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Quantifying clutter: A comparison of four methods and their relationship to bat detection

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ABSTRACT

The degree of spatial complexity in the environment, or clutter, affects the quality of foraging habitats for bats and their detection with acoustic systems. Clutter has been assessed in a variety of ways but there are no standardized methods for measuring clutter. We compared four methods (Visual Clutter, Cluster, Single Variable, and Clutter Index) and related these to the probability of detecting bat calls. From June to July, 2005–2006, we used Anabat detectors to conduct acoustic surveys for 2–4 nights at each of 71 points representing three visual clutter classes. We used a cluster analysis to identify groups of plots with similar characteristics. We used backwards stepwise discriminant analyses to identify important plot structure variables that differentiated among clutter classes and used discriminant analyses to test the effectiveness of the plot structure variables in classifying plots into visual clutter classes or clusters. Two clutter volume indices ($Index_{max}$ and $Index_{15m}$) were computed for each plot by calculating the ratio of vegetation volume to available space in the plot. We assessed the effects of the clutter estimation methods on the probability of detecting bats in low and high frequency phonic groups. Occupancy rates ranged from 0.30 to 0.78 and probability of detecting any bat was $\geqslant$0.78 for each period; however, few identifiable calls were recorded. Live tree basal area, midstory live stem count, and canopy crown volume were the most effective measures of clutter for bats because each was a plausible predictor of bat detection and the former two were important for discriminating among plots with differing structure. The use of clutter indices has promise but such methods need to be tested prior to implementation. In future studies of bat foraging habitat, quantitative measures should be used to assess clutter so it is possible to make comparisons among habitats or studies.

1. Introduction

The degree of spatial complexity in the environment, or clutter (Fenton, 1990), is an important factor in the selection of foraging habitat by insectivorous bats (Humes et al., 1999; Law and Chidel, 2002; Erickson and West, 2003; Patriquin and Barclay, 2003). Worldwide, most bat species are insectivorous (Jones and Rydell, 2003), but there is considerable variation among these species in their use of clutter. Species that forage in cluttered habitats tend to have low wing loading (mass/wing area) or small aspect ratios (wingspan^2/wing area) which make them better adapted for foraging in these environments (Norberg and Rayner, 1987). Although most Vespertilionid bats tend to have low wing loading (Norberg and Rayner, 1987), a slight change in body size can have a significant impact on habitat use. For example, Patriquin and Barclay (2003) found *Myotis* bats (wingloading 0.067–0.069, aspect ratio 6.37–6.65, Farney and Fleharty, 1969) were present in cleared, thinned, and unharvested patches of boreal forest, but silver-haired bats (*Lasionycteris noctivigans*; wingloading 0.081, aspect ratio 7.29, Farney and Fleharty, 1969) avoided unharvested patches of forest. Ability to forage effectively in clutter may also depend on echolocation call structure. High frequency broadband calls are most efficient for locating prey against a cluttered background (Siemers and Schnitzler, 2004), but even species that use such calls, like northern long-eared bats (*Myotis septentrionalis*) and little brown bats (*M. lucifugus*), modify their echolocation calls in dense vegetation by increasing frequency and slope, and decreasing call duration (Broders et al., 2004; Wund, 2006). Species with lower frequency calls, such as big brown bats

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(*Eptesicus fuscus*) and hoary bats (*Lasiurus cinereus*) tend to forage in openings (Menzel et al., 2002) or above the forest canopy (Menzel et al., 2005). As an alternative to echolocation, some species merely listen for prey-generated sounds when foraging in echo-cluttering environments (Arlettaz et al., 2001).

Clutter is also important to consider when designing acoustical studies and interpreting recorded data because dense vegetation may obscure bat calls (Patriquin et al., 2003), as well as decrease the number or types of bats that use a habitat. For example, when multiple detectors are set at a point within a forest, those oriented toward the lowest clutter record more bat passes than those facing areas of higher clutter (Weller and Zabel, 2002). Further, clutter-adapted bats may be more difficult to detect because they often use low intensity calls (e.g., *M. auriculus*, Fenton and Bell, 1979) and attenuation rate increases with call frequency (Lawrence and Simmons, 1982). However, in a study in open, thinned, and intact forest habitats in Alberta, Canada, Patriquin et al. (2003) found that 40 kHz sounds are detected 18 m from the source regardless of the complexity of habitat structure, but 25 kHz sounds are not detected as readily in intact forest patches. Missed calls may be interpreted as (false) absences or lower activity levels. Dense clutter may also affect the quality of recorded calls (but see Obrist et al., 2011). Calls from mature forests are less likely to be identifiable than calls from other habitats such as clearings and trails (Britzke, 2003), and there is a weak negative correlation between forest canopy cover and the proportion of identifiable passes (Ford et al., 2005). Poor quality calls are difficult to identify to species or may be misidentified.

Although clutter affects bat behavior and the design and interpretation of acoustic studies, and there are many methods for measuring clutter, there is no standardized global reference method. In most studies, bat activity is compared among habitat types such as thinned, unthinned, and old-growth forests (Humes et al., 1999) or open lake, open river, and forest edge (Wund, 2006), but this method does not facilitate comparisons among study areas. One technique for assessing clutter is to classify sites into predefined clutter categories by visual inspection (e.g., Loeb and O'Keefe, 2006), a method that may not be accurate unless the categories are very broad (e.g., gap or forest). Bradshaw (1996) used a camera to construct vertical profiles of clutter density based on a method developed by MacArthur and Horn (1969), but this method was not fully assessed. Law and Chidel (2002) estimated clutter for different vegetation strata by scoring clutter on a scale of 1–4. A similar method developed by the USDA, Forest Service Forest Inventory and Analysis Work Unit (1991) is the "zone percent" technique in which vegetation density is quantified by estimating the percent contribution of different types of vegetation to each of three canopy layers within an imaginary plot cylinder, but this method could be time consuming and subjective in speciose environments, such as broadleaf deciduous forest. Quantitative habitat variables such as canopy closure and canopy height (Ford et al., 2005), distance to vegetation (Broders et al., 2004), and live tree basal area (Yates and Muzika, 2006) have been used as indices for clutter in studies of bat habitat use and echolocation, but we know of no studies that have compared the efficacy of these measures as clutter indices. Avina et al. (2007) developed a method to assess clutter within an area of known volume as it relates to bat activity; however, the overall vegetation volume measurement developed by these authors was not a good predictor of bat activity (Titchenell et al., 2011). Jung et al. (2012) related bat species composition and activity to three-dimensional forest structure using Light Detection and Ranging (LiDAR) data collected via helicopter; their data show that, when available, LiDAR is an important tool for measuring the effects of clutter on forest bats.

Our goal was to develop an efficient, on-the-ground method for measuring vegetative clutter that could easily be applied to other forested ecosystems. Here we compare four methods for defining vegetative clutter. For the Visual Clutter Method, we classified survey sites into three clutter classes (high, medium, or low) based on visual assessments by one observer and used a discriminant analysis to identify important variables for differentiating among the three clutter classes. Next we applied the Cluster Method, in which we measured several plot structure variables, used a cluster analysis to identify groups of plots with similar characteristics, and then used a discriminant analysis to determine which variables best discriminated among the groups. We used the results of the discriminant analyses for the Visual Clutter and Cluster methods to determine the relative importance of individual plot structure variables as indices of clutter (Single Variable Method). Finally, we used a Clutter Index Method, creating clutter volume indices based on the ratio of vegetation volume to available space in a cylinder the same radius as the plot. With this method, our goal was to quantify clutter in a comprehensive way that was repeatable among observers and habitat types. To test the effectiveness of each method, we related measures of clutter to the probability of detecting bat calls. We assumed that probability of detection varies inversely with clutter either because bat presence or richness will decline, or because bats are more difficult to detect with increasing clutter.

2. Materials and methods

2.1. Study area

We conducted our study from June to August 2005–2006 on the Wayah Ranger District of the Nantahala National Forest in Macon County, North Carolina. Our study sites were in the Trimont Ridge (TR; 83° 29′ E, 35° 11′ N) and Wine Springs (WS; 83° 34′ E, 35° 11′ N) tracts. TR was approximately 2658 ha with elevations ranging from 700 m to 1200 m and WS was approximately 2183 ha with elevations ranging from 800 m to 1600 m. While oaks (*Quercus*) and hickories (*Carya*) were common overstory hardwoods in both tracts, yellow poplars (*Liriodendron tulipifera*) were more prevalent in TR and sugar maples (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) were common in WS. White pine (*Pinus strobus*) was the most common overstory conifer in both tracts. Upland hardwood stands dominated TR (54%; 1448 ha), followed by cove hardwood stands (35%; 936 ha), mixed pine-hardwood stands (8%; 225 ha), and white pine stands (2%; 45 ha). Upland hardwood stands also dominated WS (57%; 1239 ha), followed by cove hardwood stands (32%; 708 ha), mixed pine-hardwood stands (11%; 232 ha), and conifer stands (<1%; 4 ha). Based on stand ages in 2005, approximately 143 ha (5.4%) of TR were early successional (⩽15 yr), 325 ha (12.2%) were sapling/pole (16–39 yr), 732 ha (27.5%) were mid-successional (40–79 yr), and 1459 ha (54.9%) were late-successional (⩾80 yr). In WS, 144 ha (6.6%) of the area was early successional, 112 ha (5.1%) was sapling/pole, 500 ha (22.9%) was mid-successional, and 1428 ha (65.4%) was late-successional. Small streams (1–2 m wide) were common on the landscape, while larger streams were rare; bat activity is low near these small streams (O'Keefe et al., 2013). In summer (May–August), mean minimum and maximum daily temperatures were 16.8 °C and 28.0 °C in 2005, and 15.3 °C and 27.8 °C in 2006. Total precipitation in the same period was 45.0 cm in 2005 and 23.1 cm in 2006. Temperatures and remotely sensed precipitation estimates are for Wayah Bald, ~13 km southwest of the study area center (State Climate Office of North Carolina).

2.2. Sampling

We conducted three sampling sessions of 2–3 nights per year and sampled 12 forest stands per session. One stand was sampled twice, so a total of 71 stands were sampled. Each of the 12 survey points in a session represented a unique combination of three variables: elevation (TR = low, WS = high), aspect (general facing of N or S), and visual clutter (high, medium, or low). We numbered 311 potential stands and randomly selected stands from this list for each session. In general, low clutter stands contained $\leqslant$6 or $\geqslant$95 year old hardwoods or mixed pine-hardwoods; medium clutter stands contained 70–100 year old hardwoods; and high clutter stands contained 10–25 year old hardwoods or mixed pine-hardwoods. The senior author assigned visual clutter (high, medium, low) designations to all stands in the field. For each stand, we generated a random point using an extension to ArcView 3.2 (ESRI, Redlands, California) and set detectors at the position closest to the random point that was >25 m from the stand edge, streams, trails, or canopy gaps >10 m wide.

We used an Anabat II detector (Titley Electronics, Ballina, New South Wales, Australia) connected to a compact flash storage zero-crossings interface module (CF ZCAIM) to passively sample each point from 20:30 to 6:30 EDT for 2–4 consecutive nights during each session. Anabats and ZCAIMs were housed together in waterproof containers with the microphone nested at the base of a 45° PVC tube; boxes were set on tripods ~1.3 m high and oriented downhill in a position where no vegetation directly obstructed the microphone, which pointed upwards (Weller and Zabel, 2002). We randomly assigned detectors to points to minimize bias due to variable reception rates for different detectors (Britzke, 2004) and Anabat sensitivity was set at 7.

Acoustic data were analyzed with Analook software (v 4.9j) for MS-DOS; we used a filter to exclude call fragments and insect noise. The filter we used was identical to the default filter, except minimum frequency sweep parameter was 0 and bodyover parameter was 160 (Britzke, 2003). We verified that selected files represented bat calls by visual inspection. We did not identify most passes to species because only 21 and 66 bat passes were of sufficient quality for identification ($\geqslant$5 pulses per sequence) in 2005 and 2006, respectively. However, we visually assessed the presence of bats in high frequency (characteristic frequency, F_C > 30 kHz) and low frequency ($F_C \leqslant 30$) phonic groups for each detector night, where F_C was defined as the frequency at the end of the flattest portion of a bat call (Corben, 2004). Hoary bats, silver-haired bats, and big brown bats were the low frequency bats that occurred in the areas surveyed; high frequency bats were eastern small-footed bats (*M. leibii*), northern long-eared bats, little brown bats, tri-colored bats (*Perimyotis subflavus*), and eastern red bats (*Lasiurus borealis*; O'Keefe, 2009). We constructed comprehensive presence/absence histories (MacKenzie et al., 2006) for all surveys by assigning a one to detector-nights where $\geqslant$1 bat call was recorded and a zero to detector-nights with no bat calls. We treated each sampling night as one visit when generating detection histories by phonic group for each site. Twelve points surveyed in August 2005 were dropped from the acoustical analysis because CF cards were filled with excessive insect noise. Thus, we analyzed detection data for 60 sampling points.

2.3. Plot structure data

We collected vegetation data in 0.04 ha circular plots at each sampling point. Because we were working in steep terrain, we applied a correction factor to the plot radii in the direction of the slope to ensure that the vertically-projected area (0.04 ha) was consistent among plots. Radii for the uphill and downhill plot lines were obtained by dividing the original plot radius (11.3 m) by cos(arctan(plot slope in decimal form)) (Abella et al., 2004). Within a nested 0.01 ha circle, we measured the diameter at breast height (dbh) for all live and dead stems >1.4 m tall; stem counts were subsequently multiplied by 4 for comparison with whole plot data. Outside the nested plot, we tallied dbh for all live and dead trees >10 cm dbh and >1.4 m tall. In addition, for each quarter plot, we selected a live reference stem or tree from each of three canopy layers (understory, midstory, and canopy); first, we selected a live reference stem from any layer that was closest to plot center, then the next closest stem of another layer until we had measured trees from each layer. When possible, for the entire plot, each reference stem of a particular layer was a different tree species to account for variation in volume by species when generalizing to the entire plot. Canopy trees were defined as the tallest trees >10 cm dbh in a particular stand, the midstory layer included saplings 4–10 cm dbh with crowns completely beneath the upper canopy layer, and understory trees were saplings or shrubs >1.4 m tall and <4 cm dbh. For each reference tree, we recorded diameter at breast height (dbh) and crown width (average of the longest axis and its perpendicular). We used a clinometer to measure stem and crown heights for each reference tree. For each plot, we calculated the average volume for the stems (circular cylinder, V_{stem}) and crowns (elliptical cylinder, V_{crown}) of reference trees in each of three canopy layers. Plot data were condensed into 14 variables representing plot structure (Table 1).

We developed two clutter indices ($Index_{max}$ and $Index_{15m}$) by calculating a ratio of vegetation to available space in each plot; we considered space occupied by vegetation to be unavailable to bats in flight. To calculate $Index_{max}$, we first determined the volume occupied by all of the vegetation in each plot ($V_{veg\ total}$). To do this, we calculated total crown volume ($V_{crown\ total}$) and total stem volume ($V_{stem\ total}$) by combining measurements for V_{crown} and V_{stem} from the three canopy layers (see Table 1 for variable definitions).

$V_{crown\ total}$ was defined as:

$$(\mathrm{ulstmct})(\mathrm{mean}V_{crown\_understory}) + (\mathrm{mlstmct}) \times (\mathrm{mean}V_{crown\_midstory}) + (\mathrm{clstmct})(\mathrm{mean}V_{crown\_canopy}) \quad (1)$$

$V_{stem\ total}$ was defined as:

$$(\mathrm{ulstmct} + \mathrm{udstmct})(\mathrm{mean}V_{stem\_understory}) + (\mathrm{mlstmct} + \mathrm{mdstmct})(\mathrm{mean}V_{stem\_midstory}) + (\mathrm{clstmct} + \mathrm{cdstmct})(\mathrm{mean}V_{stem\_canopy}) \quad (2)$$

Subsequently, $V_{veg\ total}$ was defined as:

$$V_{crown\ total} + V_{stem\ total} \quad (3)$$

Next we determined the actual volume of each plot. We determined the height of the tallest reference tree in each plot ($height_{max}$) and used this value to calculate the volume of a cylinder the same height as the tallest reference tree. Thus, each plot had a unique value for volume.

Table 1
Fourteen plot structure variables measured in 0.04 ha plots at bat survey points (n = 71) in temperate deciduous forests in southwestern North Carolina, USA, June–August, 2005–2006.

Variable	Definition
ulstmct	understory live stem count/0.04 ha
udstmct	understory dead stem count/0.04 ha
ucrnvol	mean understory crown volume (m^3)
ustmvol	mean understory stem volume (m^3)
mlstmct	midstory live stem count/0.04 ha
mdstmct	midstory dead stem count/0.04 ha
mcrnvol	mean midstory crown volume (m^3)
mstmvol	mean midstory stem volume (m^3)
clstmct	canopy live stem count/0.04 ha
cdstmct	canopy dead stem count/0.04 ha
ccrnvol	mean canopy crown volume (m^3)
cstmvol	mean canopy stem volume (m^3)
ltba	live tree basal area (m^2/0.04 ha)
dtba	dead tree basal area (m^2/0.04 ha)

Maximum height plot volume ($V_{plot\ max}$) was defined as:

$$(\pi)(11.3m)^2(height_{max}) \quad (4)$$

Finally, we defined $Index_{max}$ as:

$$V_{veg\ total}/V_{plot\ max} \quad (5)$$

To calculate $Index_{15m}$, we determined the volume occupied by vegetation ⩽15 m from the ground ($V_{15m\ veg}$). We chose 15 m as a conservative estimate of the height at which we should be able to detect calls from all of the common bats in our study area (given that a 100 dB 40 kHz sound attenuates to non-detectable at ~27 m at 15 °C, 65% relative humidity; Lawrence and Simmons, 1982). For the bat community in our study area, the approximate mean F_C for calls from all bat species is 35 kHz. For each plot, we truncated the measurement data for crown and stem heights to 15 m (i.e., heights >15 m were replaced with 15 m). Next we calculated total crown volumes up to 15 m ($V_{15m\ crown\ total}$) and total stem volumes up to 15 m ($V_{15m\ stem\ total}$) by combining measurements for stem counts and crown ($V_{15m\ crown}$) and stem volumes ($V_{15m\ stem}$). $V_{15m\ crown\ total}$ was defined as:

$$(\text{ulstmct})(\text{mean}V_{15m\ crown\_understory}) + (\text{mlstmct}) \times (\text{mean}V_{15m\ crown\_midstory}) + (\text{clstmct})(\text{mean}V_{15m\ crown\_canopy}) \quad (6)$$

$V_{15m\ stem\ total}$ was defined as:

$$(\text{ulstmct} + \text{udstmct})(\text{mean}V_{15m\ stem\_understory}) + (\text{mlstmct} + \text{mdstmct})(\text{mean}V_{15m\ stem\_midstory}) + (\text{clstmct} + \text{cdstmct})(\text{mean}V_{15m\ stem\_canopy}) \quad (7)$$

Subsequently, $V_{15m\ veg}$ was defined as:

$$V_{15m\ crown\ total} + V_{15m\ stem\ total} \quad (8)$$

We determined a standard volume for all plots using 15 m for height, ($V_{15m\ plot}$):

$$(\pi)(11.3m)^2(15m) \quad (9)$$

Finally, we defined $Index_{15m}$ as:

$$V_{15m\ veg}/V_{15m\ plot} \quad (10)$$

2.4. Statistical analyses

We used SAS 9.1 (SAS Institute, Inc., 2004) to analyze plot data. To remove the effects of differing scales, we standardized (PROC STDIZE) each of the 14 plot structure variables (Table 1) by subtracting the mean and dividing by the standard deviation. To assess the Visual Clutter Method, we performed a backwards stepwise discriminant analysis (PROC STEPDISC) to identify a subset of the 14 standardized plot structure variables that best accounted for the variation among the three visual clutter groups. For each significant variable we used an analysis of variance (PROC ANOVA) with a Tukey means separation procedure to test for significant differences among the three visual clutter classes. Next, we entered significant variables into a discriminant function analysis (PROC DISCRIM) to test their effectiveness in classifying the plots into the three visual clutter classes.

For the Cluster Method, we entered the 14 plot structure variables into a cluster analysis (PROC CLUSTER) to find meaningful groupings in the data. Because there is no generally accepted clustering technique (Manly, 2005) we explored several methods and selected Ward's Minimum Variance Method, which minimizes within cluster sum of squares (SAS Institute Inc., 2004). We defined primary ($n = 2$) and secondary ($n = 4$) clusters using the first two levels of nodes encountered in a tree diagram (PROC TREE). No additional clusters were considered because we felt that >4 clutter groups would be difficult to assess visually. We performed a backwards stepwise discriminant analysis (PROC STEPDISC) to identify the subset of the 14 plot structure variables that best accounted for variation between primary clusters. For each significant variable, we used an analysis of variance (PROC ANOVA) with a Tukey means separation procedure to test for significant differences between the primary clusters. Next, we entered significant variables into a discriminant function analysis (PROC DISCRIM) to test their effectiveness in classifying the plots into the primary clusters. We repeated the stepwise discriminant analysis, ANOVA, and discriminant function analysis for plots in the secondary clusters.

For the Clutter Index Method, we tested for correlations between the clutter indices ($Index_{max}$ and $Index_{15m}$) and 14 plot structure variables (raw numbers) with Pearson product-moment correlations (PROC CORR). While we do not report correlations among the plot structure variables, only midstory stem volume X midstory crown volume and canopy stem volume X canopy crown volume were correlated at $r > 0.7$. ANOVA tests and correlations were considered significant if $P \leqslant 0.05$.

Using program PRESENCE (Hines, 2006), we measured the effects of clutter covariates on the probability of detecting bats in high and low phonic groups. The following methods were repeated for each of the 2 phonic groups. We used the null detection model as a base for 19 additional models relating probability of detection to the different methods of clutter assessment: visual clutter groups, primary clusters, secondary clusters, the plot structure variables (Table 1), $Index_{max}$, and $Index_{15m}$. All quantitative covariates were standardized in SAS by subtracting the mean and dividing by the standard deviation. We adjusted $\hat{c}$ in PRESENCE when there was a lack of evidence of model fit (MacKenzie and Bailey, 2004). We used Akaike's information theoretic procedures to rank models by their respective values for quasi-Akaike's information criterion (QAIC) and computed Akaike weights (w_i) to compare the plausibility of competing models (Burnham and Anderson, 2002). We considered the model with the lowest value for QAIC to be the best model and models with $\Delta\text{QAIC} \leqslant 2$ to be plausible.

3. Results

Bat activity was low and few of the recorded calls were identifiable. We recorded 479 echolocation sequences in 2005 (two sessions) and 790 in 2006 (three sessions). Low frequency bats were detected in 7 of 20 low clutter plots, 4 of 20 medium clutter plots, and 7 of 20 high clutter plots. High frequency bats were detected in more sites: 18 of 20 low clutter plots, 17 of 20 medium clutter plots, and 12 of 20 high clutter plots. Only 87 call sequences were identifiable; we identified calls from big brown bats, tri-colored bats, and *Myotis* bats; 82 of these sequences were recorded in 10 low clutter sites.

3.1. Visual clutter method

Five plot structure variables were important for differentiating the three visual clutter classes although only 1 variable, canopy live stem count, differed between the low and medium clutter groups (backwards stepwise discriminant analysis, Table 2). Understory and midstory live and dead stem counts were greatest in high clutter plots and lowest in low and medium clutter plots (Table 2). Canopy live stem count was high in medium clutter plots (Table 2). Using the five variables in Table 2, a discriminant analysis correctly reclassified 22 of 24 (91.7%) high clutter plots, 15 of 24 (62.5%) medium clutter plots, and 17 of 23 (73.9%) low clutter plots. One high clutter plot was misclassified as a medium clutter plot and one as a low clutter plot, nine medium clutter plots were

Table 2
Means and standard errors (S.E.s) by visual clutter class for five variables retained by stepwise discriminant analysis of 14 plot structure variables measured in 0.04 ha plots around bat survey points in temperate deciduous forests in southwestern North Carolina, USA, June–August, 2005–2006. F and P are the results of ANOVA tests for each variable.

Discriminating variable[a]	Visual clutter class (number of plots)							
	High ($n = 24$)		Medium ($n = 24$)		Low ($n = 23$)			
	Mean	S.E.	Mean	S.E.	Mean	S.E.	F	P
ulstmct	314.0A[b]	61.1	113.3B	15.7	97.4B	27.5	9.13	0.0003
udstmct	120.7A	23.7	10.3B	2.7	9.6B	2.9	20.71	<0.0001
mlstmct	87.8A	7.8	29.8B	3.8	21.9B	4.8	39.61	<0.0001
mdstmct	18.5A	3.5	4.8B	1.4	3.5B	1.0	12.97	<0.0001
clstmct	23.4AB	1.9	26.5A	1.6	18.8B	1.5	5.20	0.0079

[a] Refer to Table 1 for variable definitions.
[b] Means followed by the same letter within a row are not significantly different ($P > 0.05$).

misclassified as low clutter plots, and five low clutter plots were misclassified as medium clutter plots and one as a high clutter plot.

3.2. Cluster method

We defined two primary and four secondary clusters for the plot data from the tree graph (cluster analysis, Fig. 1). Six plot structure variables best discriminated between primary clusters A and B (backwards stepwise discriminant analysis, Table 3). Plots in cluster A were characteristic of mature stands, with greater midstory crown volume, a higher dead tree basal area, and greater live tree basal area (Table 3). Plots in cluster B had the characteristics of early successional stands, with more live understory stems and live and dead midstory stems. Using the six variables in Table 3, a discriminant analysis correctly reclassified 47 of 47 plots in cluster A and 23 of 24 plots in cluster B.

Nine variables differentiated the secondary clusters (backwards stepwise discriminant analysis, Table 4). Plots in cluster A1 had the structure of late successional stands, with fewer under and midstory stems, greater understory crown volumes, greater midstory crown volumes, fewer live canopy stems, and greater live tree basal area (Table 4). Plots in cluster A2 had the structure of mid to late successional stands, with fewer understory and midstory stems than in B1 and B2 plots, with smaller crowns than in A1 plots. Plots in cluster B1 were indicative of sapling/pole or mid-successional stands, with higher stem densities in all layers but smaller crowns and lower live tree basal area. Plots in cluster B2 had the structure of recently harvested sites, with higher stem counts in the understory and lower stem counts in both the midstory and canopy. Using the nine variables listed in Table 4, a discriminant analysis correctly reclassified all plots into their original groupings (A1, A2, B1, and B2).

3.3. Clutter index method

$Index_{max}$ ranged from 0.06 to 3.8 for 71 plots (>1 for 38 plots, see Discussion), with values of 0.06–3.49 for low visual clutter plots, 0.56–3.81 for medium clutter plots, and 0.17–2.96 for high clutter plots. $Index_{max}$ was negatively correlated with understory dead stem count ($r = -0.26$, $P = 0.03$) and midstory live stem count ($r = -0.24$, $P = 0.05$). $Index_{max}$ was positively correlated with canopy live stem count ($r = 0.35$, $P = 0.003$), live tree basal area ($r = 0.43$, $P < 0.001$), canopy stem volume ($r = 0.24$, $P = 0.04$), midstory crown volume ($r = 0.28$, $P = 0.02$), and canopy crown volume ($r = 0.5$, $P < 0.001$). $Index_{15m}$ ranged from 0.03 to 2.66 for 71 plots (>1 for 29 plots, see Discussion), with values of 0.03–2.21 for low clutter plots, 0.2–2.66 for medium clutter plots, and 0.16–2.0 for high clutter plots. $Index_{15m}$ was positively correlated with understory stem volume ($r = 0.37$, $P < 0.01$), understory crown volume ($r = 0.31$, $P < 0.01$), canopy live stem count ($r = 0.42$, $P < 0.001$), and live tree basal area ($r = 0.36$, $P < 0.01$).

3.4. Detection models

In the null models, the probability of occupancy was 0.36 ± 0.08 for low frequency bats and 0.78 ± 0.05 for high frequency bats. Bats were recorded on every survey night in 2005 and 2006 but never simultaneously in every site surveyed. Of 12 active detectors, 2–11 recorded bats on any given night.

For low frequency bats, there were two plausible models for probability of detection: live tree basal area ($w_i = 0.25$) and primary cluster ($w_i = 0.17$; Table 5). Live tree basal area was inversely related to detection probability for low frequency bats and this

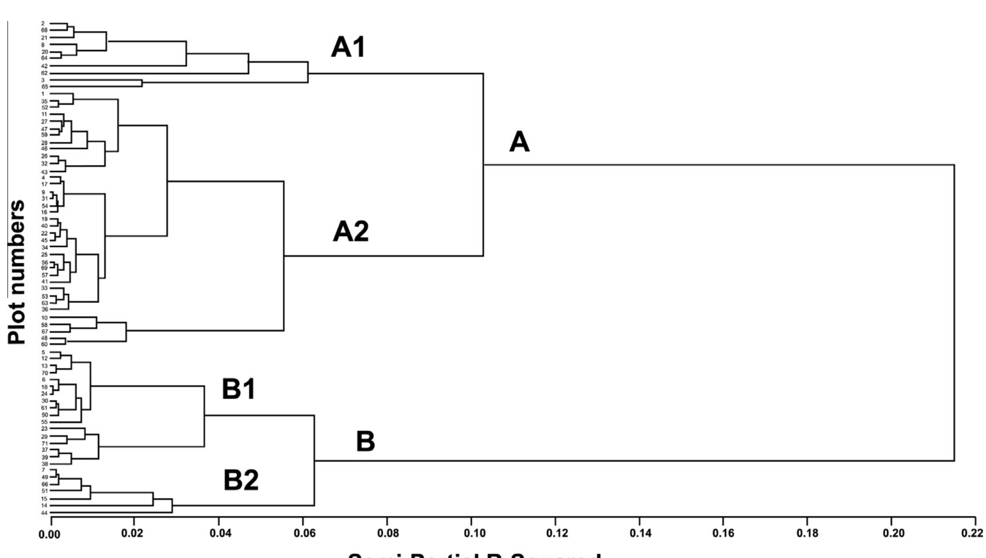

Fig. 1. Ward's minimum variance cluster groupings for bat survey points based on 14 plot structure variables measured in 0.04 ha plots in temperate deciduous forests in southwestern North Carolina, USA, June–August, 2005–2006. A and B represent the two primary clusters, and A1, A2, B1, and B2 represent the four secondary clusters.

Table 3
Means and standard errors (S.E.s) by primary clusters for six variables retained by stepwise discriminant analysis of 14 plot structure variables measured in 0.04 ha plots around bat survey points in temperate deciduous forests in southwestern North Carolina, USA, June–August, 2005–2006. F and P are the results of ANOVA tests for each variable.

Discriminating variable[a]	Primary cluster (number of plots)					
	A (n = 47)		B (n = 24)			
	Mean	S.E.	Mean	S.E.	F	P
ulstmct	94.7	10.6	335.2	61.9	26.88	<0.0001
mlstmct	25.7	3.1	88.3	7.6	82.56	<0.0001
mdstmct	4.0	0.7	18.8	3.6	28.72	<0.0001
mcrnvol	65.5	6.5	13.2	2.0	32.43	<0.0001
dtba	0.09	0.02	0.03	0.01	3.58	0.0628
ltba	1.3	0.04	0.6	0.07	64.06	<0.0001

[a] Refer to Table 1 for variable definitions.

phonic group was more likely to be detected in plots in primary cluster B (Fig. 2A and B), which had the characteristics of early successional stands (Table 3). For high frequency bats, there were two plausible models for probability of detection: canopy crown volume ($w_i = 0.35$) and midstory live stem count ($w_i = 0.13$, Table 6). Midstory live stem count was inversely related to detection probability, but canopy crown volume was directly related to detection probability (Fig. 2C and D). Visual clutter groups were not good predictors of detection probability and, aside from live tree basal area, midstory live stem count, and canopy crown volume, plot structure variables were not important predictors.

4. Discussion

We found that quantitative measurements of individual variables (Single Variable Method) were the most effective measures of clutter relative to the other methods we tested. Midstory live stem count, canopy crown volume, and live tree basal area were better predictors of bat detection in our study, and midstory live stem count and live tree basal area were important in discriminant analyses. These variables related to bat detection as expected. For high frequency bats, midstory live stem count was inversely related to detection probability and canopy crown volume was directly related to detection probability, whereas for low frequency bats live tree basal area was inversely related to detection probability. A higher midstory live stem count would characterize a plot with a cluttered midstory, while a greater crown volume should characterize a plot in which canopy trees shade out and eliminate midstory stems, thus providing a more open flyway for bats. For low frequency bats, a stand with higher live tree basal area should represent a closed canopy; bats might choose to fly above the canopy and out of the range of detection in these conditions. There was moderate support for a greater probability of detecting low frequency bats in early successional-type stands, such as those in Primary Cluster B. Midstory live stem count was also important for distinguishing among plots classified by Visual Clutter and both Cluster methods, while live tree basal area was important in distinguishing among primary and secondary clusters. Relative to the other methods we considered, there are several benefits to using a single variable to assess clutter. Measurements are easy and repeatable among observers and using a single variable facilitates comparisons among habitat types or study areas. However, because variable definitions or characteristics may vary with habitat type (e.g., the definition of midstory stems may differ for a 15 year old versus a 50 year old hardwood stand) some variation among studies or habitats may occur; thus, it is critical to provide clear variable definitions.

We found that quantitative measures of clutter were good predictors of bat detection. Although it is feasible to combine multiple

Table 5
Model parameters and standard errors (S.E.s), quasi-Akaike's Information Criterion (QAIC), difference in QAIC value when compared to the model with the lowest QAIC value (ΔQAIC), and Akaike weight (w_i) for models relating clutter methods to detection probabilities for low frequency bats at 60 survey points in southwestern North Carolina, USA, June–July, 2005–2006.

Models for low frequency bats[a]	Parameter estimate[b]	S.E.[b]	QAIC	ΔQAIC	w_i
ltba	−1.2739	0.3839	95.07	0.00	0.2509
primary cluster (A)	−2.3162	0.7313	95.82	0.75	0.1724
dtba			98.76	3.69	0.0396
ccrnvol			99.06	3.99	0.0341
secondary cluster			99.16	4.09	0.0325
visual clutter class			99.36	4.29	0.0294
cstmvol			100.04	4.97	0.0209
mdstmct			100.21	5.14	0.0192
$\text{Index}_{\text{max}}$			100.69	5.62	0.0151
ucrnvol			100.93	5.86	0.0134
udstmct			100.98	5.91	0.0131
ulstmct			101.20	6.13	0.0117
mcrnvol			101.61	6.54	0.0095
mlstmct			101.64	6.57	0.0094
cdstmct			102.33	7.26	0.0067
$\text{Index}_{\text{15m}}$			102.36	7.29	0.0066
mstmvol			103.00	7.93	0.0048
clstmct			103.56	8.49	0.0036
ustmvol			103.59	8.52	0.0035

[a] Refer to Table 1 for variable definitions.
[b] Parameter estimates and S.E.s reported only for plausible models.

Table 4
Means and standard errors (S.E.s) by secondary clusters for nine variables retained by stepwise discriminant analysis of 14 plot structure variables measured in 0.04 ha plots around bat survey points in temperate deciduous forests in southwestern North Carolina, USA, June–August, 2005–2006. F and P are the results of ANOVA tests for each variable.

Discriminating variable[a]	Secondary cluster (number of plots)									
	A1 (n = 10)		A2 (n = 37)		B1 (n = 17)		B2 (n = 7)			
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	F	P
ulstmct	75.6AB[b]	23.2	99.9A	11.9	233.4B	29.3	582.3C	174.5	19.49	<0.0001
udstmct	49.2AB	36.8	12.8A	3.7	90.8B	12.1	122.3B	72.2	6.48	0.0006
ucrnvol	9.0A	1.0	2.7B	0.2	2.0B	0.3	1.4B	0.6	42.60	<0.0001
mlstmct	22.4A	7.9	26.6A	3.3	96.5B	8.4	68.6B	14.3	30.80	<0.0001
mdstmct	2.8A	1.9	4.3A	0.8	25.9B	4.0	1.7A	1.2	26.10	<0.0001
mcrnvol	108.0A	19.9	54.0B	4.9	15.7C	2.5	7.0C	2.2	21.53	<0.0001
clstmct	18.9A	2.9	24.5AB	1.0	27.9B	1.7	8.9C	2.3	14.27	<0.0001
ltba	1.26A	0.1	1.3A	0.1	0.7B	0.1	0.4B	0.1	22.75	<0.0001
dtba	0.01A	0.01	0.1A	0.02	0.03A	0.01	0.03A	0.02	3.05	0.03

[a] Refer to Table 1 for variable definitions.
[b] Means followed by the same letter within a row are not significantly different ($P > 0.05$).

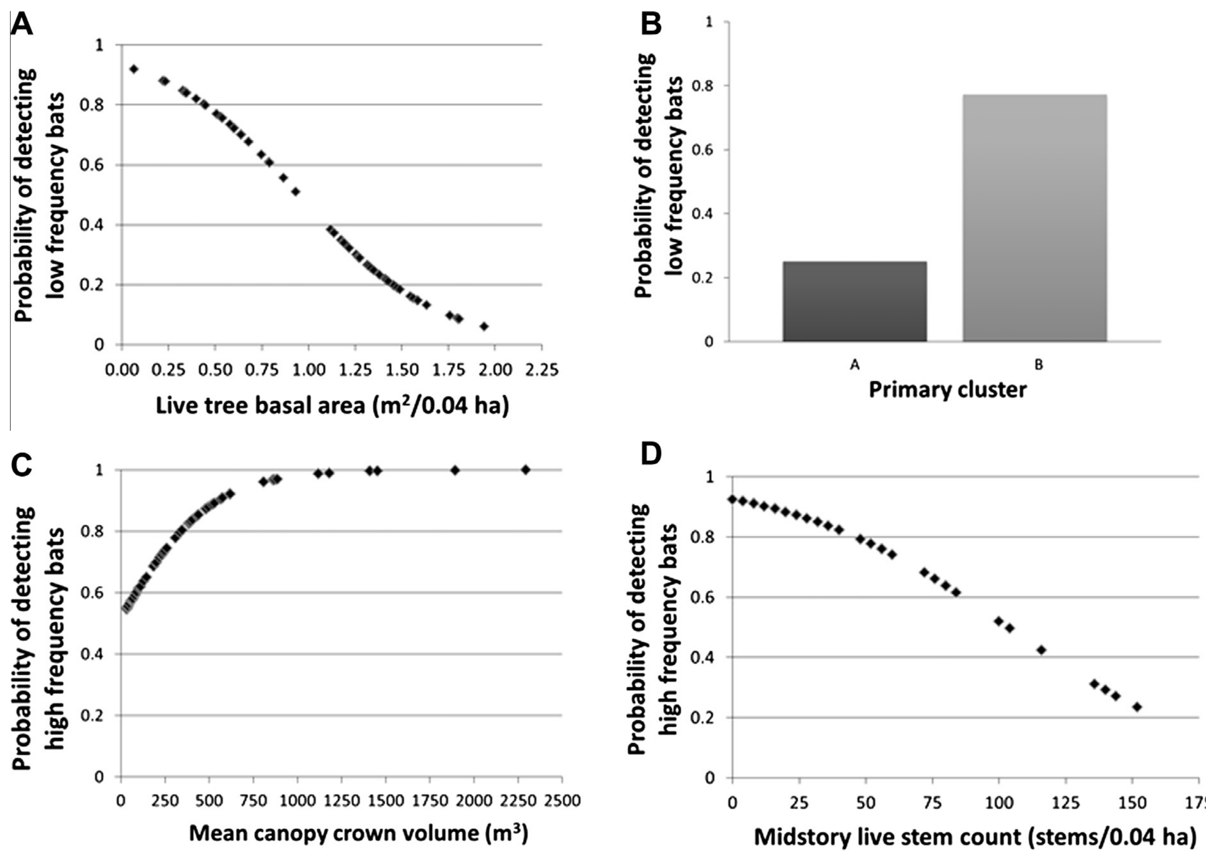

Fig. 2. Relationship between probability of detecting bats and measures of clutter. For low frequency bats, live tree basal area (A) and primary cluster (B) were important predictors. For high frequency bats, canopy crown volume (C) and midstory live stem count (D) were important predictors. X axes are labeled with untransformed data. Detection data are for acoustic survey points in temperate deciduous forests in southwestern North Carolina, USA, June–July, 2005–2006.

Table 6
Model parameters and standard errors (S.E.s), quasi-Akaike's Information Criterion (QAIC), difference in QAIC value when compared to the model with the lowest QAIC value (ΔQAIC), and Akaike weight (w_i) for models relating clutter methods to detection probabilities for high frequency bats at 60 survey points in southwestern North Carolina, USA, June–July, 2005–2006.

Models for high frequency bats[a]	Parameter estimate[b]	S.E.[b]	QAIC	ΔQAIC	w_i
ccrnvol	1.6684	0.7063	122.28	0.00	0.3468
mlstmct	−0.9810	0.2590	124.25	1.97	0.1295
$Index_{max}$			125.19	2.91	0.0809
ucrnvol			125.61	3.33	0.0656
cstmvol			126.36	4.08	0.0451
mstmvol			128.22	5.94	0.0178
visual clutter class			128.36	6.08	0.0166
ustmvol			128.59	6.31	0.0148
$Index_{15m}$			128.62	6.34	0.0146
udstmct			128.68	6.40	0.0141
ulstmct			128.87	6.59	0.0129
mcrnvol			128.98	6.70	0.0122
mdstmct			129.06	6.78	0.0117
primary cluster			129.07	6.79	0.0116
ltba			129.41	7.13	0.0098
clstmct			130.06	7.78	0.0071
dtba			130.13	7.85	0.0068
cdstmct			130.16	7.88	0.0067
secondary cluster			130.30	8.02	0.0063

[a] Refer to Table 1 for variable definitions.
[b] Parameter estimates and S.E.s reported only for plausible models.

predictors in probability of detection models, we chose to assess each measure separately to determine if a single easily-measured variable might explain probability of detection. Clutter measurements are rarely used as covariates when calculating probability of detection for bats, although several studies have examined the relationship between clutter and habitat use or activity (e.g., Erickson and West, 2003; Ford et al., 2006; Yates and Muzika, 2006; Titchenell et al., 2011). In two studies in southern Missouri, a measure of clutter was used as a covariate in detection models (Yates and Muzika, 2006; Starbuck, 2013). Understory density was the only clutter variable considered in detection probability models for bats using hard and mixed pine-hardwood forest by Yates and Muzika (2006), but this variable was not an important predictor of detection probabilities. Percent stand stocking, which was derived from 10-factor prism measurements on tree density and basal area, is negatively related to probability of detection for 4 bat species in open savannas and woodlands and closed canopy forests (Starbuck, 2013). However, detection probability for the northern long-eared bat, which emits the highest frequency echolocation calls of the bats detected in Starbuck's (2013) study, was not affected by stocking. Perhaps clutter measurements are not typically considered in models of detection because researchers simply avoid placing detectors in cluttered areas (Weller and Zabel, 2002). However, when surveying for bats in forests of varying clutter, quantitative measures of clutter may be important covariates in detection models (Patriquin et al., 2003; Starbuck, 2013, this study).

In this study, we took detailed measurements of crown volume and observed a trend for increasing canopy (tallest trees) crown volume with decreasing visual clutter. Canopy crown volume, which should be directly related to canopy closure, is probably a more reliable predictor of clutter than canopy cover because 10–25 cm dbh (i.e., midstory) tree density is lowest when the tallest trees in a stand account for a high proportion of canopy crown area

(Donoso, 2005). Jennings et al. (1999) define canopy cover as the proportion of the forest floor covered by the vertical projection of tree crowns and canopy closure as the proportion of the sky obscured by vegetation; they note that the two terms are often confused. Because canopy cover measures the presence or absence of canopy (Jennings et al., 1999), it can be high in both mature stands with little understory (which we would define as low clutter for bats) and in young stands with dense understory (high clutter); thus, canopy cover may not be a good way to assess clutter for bats. Canopy closure is less subject to sampling bias when compared to canopy cover and may be a better measure of clutter because it is directly related to tree heights within a stand (Jennings et al., 1999).

The notion of a Clutter Index Method has promise for describing plot or stand-level clutter, but this method needs to be refined to better reflect the space available to bats for foraging. At present, the measure does not account for the spatial distribution of vegetation and, thus, the distribution of clutter that might impede bat flight or block reception of ultrasounds. Although our goal was for the indices to range from 0 to 1, $Index_{max}$ and $Index_{15m}$ were >1 for 54% and 41% of plots, respectively. We also decided a priori that effective indices would be directly related to visual clutter (e.g., low visual clutter would have a low clutter index). However, we found no clear relationship between the indices and visual clutter classes. $Index_{max}$ was positively correlated with canopy crown volume; thus, overestimating the contribution of crowns may have been a primary cause of error in the Clutter Index Method. However, $Index_{15m}$ was not correlated with canopy crown volume. Clutter indices might be more reliable if crowns are measured only to the edge of a plot and for each tree or sapling in a plot rather than for a small group of reference trees. We do not have sufficient evidence to recommend one method over another. Titchenell et al. (2011) also found that an overall measure of vegetation volume was not a good predictor for bat activity.

The Visual Clutter Method was simple, but this type of classification scheme was not a good predictor of the probability of bat detection in our models, nor is it repeatable among observers or studies. Furthermore, we were less successful in discriminating between medium and low visual clutter classes with the discriminant analyses, suggesting that we were not good at visually assessing differences in clutter levels for the stands in our study area. However, it is worth noting that we recorded more identifiable echolocation sequences in forests that we designated as low clutter. In future studies of forests similar to the broadleaf deciduous forests in this study, using only two visual clutter classes (e.g., forest and open, or high and low forest clutter) may be more appropriate and effective. As further evidence of the merits of using only two groups, classification rates were higher for the two primary clusters than for the three visual clutter classes. In our southern Appalachian study area, forests might be grouped by the characters of primary clusters A and B (Table 3). Type A stands had more well-developed midstories, with higher stem densities (~25 stems in an 11.3 m radius plot) and mean crown volumes (~65 m^3). These late-successional type stands also had higher basal areas of standing live (32.5 m^2/ha) and dead (1.5 m^2/ha) trees. Type B stands had moderate understory stem counts, but low live and dead tree basal areas, suggesting they were in early stages of succession.

When the objective of a study is to relate bat activity to managed forest types and ages in a heterogeneous landscape, it may be desirable to account for at least two clutter groups when describing available habitat and calculating probability of detection. However, using a higher number of groups may yield a more accurate representation of the various levels of clutter. Although nine variables were needed to differentiate the four secondary clusters, classification rates were higher for the secondary clusters (100%) when compared to three visual clutter classes (62.5–91.7%). We suspect that classification rates were lower for visual clutter classes because we chose three classes a priori and then "forced" stands into one of the three classes. If >2 classes are to be used to describe clutter, we suggest that definitions for clutter classes be based on defined ranges of values for common stand descriptors, such as stem density or mean crown volume, in multiple canopy layers. However, because qualitative methods were not always the best predictors of detection probability, we recommend using quantitative measures to assess clutter when possible. Quantitative variables may provide a better assessment of fine-scale clutter than qualitative variables, and this is important because bats may select areas with reduced fine-scale clutter (Loeb and O'Keefe, 2006; Ober and Hayes, 2008; Smith and Gehrt, 2010), even within cluttered stands.

5. Management implications

The amount of clutter in forests has received a great deal attention as a factor that can affect bat habitat use, and managers need information on the best way to reduce clutter in many forested areas (Hayes and Loeb, 2007). However, without quantitative and repeatable measures of clutter, it is difficult for managers to transfer the results of studies in one area to their particular management areas. We present some quantitative and repeatable measures of clutter that can be used across many forest types and age classes allowing managers to develop better strategies for creating high quality bat habitat.

Bats occupied a wide range of clutter levels in forests in our study area, but were most likely to be detected in uncluttered forests (i.e., stands with low live tree basal area and midstory live stem counts, and high canopy crown volumes). We do not discount the suitability of cluttered forests as foraging or commuting habitat for some bat species, but high clutter may impede detection of such bats. Although we placed detectors at points where vegetation did not obscure the microphone (Weller and Zabel, 2002), and occupancy rates for all bats were high for most of the sites we surveyed, we recorded few high quality calls suitable for identification. Thus, for forest managers with limited resources (time and detectors) and the goal of comparing bat activity among forest types and ages, it might be more effective to place detectors in the lowest clutter point within a survey stand (e.g., on a skidder trail or in a canopy gap). Furthermore, for presence–absence surveys in forested environments, such as those now required for federally endangered species in the eastern U.S. (USFWS, 2013), it will be important to tailor methods so that clutter does not impede detection of target bat species. Active sampling, in which the researcher holds the detector and points it in the direction of bats as they are detected, may also yield more identifiable recordings (e.g., Jung et al., 2012).

In complex forests, we suggest that either a very simple classification system (i.e., two classes) or quantitative measurements will be necessary for studies that seek to relate bat activity or presence to habitat characteristics. We tested a novel method for clutter classification, the Clutter Index Method, and found that it performed poorly relative to other clutter methods. Novel methods and emerging technologies, such as LiDAR measurements of forest structure (e.g., Jung et al., 2012), should be tested thoroughly prior to implementation in long term studies.

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