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Spatio-temporal availability of soft mast in clearcuts in the Southern Appalachians

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Abstract

Soft mast is an important resource for many wild populations in the Southern Appalachians, yet the way clear-cutting affects availability of soft mast though time is not fully understood. We tested a theoretical model of temporal availability of soft mast in clearcuts using empirical data on percent cover and berry production of *Gaylussacia*, *Vaccinium*, and *Rubus* spp. plants in 100 stands that were clearcut (0–122 years old) in the Southern Appalachian Mountains. We modeled the relationship between soft mast availability and stand age, evaluated the effects of topography and forest type on soft mast, developed statistical models for predicting the spatio-temporal distribution of soft mast, and tested the hypothesis that percent cover of berry plants and berry production provided similar information about soft mast availability. We found temporal dynamics explained berry production better than it predicted percent plant cover, whereas topographic variables influenced percent plant cover more than they influenced berry production. Berry production and percent plant cover were highest in ∼2–9-year-old stands. Percent plant cover was lowest in 10–69-year-old stands and intermediate in 70+-year-old stands. Three of our spatio-temporal models performed well during model testing and they were not biased by the training data, indicating the inferences about spatio-temporal availability of soft mast extended beyond our sample data. The methods we used to estimate the distribution of soft mast may be useful for modeling distributions of other resources.
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1. Introduction

Improving habitat quality for some populations of wild animals is often considered an objective of harvesting trees on forested landscapes. Timber harvesting increases availability of soft mast (Clark et al., 1994; Mitchell et al., 2002; Noyce and Coy, 1990; Perry et al., 1999; Stransky and Roese, 1984), an important component of habitat for many wild animals (Jonkel and Cowan, 1971; Elowe and Dodge, 1989; Boddy, 1991; Castleberry et al., 2002; Thomas, 1984; Thompson and Fritzell, 1986; Willson, 1986). Availability of soft mast in harvested stands and its affect on habitat quality, however, is not static. It changes through time due to succession.

In recently harvested stands, availability of soft mast can be relatively high (Clark et al., 1994; Mitchell et al., 2002; Noyce and Coy, 1990; Perry et al., 1999; Stransky and Roese, 1984) because conditions favor early successional species, some of which produce soft mast (e.g., *Rubus* spp.; Archambault et al., 1998; Costello and Sage, 1994; McCarty et al., 2002; Perry et al., 1999). As stands age and forest canopies close, however, availability of soft mast due to early successional species declines (Mitchell et al., 2002; Mitchell and Powell, 2003). Eventually, availability of soft mast should increase again as conditions favor later successional species, some of which produce soft mast (e.g., *Vaccinium* spp. Ihalainen et al., 2003; Perry et al., 1999).

Knowing the range of stand ages in which soft mast is most available may be key to maintaining levels of soft mast on forested landscapes for wild animals. Equally important is to know the range of stand ages in which soft mast is least available because one way to optimize soft mast availability

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across a forested landscape is to minimize the proportion of area in stand ages in which soft mast is lowest.

Several studies have evaluated temporal dynamics of soft mast availability in harvested stands, but results have been incomplete. The range of stand ages in which soft mast was measured was narrow or stands were categorized, *a priori*, into arbitrary age classes. For example, Perry et al. (1999) assessed availability of soft mast in 1-, 3-, 5- and 70+-year-old stands in pine and hardwood forests in the Ouachita Mountains of Arkansas and Oklahoma and found soft mast was highest in 5-year-old shelterwood cuts and in 5-year-old clearcuts and lowest in 70+-year-old stands. Because soft mast was not measured in 6–69-year-old stands, it is unknown whether a range of stand ages between 6 and 69 years supported levels of soft mast greater than that in 5-year-old stands or lower than that in 70+-year-old stands. Costello and Sage (1994) compared availability of soft mast in 1–8, 9–16, 17–24, and 24+-year-old stands in hardwood forests in New York and found summer fruits were highest in 1–8 and 9–16-year-old stands and lowest in 24+-year-old stands. All stands >24 years were combined, which may have masked possible changes in soft mast availability that occurred as stands aged beyond 24 years.

In Minnesota, Noyce and Coy (1990) compared soft mast availability in 0–1, 2–4, 5–8, 9–12, 13–16, 30–59, and 60+-year-old stands in hardwood and boreal forests and found soft mast was highest in 5–8-year-old stands and lowest in 0–1 and 2–4-year-old stands. Importantly, they also found percent cover of berry plants was higher in 60+-year-old stands compared to that in 30–59-year-old stands, suggesting intermediate aged stands supported relatively low levels of soft mast. The last finding was detectable only because stands >30 years old were not grouped, *a priori*, into a single category.

Our first objective was to build upon previous research by evaluating how clear-cutting (i.e., removal of all trees within a stand) in the Southern Appalachian Mountains affected soft mast availability through time. Currently, little is known about temporal dynamics of soft mast in the Southern Appalachian Mountains. Brody and Stone (1987) hypothesized soft mast availability in clearcuts would be very high when clearcuts were young, but then steadily decline until stands were about 70 years old (Fig. 1). To date, this model has not been tested with empirical data. Mitchell and Powell (2003) showed soft mast in western North Carolina was higher in 0–10-year-old clearcuts compared to that in 11+-year-old stands, but all stands >10 years old were combined, making it impossible to discern changes in soft mast availability that may have occurred as stands aged beyond 10 years. We wanted to expand their work by analyzing temporal dynamics of soft mast availability in clearcuts without categorizing stands, *a priori*, into specific age groups. By using continuous data, we hoped to uncover patterns in soft mast availability that might be masked by analysis of categorical data.

Factors other than stand age also influence availability of soft mast in harvested stands. Type of harvest technique was important in Texas (Johnson and Landers, 1978), New York (Costello and Sage, 1994) and Oklahoma (Perry et al., 1999) whereas forest type was a factor in Minnesota (Noyce and Coy,
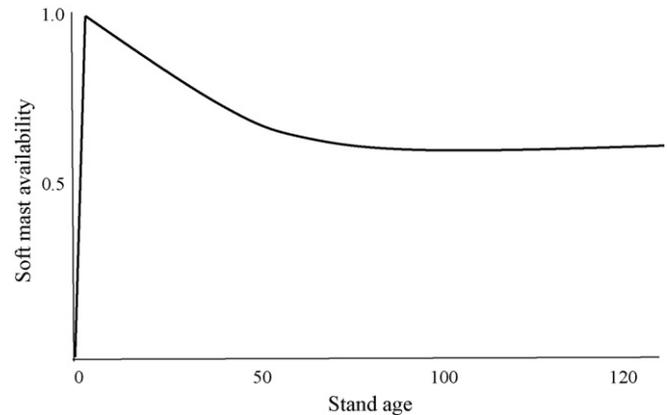
Fig. 1. Model of soft mast availability in Southern Appalachian clearcuts, as they age from 0 to 120 years, taken from Brody and Stone (1987). The *y*-axis is an index of habitat capability with respect to soft mast availability.

1990) and Arkansas (Clark et al., 1994). Topography (e.g., aspect, slope, etc.) and spatial location of a stand on the landscape (e.g., ridge top, ridge side, valley) may also affect the availability of soft mast, yet these influences have not been tested in the Southern Appalachian Mountains. Therefore, our second objective was to understand how forest type, topography and spatial location on the landscape affected soft mast availability in the Southern Appalachian Mountains. Our third objective was to combine temporal and spatial information to develop models for predicting the spatio-temporal distribution of soft mast on Southern Appalachian landscapes.

Finally, estimates of soft mast availability are influenced by how availability is defined. Some studies estimated availability of soft mast in terms of percent cover of berry plants (Mitchell et al., 2002; Mitchell and Powell, 2003), but Perry et al. (1999) showed percent cover was not always a reliable measure of potential soft mast production. In their study, poison ivy (*Toxicodendron radicans*) plants were highly available throughout the study area, but they produced few berries. Alternatively, areas could have high berry production but few berry plants. If so, estimates of only plant cover or only berry production may not provide reliable estimates of soft mast availability. Our fourth objective was to evaluate whether percent cover of berry plants and berry production provided similar estimates of soft mast availability in the Southern Appalachian Mountains.

2. Study area

We conducted our study in the Pisgah Bear Sanctuary (PBS), located in the western mountains of North Carolina (35°17′N, 82°47′W), during summers 2001 and 2002. The PBS (235 km^2) was located within the Pisgah National Forest and managed by the United States Department of Agriculture Forest Service (USDAFS) which harvested ~1000 stands during 1844–2002. Stand ages within PBS ranged from 0 to 158 years old, but most stands (~80%) were 60+ years old in 2001–2002.

Eighty-eight percent of PBS comprised oak and oak-hickory species, including northern red oak (*Quercus rubrus*), southern red oak (*Q. falcata*), white oak (*Q. alba*), chestnut oak (*Q. prinus*) and hickory (*Carya* spp.). Cove hardwoods

(*Liriodendron tulipifera*, *Magnolia* spp., *Betula* spp.) and pine-hemlock (*Pinus rigida*, *P. strobus*, *P. virginiana*, *Tsuga canadensis*) constituted approximately 4.5% and 3% of PBS, respectively. Shrub and sub-canopy species (*Rhododendron* spp., *Kalmia* spp., etc.) and a mixture of other species (*Corylus* spp., *Liquidambar styraciflua*, etc.) constituted the remaining portions of the PBS (Continuous Inventory Stand Condition Database, USDA Forest Service, 2001). The topography was mountainous with elevations ranging from 650 to 1800 m. The region was considered a temperate rainforest, with annual rainfall approaching 250 cm/year (Powell et al., 1997).

Within Pisgah Bear Sanctuary (PBS), several types of harvest prescriptions were used during 1844–2002, including thinning, selective cutting, group selection cutting, and clear-cutting. Because most stands were clearcut and allowed to naturally regenerate (∼90%), we limited our study to measuring availability of soft mast in only clearcuts. Within PBS, the genera producing the majority of berries during summer months were raspberries and blackberries (*Rubus* spp.), huckleberries (*Gaylussacia* spp.), and blueberries (*Vaccinium* spp.; Powell et al., 1997) so we measured availability of only these three genera.

3. Methods

3.1. Measuring soft mast in clearcuts

We wanted to understand how soft mast availability changed through time as clearcut stands aged from 0 to 40 years old. Before selecting our sample of stands, we first grouped all stands in PBS that were clearcut <40 years ago into age classes (i.e., 0–5, 6–10, 11–15, etc.) after which we randomly selected 5–10 stands from each group. We categorized stands to minimize bias due to cluster sampling (Ramsey and Schafer, 2002); grouping stands prior to selection was the only way we could ensure that our sample represented the full spectrum of stand ages between 0 and 40 years old. Importantly, stands were grouped by age for selection only. For all analyses, stand age was evaluated as a continuous variable.

Within each 0–40-year-old stand, we placed 200-m transects with 3-m radius circular plots placed every 50 m on each transect. To minimize edge effects, all plots were located >100 m from the stand edge and all transects were at least 100 m apart. We sampled at least two transects in each stand.

To understand longer term dynamics, we incorporated data from 41+-year-old stands (that were clearcut >41 years ago) that we collected to answer different research questions (Reynolds and Mitchell, unpublished data). Methods for data collection in 41+-year-old stands differed slightly from methods used to collect data in 0–40-year-old stands in terms of the way stands were selected and the number and placement of plots. Stands that were 41+ years old were systematically selected (stands at the intersection of odd-numbered *x* and even-numbered *y* universal transverse mercator coordinates were sampled) and five 3-m radius circular plots were sampled in each stand; one plot at the center of the intersection and one

each 100 m from the center in each of the four cardinal directions (Powell et al., 1997).

Within each 3-m radius circular plot, we visually estimated percent plant cover of *Gaylussacia*, *Vaccinium*, and *Rubus* spp. and we indexed berry production according to the following scale: 0 = no fruit, 1 = fruits covering between 0 and 33% of the plants, 2 = fruits covering between 34 and 67% of the plants, and, 3 = fruits covering >67% of the plants (Noyce and Coy, 1990). Values of berry production index were unit-less because we did not measure berry production directly (e.g., kg fruit/m^2). We sampled stands during peak fruiting season, between July and August in 2001 and 2002. Flowers and fruit caps were counted as fruit on plants that hadn't yet fruited or where fruit had obviously been eaten. We pooled data between years to increase sample size. Neither percent cover in berry plants ($F_{1,99} = 0.08$; $P > 0.36$; $r^2 = 0.00$) nor production index ($F_{1,99} = 3.01$; $P = 0.08$; $r^2 = 0.02$) differed among years.

Within each plot, we documented landform type (ridge top, ridge side, valley) slope (flat = 0–10 degree slope, moderate = 11–25 degree slope, or steep = >25 degree slope), and aspect (NE, NW, SE, SW). We recorded "no aspect" for plots that were flat. Finally, we categorized each clearcut as either hardwood (stands in which ≥70% trees were hardwoods; USDA Forest Service stand codes 50–98; Continuous Inventory Stand Condition, 2001), softwood (stands in which ≥70% trees were softwoods; USDA Forest Service codes 2–7, 21–26, and 31–39), or mixed (stands with a mixture of hardwood and softwood species; USDA Forest Service codes 8–20 and 40–49). To minimize observer bias, only three observers collected field data and all observers were extensively trained.

3.2. Time

To understand temporal dynamics of soft mast availability, we conducted two sets of analyses. First, we included data from only 0–40-year-old stands because our sampling methods for these stands differed slightly from sampling methods for 41+-year-old stands. We used results from the first analysis to make inferences about clearcut stands that were 0–40 years old. We then combined data from 0 to 40-year-old stands with data from 41+-year-old stands for our second analysis and used these results to make inferences about clearcut stands that were 41+ years old.

To determine the range of stand ages in which soft mast was highest and lowest, we modeled mean percent plant cover (*C*) as a function of stand age for all genera combined. A curvilinear relationship may exist between *C* and stand age because percent cover of early successional berry plants (e.g., *Rubus* spp.; Archambault et al., 1998; Costello and Sage, 1994; McCarty et al., 2002; Perry et al., 1999) should be highest in young stands and decrease as stands age, whereas percent cover of later successional berry plants (e.g., *Vaccinium* spp.; Ihalainen et al., 2003; Perry et al., 1999) should be lowest in young stands and increase as stands age. Therefore, a simple linear relationship was unlikely to capture the overall dynamics between *C* and stand age. We modeled the statistical relationship between *C* and stand age for early successional

berry plants by considering two transformations of stand age (stand age^{-1} and stand age$^{-1/2}$), both of which have a decreasing function. We considered both transformations, even though their functions were similar, because slopes differed between the transformations (stand age^{-1} had a smaller slope) and we did not know, *a priori*, which slope best represented the relationship between C and stand age for early successional berry plants. We modeled temporal dynamics of C and stand age for later successional berry plants by transforming stand age (stand age^2; Johnson et al., 2004), which had an increasing function. To develop a global model of C for both early and later successional berry plants combined, therefore, we randomly selected 70% of the data and used stand age, stand age^{-1}, stand age$^{-1/2}$, and stand age^2 as predictor variables (Proc Reg: SAS Institute, 2000). We considered stand age as an explanatory variable because C for later successional berry plants may have been very low and relatively constant for a long time during the early and mid stages of succession. We developed a suite of nested models from the global model and we considered the null model to be the intercept-only model. We used Akaike's information criterion, with an adjustment for small sample bias (AIC$_c$; Akaike, 1973; Anderson et al., 1994) to rank the models in terms of their ability to explain the data. We used the remaining 30% of the data to test the top-ranked model. We used the same method to model berry production index (P).

We used results from the above regression analysis to estimate the range of stand ages in which C was high, low, and intermediate. To test if C was statistically different among the three ranges of stand ages that were estimated using regression analysis, we categorized data on percent cover into the three age groups and compared mean C among the groups (Proc GLM: SAS Institute, 2000; alpha = .10). For example, if the regression analysis indicated C was highest in 0–10-year-old stands, intermediate in 11–69-year-old stands and lowest in 70+-year-old stands (Brody and Stone, 1987; Fig. 1), then we categorized percent cover data into 0–10, 11–69, and 70+ age groups and compared mean C among the three groups. We used the same method to test for statistical differences in P among stand age groups.

Although data on both percent plant cover and berry production contained zeros, we did not adjust for zero inflation because the goal of this research was to understand how clear-cutting affected the temporal availability of soft mast through time. Zeros were important to retain because we wanted to estimate mean soft mast availability as a function of stand age. Had we first modeled the probability of plant cover of berry plants and then modeled the probability of berry production, our results would have reflected the likelihood of berry production given the presence of berry plants, which was not the purpose of this study.

3.3. Topography

To understand how topography affected soft mast availability, we developed a suite of models for C for all genera combined using aspect, slope, and topographic position as predictor variables. We used AIC for model selection. Sample size was based on number of plots because topography and spatial location were heterogeneous within stands. To understand how forest type affected soft mast availability, we compared differences in mean C and differences in mean P among forest types (Proc GLM: SAS Institute, 2000). Because the category forest type was homogeneous within a given stand, sample size was based on number of stands (Hurlbert, 1984).

3.4. Spatio-temporal models

We developed statistical models for predicting C on the landscape using both temporal and topographic parameters. For each sampled stand, we extracted mean values of slope, elevation and aspect (Beers transformation of aspect; Beers et al., 1966) using a geographic information system (GIS) at a 30 m resolution. We also extracted mean values for curvature of the land, plane of the curvature, profile of the curvature (DEMAT Behrens 2000), and distance to water (Mitchell et al., 2002). We did not include soil data because soil type did not differ on over 95% of our plots (Hermann, 1996).

We regressed each topographic parameter and its square (e.g., elevation and elevation^2; Johnson et al., 2004) as well as stand age and three transformations of stand age (stand age^2, stand age^{-1}, stand age$^{-1/2}$; Proc Reg; SAS Institute, 2000) to develop a global model of C using 70% of the randomly selected data. We generated a suite of nested models from the global model, selected the best approximating model using AIC$_c$ and tested the top-ranked model using the remaining 30% of the data (Proc Reg; SAS Institute, 2000). We used the same method to develop and test a model for predicting the spatio-temporal distribution of P. Because soft mast availability might be best explained by combining measures of C and P (Clark et al., 1994), we also developed and tested a model for predicting $C \times P$.

During model testing, we evaluated model bias. If training data (i.e., data used during model development) are unbiased estimators of the population, the amount of variability explained during model development will be similar to the amount of variability explained during model testing (Neter et al., 1996). For each model of C, P, and $C \times P$, we compared values of coefficient of determination (r^2) between training and testing models.

3.5. Cover in berry plants versus berry production

To test if C and P provided similar estimates of soft mast availability, we evaluated three predictions. First, we evaluated the degree to which stand age and topographic variables each explained C and P. If C and P provided similar information about soft mast availability, we predicted the effects of stand age and topography on C would be similar to the effects of stand age and topography on P. Second, we modeled C and P using berry genus as the predictor variable and used AIC to compare the ability of this model to explain the data relative to the ability of a null model (i.e., an intercept only model). If C and P provided similar information, we predicted C values for each
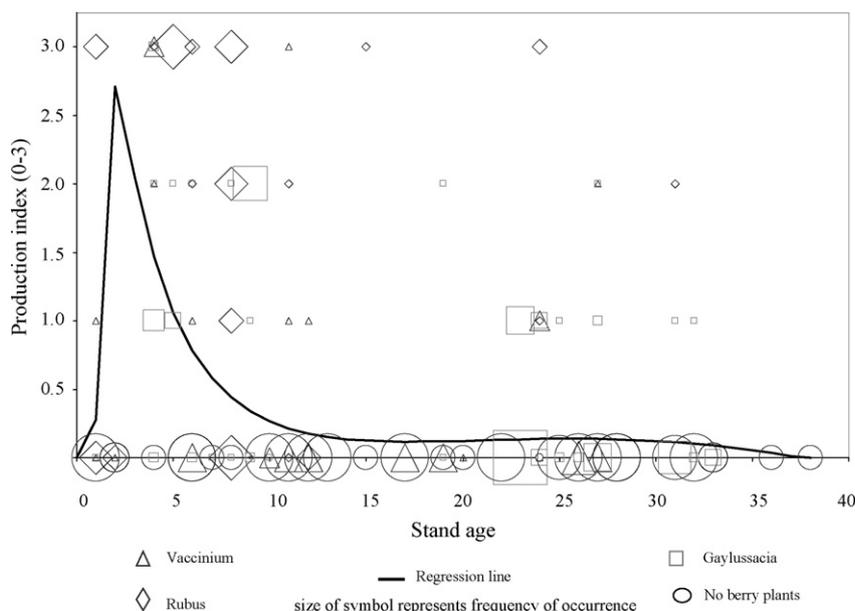
Fig. 2. Berry production index (P) of *Vaccinium*, *Rubus*, and *Gaylussacia* spp. combined in 579 plots in 0–40-year-old clearcuts in Pisgah Bear Sanctuary, North Carolina, 2001. Data for each plot are shown by genus, but the regression line predicts mean P of all three genera combined and was based on mean P per stand ($n = 57$).

genus would be similar to P values. Third, we used least squares regression (Proc Reg; SAS Institute, 2000) to examine the variability in P explained by C. If C and P provided similar information, we predicted C would explain P reasonably well.

4. Results

We collected data in 57 stands that were 0–38 years (no stands in Pisgah Bear Sanctuary were 39 or 40 years old in 2001 or 2002); within which we sampled 579 plots. Percent plant cover of *Gaylussacia*, *Vacinnium*, or *Rubus*, spp. was >0 in 205 plots (34%). Of the 205 plots, *Gaylussacia* spp. were found in 43% ($n = 88$), *Vaccinium* spp. were found in 34% ($n = 70$), and

Rubus spp. were found in 23% ($n = 47$). We collected data in 43 stands that were 41–122 years old, within which we sampled 215 plots. Percent plant cover was >0 in 93 plots (43%). Of the 93 plots, *Gaylussacia* spp. were in 29% ($n = 27$), *Vaccinium* spp. were in 61% ($n = 57$) and *Rubus* spp. were in 10% ($n = 9$).

4.1. Time

The top-ranked model for P when all genera were combined for 0–40-year-old stands included stand age, stand age^2, stand age$^{1/2}$, and stand age$^{-1/2}$ ($r^2 = 0.37$; Fig. 2). The top-ranked model for C when all genera were combined for 0–40-year-old stands was the null model (i.e., intercept-only model; Fig. 3).
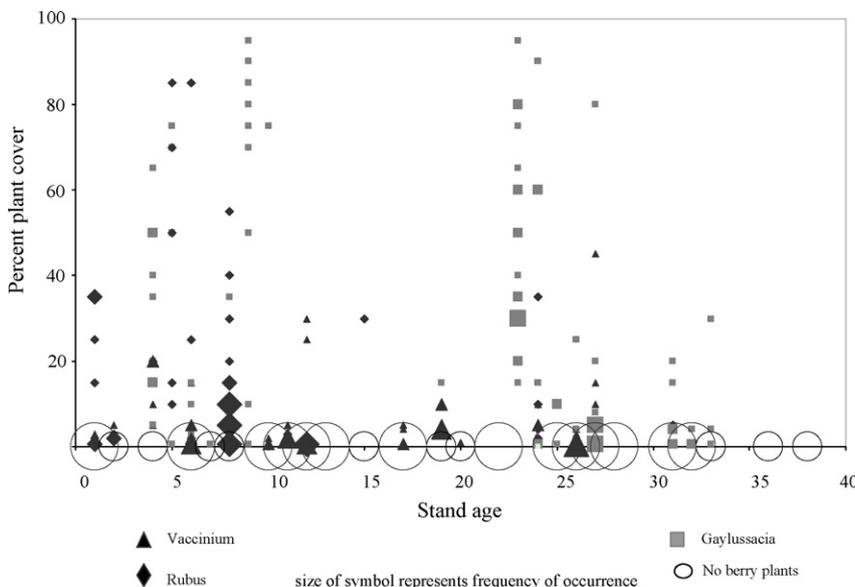
Fig. 3. Percent plant cover (C) of *Vaccinium*, *Rubus*, and *Gaylussacia* spp. combined in 579 plots in 0–40-year-old clearcuts in Pisgah Bear Sanctuary, North Carolina, 2001. Data for each plot are shown by genus. A regression line is not included because stand age was a poor predictor of mean C in 0–40-year-old clearcuts.
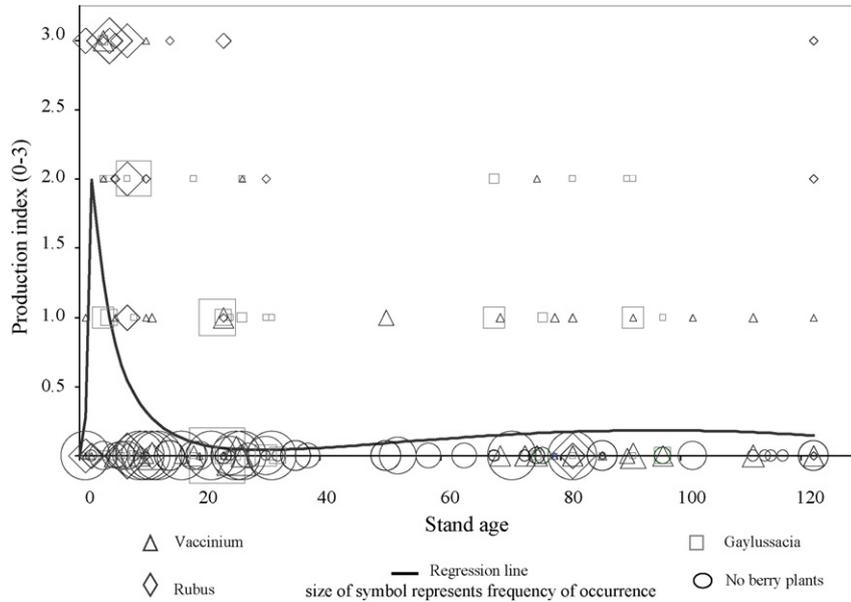
Fig. 4. Berry production index (*P*) for *Vaccinium*, *Rubus*, and *Gaylussacia* spp. combined in 794 plots in 0–122-year-old clearcuts in Pisgah Bear Sanctuary, North Carolina, 2001–2002. Data for each plot are shown by genus, but the regression line predicts mean *P* of all three genera combined and was based on mean *P* per stand (*n* = 100).

Results of model testing showed the temporal model of *P* explained 43% variability in predicted *P*. *P* was highest in ~2–9-year-old stands (Fig. 2). Data for *C* did not always correlate with data for *P*. For example, several values of *C* for *Gaylussacia* spp. at stand age 23 were high (Fig. 3), but all values of *P* for *Gaylussacia* spp. at stand age 23 were low or zero (Fig. 2).

The top ranked model for *P* when all genera were combined for 0–122-year-old stands included stand age, stand age^2, stand age$^{1/2}$, and stand age$^{-1/2}$ ($r^2 = 0.32$; Fig. 4). The top ranked model for *C* when all general were combined for 0–122-year-old stands was the null model (Fig. 5). Results of model testing

showed the temporal model of *P* predicted 28% variability in predicted *P*, indicating the training data did not bias the model. Based on the regression line, *P* was lowest in ~14–49-year-old stands (Fig. 4). Based on data, *P* was lowest in ~30–68-year-old stands (Fig. 4) and berry plants were notably missing in 34–69-year-old stands (Fig. 5). Although we sampled 50 plots in 34–69-year-old stands, we found berry plants in only 4% of the plots (*n* = 2).

Based on the relationship between stand age and *P* predicted by our regression analysis (Figs. 2 and 4), soft mast appeared to be highest in ~2–9-year-old stands and lowest in ~10–69-year-old stands. *P* appeared to increase as stands aged beyond ~70
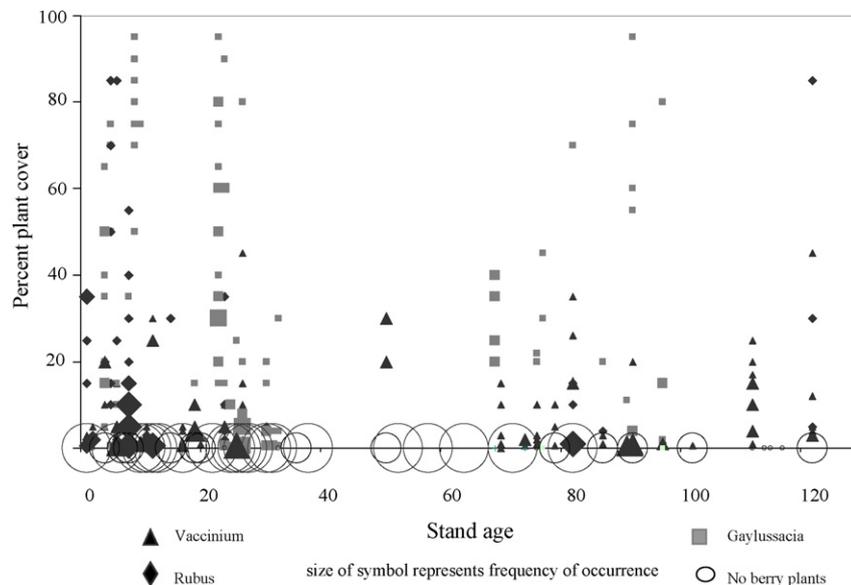
Fig. 5. Percent plant cover (*C*) of *Vaccinium*, *Rubus*, and *Gaylussacia* spp. combined in 794 plots in 0–122-year-old clearcuts in Pisgah Bear Sanctuary, North Carolina, 2001–2002. Data for each plot are shown by genus. A regression line is not included because stand age was a poor predictor of mean *C* in 0–122-year-old clearcuts.

Table 1

Mean values of percent plant cover (*C*) and berry production index (*P*) of *Vaccinium*, *Rubus*, and *Gaylussacia* spp. (combined) among different levels of topographic position, aspect, and slope

	Percent plant cover	S.E.	Berry production index	S.E.	*n*
Landform					
Ridge top	6.22	1.60	0.22	0.06	102
Ridge side	5.69	0.74	0.24	0.03	512
Valley	11.24	2.01	0.28	0.06	127
Aspect					
NE	6.00	1.22	0.22	0.05	179
NW	16.24	2.70	0.36	0.06	114
SE	4.06	0.76	0.17	0.04	212
SW	3.09	0.74	0.19	0.05	181
Slope					
Flat	10.44	1.72	0.18	0.04	163
Moderate	6.29	0.94	0.26	0.04	363
Steep	4.57	0.89	0.25	0.05	215

Data were collected within 741 plots in 0–122-year-old clearcuts in Pisgah Bear Sanctuary in North Carolina during 2001 and 2002.

Table 3

Slope estimates and standard errors for variables in the top-ranked model for predicting the spatio-temporal distribution of percent plant cover (*C*) of *Vaccinium*, *Rubus*, and *Gaylussacia* spp. (combined) in 0–40-year-old clearcuts (*n* = 57) and in 0–122-year-old clearcuts (*n* = 100) in Pisgah Bear Sanctuary in western North Carolina, 2001–2002

Model	Slope	S.E.	r^2
C in 0–40-year-old clearcuts			
Intercept	60.97205	10.27	0.66
Stand age^{-1}	151.37519	47.42	
Stand age$^{-1/2}$	−143.8855	44.43	
Slope	−7.93037	1.38	
Slope^2	0.21155	0.05	
Distance to water^2	0.00006	0.00	
C in 0–122-year-old clearcuts			
Intercept	26.187	9.56	0.57
Stand age	0.11896	0.04	
Stand age^{-1}	145.22699	34.03	
Stand age$^{-1/2}$	−134.36371	31.13	
Slope	−6.03658	0.84	
Slope^2	0.14947	0.02	
Elevation	0.01929	0.01	
Distance to water	0.02429	0.01	

years. When we categorized plots into 2–9, 10–69, and 70+ age groups to test for statistical differences, we found mean *P* in 2–9-year-old stands differed from mean *P* in 10–69 and 70+-year-old stands ($F_{2,748} = 63.17$; $r^2 = 0.14$; $P < 0.0001$), but mean *P* in 10–69-year-old stands did not differ from mean *P* in 70+-year-old stands. Mean *C*, however, differed among all three stand age groups ($F_{2,748} = 22.75$; $r^2 = 0.06$; $P < 0.0001$). Mean *C* was highest in 2–9-year-old stands (mean percent cover = 16.1; S.E. = 2.42), lowest in 10–69-year-old stands (mean percent cover = 4.2; S.E. = 0.65), and intermediate in 70+-year-old stands (mean percent cover = 7.1; S.E. = 1.13).

4.2. Topography

The top ranked model for *C* in sampled plots included slope, topographic position, and aspect. Percent cover in berry plants was highest on flat slopes, in valleys, and in areas with NW aspects (Table 1). The top ranked model for *P* included only aspect. Production index was highest on NW aspects (Table 1). Of the 100 stands we sampled, 91 were classified as hardwood, 7 were softwood, and 2 were mixed hardwood and softwood. Forest type affected neither *C* ($F_{2,99} = 0.25$; $P = 0.86$) nor *P* ($F_{2,99} = 0.68$; $P = 0.56$).

4.3. Spatio-temporal models

The top-ranked model for predicting *C* included temporal and topographic parameters. The model that best supported the data on *C* in 0–40-year-old stands included stand age^{-1}, stand age$^{-1/2}$, slope, slope^2, and distance to water^2 (Table 2), slope estimates for variables are provided in Table 3. The null model ranked very low and had low model weight. The top-ranked model performed well during model testing ($F_{1,11} = 24.64$; $r^2 = 0.71$; $P = 0.0006$; Table 4). The model that best fit the data on *C* in 0–122-year-old stands (Table 2) performed reasonably well during model testing ($F_{1,28} = 23.98$; $r^2 = 0.47$; $P = 0.0001$; Table 4).

Table 2

Model rankings for cover of berry plants (*C*) in (A) 0–40-year-old clearcuts and (B) 0–122-year-old clearcuts in Pisgah Bear Sanctuary in western North Carolina, 2001–2002

Model	AIC$_c$	ΔAIC$_c$	Model likelihood	*K*
(A) *C* in 0–40-year-old clearcuts				
Age^{-1}, age$^{-1/2}$, slope, slope^2, distance to water	216.60	0.00	1.00	6
Age^{-1}, age$^{-1/2}$, slope, slope^2, curvature, aspect, distance to water	216.98	0.38	0.83	8
Age^2, age^{-1}, age$^{-1/2}$, slope, slope^2 distance to water^2	218.31	1.71	0.43	7
Age^{-1}, age$^{-1/2}$, slope, slope^2, curvature^2, distance to water^2	218.40	1.80	0.41	7
Null	259.77	43.17	0.001	
(B) *C* in 0–122-year-old clearcuts				
Age, age^{-1}, age$^{-1/2}$, slope, slope^2, elevation, distance to water	404.25	0.00	1.00	8
Age^2, age^{-1}, age$^{-1/2}$, slope, slope^2, elevation^2, distance to water	405.24	0.99	0.61	8
Age^2, age^{-1}, age$^{-1/2}$, slope, slope^2, elevation, distance to water	405.98	1.73	0.42	8
Age, age^2, age^{-1}, age$^{-1/2}$, slope, slope^2, elevation, elevation^2, distance to water	406.41	2.16	0.34	10
Null	465.72	61.47	0.001	

Only the top four models and the null model are presented.

Table 4
Results of model testing using training data (70% of data, randomly selected) and testing data (30% of data) for spatio-temporal models of percent cover of berry plants (C), spatio-temporal models of berry production index (P), and spatio-temporal models of $C \times P$

Model	F	d.f.	r^2	P-value
C in 0–40-year-old clearcuts				
Training data	12.09	5, 36	0.66	<0.0001
Testing data	24.64	1, 11	0.71	0.0006
C in 0–122-year-old clearcuts				
Training data	9.39	6, 64	0.57	<0.0001
Testing data	23.98	1, 28	0.47	0.0001
P in 0–40-year-old clearcuts				
Training data	8.13	6, 36	0.62	<0.0001
Testing data	16.03	1, 11	0.61	0.002
P in 0–122-year-old clearcuts				
Training data	9.28	6, 64	0.49	<0.0001
Testing data	6.19	1, 28	0.18	0.019
$C \times P$ in 0–40-year-old clearcuts				
Training data	7.44	4, 36	0.48	<0.0002
Testing data	0.7	1, 11	0.06	0.42
$C \times P$ in 0–122-year-old clearcuts				
Training data	5.64	6, 64	0.37	<0.0001
Testing data	3.54	1, 28	0.12	0.07

Berry plants measured included *Vacinnium*, *Rubus*, and *Gaylussacia* spp. (combined) collected in 0–40-year-old clearcuts (n = 57) and in 0–122-year-old clearcuts (n = 100) in Pisgah Bear Sanctuary in North Carolina, 2001–2002.

Table 6
Slope estimates and standard errors for variables in the top-ranked model for predicting the spatio-temporal distribution of percent plant cover (P) of *Vaccinium*, *Rubus*, and *Gaylussacia* spp. (combined) in 0–40-year-old clearcuts (n = 57) and in 0–122-year-old clearcuts (n = 100) in Pisgah Bear Sanctuary in western North Carolina, 2001–2002

Model	Slope	S.E.	r^2
P in 0–40-year-old clearcuts			
Intercept	−6.34536	5.74	0.62
Stand age	0.02317	0.02	
Stand age^{-1}	13.04812	3.67	
Stand age$^{-1/2}$	−11.64471	3.19	
Elevation	0.01144	0.00	
Elevation^2	−0.00000633	0.01	
Distance to water	0.00115	0.00	
P in 0–122-year-old clearcuts			
Intercept	0.00891	0.33	0.49
Stand age	0.0059	0.01	
Stand age^{-1}	8.5777	1.48	
Stand age$^{-1/2}$	−7.76266	1.36	
Slope	−0.07351	0.04	
Slope^2	0.00191	0.00	
Distance water	0.00094367	0.00	

The top-ranked model for predicting P in 0–40-year-old stands also included temporal and topographic variables (Table 5), slope estimates for variables are provided in Table 6. The top-ranked model performed well during model testing ($F_{1,11} = 16.03$; $r^2 = 0.61$; $P = 0.002$; Table 4). The model that best fit the data on P in 0–122-year-old stands included both temporal and spatial parameters (Table 5), but the top-ranked model did not perform well during model testing ($F_{1,28} = 6.19$; $r^2 = 0.18$; $P = 0.019$; Table 4).

Evaluation of model bias showed both spatio-temporal models of C were not biased by the training data, but one model of P was biased. The variability in C explained by the training data for 0–40-year-old stands (66%; Table 4) was similar to the variability in predicted C (71%; Table 4). Similar results were found for the model of C in 0–122-year-old stands and the model of P in 0–40-year-old stands (Table 4). However, the variability in P explained by the training data for 0–122-year-old stands (49%; Table 4) was not similar to the variability in predicted P (18%; Table 4).

The top-ranked model for predicting the spatio-temporal distribution of $C \times P$ in 0–40-year-old stands included stand age^{-1}, stand age$^{-1/2}$, aspect^2, and distance to water^2 ($F_{4,36} = 7.44$; $r^2 = 0.48$; $P = 0.0001$), but this model performed poorly during model testing ($F_{1,11} = 0.70$; $r^2 = 0.06$; $P = 0.42$; Table 4). Similarly, the model that best fit the data on $C \times P$ in 0–122-year-old stands ($F_{6,64} = 5.64$; $r^2 = 0.37$; $P = 0.0001$) performed poorly during model testing (Table 4). Both models of $C \times P$ were biased by the training data (Table 4).

Table 5
Model rankings for berry production index (P) in (A) 0–40-year-old clearcuts and (B) 0–122-year-old clearcuts in Pisgah Bear Sanctuary in western North Carolina, 2001–2002

Model	AIC_c	ΔAIC_c	Model likelihood	K
(A) P in 0–40-year-old clearcuts				
Age, age^{-1}, age$^{-1/2}$, elevation, elevation^2, distance to water	−86.21	0.00	1.00	7
Age^{-1}, age$^{-1/2}$, distance to water	−84.54	1.67	0.37	4
Age^{-1}, age$^{-1/2}$, elevation, elevation^2, distance to water	−84.24	1.97	0.43	6
Age^{-1}, age$^{-1/2}$, distance to water^2	−83.81	2.40	0.30	4
Null	−62.24	23.97	0.001	
(B) P in 0–122-year-old clearcuts				
Age, age^{-1}, age$^{-1/2}$, slope, slope^2, distance to water	−202.80	0.00	1.00	7
Age, age^{-1}, age$^{-1/2}$, distance to water	−201.48	1.32	0.52	5
Age, age^2, age^{-1}, age$^{-1/2}$, slope, slope^2, distance to water^2	−201.44	1.36	0.51	8
Age, age^{-1}, age$^{-1/2}$, slope, distance to water	−200.62	2.18	0.34	6
Null	−120.85	81.95	0.001	

Only the top four models and the null model are presented.
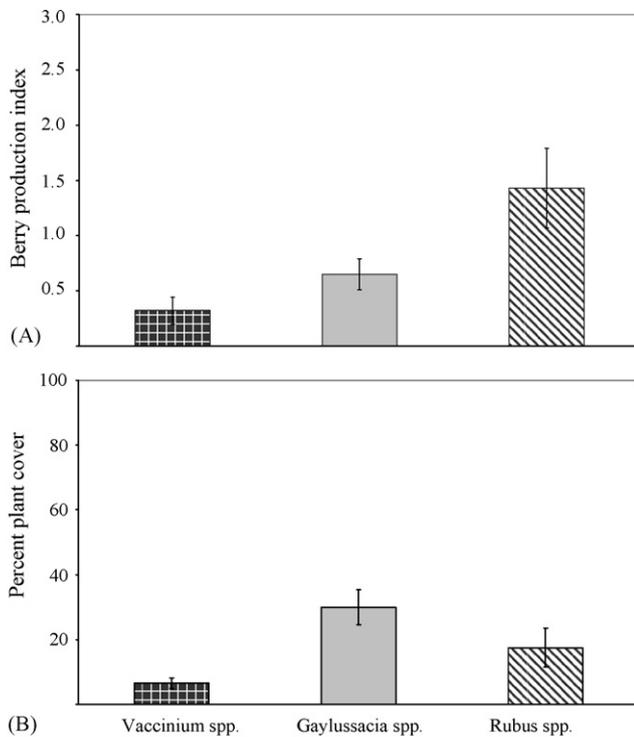
Fig. 6. Percent plant cover, with 95% confidence intervals (A), and berry production index, with 95% confidence intervals (B), for *Vaccinium*, *Rubus*, and *Gaylussacia* spp. in 794 plots in 0–122-year-old clearcuts in Pisgah Bear Sanctuary, North Carolina, 2001–2002.

4.4. Cover in berry plants versus berry production

Stand age and topography affected *C* differently than they affected *P*. In 0–122-year-old stands, temporal dynamics explained *P* (Fig. 4) but not *C* (the null model ranked highest for *C*; Fig. 5), whereas topographic variables influenced *C* more than they influenced *P* (Table 1). Moreover, the top-ranked model for both *C* and *P* included berry genera. Based on 95% confidence intervals, *C* and *P* differed among berry genera (Fig. 6). Mean *P* was highest in *Rubus* spp. whereas mean *C* was highest in *Gaylussacia* spp. Results of least squares regression showed mean *C* predicted mean *P* ($F_{1,99} = 66.78$; $r^2 = 0.41$; $P < 0.0001$).

5. Discussion

The relationship between clear-cutting and its effect on habitat for wild animals is complex. Distilling this complexity requires understanding how clear-cutting affects the availability of resources that are important to populations of wild animals. The focus of this paper was to understand how clear-cutting in the Southern Appalachians affected the spatio-temporal availability of soft mast.

We found berry production of *Rubus*, *Gaylussacia*, and *Vacinnium* spp. combined was highest in ~2–9-year-old clearcut stands (Fig. 2). It appeared that berry production was lowest in ~10–69-year-old stands and increased as stands aged beyond ~70 years (Figs. 2 and 4), but we found no statistical difference in mean berry production between 10–69

and 70+-year-old stands. Based on analysis of continuous data, we did not find a relationship between stand age and percent cover in berry plants. When data on percent cover were grouped into 2–9, 10–69, and 70+ age classes, however, percent cover differed among all three groups. Percent cover in berry plants was highest in 2–9-year-old stands, lowest in 10–69-year-old stands, and intermediate in 70+-year-old stands.

Presence of berry plants did not guarantee berry production. In 0–40-year-old stands, percent cover of *Gaylussacia* spp. plants was approximately equally distributed among stand ages, but berry production was not. Of the 57 plots in which *Gaylussacia* spp. were present in 10–38-year-old stands, 70% ($n = 40$) had zero berry production whereas only 20% of the 25 plots in which *Gaylussacia* spp. were present in 2–9-year-old stands had zero berry production. Similarly, *Vaccinium* spp. plants were approximately equally distributed among 2–38-year-old clearcuts (Fig. 3), but *Vaccinium* spp. in 2–9-year-old stands were three times more likely to be productive than *Vaccinium* spp. in 10–38-year-old stands (Fig. 2). These results indicate that although *Gaylussacia* and *Vaccinium* spp. were present in 2–38-year-old stands, they were highly productive in only ~2–9-year-old stands. Moola and Mallik (1998) similarly found *Vaccinium myrtilloides* plants persisted in both clearcut stands and older stands, but plants in older stands were relatively unproductive. *V. myrtilloides* demonstrate morphological plasticity in that leaf area, leaf weight, and proportion of total biomass in stems and foliage change along a light gradient (Moola and Mallik, 1998), which may help explain why these plants can persist in both open and closed canopies. Assuming sunlight is a necessary prerequisite to berry production, however, berry production of *Vaccinium* spp. plants located in stands with relatively high canopy cover are unlikely to be productive.

Beyond stand age 40, availability of soft mast in our study remained relatively low until, at most, stand age 70 (Figs. 4 and 5). Of the 50 plots we sampled that were located in 34–69-year-old stands, we found berry plants in only two plots (4%; Fig. 5), suggesting the range of stand ages in which soft mast was lowest was ~10–69 years. Our ability to detect soft mast availability in 34–69-year-old stands may have been compromised because our sample size of these stands was relatively small (few stands in our study site during 2001–2002 were 34–69 years old). A conservative estimate of the range of stand ages in which soft mast was lowest is ~10–40-year-old stands. Future research should test our results by measuring soft mast in other Southern Appalachian forests that contain a larger sample of 34–69-year-old clearcut stands.

Our results did not support Brody and Stone's (1987) hypothesis about the temporal dynamics of soft mast availability in Southern Appalachian clearcuts (Fig. 1). They hypothesized soft mast availability would be highest in young stands, after which it would gradually decline and asymptote when stands reach age ~70. Our data showed berry production peaked in ~2–9-year-old stands, but then plummeted and remained very low for 30–60 years (Figs. 2 and 4), after which it appeared to increase. Importantly, Brody and Stone (1987)

hypothesized soft mast availability would be lowest in stands 70+ years old, but we found soft mast availability was lowest in intermediate aged stands. This finding is significant because it suggests that area in intermediate aged stands, not area in older stands, should be minimized to optimize availability of soft mast on forested landscapes in the Southern Appalachians.

Our results regarding the high availability of soft mast in young stands generally agreed with findings from previous studies on harvesting effects in Minnesota (Noyce and Coy, 1990), Maryland (Matlack et al., 1993), New York (Costello and Sage, 1994), Quebec (Archambault et al., 1998), Arkansas (Perry et al., 1999) and North Carolina (Mitchell and Powell, 2003) as well as findings from previous studies on burn effects in western North Carolina (Elliott et al., 1999) and New Jersey (Matlack et al., 1993). Our results regarding the low availability of soft mast in intermediate-aged stands corroborated findings by Noyce and Coy (1990) who found percent cover in berry plants was higher in 60+-year-old stands compared to that in 30–59-year-old stands. Similarly, Ihalainen et al. (2003) found *Vaccinium myrtillus* was most abundant in mature stands in a boreal forest in Finland, not intermediate aged stands.

The temporal dynamics in soft mast availability we found were probably due to changes in canopy closure. In recently harvested stands, the forest canopy is relatively open providing opportunities for early successional plants, such as *Rubus* spp., to flourish. We also found that *Vaccinium* spp. and *Gaylusacia* spp. established and produced berries in young stands (Figs. 2–5), which corroborated previous findings by Moola and Mallik (1998).

After stands aged beyond ∼10 years, the sharp decline in soft mast availability probably occurred because forest canopies began to close, making forest conditions less ideal for early successional species (e.g., *Rubus* spp.) and other species (e.g., *Vaccinium* and *Gaylussacia* spp.). Canopy closure in intermediate aged stands may have been too high for berry production, which would help explain why soft mast availability was relatively low in intermediate aged stands. Older stands (70+ years old) have relatively closed forest canopies, but sunlight can often reach the forest floor due to occasional tree gaps (Frelich and Reich, 1995; Johnston, 1996), which may help explain why soft mast availability in 70+-year-old stands was higher than that in 10–69-year-old stands.

We did not test if canopy closure was the mechanism underlying the temporal trends we documented, but results from a previous study supports predictions from this hypothesis. Although rate of forest succession depends on numerous variables including moisture, temperature, duration of solar radiation, soil fertility, site condition, species availability, and herbivory (Donnegan and Rebertus, 1999; Gleeson and Tilman, 1990; Pickett and McDonnell, 1989), forests in the northeast and far upper midwest should have slower successional rates than forests in the Southern Appalachians, on average, because the growing season is shorter in the former. Therefore, forest canopies in the northeast should close slower after clear-cutting compared to rate of canopy closure in the Southern Appalachians. Hence, the range of stand ages in which soft mast availability peaks should be higher in the northeast

compared to that in the Southern Appalachians. Soft mast availability in New York was highest in 1–16-year-old stands (Costello and Sage, 1994), whereas it was highest in 2–9-year-old stands in our study.

Our findings yielded two additional insights regarding soft mast availability at a landscape scale. Although mean P was highest for *Rubus* spp. (Fig. 5) and *Vacinnium* spp. were found in the most number of plots (129 plots), *Gaylussacia* spp. probably contributed most to total soft mast availability on the Pisgah Bear Sanctuary landscape. Intuitively, the contribution each genus makes to total soft mast should be a function of the number of plots in which the genus was found, C, and P. *Gaylussacia* spp. were located in 115 plots, within which mean C was 30% and mean P was 0.65. Alternatively, *Rubus* spp. were located in 56 plots, mean C was 17%, and mean P was 1.43. Finally, *Vaccinium* spp. were located in 129 plots, mean C was 6.5%, and mean P was 0.32. Assuming the contribution each genus makes to total soft mast availability is based on the interaction of all three measures of soft mast, *Gaylussacia* spp. contributed most ($115 \times 0.30 \times 0.65 = 22.42$), *Rubus* spp. contributed the second most ($56 \times 0.17 \times 1.43 = 13.61$), and *Vaccinium* spp. contributed the least ($129 \times 0.065 \times 0.32 = 2.68$).

Surprisingly, *Vaccinium* spp. contributed the least to total availability of soft mast on the landscape, even though it was found in more plots than either *Gaylussacia* spp. or *Rubus* spp. Such counterintuitive results provide insights not only about the ecological system in our study site, but also about research techniques that measure resource availability with only presence/absence data. Clearly, presence/absence data alone may lead to biased inferences.

Estimates of C and P did not always provide similar information about soft mast availability. Topography and spatial location on the landscape influenced C more than it influenced P (Table 1), whereas the relationship between stand age and P ($F_{4,69} = 6.33$; $r^2 = 0.28$; $P < 0.0002$; Fig. 4) was stronger than the relationship between stand age and C ($F_{4,69} = 1.50$; $r^2 = 0.08$; $P = 0.21$). Moreover, analysis of only P suggested *Rubus* spp. contributed most to total soft mast availability, whereas analysis of only C suggested *Gaylussacia* spp. contributed most (Fig. 6). In addition, data for C did not always correlate with data for P, particularly as stands aged beyond 10 years (Figs. 2 and 3).

We were unable to develop an unbiased model for predicting the spatio-temporal distribution of $C \times P$ on forested landscapes in the Southern Appalachians. Our statistical models of $C \times P$ had fairly high r^2 values during model development, but they performed poorly during model testing (Table 4). Our sample size may have been too small to capture both temporal and spatial variability necessary to model $C \times P$, given P was most affected by temporal dynamics whereas C was most affected by topography and spatial location.

We were able to predict the spatio-temporal distribution of C. The model for C in 0–40-year-old stands explained 71% variability in predicted C and the model for C in 0–122-year-old stands explained 47% variability in predicted C. Importantly, both models were unbiased, indicating the inferences about the

spatio-temporal distribution of C extended beyond our sampled data. Therefore, our models can be used to map the spatio-temporal distribution of C on forested landscapes in the Southern Appalachian Mountains. In addition, the methods we used to estimate the distribution of C may be useful for estimating distributions of other resources.

6. Summary and conservation implications

Although soft mast availability was highest in young stands (2–9 years old), the duration of availability was short (∼7 years). Alternatively, soft mast availability was very low in intermediate-aged stands and remained very low for a long time (∼30–60 years). Older stands (∼70+ years) supported intermediate levels of soft mast for a relatively long period (50+ years). These results indicate that both young stands (2–9 years old) and older stands (70+ years old) should be maintained to sustain availability of soft mast across forested landscapes in the Southern Appalachians. Simultaneously, area of intermediate aged stands, where soft mast availability is lowest, should be minimized. One way to achieve this goal is to burn or harvest intermediate aged stands.

In both our study and the study by Noyce and Coy (1990), availability of soft mast was lowest in intermediate aged stands. If older stands (which support intermediate levels of soft mast) are clearcut for the purpose of increasing soft mast availability, the immediate benefits of increased soft mast over a short duration (i.e., when stands are ∼2–9 years old) may or may not outweigh the longer term costs of decreased soft mast over a long duration (when stands are ∼10–69 years old). Any conservation plan that uses clear-cutting to increase soft mast availability, therefore, must carefully consider the tradeoffs associated with short-term benefits and longer-term costs. This tradeoff is more compelling when other management objectives are also considered. For example, managers in the Southern Appalachian Mountains are often tasked to maintain simultaneous availabilities of soft mast and hard mast. While clearcuts affect the availability of soft mast positively, at least for ∼7 years, clearcuts affect the availability of hard mast negatively for 25–50 years, the time required for regenerating hardwoods to reach reproductive age in the Southern Appalachians (Burns and Honkala, 1990). How these tradeoffs are evaluated for any system may differ depending on management goals and the stand age distribution of the managed forest, but our results suggest managers can maximize both soft mast and hard mast by, at least, minimizing the proportion of the landscape that provides neither soft mast nor hard mast (i.e., stand ages 10–25 years old).

We found percent cover of soft mast plants was affected by landscape position, slope, and aspect whereas berry production was influenced by aspect. If a management objective is to increase levels of soft mast on forested landscapes in the Southern Appalachians by using clearcutting, then clearcuts should be placed in flat valleys with NW aspects to maximize the probability that berry plants will establish and be productive.

References

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B., Cazakil, F. (Eds.), Proceedings of the Second International Symposium on Information Theory, Aakademiai Kidao, Budapest.

Anderson, D.R., Burnham, K.P., White, G.C., 1994. AIC model selection in overdispersed capture-recapture data. Ecology 75, 1780–1793.

Archambault, L., Morissette, J., Bernier-Cardow, M., 1998. Forest succession over a 20-year period following clearcutting in balsam fir-yellow birch ecosystems of eastern Quebec, Canada. For. Ecol. Manage. 102, 61–74.

Beers, T.W., Dress, P.E., Wensel, L.C., 1966. Aspect transformation in site productivity research. J. Forest. 64, 691–692.

Boddy, M., 1991. Some aspects of frugivory by bird populations using coastal dune scrub in Lincholnshire. Bird Study 38, 188–199.

Brody, A.J., Stone, J.N., 1987. Timber harvest and black bear population dynamics in a Southern Appalachian forest. Int. Conf. Bear Res. Manage. 7, 243–250.

Burns, R.M., Honkala, B.H., 1990. Silvics of North America. U.S. Dept. of Agriculture, Forest Service, Washington, DC.

Castleberry, N.L., Castleberry, S.B., Ford, W.M., Wood, P.B., Mengak, M.T., 2002. Allegheny woodrat (*Neotoma magister*) food habits in the central Appalachians American midland naturalist 147, 80–92.

Clark, J.D., Clapp, E.L., Smith, K.G., Ederington, B., 1994. Black bear habitat use in relation to food availability in the interior highlands of Arkansas. Int. Conf. Bear Res. Manage. 9, 309–318.

Continuous Inventory Stand Condition Database, Pisgah Ranger District, USDA Forest Service, 2001. in press.

Costello, C.M., Sage, R.W., 1994. Predicting black bear habitat selection from food abundance under 3 forest management systems. Int. Conf. Bear Res. Manage. 9, 375–387.

Donnegan, J.A., Rebertus, A.J., 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. Ecology 80, 1370–1384.

Elliott, K.J., Hendrick, R.L., Major, A.E., Vose, J.M., Swank, W.T., 1999. Vegetation dynamics after a prescribed fire in the Southern Appalachians. For. Ecol. Manage. 114, 199–213.

Elowe, K.D., Dodge, W.E., 1989. Factors affecting black bear reproductive success and cubsurvival. J. Wildlife Manage. 53, 962–968.

Frelich, L.E., Reich, P.B., 1995. Spatial patterns and succession in a Minnesota southern boreal forest. Ecol. Monogr. 65, 325–346.

Gleeson, S.K., Tilman, D., 1990. Allocation and the transient dynamics of succession on poor soils. Ecology 71, 1144–1155.

Hermann, K.A. (Ed.), 1996. The Southern Appalachian Assessment GIS Data Base CD ROM Set. Southern Appalachian Man and the Biosphere Program, Norris, TN.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Ihalainen, M., Salo, K., Pukkala, T., 2003. Empirical predictions models for *Vaccinium myrtillus* and *V. vitis-idaea* berry yields in North Karelia, Finland. Silva Fennica 37, 95–108.

Johnson, A.S., Landers, J.L., 1978. Fruit production in slash pine plantations in Georgia. J. Wildlife Manage. 42, 1978.

Johnson, C.J., Seip, D.R., Boyce, M.S., 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. J. Appl. Ecol. 41, 238–251.

Johnston, M., 1996. The role of disturbance in boreal mixedwood forests of Ontario. In: Smith, C.R., Crook, G.W. (Eds.), Proceedings of the Workshop on Advancing Boreal Mixedwood Management in Ontario, October 17–19, 1995, Sault Ste. Marie, Ont, Natural Resources Canada, Canadian Forest Service and Ontario Ministry of Natural Resources, Sault Ste Marie, Ont, pp. 33–40.

Jonkel, C.J., Cowan, I.M., 1971. The black bear in the spruce-fir forest. Wildlife Monogr. 27 .

Matlack, G.R., Gibson, D.J., Good, R.E., 1993. Regeneration of the shrub *Gaylussacia baccata* and associated species after low intensity fire in an Atlantic coastal plain forest. Am. J. Bot. 80, 119–126.

McCarty, J.P., Levey, D.J., Greenberg, C.H., Sargent, S., 2002. Spatial and temporal variation in fruit use by wildlife in a forested landscape. For. Ecol. Manage. 164, 277–291.

Mitchell, M.S., Zimmerman, J.W., Powell, R.A., 2002. Test of a habitat suitability index for black bears in the Southern Appalachians. Wildlife Soc. Bull. 30, 794–808.

Mitchell, M.S., Powell, R.A., 2003. Response of black bears to forest management in the Southern Appalachian Mountains. J. Wildlife Manage. 67, 692–705.

Moola, F.M., Mallik, A.U., 1998. Morphological plasticity and regeneration strategies of velvet leaf blueberry (*Vaccinium myrtilloides* Michx) following canopy disturbance in boreal mixedwood forests. For. Ecol. Manage. 111, 35–50.

Neter, J., Kutner, M.H., Nachtsheim, C.J., Wasserman, W., 1996. Applied Linear Statistical Models, 4th ed. The McGraw-Hill Companies Inc., New York.

Noyce, K.V., Coy, P.L., 1990. Abundance and productivity of bear food species in different forest types of northcentral Minnesota. Int. Conf. Bear Res. Manage. 8, 169–181.

Perry, R.W., Thill, R.E., Peitz, D.G., Tappe, P.A., 1999. Effects of different silvicultural systems on initial soft mast production. Wildlife Soc. Bull. 27, 915–923.

Pickett, S.T.A., McDonnell, M.J., 1989. Changing perspectives in community dynamics: a theory of successional forces. Trends Ecol. Evol. 42, 241–245.

Powell, R.A., Zimmerman, J.W., Seaman, D.E., 1997. Ecology and Behavior North American Black Bears: Home Ranges, Habitat and Social Organization. Chapman and Hall Publishers, London.

Ramsey, F.L., Schafer, D.W., 2002. The Statistical Sleuth: A Course in Methods of Data Analysis, 2nd ed. Duxbury, Pacific Grove, CA, USA.

SAS Institute Inc., 2000. SAS/STAT User's Guide. Version 6. SAS Institute Inc., Cary, NC, USA.

Stransky, J.J., Roese, J.H., 1984. Promoting soft mast for wildlife in intensively managed forests. Wildlife Soc. Bull. 12, 234–239.

Thomas, D.W., 1984. Fruit intake and energy budgets of frugivorous bats. Physiol. Zool. 57, 457–467.

Thompson III, F.R., Fritzell, E.K., 1986. Fall foods and nutrition of ruffed grouse in Missouri USA. Trans. Missouri Acad. Sci. 20, 45–48.

Willson, M.F., 1986. Avian frugivory and seed dispersal in eastern North America. Curr. Ornithol. 3, 223–279.