726	0.00	0.07
LOI composition				
Number_of_Stands	−0.002	0.943	0.00	−0.08
Aspen_Proportion	−0.280	0.347	0.02	0.06
Hardwood_Proportion	−0.026	0.911	0.00	0.09
LC_Proportion	**1.130**	**0.030**	**0.09**	**0.17**
Hardwood stands structure				
Hardwood_DBH (cm)	**−0.024**	**0.021**	**0.10**	**0.22**
Hardwood_BA (m²/ha)	*−0.024*	*0.081*	*0.06*	*0.16*
Hardwood_DBH_Range	0.018	0.182	0.10	0.22
Hardwood_BA_Range	−0.009	0.678	0.01	0.10

[a] Kendall rank correlation coefficient.

deer density for a site are ranked at the same position in the entire sample of sites. Results for fivefold cross-validation indicate the model performs less well when predicting observations not used in model calibration, but also that performance decreases less for the 'best' model versus the 'full' model (Table 2).

Results from BMA analyses indicate that from our set of five variables, those with highest probability of being in the best candidate model are *Distance_LC* (0.59) and *Hardwood_DBH* (0.57) (Fig. 4). These variables are present in the most probable model alone, and with *Hardwood_BA* are the only variables in the five most probable models (with cumulative probability of 0.41). *LC_Proportion* does not appear in any of the five most probable models, but has a greater probability than *Hardwood_BA* of being in the best candidate model. This is because *LC_Proportion* has a greater probability of being present in a model when *Distance_LC* is absent. An OLS regression of the best candidate model from BMA has $P = 0.004$ (Table 2) and a probability of 0.66 that observed and modeled deer density for a site will be ranked at the same position in a sample of sites.

Spatial patterns of deer density estimated by model ensembles are similar between 'best' and averaged Bayesian regression
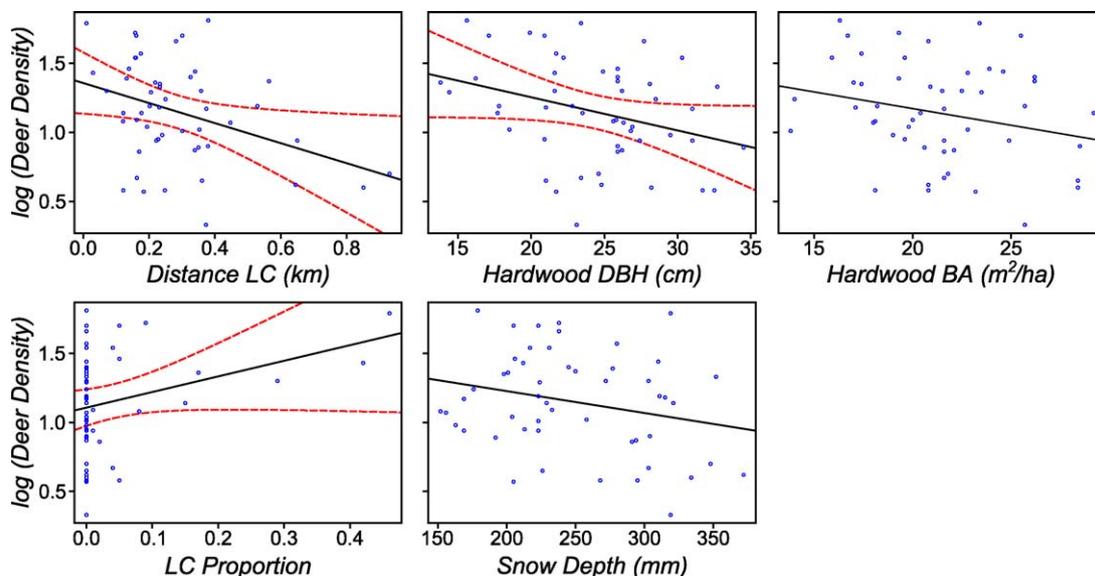
Fig. 3. Univariate relationships between (log) deer density and independent variables with $P < 0.10$. Ordinary least squares regression lines are shown for all variables. Confidence bands (95%) are shown for relationships with $P < 0.05$.

Table 2

'Full' and 'Best' ordinary least squares linear regression models of (log) deer density. Variables statistically significant at $P < 0.05$ are shown in bold and at $P < 0.10$ in italics. Error estimates for cross-validation results are 95% confidence intervals calculated from mean and variance of 100 repetitions. Models use data with $n = 51$.
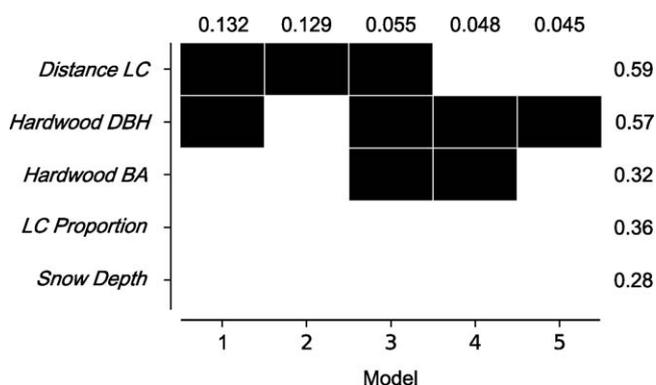
	'Full' model		'Best' model	
	β	P	β	P
Intercept	**2.254**	**<0.001**	**1.815**	**<0.001**
Distance_LC (km)	−0.326	0.276	**−0.624**	**0.019**
Hardwood_DBH (cm)	*−0.019*	*0.063*	*−0.019*	*0.056*
Hardwood_BA (m²/ha)	−0.017	0.216	–	–
LC_Proportion	0.673	0.216	–	–
Snow_Depth (mm)	−0.001	0.312	–	–
Model *P*-value	0.011		0.004	
Model R^2	0.28		0.20	
Model τ[a] (P)[b]	0.38 (0.69)		0.31 (0.66)	
Fivefold cross-validation, R^2	0.11 (±0.005)		0.12 (±0.004)	
Fivefold cross-validation, τ	0.23 (±0.005)		0.23 (±0.004)	

[a] Kendall rank correlation coefficient.
[b] Values in brackets (P) for τ are the probability that observed and modeled deer densities for the same site are ranked at the same position in the entire sample of sites (calculated as $[1 + \tau]/2$).

Table 3

'Best' and averaged Bayesian linear regression models of (log) deer density found by Bayesian model averaging. A dash (–) indicates the variable was not present in the model.

	'Best' model		Averaged model	
	Mean β	Std. Dev.	Mean β	Std. Dev.
Intercept	1.817	0.252	1.760	0.421
Distance_LC (km)	−0.627	0.264	−0.354	0.365
Hardwood_DBH (cm)	−0.020	0.010	−0.012	0.013
Hardwood_BA (m²/ha)	–	–	−0.007	0.012
LC_Proportion	–	–	0.316	0.532
Snow_Depth (mm)	–	–	−0.000	0.001

models (Fig. 5, models are presented in Table 3). Maximum deer density (47 and 50 deer/km² for 'best' and averaged models, respectively) and minimum deer density (9 and 12 deer/km² for 'best' and averaged models, respectively) are also similar. Lower deer densities away from the edges of northern hardwood stands are observed for both models (Fig. 5a and b), as expected given the important negative relationship between Distance_LC and deer density (Table 1, Figs. 3 and 4). However, greatest pixel estimate standard deviations (i.e., uncertainty) are also generally greater away from the edges of northern hardwood stands, reflecting the influence of the combination of high Distance_LC values with uncertainty in the parameter estimate (Fig. 5c and d, Table 3). Uncertainty in pixel deer density estimates is low at the edge of many northern hardwood stands because uncertainty in the intercept value of the regression models is low (i.e., relatively low standard deviation compared to the estimate mean, Table 3).

Greatest differences in deer density estimates between 'best' and averaged model ensemble maps are in areas with low Distance_LC and high LC_Proportion, with greater densities generally predicted by the averaged model (e.g., area highlighted by circles in Fig. 5a and b). Uncertainty is greater in all areas for the averaged model compared with the 'best' model (Fig. 5c and d). Mean pixel standard deviations are 2.2 and 4.2 deer/km² for 'best' and averaged model uncertainty maps, respectively. Greater uncertainty in deer density estimates for the averaged model is
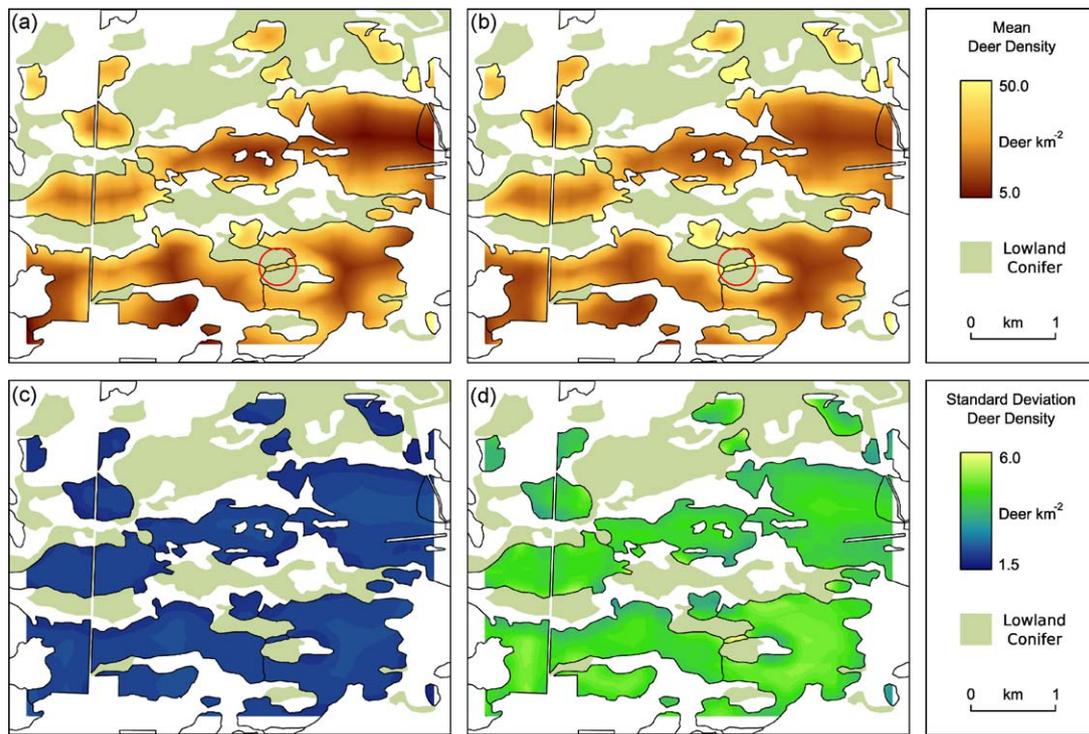
a result of the addition of variables with large standard deviations relative to their mean estimate values (Hardwood_BA, LC_Proportion and Snow_Depth, Table 3).

4. Discussion

4.1. Determinants of winter deer density

Our results highlight the importance of lowland conifer cover for winter deer habitat and show that it is an important driver of deer density in northern hardwood stands of mixed hardwood-conifer forests. The negative relationship of deer density with Distance_LC (Table 1, Fig. 3) implies deer densities are greater nearer lowland conifer stands (which provide thermal cover) and the positive relationship with LC_Proportion (Table 1, Fig. 3) indicates more deer in areas with greater lowland conifer forest cover (again providing thermal cover). Our results also suggest that local northern hardwood stand structure (mainly Hardwood_DBH) is important for deer density. The importance of Hardwood_DBH (Table 1, Figs. 3 and 4) is less easy to interpret than lowland conifer variables. Hardwood_DBH was unassociated with particular tree species relative abundance or tree diversity $(P > 0.19)$ or with time since last partial harvest $(P = 0.125)$. Although we expected aspects of forest management to be influential, we are currently unable to provide a convincing reason for the importance of Hardwood_DBH on deer density. However, our results for Hardwood_DBH are similar to those from the only other known study of this type (Dumont et al., 1998), which found local deciduous forest DBH was an important driver of winter white-tailed deer density at a study site in eastern Quebec, Canada.

We examined the influence of regional variables (e.g., mean daily snow depth and Albert's ecoregion subsection boundaries) because deer density in northern hardwood stands over our 4000 km² study area could be modified by factors that vary at this scale. Although snow depth varied across our study area, the limited influence of Snow_Depth on deer density may be attributable to the relatively shallow snow depths in our study area. Compared with the depth at which snow begins to significantly impair deer movement and increase energy costs (around 400 mm, e.g., Parker et al., 1984; Pauley et al., 1993), our mean daily snow depths (150–370 mm with a mean of 250 mm) indicate that snow is not such a hindrance to deer movement in our study area as it might be in others. Shi et al. (2006) found snow depth to be very important for driving regional variation in deer distribution for a study area larger than ours in Michigan's western U.P. (e.g., on the Keweenaw Peninsula where winter snowfall is greater). They found snow depth was less important in the vicinity of our study area. We suggest that our methods may be applicable to other regions with similar forests (e.g., much of the mixed hardwood-conifer forests of the Great Lakes region), although the importance of variables (such as snow depth) may vary.

Fig. 4. Bayesian model averaging. Results for the five models with highest posterior probability of being the best candidate model in each model set are shown (probability for each model shown at top). Dark blocks indicate the corresponding variable (row) is included in a given model. Posterior probabilities of variables being included in the best model are shown to the right of the blocks.

Fig. 5. Spatial estimates of deer density from regression model ensembles. (a) Mean of ensemble estimates from best Bayesian regression model, (b) mean of ensemble estimates from averaged Bayesian regression model, (c) standard deviation of ensemble estimates from best Bayesian regression model, and (d) standard deviation of ensemble estimates from averaged Bayesian regression model (regression model details in Table 3). Each model ensemble is composed of 1000 regressions using parameter estimates sampled from ensemble posterior probability distributions. Original forest cover map is shown in Fig. 1c. Red circles highlight an example area of a relatively great difference between deer density model estimates, due to high LC_Proportion (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article).

Interestingly, Shi et al. (2006) also found that for our study area, patch area of white cedar canopy cover >70% is more important than snow for determining regional deer density. We found that Distance_LC is likely more important than LC_Proportion for explaining deer density (Table 1, Fig. 4) but that the two variables are somewhat correlated (Pearson's correlation coefficient = −0.43). We suggest the results of Shi et al. (2006) might be due to colinearity between patch area of cedar cover and distances to those patches within pixels of the coarse grain data they used (23 km^2). Although our fine-scale stand-level data have restricted the number of data points for analysis, they allow us to refine understanding about the mechanisms of spatial relationships—in this case that deer density is influenced more by proximity to the thermal cover of lowland conifer stands than the local abundance of lowland conifer.

We included Ecoregion in our analyses as a proxy for regional-scale variation in land cover pattern between southeast and northwest of our study area. Although Ecoregion was not an important predictor of our deer density estimates, parameter estimates from Geographically Weighted Regression analyses (not presented, Fotheringham et al., 2002) suggest greater influence of Distance_LC than Hardwood_DBH and Hardwood_BA in the north and west of the study, and vice versa in the south and east. However, these spatial patterns are not significantly different from a random distribution (Hope's 1968 Monte Carlo significance test at $P < 0.05$), and the absence of spatial pattern in residuals from our OLS regression models suggests that any regional differences in forest cover in our study area are not important for the models we have investigated above. This implies that our 'global' models (i.e., for the full extent of our study area, Tables 2 and 3) are appropriate, and that potential differences in the importance of variables across our study area are due to variation in the distribution of independent variables rather than in how those variables influence deer density.

4.2. Management implications

The ability to predict white-tailed deer density in northern hardwood stands would be valuable to managers for a number of reasons, including efforts to achieve desirable levels of both tree regeneration and deer in a managed forested landscape. Management activities aimed at mitigating the impact of white-tailed deer on ecological processes should be targeted at areas with relatively high deer density, as magnitude of deer impact on ecological processes such as tree regeneration is likely to be greatest in these areas (Rooney and Waller, 2003). Information about the types of variables that we found to be important in predicting variation in deer density in northern hardwood stands (cover type, size/density, distance) is usually available to land managers in inventory and GIS databases. Thus, using readily accessible data, land managers could estimate relative winter deer density across their management areas, as shown in our spatial estimates (e.g., Fig. 5). We suggest maps such as these are best used as indicators of relative deer density across a landscape, given the many assumptions needed to use counts of deer fecal pellet groups as a proxy for deer density (for example, our 'best' regression model explains 20% of variance in deer density, but has a 66% chance of correctly ranking a site, Table 2).

By adopting an ensemble modeling approach, in which multiple realizations of a regression model are generated by sampling from the probability distributions provided by the Bayesian linear regression, we are able to produce 'uncertainty' maps to accompany our deer density estimates (Fig. 5c and d). Measures of uncertainty in deer density estimates produced by Bayesian ensemble models are equally as important as the deer density estimates themselves. Although it has been argued that predictions using Bayesian model averaging can outperform predictions based on a single 'best' model (Raftery et al., 1997; Clark, 2007),
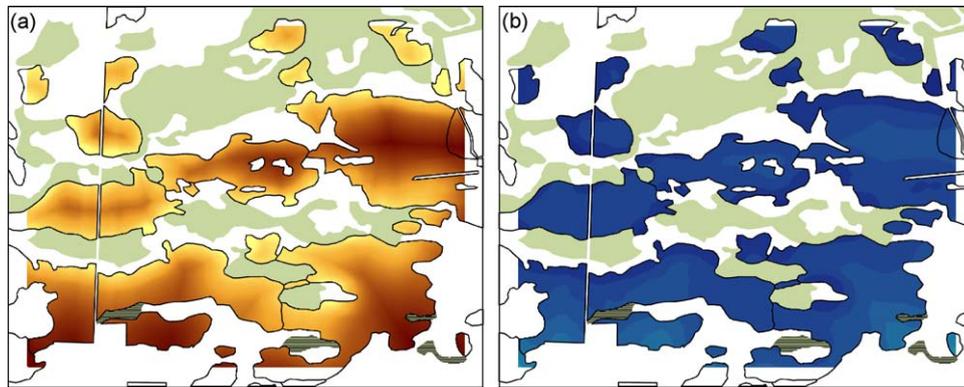
Fig. 6. Spatial estimates of deer density for scenario with four lowland conifer stands removed. (a) Mean of ensemble estimates from best Bayesian regression model, (b) standard deviation of ensemble estimates from best Bayesian regression model (regression model details in Table 3). Legend as for Fig. 5—the four horizontally striped lowland conifer stands are assumed to be removed for this model ensemble. Compare mean and standard deviation of deer density estimates with Fig. 5a and c, respectively. Original forest cover map is shown in Fig. 1c.

others caution that the method is still in its infancy and requires further testing (Stephens et al., 2007). For forest managers working under data constraints, parsimonious models are of particular value. In our case, we suggest that the relatively large uncertainty in the averaged model parameter estimates means that the model from our suite of variables with the greatest posterior probability (the 'best' model) is most useful.

A variety of management practices can be prescribed to control deer density and moderate browse impacts on vegetation in forest stands. For example, our results show that the proximity of lowland conifer cover is positively correlated with winter deer density, so judiciously chosen conifer stands could be removed to reduce the suitability of nearby areas for winter deer habitat. The current conservative philosophy toward harvesting lowland conifer stands is seemingly at odds with this suggestion. Managers are reticent to harvest these stands given the difficulty of regenerating them and, like northern hardwood stands, deer browse is implicated for their regeneration failure (Anderson and Loucks, 1979; Rooney et al., 2002). However, management that includes high intensity harvests but retains few residual mature trees at low density (e.g., seed tree silvicultural systems) may both provide adequate seed for regeneration and reduce winter deer density (via eliminating thermal cover) long enough for regeneration in both the former lowland stand and adjacent hardwood stands to outgrow the reach of deer. There is evidence that many cedar-dominated lowland conifer stands in the vicinity of our study area are even-aged in origin (Heitzman et al., 1997), supporting the notion that even-aged techniques (i.e., total or near-total stand replacement) would be a viable means for regenerating cedar given low deer density. Empirical trials should investigate the efficacy of higher intensity harvests in lowland conifer stands with the aim of decreasing deer populations to promote regeneration in lowland conifer and/or adjacent hardwood stands.

As our data show, the design of these trials should explicitly consider the spatial effects of adjacent stands as a factor influencing deer populations. We can inform this design using our spatial estimates of deer density. For example, from the land cover map for the section of our study area examined above, we removed four small lowland conifer stands (total area 0.18 km^2) that have a large area of surrounding hardwood stands with relatively high estimated deer density and low uncertainty (indicated by the horizontal stripes in Fig. 6). These characteristics suggest the removal of these stands will maximize the area and magnitude of decreases in deer density whilst minimizing the total area of lowland conifers harvested. Using the 'best' model from our Bayesian analysis (Table 3), we produce a model

ensemble with the new scenario forest cover map (DBH of northern hardwood stands is assumed to be unaffected in this scenario). The spatial estimates for this scenario predict that by removing the four lowland conifer stands (area 0.18 km^2), mean deer density in the 1.48 km^2 of adjacent northern hardwood stands is reduced from 18.2 to 7.9 deer/km^2 (compare Figs. 6a and 5a). Uncertainty for these areas with lower estimated deer density is slightly greater than that in our previous map because distance to conifer has increased (compare Figs. 6b and 5c), but it is still low relative to the mean decrease in deer density for the area (maximum standard deviation of pixel estimates is 2.6 deer/km^2 in the scenario map). It is important to highlight that even though our model construction and inference is based on the best current understanding of winter survival requirements for deer, there is the possibility of incorrectly assuming that high quality deer habitat is inexorably linked to high deer densities (van Horne, 1983). Consequently, although spatial estimates of deer density for multiple scenarios of timber harvest removal like ours will be useful to guide where trials may be best located, they are no substitute for empirical study of such management actions.

5. Conclusions

In this paper we have quantified the effects of local and regional landscape characteristics on the spatial distribution of white-tailed deer, produced maps of estimated deer density (and associated uncertainty) using these quantified relationships, and shown how this information can be used to guide co-management of deer and forest regeneration. Winter white-tailed deer density in northern hardwood stands of Michigan's U.P. is negatively related to distance to lowland conifer stands and mean northern hardwood diameter-at-breast-height in the surrounding 12.5 ha. The estimated deer density maps produced using Bayesian regression model ensembles, with their associated uncertainty maps, provide a means to identify areas where managers may most effectively focus their actions. Information such as spatial distributions of wildlife species as a consequence of local forest structure and regional forest cover can aid the co-management of wildlife and forests for ecological and economic sustainability.

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