

Northern Snakes Appear Much More Abundant in Old Fields than in Forests

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Temperature is one of the most important factors regulating habitat selection by ectotherms. Through behavioural thermoregulation, reptiles maintain preferred body temperatures and thereby maximize fitness. At northern latitudes, small colubrids appear to use forest habitat rarely because of thermal constraints. In cool environments, open habitats such as old fields offer more favourable thermal conditions than forest. We studied two northern colubrid snakes, Red-bellied Snake (*Storeria occipitomaculata*) and Common Gartersnake (*Thamnophis sirtalis*), in Gatineau Park, Quebec, Canada, to test the hypothesis that small northern snakes are more abundant in open than in closed habitats because open habitats provide better opportunities for thermoregulation. Snakes were sampled using large arrays of tin and plywood coverboards. Snakes were indeed much more abundant in old fields than in forest, and fields offered more favourable thermal conditions. Most snakes were captured in spring and summer (May to August) when temperatures were highest. *Storeria occipitomaculata* preferred tin over plywood coverboards. We confirmed an apparent strong preference for open habitats in northern snakes.

Key Words: Habitat selection; behavioural thermoregulation; Common Gartersnake; *Thamnophis sirtalis*; Red-bellied Snake; *Storeria occipitomaculata*; population density; Gatineau Park

Introduction

Species face different environmental conditions across their geographic ranges, and these environmental conditions limit their distribution and abundance. The abundant centre hypothesis states that a species' abundance is highest at the centre of its geographic distribution and gradually decreases toward the edges (Brown 1984; Sagarin *et al.* 2006). At higher latitudes, abiotic factors, such as temperature and sunlight, are believed to limit abundance and distribution of terrestrial species, whereas at lower latitudes biotic factors are believed to be the main limit (Dobzhansky 1950; MacArthur 1972).

The spatial distribution of reptiles is influenced by numerous factors, such as prey density (Madsen and Shine 1996), availability of hibernation sites (Reinert and Kodrich 1982), and proximity to retreat sites (Martino *et al.* 2011). For the Squamata, temperature is considered to be one of the most important factors regulating habitat selection (Reinert 1993). In ectothermic animals, the necessity to maintain an adequate body temperature is vital for physiological and developmental processes (Peterson *et al.* 1993). Indeed, body temperature affects physiological, reproductive, and ecological performance (Huey 1982). By adjusting microhabitat selection and timing of activity, ectotherms can thermoregulate effectively (Huey *et al.* 1989; Krohmer 1989).

In northern latitudes, colubrids appear to use forest rarely, probably because of thermal constraints (Charland and Gregory 1995; Halliday and Blouin-Demers 2016). Black Ratsnakes (*Elaphe obsoleta*) prefer edges of open habitats because they provide the best opportu-

nities for thermoregulation (Blouin-Demers and Weatherhead 2001). Milksnakes (*Lampropeltis triangulum*) also prefer open habitats with high thermal quality (Row and Blouin-Demers 2006a). Habitats with high thermal quality have a minimal difference between the operative environmental temperature and the preferred body temperature of individuals. Because forest vegetation is dense and does not allow sufficient exposure to sunlight, snakes are expected to use open habitats so that they can bask and achieve preferred body temperatures (Row and Blouin-Demers 2006b).

We tested the hypothesis that small northern snakes are more abundant in open than in closed habitats because open habitats provide better opportunities for thermoregulation. More specifically, we tested the prediction that the number of captures of Common Gartersnakes (*Thamnophis sirtalis*) and Red-bellied Snakes (*Storeria occipitomaculata*), both small northern snakes, should be significantly higher in old fields than in forest. We monitored the abundance of small snakes in arrays of coverboards in old fields and in forest in Gatineau Park, Quebec, during their active season in 2015.

Coverboards are effective for sampling snakes (Grant *et al.* 1992; Houze and Chandler 2002; Ryan *et al.* 2002), particularly cryptic species (Halliday and Blouin-Demers 2015). Coverboards of different sizes (Hecnar and Hecnar 2011) and materials (Engelsoft and Ovaska 2000) can attract different species based on their microhabitat preferences (Hyde and Simons 2001). Coverboards can provide protection from predation as well as thermal benefits (Cooper *et al.* 1999; Goldsbrough *et al.* 2006). Coverboards are often made of tin or plywood.

Tin was more effective than plywood for sampling Common Gartersnakes, Western Terrestrial Gartersnakes (*Thamnophis elegans*), and Sharp-tailed Snakes (*Contia tenuis*) in British-Columbia (Engelstoft and Ovaska 2000). Coverboards are preferred over traps because they are economical and safe (Ryan *et al.* 2002). A secondary objective of our study was to quantify the efficacy of tin and plywood coverboards at attracting small snakes.

Methods

We sampled snakes at four sites in Gatineau Park (45.50°N, 76.00°W), Quebec, in summer 2015. All sites were less than 25 km apart. Although Red-bellied Snake, Common Gartersnake, Smooth Greensnake (*Liochlorophis vernalis*), Ring-necked Snake (*Diadophis punctatus*), and Milksnake (*Lampropeltis triangulum*) were all captured, we only obtained sufficient captures for analysis of Common Gartersnake and Red-bellied Snake. At each of the four sites, we set up two 200-m transects with pairs of coverboards (one roofing tin, one 3/4-inch [2-cm] plywood, both 90 × 60 cm) installed every 10 m, for a total of 320 coverboards. At each site, the transects were parallel to and 50 m from the edge between old field and forest, one transect in the field and one transect in the forest. The plant community in the old fields consisted mainly of *Aster* sp., *Rhamnus* sp., *Asclepias* sp., *Cirsium* sp., and *Poa* spp. All forests were mostly composed of White Birch (*Betula papyrifera* Marshall), Sugar Maple (*Acer saccharum* Marshall), and American Beech (*Fagus grandifolia* Ehrhart). Detailed site descriptions and photographs are available in Appendix S1.

We sampled snakes weekly from 14 May to 16 November 2015. The four sites were visited on the same sunny day between 0800 and 1800 with a weekly rotation in the order in which sites were visited so that they were visited at different times of day. Snakes were hand captured under the coverboards and each individual was marked by branding one ventral scale with a medical cautery unit (Bovie Aaron Low-Temp Reusable Cautery Unit, Clearwater, Florida, USA; Winne *et al.* 2006). The date, time, air temperature (at about waist height), temperature under the coverboard, coverboard type (tin or plywood), and habitat type (forest or old field) were recorded for each capture. Individuals were then released immediately at their point of capture. We placed 18 temperature data loggers (iButton thermochron, model DS1921L, Dallas, Sunnyvale, California, USA) under coverboards of both materials and in both habitats at the four sites. The loggers were programmed to measure temperature on the hour between 0800 and 1800 for two periods: from 12 May to 30 July and from 10 September to 23 October.

For both species, we compared the total number of snakes captured (including recaptures) in forest with those captured in field and the total number of snakes

captured under tin with those captured under plywood using generalized linear mixed-effects models with a Poisson distribution in R (R Core Team 2012; package lme4; function glmer; family Poisson; Bates *et al.* 2012). We used a Poisson distribution because the data were zero inflated. Month, habitat, time of capture, ambient temperature, coverboard material, and all interactions were fixed effects, and site identity was a random effect. We compared maximum temperature under tin and plywood coverboards in forest and old field using a linear mixed-effects model in R (package nlme; function lme; Pinheiro *et al.* 2012). Habitat, cover type, and all interactions were fixed effects and site identity was a random effect.

Results

We captured 353 snakes (including recaptures) of five species during the 25 weekly visits. Captures remained constant from May until late August and then decreased slowly until November. Common Gartersnakes ($n = 90$) and Red-bellied Snakes ($n = 242$) were the two most abundant species. Rarer species included Smooth Greensnake ($n = 2$), Ring-necked Snake ($n = 2$), and Milksnake ($n = 17$). Total unique captures comprised two Ring-necked Snakes, two Smooth Greensnakes, 13 Milksnakes, 57 Common Gartersnakes, and 171 Red-bellied Snakes.

Controlling for the effects of month, site, and time of capture, we captured significantly more Common Gartersnakes ($z = 4.47$, $P < 0.001$) and Red-bellied Snakes ($z = 9.196$, $P < 0.001$) in the field than in forest (Figure 1). In fact, only one Common Gartersnake and seven Red-bellied Snakes were captured in forest. We also captured more snakes in mid-season (June to July) than in early (May) and in late season (September to November): Common Gartersnake: $z = 2.42$, $P = 0.016$; Red-bellied Snake: $z = 2.875$, $P = 0.004$ (Figure 2). Whereas Common Gartersnakes did not seem to have a preference between tin and plywood coverboards ($z = 0.11$, $P = 0.91$; Figure 1), we captured more Red-bellied Snakes under tin than plywood coverboards ($z = 5.78$, $P < 0.001$; Figure 1).

Temperature did not vary significantly between plywood and tin coverboards ($t = 0.16$, $P = 0.87$; Figure 3). Temperature varied significantly between coverboards in forest and those in fields only during the warmer months (May, June, and July). During these months, temperatures under coverboards in fields were on average 8.8°C higher than under coverboards in forest ($t = 3.46$, $P < 0.001$; Figure 3). Coverboards in forests never warmed to the preferred temperature range of either Red-bellied Snakes (about 26.5°C; Brattstrom 1965) or Common Gartersnakes (24.5°–30.7°C, Peterson *et al.* 1987; $25.5 \pm 0.4^\circ\text{C}$ [SE] to $27.4 \pm 0.3^\circ\text{C}$, Halliday and Blouin-Demers 2016; Figure 3).

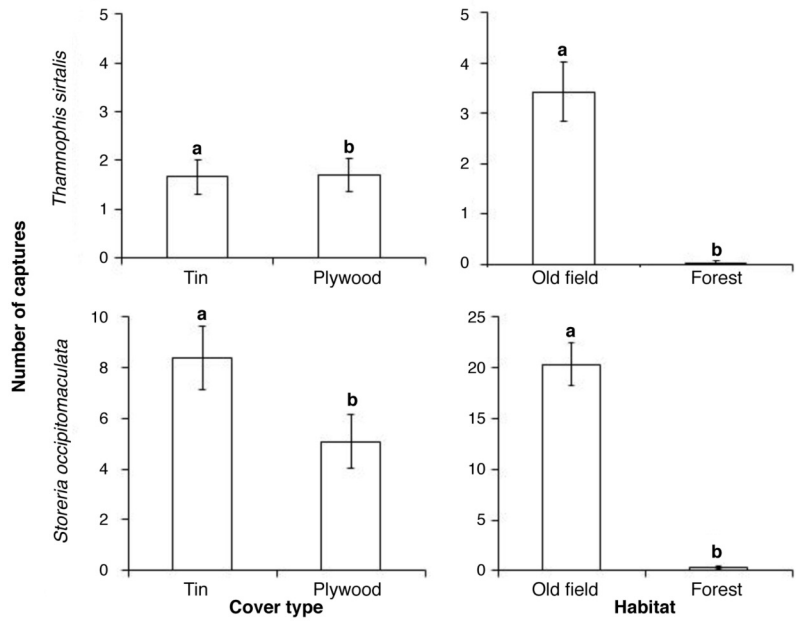


FIGURE 1. Number of captures of Red-bellied Snakes (*Storeria occipitomaculata*; $n = 242$) and Common Gartersnakes (*Thamnophis sirtalis*; $n = 90$) under plywood and tin coverboards in old field and forest in Gatineau Park, Quebec, Canada, 14 May to 16 November 2015. Each bar represents mean daily captures across four study sites. In each graph, means with the same letter are not significantly different, and error bars represent the standard error.

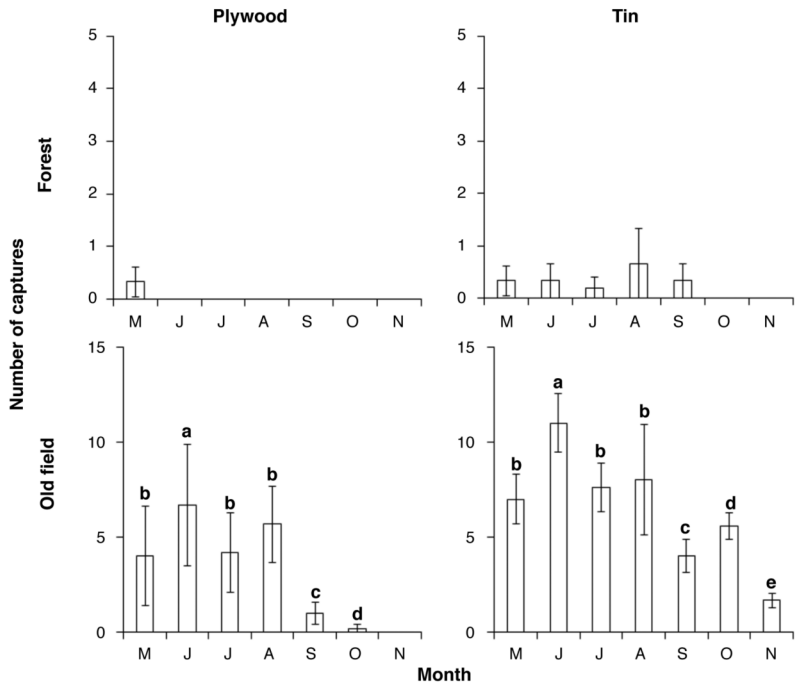


FIGURE 2. Number of captures by month of Red-bellied Snakes (*Storeria occipitomaculata*; $n = 242$) under plywood and tin coverboards in old field and forest in Gatineau Park, Quebec, Canada, 14 May to 16 November 2015. Each bar represents mean monthly captures across all four study sites. In each graph, means with the same letter are not significantly different, and error bars represent the standard error.

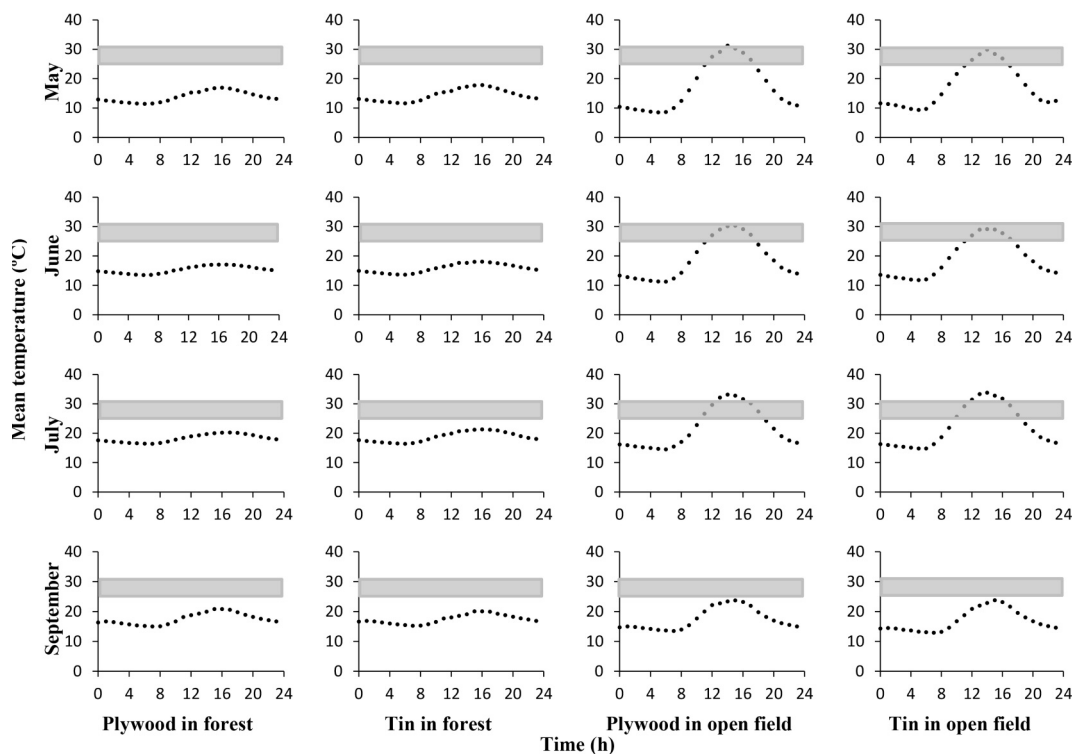


FIGURE 3. Mean temperature profiles under plywood and tin coverboards in old field and forest in Gatineau Park, Quebec, Canada, 2015. The grey rectangle represents the mean preferred temperature of Common Gartersnakes (*Thamnophis sirtalis*): 24.5–30.7°C (Peterson 1987).

Discussion

Both Common Gartersnakes and Red-bellied Snakes strongly preferred old field over forests, a pattern also observed in previous studies of other snakes (Charland and Gregory 1995; Row and Blouin-Demers 2006b; Kapfer *et al.* 2008; Lagory *et al.* 2009; Halliday and Blouin-Demers 2016). Old fields offered significantly higher temperatures than forests, particularly in May, June, and July. These patterns are consistent with the hypothesis that northern snakes are more abundant in open habitats because of their high thermal quality. Halliday and Blouin-Demers (2016) demonstrated that Common Gartersnakes prefer open habitats and that open habitats offer the best thermal conditions and the greatest fitness in terms of reproductive output and growth rate. Similarly, Black Ratsnakes use open habitats to increase fitness (measured by locomotor performance; Blouin-Demers and Weatherhead 2008). It is important to note that, although open habitats are preferred by many snake species, forest can still be important. For example, Eastern Massasauga Rattlesnakes (*Sistrurus catenatus*) prefer forest for hibernation (Harvey and Weatherhead 2006).

Most Common Gartersnakes and Red-bellied Snakes were captured from May to August with a peak in June and July, which corresponds with the highest maximum temperatures. Because body temperature directly affects physiological, reproductive, and ecological performance (Huey 1982), it is likely that the high number of captures during warmer months results from favourable thermal conditions. From May to August, high solar radiation heated the coverboards in old fields rendering them useful for behavioural thermoregulation.

It is worth noting that this study took place in a challenging thermal environment for ectotherms, where thermal quality is expected to be a strong predictor of habitat selection. In more southern and tropical locations, snakes often use forest (Luiselli and Capizzi 1997; Baxley *et al.* 2011; Steen *et al.* 2012), suggesting that thermal quality may not be a strong predictor of habitat selection in warmer areas. In Illinois, a less thermally challenging environment, Black Ratsnakes use forest more and forest edges less than populations of the same species in Ontario (Carfagno and Weatherhead 2006). Similarly, Five-lined Skink (*Plestiodon fasciatus*) uses open habitats in the northern part of its

range (Quirt *et al.* 2006; Brazeau 2016), whereas it is found in forests in the southern part of its range (Watson and Gough 2012). Therefore, although northern populations of species, such as Common Gartersnake and Red-bellied Snake, prefer open habitats because of their thermal needs, southern populations of the same species may prefer different habitats for other reasons, such as prey density (Madsen and Shine 1996; Wasko and Sasa 2012).

Another possible explanation for the preference of northern snakes for open habitats is that coverboards act as refuges reducing predation risk associated with open habitats. Cover serves both as a resting place to avoid detection (Webb and Whiting 2005) and as a refuge for individuals that have been detected in open habitats (Martin and Lopez 2015). In fact, small snakes are found more frequently under cover in open habitats than large snakes, most likely because small snakes use cover as protection from predators (Gregory and Tuttle 2016).

Tin was preferred over plywood coverboards by Red-bellied Snakes, as also observed in some other snakes (Engelstoft and Ovaska 2000; Halliday and Blouin-Demers 2015). Although Engelstoft and Ovaska (2000) believed this was because tin is a better thermal conductor than plywood, we did not detect a significant difference between temperatures under tin and plywood coverboards. Furthermore, Common Gartersnakes did not prefer tin coverboards, but this may be a result of fewer captures (90 Common Gartersnakes versus 242 Red-bellied Snakes) and, thus, less power to detect a preference. The intriguing preference for tin over plywood coverboards in several snakes warrants further study.

In conclusion, Common Gartersnakes and Red-bellied Snakes were more abundant in old fields than in forest, confirming the preference of northern snakes for open habitats, likely because such habitats facilitate behavioural thermoregulation. However, an important caveat must be made: snakes were sampled exclusively with coverboards, and coverboards may be more attractive to snakes in open habitats than in closed habitats. For instance, we showed that coverboards in fields became warmer than coverboards in forest because they received more solar radiation. In fact, coverboards in forest never reached the preferred body temperature range of small northern snakes. Therefore, it is possible that coverboards in fields are more attractive to snakes because of their superior thermal attributes and, thus, are used more than coverboards in forest. If this is the case, the number of captures under coverboards may not be an accurate reflection of the relative density of snakes in the two habitats. This potential bias clearly deserves further study using different sampling methods.

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SUPPLEMENTARY MATERIAL:

APPENDIX S1: Detailed descriptions of the study sites, provided by Audrey Paquette and Mélanie Routh under the supervision of Jocelyne Jacob, National Capital Commission, Gatineau Park.

APPENDIX S1. Detailed descriptions of the study sites, provided by Audrey Paquette and Mélanie Routh under the supervision of Jocelyne Jacob, National Capital Commission, Gatineau Park. Photos: F. R. Diaz.

SITE 1. Luskville Falls, located along the Eardley escarpment. The site is located along an old agricultural field along a forest at the base of the Eardley escarpment.



The field is composed of an about 1 m high herbaceous plant community. Some patches of shrubs and smaller trees are located directly in the field, composed mainly of *Myrica gale*. Various semi-mature *Fraxinus nigra*, *Pinus strobus*, and *Acer saccharum* are also found in the field. The herbaceous plant community consists of *Asclepias* spp., *Carex* spp., *Poa* spp., *Ranunculus acris*, *Trifolium pretense*, *Trifolium repens*, *Vicia cracca*, *Onoclea sensibilis*, *Dryopteris phegopteris*, *Galium* spp., *Anemone canadensis*, *Potentilla recta*, *Rhus typhina*, and *Parthenocissus quinquefolia*.



The forest is dominated by *Acer saccharum* (40%), *Ulmus americana* (40%), and *Fraxinus* spp. (20%).

SITE 2. Pilon Road, located along the Eardley escarpment. The site is located along an old agricultural field along a forest at the base of the Eardley escarpment.



The field is composed of an about 50 cm high herbaceous plant community. Some patches of shrubs and smaller trees are located directly in the field, composed mainly of *Myrica gale* and *Fraxinus nigra*.

The herbaceous plant community consists of *Asclepias* spp., *Carex* spp., *Poa* spp., *Ranunculus acris*, *Trifolium pretense*, *Trifolium repens*, *Vicia cracca*, *Onoclea sensibilis*, *Dryopteris phegopteris*, *Galium* spp., *Anemone canadensis*, *Cirsium arvense*, *Lotus corniculatus*, and *Mentha arvensis*.



The forest surrounding the field is dominated by *Acer saccharum* (30%), *Quercus rubra* (25%), *Quercus macrocarpa* (25%), *Acer rubrum* (10%), and *Fraxinus* spp. (10%).

Rubus odoratus, *Rubus allegheniensis*, *Maianthemum racemosum*, *Aster macrophyllus*, *Osmunda claytoniana*, *Onoclea sensibilis*, and *Dryopteris phegopteris* are also found along the forest edges.

SITE 3. This site is located near the Dennison Dam and is the site closest to an urban area; the site is bordered by a cycling pathway.



The field consists of about 70% herbaceous plants with a height of approximately 1 m. Very few smaller trees are found in this field. About 15% of this field consists of small herbaceous plants such as *Vicia cracca*, *Lotus corniculatus*, *Parthenocissus quinquefolia*, *Asclepias* spp., *Anemone canadensis*, *Potentilla recta*, *Trifolium pratense*, *Trifolium repens*, *Hypericum perforatum*, *Ranunculus acris*, *Gallium mollugo*, and *Leucanthemum vulgare*.

The other 15% of the field consists of various shrub trees and semi-mature tree species such as *Pinus strobus*, *Fraxinus americana*, *Ulmus americana*, *Rhamnus cathartica*, and *Rhamnus frangula*.

The forest community along the field is composed mainly of *Acer saccharum* (5%), *Ulmus americana* (30%), *Pinus strobus* (10%), *Populus grandidentata* (5%), *Quercus rubra* (30%), and *Fraxinus americana* (20%).

SITE 4. This site is located in the Meech Creek Valley, where agriculture was once dominant.



The field consists of about 10% invasive species (*Vicia cracca*, *Lotus corniculatus*, and *Cirsium vulgare*), 10% *Asclepias* spp., and 85% herbaceous plants with a height of approximately 1.5 to 2 m. Very few semi-mature trees are found in this field.



The forest community along the field is composed mainly of *Acer saccharum* (40%), *Ulmus americana* (40%), *Pinus strobus* (10%), and *Picea glauca* (10%).