

Habitat Associations of Hypogeous Fungi in the Southern Appalachians: Implications for the Endangered Northern Flying Squirrel (*Glaucomys sabrinus coloratus*)

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ABSTRACT. gporocarps of hypogeous mycorrhizal fungi (truffles) are the major food of northern flying squirrels (*Glaucomys sabrinus*). The two subspecies of northern flying squirrels that occur in the southern Appalachians, *G. s. coloratus* and *G. s. fuscus*, are endangered species which are primarily found in the ecotone between high-elevation spruce-fir and northern hardwood forests. Our objective was to determine the microhabitat and macrohabitat characteristics associated with the presence and abundance of truffles in suitable habitat for northern flying squirrels. We sampled for truffles in 24-26, 1-m² plots on each of 10 northern flying squirrel sites in North Carolina and measured micro- and macrohabitat characteristics associated with sample plots and sites. *Elaphomyces granulatus* was the most common species of truffle found (78.7%). Red spruce (*Picea rubra*) was significantly more likely to be one of the three closest trees to plots with truffles. Further, spruce was the most important species in plots with truffles, followed by beech (*Fagus grandifolia*), red oak (*Quercus rubra*) and yellow birch (*Betula lutea*), whereas the most important species in plots with no truffles were beech, followed by yellow birch, spruce and red oak. At the macrohabitat (site) level, spruce was the most important species in sites with high truffle production followed by beech and red oak, whereas the most important species in sites with low truffle production were beech, yellow birch, spruce and rhododendron (*Rhododendron* spp.). Significant variables entered into a linear regression model predicting the number of truffles in a site were the importance values of fir (*Abies fraseri*), spruce and silverbell (*Halesia carolina*). Our data suggest that spruce-fir or mixed spruce-fir/hardwood stands are important foraging sites for northern flying squirrels in the southern Appalachians.

INTRODUCTION

The northern flying squirrel (*Glaucomys sabrinus*) is relatively common in conifer and hardwood forests throughout much of northern and western U.S. and Canada (Wells-Gosling and Heaney, 1984). However, northern flying squirrels found in the southern Appalachians predominantly inhabit high-elevation spruce-fir/northern hardwood forests (Weigl et al., 1992), which are among the rarest and most threatened forest types in the South (White et al., 1993). Because these forests mostly occur at elevations > 1350 m, the habitat is naturally fragmented and island-like. Logging, road-building, pollution and the introduced balsam woolly adelgid (*Adelges piceae*) have caused further habitat loss, degradation and fragmentation (White, 1983). Because squirrel populations declined with the continual loss of habitat, the two southern Appalachian subspecies *Glaucomys s. fuscus* and *G. s.*

coloratus were listed as endangered species by the U.S. Fish and Wildlife Service in 1985 (U.S. Fish and Wildlife Service, 1990).

Conservation and management of habitat are critical to the recovery of northern flying squirrels. Although their preferred habitat generally has been defined as the ecotone between spruce-fir and northern hardwood forests, usually on north facing slopes above 1540 m and with numerous logs and snags, little is known about the specific habitat features that meet the squirrels' requirements (Payne *et al.*, 1989; Weigl *et al.*, 1992). Attempts to define distinctive structural or compositional characteristics of high quality northern flying squirrel habitat have failed in both the southern Appalachians (Weigl *et al.*, 1992) and the Pacific Northwest (Rosenberg and Anthony, 1992; Waters and Zabel, 1995). This has led to the suggestion that factors such as food supply may be important determinants of squirrel habitat quality (Carey *et al.*, 1992; Rosenberg and Anthony, 1992; Weigl *et al.*, 1992; Witt, 1992).

The diets of northern flying squirrels in the western U.S. consist primarily of hypogeous sporocarps of mycorrhizal fungi (truffles) and lichens (McKeever, 1960; Maser *et al.*, 1985; Maser *et al.*, 1986; Hall, 1991; Waters and Zabel, 1995; Rosentreter *et al.*, 1997). Truffles, particularly *Geopora* and *Elaphomyces*, are also common components of the diets of *Glaucomys s. coloratus* and *G. s. fuscus* (Weigl *et al.*, 1992). Waters and Zabel (1995) found that northern flying squirrel densities were positively correlated with truffle frequencies in northeastern California. Cázares *et al.* (1999) also concluded that truffle abundance is important in determining northern flying squirrel abundance in western Oregon, but that other factors such as tree basal area, snags, logs and cavities are also important. Thus, the species composition and abundance of truffles may be important determinants of northern flying squirrel distribution and abundance in the southern Appalachians.

Several factors, including forest management practices, affect the abundance and species composition of truffles. For example, truffle abundance is positively associated with the presence of downed logs (Amaranthus *et al.*, 1994; Clarkson and Mills, 1994). Thinning and burning of 70–100 y-old white and red fir stands (*Abies concolor* and *A. magnifica*) in northeastern California affect truffle species composition but not total abundance or frequency (Waters *et al.*, 1994). In contrast, clearcutting negatively affected truffle abundance in southwestern Oregon (Amaranthus *et al.*, 1994; Clarkson and Mills, 1994; Mills, 1995). Further, the abundance of truffles in managed young western hemlock (*Tsuga heterophylla*) stands is significantly lower than in natural mature and oldgrowth stands (North *et al.*, 1997). Size of the mature stands may also affect truffle abundance, which increases with distance from the forest/clear-cut edge (Mills, 1995). Little research has been conducted on hypogeous mycorrhizal fungal communities in the southern Appalachians (Petersen, 1984). Our objective was to determine the micro- and macrohabitat characteristics associated with truffle presence and abundance.

STUDY AREA AND METHODS

Ten sites in the southern Appalachians were sampled for truffles in August-October 1995 and June-August 1996. Nine sites were in the Balsam Mountains of North Carolina and one site (Carver's Gap) was on Roan Mountain, North Carolina. All sites were mature (>70 y) spruce-fir/northern hardwood or spruce-fir/red-oak stands \geq 1450-m elevation. Northern flying squirrels have been found in 8 of the 10 sites (Weigl *et al.*, 1992; C. McGrath, pers. comm.); based on forest type and age, the other two were considered potential northern flying squirrel sites.

We sampled for truffles on two sites (Carver's Gap and Devil's Courthouse) in 1995 and on the remaining eight in 1996. Our sampling procedures the second year were somewhat

different from those we followed the first year. However, the differences in sampling procedures had little effect on the results (see Discussion). At Carver's Gap and Devil's Courthouse we established one 5 X 5 grid at each site with 25-m spacing between grid points and sampled at each of the grid points. No nest boxes were associated with these points. The eight sites sampled in 1996 each contained 15 flying squirrel nest boxes arranged in lines that generally paralleled trails or slope contours. Nest box lines were used simply for reference. We established 26 points associated with the central 13 nest boxes. On most sites we established one point 50 m downslope and another point 50 m upslope from each nest box. On sites where it was not possible to establish a point 50 m upslope from the nest box we established the second point 25 m from the nest box and along the line of boxes.

At all sites we established a 1 X 1 m plot at each of the sample points. Because the organic soil layer was very deep, we could not sample the plots with rakes as is commonly done in the western U.S. (e.g., *Amaranthus et al.*, 1994; *Waters et al.*, 1994; *North et al.*, 1997). Instead, we dug up the entire 1 X 1 m plot to the mineral soil layer and placed the litter and organic soil layers on a plastic sheet next to the plot. We then searched the top 2-3 cm of mineral soil for truffles and sifted the entire organic soil layer and litter layer by hand. Following the search, we returned the soil to the plot. We placed truffles in labeled (site, plot number, date) wax paper bags and kept them on ice until we transferred them to the laboratory which occurred within 4 d.

Truffles were gently washed to remove soil particles, the outer mycelial covering and root fragments. Each truffle was blotted dry with paper towels, assigned an accession number and weighed. After recording the length, width and thickness, we dried each truffle at 80 C for 24 h in a forced draft oven and reweighed it. Each truffle was sliced in half with a razor blade and identified to genus or species using the key of *Castellano et al.* (1989).

At each plot on all sites we recorded the depth of the litter and organic soil layers, the distance to the nearest downed wood >10 cm in diameter at the midpoint and the distance, diameter at breast height (dbh), species, position (canopy or midstory) and decomposition stage of the three closest trees (>10 cm dbh) to the plot center. Decomposition stages followed *Thomas et al.* (1979) and ranged from 1 (healthy) to 9 (stump). In 1996 we established 8 m radius (200 m²) circular plots around each plot center and recorded the species, dbh, position and decomposition stage of all trees > 10 cm dbh and the midpoint diameter and decomposition class (*Maser et al.*, 1979) of all logs > 10 cm at the midpoint. Log decomposition classes ranged from sound (1) to highly decayed (5). Logs were later classified as nondecayed (classes 1-3) or decayed (classes 4-5). We estimated canopy cover at the center of each plot by averaging spherical densiometer readings made in each of the four cardinal directions. In 1995 we collected the same vegetation, log and canopy cover data but only sampled at three randomly selected 200 m² plots within each site.

We calculated the importance values of each tree species for each plot and for the entire site (all plots). Importance values at the plot level were calculated as (% relative basal area + % relative density; *Barbour et al.*, 1980). At the macrohabitat (site) level, importance values were calculated as (% relative basal area + % relative density + % relative frequency). Several species (basswood, *Tilia heterophylla*; bladdernut, *Staphylea trifolia*; hawthorn, *Crataegus* spp.; locust, *Robinia* spp.; mountain ash, *Sorbus umericuna* and river birch, *Betula niger*) occurred on only a few sites. These species were combined and designated as "other." In addition, we combined maples that could not be positively identified and uncommon species such as striped maple (*Acer pennsylvanicum*) and sugar maple (*A. saccharum*) and referred to them collectively as maples.

We used logistic regression procedures (PROC LOGISTIC; SAS 1990) to determine the structural (soil characteristics, logs, snags, canopy cover) and vegetation characteristics that

TABLE 1.—Number of 1 m² plots in which truffles were found and number of sporocarps of each hypogeous mycorrhizal species found in each of 10 sites in North Carolina sampled in either August–October 1995 (DC and CG) or June–August 1996 (all others). The number of plots in which each species was found is given in parentheses. Twenty-four to 26 plots were sampled per site

Site ¹	No. plots with truffles	<i>Elaphomyces granulatus</i>	<i>E. leveilli</i>	<i>E. muricatus</i>	Other	Immature	Total
DC	7	16 (4)	3 (3)	0	0	3 (2)	22
CG	3	66 (2)	0	0	1 (1)	4 (2)	71
RG	4	27 (3)	2 (1)	0	1 (1)	5 (3)	35
HG	3	4 (2)	2 (1)	1 (1)	0	1 (1)	8
BC	2	4 (1)	0	0	1 (1)	0	5
SS	1	4 (1)	0	0	0	2 (1)	6
RB	1	1 (1)	0	0	0	5 (1)	6
LS	1	0	0	0	0	2 (1)	2
BG	0	0	0	0	0	0	0
HB	0	0	0	0	0	0	0

¹ DC = Devil's Courthouse, CG = Carver's Gap, RG = Reinhart Gap South, HG = Haywood Gap, BC = Buckeye Creek, SS = Sweetwater Springs, RB = Rough Butt Bald, LS = Little Sam Knob, BG = Beech Gap, HB = Horse Bone Gap

were related to the presence of truffles at the microhabitat (plot) level. Only the three randomly selected sites from Carver's Gap and Devil's Courthouse were used in the analyses. At the macrohabitat level, we classified sites as high truffle production (Carver's Gap, Devil's Courthouse, Reinhart and Haywood Gap) and low truffle production (Little Sam's Knob, Beech Gap, Buckeye Gap, Rough Butt Bald, Horsebone Gap and Sweetwater Springs) and used logistic regression to determine which vegetation characteristics were associated with high truffle production. Sites considered to have high truffle production had ≥ 3 plots with truffles (Table 1). We used linear regression procedures (PROC REG, Freund and Littell, 1991) to determine important structural and vegetation characteristics associated with the number of truffles among all plots and the number of truffles among plots with truffles at the microhabitat scale and structural and vegetation characteristics and the number of truffles per site at the macrohabitat scale. Variables included in both the logistic and linear models were selected using stepwise selection procedures with $\alpha = 0.05$ for entry and removal. We used G-tests of goodness of fit to test whether the species, position and status (live versus dead) of the three trees nearest to plots with and without truffles differed from expected frequencies.

RESULTS

Truffles were found in 8 of the 10 sites (Table 1). The majority (78.7%) of truffles were mature *Elaphomyces granulatus*. Other species found were *E. leveilli*, *E. muricatus*, *Scleroderma* spp., *Alpova* spp. and an unidentified species. Twenty-two truffles were too immature for identification.

Litter depth, organic soil depth, canopy cover, number of logs within 8 m, number of decayed logs within 8 m, the distance to the closest log and number of snags within 8 m were similar between plots with and without truffles although distance to the closest trees tended to be less for plots with truffles (Table 2). None of the structural variables significantly predicted the presence of truffles within plots; however, among plots with truffles, canopy cover was significantly negatively related to the number of truffles within those plots

TABLE 2.—Structural characteristics of plots with and without truffles

Plot characteristic	Truffles present		Truffles absent	
	n	$\bar{x} \pm SE$	n	$\bar{x} \pm SE$
Litter depth (cm)	22	4.18 ± 0.35	235	4.17 ± 0.12
Organic soil depth (cm)	22	13.14 ± 1.06	235	13.40 ± 0.41
Canopy cover (%)	12	95.48 ± 1.09	196	93.28 ± 0.80
Logs within 8 m	12	7.85 ± 1.49	196	6.91 ± 0.43
Decayed logs within 8 m	12	3.77 ± 0.92	196	3.39 ± 0.25
Distance to closest log (m)	20	2.22 ± 0.39	210	2.44 ± 0.11
Snags within 8 m	12	2.30 ± 0.46	196	1.88 ± 0.15
Distance closest tree (m)	22	1.74 ± 0.14	235	1.97 ± 0.06
Distance 2nd closest tree (m)	22	2.54 ± 2.54	235	2.82 ± 0.07
Distance 3rd closest tree (m)	22	3.23 ± 0.20	235	3.77 ± 0.10
Mean distance 3 closest trees (m)	22	2.50 ± 0.15	235	2.85 ± 0.07

(Table 3). The species of the closest tree to plots with truffles were significantly different from expected ($G = 35.02$, $df = 8$, $P = 0.0002$). Spruce (*Picea rubra*) was found in far greater frequency than expected near plots with truffles, whereas beech (*Fagus grandifolia*) and yellow birch (*Betula lutea*) were found in lower frequencies than expected (Fig. 1a). In contrast, the three closest trees to plots without truffles were found in their expected frequencies ($G = 4.02$, $df = 8$, $P = 0.85$; Fig 1b). The decomposition stage and canopy position of the three closest trees did not differ from expected frequencies for plots with ($G = 2.43$, $df = 1$, $P = 0.12$ and $G = 2.15$, $df = 1$, $P = 0.14$, respectively) and without truffles ($G = 0.18$, $df = 1$, $P = 0.76$ and $G = 0.20$, $df = 1$, $P = 0.66$, respectively). Eighty-one percent of the three closest trees to plots with truffles were in the canopy and 72.3% of the three closest trees to plots without truffles were in the canopy; 4.6% of the three closest trees to plots with truffles were snags and 10.1% of the three closest trees to plots without truffles were snags.

Spruce was the most important species surrounding plots with truffles, followed by beech, red oak (*Quercus rubra*) and yellow birch (Table 4). In contrast, the most important species surrounding plots with no truffles was beech, followed by yellow birch, spruce and red oak

TABLE 5.—Results of linear regression models predicting the number of truffles at the microhabitat (plot) and macrohabitat (site) scales

Model/variable	Parameter estimate	SE	Partial r ²	P
Structural characteristics-Plot				
Canopy cover	-1.28	0.29	0.66	0.0013
Vegetation characteristics-Ah plots				
Spruce	0.02	0.004	0.09	0.0001
Vegetation characteristics-Truffle plots				
Spruce	0.13	0.03	0.57	0.0027
Vegetation characteristics-Site				
Fir	0.65	0.13	0.70	0.003
Spruce	0.41	0.15	0.14	0.05
Silverbell	0.11	0.03	0.09	0.04

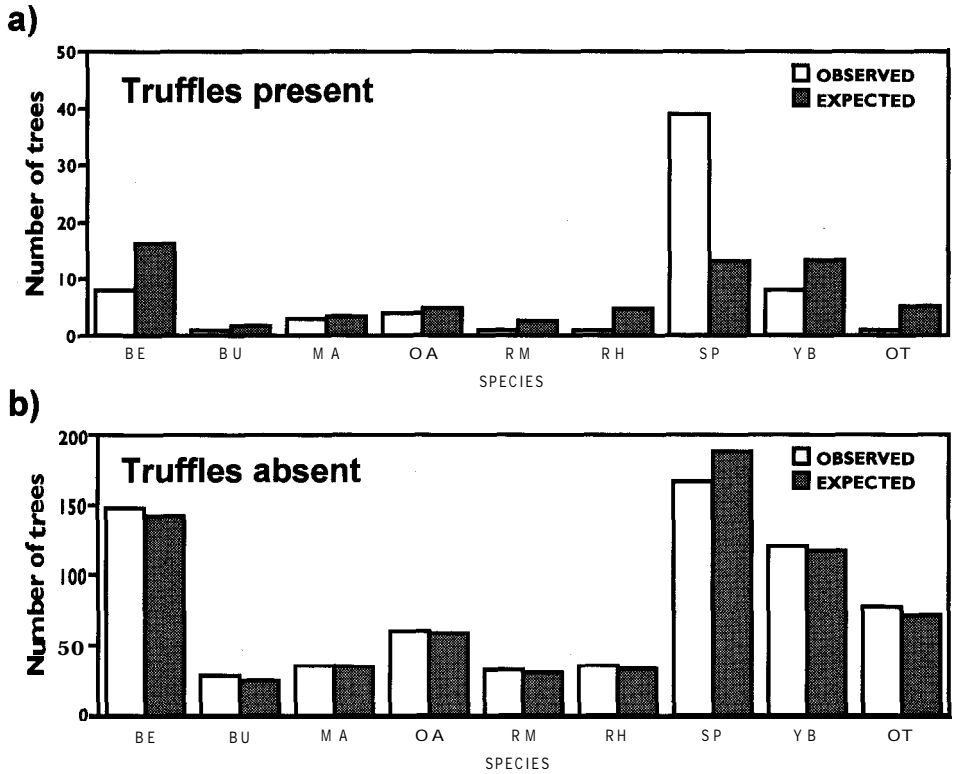


FIG. 1.—Observed and expected frequencies of each tree species surrounding plots with truffles (a) and without truffles (b). Species abbreviations: BE = beech, BU = buckeye, MA = maples, OA = red oak, RM = red maple, RH = rhododendron, SP = spruce, YB = yellow birch, OT = other

(Table 4). The importance value of spruce was the only vegetation variable that remained in the logistic regression model predicting the presence of truffles at the microhabitat level (Parameter estimate = 0.009, $SE = 0.004$, Wald chi square = 3.91, $df = 1$, $P = 0.05$). Further, the importance value of spruce was the only significant variable entered into the linear regression model predicting the number of truffles per plot among all plots and among only plots with truffles (Table 3).

At the macrohabitat level, spruce was the most important species in sites with high truffle production followed by beech and red oak whereas the most important species (in descending order) in sites with low truffle production were beech, yellow birch, spruce and rhododendron (*Rhododendron* spp.; Table 4). No tree importance values significantly predicted high truffle production. However, the importance values of fir (*Abies fraseri*), spruce and silverbell (*Halesia Carolina*) were significant variables in the linear regression model predicting the number of truffles in a site (Table 3).

DISCUSSION

Although we sampled in slightly different ways and in slightly different seasons (summer vs. late summer-early fall) between the 2 y of the study, *Elaphomyces granulatus* was the

TABLE 4.—Mean (± 1 SE) importance values of trees in plots with and without truffles (microhabitat scale) and sites with high and low truffle production (macrohabitat scale)

Species	Microhabitat (plot)		Macrohabitat (site)	
	Truffles present (n = 13)	Truffles absent (n = 201)	Truffles high (n = 4)	Truffles low (n = 6)
Beech (<i>Fagus grandifolia</i>)	52.09 \pm 16.05	52.58 \pm 4.51	74.73 \pm 37.90	100.69 \pm 41.45
Buckeye (<i>Aesculus octandra</i>)	1.62 \pm 1.62	8.00 \pm 1.69	5.29 \pm 3.05	25.32 \pm 10.96
Cherry (<i>Prunus serotina</i>)	1.80 \pm 1.80	4.35 \pm 1.01	3.30 \pm 3.30	20.38 \pm 14.48
Dogwood (<i>Cornus florida</i>)	0.0	1.14 \pm 0.58	0.0	3.91 \pm 3.91
Elm (<i>Ulmus rubra</i>)	1.38 \pm 1.38	3.89 \pm 1.10	8.73 \pm 8.73	15.54 \pm 5.07
Fir (<i>Abies fraseri</i>)	0 . 0	0.84 \pm 0.43	18.23 \pm 18.26	3.08 \pm 1.95
Maples (<i>Acer</i> spp.)	4.56 \pm 2.96	8.18 \pm 1.30	24.88 \pm 18.94	23.35 \pm 6.50
Mountain maple (<i>A. spicatum</i>)	4.30 \pm 2.42	1.89 \pm 0.51	1.04 \pm 1.04	13.64 \pm 2.01
Red oak (<i>Quercus rubra</i>)	29.17 \pm 16.34	21.78 \pm 3.20	48.46 \pm 45.24	29.82 \pm 29.82
Red maple (<i>A. rubrum</i>)	7.66 \pm 4.85	9.95 \pm 1.75	16.69 \pm 15.14	29.52 \pm 11.15
Rhododendron (<i>Rhododendron</i> spp.)	2.66 \pm 2.12	11.13 \pm 1.78	17.81 \pm 9.42	43.62 \pm 20.73
Serviceberry (<i>Amelanchier arborea</i>)	6.70 \pm 4.54	1.51 \pm 0.59	7.81 \pm 7.81	6.91 \pm 3.97
Silver maple (<i>A. saccharinum</i>)	0.0	1.90 \pm 0.64	2.21 \pm 2.21	8.36 \pm 6.00
Silverbell (<i>Halesia carolina</i>)	0.0	3.08 \pm 0.87	12.66 \pm 12.66	7.02 \pm 4.36
Spruce (<i>Picea rubens</i>)	57.22 \pm 20.17	28.67 \pm 3.25	186.45 \pm 54.74	67.20 \pm 14.40
Yellow birch (<i>B. lutea</i>)	27.63 \pm 14.57	38.25 \pm 3.81	52.94 \pm 9.07	97.09 \pm 28.40
Other	3.23 \pm 2.19	1.62 \pm 0.46	5.55 \pm 5.55	11.73 \pm 4.97

dominant species of hypogeous mycorrhizal fungi in both years and in every site (Table 1). *Elaphomyces granulatus* is one of the most common and widely distributed species of hypogeous fungi in the northern hemisphere and is found in a variety of habitats including pine, chestnut, beech and oak forests (Smith *et al.*, 1981; Zhang and Minter, 1989). North *et al.* (1997) also found a predominance of *E. granulatus* (93%) in their study of hypogeous mycorrhizal fungi in managed-young, natural-mature and oldgrowth western hemlock forests in Washington; and Luoma *et al.* (1991) considered *E. granulatus* a dominant or co-dominant species in the hypogeous mycorrhizal communities of mature and old-growth Douglas-fir forests of southwestern Oregon. However, we cannot conclude that *E. granulatus* is the dominant species of hypogeous fungi in high-elevation spruce-fir forests of the southern Appalachians because each site was sampled only once during summer or early fall. Greater species richness and diversity may be found on these sites if samples are collected year-round (Luoma *et al.*, 1991). However, annual variation in truffle presence and abundance was probably not an important factor affecting our results. For example, Fogel (1976) found some annual variation in the number of truffles in a Douglas-fir stand in western Oregon. However, species that were abundant in one year were abundant in all years and species, that were rare in one year were rare in all years.

The presence of truffles in our study was not related to soil or litter characteristics, canopy cover or coarse woody debris abundance or proximity. In contrast, truffles and downed woody debris are positively associated in the western U.S., particularly during dry periods (Amaranthus *et al.*, 1994, Clarkson and Mills, 1994). Coarse woody debris retains moisture and provides favorable fungal fruiting conditions during the dry summers characteristic of many areas in the West (Amaranthus *et al.*, 1994). We conducted our study in the high-rainfall belt of the southern Appalachians, which receives rain throughout the year and seldom experiences true drought (Helvey and Hewlett, 1962). Because of the almost continual cool and moist conditions, fungi in the southern Appalachians may not have to rely on the presence of logs for proper microclimatic conditions, so fruiting may occur within a much broader array of microsites.

In Canada, *Elaphomyces granulatus* is usually associated with *Picea* spp., *Abies* spp. and *Pinus banksiana* although in Europe it is associated with both pines and oaks (Zhang and Minter, 1989). In the southern Appalachians, the presence and abundance of truffles, primarily *E. granulatus*, were strongly associated with the presence and importance of spruce at the microhabitat scale and the importance of spruce, fir and silverbell at the macrohabitat scale. In contrast, hardwoods such as beech and yellow birch were the dominant species in plots with no truffles and in sites with low truffle production.

No quantitative studies of *Glaucomys sabrinus coloratus* food habits have been conducted, although Weigl *et al.* (1992) found that *Geopora* spp. and *Elaphomyces* spp. were common dietary items of northern flying squirrels. Therefore, it has been assumed that the diet of *G. s. coloratus* is similar to that of northern flying squirrels in the western U.S. and is comprised primarily of truffles and lichens (U.S. Fish and Wildlife Service, 1990). The low number of truffles found in this study may suggest that they are not an important food item for northern flying squirrels in the southern Appalachians. However, truffles tend to have a very patchy distribution but are often found in high numbers within those patches (Fogel, 1976; Luoma *et al.*, 1991; Amaranthus *et al.*, 1994). For example, at Carver's Gap we found 44 truffles in one 1 m² plot and 26 truffles in another plot that was only 35 m away. Truffles emit strong odors when they are mature (Fogel and Trappe, 1978) and flying squirrels are presumably able to locate them with their well developed sense of smell (Trappe and Maser, 1977). Therefore, although we did not find high numbers of truffles in our systematic sampling procedures, it is likely that northern flying squirrels are far more effi-

cient at locating and harvesting large clumps of truffles where they exist and can thus, rely on them as a food item.

The patchy distribution of truffles suggests their dispersion and abundance should have a large effect on habitat use by northern flying squirrels in the southern Appalachians. The few studies conducted on the habitat associations of northern flying squirrels in the southern Appalachians indicate that the presence of both spruce/fir and northern hardwoods is important in determining the squirrel's distributions (Payne *et al.*, 1989; Pagels, 1990; Weigl *et al.*, 1992). However, squirrels are most often captured in northern hardwood stands adjacent to spruce-fir forests (Weigl, 1987) and rarely use pure stands of spruce-fir (Weigl *et al.*, 1992). These observations raise questions about the importance of spruce-fir forests to northern flying squirrels. Our results suggest that spruce-fir and mixed spruce-fir/northern hardwood forests may be important because they support truffles and, therefore, represent important foraging habitat for *Glaucomys s. coloratus*, at least during part of the year. Although hardwood stands constitute primary habitat for northern flying squirrels in the southern Appalachians, the negative association between truffle abundance and many hardwood species suggests that they do not meet all of the squirrels' requirements. Northern hardwood stands, particularly those containing yellow birch, may be especially important for nesting (Weigl *et al.* 1992; C. McGrath, pers. comm.), but northern hardwood stands that are adjacent to spruce-fir forests may be more highly preferred because they provide ready access to an important dietary item. This suggests that the dispersion of habitat types across the landscape may be as important as their age, composition, structure or size in determining their relative quality for northern flying squirrels.

Our data suggest that management and conservation of spruce-fir forests, particularly those adjacent to northern hardwood stands, are critical to the recovery of northern flying squirrel populations. However, because there is a symbiotic relationship between mycorrhizal fungi and their host plants, spruce and its mycorrhizal fungi are interdependent. Further, hypogeous mycorrhizal fungi depend on animals, primarily mammals, for spore dispersal (Trappe and Maser, 1977; Fogel and Trappe, 1978; Johnson, 1996). Many other mammals inhabit the spruce-fir zone of the southern Appalachians (Pelton, 1984) and some eat truffles (Maser *et al.*, 1978). However, the northern flying squirrel has a larger home range than many of the other mycophagist species (e.g., Gapper's red-backed vole, *Clethrionomys gapperi*) and, thus, may be an important vector of fungal spores across the landscape. The positive associations among northern flying squirrels, truffles and spruce in the southern Appalachians suggest that each component of the system may depend on the presence of the other two. Thus, forest management practices and other human impacts such as development, pollution and introduced pests that negatively impact one component may negatively affect the entire system. The juxtaposition of forest types may also be important in the dispersal of spores to new areas.

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