SPECIES COMPOSITION AND METAPOPULATION ANALYSIS OF THREE FOREST OPENING SITES WITHIN SHAWNEE NATIONAL FOREST, ILLINOIS

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Table of Contents

Summary

Forest openings are prairie-like habitats found within dry forests. These openings contain a different plant species composition than the surrounding forest, leading to increased biodiversity in areas containing forest openings. Forest openings are threatened by the encroachment of woody species due to fire suppression. Many forest openings are reduced to series of habitat patches along ridge-tops, leading to the possibility that some plant species within these habitat patches exist as metapopulations. We conducted floristic surveys of 36 forest opening within three sites to determine whether any of the vascular plant species in the forest opening behaved as metapopulations according to an incidence-function metapopulation model developed by Hanski (1994), and adapted by Quintana-Ascencio and Menges (1996). We found 123 species of vascular plants at the three sites, of which 53 have the potential to be metapopulation species, according to the model. Careful implementation of measures (tree removal, burning) to maintain the integrity of the forest opening as open habitat is recommended to ensure the survival of the metapopulation species.

Introduction

Forest openings are defined as areas of prairie-like habitat found within xeric forests (Heikens, 1991; Heikens & Robertson, 1995). Based upon bedrock type, these have been given different names, such as barrens, glades, and hill prairies (Heikens & Robertson, 1995), but they share characteristics that allow them to be grouped together into a common habitat type. Forest openings are characterized by thin, often rocky, soil, and microhabitat conditions, which are hotter and drier than that of the surrounding forest. Since south and southwest-facing slopes receive more direct sun exposure, hence leading to hotter, drier microhabitat conditions, forest openings are most often found on south or southwest-facing slopes. Forest openings differ from treefall gaps in their size (forest openings are larger) and origin (the climate conditions of forest openings generally deter trees from becoming established). However, fire-suppression has allowed eastern red cedar (*Juniperus virginiana*) and other species to encroach upon previously open areas, and close the canopy, resulting in less sunlight reaching the ground. This succession leads from an open, prairie-like habitat, characterized by scattered trees such as *Quercus stellata*, with a ground layer of *Vaccinium arboreum* and *Schizachyrium scoparium*, to an open forest characterized by tree species such as *Acer saccharum*, *Diospyros virginiana*, and *Ostrya virginiana*. Due to this, plant species that have adapted to living in the hot, dry conditions of forest openings suffer a decrease in recruitment and establishment, eventually resulting in the extirpation of those plant species from the landscape.

Where forest openings persist, the resulting habitat diversity causes an increase in plant species diversity across the landscape. However, due to continual woody species encroachment, even large expanses of remaining forest openings (barrens, glades, etc.) have been fragmented into smaller patches of habitat that are more-or-less connected through dispersal along dry xeric ridges. This fragmentation of forest openings is comparable to forest habitat fragmentation resulting from urban development. In both cases, species persistence may depend upon the ability of individual species to either 1) maintain a viable population in the smaller habitat area, or 2) interact through dispersal with nearby habitat patches, as a source-sink population or a metapopulation.

The purpose of this study is to determine whether herbaceous vascular plant species within dry forest openings are behaving as metapopulations. Metapopulations, loosely defined, are collections of local populations of a given species that interact through dispersal, so that the regional persistence of the species depends upon the rate of dispersal between forest openings being higher than the rate of extinction of the local populations (Hanski, 1999). Most often, metapopulations are depicted as occurring on a set of "islands" of suitable habitat within an inhospitable "matrix" of unsuitable habitat. In this case (that of prairie-like patches within a dry forest), however, this assumption must be relaxed slightly, as most of the species that occur within forest openings can survive to some extent in light gaps within the forest itself.

The knowledge of the type of regional dynamics that species (for example, a rare species or an invasive species) have can be useful for management decisions for that species. If a species is found to consist of isolated local populations, then each local population must be managed separately. However, if a species is found to behave as a metapopulation, then the collection of local populations can be managed as a group. Since the extinction of local populations in a metapopulation is normal, the local extinction of say, an invasive species, does not necessary mean that that species is gone permanently from a given area. Rather, an invasive species that behaves as a metapopulation will likely return in subsequent years unless all potential sources of volunteers (e.g. all other local populations) are eliminated as well.

Study Sites

Three groups of forest opening patches (hereafter referred to as "patches") were selected in the Shawnee National Forest region of southern Illinois. Potential forest openings sites were selected by use of GIS (Geographical Information System), based upon criteria of state ownership, slope, aspect, and cover type. Potential sites were ground-truthed to ensure that the requisite number (12 or more) of patches were present. Of the potential 10-12 sites, only three (Giant City State Park, Berryville Shale Barren, McClure School Shale Barren) contained enough patches to be considered for the study. Giant City State Park (GC) (N 37° 36.48, W 89° 11.49'), Makanda, Illinois, is located within the Shawnee Hills physiographic subdivision. Soils within forest opening patches here are relatively thick compared to the other sites (> 10 cm depth in places), but are interspersed with areas of exposed sandstone bedrock. Twelve patches were located here, spread out over a 3-km^2 area. McClure School Shale Barrens (MC) (N 37° 26.19', W 89° 17.31') and Berryville Shale Barrens (BE) (N 37° 26.99', W 89° 17.57'), both in Jonesboro, Illinois, are located within the Ozark Hills subdivision. Soils within these two sites are relatively thin (approx. < 5 cm depth), and very gravelly, the gravel consisting of small (~ 1 cm) flakes of the shale parent material. Bedrock is exposed in many places within these two sites. Fourteen patches were located at McClure, and twelve patches were found at Berryville. Spacing of patches at these sites is different from that of Giant City: at Berryville and McClure, patches are located along one long (0.5 km) ridge each, while at Giant City, patches are scattered along several short (100-200 m) ridges.

Methods

Potential forest opening sites were found using the above method (see "Study Sites"). In order for the metapopulation model (see below) to give the best estimate of parameters, at least 50 patches (in this case, at least 17 patches per site) is most preferable; however, the number of distinct patches was a limiting factor at most sites, so the sites with the most patches per site were used. Of the three sites, McClure had the most acceptable patches (14), while Berryville and Giant City had even fewer (12 each). Patch acceptance criteria were: size between 0.1-0.5 ha (for feasibility of surveys), total (hemispheric) canopy cover greater than 20%, and the presence of xeric species, such as the grasses *Shizachyrium scoparium*, *Vulpia octoflora*, or *Sorghastrum nutans*. Potential sites and patches were surveyed for these characteristics in the summer of 2004.

The patches in the three sites were surveyed again during the 2005 growing season (Mar.-Oct.), and voucher specimens were collected of the vascular plant flora, and are deposited in the SIUC Herbarium. Nomenclature follows Mohlenbrock (2002). Incidence data (presence or absence) of each species was noted, and percent canopy cover of each species also was estimated in each patch. Patch area was measured in the field, and coordinates of each patch were taken using a Trimble GeoXM GPS unit. Using these data, the distance between patches was measured using Trimble GIS Office software. The parameters (species incidence in each patch, patch size, and patch distance) were then used in a metapopulation model to determine whether species occurrence was consistent with that of a metapopulation.

A two-state Markov-chain metapopulation model (Hanski, 1994; Quintana-Ascencio & Menges, 1996) was used to estimate parameters necessary to determine whether a species behaved as metapopulation. This method has the advantage that one can quickly determine whether all species in a region of interest behave as metapopulations, based upon the model. It also is advantageous in terms of cost, as molecular methods to do the same would be exorbitant (and time-consuming) if one were to study all species in a given habitat type. However, the use of molecular and genetic data to examine metapopulations of a single species usually is preferred, as these generally provide a more complete and accurate picture of the species dispersal patterns than modeling alone (Cain et al., 2000).

Using data collected in the field (patch size, patch distance, and species incidence), an isolation index (S_i) is calculated for each local population ($_i$), using the equation

$$S_i = \sum p_j \exp(-\alpha d_{ij}) A_j \, ,$$

where p_j is the incidence (1 for occupied patches, 0 for unoccupied patches, estimated using maximum likelihood methods) of the species in the destination patch j, α is a constant representing the ability of the species to survive over distance, d_{ij} is the distance from origin patch i to destination patch j, and A_j is the area of patch j (Hanski, 1994; Quintana-Ascencio & Menges, 1996). "Local population" is defined as the population of the focal species occurring within a patch. Although values of this index are negative, lower index values (i.e., more negative) mean that the local population is more likely to have a connection to the other local populations. Higher values (less negative) mean that a local population is more isolated from the other local populations. For each species, patch size (A_i), incidence (J_i) and patch isolation (S_i) for each patch are input into the metapopulation model. The model is given as

$$J_i = 1/\ (1 + (e'/(S^2{}_i A^x{}_i))),$$

where *e*' is a composite parameter (*e*' = *ey*') that includes the extinction probability (*e*) for the species in the focal patch, and the colonization ability (*y*'), and *x*, which describes the speed at which the probability of extinction decreases as patch size increases.

Both *y*' and *x* were estimated in SAS (PROC NLMIXED) (SAS, 2003) using the nonlinear model (described above) and the known parameters. *If the estimated extinction parameter* x *is a positive value, then the species behaves according to the assumptions of the model and is considered to be a metapopulation.* In this model, a value of *x* that is approximately 1 means that the metapopulation is stable, while a number less than 1 means that the metapopulation is declining, and heading toward extinction. This process is repeated for each species of interest, and can be used to determine whether the species in a given area act as metapopulations.

Results

A total of 123 vascular plant species were found at the three sites within patches. There were 85 species at Giant City, 61 species at Berryville, and 57 species at McClure (see Tables 1-4). Of these, 34 species were present at two of the sites, while 23 species were present at all three sites. These numbers do not include species that are found within the forests surrounding the openings; only species found within forest openings are included here. According to the metapopulation model, 52 species have the incidence pattern indicative of metapopulation species (26 at Giant City, 19 each at Berryville and McClure). Of these, 12 species form metapopulations at more than one site (Tables 5-8) (i.e., *Ambrosia artemisiifolia, Asclepias tuberosa, Cunila origanoides, Dichanthelium praecocious, Erigeron strigosus, Euphorbia corollata, Houstonia pusilla, Hypericum punctatum, Oxalis violacea, Rosa setigera , Schizachyrium scoparium, Stylosanthes biflora)*.

Discussion

There appear to be more species found at Giant City compared with the other two sites. This difference is likely due to the nature of the forest openings at Giant City. As detailed in the "Study Sites" section, forest openings within Giant City State Park occur on deeper soils than the other two sites. It is extremely likely that the dry, thin, gravelly soil at McClure and Berryville is less amenable to supporting plant life than that of Giant City. While soil conditions (thickness, texture) in the surrounding forests are similar to that of the forest openings at all sites, the differences between environmental conditions between forest and opening at Giant City are probably less distinct than that of Berryville or McClure (this will be tested empirically during the 2006 season). As a result, many forest and forest-edge species (such as *Parthenocissus quinquefolia* and *Toxicodendron radicans*) can be found at the edges of forest openings at Giant City. This type of species is less frequent or absent from McClure or Berryville forest openings.

The flora of the forest openings at the three sites also differed in terms of dominant species. Forest openings at Giant City have the highest total percent cover of the invasive species *Lonicera japonica*. This is due to the dominance of this plant in patches in which it occurs, mainly in the Post Oak Trail area. Other dominant species, such as *Danthonia spicata* and *Schizachyrium scoparium*, occur in more patches, but occupy less area within them. At McClure, the most dominant species is the spring herb *Nothoscordum bivalve*. This plant and other spring herbs such as *Oxalis violacea* take advantage of the lack of competition in the early spring to proliferate before late-spring species appear. Dominant plants in McClure tend to occur in most patches, unlike those at Giant City. At Berryville, dominant species are a mixture of early-spring herbs such as *Oxalis violacea* and *Nothoscordum bivalve*, and grasses such as *Schizachyrium scoparium* and *Danthonia spicata*. All of these are well-distributed, occurring in most patches. The latter two sites (Berryville and McClure) tend to have similar species compositions in all patches, while Giant City has more variability between patches. This is most likely a reflection of the spatial orientation of the patches. Since all of the patches at McClure and Berryville are each found along one long ridgeline, dispersal distance is relatively low between patches, and microhabitat conditions in patches have low variability at these sites. At Giant City, patches are scattered along several shorter ridgelines, leading to larger dispersal distance between patches, and possibly more microhabitat variation between patches. It is therefore no surprise that Berryville and McClure would have lower beta-diversity than Giant City.

Few non-native, invasive species occur in forest openings. Although species such as *Rosa multiflora* and *Lonicera japonica* do occur in forest openings at Giant City State

Park, they do not occur in many of the forest openings. This is likely due to the fact that these species prefer more mesic habitats to dry forest openings. The patches in which these species do occur in Giant City may be less distinct from the surrounding forest, i.e., they may have overall environmental characteristics that fall within the range of conditions that the invasives require. *Lonicera japonica* grows within the forest, and spreads vegetatively into forest openings, whereas *Rosa multiflora* grows in forest opening patches near a path at Post Oak Trail. Invasive species tend not to form metapopulations in forest openings because they are generalists, rather than specialists. Therefore, they can grow in a variety of habitats and are not limited to specialized sites such as forest openings. Invasive species tend not to occur in openings at McClure or Berryville, although invasive plant species may be found in the nearby forests at both preserves. It is likely too dry at these sites to sustain populations of Illinois' most noxious invasive species, although non-native species can be found in forest openings (West, 2005).

The metapopulation model found that approximately 30-33% of species occurring in forest openings at each site had the spatial characteristics indicative of metapopulations. This is a comparable percentage to that of Quintana-Ascencio and Menges (1996), who found that 25 out of 80 (31.25%) Florida rosemary scrub species that were tested fit the metapopulation model. However, some of the forest opening species that were tested are shrub species, and others are not exclusive to forest openings. Therefore, one cannot conclude with certainty that these species indeed exist as metapopulations in the classical sense. It is more likely that species that occur only in forest openings, such as *S. scoparium*, or short-lived species, such as *Erigeron strigosus* exist as metapopulations, as these are either limited by their habitat, or must reproduce and disperse to new areas in order to maintain a regional population.

Management Recommendations

The largest threat to the species within forest openings in southern Illinois is habitat loss. As previously discussed, forest openings are distinct habitat types within dry forests that are maintained by having environmental conditions that are too dry for most shrub and tree species to survive. This in turn keeps the canopy cover low, which allows prairie species to maintain viable populations. However, there are a few species of trees, most notably *Juniperus virginiana*, which can tolerate dry conditions well enough to grow and shade out herbaceous species. In the past, xerophyllic trees were controlled by sporadic fires, which killed saplings and damaged adults so as to reduce fitness to reproduce. Since fire-suppression policies have been instituted, the lack of killing fires has allowed *J. virginiana* to encroach upon and shade out many forest opening habitats.

Therefore we recommend management practices that discourage the growth of tree species such as *J. virginiana* in forest opening habitats. Either physical removal of trees or selective burning of forest openings will prevent forest opening species from being out-competed for light. This method has met with some success at Collier Glade in Hardin County, Illinois (Delong et al., 2005). However, we caution against using these techniques on a widespread basis until more is known about the nature of the metapopulation-forming species in the forest openings. It is unknown at this time whether species in forest openings form metapopulations as a response to habitat fragmentation, or whether metapopulations result from dispersal between naturallyoccurring local populations, which may be patchy on the landscape. Rather, we recommend that tree-removal should be tried at some forest opening sites, with careful monitoring of metapopulation species to see if they respond positively to these management practices or not.

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Table 1. Species list at Giant City State Park. Species are listed alphabetically by genus. # plots = number of incidences in 12 plots. ttl% = total percent cover of species. % freq = percentage of patches in which species occurs. % all plots = species abundance within forest openings.

Species	# plots	ttl %	% freq	% all plots
Agalinis skinneriana (Wood) Britt.	1	2	8.3%	0.17%
Ageratina altissima (L.) R.M. King & H. Robins	6	16	50.0%	1.33%
Allium canadense L.	1	2	8.3%	0.17%
Ambrosia artemisiifolia L.	3	8	25.0%	0.67%
Apocynum cannabinum L.	4	20	33.3%	1.67%
Aristida oligantha Michx.	3	12	25.0%	1.00%
Ascyrium multicaule Michx.	3	14	25.0%	1.17%
Asplenium platyneuron (L.) B.S.P.	7	13	58.3%	1.08%
Aster laevis L.	2	5	16.7%	0.42%
Aster lanceolatus Willd.	1	1	8.3%	0.08%
Bidens bipinnata L.	4	25	33.3%	2.08%
Cardamine hirsuta L.	1	3	8.3%	0.25%
Cardamine parviflora L. *var. arenicola* (Britt.) O.E. Schultz	4	8.5	33.3%	0.71%
Carex albursina Sheldon	2	2	16.7%	0.17%
Carex bushii Mackenzie	8	23	66.7%	1.92%
Carex granularis var. *haleana* (Olney) Porter	2	2	16.7%	0.17%
Cerastium fontanum Baum.	1	2	8.3%	0.17%
Chamaecrista nictitans (L.) Moench	3	5	25.0%	0.42%
Chasmanthium latifolium (Michx.) Yates	3	11	25.0%	0.92%
Claytonia virginica L.	5	16	41.7%	1.33%
Clitoria mariana L.	1	1	8.3%	0.08%
Cunila origanioides (L.) Britt	5	10	41.7%	0.83%
Danthonia spicata (L.) Beauv. ex Roemer & J.A. Schultes	11	62	91.7%	5.17%
Dichanthelium boscii (Poir.) Gould & Clark	7	15	58.3%	1.25%
Dichanthelium microcarpon (Muhl.) Mohlenbr.	9	21	75.0%	1.75%
Dichanthelium polyanthes (Schult.) Mohlenbr.	5	16	41.7%	1.33%
Dichanthelium praecocius (Hitchc. & Chase) Mohlenbr.	6	15.5	50.0%	1.29%
Elaeagnus angustifolia L.	1	4	8.3%	0.33%
Elymus canadensis L.	7	23	58.3%	1.92%
Eragrostis spectabilis (Pursh) Steud.	1	1	8.3%	0.08%
Erigeron strigosus Muhl. ex Willd.	3	5	25.0%	0.42%
Euphorbia corollata L.	4	8	33.3%	0.67%
Galactia regularis (L.) B.S.P.	1	1	8.3%	0.08%
Galium aparine L.	4	39	33.3%	3.25%
Galium circaezans Michx.	3	7	25.0%	0.58%
Galium pilosum Ait.	4	7	33.3%	0.58%
Galium triflorum Michx.	1	1	8.3%	0.08%
Geranium maculatum L.	2	4	16.7%	0.33%
Heuchera americana L.	1	1	8.3%	0.08%
Houstonia pusilla Schoepf	7	13.5	58.3%	1.13%
Hypericum prolificum L.	1	2	8.3%	0.17%
Hypericum punctatum Lam.	2	1.5	16.7%	0.13%
Hypoxis hirsuta (L.) Coville	1	0.5	8.3%	0.04%
Juniperus virginiana L.	1	1	8.3%	0.08%

Krigia biflora (Walt.) Blake	1	1	8.3%	0.08%
Krigia dandelion (L.) Nutt.	3	7	25.0%	0.58%
Lobelia inflata L.	1	1	8.3%	0.08%
Lonicera japonica Thunb.	5	138	41.7%	11.50%
Luzula multiflora (Ehrh.) Lej.	4	5.5	33.3%	0.46%
Manfreda virginica (L.) Salisb. ex Rose	2	4	16.7%	0.33%
Myosotis verna Nutt.	2	1.5	16.7%	0.13%
Nothoscordum bivalve (L.) Britt.	5	40	41.7%	3.33%
Opuntia humifusa (Raf.) Raf.	2	6	16.7%	0.50%
Oxalis stricta L.	1	1	8.3%	0.08%
Oxalis violacea L.	5	12	41.7%	1.00%
Parthenocissus quinquefolia (L.) Planch.	11	36	91.7%	3.00%
Penstemon pallidus Small	3	6.5	25.0%	0.54%
Podophyllum peltatum L.	1	8	8.3%	0.67%
Polystichum acrostichoides (Michx.) Schott	1	4	8.3%	0.33%
Prunella vulgaris L.	1	2	8.3%	0.17%
Pycnanthemum tenuifolium Schrad.	4	10	33.3%	0.83%
Ranunculus micranthus Torr. & Gray	1	3	8.3%	0.25%
Rhus aromatica Ait.	1	6	8.3%	0.50%
Rhus coppalina L.	1	1	8.3%	0.08%
Rosa multiflora Thunb. ex Murr.	2	8	16.7%	0.67%
Rosa setigera Michx.	5	6.5	41.7%	0.54%
Rubus pensilvanicus Poir.	3	6	25.0%	0.50%
Sanicula canadensis L.	1	1	8.3%	0.08%
Schizachyrium scoparium (Michx.) Nash	8	49	66.7%	4.08%
Scleria pauciflora var. pauciflora Muhl. ex Willd.	3	3.5	25.0%	0.29%
Scutellaria incana Biehler	3	11	25.0%	0.92%
Sedum pulchellum Michx.	1	2	8.3%	0.17%
Smilax bona-nox L.	1	1	8.3%	0.08%
Smilax glauca Walt.	1	1	8.3%	0.08%
Solanum carolinense L.	1	1	8.3%	0.08%
Solidago nemoralis Ait.	3	4	25.0%	0.33%
Sorghastrum nutans (L.) Nash	1	1	8.3%	0.08%
Stylosanthes biflora (L.) B.S.P.	6	70.5	50.0%	5.88%
Toxicodendron radicans (L.) Kuntze	2	3	16.7%	0.25%
Tradescantia virginiana L.	4	15	33.3%	1.25%
Triodanis perfoliata (L.) Nieuwl.	4	16	33.3%	1.33%
Viola rafinesquii Greene	4	9.5	33.3%	0.79%
Viola sororia Willd.	2	3	16.7%	0.25%
Vulpia myuros (L.) K.C. Gmel.	1	1	8.3%	0.08%
Woodsia obtusa (Spreng.) Torr.	4	12	33.3%	1.00%

Table 2. Species list at McClure School Shale Barrens. Species are listed alphabetically by genus. #plots = number of incidences in 14 plots. ttl% = total percent cover of species. % freq = percentage of patches in which species occurs. % all plots = species abundance within forest openings.

Species	# plots	ttl %	% freq	% all plots
Agalinis skinneriana (Wood) Britt.	7	18	50.0%	1.29%
Allium canadense L.	2	4	14.3%	0.29%
Ambrosia artemisiifolia L.	3	10	21.4%	0.71%
Asclepias tuberosa L. ssp. *interior* Woodson	3	4	21.4%	0.29%
Asplenium platyneuron (L.) B.S.P.	2	4	14.3%	0.29%
Cardamine hirsuta L.	1	5	7.1%	0.36%
Cardamine parviflora L. var. *arenicola* (Britt.) O.E. Schultz	10	31.5	71.4%	2.25%
Carex bushii Mackenzie	2	5	14.3%	0.36%
Carex granularis var. haleana (Olney) Porter	1	1	7.1%	0.07%
Chamaecrista nictitans (L.) Moench	3	5	21.4%	0.36%
Cheilanthes feei T. Moore	6	82	42.9%	5.86%
Clitoria mariana L.	3	4	21.4%	0.29%
Cunila origanioides (L.) Britt	10	26	71.4%	1.86%
Danthonia spicata (L.) Beauv. ex Roemer & J.A. Schultes	9	31	64.3%	2.21%
Desmodium marilandicum (L.) DC	2	2	14.3%	0.14%
Dichanthelium boscii (Poir.) Gould & Clark	1	7	7.1%	0.50%
Dichanthelium dichotomum (L.) Gould var. *barbulatum* (Michx.) Mohlenbr.	12	69	85.7%	4.93%
Dichanthelium polyanthes (Schult.) Mohlenbr.	2	7	14.3%	0.50%
Eragrostis spectabilis (Pursh) Steud.	2	4	14.3%	0.29%
Erigeron strigosus Muhl. ex Willd.	3	4.5	21.4%	0.32%
Euphorbia corollata L.	12	20	85.7%	1.43%
Galium aparine L.	1	3	7.1%	0.21%
Galium pilosum Ait.	1	1	7.1%	0.07%
Houstonia pusilla Schoepf	3	6	21.4%	0.43%
Isanthus brachiatus (L.) BSP	1	2	7.1%	0.14%
Lespedeza intermedia (S. Wats.) Britt.	7	29	50.0%	2.07%
Lespedeza virginica (L.) Britt.	6	10	42.9%	0.71%
Manfreda virginica (L.) Salisb. ex Rose	11	30	78.6%	2.14%
Myosotis verna Nutt.	6	12.5	42.9%	0.89%
Nothoscordum bivalve (L.) Britt.	13	496	92.9%	35.43%
Oxalis stricta L.	11	19.5	78.6%	1.39%
Oxalis violacea L.	10	90	71.4%	6.43%
Parthenocissus quinquefolia (L.) Planch.	1	5	7.1%	0.36%
Penstemon pallidus Small	8	18	57.1%	1.29%
Plantago aristata Michx.	1	12	7.1%	0.86%
Polygonum ramosissimum Michx.	1	7	7.1%	0.50%
Ranunculus fascicluaris Bigel.	3	4.5	21.4%	0.32%
Rhus aromatica Ait.	6	28	42.9%	2.00%
Rhus coppalina L.	1	3	7.1%	0.21%
Rosa carolina L.	2	9	14.3%	0.64%
Ruellia strepens L.	1	5	7.1%	0.36%
Ruellia pedunculata Torr.	2	20	14.3%	1.43%
Sanicula canadensis L.	1	1	7.1%	0.07%
Scutellaria incana Biehler	2	6	14.3%	0.43%

Setaria glauca (L.) P. Beauv.	1	7	7.1%	0.50%
Silphium integrifolium Michx.	10	30	71.4%	2.14%
Smilax bona-nox L.	4	18	28.6%	1.29%
Solidago ulmifolia Muhl.	6	20	42.9%	1.43%
Sphenopholis obtusata (Michx.) Scribn.	2	4	14.3%	0.29%
Stylosanthes biflora (L.) B.S.P.	7	30	50.0%	2.14%
Tradescantia virginiana L.	1	3	7.1%	0.21%
Triodanis perfoliata (L.) Nieuwl.	13	107	92.9%	7.64%
Vaccinium arboreum Marsh.	3	8	21.4%	0.57%
Viola rafinesquii Greene	5	29.5	35.7%	2.11%
Vitis aestivalis Michx.	2	3	14.3%	0.21%
Vulpia octoflora (Walt.) Rydb. var. *tenella* (Willd.) Fern.	6	20.5	42.9%	1.46%
Woodsia obtusa (Spreng.) Torr.	1	2	7.1%	0.14%

Table 3. Species list at Berryville Shale Barrens. Species are listed alphabetically by genus. #plots = number of incidences in 12 plots. ttl% = total percent cover of species. % freq = percentage of patches in which species occurs. % all plots = species abundance within forest openings.

Species	# plots	ttl %	% freq	% all plots
Agalinis skinneriana (Wood) Britt.	3	2.5	33.3%	0.21%
Allium canadense L.	4	14	8.3%	1.17%
Ambrosia artemisiifolia L.	1	2	16.7%	0.17%
Ampelopsis cordata Michx.	2	3	8.3%	0.25%
Arisaema dracontium (L.) Schott.	1	1	16.7%	0.08%
Asclepias tuberosa L. ssp. i*nterior Woodson*	2	6	16.7%	0.50%
Ascyrium multicaule Michx.	2	3	25.0%	0.25%
Asplenium platyneuron (L.) B.S.P.	3	5	8.3%	0.42%
Aster anomalus Engelm.	1	3	8.3%	0.25%
Aster lanceolatus Willd.	1	2	16.7%	0.17%
Aster novae-angliae L.	2	5	8.3%	0.42%
Aster turbinellus Lindl.	1	2	16.7%	0.17%
Bidens bipinnata L.	2	4	8.3%	0.33%
Brachyelytrum erectum (Roth) P. Beauv.	1	1	16.7%	0.08%
Cardamine parviflora L. *var. arenicola* (Britt.) O.E. Schultz	2	4.5	8.3%	0.38%
Carex albicans Willd.	1	3	16.7%	0.25%
Chamaecrista fasciculata (Michx.) Greene	3	13	25.0%	1.08%
Chamaecrista nictitans (L.) Moench	2	2	41.7%	0.17%
Cheilanthes feei T. Moore	5	48	8.3%	4.00%
Clitoria mariana L.	1	1	25.0%	0.08%
Cunila origanioides (L.) Britt	11	68	91.7%	5.67%
Danthonia spicata (L.) Beauv. ex Roemer & J.A. Schultes	11	51	91.7%	4.25%
Dichanthelium praecocius (Hitchc. & Chase) Mohlenbr.	8	14	66.7%	1.17%
Dodecatheon meadia L.	1	3	8.3%	0.25%
Euphorbia corollata L.	5	9	41.7%	0.75%
Galium aparine L.	1	1	8.3%	0.08%
Geranium maculatum L.	1	1	8.3%	0.08%
Hedeoma pulegioides (L.) Pers.	1	1	8.3%	0.08%
Houstonia pusilla Schoepf	4	12	33.3%	1.00%
Hybanthus concolor (T.F. Forst.) Spreng.	2	29	16.7%	2.42%
Hypericum punctatum Lam.	2	2	16.7%	0.17%
Juniperus virginiana L.	3	6	25.0%	0.50%
Krigia biflora (Walt.) Blake	3	12	16.7%	1.00%
Lepidium virginicum L.	2	5	16.7%	0.42%
Lespedeza procumbens Michx.	2	9	8.3%	0.75%
Luzula multiflora (Ehrh.) Lej.	1	5	58.3%	0.42%
Nothoscordum bivalve (L.) Britt.	7	51	25.0%	4.25%
Oxalis stricta L.	3	6	83.3%	0.50%
Oxalis violacea L.	10	92	16.7%	7.67%
Parthenocissus quinquefolia (L.) Planch.	2	4	33.3%	0.33%
Penstemon pallidus Small	4	6.5	8.3%	0.54%
Physalis pubescens L.	1	1	8.3%	0.08%
Phytolacca americana L.	1	1	16.7%	0.08%
Quercus marilandica Muench.	2	6	25.0%	0.50%

Ranunculus fascicluaris Bigel.	3	7	16.7%	0.58%
Rhus aromatica Ait.	2	9	16.7%	0.75%
Rhus coppalina L.	2	4	16.7%	0.33%
Rosa setigera Michx.	2	37	8.3%	3.08%
Ruellia pedunculata Torr.	1	1	58.3%	0.08%
Schizachyrium scoparium (Michx.) Nash	7	52	66.7%	4.33%
Silphium integrifolium Michx.	8	24	8.3%	2.00%
Smilax glauca Walt.	1	1	8.3%	0.08%
Solidago nemoralis Ait.	1	1	16.7%	0.08%
Solidago radula Nutt.	2	5	25.0%	0.42%
Stylosanthes biflora (L.) B.S.P.	3	4	8.3%	0.33%
Torilis japonica (Houtt.) DC.	1	2	58.3%	0.17%
Triodanis perfoliata (L.) Nieuwl.	7	9	50.0%	0.75%
Vaccinium arboreum Marsh.	6	27	25.0%	2.25%
Viola rafinesquii Greene	3	5	8.3%	0.42%
Vitis aestivalis Michx.	1	1	8.3%	0.08%
Woodsia obtusa (Spreng.) Torr.	1	3	33.3%	0.25%

Table 4. Combined species list for forest openings at all sites. a = annual, b = biennial, p = perennial.

Species	Family	Life History
Agalinis skinneriana (Wood) Britt.	Scrophulariaceae	a
Ageratina altissima (L.) R.M. King & H. Robins	Asteraceae	p
Allium canadense L.	Liliaceae	p
Ambrosia artemisiifolia L.	Asteraceae	a
Ampelopsis cordata Michx.	Vitaceae	p
Apocynum cannabinum L.	Apocynaceae	p
Arisaema dracontium (L.) Schott.	Araceae	p
Aristida oligantha Michx.	Poaceae	a
Asclepias tuberosa L. ssp. i*nterior Woodson*	Asclepiadaceae	p
Ascyrium multicaule Michx.	Hypericaceae	p
Asplenium platyneuron (L.) B.S.P.	Aspleniaceae	p
Aster anomalus Engelm.	Asteraceae	p
Aster laevis L.	Asteraceae	p
Aster lanceolatus Willd.	Asteraceae	p
Aster novae-angliae L.	Asteraceae	p
Aster turbinellus Lindl.	Asteraceae	p
Bidens bipinnata L.	Asteraceae	a
Brachyelytrum erectum (Roth) P. Beauv.	Poaceae	p
Cardamine hirsuta L.	Brassicaceae	a
Cardamine parviflora L. *var. arenicola* (Britt.) O.E. Schultz	Brassicaceae	a
Carex albicans Willd.	Cyperaceae	p
Carex albursina Sheldon	Cyperaceae	p
Carex bushii Mackenzie	Cyperaceae	p
Carex granularis var. haleana (Olney) Porter	Cyperaceae	p
Cerastium fontanum Baum.	Caryophyllaceae	b
Chamaecrista fasciculata (Michx.) Greene	Caesalpiniaceae	a
Chamaecrista nictitans (L.) Moench	Caesalpiniaceae	a
Chasmanthium latifolium (Michx.) Yates	Poaceae	p
Cheilanthes feei T. Moore	Pteridaceae	p
Claytonia virginica L.	Portulacaceae	p
Clitoria mariana L.	Fabaceae	p
Cunila origanioides (L.) Britt	Lamiaceae	p
Danthonia spicata (L.) Beauv. ex Roemer & J.A. Schultes	Poaceae	p
Desmodium marilandicum (L.) DC	Fabaceae	p
Dichanthelium boscii (Poir.) Gould & Clark	Poaceae	p
Dichanthelium dichotomum (L.) Gould var. *barbulatum* (Michx.) Mohlenbr.	Poaceae	p
Dichanthelium microcarpon (Muhl.) Mohlenbr.	Poaceae	p
Dichanthelium polyanthes (Schult.) Mohlenbr.	Poaceae	p
Dichanthelium praecocius (Hitchc. & Chase) Mohlenbr.	Poaceae	p
Dodecatheon meadia L.	Primulaceae	p
Elaeagnus angustifolia L.	Elaeagnaceae	p
Elymus canadensis L.	Poaceae	p
Eragrostis spectabilis (Pursh) Steud.	Poaceae	p
Erigeron strigosus Muhl. ex Willd.	Asteraceae	a
Euphorbia corollata L.	Euphorbiaceae	p

Galactia regularis (L.) B.S.P.	Fabaceae	p
Galium aparine L.	Rubiaceae	a
Galium circaezans Michx.	Rubiaceae	p
Galium pilosum Ait.	Rubiaceae	p
Galium triflorum Michx.	Rubiaceae	p
Geranium maculatum L.	Geraniaceae	p
Hedeoma pulegioides (L.) Pers.	Lamiaceae	a
Heuchera americana L.	Saxifragaceae	p
Houstonia pusilla Schoepf	Rubiaceae	a
Hybanthus concolor (T.F. Forst.) Spreng.	Violaceae	p
Hypericum prolificum L.	Hypericaceae	p
Hypericum punctatum Lam.	Hypericaceae	p
Hypoxis hirsuta (L.) Coville	Amaryllidaceae	p
Isanthus brachiatus (L.) BSP	Lamiaceae	a
Juniperus virginiana L.	Cupressaceae	p
Krigia biflora (Walt.) Blake	Asteraceae	p
Krigia dandelion (L.) Nutt.	Asteraceae	p
Lepidium virginicum L.	Brassicaceae	a
Lespedeza intermedia (S. Wats.) Britt.	Fabaceae	p
Lespedeza procumbens Michx.	Fabaceae	p
Lespedeza virginica (L.) Britt.	Fabaceae	p
Lobelia inflata L.	Campanulaceae	a
Lonicera japonica Thunb.	Caprifoliaceae	p
Luzula multiflora (Ehrh.) Lej.	Juncaceae	p
Manfreda virginica (L.) Salisb. ex Rose	Agavaceae	p
Myosotis verna Nutt.	Boraginaceae	a
Nothoscordum bivalve (L.) Britt.	Liliaceae	p
Opuntia humifusa (Raf.) Raf.	Cactaceae	p
Oxalis stricta L.	Oxalidaceae	p
Oxalis violacea L.	Oxalidaceae	p
Parthenocissus quinquefolia (L.) Planch.	Vitaceae	p
Penstemon pallidus Small	Scrophulariaceae	p
Physalis pubescens L.	Solanaceae	a
Phytolacca americana L.	Phytolaccaceae	p
Plantago aristata Michx.	Plantaginaceae	a
Podophyllum peltatum L.	Berberidaceae	p
Polygonum ramosissimum Michx.	Polygonaceae	a
Polystichum acrostichoides (Michx.) Schott	Dryopteridaceae	p
Prunella vulgaris L.	Lamiaceae	p
Pycnanthemum tenuifolium Schrad.	Lamiaceae	p
Quercus marilandica Muench.	Fagaceae	p
Ranunculus fascicluaris Bigel.	Ranunculaceae	p
Ranunculus micranthus Torr. & Gray	Ranunculaceae	p
Rhus aromatica Ait.	Anacardiaceae	p
Rhus coppalina L.	Anacardiaceae	p
Rosa carolina L.	Rosaceae	p
Rosa multiflora Thunb. ex Murr.	Rosaceae	p
Rubus pensilvanicus Poir.	Rosaceae	p
Ruellia pedunculata Torr.	Acanthaceae	p
Ruellia strepens L.	Acanthaceae	p

Sanicula canadensis L.	Apiaceae	b
Schizachyrium scoparium (Michx.) Nash	Poaceae	p
Scleria pauciflora var. pauciflora Muhl. ex Willd.	Cyperaceae	p
Scutellaria incana Biehler	Lamiaceae	p
Sedum pulchellum Michx.	Crassulaceae	a
Setaria glauca (L.) P. Beauv.	Poaceae	a
Silphium integrifolium Michx.	Asteraceae	p
Smilax bona-nox L.	Smilacaceae	p
Smilax glauca Walt.	Smilacaceae	p
Solanum carolinense L.	Solanaceae	p
Solidago nemoralis Ait.	Asteraceae	p
Solidago radula Nutt.	Asteraceae	p
Solidago ulmifolia Muhl.	Asteraceae	p
Sorghastrum nutans (L.) Nash	Poaceae	p
Sphenopholis obtusata (Michx.) Scribn.	Poaceae	a
Stylosanthes biflora (L.) B.S.P.	Fabaceae	p
Torilis japonica (Houtt.) DC.	Apiaceae	a
Toxicodendron radicans (L.) Kuntze	Anacardiaceae	p
Tradescantia virginiana L.	Commelinaceae	p
Triodanis perfoliata (L.) Nieuwl.	Campanulaceae	a
Vaccinium arboreum Marsh.	Ericaceae	p
Viola rafinesquii Greene	Violaceae	a
Viola sororia Willd.	Violaceae	a
Vitis aestivalis Michx.	Vitaceae	p
Vulpia myuros (L.) K.C. Gmel.	Poaceae	a
Vulpia octoflora (Walt.) Rydb. var. *tenella* (Willd.) Fern.	Poaceae	a
Woodsia obtusa (Spreng.) Torr.	Dryopteridaceae	p

Table 5. Metapopulation species at Giant City State Park. Species are listed alphabetically by genus, with *x* values. Positive *x* values indicate that a species behaves according to the metapopulation model. See "Methods" section for details.

Species	x
Ambrosia artemisiifolia	1.4346
Aristida oligantha	1.2372
Asplenium platyneuron	0.4471
Aster laevis	1.7002
Carex albursina	3.0885
Claytonia virginica	0.6261
Cunila origanoides	2.8923
Dichanthelium microcarpon	2.0243
Dichanthelium praecocius	0.6623
Erigeron strigosus	1.0747
Euphorbia corollata	3.3537
Galium circaezans	0.8359
Galium pilosum	1.6328
Houstonia pusilla	0.9557
Hypericum punctatum	0.7135
Krigia dandelion	0.9064
Opuntia humifusa	1.4471
Oxalis violacea	0.4226
Rosa setigera	3.5486
Rubus pensilvanicus	0.6748
Schizachyrium scoparium	1.1625
Scleria pauciflora var. *pauciflora*	0.4245
Solidago nemoralis	1.4726
Stylosanthes biflora	2.0883
Toxicodendron radicans	1.4471
Tradescantia virginiana	0.6329

Table 6. Metapopulation species at McClure School Shale Barrens. Species are listed alphabetically by genus, with *x* values. Positive *x* values indicate that a species behaves according to the metapopulation model. See "Methods" section for details.

Species	x
Ambrosia artemisiifolia	2.4754
Asclepias tuberosa	3.7259
Carex bushii	2.6513
Cunila origanoides	0.479
Desmodium marilandicum	4.3164
Erigeron strigosus	0.6764
Lespedeza virginica	1.6155
Manfreda virginica	2.0747
Myosotis verna	0.899
Oxalis violacea	0.7915
Penstemon pallidus	3.0029
Rhus aromatica	0.4488
Rosa carolina	1.7039
Smilax bona-nox	0.4755
Solidago ulmifolia	1.3895
Sphenopholis obtusata	2.6512
Stylosanthes biflora	0.7603
Vaccinium arboreum	1.6563
Vulpia octoflora var. *tenella*	1.4411

Table 7. Metapopulation species at Berryville Shale Barrens. Species are listed alphabetically by genus, with *x* values. Positive *x* values indicate that a species behaves according to the metapopulation model. See "Methods" section for details.

Species	x
Agalinis skinneriana	0.9682
Ampelopsis cordata	5.0122
Asclepias tuberosa	5.0122
Ascyrium multicaule	1.367
Chamaecrista nictitans	1.022
Cheilanthes feei	1.2215
Dichanthelium praecocious	2.3165
Euphorbia corollata	1.2215
Hedeoma pulegioides	1.124
Houstonia pusilla	1.5432
Hypericum punctatum	5.0122
Krigia biflora	0.9682
Nothoscordum bivalve	0.8544
Oxalis stricta	0.4683
Ranunculus fascicularis	0.7123
Rosa setigera	5.0122
Schizachyrium scoparium	0.5865
Solidago radula	1.0512
Triodanis perfoliata	0.3559

Photos of study sites in Delong and Gibson study

1. Photo of forest opening at Berryville Shale Glade showing abundant *Danthonia spicata* ground cover. Photo was taken late spring/early summer 2005 by M. Delong.

2. Photo of forest opening at Berryville showing gravelly texture of soil and sparse ground cover that occurs in many places at both Berryville and McClure. Photo was taken late spring/early summer 2005 by M. Delong.

3. Photo at Stone Fort of Giant City State Park, July/August 2005. Numerous species can be found here that are indicative of forest openings including *Manfreda virginica*, *Stylosanthes biflora*, and *Euphorbia corollata*. Photo by M. Delong.

4. Photo at Giant City State Park, May 2005. Forest openings at Giant City may have soil characteristics similar to that of the surrounding forests, and have more organic material than at McClure or Berryville. Photo by M. Delong.

5. Photo of forest opening at Giant City State Park, May 2005. Photo by M. Delong.

6. Photo at Giant City State Park, May 2005. Xerophytic trees such as *Quercus stellata* and *Quercus marilandica* commonly are found in association with forest openings, usually comprising the "border" between forest and forest opening. Photo by M. Delong.

7. Photo at Giant City State Park, May 2005. Forest openings at Giant City may contain a mix of forest species and open/prairie species. This patch was found to have *Podophyllum peltatum*, a forest species, and *Scleria pauciflora*, a species of open habitats. Photo by M. Delong.