CONSERVATION ASSESSMENT OF CALCAREOUS ECOSYSTEMS IN PENNSYLVANIA



CONSERVATION ASSESSMENT OF CALCAREOUS ECOSYSTEMS IN PENNSYLVANIA

Jessica I. McPherson October 2013

Funded by:

Wild Resources Conservation Program

Pennsylvania Department of Natural Resources 400 Market Street, 6th floor Harrisburg, PA 17101

Prepared by:

Pennsylvania Natural Heritage Program

Western Pennsylvania Conservancy 800 Waterfront Drive Pittsburgh, PA 15222



This report may be cited as: McPherson, J. I. 2013. Conservation Assessment of Calcareous Ecosystems. Pennsylvania Natural Heritage Program at Western Pennsylvania Conservancy. Pittsburgh, PA. Report to Wild Resources Conservation Program, Grant #10391. 152 pg.

Acknowledgements

I would like to thank all of the many people who have contributed skills, time, effort, and funding towards the completion of this study:

Steven Grund and John Kunsman contributed their botanical expertise to most of our field visits. Steven and John also provided helpful comments and insights throughout the project, from site selection to the habitat preferences of individual taxa. Dr. Larry Klotz also helped select sites in Franklin County and joined our field survey team there.

Steven Grund, Anthony Davis, Bonnie Isaac, Joseph Isaac, Dr. Larry Klotz, John Kunsman, Dr. Ann Rhoads, and Ephraim Zimmerman all contributed to the panel of expert botanists that created the pH categorization of the Pennsylvania flora; immeasurable thanks for their time and effort to join the panel and their willingness to share their extensive knowledge of the state flora, without which this endeavor would have been impossible.

Ephraim Zimmerman provided insight and expertise in many facets of plant ecology addressed in the report, including plant community analysis and floristic quality assessment; and editorial review to improve the clarity of the presentation of the report. Chris Tracey provided assistance in setting up the MaxEnt models and review of the modeling section of the report.

The Wild Resources Conservation Program and the Western Pennsylvania Conservancy provided funding for this project.

Table of Contents

Table of Figures	4
List of Tables	6
Introduction	7
Background	8
Plants and Substratum Chemistry	8
Distribution of Calcareous Geology in Pennsylvania	9
Influence of geology and other environmental factors on soil pH	9
I. Assessing the Pennsylvania Vascular Flora for pH-specialist Taxa	11
Methods	11
Results and Discussion	
II. Plant Communities of Calcareous Habitats in Pennsylvania	15
Wetlands	
Terrestrial Communities	16
Methods	
Results and Discussion	18
Community Type Descriptions	
III. Extent of limestone habitats in Pennsylvania	34
Methods	34
Upland Calcareous Habitat	
Species and Community Habitat Models	38
Wetland Calcareous Habitat	
Protected Areas	
Results and Discussion	
Upland calcareous habitats	
Species and Community Habitat Models	
Wetland Calcareous Habitat	
Protected areas	
IV. Conservation Assessment of Calcareous Flora and Plant Communities	
Biogeography of Pennsylvania Calciphile Taxa	
Methods	
Results & Discussion	
Habitat analysis of calciphile taxa	
Methods	
Results & Discussion	
Summary of Conservation Significance	99
Conservation Needs of Calcareous Vascular Plants and Their Habitats	
Habitat isolation and fragmentation	
Land Protection	
Invasive species	
Climate Change	
Wetlands	
Grasslands	
Woodlands	
Mesic Outcrops	
Forests	
Future Study Needs	
Literature Cited	
Appendix 1: Study Site Profiles	
Appendix 2: Calciphile Taxa Habitat Preferences	. 142

Terrestrial Taxa Habitat Preferences	
Wetland taxa habitat preferences	147
Appendix 3: Calcareous Wetland Taxa With Range Contractions	

Table of Figures

Figure 1. Rare calciphiles by s-rank. Figure 2. Rare acidophiles by s-rank.	
Figure 3. Study site locations.	
Figure 4. NMS graph, all plots	
Figure 5. Cluster diagram, all plots	
Figure 6. NMS graph, grassland plots	
Figure 7. Cluster analysis, woodland plots.	
Figure 8. NMS graph, woodland plots	
Figure 9. Cluster diagram, woodland plots, with aspect	
Figure 10. Cluster diagram, forest plots	
Figure 11. NMS graph, forest plots	
Figure 12. Pennsylvania's 97 surface geology map units.	
Figure 13. Pennsylvania's surface geology, categorized by composition.	36
Figure 14. Example graph for MaxEnt model quality metric "Average Omission."	39
Figure 15. Example graph for MaxEnt model quality metric "AUC."	
Figure 16. Proportion of Pennsylvania land area in various surface geology categories	41
Figure 17. Calcareous surface geology in Pennsylvania, with percent of state total found in each	
physiographic province.	42
Figure 18 (left). Proportion of state in various land cover categories, NLCD data	43
Figure 19 (right). Proportion of calcareous geology lands in various land cover categories, NLCD data	
Figure 20. Forest acreage by block size,	
Figure 21. Forest acreage by block size, on calcareous geology.	
Figure 22. Forest acres by block size; blocks on calcareous geology considered with adjacent forest	
cover	45
Figure 23. Patches of contiguous upland habitat with calcareous surface geology remaining in natural	
land cover in PA.	
Figure 24. Arabis patens model habitat, a subset of available terrestrial calcareous habitat.	
Figure 25. MaxEnt habitat model for <i>Arabis patens</i> in PA	
Figure 26. MaxEnt model for <i>Bouteloua curtipendula</i> in PA	
Figure 27. MaxEnt model for <i>Delphinium exaltatum</i> in PA	
Figure 28. MaxEnt model for red oak woodland community type in PA.	
Figure 29. MaxEnt model for sideoats grama grassland community type in PA	
Figure 30. MaxEnt model for yellow oak - redbud community type in PA.	
Figure 31. MaxEnt model for yellow oak forest community type in PA	
Figure 32. Fraction of PA's known calcareous wetland plant taxa in each physiographic province & a	
section.	
Figure 33. Fraction of PA's known calcareous wetland sites in each physiographic province and section	
Eigure 24 Calcorrows watland plant logations (DNDI data shown in red) in DA with physicorrophic	01
Figure 34. Calcareous wetland plant locations (PNDI data, shown in red) in PA, with physiographic	(\mathbf{c})
provinces.	
Figure 35. Protection status of calcareous wetland sites in Pennsylvania.	03
Figure 36. North American distribution for <i>Carex prairea</i> , a typical northern fen species, rare in	70
Pennsylvania	
Figure 37. North American distribution for <i>Carex interior</i> , a northern species not rare in Pennsylvania	ı /U
Figure 38. North American distribution for <i>Platanthera aquilonis</i> , a northern fen species confined to	- 1
glaciated regions in PA.	/ I
Figure 39. North American distribution for <i>Symphoricarpos albus var. albus</i> , a northern species	- 1
inhabiting limestone outcrops in PA.	/1
Figure 40. North American distribution for <i>Chrysogonum virginianum</i> , a southern species barely	
extending into PA.	73

Figure 41. North American distribution for <i>Symphyotrichum phlogifolium</i> , a species whose northern rang edge falls in PA7	
Figure 42. North American distribution of <i>Rhamnus lanceolata</i> , southern distribution with disjunct	•
Midwestern & Appalachian populations	'4
Figure 43. North American distribution of <i>Dodecatheon meadia</i>	
Figure 44. North American distribution of <i>Thalictrum coriaceum</i> , southern Appalachian mountain specie	
with northern range limit in PA	
Figure 45. North American distribution for <i>Bouteloua curtipendula</i> , prairie species with eastern disjunct	-
population	
Figure 46. North American distribution of <i>Zanthoxylum americanum</i> , a northern-centered midwest /	
eastern disjunct distribution	7
Figure 47. North American range of <i>Muhlenbergia sobolifera</i> 7	
Figure 48. North American distribution of <i>Ruellia humilis</i> , midwest / eastern disjunct populations	-
centered south of Pennsylvania	8
Figure 49. North American distribution of Jeffersonia diphylla, typical midwestern forest species pattern	
Figure 50. North American distribution of <i>Carex careyana</i> (G4)	
Figure 51. North American distribution of Trillium nivale, midwestern forest species with eastern edge of	
range in PA	
Figure 52. North American distribution of Diplazium pycnocarpon8	51
Figure 53. North American distribution of <i>Triosteum perfoliatum</i> , intermediate between Midwestern	
forest and prairie disjunct patterns	51
Figure 54. North American distribution of <i>Ranunculus allegheniensis</i> , mountain species centered	
northwards	2
Figure 55. North American distribution of Asplenium ruta-muraria, Appalachian mountain species8	2
Figure 56. North American distribution of Shepherdia canadensis, a Great Lakes dune & shore specialist	i.
	3
Figure 57. North American distribution of Juncus alpinoarticulatus, species primarily of Great Lakes	
shores extending to some inland wetlands	
Figure 58. Calciphile taxa per habitat type, with # of taxa exclusive to each type	8
Figure 59. Number of habitat types occupied by terrestrial calciphile taxa8	
Figure 60. Habitat specificity of terrestrial calciphiles, by habitat type	;9
Figure 61. Mean C, # exclusive calciphiles, and total # of calciphiles per plot, averaged for each	
community type (with standard deviation error bars)9	
Figure 62. State distribution of Conioselinum chinense	
Figure 63. State distribution of <i>Cypripedium reginae</i>	
Figure 64. Statewide distribution of <i>Eriophorum gracile</i> 15	
Figure 65. Statewide distribution for Juncus brachycephalus15	
Figure 66. Statewide distribution for Malaxis monophyllos	
Figure 67. Statewide distribution for Salix serissima	2

List of Tables

Table 1. Native Vascular Plant Taxa in PA, summarized by pH preference	13
Table 2. Conservation Status of Plants of pH extremes - calciphiles & acidophiles	14
Table 3. Calcareous wetland community types described in Pennsylvania community classification	16
Table 4. Environmental variables with high significance in NMS analysis, all plots	19
Table 5. Woodland Plots, Plot Groupings, and Community Types.	23
Table 6. Surface Geology Categories, per Anderson and Ferree.	35
Table 7. Environmental Variables used for MaxEnt Distribution Models.	
Table 8. Remaining forest cover over limestone geology, by physiographic province	43
Table 9. Model quality as indicated by AUC.	
Table 10. Summary of calcareous wetland plant locations (PNDI data) and calcareous habitat sites, b	
physiographic province.	-
Table 11. Protected areas in Pennsylvania by surface geology category.	64
Table 12. Protection status of calcareous wetland sites and plant popululations in Pennsylvania by	
physiographic province and section.	65
Table 13. Totals for geographic distribution patterns in calciphile species found in PA	68
Table 14. Calciphile taxa with northern distributions.	68
Table 15. Northern calciphiles, categorized according to whether they are calciphiles throughout their	ir
range	
Table 16. Calciphile taxa with southern distributions	72
Table 17. Southern distribution species, calciphile status in PA vs. center of range	72
Table 18. Calciphile taxa with prairie/savannah distributions and and disjunct eastern mountain	
populations	
Table 19. Calciphile taxa with Midwestern forest distributions.	79
Table 20. Calciphile taxa with Appalachian Mountain distributions	
Table 21. Calciphile taxa with Great Lakes Shore distributions	83
Table 22. Habitat types of calciphile species.	
Table 23. Average coefficients of conservatism for calciphiles compared to all PA native species	91
Table 24. Single-factor ANOVA results for mean C and plot community type	93
Table 25. Single factor ANOVA results for mean C' and plot community type	93
Table 26. Single factor ANOVA results for mean C and plot physiognomy	94
Table 27. Single factor ANOVA results for community type and # calciphiles per plot	94
Table 28. Single factor ANOVA results for strict calciphiles (002) and community type	95
Table 29. Climate Change Vulnerability Index results for selected calciphile species in PA/	

Introduction

This report provides a statewide assessment of the conservation value and status of calcareous habitats, both upland and wetland, primarily from a plant ecology perspective. In Pennsylvania, calcareous rock is a minority component in the state's surface geology. There has long been an informal understanding among botanists that calcareous habitats are particularly interesting and host some unusual plants that are not found on other bedrock types. Many experts also suspect, from field observations, that calcareous ecosystems such as fens, limestone grasslands, rock outcrops, and calcareous slopes are under threat from a variety of sources, including development, exotic species invasion, fire suppression, and habitat isolation. However, with the exception of limestone grasslands, there has been little systematic study of these habitats. We attempt to synthesize expert knowledge and a variety of data sources, including new fieldwork, to assess the contribution of calcareous ecosystems to the state's botanical diversity, the extent of calcareous ecosystems remaining in the state, and the conservation needs of these ecosystems. We hope this baseline assessment can provide science-based guidance for conservation and stewardship efforts, and also identify knowledge gaps to help direct future research.

In section I, we report how many of Pennsylvania's vascular plant species are dependent on calcareous ecosystems. A panel of expert botanists rated the state's entire vascular flora according to pH preferences in habitat. The result is a new reference that can be used by amateurs and professionals alike to advance understanding of our state's native plant species; there are a variety of potential applications in environmental education, conservation, and restoration.

In section II, we analyzed plot data from this study and an additional Pennsylvania Natural Heritage Program study to identify upland plant community types typical of calcareous geology. Forty-five plots were collected at 26 sites over the course of July – September 2011 and May – August 2012; these data were combined with a 2008 study with 45 plots from 11 sites. This work provides quantitative input into ongoing efforts to update and improve the Pennsylvania Plant Community Classification. Mapping natural lands using the plant community classification provides an estimate of habitat diversity and extent.

In section III, we assessed the extent of the remaining calcareous habitats in Pennsylvania. For wetlands, we compiled a map of all known calcareous wetland sites in the state, using Pennsylvania Natural Heritage Program data. For upland habitats, we used GIS analysis to identify areas remaining in natural vegetation on calcareous geology. We compared habitat loss on calcareous geology to habitat loss in the state overall, and assessed the habitat contiguity of calcareous upland ecosystems. We also examined the protection status of wetland and upland calcareous habitats.

Section IV provides a conservation assessment of Pennsylvania's calcareous flora and habitats. We analyzed the calcareous portion of the state's flora in relation to patterns of rarity, biogeographical distribution, species and habitat conservatism, and habitat preference. We assessed the vulnerability of Pennsylvania's calcareous species to climate change, using NatureServe's Climate Change Vulnerability Index tool. This section also summarizes and interprets the report's findings to present the conservation importance, threats, and management needs of calcareous ecosystems in Pennsylvania.

Background

Plants and Substratum Chemistry

The separation of plant species on the landscape according to their tolerance of calcareous substrate and/or high soil pH has been noted for several centuries. Naturalists in Europe and North America observed and documented distinctions based on geology even before the concept of soil reaction was defined (Schimper 1898; Fernald 1907). Because calcium from carbonate-based rock is the primary means by which soils become alkaline in humid temperate regions, calcareous soils and high pH are often treated more and less interchangeably. European authors term plants that are found in high pH environments "calcicoles" and plants found in acidic environments "calcifuges." North American authors more commonly used the term "calciphile" in place of "calcicole".

A variety of systems have been devised to categorize plants based on their calcium or pH tolerance, although none have been adopted widely in North America (Landolt 1977; H. Ellenberg 1979; H. H. Ellenberg 1988; H. Ellenberg et al. 1991; M. O. Hill et al. 1999; Wherry 1927). Ellenberg et al. created a system of numerical indicator values for several hundred plant species in the Central European flora. Indicator values were calculated (based on averaged data from releve plots) for several habitat characteristics: soil reaction, nitrogen, moisture, temperature, and coastal vs. inland location. Wherry compared the soil pH preferences of related species using field measurements of soil reaction. He indicated the range of soil pH conditions tolerated by a plant by placing it in one or more of five categories on a scale.

Work over the last few decades has improved understanding of the physiological mechanisms underlying plant species' pH tolerance. The availability of soil nutrients is highly dependent on soil pH (Brady 1990). In the range between pH 5.5 and pH 6.5, most nutrients are available. Below 5.5, metals (iron, manganese, zinc, copper, aluminum) become soluble to the point of potential toxicity, while nitrogen, potassium, and phosphorus become less available. Above 6.5, the metals become immobilized, and above 7.0, phosphorus availability is very low. Plants that specialize in one portion of the pH scale appear to have mechanisms to compensate for the nutrient limitations in that range (Zohlen and Tyler 2004; Ström 1997; Misra and Tyler 1999). Competition may also play a role; several studies have documented that some species only observed on calcareous substrates in nature can grow or even thrive in non-calcareous soils in the absence of competition (Tansley 1917; Veblen and Young 2009).

A number of quantitative studies of plant locations and corresponding soil pH values have documented that there is great variation in the shape of species' distributions on the pH scale (Wherry 1927; Gignac et al. 2004; Schaffers and Sykora 2000). Schaffers and Sykora report that species at either end of the scale have narrow distributions, while species in the middle tend to have broader distributions. Lawesson's study of Danish forests found that most species have unimodal distributions, but a substantial portion (27%) have linear or plateau distributions; of the unimodal species, 19% had skewed distributions (Lawesson 2003).

There are also some documented cases in which the range and optimum pH value for a species changes in different parts of its range (Schaffers and Sykora 2000). It is believed to be a common pattern for a species to have a broad tolerance in the middle of its range, but to be a calciphile at the edges of its range; however, this phenomenon has received sparse attention in published literature (S. R. Hill 1992; Schaffers and Sykora 2000; Steele 1955; Ware and Ware 1992).

Distribution of Calcareous Geology in Pennsylvania

Sedimentary limestone layers are the major contributor to calcareous habitat in Pennsylvania. The purity of limestone layers varies regionally. Calcareous shales and sandstones are important in some areas as well (Schultz 1999).

The majority of the state's limestone is found in the Ridge and Valley and Piedmont physiographic provinces. It occurs mainly in valleys. The formations tend to be folded and steeply dipping. These limestone layers tend to be more pure and high calcium than those of other regions. The piedmont region is more complexly folded and includes some metamorphic features (PA DCNR 1990). The soils formed from limestone in the Ridge and Valley and Piedmont are also prime farmland, and large portions have been converted for farming and residential development. Quarrying has also impacted habitat significantly.

In the Allegheny Mountains and along Allegheny Front, the surface geology is primarily sandstone and shale, but the Mauch Chunk formation includes several narrow bands of limestone that outcrop frequently on steep slopes (Berg et al. 1980). Land use is primarily forested, although quarrying activities have impacted the limestone in places.

In the Appalachian Plateau province, the most influential limestone is in the Monongahela formation, which surfaces across southwestern Pennsylvania. This formation tends to be more flat-lying rather than folded, and its limestone is not as thick, pure, or consistently present as the Ridge and Valley formations. It does include calcareous shale and sandstone that can influence surface habitat conditions. However, this formation also includes the Pittsburgh coal seam, and areas where it surfaces have been heavily impacted by strip mining. The Vanport limestone of the Allegheny formation was widespread in counties north of Pittsburgh, but its impact on surface habitat is much less than might be expected. It has been very extensively mined, and it also rarely forms outcrops because highly erodible layers surround it (PA DCNR 1990).

Influence of Geology and Other Environmental Factors on Soil pH

Soils are created through the weathering of bedrock, and the composition of soil at a given site is influenced by the composition of the parent rock, the kinds of weathering processes it has undergone, and transportation processes moving sediments onto or off of the site (Brady 1990). Most of Pennsylvania's surface geology is sedimentary materials such as shale, sandstone, siltstone, limestone, and coal (Schultz 1999). In unglaciated areas, it is generally true that soil composition aligns with surface geology composition (Blumberg and Cunningham 1982). Most soils are weathered in place (residuum) or on steeper slopes, formed by colluvial transport of materials from upslope.

Geological parent materials exert a large influence on soil pH. In Pennsylvania, soils in unglaciated areas are generally acidic, in the range of pH 4.0 -5.5, unless they are formed from limestone or other calcareous rock. Soils formed from calcareous materials generally have higher pH, in the range of 5.5-8. Limestone dust may have a pH of 7.5-8.7; however, because precipitation levels are sufficient in our climate to cause significant leaching of calcium from soils, even soils formed from limestone rarely have pH above 6.5 (Blumberg and Cunningham 1982). Soil reaction values above 6.5 are of particular interest because this is the range where the nutrient limitations that appear to drive floristic specialization are manifest. Higher pH values appear to be found where there is a source to recharge the leached calcium. This may be colluvial or alluvial inputs of materials weathered from calcareous rock, a high fraction of

calcareous rock fragments in the surface layers of the soil, or seepage flow of groundwater passing through calcareous materials. In effect, this means that rocky slopes, floodplains, and calcareous seeps are the most likely settings to find unlimed soils with pH 7.0 or above. Flatter terrain is more likely to have a lower pH value even if the underlying rock is limestone, unless it is very shallow to bedrock.

A wide variety of calcareous rock formations surface in Pennsylvania, ranging from thick, pure limestone underlying the valleys of the Central Appalachian mountain region, to thinner layers of limestone, to calcareous shales and sandstones (Schultz 1999). Calcareous and non-calcareous layers often occur in the same geological map unit. In formations of mixed materials, soils are more likely to be calcareous if formed from colluvium rather than weathered in place, because colluvial transport can mix the calcareous and non-calcareous layers. Residual weathering is less likely to produce strongly calcareous soils because most of the parent material, and all of the calcite, is dissolved in the process (Ciolkosz et al. 1995). It appears to require calcareous layers of a fairly significant size near the surface for the creation of calcareous soil/rock substrate large enough in extent to support more than one or a few terrestrial indicator species.

In glaciated areas, soils may be a product of the weathering of glacial deposits, which can include bedrock materials from a wide geographic range. Pennsylvania's glacial deposits in the northwestern part of the state do include significant amounts of calcareous material, but it generally does not influence soils enough to create neutral or basic conditions except through seepage of groundwater. Calcareous seepages and fens are relatively abundant in the glaciated northwestern portion of the state, but calcareous upland habitats are not known to occur (Bissell, personal communication).

A great deal of research has been conducted on limestone grasslands in Britain over the past century and a half, resulting in detailed understanding of the interplay of soil parent materials, topography, soil pH and calcareous vegetation. As this region has a similar moist-temperate climate and history of anthropogenic disturbance, some of these insights may be applicable to Pennsylvania's calcareous systems. Balme describes in detail the variation in soil formation processes and soil nutrient status across a topographic gradient over carboniferous limestones in northwestern Britain, and correspondant variations in vegetative community composition (Balme 1953). Low flat areas with poorly drained soils have high pH because they are recharged from base materials. Steep slopes have shallow, young soils with continual erosion and a high proportion of rock fragments, with high pH and low available phosphorus; these areas host limestone grasslands. Upland flat areas have low pH even though they are derived from limestone soil, because of leaching of carbonates; these areas host non-calcareous plant communities. A follow-up study conducted fifty years later found that limestone communities were reduced in extent at that site and at limestone grasslands across Britain (Bennie et al. 2006). However, the slowest change was observed on steep south-facing slopes where high soil pH, low available phosphorus, and higher solar radiation combine to produce conditions where calciphiles may be at greatest advantage over other species.

It is also important to note that while the relationship between surface geology and soil pH has a large influence on plant growth, surface geology may also influence plant growth in other ways. Some geological substrates are characterized by superabundance or deficiency of other minerals, metals, and salts. Serpentine and diabase are two other geology types in our region that weather to create soils with distinctive mineral profiles, and also host distinctive floristic elements. Serpentine, diabase, and limestone soils are similar in that all can have abundant base cations (Ca⁺ and Mg⁺). However, serpentine and diabase soils differ from limestone in the ratio of Mg⁺ to Ca⁺ present and in the abundance of other mineral elements such as metals; these soils present distinct challenges for plant nutrient uptake. Diabase flora has significant overlap with limestone flora; serpentine flora has fewer species in common. Physical characteristics of rock types also influence habitat, such as fissile shale outcroppings with unique "shale barren" flora adapted to high temperatures, little soil, and frequent shifting of fragile substrate rocks.

I. Assessing the Pennsylvania Vascular Flora for pH-specialist Taxa

This section provides a qualitative expert assessment of the pH preferences of all vascular plant species found in Pennsylvania. From this assessment we derived a list of specialist taxa, those that are found mainly or exclusively in acidic or alkaline environments. We also discuss the conservation status of pH specialist taxa in this section.

Methods

A panel of expert botanists¹ reviewed all species in the flora and assigned each a range on a categorical pH scale. The scale included three categories, acidophile, mid-range, and calciphile. It is adapted from a system devised by Wherry (Wherry 1927).

acidophile: bogs, coastal plain, acid forests, plants of sandstone **mid-range**: "rich woods", floodplain plants, diabase & shale. (Usually if plant was rated midrange because of diabase or shale occurrence, a geology note should accompany.) Native "weeds" (mostly meaning ruderals) found on roadsides, fields, etc.. **calciphile:** limestone, limestone-derived soils, mineral rich fens. Also includes ruderals that show preference for limed areas, limed artificial substrates like sidewalks.

For each category, a plant was assigned "0," "1," or "2" to denote the strength of that species' presence in habitats of that category.

"0" - the species is absent from habitats of this pH category

"1" - the species is found relatively infrequently in habitats of this pH category; it may also appear to be nutrient-deficient or growth-inhibited when found in habitats of this category.
"2" - many of the species' occupied habitats are this category, and populations generally appear to have normal vigor.

The experience of the expert botanical panel was primarily based on knowledge of substrate factors that contribute to pH (including surface geology, soil type, field recognition of rock type, etc.) rather than direct testing of soil pH in areas surveyed.

Diabase geology results in soils with a unique mineral composition and a corresponding unique flora. It is not high in pH, but a substantial portion of diabase specialist taxa also occur on calcareous substrates. Preference for diabase was noted separately from pH preferences, to capture the taxa which are found exclusively on these two substrates.

¹ Anthony Davis (Ecologist, PNHP), Steve Grund (Botanist, PNHP), Bonnie Isaac (Carnegie Museum of Natural History), Joseph Isaac (Botanist, CEC), Dr. Larry Klotz (Shippensburg University), John Kunsman (Botanist, PNHP), Jessica McPherson (Ecologist, PNHP), Dr. Ann Rhoads (Senior Botanist, retired; Morris Arboretum of the University of Pennsylvania), Ephraim Zimmerman (Ecologist, PNHP).

Results and Discussion

Appendix A lists the entire Pennsylvania vascular flora with pH preference ratings and geologic substrate preference notes. Of 1973 native vascular plant taxa extant in Pennsylvania, 1655 were rated for all pH categories. One hundred and twenty-two were rated incompletely, and 194 were given no rating, based on lack of experience within the group to confidently assign ratings in all pH categories. The term "taxa" is used to include species, varieties and subspecies. The majority of the unrated or partially rated taxa were hybrids, species that are uncommon in the state, or sub-specific taxa (varieties or subspecies) for which a more common taxon was rated.

Among those unrated are 55 hybrid taxa; 32 varieties and 6 subspecies for which the more common related taxon was rated; and 37 taxa of special concern (rare, threatened, or endangered). The 122 partially rated taxa include 61 taxa of special concern (rare, threatened, or endangered), and 5 varieties and 1 subspecies for which the more common related taxa was rated. The 104 taxa classified as native but no longer extant in the state (historic or extirpated) were also not rated, as experience with these taxa in Pennsylvania was inherently none or minimal.

Of the 1973 extant native vascular plant taxa in Pennsylvania, 25% are habitat specialists requiring acid or alkaline pH conditions (Table 1). This includes taxa which are found exclusively in acid or alkaline conditions, and those found mainly but not exclusively in such conditions. There are 30% more acidophiles (301) than calciphiles (197).

There is a relatively large group of plants that were rated as occupying calcareous habitats, and a smaller subset of these are habitat specialists. Five hundred and thirteen taxa (30.1% of those rated) were given a '2' rating for calcareous habitats. This group includes 10% which are calcareous habitat specialists, rated either "0 0 2", "0 1 2", or "0 2 2" because they occur exclusively on calcium and diabase. The remaining 20% of those rated "2" for calcareous habitats are not considered specialists because they were rated to equally prefer mid-range or acidic habitats.

Among the partially rated taxa, there are 55 which are potential calcareous habitat specialists. Fourteen were rated '0?2'; 35 were rated '0??'; and 4 were rated '00?'. Further field work is needed to gain experience with the habitat preferences of these taxa in PA in order to fully rate them and identify any additional calcareous habitat specialists.

There were 945 introduced taxa; 527 of them were not rated and 15 were partially rated, due to insufficient experience with the taxa among our experts or small geographic extent in the state. Only six taxa were rated to be exclusive calciphiles, and 3 taxa strong calciphiles; this is a far lower proportion of habitat specialists than the native taxa. However, 128 species (30% of those rated) were rated '2' in calciphile habitats. Roughly the same percentages of introduced and native taxa were rated '2' for calciphile habitats.

To our knowledge, this is the first attempt to rate pH tolerance for a regional flora in eastern North America. Caution should be used in applying the ratings outside of Pennsylvania. Because a taxon's pH requirements can change at the edge of its range, the ratings will likely be most reliable for areas that occupy a similar portion of the taxon in question's range; i.e., if Pennsylvania falls in the central part of the range, the PA rating may work for other areas also in the central part of its range. If Pennsylvania is at the southern edge of the range, it may work for other regions also at the southern edge, but may not be suitable for regions further north towards the center of the range. Another consideration that may affect the utility of the ratings outside of Pennsylvania is the relative prevalence of high-pH substrates in

different regions. In regions where high pH substrates are either much more or much less abundant than Pennsylvania, botanists' sense of "calciphile" taxa will likely be different. For example, in northeastern areas with predominantly igneous geology where high pH substrates are very uncommon, pH 6.0 may be considered very high, and taxa found in such locations strong calciphiles. In Pennsylvania, pH 6.0 is moderately high and taxa found in such locations were often rated as occupying but not exclusively preferring high pH substrates. In Midwestern regions with abundant limestone geology, taxa such as *Trillium nivale* or *Jeffersonia diphylla* may merely be considered rich forest species, rather than distinctly restricted to high pH soils as they are perceived in Pennsylvania.

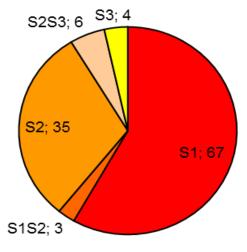
Conservation Status of pH-specialist Vascular Plant Taxa

Acidophile species and calciphile taxa together contribute 45% of the state's rare plant taxa (Table 2). Calciphile taxa form a smaller portion of the total flora than acidophiles (10.0% vs. 15.3%), but represent a higher fraction of rare taxa (23.8% vs. 20.3% of all rare taxa). Almost 80% of the plant taxa found exclusively in calcareous habitats are rare, while 40% of exclusive acidophiles are rare. A much smaller proportion of the taxa rated as strongly but not exclusively calciphilic or acidophilic are rare.

For both acidophile and calciphile taxa, most of the rare species are critically imperiled (S1 status), while smaller fractions are imperiled (S2) or vulnerable (S3) in the state (Figure 1, 2). While about the same fraction of rare acidophiles and rare calciphiles are rated critically imperiled, a larger fraction of calciphiles are rated imperiled, while a larger fraction of acidophiles are rated vulnerable.

Exclusive	Strong	Calcium &	Calciphile	Exclusive	Strong	Acidophile
calciphiles	calciphiles	diabase	total	acidophiles	acidophiles	total
(002)	(012)	(022 d)		(200)	(210)	
110	64	23	197	204	97	301
5.6%	3.2%	1.2%	10.0%	10.3%	4.9%	15.3%
	calciphiles (002) 110	calciphiles calciphiles (002) (012) 110 64	calciphiles calciphiles diabase (002) (012) (022 d) 110 64 23	calciphiles calciphiles diabase total (002) (012) (022 d) 110 64 23 197	calciphiles (002)calciphiles (012)diabase (022 d)total (200)acidophiles (200)1106423197204	calciphiles (002)calciphiles (012)diabase (022 d)totalacidophiles (200)acidophiles (210)110642319720497

Table 1. Native Vascular Plant Taxa in PA, summarized by pH preference





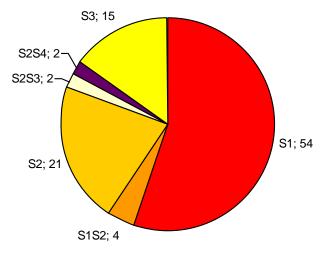


Figure 2. Rare acidophiles by s-rank.

Table 2. Conservation Status of Plants of pH extremes – calcipnies & actophiles								
		Exclusive	Strong	Calcium	Calciphile	Exclusive	Strong	Acidophile
	Total	calciphiles	calciphiles	& diabase	total	acidophiles	acidophiles	total
	taxa	(002)	(012)	(022 d)		(200)	(210)	
Extant PA								
native plant								
taxa	1973	110	64	23	197	204	97	301
Rare native								
plants (s1-s3)	478	86	21	7	114	82	15	97
Percent of								
flora	100%	5.6%	3.2%	1.2%	10.0%	10.3%	4.9%	15.3%
Percentage of								
all rare plants	100%	18.0%	4.4%	1.5%	23.8%	17.2%	3.1%	20.3%
Percent of								
extant in								
category that								
are rare	16.1%	76.3%	34.3%	22.2%	56.9%	40.2%	15.5%	32.2%

Table 2. Conservation Status of Plants of pH extremes – calciphiles & acidophiles

II. Plant Communities of Calcareous Habitats in Pennsylvania

Plant community types are a framework that can be used to assess the diversity of natural habitats found on the landscape. Plant communities are groups of plant species that occur together repeatedly across the landscape, usually in locations with similar environmental characteristics. They are named according the dominant species and sometimes important environmental characteristics; examples include "sugar maple – basswood forest" found on mesic slopes with rich soil; "hemlock palustrine forest" found in cool basin wetlands; or "cattail marsh". Community types are shaped by environmental variables such as slope, aspect, soil moisture and nutrition, or hydrological regime. They are also shaped by land use history and disturbances such as fire or flooding.

Plant communities are useful for mapping natural landscapes, assessing habitat diversity, and planning for conservation. Defining community types of calcareous habitats provides units to map known sites, compare their distribution and relative rarity, and identify habitat-specific conservation needs. Conservation efforts can be aimed at communities that are rare on the landscape, particularly important to biodiversity, or formed over a long period of time and difficult to replace if lost.

This section lists the calcareous community types already defined in the Pennsylvania Plant Community Classification for wetlands, and analyzes plot data from terrestrial calcareous sites to provide quantitatively derived community type definitions.

Wetlands

We did no additional fieldwork in wetlands for this project, because extensive quantitative work has been done to inventory, define, and classify calcareous wetland communities. This work is summarized below. Calcareous wetlands were addressed through "A Study of Seepage Wetlands in Pennsylvania." (1998), "A Study of Calcareous Fen Communities in Pennsylvania" (1995), and several floodplain studies (Zimmerman and Podniesinski 2008; "Classification, Assessment and Protection of Forested Floodplain Wetlands of the Susquehanna Drainage." 2002; "Classification, Assessment and Protection of Non-Forested Floodplain Wetlands of the Susquehanna Drainage." 2004). The seep and fen studies were both targeted at circumneutral to high-pH environments, while the floodplains studies were focused by major river watershed, stream order, and physiognomic type, and thus included a broad pH range of sites.

In 2012, the Pennsylvania Natural Heritage program completed an update to wetland plant communities of Pennsylvania, with updated wetland plant community types based on these studies and additional quantitative and qualitative field survey work ("Terrestrial and Palustrine Plant Communities of Pennsylvania, 2nd Edition" 2012). Table 3 (next page) lists the calcareous wetland communities that are presently included in the Pennsylvania classification:

Name	Subsystem	PA Ecological	Global	State
		Group	Rank	Rank
Sugar Maple – Mixed Hardwood Floodplain Forest	Forest	River floodplain	GNR	S4
Red Maple – Black Ash Palustrine Forest	Forest	Basin wetland	G2G4	S2S3
Alder-leaved Buckthorn – Inland Sedge – Golden Ragwort Shrubland	Shrubland	Peatland wetland	G2Q	S2
Circumneutral Mixed Shrub Wetland	Shrubland	Basin wetland	G4G5	S 3
Great Lakes Bayberry – Mixed Shrub Wetland	Shrubland	Great Lakes Region	GNR	S 1
Great Lakes Bluff Seep	Shrubland	Great Lakes Region	GNR	S 1
Poison Sumac – Red-Cedar – Bayberry Fen	Shrubland	Peatland wetland	GNR	S 1
Golden Saxifrage – Sedge Rich Seep	Herbaceous	Seepage wetland	GNR	S2
Great Lakes Palustrine Sandplain	Herbaceous	Great Lakes Region	GNR	S 1
River Bluff Seep	Herbaceous	Great Lakes region	GNR	S 1
Sedge – Mixed Forb Fen	Herbaceous	Great Lakes Region	GNR	S1
Skunk Cabbage – Golden Saxifrage Seep (calcareous subtype)	Herbaceous	Seepage wetland	GNR	S4S5

Table 3. Calcareous wetland community types described in Pennsylvania community classification.

Terrestrial Communities

We analyzed field data from this project and a 2008 project that also collected terrestrial community data to identify terrestrial plant community types situated on calcareous geology. The Pennsylvania plant community classification currently includes several calcareous types based on qualitative data, and this study will help to refine these types and their descriptions.

Methods

Data were collected at 45 releve plots at 26 sites as part of the current study, over the course of July – September 2011 and May – August 2012. The 2008 study included 45 plots at 11 sites, although not all were strongly calcareous (pH ranged from 4.5 - 8.0). Figure 3 shows the locations of all sites, and Appendix 1: Study Site Profiles provides more detailed information about each site. In the current study, sites were selected to include a range of physiognomic types from grassland to forest, and to encompass the geographic range in which calcareous habitats occur in the state. To ensure that sites had calcareous flora, surface geology maps and PNDI field survey data for calcareous plant populations were also consulted in site selection.

All vegetation data were collected following Natural Heritage sampling protocols developed for the quantitative characterization of plant communities (Strakosch-Walz 2001). For forests, plots of 20m x 20m were used; for woodlands, plots of 15m x 15 m were used; for shrublands, plots of 10m x 10m, and for herbaceous areas, plots of 5m x 5m. Plots were established within homogenous vegetation patches that were representative of the community (Mueller-Dombois and Ellenberg 1974). When site conditions

did not allow for the establishment of a square plot, rectangular plots were used with dimensions to produce equivalent area.

Vegetation was visually divided into 8 strata: emergent trees (variable height), canopy trees (variable height), subcanopy trees (> 5 m in height), tall shrubs (2m-5m in height), short shrubs (0-2 m in height), herbaceous, non-vascular, and vines. Total cover for each stratum was estimated, and percent cover was estimated for each species in each stratum using modified Braun-Blanquet cover classes. Specimens were collected for species not identified in the field, and deposited in the Carnegie Museum of Natural History in Pittsburgh.

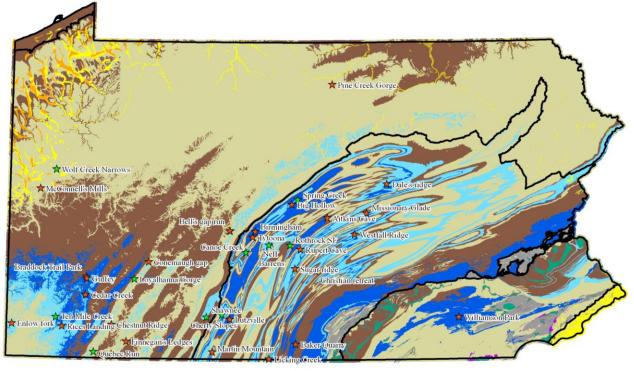
In addition to floristic information, the following environmental variables were recorded for each site: slope, aspect, topographic position, hydrologic regime, and soil pH. Soil pH was measured in the field using a hellig-truog soil pH test kit. Three soil pits were dug in each plot to bedrock. Each stratum in each pit was tested; any differences were noted, and values averaged to generate a value for field pH at the site. Soil samples were also collected and sent for analysis to University of Massachusetts – Amherst. The following values were measured: pH, aluminum, percent organic matter, phosphorus (ppm), potassium (ppm), calcium (ppm), magnesium (ppm), zinc (ppm), copper (ppm), iron (ppm), sulfur (ppm), and lead. Field and lab pH values had significant discrepancies, possibly due to delay in sample processing. Lab values differing from field values by more than .5 were discarded, and final site pH values were generated by averaging field and lab values.

Species cover and environmental variables were analyzed using hierarchical agglomerative cluster analysis and non-metric multidimensional scaling (NMS) in PC-ORD. For grassland and woodland types, cover categories were used for all species instead of cover values, in order to create a more balanced weighting of herbaceous and canopy species in the results. Indicator species analysis (Dufrene and Legendre 1997) was conducted and used to evaluate the groupings suggested by NMS and cluster analysis.

Cover	1	2	3	4	5	6	7	8
category Cover value	0 <x≤.1%< td=""><td>.1<x≤1%< td=""><td>1<x≤5%< td=""><td>5<x≤12%< td=""><td>12<x≤25%< td=""><td>25<x≤50%< td=""><td>50<x≤75%< td=""><td>75<x≤100%< td=""></x≤100%<></td></x≤75%<></td></x≤50%<></td></x≤25%<></td></x≤12%<></td></x≤5%<></td></x≤1%<></td></x≤.1%<>	.1 <x≤1%< td=""><td>1<x≤5%< td=""><td>5<x≤12%< td=""><td>12<x≤25%< td=""><td>25<x≤50%< td=""><td>50<x≤75%< td=""><td>75<x≤100%< td=""></x≤100%<></td></x≤75%<></td></x≤50%<></td></x≤25%<></td></x≤12%<></td></x≤5%<></td></x≤1%<>	1 <x≤5%< td=""><td>5<x≤12%< td=""><td>12<x≤25%< td=""><td>25<x≤50%< td=""><td>50<x≤75%< td=""><td>75<x≤100%< td=""></x≤100%<></td></x≤75%<></td></x≤50%<></td></x≤25%<></td></x≤12%<></td></x≤5%<>	5 <x≤12%< td=""><td>12<x≤25%< td=""><td>25<x≤50%< td=""><td>50<x≤75%< td=""><td>75<x≤100%< td=""></x≤100%<></td></x≤75%<></td></x≤50%<></td></x≤25%<></td></x≤12%<>	12 <x≤25%< td=""><td>25<x≤50%< td=""><td>50<x≤75%< td=""><td>75<x≤100%< td=""></x≤100%<></td></x≤75%<></td></x≤50%<></td></x≤25%<>	25 <x≤50%< td=""><td>50<x≤75%< td=""><td>75<x≤100%< td=""></x≤100%<></td></x≤75%<></td></x≤50%<>	50 <x≤75%< td=""><td>75<x≤100%< td=""></x≤100%<></td></x≤75%<>	75 <x≤100%< td=""></x≤100%<>

Parameters used for the NMS analysis were the Sorenson (Bray-Curtis) distance measure, random starting configuration, 50 runs with real data, a stability criterion of .00001, and a maximum of 250 runs.

Parameters used in the cluster analysis were the Sorenson (Bray-Curtis) distance measure and flexible beta group linkage method (-.25).



★ study sites 2011-12 ★ study sites 2006 physiographic provinces

Figure 3. Study site locations.

Results and Discussion

When all 47 plots were analyzed together, cluster analysis (Figure 5), and NMS (Figure 4) show distinct groupings by physiognomic category. Tree canopy (T2) and sub-canopy (T3) height, and tree canopy (T2) percent cover are significantly correlated with the NMS axes (Table 4). Herbaceous plots separate early in the cluster analysis from all other plots, and form a visible group in the NMS graph space. All herbaceous plots in the study had graminoid vegetation; this group will be referred to as "grasslands." Three woodlands fall within the grassland cluster, all of which were grasslands in the past and have succeeded to woodland, showing that differences in species composition persist as grasslands succeed.

The next split in the cluster analysis identifies a group of forests plots and a group of woodland/outcrop plots, although there is some overlap. Woodland and forest plots are incompletely segregated in the NMS graph, with the forest plots at the opposite end of Axis 1 from the grassland plots. In most cases, plots falling outside their physiognomic class cluster grouped with other plots from the same site, reflecting the similarity of species composition within sites. Outcrop plots were assigned to the "sparse vegetation" category regardless of their actual canopy cover; this category also all falls within one quadrant of the NMS graph, although it is not tightly clustered, likely because of the variation in canopy cover within the group.

Because the analysis including all plots is so heavily reflective of physiognomic differences, we analyzed each physiognomic class separately as well. Discussion for each group follows.

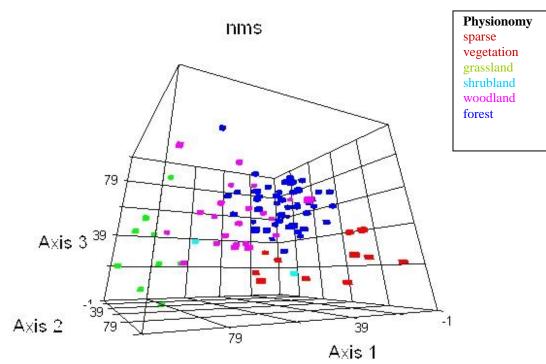


Figure 4. NMS graph, all plots.

Table 4. Environmental variables with high significance in NMS analysis, all plots.

Tuble II Elli II ommenical (artab	es with ingh significance	in ruito unuigoio, un proto-
Variable	Axis	r^2 value
Soil pH	1	.312
T2 height	1, 2	.255, .303
Canopy cover (T2) %	1, 2	.366, .234
Subcanopy (T3) height	3	.302
Longitude	3	.617

cluster

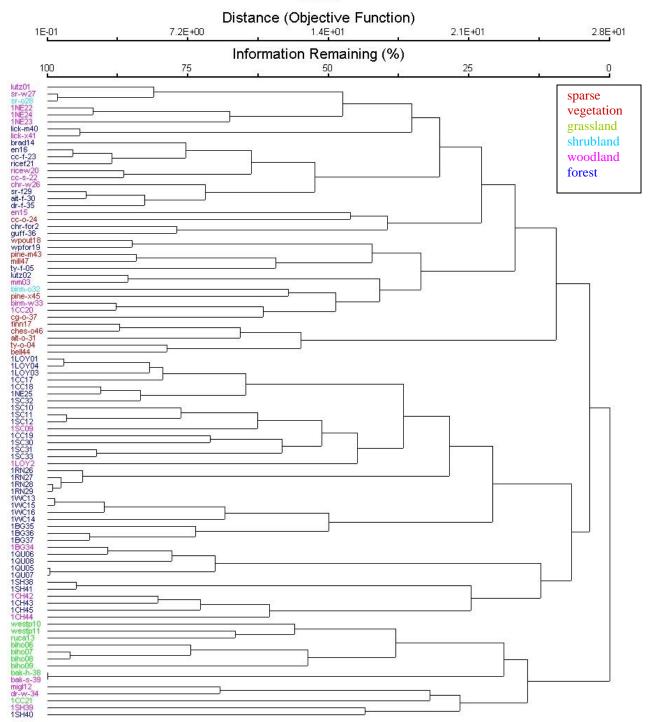


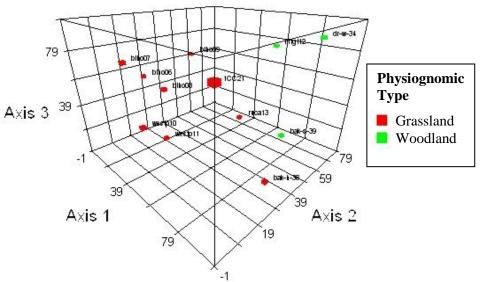
Figure 5. Cluster diagram, all plots.

Grasslands

The grassland plots form a distinct group when all plots are analyzed together. Indicator species analysis of grassland plots vs. all other plots illustrates the fundamental influence of physiognomy; indicators for grassland plots include generalist dry open field species such as Queen Anne's lace (*Daucus carota*), spotted knapweed (*Centaurea biebersteinii*), gray goldenrod (*Solidago nemoralis*), and (*Ambrosia artemisiifolia*), while the strongest indicators for non-grassland plots are the generalist forest species sugar maple (*Acer saccharum*), bluestem goldenrod (*Solidago caesia*), and white wood aster (*Eurybia divaricata*).

However, grassland indicator species also include a large number of species that primarily inhabit calcareous grasslands, including sideoats grama grass (*Bouteloua curtipendula*), stiff goldenrod (*Oligoneuron rigidum*), grooved yellow flax (*Linum sulcatum*), (*Dichanthelium oligosanthes*), field thistle (*Cirsium discolor*), whorled milkweed (*Asclepias verticillata*), green comet milkweed (*Asclepias viridiflora*), false boneset (*Brickellia eupatorioides*), hairy bedstraw (*Galium pilosum*), panicled leaf tick trefoil (*Desmodium paniculatum*), hairy beardtongue (*Penstemon hirsutus*), and hoary mountain mint (*Pycnanthemum incanum*). Many of the grassland species have a primarily Midwestern distribution, and their Pennsylvania populations are disjunct to varying degrees with the major portion of the range (see pg. 76 for further discussion of this biogeographical pattern). Calcareous grasslands are the only habitats occupied by some of these disjunct species, while others are also found on herbaceous communities of diabase and serpentine geology; all of these habitats are quite limited in extent in Pennsylvania. The results of this study are consistent with Laughlin's work on Pennsylvania's calcareous grasslands, which also provides an indicator species list, environmental characterization of 11 sites, and assessment of the biogeography of the calcareous grassland flora (Laughlin and Uhl 2003; Laughlin 2004b).

Cluster analysis and NMS (Figure 6) of the grassland plots plus the three woodland plots that grouped with them do not support further division into multiple grassland types; however there is a separation between two of the woodland sites and the grassland sites. The Pennsylvania Plant Community Classification presently includes one calcareous grassland type, the "Sideoats Grama Grassland", based on Laughlin's work and qualitative PNHP surveys. The Sideoats Grama Grassland is synonymous with Laughlin's concept, although Laughlin terms the community "Xeric Limestone Prairie." The results of our analysis support this existing concept, with some refinements and quantitatively derived indicator species offered in the community type description (pg. 29). Laughlin's work emphasized the importance



of anthropogenic disturbance in maintaining the open physiognomy of these communities, and the tendency towards woody plant invasion and loss of prairie disjunct taxa in the absence of disturbance (Laughlin 2004a).

Figure 6. NMS graph, grassland plots.

Woodlands

The woodland group included outcrops with varying levels of forest cover as well as steep slopes with less than 75% forest cover. Cluster analysis (Cluster analysis % chaining = 10.85

Figure 7) and NMS (Figure 8) show a separation into six groupings of plots; there is strong evidence for three community types based on these groupings, and provisional evidence for two additional community types. Table 5 lists the groups, the plots included in each, and the corresponding community type.

Group 1: Mesic Outcrops

The mesic outcrop plots separate early in the cluster analysis from the rest of the woodland plots (Figure 7), and also appear in a distinct cluster in the NMS (group 1 in Figure 8). This separation can be seen as well in the NMS graph of all plot data (Figure 4). From a physiognomic standpoint, not all "mesic outcrops" strictly meet the criteria for woodlands, 25%-75% tree canopy cover, because some have almost complete canopy cover. However, the distinctness of this group despite the variability in canopy cover indicates it is a physical setting with a floristically distinct community.

This group spans a broad geographic range and shares a common set of environmental characteristics, including north or east facing aspect (Figure 9), lower slope position, mesic hydrology, and high bryophyte cover (20% or above). It includes three sites on Loyalhanna limestone (two in the southwestern part of the state and one along Allegheny Front); and two outcroppings associated with caves in central Pennsylvania. One additional site in Lawrence County on Vanport limestone shares similar environmental characteristics and falls with this group in the NMS, although it is placed separately in the cluster analysis. The distinct combination of environmental factors – cool microclimate, mesic hydrology, and calcareous rock – are clearly reflected in the flora, through high bryophyte cover and vascular indicator species including bulblet bladderfern (*Cystopteris bulbifera*), twoleaf miterwort (*Mitella diphylla*), mountain maple (*Acer spicatum*), clearweed (*Pilea sp.*), and walking fern (*Asplenium rhizophyllum*). We propose a "mesic calcareous outcrop" community type based on these data.

Group 2: no type designated

Group 2 includes two plots from a single site that is situated alongside the Pennsylvania turnpike. These plots split early in the cluster analysis from the others, and also appear as outliers in the NMS graph. There are no indicator species for this group; the disturbed character of the site may be the reason for its position in the NMS and cluster analysis. These plots are considered outliers and no community type is designated based on this group.

Group 4: Red Oak - Mixed Hardwood Calcareous Woodland

Group four is the most variable group; although there is fairly good similarity in species composition, the environmental characteristics of the plots are somewhat disparate. It includes three outcrop plots that are geographical outliers (Tioga County and Lancaster County) and cluster together; two additional outcrop plots in the central and southwestern portions of the state that also cluster together; and three woodland plots from the south-central part of the state that cluster together. Aspect (Figure 9) and soil depth are variable; canopy cover tends to be higher in this group than in the remaining woodland types, with sugar maple and red oak dominant species. Shrub cover is also lower than other groups. We propose a red oak – mixed hardwood calcareous woodland type based on this grouping, that includes dry woodlands and outcrops with moderate canopy cover and moderately exposed sites; sites that are much drier than the mesic outcrop type, but less xeric than the "yellow oak – redbud" woodland type.

Group 5, 6, 3: Xeric Calcareous Woodlands: Juniper Woodland, Yellow oak – Redbud Woodland, Yellow oak – Redbud Woodland SW Variant.

Groups 5, 6, and 3 are three groups of xeric woodlands adjacent in the cluster analysis and more related to each other than to the other plots in the analysis. These plots are all are south and west facing (Figure 9), and tend to have low bryophyte cover (less than 15%). Soil depth and elevation are variable. These environmental data suggest a more xeric character for these groups than the other woodland groups.

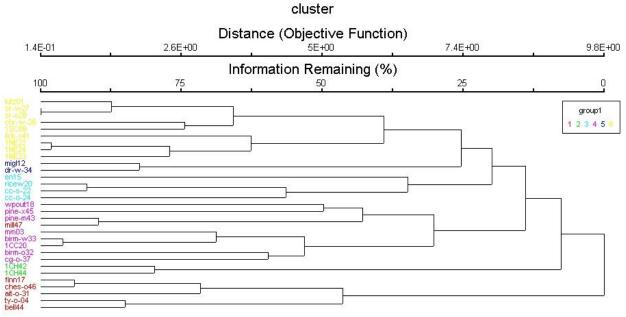
Group five are the two woodlands that grouped with grasslands in the analysis of all plots; these have high red cedar cover and low yellow oak cover, as well as common species with the grassland type. We provisionally propose a "Juniper Woodland" type based on this grouping, as a later-successional form of the sideoats grama grassland. However, there is not sufficient data available to confirm this type. A third woodland plot at Baker Quarry ("bak-s-39") also grouped with the grasslands, but did not group with these plots in the NMS or cluster analysis. This plot grouped most closely with the grassland plot from the same site. Because the site is in Franklin County at the very southern edge of Pennsylvania, these plots' distinct position in the analysis may arise because of geographically driven floristic differences.

Group three and **six** are woodlands with high yellow oak and redbud cover. Group three separates due to regional differences in the flora in the southwestern part of the state, and also has lower shrub cover.

Our results support the "Yellow oak – Redbud Woodland" type, described qualitatively in the current classification, based on this split. The grouping of plots from the southwestern sites may also merit segregation into a separate type based on floristic and environmental differences; however, only four plots from three sites are known at this time. All Yellow oak - Redbud plots were on steep slopes with high diversity, including many of the dry-site calciphile species such as low false bindweed (Calystegia spithamaea var. purshiana), fourleaf milkweed (Asclepias quadrifolia), golden ragwort (Packera obovata), Virginia snakeroot (Aristolochia serpentaria), and American bittersweet (Celastrus scandens). Environmental differences were that the SW plots occurred on steep slopes above medium or small tributaries, while the ridge and valley Yellow oak - Redbud Woodlands were above larger streams or rivers; and SW plots had higher canopy cover. Floristic differences included Pawpaw (Asimina triloba) and buckeye species (Aesculus spp.) in the shrub or understory for the SW type; the presence of a number of southwestern regional species such as whorled rosinweed (*Silphium trifoliatum*), starry false lily-ofthe-valley (Maianthemum stellatum), great yellow wood sorrel (Oxalis grandis), Short's aster (Symphyotrichum shortii), and small woodland sunflower (Helianthus microcephalus). The SW type also tends to include more mesic species such as woodland stonecrop (Sedum ternatum), spotted geranium (Geranium maculatum), green violet (Hybanthus concolor), orangefruit horse-gentian (Triosteum aurantiacum), and Canadian honewort (Cryptotaenia canadensis) than the Ridge and Valley type.

Group #	Plot #s	Community Type
1	mill47, finn17, ches-046, ait-031, ty-0-04, bell44	Mesic Outcrop
2	1CH42, 1CH43	None
3	en15, ricew20, cc-s22, cc-o24	Yellow Oak – Redbud
		Woodland, Southwest Variant
4	wpout18, pine-x45, pine-m43, mm03, birm-w33, 1CC20,	Red oak – Mixed Hardwood
	birm-o32, cg-o37	Calcareous Woodland
5	migl-12, dr-w-34	Juniper Woodland
6	lutz01, sr-w27, sr-o28, chr-w26, 1SC09, lick-x41, 1NE22,	Yellow Oak – Redbud Woodland
	1NE23, 1NE24	

Table 5. Woodland Plots, Plot Groupings, and Community Types.



Cluster analysis % chaining = 10.85

Figure 7. Cluster analysis, woodland plots.

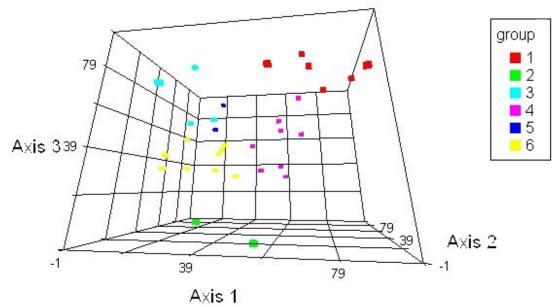


Figure 8. NMS graph, woodland plots.

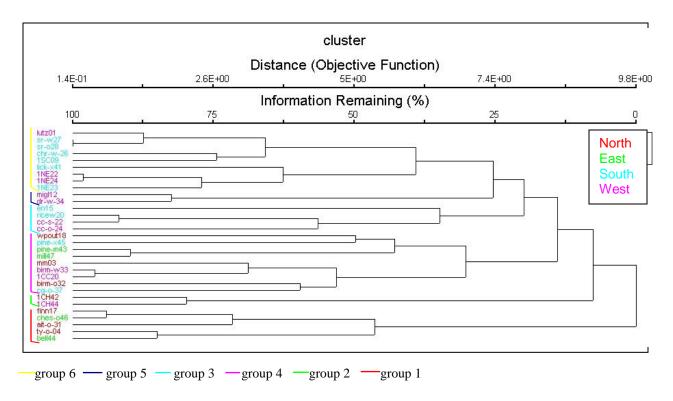


Figure 9. Cluster diagram, woodland plots, with aspect.

Forests

The forest plots show few strong groupings in the NMS (Figure 11) or cluster analysis (Figure 10). The clearest groups are a yellow oak forest group with a number of calciphile indicators in the understory layer (group 1, in red), and a more acidic forest group that can be distinguished by canopy and herbaceous indicator species (group 4, in purple).

Group 1, 9: Yellow Oak Forest

Groups 1 and 9 separate from the other plots very early in the cluster diagram. However, these groups may not be closely related to each other; they do not group together in the NMS graph, and they separate early from each other in the cluster analysis. Two of the three plots in group 9 are from a disturbed site adjacent to the Pennsylvania turnpike. Because of the disturbed character of the plots, and because indicator species analysis did not produce distinct results for this group, this group did not merit description of a unique community type.

The plots in group 1 do not group together strongly in the NMS graph, but they occupy a distinct region of the NMS space that is separated from the other plots. Indicator species analysis provides a good number of species with high p values for this group, most of which are calciphile species, reinforcing the strength of this type. These data support the "Yellow Oak Forest" type described qualitatively in the current classification.

Group 2: no type identified

The second fork in the cluster analysis (group 2) groups four plots from a single site in Rothrock State Forest which vary in pH. Although they are all placed near each other in the NMS graph, individual plots are not closer to each other than to other plots outside of the group, so the group does not appear distinct from the other plots. Indicator species analysis provides strong results, but this is likely caused by the geographic proximity of the plots. There are no identifiable distinctions in environmental variables correlated with the grouping or the indicator species. Indicator species with p values < .005 for this group included *Uvularia perfoliata, Carya glabra, Dichanthelium clandestinum, Ostrya virginiana, Magnolia acuminata, Hepatica nobilis, Pinus strobus, Carex pensylvanica*, and *Potentilla simplex*. There is insufficient data at this time to designate a community type based on this group.

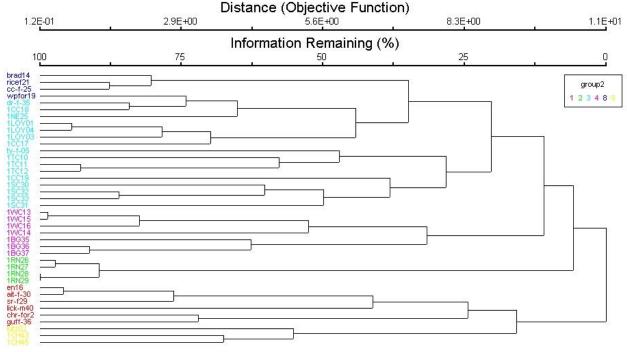
Group 4: acidic forest

The third fork in the cluster analysis separates the acidic plots (8 plots from 4 sites) into a group. These plots segregate fairly well in the NMS graph. Indicator species analysis also provides a good number of canopy and herbaceous species with low p values (*Prunus serotina, Dryopteris intermedia, Acer rubrum, Fagus grandifolia, Maianthemum canadense, Tsuga canadensis, Acer pensylvanicum*). Because only a few plots of acidic character were included in the analysis, while many more are available statewide, the results from this analysis should not be used to describe a community type. However, the indicator species can provide contrast to help distinguish calcareous types.

Group 3, 8: no type identified

The remaining 20 plots do not separate clearly into groups, and also do not demonstrate enough similarity to consider them a single type. Indicator species analysis yielded only three generalist species with p values below .05, and canopy composition varies significantly within the group. Geographic proximity

appears to be highly influential, as 10 of the plots are from just 3 sites, and the plots from each of these sites all group together. Group 8 is based on a cluster observed in the NMS graph, and is supported by a fork in the cluster that groups 3 of the 4 plots together. The three plots grouped in the cluster analysis are all in southwestern Pennsylvania, while the fourth plot is in Lancaster County. However, the physical setting for all plots is similar, mesic to dry-mesic moderately steep mid-slopes. Indicator species analysis provides a good number of species with low p values, but most occur at only half the four plots, or also occur on at least as many other plots outside of the group. The plots in group 8 suggest a tentative concept (southwestern mid-slope rich mesic forest) that needs more data to fully develop.



Cluster analysis % chaining = 5.97

Figure 10. Cluster diagram, forest plots.

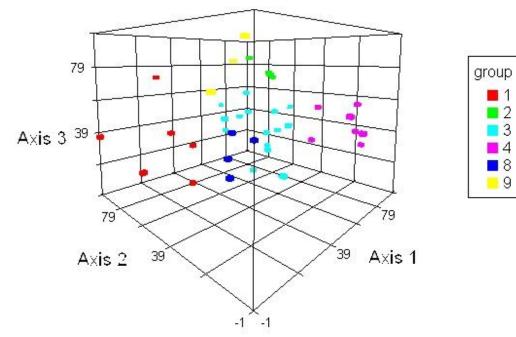


Figure 11. NMS graph, forest plots.

Community Type Descriptions

Sideoats Grama Grassland

This calcareous grassland type is found in the ridge and valley province. Sideoats grama grass (*Bouteloua curtipendula*) is an indicator species, and usually a co-dominant species, although it may be sparse at sites where succession is advancing. Co-occuring grass species are somewhat variable but may include little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), and purpletop tridens (*Tridens flavus*). Wild bergamot (*Monarda fistulosa*) is a common co-dominant. Other distinctive indicator species include field thistle (*Cirsium discolor*), whorled milkweed (*Asclepias verticillata*), green comet milkweed (*Asclepias viridiflora*), false boneset (*Brickellia eupatorioides*), hairy bedstraw (*Galium pilosum*), panicled leaf tick trefoil (*Desmodium paniculatum*), hairy beardtongue (*Penstemon hirsutus*), and hoary mountain mint (*Pycnanthemum incanum*). There is also a sizeable number of indicator species that are rare in the state, for which this community is their primary or exclusive habitat: Heller's rosette grass (*Dichanthelium oligosanthes*), grooved flax (*Linum sulcatum*), stiff goldenrod (*Oligoneuron rigidum*), hoary puccoon (*Lithospermum canescens*), false gromwell (*Onosmodium molle ssp. hispidissimum*), arctic brome (*Bromus kalmii*), and devil's bit (*Liatris scariosa var. scariosa*).



This type now often occurs as small open areas in a matrix of succeeding shrublands or young forest. Shrub species can include redbud (*Cercis canadensis*), red cedar (*Juniperus virginiana*), dwarf hackberry (*Celtis tenuifolia*), and blackberry spp. (*Rubus sp.*), as well as a variety of hardwood seedlings including black walnut (*Juglans nigra*), slippery elm (*Ulmus rubra*), and red oak (*Quercus rubra*). At some sites the successional pathway includes heavy dominance by red cedar.

Daniel Laughlin produced a number of research studies on this system, including extensive floristic documentation at most known examples of this grassland type in Pennsylvania, and assessment of their biogeographic history (Laughlin 2003a; Laughlin and Uhl 2003; Laughlin 2004a; Laughlin 2003b; Laughlin 2004b).

This type likely depends on disturbance such as fire or grazing to persist in grassland form. Laughlin's research found that calcareous grasslands were more extensive at the time of European settlement, and aerial photographs from the past century show

dramatic loss of grassland area at many sites due to succession.

Mesic Calcareous Outcrop



This community is found on mesic, north- or east- facing outcroppings of limestone or other calcareous rock. It is often in a mid-slope or lower slope position, and in central Pennsylvania may be associated with caves. The sites are usually forested, with sugar maple (Acer saccharum), basswood (Tilia americana), and often some hemlock (Tsuga canadensis). The flora reflects the cool, mesic environment; indicator species include bulblet bladderfern (Cystopteris bulbifera), twoleaf miterwort (Mitella diphylla), mountain maple (Acer spicatum), clearweed (Pilea sp.), and walking fern (Asplenium rhizophyllum). A variety of other species of rich woods and outcrops are also found in this type, such as

wild ginger (*Asarum canadense*), jack-in-the-pulpit (*Arisaema triphyllum*), zigzag goldenrod (*Solidago flexicaulis*), jewelweed (*Impatiens sp.*), and wild hydrangea (*Hydrangea arborescens*). In the southwestern part of the state these sites can host blue monkshood (*Aconitum uncinatum*) and American bugbane (*Cimicifuga americana*). Bryophyte cover is often high, above 20%.



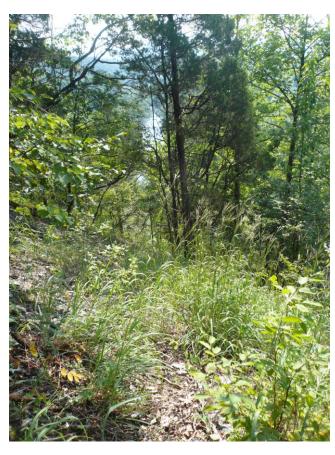
Red Oak – Mixed Hardwood Calcareous Woodland

This type is found in a variety of environmental settings, primarily in the Ridge and Valley province but possibly elsewhere as well. Typically it is on moderately steep to very steep upper slopes, which may have outcroppings or not; aspect and soil depth are variable. The canopy is often thinner and more stunted than surrounding forest due to a combination of slope, exposure, and soil depth. Red oak (Quercus rubra) and sugar maple (Acer saccharum) are the dominant canopy species, with chestnut oak (Quercus prinus) often present as well. Other canopy species may include basswood (Tilia americana), pignut hickory (Carya glabra), shagbark hickory (Carya ovata) and American hop-hornbeam (Ostrya virginiana) in the subcanopy. Yellow oak (Quercus muhlenbergii) and redbud (Cercis canadensis) are absent or uncommon in this type. Canopy cover is also typically slightly greater than at Yellow oak - redbud woodland sites, and some calciphile species with higher light requirements are excluded.

The herbaceous layer includes calcareous species such as golden ragwort (*Packera obovata*), early meadow-rue (*Thalictrum dioicum*), yellow pimpernel (*Taenidia integerrima*), nodding onion (*Allium cernuum*), and fourleaf milkweed (*Asclepias quadrifolia*); if outcroppings are present, purple cliffbrake (*Pellaea atropurpurea*), lyrate rockcress (*Arabis lyrata*), and red columbine (*Aquilegia canadensis*) are likely as well. The following species are indicators likely to be more frequent and abundant at this type than at other calcareous woodland types: Seneca snakeroot (*Polygala senega*), blackseed ricegrass (*Piptatherum racemosum*), meadow zizia (*Zizia aptera*), broadleaf sedge (*Carex platyphylla*), and mapleleaf viburnum (*Viburnum acerifolium*). Bryophyte cover is generally fairly low, although can be higher at sites where shaded outcroppings are common.

Yellow Oak - Redbud Woodland

This type occurs on steep, south- or west- facing slopes, often above major streams or rivers. Yellow oak is dominant or co-dominant in the canopy, and redbud is dominant or co-dominant in the shrub layer. Tree cover may be 30-75%; rock outcroppings are often present. Other tree species may include red oak



(Quercus rubra), white oak (Quercus alba), slippery elm (Ulmus rubra), white ash (Fraxinus americana), American hop-hornbeam (Ostrya virginiana), shagbark hickory (Carya ovata), or pignut hickory (Carya glabra).

The shrub layer can be diverse, with calciphiles redbud (*Cercis canadensis*), dwarf hackberry (*Celtis tenuifolia*), red cedar (*Juniperus virginiana*), and fragrant sumac (*Rhus aromatica*); flowering dogwood (*Cornus florida*) and are also common, as are the tree canopy species.

The herbaceous layer also includes a diverse assemblage of calciphiles and rich upland species, such as low false bindweed (*Calystegia spithamaea var. purshiana*), fourleaf milkweed (*Asclepias quadrifolia*), golden ragwort (*Packera obovata*), early meadow-rue (*Thalictrum dioicum*), wild comfrey (*Cynoglossum virginianum*), upland boneset (*Eupatorium sessilifolium*), hoary puccoon (*Lithospermum canescens*), spreading rockcress (*Arabis patens*), Virginia snakeroot (*Aristolochia serpentaria*), licorice bedstraw (*Galium circaezans*), early blue violet (*Viola palmata*), bloodroot (*Sanguinaria*

canadensis), hairy Solomon's seal (*Polygonatum pubescens*), and sedges (*Carex albursina, Carex laxiflora*).

Southwestern Yellow Oak - Redbud Woodland



This type is a yellow oak - redbud woodland with a southwestern regional influence in the flora. In addition to redbud (Cercis canadensis), Pawpaw (Asimina triloba) and buckeye species (Aesculus spp.) may be in the shrub or understory. The environmental setting in the southwest is steep south- or west- facing slopes above medium sized tributaries. The extent of the communities is often quite small, but species diversity is high. This type may host many of the drysite calciphile species such as low false bindweed (Calystegia spithamaea var. purshiana), fourleaf milkweed (Asclepias quadrifolia), golden ragwort (Packera obovata), Virginia snakeroot (Aristolochia

serpentaria), and American bittersweet (*Celastrus scandens*). It characteristically hosts a number of southwestern regional species such as whorled rosinweed (*Silphium trifoliatum*), starry false lily-of-the-valley (*Maianthemum stellatum*), great yellow wood sorrel (*Oxalis grandis*), Short's aster (*Symphyotrichum shortii*), and small woodland sunflower (*Helianthus microcephalus*). This type also tends to include more mesic species such as woodland stonecrop (*Sedum ternatum*), spotted geranium (*Geranium maculatum*), green violet (*Hybanthus concolor*), orangefruit horse-gentian (*Triosteum aurantiacum*), and Canadian honewort (*Cryptotaenia canadensis*) than the Ridge and Valley type.

Red Cedar Woodland



This type occurs when a calcareous grassland succeeds to woodland. Red cedar (Juniperus virginiana) is a dominant or codominant species; the early successional species black walnut (Juglans nigra) and white pine (Pinus strobus) may also be present at higher cover than other woodlands. The presence, albeit often sparse, of herbaceous grassland species is another indicator differentiating this type from other calcareous woodlands. Examples may include field thistle (Cirsium discolor), whorled milkweed (Asclepias verticillata), green comet milkweed (Asclepias viridiflora), grooved yellow flax (*Linum sulcatum*), sideoats grama grass

(Bouteloua curtipendula), ground cherry (Physalis sp.), and false boneset (Brickellia eupatorioides). Because it is successional, this type also tends to be weedy, with introduced old field species such as Queen Anne's lace (Daucus carota), Canada bluegrass (Poa compressa), and annual ragweed (Ambrosia artemisiifolia).

Yellow Oak - Mixed Hardwood Forest



The canopy for this type includes a substantial component of yellow oak (Quercus muhlenbergii); other typical species include sugar maple (Acer saccharum), black walnut (Juglans nigra), hackberry (Celtis occidentalis), white ash (Fraxinus americana), and red oak (*Quercus rubra*). The shrub layer may include redbud (Cercis canadensis), which is a good indicator, although it is not uniformly present. Calciphile indicator species in the herbaceous layer include hairy woodland brome (Bromus pubescens), James' sedge (Carex jamesii), nodding fescue (Festuca subverticillata), twinleaf (Jeffersonia diphylla); other indicators

include woodland bluegrass (*Poa sylvestris*), shining bedstraw (*Galium concinnum*), and thinleaf sunflower (*Helianthus decapetalus*). The setting is usually south or west facing upper slopes.

III. Extent of Limestone Habitats in Pennsylvania

In order to assess the conservation status in Pennsylvania of species and communities that depend on calcareous habitat conditions, it is important to understand the extent of this habitat in the state. We define calcareous habitat as an environmental setting with strong influence of calcium in the substrate, with relatively intact natural ecosystems present. We exclude from this definition areas that have experienced disturbances that remove the seed bank, such as tillage, residential development, or strip mining. These areas are not considered to presently provide viable habitat, due to removal of all natural vegetation.

Calcareous geology is a minority component of the state's overall landscape, and the regions where this geology is most abundant have seen extensive development for agriculture, residential use, quarrying, and coal mining. In this section we attempt to develop a quantitative estimate of how much calcareous habitat, both upland and wetland, remains in the state; and to map these areas. We examine remaining habitat area by physiographic province, in order to provide an ecologically meaningful frame for understanding local conservation needs. For uplands, we use a combination of GIS overlays and modeling, based on surface geology, land cover, slope, aspect, and climate data, to identify calcareous habitat area and calculate its extent. For wetland habitats, we use PNHP survey data to identify habitat area and calculate extent. We also assess the landscape context of upland calcareous habitats, by examining patch size and contiguity. Finally, we assess how much calcareous habitat is currently included in Pennsylvania's protected lands.

Methods

Upland Calcareous Habitat

Our analysis of upland habitats included the following basic steps, described in more detail below. In order to identify the extent of areas that potentially have a strong influence of calcium in the substrate, we developed an estimate of how much land area in Pennsylvania has calcareous surface geology, based on a surface geology map classified into ecologically meaningful groups. We then overlaid NLCD satellite land cover data (Fry et al. 2011) with the categorized surface geology dataset to estimate the extent of calcareous lands that remain in relatively natural condition, and compare this to the extent of other geology types that remain in natural condition. We overlaid forest block data with calcareous lands in natural condition to assess the contiguity and patch size of calcareous habitats. Finally, we used a variety of environmental data layers in the MaxEnt modeling program to create predictive models of the extent of habitat available to selected individual species and community types.

Surface Geology

Standard geological formations are categorized based mainly on the age of rocks rather than their composition. A single formation may often include layers of many different kinds of rock, and thus a single map unit can vary widely at different locations in its influence on the pH and mineral composition of surface habitat, depending on exactly which layers are at the surface or contributed to soil formation. The standard surface geology map for Pennsylvania has 97 types of map units, shown in Figure 12 (Berg et al. 1980). Anderson and Ferree developed a surface geology dataset which categorized geological formations throughout northeastern United States (including Pennsylvania) based on the dominant materials in the formation (Anderson and Ferree 2010). Table 6 lists the 9 categories and their definitions. Two calcareous categories are included: "calcareous sedimentary," and "moderately calcareous sedimentary/metasedimentary." The dataset also includes two categories of

surface sediment deposits, and maps these units in areas where sediment deposition has a stronger influence than geology (glaciated and coastal plain regions).

We modified this map to include the Monongahela formation in the "calcareous" category. Many of the formations mapped as moderately calcareous include thinner or less pure calcareous layers, often intermixed with acidic layers. While the Monongahela formation's calcareous layers are heterogeneous and relatively impure, a large portion of the formation is calcareous. It has the largest calcareous component of any formation in the western portion of the state and underlies most known locations of limestone communities in the west. Figure 17 shows the modified geology map for Pennsylvania. We then assessed the acreage of lands with calcareous surface geology in the state, and in each physiographic province.

Table 0. Surface Geology Categories, per Alderson a	nu rente.
Geology Class	Included Lithologies Occurring in PA
Ultramafic: magnesium rich alkaline rock	Serpentine, pyroxenite
Mafic : quartz poor alkaline to slightly acidic rock.	Anorthosite, gabbro, diabase, basalt. Metamorphic equivalents: greenstone, amphibolites.
Acidic Granitic: quartz rich, acidic igneous and metamorphic rock.	Granite, granodiorite, rhyolite, pegmatite, Metamorphic equivalents: Granitic gneiss.
Acidic Sedimentary: fine to coarse grained, acidic sedimentary rock	Mudstone, claystone, siltstone, non-fissile shale, sandstone, conglomerate, graywacke. Metamorphic equivalents: slate, phyllite, schist, quartzite.
Acidic Shale: fine grained acidic sedimentary rock with fissile texture.	Fissile shale.
Calcareous Sedimentary: alkaline, soft	Limestone, dolomite, other carbonate-rich clastic
sedimentary rock with high calcium content	rocks. Metamorphic equivalents: marble
Moderately Calcareous Sedimentary: Neutral sedimentary rock with some calcium.	Calcareous shale and sandstone. Metamorphic equivalents: calcareous schists and phyllite.
Fine Sediment: fine grained surficial sediments.	Unconsolidated mud, clay, drift, ancient lake deposits.
Coarse Sediment : coarse-grained surficial sediments.	Unconsolidated sand, gravel, pebble, till.

Table 6. Surface Geology Categories, per Anderson and Ferree.

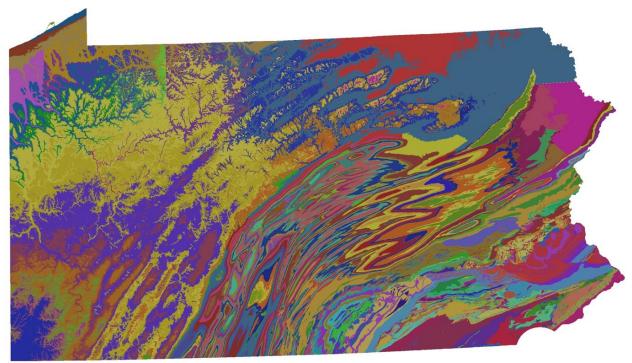


Figure 12. Pennsylvania's 97 surface geology map units.

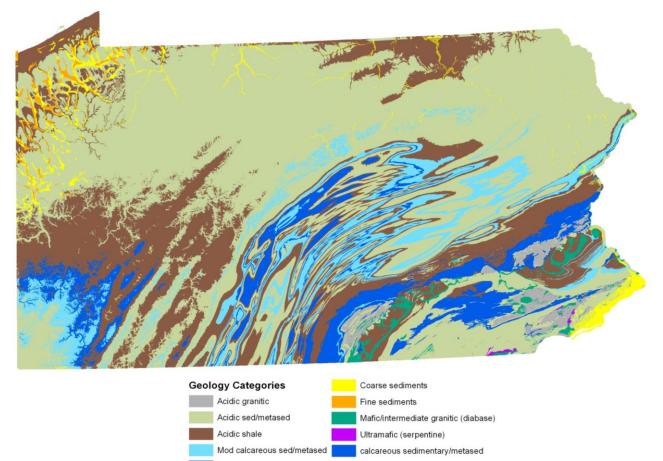


Figure 13. Pennsylvania's surface geology, categorized by composition.

Habitat Contiguity

We assessed habitat contiguity for upland areas only. To create a dataset of limestone forest patches, we intersected the geology category layer with a forest block layer for the entire state (WPC and TNC 2007), then separated any multipart polygons. The resulting layer contains only those portions of forest blocks occurring on limestone geology. We then calculated the acreage of these patches. This data was used to calculate the proportion of the upland calcareous habitat patches remaining in the state that fall into various size classes, per physiographic province. We compare the results to the patch size distribution for all forest regardless of geology type.

Physiographic province location for forest blocks was determined using a spatial join. Since spatial join does not assign values when a polygon falls in more than one category, where forest blocks included area in more than one physiographic province or section, they were manually assigned to the province or section where the majority of its area occurred. Blocks under 50 acres were not reviewed.

However, since limestone forest can and often does occur as part of a forest block that includes multiple geology types, and many of the ecological benefits of forest contiguity are not sensitive to geology type, we also assessed the limestone forest patches according the size of the forest block each fell within. Although limestone habitat specialists cannot utilize non-calcareous forest directly, adjacent non-calcareous forest may still provide corridors for pollinators and animal dispersal agents, and protection against edge conditions that facilitate invasive species establishment.

To assess the contiguity of calcareous habitat areas in natural cover, relative to contiguity of natural habitat on other geology types, we compared the size of forest blocks falling mainly on calcareous geology to block sizes on other geology types.

Species and Community Habitat Models

To provide a more refined estimate of habitat availability for individual species and communities, we generated predictive models using the Maximum Entropy algorithm with known locations and environmental datasets for geology category, slope, elevation, land use, aspect, annual temperature, and annual rainfall (Table 7). We used PNDI data for *Arabis patens, Bouteloua curtipendula*, and *Delphinium exaltatum*. These species were chosen because *Arabis patens* and *Delphinium exaltatum* are both globally imperiled (G3) and serve as indicators of xeric woodland habitats, while *Bouteloua curtipendula* is an indicator of grassland habitat. We also used known locations for several community types. We used Maximum Entropy techniques to create the models (MaxEnt v3.3). MaxEnt is a machine learning technique that compares known species occurrences over a study area to a set of relevant environmental factors, such as vegetation or soil. The program estimates spatial distribution of the species by assuming nothing about which is unknown (maximizing entropy) but by matching the occurrence data with underlying environmental variables. It is useful for rare and endangered species, since absence data are not required, and it can perform well with a relatively small number of occurrence points (R. G. Pearson et al. 2007).

Our models were generated by averaging four replicate runs that each used cross-validation of data (for each training run, a fraction of randomly selected presence data were excluded from the model and used as test data). Thirty meter grid size was used for input raster data layers.

The model outputs a raster layer with the probability of suitable habitat across the state, on a logarithmic scale. MaxEnt generates a "Maximum training sensitivity plus specificity logistic threshold" (MTSSL threshold) for each model, which is a cutoff to separate suitable habitat from unsuitable habitat.

Variable	Data Type	Source
Surface geology	Categorical	Pennsylvania Geological Survey Geologic Map of
lithology		Pennsylvania (Berg et al. 1980)
Physiographic province	Categorical	Pennsylvania Geological Survey (W. D. Sevon 2000)
Annual precipitation	Continuous	ClimateWizard downscaled climate data (Girvetz et al. 2009)
Land cover	Categorical	2006 National Land Cover Dataset satellite land cover (Fry et
		al. 2011)
Elevation	Continuous	Digital Elevation Model (DEM) ("7.5 Minute Digital
		Elevation Models (DEM) for Pennsylvania (30 M)" 2000)
Slope	Continuous	Derived from DEM using ArcGIS Spatial Analyst
Historical temperature variation	Continuous	ClimateWizard downscaled climate data (Girvetz et al. 2009)
Historical precipitation	Continuous	ClimateWizard downscaled climate data (Girvetz et al. 2009)
variation		
Aspect	Continuous	Derived from DEM using ArcGIS Spatial Analyst

We used two metrics generated by MaxEnt to evaluate the quality of the model. Results from the *Arabis patens* model, which performed well, are provided below to illustrate these metrics.

"Average Omission and Predicted Area" (Figure 14) compares the model's actual omission of test data against the fraction of data that should be excluded across a range of predicted occurrence probability. The "cumulative threshold" on the x-axis is defined to vary from 0-1, with no occurrences included at 0 and all occurrences included at 1. A good model should display a 1:1 line, with the actual omission rate

matching the predicted omission rate across all values of the cumulative threshold. (Phillips, Anderson, and Schapire 2006).

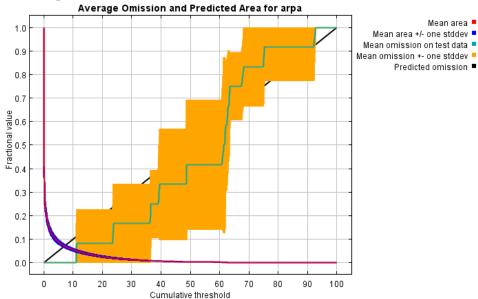


Figure 14. Example graph for MaxEnt model quality metric "Average Omission."

The "receiver operating characteristic" curve shows how well the model predicts occurrence points compared to a random selection of points, and is used to generate the area under the curve (AUC) statistic that indicates quality of the model. The proportion of occurrences captured by the model is graphed against the proportion of the area selected; a perfect model will select occurrences only, requiring only the small fraction of area actually occupied, and appear as a right angle. A random model will increase the proportion of occurrences captured exactly as the proportion of area selected increases, resulting in a 1:1 line. The area under the curve (AUC) statistic summarizes this graph; a perfect model has AUC = 1, while a random model has AUC = .5. AUC is averaged for all model runs, and standard deviation calculated. For the Arabis patens model shown in ,average test AUC (Area under Curve) = 0.991, stdev = = 0.006

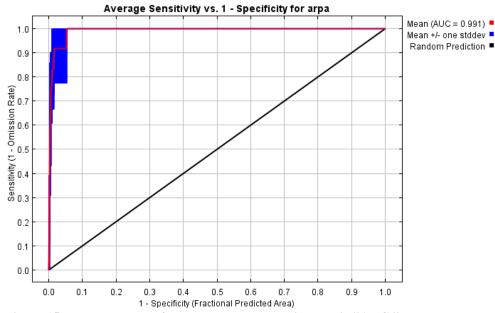


Figure 15. Example graph for MaxEnt model quality metric "AUC."

Wetland Calcareous Habitat

We used the PNDI dataset as the basis for mapping wetland habitat. We selected all calcareous (002, 012, 022 diabase) wetland plant species records in the database, then removed those older than 1970 and mapped with low precision. The PNDI dataset includes herbarium specimen records from all major collections in the region, and field surveys conducted by PNHP staff, state natural resource agency staff, consultants, and others.

We conducted a spatial join with PNDI plant records and the geology category dataset to evaluate how often calcareous wetland plant locations occurred in areas mapped with calcareous surface geology. Where records fell across multiple geology categories, a geology category was assigned by hand; if any portion of the population fell on "moderately calcareous", "strongly calcareous", "coarse sediments", or "fine sediments", this category was assigned. If the population fell across multiple categories within this subset, the determination was based on where the majority of the population occurred.

To further refine the habitat map, we reviewed all records of calcareous plants that did not fall in areas mapped with calcareous geology, considering further information about the site such as species lists and survey notes to determine whether the site represented a habitat with a strong calcareous influence or not. Sites where only one calcareous species was documented were not considered strongly calcareous, and removed from the habitat map.

From this dataset of calcareous plant locations, we attempted a rough calculation of the number of calcareous wetland sites in the state. The number of calcareous plant records in the previously described dataset does not reflect the number of calcareous wetland sites, because often more than one rare plant record occurs at the same site. The PNDI dataset includes site names for most of the rare plant records, but some records were not assigned site names, and some inconsistencies in site names between records exist. We combined the two data fields that contain site names, "site name" and "survey site,", and combined any alternate names that referred to the same sites. We reviewed any records with no site names, and either filled in an existing site names, or provided a new name if the site was unnamed, as appropriate. Then we summarized the number of unique sites.

We calculated the known acreage of calcareous wetland habitat by summing all area mapped in the calcareous wetland plant records in PNDI. Where records overlapped, the overlapping area was counted only once.

Protected Areas

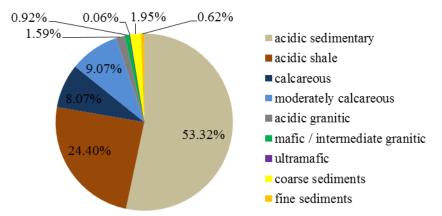
We calculated the acreage of protected areas in each geological category, using a managed lands layer including state forest, state parks, state game lands, national forest, national parks, national natural landmarks, local and county parks, and properties held by several private conservancies.

We also used this layer to calculate how many of the calcareous wetland sites are on protected lands, and how much acreage this represents.

Results and Discussion

This section presents habitat mapping results, and discussion of their accuracy and any methodological issues. Discussion of the broader ecological and conservation significance of the habitat mapping results is addressed in the discussion section of the Conservation Needs of Calcareous Vascular Plants and Their Habitats section of the report (pg. 100).

Upland Calcareous Habitats



Calcareous Surface Geology in Pennsylvania

Figure 16. Proportion of Pennsylvania land area in various surface geology categories.

Calcareous bedrock is substantially more common in Pennsylvania than the other geology types that host unique flora (ultramafic/serpentine and mafic/diabase), but still underlies a minority proportion of the state's land area. Eight percent of Pennsylvania's land area is underlain by calcareous geology, and an additional 9% is underlain by moderately calcareous geology. The vast majority of the state, over 75% of its total land area, is underlain by acidic bedrock. The remaining five geology categories are very scarce in the state, together forming 6% of the state's land area.

Pennsylvania's three largest physiographic provinces all contain a high percentage of the state's total land with calcareous surface geology (Figure 17). The Ridge and Valley has the most land area with calcareous geology (59% of all calcareous land in the state), and the highest proportion of calcareous to non-calcareous surface geology within the province. The Appalachian plateau contains 25% of the state's calcareous lands, concentrated in the southwest where the Monongahela formation surfaces. The majority of this very large province has acidic sedimentary or acidic shale surface geology. The Piedmont physiographic province also contains 16% of the state's calcareous lands.

This map omits the areas of calcareous surface geology in Pennsylvania that are found outside of those formations classified as "calcareous". In most cases, these are calcareous geology layers that are relatively thin, and embedded in non-calcareous layers. They often also have lower calcareous content, as in calcareous shales or sandstones. Because of these factors, these geology layers generally exert only a weakly calcareous influence on the surface, or influence the surface only in very small patches, on the order of 1 to several meters in width, that are often surrounded by more acidic habitat. The ecological significance of these small patches is reduced because they can only host very small populations rather than communities, and many taxa may have difficulty dispersing to them. However, for individual taxa, these minor layers may be important and worth further examination. For example, field experience

suggests that the Ames limestone, a thin layer within the predominantly acidic Glenshaw formation, is often correlated with snow trillium (*Trillium nivale*) locations; these locations also often have few or no additional calciphile species.

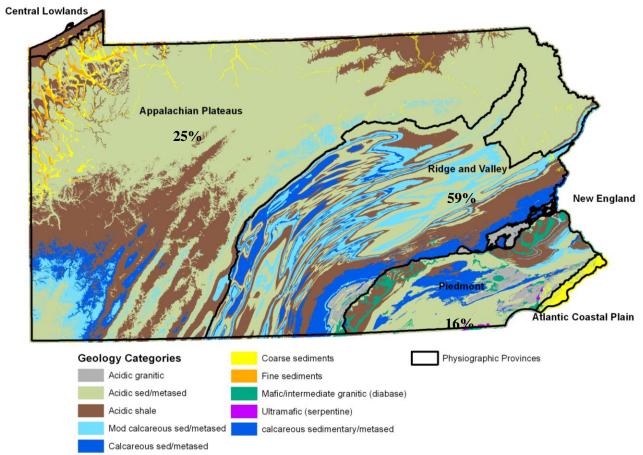
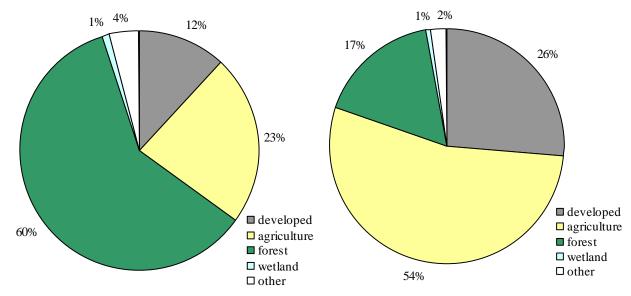


Figure 17. Calcareous surface geology in Pennsylvania, with percent of state total found in each physiographic province.

It is also likely, however, that our use of the "calcareous" surface geology category to estimate potential habitat overpredicts the area where the surface substrate is actually influenced strongly enough by calcium to provide habitat for exclusive calciphile taxa. Soil pH must generally be 6.5 or above in order to cause the nutrient limitations that appear to drive floristic specialization (see background, pg. 8, for more information). There is some evidence that the pH of even limestone-derived soils in our region is often lower than 6.5, due to leaching, unless there is an active mechanism for replenishment of calcium from bedrock materials (see background, pg. 9). This factor further reduces the likelihood that minor calcareous geology layers will result in ecologically significant areas of calcareous habitat.

We do not yet have a method to predict where substrate pH is above 6.5 using remote data, and therefore we cannot assess the extent of this type of over-prediction in our estimate of potentially calcareous lands in Pennsylvania. Soil survey data are not useful because they usually provide pH data in a broad range for individual map units (e.g., Leck Kill soil pH 5.5-7.0), they often lump map units on steep slopes because these areas are not economically valuable, and map units are not designated consistently between counties.



Calcareous Lands in Natural Land Cover

Figure 18 (left). Proportion of state in various land cover categories, NLCD data Figure 19 (right). Proportion of calcareous geology lands in various land cover categories, NLCD data.

Statewide, 60% of Pennsylvania's land area is in forest cover, according to NLCD satellite data. However, only 17% of areas with calcareous bedrock are in forest cover. The fraction of calcareous lands that have been converted to agriculture and developed land cover types is more than double the fraction of the state as a whole that has been converted to these types (Figure 18, Figure 19).

Table 8 shows that conversion of limestone-underlain lands to non-forest land uses has been more extensive in some parts of the state than in others.

Physiographic	Section	% of calc	% remaining	% of PA's	Acres of
Province		bedrock in	in forest	remaining forested	forested
		state		limestone	limestone
Appalachian Plateaus	Waynesburg Hills	12.1%	50.0%	26.2%	141,983
	Pittsburgh Low Plateau	11.9%	42.4%	21.9%	118,973
Ridge and Valley	Appalachian Mountains	22.7%	31.8%	31.3%	169,888
	Great Valley	29.4%	9.1%	11.6%	62,810
	Susquehanna Lowlands	4.6%	18.3%	3.6%	19,744
Piedmont	Piedmont Lowlands	15.7%	5.7%	5.4%	29,291

T-11.0	D		1 1
I able 8.	Remaining forest cove	r over iimestone geology	, by physiographic province.

The Appalachian Plateau Province appears to have the highest fraction of its calcareous lands in forest cover, at nearly 50%. While this province only has 25% of the state's strongly calcareous land, it now contains almost half the calcareous land still remaining in forest cover.

However, it is likely that this figure includes substantial areas which have been strip mined for coal. The Monongahela formation, which includes the largest calcareous rock layers in the southwest, also includes

the heavily mined Pittsburgh coal seam. Visual comparison of USGS topographic maps that delineate strip mined areas with NLCD land cover data confirms that many strip mined areas in the region are categorized as forest cover in the NLCD. Previously stripped lands are notoriously difficult to restore to natural forest ecosystems; it is possible that these areas have formed young, thin forest, or even thickets of invasive species, that were categorized as forest through the remote sensing algorithm used to create the NLCD. However, it is unlikely that strip mined areas now provide habitat for limestone species. Strip mining would have eliminated the seed bank, and many limestone species are highly conservative. Furthermore, disruption and removal of bedrock layers could result in alteration or removal of the influence of calcareous bedrock on the surface substrate.

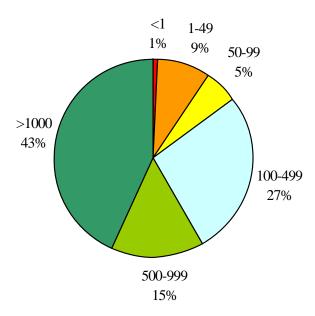
In the Ridge and Valley Province, the overall fraction of forest cover is lower, and the fraction varies substantially in different sections. The Appalachian Mountain section has the largest proportion of calcareous land still in forest cover, at roughly 30%. This relatively large region still contributes 30% of the state's total remaining calcareous land in forest cover. The Great Valley has an extremely low fraction of forest cover, 9%, because most of the valley has been converted to agriculture. While this extensive limestone valley represents almost 30% of all calcareous land in the state, it now has only about 10% of the state's remaining forested limestone lands.

The Piedmont province has 15.7% of the state's calcareous land, but today has the lowest fraction of forest cover, at 6%. Agriculture and residential/commercial land development are nearly ubiquitous in the calcareous areas of this province.

Habitat Contiguity

Forest cover on calcareous geology is much more fragmented and occurs in smaller patches than all forest cover statewide. While 43% of forest cover statewide occurs in contiguous blocks greater than 1000 acres in size (Figure 20), only 3% of forest on calcareous geology occurs in contiguous blocks greater than 1000 acres in size (Figure 21). There are only 9 such blocks remaining in PA, all in the Appalachian Mountain section of the Ridge and Valley Province (Figure 23). Over 50% of forest on calcareous geology is less than 100 acres in size, while only 15% of all forest acreage statewide occurs in blocks less than 100 acres in size.

While these figures reflect the size of contiguous limestone forest habitat, limestone forest can occur adjacent to forest on other geology, so we analyzed the size of forest blocks including any calcareous forest separately (Figure 22). Sixteen percent of forest on calcareous geology occurs as part of a forest block that is larger than 1000 acres when forests on all geology types are considered together. Forty-two percent of forest on calcareous geology occurs in blocks less than 100 acres in size.



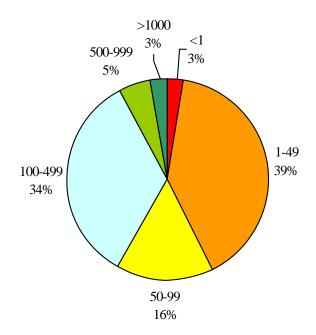


Figure 20. Forest acreage by block size, statewide.

Figure 21. Forest acreage by block size, on calcareous geology.

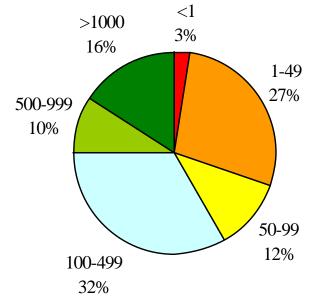


Figure 22. Forest acres by block size; blocks on calcareous geology considered with adjacent forest cover.

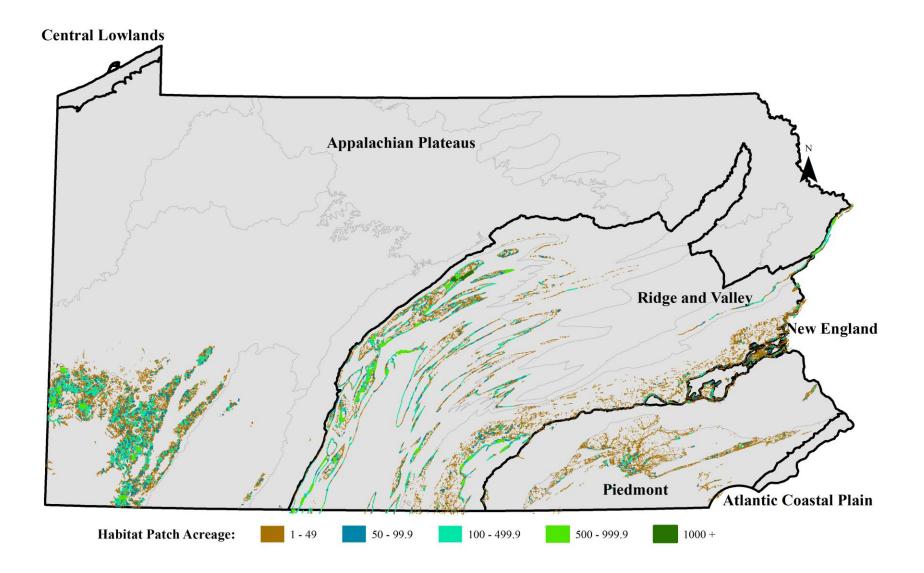


Figure 23. Patches of contiguous upland habitat with calcareous surface geology remaining in natural land cover in PA.

Species and Community Habitat Models

Models for two of the selected species, *Arabis patens* and *Bouteloua curtipendula*, performed very well, with high AUC and low variation between model runs (Table 9). The *Delphinium exaltatum* model performed moderately well, with high AUC but also a high standard deviation showing that the model runs were less consistent in their results.

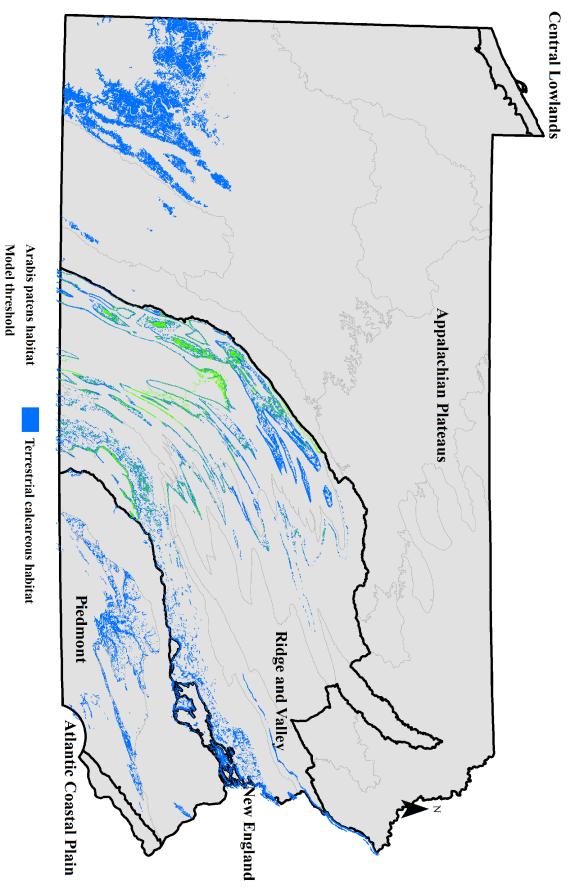
In general, the well-performing models demonstrate that the species modeled can each utilize only a fraction of all terrestrial calcareous habitat remaining in natural condition in the state. Spreading rockcress, for example, is a southern-distributed Appalachian mountain species and only extends into the Ridge and Valley physiographic province of Pennsylvania. The model shows that it is indeed limited to areas with calcareous bedrock and natural land cover, the characteristics that define our calculation of available terrestrial calcareous habitat. However, the model indicates that slope and annual precipitation are also important, and it occurs exclusively in the deciduous forest land cover category. The species' requirement for dry, moderate-to-steeply sloped sites with deciduous forest limits its potential available habitat area to a subset of the calcareous habitat remaining in the state.

The community models did not perform as well, with the exception of the red oak - mixed hardwood calcareous woodland and sideoats grama grassland types. For the other community models, AUC scores are low, and large areas are identified as predicted habitat because the models have low ability to accurately distinguish actual habitat. Limited datasets may be one cause of the poor performance of these models; among all the models, the best results were obtained for the two with the largest number of input occurrences. Another factor may be that some variables important to defining the environmental niche of these communities were not included in the analysis. Scale can also be important; if variation occurs over a smaller scale than the grid square sized used in the model (30 m), the values calculated for occurrence locations may be inaccurate, which would lead to inability of the model to correctly incorporate the environmental parameter. This may occur with slope or aspect.

The following graphics representing model habitat distribution and statistics on model performance were generated using the MaxEnt 3.3 software package. (See methods, pg. 38, for further information on interpreting the model maps and quality metrics).

Model target	AUC (avg 4 model runs)	Standard Deviation	# Input locations
Spreading rockcress (Arabis patens)	.991	.006	12
Sideoats grama grass (<i>Bouteloua curtipendula</i>)	.983	.018	18
Tall larkspur (<i>Delphinium exaltatum</i>)	.966	.051	8
Mesic outcrop community	.658	.324	6
Red oak – mixed hardwood calcareous woodland	.988	.006	8
Sideoats grama grassland	.993	.006	8
Yellow oak - redbud woodland	.960	.025	10
Yellow oak forest	.976	.020	6

Table 9. Model quality as indicated by AUC.



0 - 0.42 (unsuitable) 0.43 - 0.9 (suitable)

Figure 24. Arabis patens model habitat, a subset of available terrestrial calcareous habitat.

Spreading rockcress (Arabis patens)

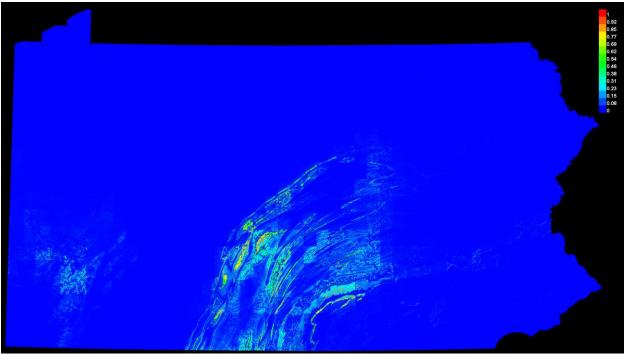
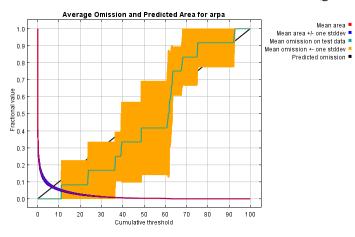


Figure 25. MaxEnt habitat model for *Arabis patens* in PA. MTSSL threshold = .46; values above the threshold (green through red) are suitable habitat.



Variable	Percent contribution	Permutation importance
Surface geology lithology	35.1	19.1
Physiographic province	24.5	3.5
Annual precipitation	19	51.3
Land cover (NLCD)	16.3	16.5
Elevation	5	9.6
Slope	0.1	0
Historical temperature variation	0	0
Historical precipitation variation	0	0
Aspect	0	0

Sideoats grama grass (Bouteloua curtipendula)

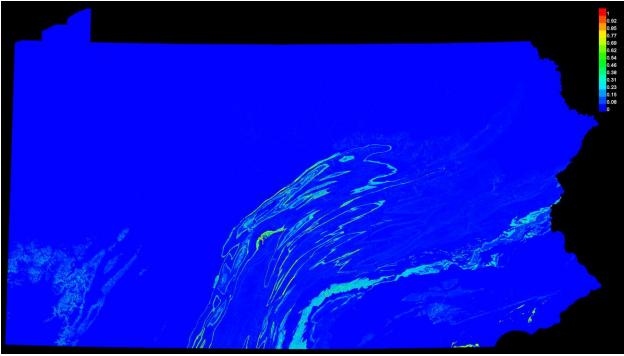
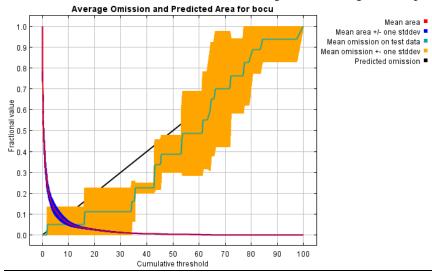


Figure 26. MaxEnt model for *Bouteloua curtipendula* **in PA.** MTSSL threshold: suitable habitat > .1877 (light blue through red display colors are suitable habitat)



Percent contribution	Permutation importance
69.5	87.6
13.3	5
12	5.2
4.1	1.4
0.6	0.2
0.4	0.6
0	0
0	0
0	0
	69.5 13.3 12 4.1 0.6 0.4 0 0

Tall larkspur (Delphinium exaltatum)

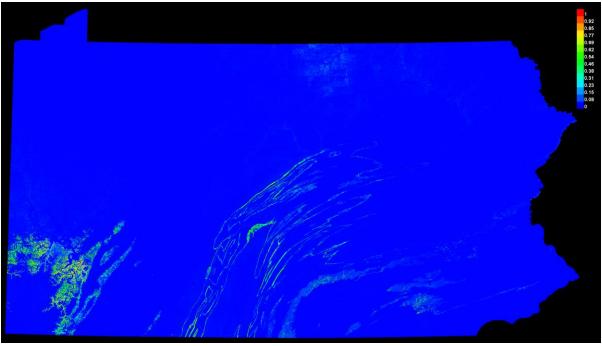
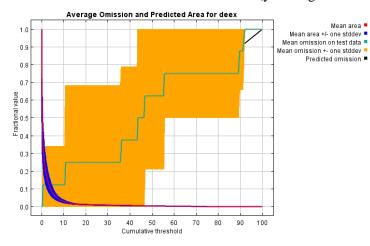
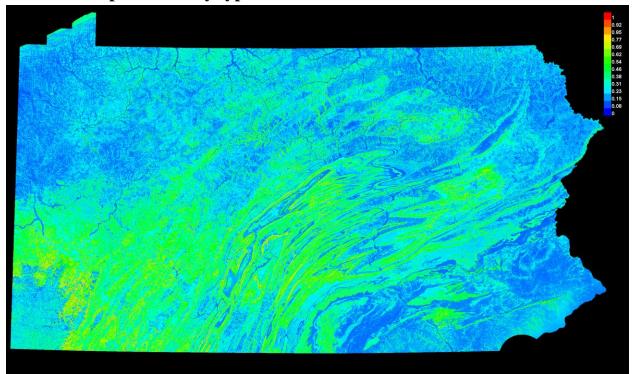


Figure 27. MaxEnt model for *Delphinium exaltatum* **in PA.** MTSSL threshold: suitable habitat > .651 (yellow-green through red display colors are suitable habitat)

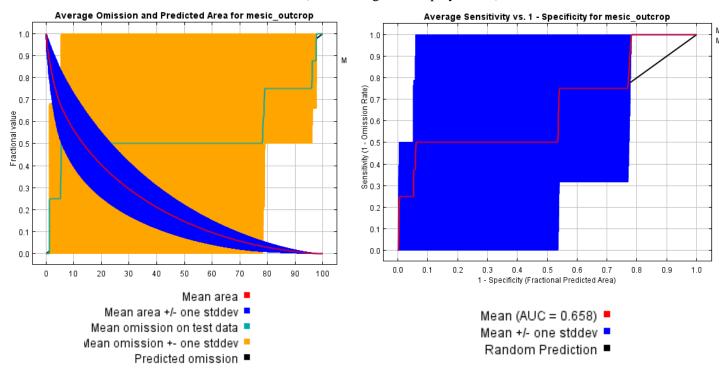


Variable	Percent contribution	Permutation importance
Surface geology lithology	69.1	56.1
Land cover (NLCD)	18.9	18.3
Historical precipitation variation	4.8	3.8
Elevation	2.8	16.2
Physiographic province	2.8	5.1
aspect	1.4	0
slope	0.2	0.5
Annual precipitation	0	0
Historical temperature variation	0	0

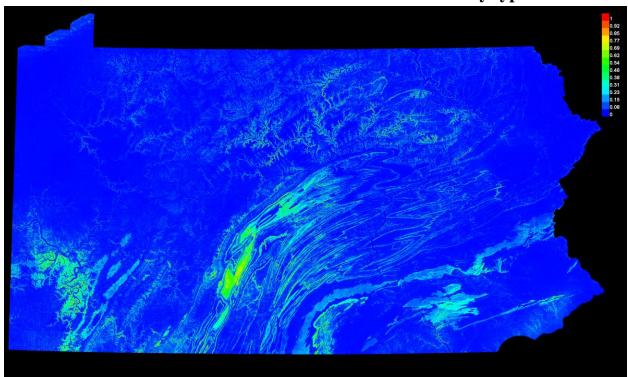
Mesic outcrop community type



MTSSL threshold: suitable habitat >.7142 (Gold through red display colors). Model: 6 known locations.

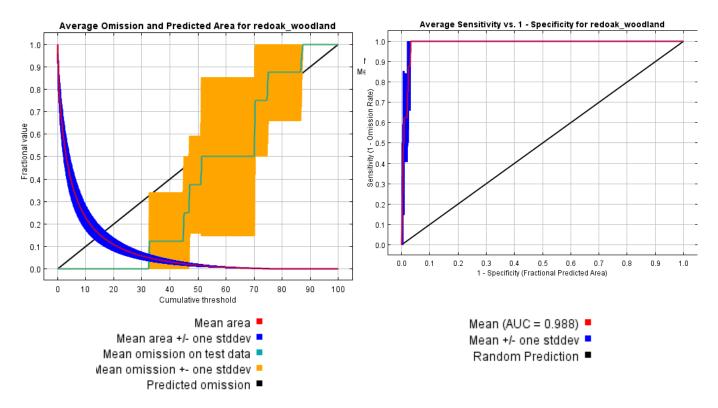


The average test AUC for the replicate runs is 0.658, and the standard deviation is 0.324. This model performed poorly, with extremely low specificity.



Red oak - mixed hardwood calcareous woodland community type

Figure 28. MaxEnt model for red oak woodland community type in PA. MTSSL threshold: suitable habitat >.46 (Green through red display colors). Model: 8 known locations



The average test AUC for the replicate runs is 0.988, and the standard deviation is 0.006.

Sideoats grama grassland community

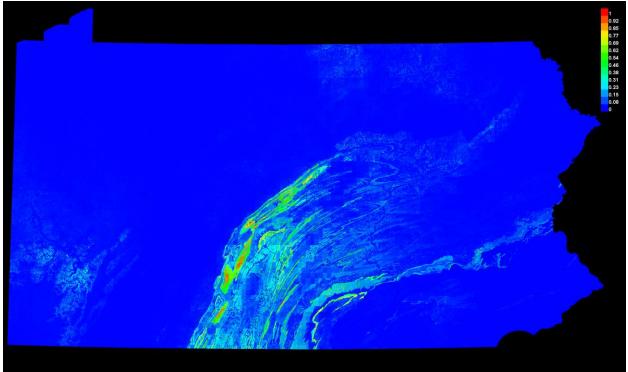
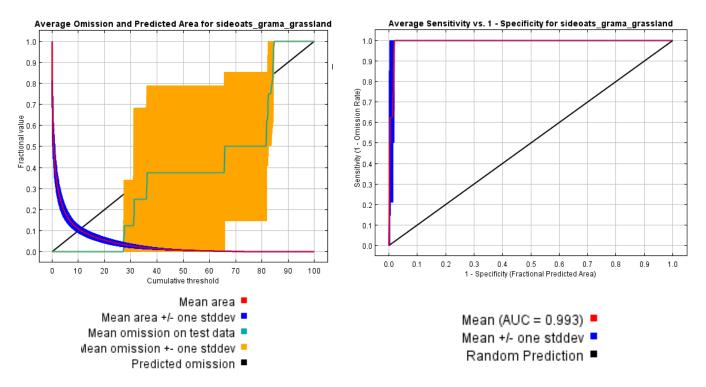


Figure 29. MaxEnt model for sideoats grama grassland community type in PA. MTSSL threshold: suitable habitat >.4867 (Green through red display colors). Model: 8 known locations



Yellow oak - redbud woodland community

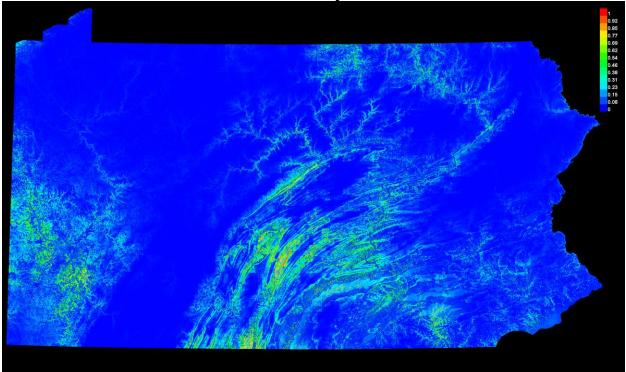
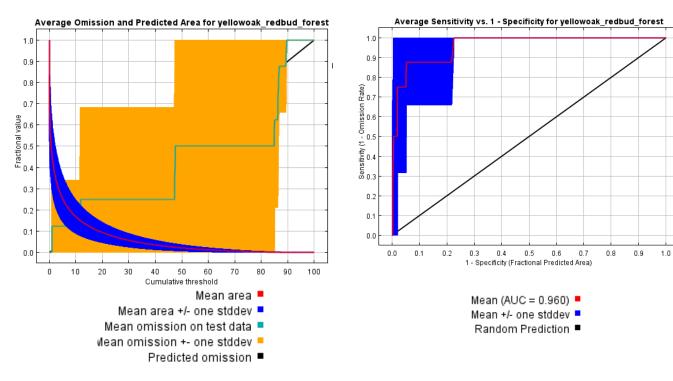


Figure 30. MaxEnt model for yellow oak - redbud community type in PA. MTSSL threshold: suitable habitat >.333 (Green through red display colors). Model: 10 known locations



Yellow oak forest community

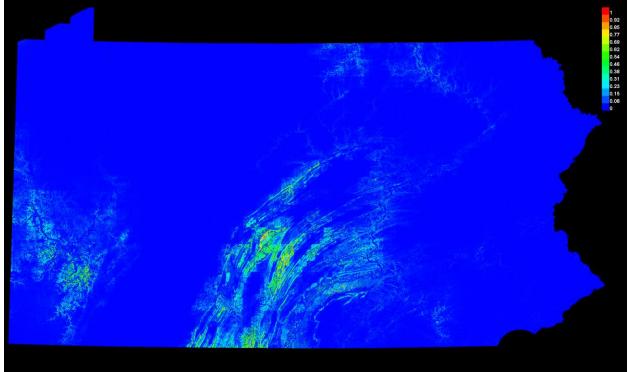
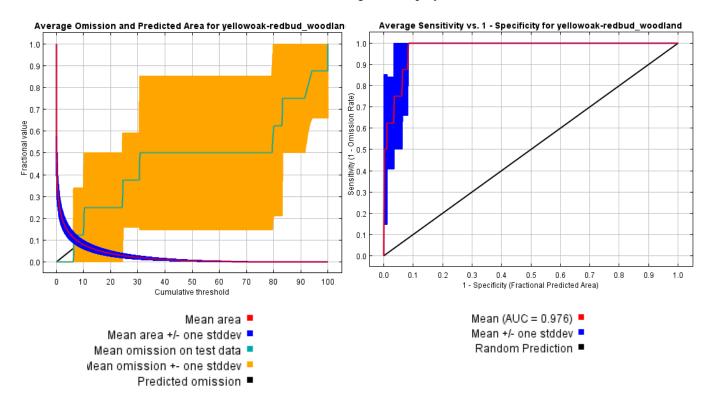


Figure 31. MaxEnt model for yellow oak forest community type in PA. MTSSL threshold: suitable habitat >.38 (Green through red display colors). Model: 6 known locations.



	I	5 51
Variable	Percent contribution	Permutation importance
Geology	38.8	53.3
Landcover	27.4	26.5
slope	24.8	9
histempv	8.7	10.7
histprecip	0.2	0
aspect	0.2	0.3
physprov	0	0.4
Ann-precip	0	0
elevation	0	0

Mesic outcrop community type

Red oak woodland community type

Variable	Percent contribution	Permutation importance
Slope	49.6	66.8
Geology	29.2	25.3
Landcover	10.6	3.6
Histempv	7.3	2.5
Ann-precip	2.1	1
Physprov	1.2	0.8
Histprecip	0.1	0.1
Elevation	0	0
Aspect	0	0

Sideoats grama grassland community type

Variable	Percent contribution	Permutation importance
Geology	38.5	45.9
Physprov	27	4.7
Landcover	16.5	34.6
Ann-precip	15.5	8
Histprecip	1.9	5.9
Elevation	0.5	0.1
Slope	0.1	0.8
Aspect	0	0
Histempv	0	0

Yellow oa	k – redbud	woodland	community type

Variable	Percent contribution	Permutation importance
Geology	22.2	3.2
Elevation	21.7	32.8
Landcover	21	39.2
Annual precip	14.7	0
Histprecip	9.1	14.5
Slope	6.5	9.6
Physprov	4.7	0.6
Aspect	0	0
Histempv	0	0

Yellow oak forest community type

Variable	Percent contribution	Permutation importance
Geology	22.2	3.2
Elevation	21.7	32.8
Landcover	21	39.2
Annual precip	14.7	0
Histprecip	9.1	14.5
Slope	6.5	9.6
Physprov	4.7	0.6
Aspect	0	0
Histempv	0	0

Wetland Calcareous Habitat

Figure 34 presents a map of calcareous wetland habitats in Pennsylvania, based on PNDI data for populations of rare calcareous wetland plant species. Table 10 summarizes the number of plant populations and calcareous wetland sites per physiographic province.

Calcareous wetland sites are clearly concentrated most heavily in the glaciated northwestern part of the state, with half of all known sites in the Central Lowlands Province (Lake Erie Floodplain) and the Northwestern Glaciated Plateau Section of the Appalachian Plateaus Province (Figure 33). The glaciation processes that shaped this region resulted in a landscape in which wetlands are much more abundant than in other portions of the state, and many of these wetlands are calcareous. Calcareous wetlands are strongly correlated with the "coarse sediment" and "fine sediment" geology categories (shown in yellow and orange in Figure 34), which map thick glacial deposits. In Northwest PA, these deposits often contain calcareous materials (PA DCNR 2013), and wetlands fed by groundwater that flows through them receive calcareous mineral input. The areas mapped as "coarse sediments" correspond to "kames, kame terraces, kame moraines, and eskers" in the Pennsylvania Geological Survey's "Map of the Glacial Deposits of Northwestern Pennsylvania" (Shepps et al. 1959). These deposits are of sand and gravel materials. Areas mapped as "fine sediment" correspond to "outwash, river terraces, and lake deposits" of bedded sand, silt, and clay, as well as sand and gravel materials. "Stream alluvium and bedrock" areas also correspond to areas mapped in the "fine sediment" category.

The Northwestern PA glaciated areas also tend to have more calcareous taxa per site than other regions of the state. While these two physiographic province sections include half the state's calcareous wetland sites, these sites contain almost ³/₄ of the known rare plant populations (Figure 32).

The Central Lowlands Province is particularly notable for the density of calcareous wetland habitats within a small area. The average number of taxa per site is highest of any section, at 4.2. However, this province includes Presque Isle, which has a great density of rare plants because it is the only habitat in Pennsylvania for Great Lakes dune ecosystem specialists. Without Presque Isle, the Central Lowlands province still has 20 sites, with an average of 2.2 taxa per site, which is lower than the Northwestern Glaciated Plateau section but greater than the average taxa for any section in the Ridge and Valley or Piedmont Provinces. This includes fens as well as bluff seepages.

Outside of the Northwestern Glaciated Plateau Section, calcareous wetlands are very scarce in the Appalachian Plateau Province. The glaciation that occurred in north central and eastern Pennsylvania was dominated by erosional processes rather than depositional processes, and thus the landscape now has extremely thin soils above bedrock rather than layers of glacial till. Furthermore, soils and glacial formations are dominated by local bedrock materials, which contain very little calcareous material (PA DCNR 2013; William D. Sevon, Fleeger, and Shepps 1999). While wetlands are common in these glaciated landscapes, they very rarely receive significant calcareous input. Outside of glaciated areas, wetlands are much less common in general. The southwestern portion of the state, which does have a significant amount of terrestrial calcareous habitat, has only one known calcareous wetland habitat.

The Ridge and Valley Province is also an important region for calcareous wetlands in the state, with 36% of known calcareous wetland sites. These sites occur in the relatively flat and low valleys of the province, which are also usually the areas underlain with calcareous geology, because the valleys were created from folded limestone layers weathering faster than the more resistant sandstone and shale that became the ridges (Schultz 1999). The Ridge and Valley calcareous wetlands have an intermediate number of

calcareous taxa per site, averaging more than one taxon per site, but not as many as the Northwestern region.

The Piedmont Province has a small fraction of the state's calcareous wetland sites, and these tend to have one calcareous plant taxon documented per site.

The total area mapped as current known habitat for calcareous wetland plant species in Figure 34 is 6400 acres. However, this estimate is limited by the quality of the PNDI data in representing the actual extent of populations on the ground. For each PNDI record, the known occupied area for the population is mapped. However, there are several reasons the area mapped may not correspond to the actual occupied area on the ground. The full extent of potential habitat is not always surveyed, so more plants may exist beyond the mapped area. Some records are created from specimen data or surveys where limited information is given about the extent of the population; the mapped areas may underestimate or overestimate the actual occupied area in these cases. Where records overlapped, the area was only counted once.

We used empirical data rather than GIS modeling because we had relatively good survey-based data available, while there are a number of problems with the available remote datasets that make it unlikely modeling would provide good results. Calcareous wetlands have been fairly comprehensively surveyed across the state. Most calcareous wetland plant species have been assigned special concern status (rare, threatened, or endangered in PA) and are therefore included in the PNHP database.

Several factors complicate accurate mapping of calcareous wetland habitats with remote datasets. Groundwater can be influenced by materials distant from the point at which the groundwater reaches the surface, and thus some wetlands can be located in places where calcareous surface geology is not mapped, but calcareous groundwater does emerge. Furthermore, the only statewide wetland datasets are the National Wetlands Inventory (NWI) and NLCD, and casual examination of known calcareous wetland plant populations in the PNDI dataset shows that many are mapped outside of areas mapped as wetland in either the NWI or the NLCD. Of known calcareous plant locations, 24% do not intersect with NWI wetlands at all, while at least 31% do not intersect with NLCD wetlands or open water (class 95, 90, or 11). Seventeen percent do not intersect with wetlands in either dataset.

Province	Section	# calc plant	# sites	Average #
		populations		taxa per site
Appalachian	Allegheny Front	3	3	1
Plateaus				
(total plants: 280)	Glaciated High Plateau	3	3	1
(total sites: 108)	Glaciated Low Plateau	9	8	1.1
	Northwestern Glaciated	261	90	2.9
	Plateau			
	Pittsburgh Low Plateau	3	3	1
	Waynesburg Hills	1	1	1
Central Lowlands	Eastern Lake	89	21	4.2
(total plants: 89)				
(total sites: 21)				
Piedmont	Gettysburg-Newark Lowland	9	7	1.3
(total plants: 18)	Piedmont Lowland	1	1	1
(total sites: 16)	Piedmont Upland	8	8	1
Ridge and Valley	Anthracite Upland	1	1	1
(total plants: 138)	Appalachian Mountain	49	27	1.8
(total sites: 74)	Blue Mountain	23	13	1.8
	Deep Valleys	1	1	1
	Great Valley	51	20	2.1
	South Mountain	5	2	3
	Susquehanna Lowland	7	6	1.2
TOTALS FOR		524	212	2.6
ALL PA:				

Table 10. Summary of calcareous wetland plant locations (PNDI data) and calcareous habitat sites, by physiographic province.

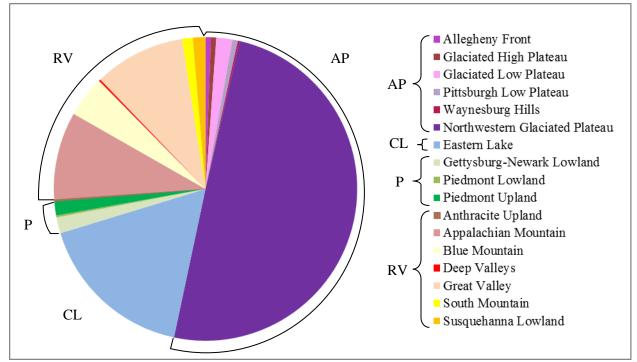


Figure 32. Fraction of PA's known calcareous wetland plant taxa in each physiographic province & and section.

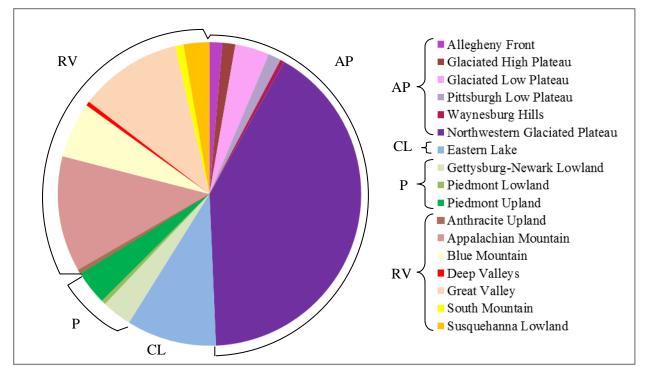


Figure 33. Fraction of PA's known calcareous wetland sites in each physiographic province and section.

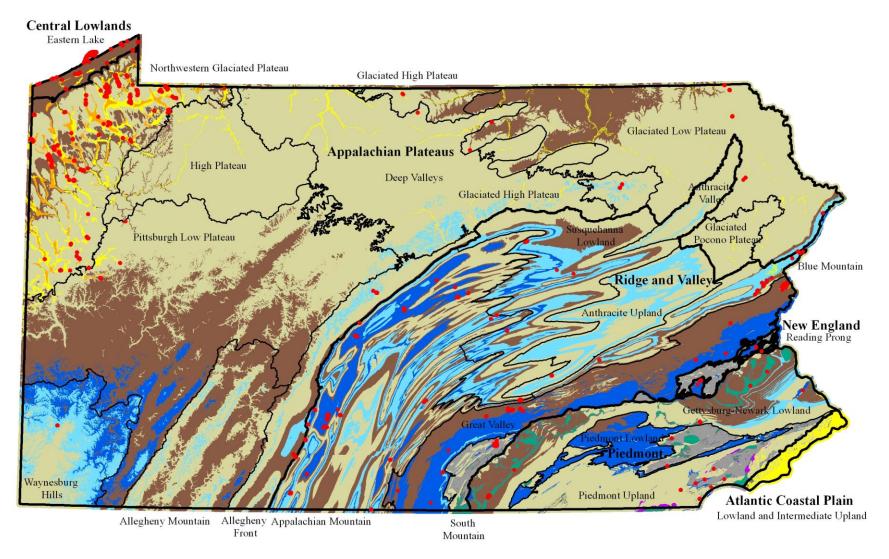


Figure 34. Calcareous wetland plant locations (PNDI data, shown in red) in PA, with physiographic provinces.

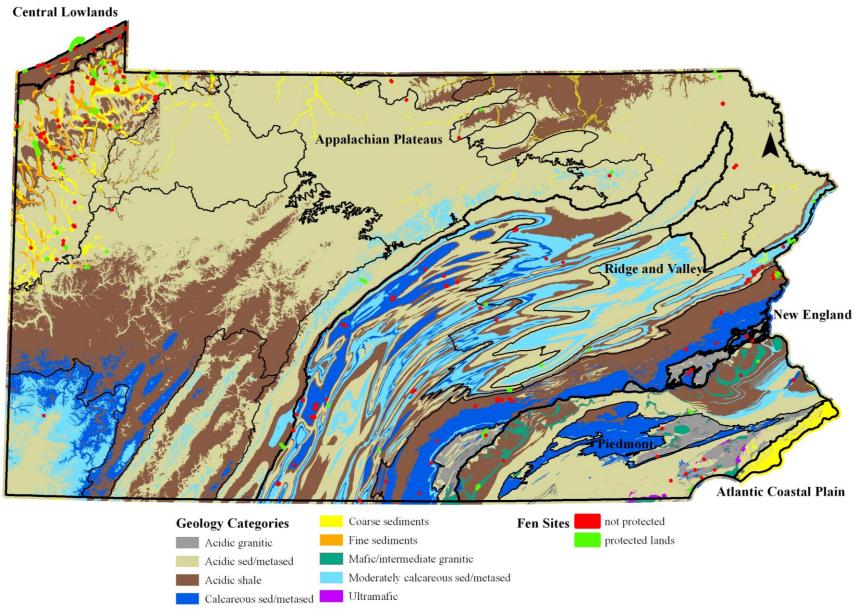


Figure 35. Protection status of calcareous wetland sites in Pennsylvania.

Protected areas

Calcareous habitats are disproportionately lacking from Pennsylvania's protected land system. Although 8% of the state's land area is calcareous geology and 9% is moderately calcareous geology, less than 1% of all protected lands in the state are on calcareous geology, and only 7% are on moderately calcareous geology. While other minority geology categories in the state are proportionately represented in protected lands, calcareous geology is very much underrepresented in protected lands (Table 11).

A much larger proportion of known calcareous wetland habitat is protected than terrestrial habitat, but there remains significant room for improvement, and protected wetland sites are not evenly distributed across the state. Figure 35 maps calcareous wetlands according to their protection status. Only 34% of the known calcareous wetland sites in Pennsylvania are on protected lands, although 47% of this acreage is protected (Table 12). The Northwestern Glaciated Plateau section of the Appalachian Plateau Province has by far the most sites of any section, and also has a relatively high proportion of protected sites, 46%. However, the adjacent lakeplain of Lake Erie (Central Lowlands Province), which has a great density of sites in a small area, has only 2 of 20 sites protected. The Ridge and Valley Province, which has about a third of the state's calcareous wetland sites, has a much lower proportion of protected sites than the Northwest: only 15 of 70 (21%). A quarter of the sites in the Piedmont Province (4 of 16) are protected.

Although there is a large variation in the number of calcareous taxa known to occur at sites, the protected fraction of all known calcareous plant populations matches the protected fraction of sites exactly; both are 34%. This is also fairly consistent at a regional scale as well; in most physiographic province sections, the fraction of plant populations protected is close to the fraction of sites protected (Table 12). In five of the seven sections where there is more than a 5% difference between these fractions, the fraction of plants protected is greater than the fraction of sites protected. The only regions where the fraction of plants protected is much lower than the fraction of sites protected are the South Mountain and Appalachian Mountain sections of the Ridge and Valley Province.

Geology category	Protected Acres	% of all protected	% of state land area
		areas	
acidic sedimentary	3,567,211	81.70%	53.32%
acidic shale	335,172	7.68%	24.40%
calcareous	31,044	0.71%	8.07%
moderately calcareous	288,435	6.61%	9.07%
acidic granitic	57,570	1.32%	1.59%
mafic / intermediate granitic	19,537	0.45%	0.92%
ultramafic	1,609	0.04%	0.06%
coarse sediments	36,615	0.84%	1.95%
fine sediments	29,303	0.67%	0.62%
total protected lands	4,366,496		14.69%

Table 11. Protected areas in Pennsylvania by surface geology category.

Province	Section	# calc plant	%	#	# sites	%
		populations	protected	sites	protected	protected
Appalachian	Allegheny Front	3	100%	3	3	100%
Plateaus	Glaciated High Plateau	3	33%	3	1	33%
(total: 280 plants,	Glaciated Low Plateau	9	56%	8	4	50%
108 sites)	Northwestern Glaciated Plateau	261	46%	90	42	47%
	Pittsburgh Low Plateau	3	66%	3	2	66%
	Waynesburg Hills	1	0%	1	0	0%
Central Lowlands (total: 89 plants, 21 sites)	Eastern Lake	89	16%	21	2	10%
Piedmont	Gettysburg-Newark Lowland	9	66%	7	3	43%
(total: 18 plants,	Piedmont Lowland	1	0%	1	0	0%
16 sites)	Piedmont Upland	8	13%	8	1	13%
Ridge and Valley	Anthracite Upland	1	100%	1	1	100%
(total: 137 plants,	Appalachian Mountain	49	6%	27	6	22%
70 sites)	Blue Mountain	23	30%	13	4	31%
	Deep Valleys	1	0%	1	0	0%
	Great Valley	51	20%	20	1	5%
	South Mountain	5	20%	2	1	50%
	Susquehanna Lowland	7	43%	6	2	33%
TOTALS FOR ALL PA:		524	34%	212	73	34%
Acreage:				6,394	3,033	47%

Table 12. Protection status of calcareous wetland sites and plant populations in Pennsylvania by physiographic province and section.

IV. Conservation Assessment of Calcareous Flora and Plant Communities

In this section we used a variety of tools to assess the conservation significance of Pennsylvania's calcareous taxa and plant communities. We examined the biogeography of these species to assess patterns in range-wide distributions among calciphiles found in Pennsylvania, which are often relevant to the conservation needs and significance of these taxa. We analyzed the habitat preferences of Pennsylvania calciphiles in order to make connections, where possible, between conservation units such as natural communities and individual taxa. We also applied Floristic Quality Assessment and Climate Change Vulnerability indices to better understand the conservation needs of Pennsylvania's calcareous taxa and communities.

Biogeography of Pennsylvania Calciphile Taxa

Previous work has addressed biogeographical patterns in the Pennsylvania flora, listing taxa that fall into various categories such as glacial taxa regional endemics, and taxa limited to particular physiographic regions (Keener and Park 1986). Our study differs in specifically assessing the calcareous portion of the flora. Furthermore, many new tools have become available that greatly facilitate assessment of range-wide patterns and corresponding ecological variables.

Biogeographical patterns have great importance to conservation. Many of the taxa considered rare in state jurisdictions are rare because the state includes the edge of their geographic range. Populations at the edge of a species' range are often considered to be potentially unique genetically, because they survive in environments which are different than the main portion of the range. There is also a pattern observed among some species to have more specific habitat requirements at the edge of their range, where temperature or rainfall differences from the main portion of the range may push the species' physiological limits. One way this manifests is for a species to have a broad pH tolerance in the major portion of its range, but to inhabit calcareous habitats at the edge of their range (Steele 1955; Ware and Ware 1992).

Methods

We reviewed the taxa which were considered exclusive calciphiles (002) to determine if there were any consistent patterns in their North American geographic distributions, and their distributions in Pennsylvania. Distribution data in North America are from the Biota of North America Project (BONAP) by John Kartesz. Distribution data in Pennsylvania are from the Pennsylvania Flora Project atlas (records of collections submitted to state herbariums, compiled in 1993), the Pennsylvania Natural Heritage Program database (mainly rare species), and other field identifications documented in PNHP surveys.

For taxa where the edge of the range falls in or near Pennsylvania, we also reviewed habitat descriptions across the eastern North American range, to determine if the taxon behaves as a calciphile throughout the range. To make this determination we consulted qualitative assessments from expert botanists in published sources, including the following:

Flora of North America (Flora of North America Editorial Committee, eds. 1993) Michigan Flora (Reznicek, Voss, and Walters 2011; Voss 1972) New York Flora Atlas (Weldy and Werier 2012) Minnesota Department of Natural Resources Rare Species Guides (Minnesota DNR 2012) Wisconsin Botanical Information System (Wisconsin State Herbarium 2012) Flora of the Southern and Mid-Atlantic States (Weakley 2012)

For the state floras, habitat information was interpreted based on the location of the state within the taxa's range in eastern North America. If calciphilic habitat preference was specified in Flora of North America, or in a state which included significant area not at the edge of range, the taxa was categorized as a calciphile throughout the range.

If Flora of North America or another source did not specify calciphilic preference, and included terms such as "bog" "acid" "marsh" "ditch" "streamside" "wet woods" "barrens" "a variety of habitats" or "diverse habitats", the taxa was considered to have a broader habitat tolerance further north. If no clear indicators of more acid habitats were included in the description, but calciphilic habitat preference was not specified in Flora of North America (or in most of the other sources, when FNA information was not available), the taxa was categorized as "inconclusive".

Results & Discussion

Several distinct geographic patterns can be observed in the distributions of Pennsylvania's calcareous species.

Table 1	Table 15. Totals for geographic distribution patterns in calcipline species found in FA.						
	southern	northern	Prairie	Midwest	great	Appalachian mountains (mainly	Great lakes/ coastal
	distribution	distribution	disjunct	forest	lakes	southern)	plain
# tax	a 24	53	14	12	5	12	2

Table 13.	Totals for geograp	hic distribution	patterns in cal	ciphile spec	ies found in PA.
I GOIC IC.	I Officially I of Scolling	me anotino attor	putter mo mi cun	cipinie spec	too tound in this

Northern Taxa

The largest proportion of the species had their North American range centered north of Pennsylvania, with the edge of their geographic range falling near or within the state. Some species extended further south in the Appalachian Mountains, but outside of the mountains the edge of range was in or near Pennsylvania's latitude. Most, but not all, of the species with northern distributions were wetland species.

Table 14. Calciphile taxa with northern distributions.	
Anemone cylindrica	Galium boreale
Arabis hirsuta var. pycnocarpa	Galium labradoricum
Astragalus neglectus	Gentianopsis crinita
Cardamine pratensis var. Palustris	Gentianopsis virgata
Carex aurea (G)	Geum rivale
Carex bebbii (~G)	Juncus alpinoarticulatus ssp. nodulosus
Carex crawfordii	Lathyrus palustris
Carex cryptolepis (G)	Lobelia kalmii (G)
Carex eburnea	Maianthemum stellatum
Carex flava (G)	Malaxis monophyllos var. brachypoda (G)
Carex formosa	Mitella nuda (G)
Carex garberi	Myriophyllum verticillatum
Carex interior	Parnassia glauca (G)
Carex prairea (G)	Platanthera aquilonis (G)
Carex schweinitzii	Platanthera dilatata var. dilatata (G)
Carex sterilis	Potamogeton friesii (G)
Carex viridula	Potamogeton praelongus
Clematis occidentalis	Potentilla fruticosa
Conioselinum chinense	Rhamnus alnifolia
Cryptogramma stelleri	Ribes americanum
Cypripedium reginae	Ribes hirtellum
Eleocharis quinqueflora	Ribes triste (G)
Equisetum scirpoides	Salix candida (G)
Equisetum variegatum	Salix serissima (G)
Eriophorum gracile	Spiranthes romanzoffiana (G)
Eriophorum viridicarinatum	Symphoricarpos albus var. albus
Fragaria vesca ssp. Americana	Symphyotrichum boreale (G)
-	Viburnum trilobum

Table 14. Calciphile taxa with northern distributions

Our review of North American habitat descriptions indicates that among the species rated as strict calciphiles in Pennsylvania, close to half of those with a northern distribution do not behave as calciphiles throughout their range.

Calciphiles throughout range	Broader habitat northwards	Inconclusive
Astragalus neglectus	Anemone cylindrica	Carex viridula
Carex bebbii	Arabis hirsuta var.	Eleocharis quinqueflora
	pycnocarpa	
Carex flava	Carex cryptolepis	Fragaria vesca ssp. Americana
Carex formosa	Carex eburnea	Gentianopsis crinita
Carex garberi	Conioselinum chinense	Galium boreale
Carex interior	Equisetum scirpoides	Geum rivale
Carex prairea	Equisetum variegatum	Lathyrus palustris
Carex schweinitzii	Eriophorum gracile	Lobelia kalmii
Carex sterilis	Eriophorum viridicarinatum	Myriophyllum verticillatum
Clematis occidentalis	Galium labradoricum	Potamogeton friesii
Cryptogramma stelleri	Mitella nuda	Potamogeton praelongus
Cypripedium reginae	Platanthera aquilonis	Viburnum trilobum
Gentianopsis virgata	Ribes triste	
Juncus alpinoarticulatus ssp. nodulosus	Symphoricarpos albus var. all	pus
Parnassia glauca	(?) Cardamine pratensis var. J	palustris
Potentilla fruticosa	(?) Maianthemum stellatum	
Salix candida	(?) Platanthera dilatata var. L	Dilatata
Symphyotrichum boreale	(?) Ribes hirtellum	
(?) Carex aurea	(?) Spiranthes romanzoffiana	
(?) Rhamnus alnifolia		
(?) Salix serissima		
(?) Malaxis monophyllos var.		
brachypoda		
(?) Ribes americanum		
Total # taxa = $18 + 5(?)$	14 + 5(?)	11

Table 15. Northern calciphiles, categorized according to whether they are calciphiles throughout their range. (?) = habitat descriptions suggest or imply status but are not conclusive.

The following species show examples of typical distribution patterns for northern species reaching their southern limits in or near Pennsylvania. *Carex prairea* (Figure 36) is an example of a fen specialist for which Pennsylvania is at the southern edge of the range, and the species is rare in the state. It is a calciphile throughout its range. Within the state, its distribution corresponds closely to the regions of the state where strongly calcareous wetlands are found; northwestern Pennsylvania, the valleys of the Ridge and Valley Province, and a vertical band in eastern Pennsylvania. Many other calcareous wetland species exhibit similar distribution patterns in the state.

Carex interior (Figure 37) is also a fen specialist throughout its range, which is not presently considered rare in Pennsylvania. Its range extends further south into the mountains of Virginia and West Virginia, and slightly into Maryland. Within Pennsylvania, it has a broader distribution than the more northern species. However, southern Pennsylvania populations should also be considered at the edge of the species' geographic range, and may merit special conservation consideration.

Platanthera aquilonis (Figure 38) is a fen species that is restricted to glaciated areas, and is not found in calcareous wetlands of non-glaciated portions of the state. There are 15 northern species with roughly similar distributions. Some of these also include eastern glaciated sites but not unglaciated ridge and valley sites (*Eriophorum viridicarinatum, Mitella nuda, Parnassia glauca, Ribes triste, Symphyotrichum boreale*). All of these are taxa of wetland habitats, and their range may reflect preference for features resulting from glaciation such as broad, mucky swamps; or it may reflect restriction to the coolest climate regions of the state. *Ribes triste* and *Symphyotrichum boreale* both have isolated populations in West Virginia, which are south of the line of glaciation but at higher elevations.

Symphoricarpos albus var. albus (Figure 39) is a northern species near the southern edge of its range in Pennsylvania, only extending further south in the mountains. Its habitat is limestone outcrops and steep slopes. Within the state, its distribution follows the same limestone-region pattern as *Carex prairea*. *Carex eburnea* (002), *Clematis occidentalis* (002), and *Piptatherum racemosum* (012) are also limestone outcrop/steep slope terrestrial species with similar distribution patterns.

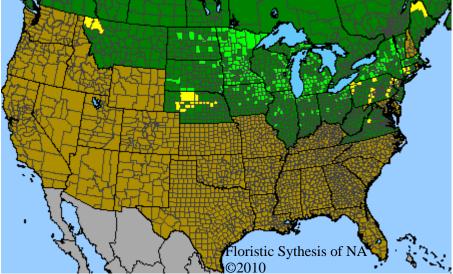


Figure 36. North American distribution for *Carex prairea*, a typical northern fen species, rare in Pennsylvania.

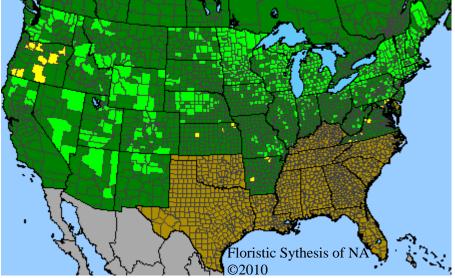
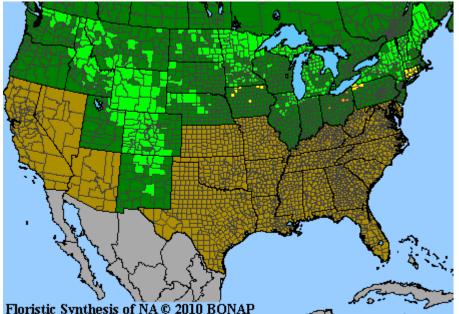
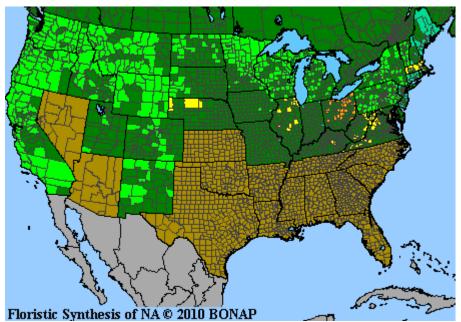


Figure 37. North American distribution for Carex interior, a northern species not rare in Pennsylvania.



Floristic Synthesis of NA © 2010 BONAP Figure 38. North American distribution for *Platanthera aquilonis*, a northern fen species confined to glaciated regions in PA.



Floristic Synthesis of NA © 2010 BONAP Figure 39. North American distribution for *Symphoricarpos albus var. albus*, a northern species inhabiting limestone outcrops in PA.

Southern Taxa

Twenty-four species have their range centered to the south of Pennsylvania, with the northern edge of range falling in or near the state.

Table 16. Calciphile taxa with southern distributions.	
Arabis patens	Paxistima canbyi
Asplenium resiliens	Persicaria setacea
Carex mitchelliana	Poa cuspidata (012 diabase)
Chrysogonum virginianum	Prunus alleghaniensis
Clematis viorna	Rhamnus lanceolata
Corallorhiza wisteriana	Ruellia caroliniensis
Cystopteris tennesseensis	Ruellia humilis
Dodecatheon meadia	Silphium asteriscis var. asteriscis
Juncus brachycarpus	Symphyotrichum lowrieanum
Melica nitens (012 diabase)	Symphyotrichum phlogifolium
Obolaria virginica	Thalictrum coriaceum
Ophioglossum engelmannii	Triadenum walteri

Table 16. Calciphile taxa with southern distributions.

Table 17. Southern distribution species, calciphile status in PA vs. center of rang	Table 17.	7. Southern	distribution s	species, calo	iphile status	in PA	vs. center of range
-------------------------------------------------------------------------------------	-----------	-------------	----------------	---------------	---------------	-------	---------------------

Calciphiles throughout	Broader habitat	Inconclusive
range	southwards	
Arabis patens	Carex mitchelliana	Triadenum walteri
Asplenium resiliens	Chrysogonum virginianum	Ruellia caroliniensis
Cystopteris tennesseensis	Clematis viorna	Prunus alleghaniensis
Dodecatheon meadia	Corallorhiza wisteriana	Symphyotrichum phlogifolium
Ophioglossum engelmannii	Persicaria setacea	Thalictrum coriaceum
Paxistima canbyi	Symphyotrichum lowrieanum	Obolaria virginica
Rhamnus lanceolata	(?) Juncus brachycarpus	Silphium asteriscus var. trifoliatum
Ruellia humilis	(?) Galium concinnum	
Trillium flexipes		
Total # taxa: 9	6 + 2 (?)	7

For the southern species reaching their northern edge of range in Pennsylvania, slightly less than 1/3 seem to have broader habitat tolerances in the main part of their range than they exhibit in Pennsylvania. This is a lower fraction than among the northern species. However, 1/3 of the southern species could not be conclusively assessed in regards to their calcium affinity throughout their range.

Among the taxa with distributions centered south of Pennsylvania, there are several distinct distribution patterns.

One group of taxa has distributions centered on the southeast that reach the northern edge of their range at the very southern edge of Pennsylvania. For *Chrysogonom virginianum* (Figure 40), the southernmost counties in the Ridge and Valley province of Pennsylvania are at the very northern extent of the range,

except for a few disjunct populations in Ohio and New York. *Asplenium resiliens, Ophioglossum engelmannii,* and *Ruellia caroliniensis* (piedmont region) also have this distribution pattern. All of these taxa are considered rare in Pennsylvania primarily due to their extremely limited distribution in the state.

A few species have the northern edge of their range in Pennsylvania's middle latitudes. *Symphyotrichum phlogifolium* (Figure 41) and Poa cuspidata follow this pattern. These taxa have a much greater occupied range within the state and are not considered rare. In these cases the edge-of-range populations do not receive protection.

Another group of taxa have southern-centered distributions that extend much further west, sometimes with disjunct eastern and Midwest populations. *Rhamnus lanceolata* (Figure 42) has the major portion of its' range further west, and a disjunct portion of its range in the Appalachian mountains, with the northernmost extent of this portion falling in Pennsylvania. *Melica nitens* has a very similar distribution. *Ophioglossum engelmannii* and *Ruellia humilis* follow a similar pattern, although these species reach only into Franklin County. *Dodecatheon meadia* (Figure 43), *Cystopteris tennesseensis*, *Brickellia eupatorioides* (012), *Cirsium altissimum* (012), *Corallorhiza wisteriana*, and *Carex shortiana* (012) exhibit a similar pattern, but without the distinct segregation of mountain and central populations.

Thalictrum coriaceum (Figure 44) is a southern Appalachian mountain species that reaches the northern extent of its range in Pennsylvania. The globally rare *Paxistima canbyi, Arabis patens*, and *Euphorbia purpurea* (012-diabase) follow a similar distribution. *Prunus allegheniensis*, a G4 species, has three disjunct portions of its range: the central Appalachians mainly in Pennsylvania; Michigan; and coastal plain New Jersey.

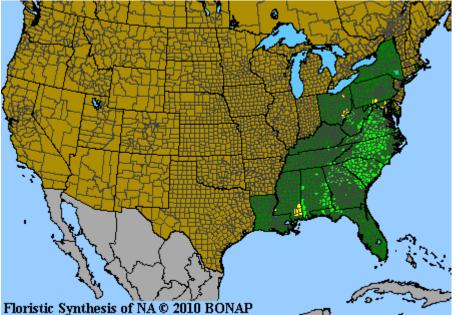
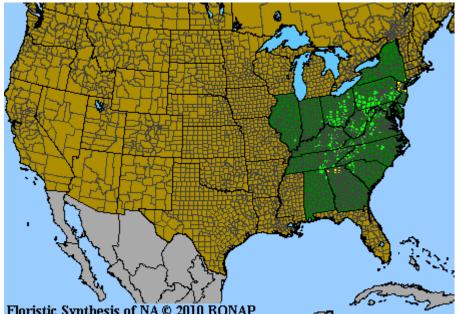


Figure 40. North American distribution for *Chrysogonum virginianum*, a southern species barely extending into PA.



Floristic Synthesis of NA © 2010 BONAP Figure 41. North American distribution for *Symphyotrichum phlogifolium*, a species whose northern range edge falls in PA.

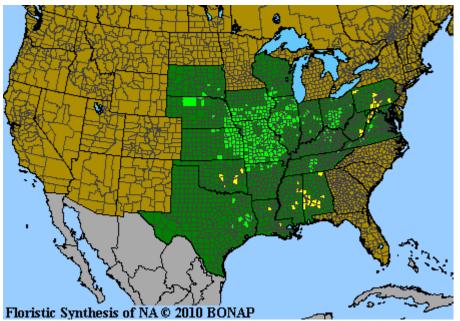
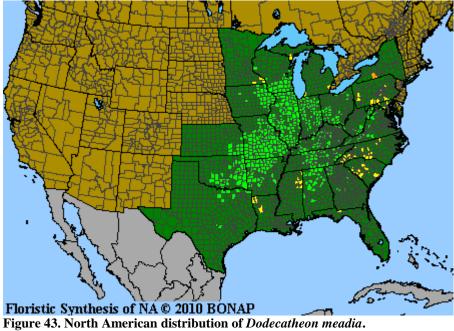
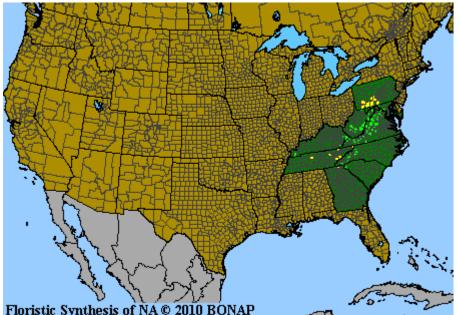


Figure 42. North American distribution of *Rhamnus lanceolata*, southern distribution with disjunct Midwestern & Appalachian populations.





Floristic Synthesis of NA © 2010 BONAP Figure 44. North American distribution of *Thalictrum coriaceum*, southern Appalachian mountain species with northern range limit in PA.

Prairie/Savannah with Eastern Mountain Disjunct Population

There are fourteen taxa whose ranges are centered in the Midwest, with an eastern population that is more or less disjunct. The habitats for these plants are mostly prairie, savannah, and woodland (*Euonymous atropurpureus* is unique in its preference for mesic floodplain forest habitats). In the east, these taxa may be found on limestone glades, grasslands, woodlands, and outcrops. The extent of these habitats is very limited, in small patches. Because the eastern populations are disjunct, they may have unique genetics and conservation significance. The degree of disjuncture varies, as does the size of the eastern population, but in the majority of cases, the taxa is considered rare in at least two eastern states. This group includes several of the rare taxa of the "xeric limestone prairies" extensively studied by Daniel Laughlin, although many of these species are also found in woodland or outcrop habitats in Pennsylvania.

Table 18. Calciphile taxa with prairie/savannah distributions and disjunct eastern mountain populations.

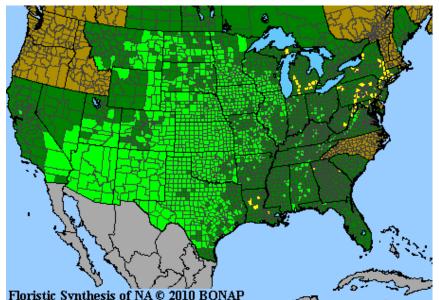
Bouteloua curtipendula	Onosmodium molle var. hispidissimum
Carex pellita	Ophioglossum engelmannii
Dichanthelium oligosanthes	Rhamnus lanceolata
Dodecatheon meadia	Ruellia humilis
Euonymous atropurpureus	Solidago rigida var. rigida
Melica nitens	Triosteum perfoliatum
Muhlenbergia sobolifera	Zanthoxylum americanum

Bouteloua curtipendula (Figure 45)is a good example of a species with a large western range and a much smaller, essentially disjunct population following the Appalachian Mountains in the east. The soils of the west tend to be alkaline because the limited rainfall does not leach them as rapidly. In the east, the species behaves as a calciphile and prefers open habitats, which may be because these conditions most closely mimic its western habitat, or it may be an example of out-of-range specialization in calcareous habitats. Laughlin proposed a mechanism for the establishment of the eastern disjunct population (Laughlin 2003a). *Onosmodium molle var. hispidissimum* is more scattered but follows a similar pattern, as does *Carex pellita* and *Dichanthelium oligosanthes* (except that its eastern populations follow the mountains less closely and are less contiguous; the species is likely under-documented due to identification difficulties).

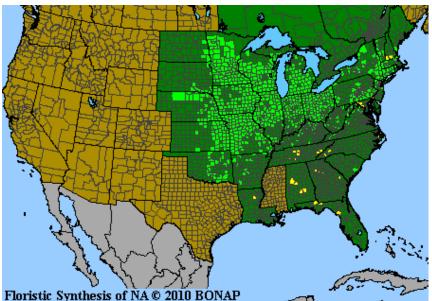
The ranges of the other species with this pattern do not extend as far west, usually ending in Missouri or eastern Kansas. These species tend towards savannah or dry woodland rather than prairie habitats. *Lithospermum canescens, Zanthoxylem americanum* (Figure 46), and *Triosteum perfoliatum* have very similar ranges that are more northern centered.

Muhlenbergia sobolifera (Figure 47) has a centrally situated range, and a less clear disjuncture between the eastern and Midwestern populations.

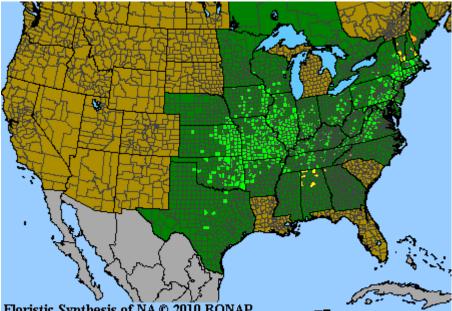
The remaining species in this group (*Ophioglossum engelmannii, Rhamnus lanceolata, Ruellia humilis* - Figure 48, *Melica nitens, and Dodecatheon meadia*) are both Midwest centered and have the northern edge of their range in Pennsylvania. Although the overall pattern is similar, degree of disjuncture between eastern and Midwestern population varies.



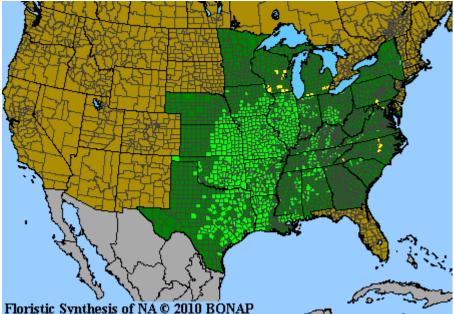
Floristic Synthesis of NA © 2010 BONAP Figure 45. North American distribution for *Bouteloua curtipendula*, prairie species with eastern disjunct population.



Floristic Synthesis of NA © 2010 BONAP Figure 46. North American distribution of *Zanthoxylum americanum*, a northern-centered Midwest / eastern disjunct distribution.



Floristic Synthesis of NA © 2010 BONAP Figure 47. North American range of Muhlenbergia sobolifera.



Floristic Synthesis of NA © 2010 BONAP Figure 48. North American distribution of *Ruellia humilis*, Midwest / eastern disjunct populations centered south of Pennsylvania.

Midwestern Forest Species

Twelve species have distributions centered on forested regions of the Midwest. Their habitat is rich, mesic forests, and most of them are calciphiles throughout their ranges. The requirement for mesic habitats likely creates the western bound of the range, while the requirement for calcareous soils may explain their limitation to Midwestern forests, where limestone soils are much more common than in eastern North America. In Pennsylvania, several of these species are more abundant westward and reach their eastern range limit within the state.

Table 19. Calcipinie taxa with Mildwestern forest distributions.				
Carex careyana	Hybanthus concolor			
Carex hitchcockiana	Hydrastis canadensis			
Carex oligocarpa	Jeffersonia diphylla			
Diplazium pycnocarpon	Trillium flexipes			
Euonymus atropurpureus	Trillium nivale			
Galium concinnum	Triosteum perfoliatum			

Table 19. Calciphile taxa with Midwestern forest distribution	ons.
---------------------------------------------------------------	------

Jeffersonia diphylla, Hydrastis canadensis, Hybanthus concolor, and Trillium flexipes all have very similar distributions. Figure 49 shows the distribution for *Jeffersonia diphylla*. *Carex careyana* (Figure 50) is a species of global concern, with a nearly identical range, but less densely populated distribution within the range. *Carex hitchcockiana* is another globally uncommon species that follows a similar pattern. *Trillium nivale* (Figure 51) has a smaller, more latitudinally compressed range, and clearly reaches its northern and eastern bound in western Pennsylvania. *Carex shortiana* (012) follows a similar pattern. *Diplazium pycnocarpon* (Figure 52) and *Carex oligocarpa* have somewhat broader distributions.

Euonymous atropurpurea and *Triosteum perfoliatum* (Figure 53) have distributions that are intermediate between the prairie disjunct and Midwest forest patterns, likely because these species have intermediate habitat requirements, occupying both rich forests and dry woodlands. *Euonymous atropurpurea* reaches farther west than the other species, while *Triosteum perfoliatum* reaches slightly further west and has a distinct constriction between Midwestern and eastern-mountain focused population centers, bridged narrowly across Ohio.

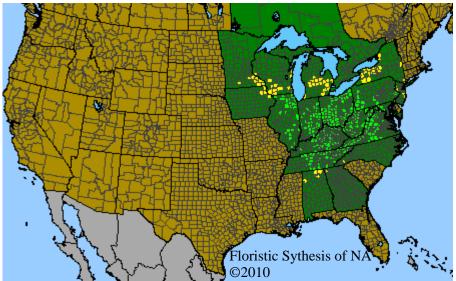
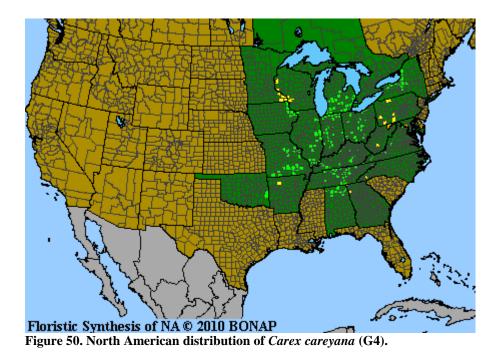
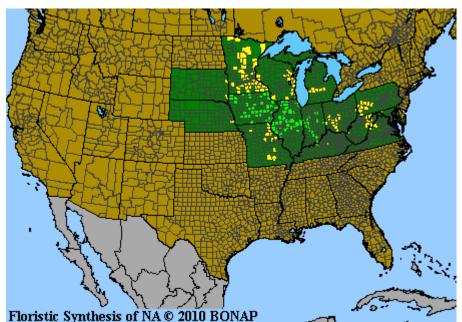
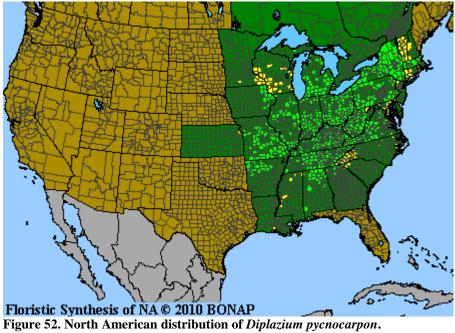


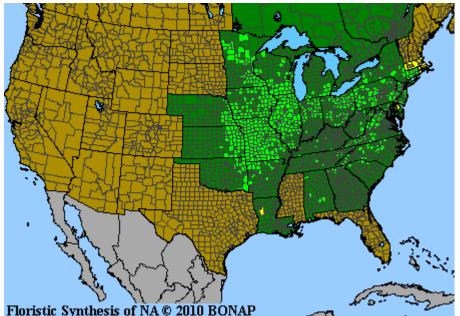
Figure 49. North American distribution of *Jeffersonia diphylla*, typical Midwestern forest species pattern.





Floristic Synthesis of NA © 2010 BONAP Figure 51. North American distribution of *Trillium nivale*, Midwestern forest species with eastern edge of range in PA.





Floristic Synthesis of NA © 2010 BONAP Figure 53. North American distribution of *Triosteum perfoliatum*, intermediate between Midwestern forest and prairie disjunct patterns.

Appalachian Mountain Species

Twelve species have their ranges centered on the Appalachian Mountains. Almost all of these species are centered on the southern Appalachians, and have the northern edge of their range in Pennsylvania. However, two species have ranges that extend further northwards; *Ranunculus allegheniensis* (Figure 54) and *Asplenium ruta-muraria* (Figure 55). This group includes most of the globally rare calciphile taxa that occur in Pennsylvania.

Table 20. Calciphile taxa with Appalachian Mountain distributions.

Arabis patens (G3) Asplenium resiliens (G5) Asplenium ruta-muraria var. cryptolepis (G5) Delphinium exaltatum (G3) Paxistima canbyi (G2) Prunus alleghaniensis (G4) Ranunculus allegheniensis (G4G5) Rhamnus lanceolata (G5) - Figure 42 Symphyotrichum lowrieanum (G3G5Q) Symphyotrichum phlogifolium (G5) Thalictrum coriaceum (G4) - Figure 44 Veratrum latifolium (G5)

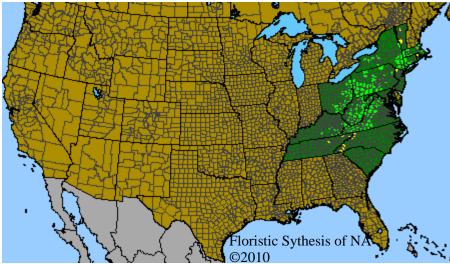


Figure 54. North American distribution of *Ranunculus allegheniensis*, mountain species centered northwards.

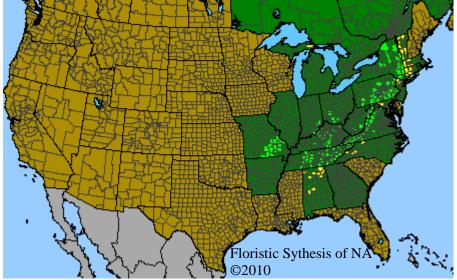


Figure 55. North American distribution of Asplenium ruta-muraria, Appalachian mountain species.

Great Lakes Shores Species

A final distribution pattern evident among a number of Pennsylvania calciphiles is a range that closely follows the shores of the Great Lakes. Great Lakes shores can include a variety of calcareous habitats. The only lakeshore habitat associated with the Great Lakes in Pennsylvania is the portion of Erie County that touches Lake Erie, so this group of plants has very limited habitat in Pennsylvania. These taxa are confined to Presque Isle and a few additional locations in the Lake Plain in Erie County.

Table 21. Calciphile taxa with Great Lakes Shore distributions.

Carex garberi Carex viridula Gentianopsis virgata Juncus alpinoarticulatus ssp. nodulosus Lathyrus japonicus var. glaber Shepherdia canadensis

Shepherdia canadensis (Figure 56) and *Lathyrus japonicus var. glaber* are relatively upland species of dune and sandy shore habitats, whose ranges closely follow the shores of the Great Lakes. *Carex garberi* is a wetland species that also has a very similar distribution tightly confined to the lake shore.

Juncus alpinoarticulatus (Figure 57), *Carex viridula*, and *Gentianopsis virgata* are species that are found extensively on lake shores and associated sandy wet habitats such as interdunal wetlands, but also found inland to some degree. In Pennsylvania they are only known from Presque Isle.

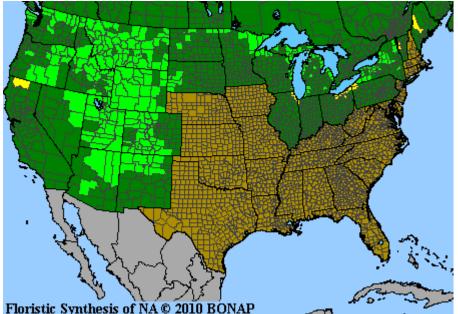
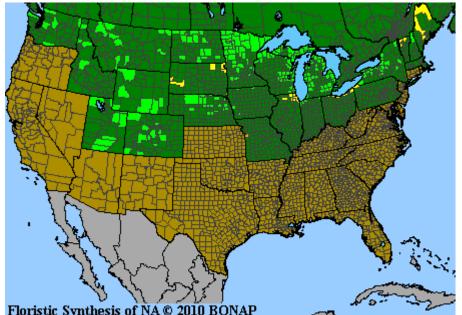


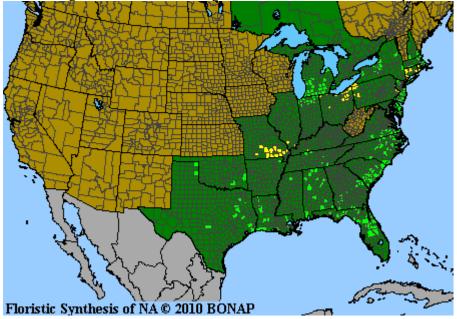
Figure 56. North American distribution of Shepherdia canadensis, a Great Lakes dune & shore specialist.



Floristic Synthesis of NA © 2010 BONAP Figure 57. North American distribution of *Juncus alpinoarticulatus*, species primarily of Great Lakes shores extending to some inland wetlands.

Coastal Plain – Great Lakes species

Carex alata and *Lathyrus japonicus* show the interesting pattern of two disjunct populations centered around the glaciated Great Lakes region and on the Atlantic coastal plain.



Habitat Analysis of Calciphile Taxa

In this section we assessed patterns in the habitat preferences of the calciphile portion of Pennsylvania's flora, in order to aid in targeting and prioritizing conservation efforts. The purpose of this analysis is to compare the ecology of habitat types and the ecology of the calciphile taxa that occupy them. With 206 calciphile taxa in the state, conservation efforts will be greatly simplified if it is possible to develop guidelines for management of habitats that benefit groups of taxa. For each taxon, we assessed the primary habitat type(s) it occupies, based on expert field experience, botanical references, and field data. We then examined the group of taxa found in each habitat type for patterns in conservatism, biogeography, number of calciphile taxa present exclusively in a single habitat type, and vulnerability to climate change.

Where possible, we considered habitat types at the specificity of the community types identified in section III. However, for many taxa sufficient data are not available to assess patterns at this level, so we also used a broader categorization of habitat types based on upland/wetland status and physiognomy.

We analyzed the conservatism of the calcareous flora and community types using Floristic Quality Assessment metrics, including coefficients of conservatism and site index values. Coefficients of conservatism rank the likelihood that a species is found exclusively in a high quality natural habitat. The Coefficients of Conservatism (C) applied in this study were developed by the Mid-Atlantic Floristic Quality Assessment Project (Chamberlain and Ingram 2012). Floristic Quality Assessment is a system for assessing the natural quality of sites based on the plants inhabiting the site using the concept of species "conservatism" (Swink and Wilhelm 1994). The C of a species is an estimate of the tolerance to disturbance as well as the degree of fidelity to specific habitat integrity (ibid).

Finally, we assess the vulnerability of calciphile taxa to climate change using NatureServe's Climate Change Vulnerability Assessment tool, and interpret these results in terms of habitat conservation needs.

Methods

Habitat Preference of Calciphile Taxa

We first rated all calciphile taxa (012, 002, and 022 diabase) using a broad habitat categorization based on upland/wetland and physiognomy. Because this project included field study of terrestrial sites we were able to examine the habitat preferences of terrestrial calciphile taxa in more depth than wetland taxa. Sufficient data were not available for all taxa to determine trends in taxon fidelity to the specificity of the community types identified in section III, so we simplified these types into "habitat types". The terrestrial habitat types match the community types except that all woodland types are combined, and all mesic forests are considered one habitat type.

Ratings are based on field experience and consultation of published literature, including flora habitat descriptions and U.S. Fish and Wildlife Service wetland codes. Taxa were assigned more than one category where appropriate. The following habitat categories were included: calcareous grasslands, woodlands, dry forests, mesic forests, mesic outcrops, rock specialists, wetlands, floodplains, aquatic, and great lakes shores.

The "rock specialist" category is used to indicate whether a species grows mainly or exclusively on rock outcroppings. "Fac-r" is assigned to taxa which are often but not exclusively found on rock outcroppings, while "obl" is assigned to species that only occur on rocks. This category was added because rock

outcroppings vary in size, and many rock specialists can be found on small rock piles in forested landscapes in addition to larger outcroppings.

For terrestrial taxa, we used plot data to refine the categorization, and to further assess habitat preferences based on presence/absence in plant community types (see Appendix 2 for more detail). We did not attempt to analyze patterns of occurrence in individual community types more specifically than the habitat categories identified above, because sample sizes were too small for most taxa.

Floristic Quality Assessment Index

The Mid-Atlantic Floristic Quality Assessment Project assigned C values for species for each ecoregion in which they occur (Chamberlain and Ingram 2012). For the purposes of this project, we averaged the regional C values, excluding the coastal plain, because Pennsylvania has almost no coastal plain habitat. In most cases the values were the same for each ecoregion (or differed only in the excluded coastal plain region), so there was no difference between the regional and averaged values.

Because the pH preference rankings for the flora were done using Pennsylvania Flora Project taxonomy, while the Mid-Atlantic Floristic Quality Assessment Project used the USDA Plants taxonomy, the two had to be rectified in order to match C values with pH preference values.

To assess the relative conservatism of the calciphile portion of the PA flora in comparison with other native species, we averaged the C values for all native calciphile species, and then for all native species.

We also calculated the mean C and C' values for the species lists from the plot data collected. Species lists were evaluated per plot rather than per site because the area surveyed varied widely at different sites; while I values have been shown to vary significantly depending on area, mean C values are less dependent on survey area (Matthews et al. 2005; Bourdaghs, Johnston, and Regal 2006).

FQI and mean C are intended to be used as an estimate of conservation value for sites (Swink and Wilhelm 1994). In order to determine whether mean C value can serve as a surrogate for the conservation value of sites specifically in regards to calcareous taxa, we calculated the number of calciphile taxa present in each plot, and the number of strict calciphile taxa (rated 002), and compared these to plot mean C value using regression analysis. If mean C and numbers of calciphile taxa, and mean C is a good summary metric for site conservation value for calcareous taxa. However, if mean C and number of calciphile taxa present are not correlated, mean C should not be used in isolation to estimate conservation value of calcareous sites.

FQI assessment methodology is sometimes used compare the conservation value of sites that have different and/or multiple community types present (Matthews et al. 2005; Miller and Wardrop 2006). Other authors have used FQI only to compare instances of the same community type at different sites (Nichols, Perry, and DeBerry 2006; Bourdaghs, Johnston, and Regal 2006). We tested whether mean C values for plots differed significantly for different communities, using ANOVA to compare whether variation in plot mean C values independently from community type, we also used ANOVA to compare mean C values and physiognomic categories. We also assessed whether community type was significantly correlated with variation in the number of calciphile and number of strict calciphile taxa, using ANOVA to determine whether variation is greater within or between plots grouped by community type. Almost all grassland, shrubland, or woodland plots were able to be assigned to a community type. However, most of the forest plots were not able to be classified, because our attempt at classification of mesic forests did not result in identification of distinct types. For the purpose of these analyses, an additional community type category was added to include the forest plots. "Forest" includes all forest plots with pH above 6.0 that were not able to be classified.

Climate Change Vulnerability Analysis

The Climate Change Vulnerability Index is a tool developed by NatureServe to assess the potential vulnerability of different species to the changes that are likely to occur in our climate as a result of increased levels of greenhouse gases in the atmosphere. The Index rates individual species using a scale of five categories, ranging from "somewhat decrease vulnerability" to "greatly increase vulnerability".

The CCVI rating is calculated using a scoring system that integrates a species' predicted exposure to climate change within an assessment area and three sets of factors associated with climate change sensitivity, each supported by published studies: 1) indirect exposure to climate change, 2) species-specific factors (including dispersal ability, temperature and precipitation sensitivity, physical habitat specificity, interspecific interactions, and genetic factors), and 3) documented response to climate change (Young et al. 2011).

We chose species for CCVI analysis whose ranges are centered north of Pennsylvania, and which were assigned high Coefficients of Conservatism. Conservative species may require specialized habitats, ecologically intact habitats, and/or have limited dispersal ability, and thus may have diminished capacity to respond to climate change.

An additional group of calcareous species were assessed by researchers at the Carnegies Museum, focusing on species in Bedford County. This group includes many species with southern distributions. The results are analyzed together.

Results & Discussion

Habitat Preference of Calcareous Taxa

Of a total of 204 calciphile taxa, 112 inhabit terrestrial habitats, 82 are wetland taxa, and 7 are aquatic (Figure 58, Table 22). *Appendix 2: Calciphile Taxa Habitat Preferences* lists the habitat preferences of all calciphile species. Wetlands support the largest number of taxa, and the vast majority of these occur exclusively in wetland habitat. There are 3 taxa that inhabit both terrestrial and wetland habitats. Floodplains (12 taxa) have very few exclusive taxa; 5 are also wetland taxa, while 5 also occupy a terrestrial habitat type., and 3 occur exclusively in floodplains. All aquatic taxa occur exclusively in aquatic habitats.

Most of the calciphile species of terrestrial habitats occupied more than one type of habitat, but a significant fraction (41%, 47 taxa) occupied only one habitat type (Figure 59). Woodlands provide habitat for by far the greatest number of taxa (77), followed by yellow oak forest (47) and mesic forest (39 taxa; Figure 58, Table 22). Almost as many taxa occur in woodlands as occur in wetlands, but a far lower proportion occur exclusively in woodland habitat. While all terrestrial habitat types have some species found exclusively in that type, grasslands (46%) and rock specialists (33%) have the highest fraction of exclusive taxa (Table 22, Figure 60). Because of the high number of taxa supported by woodlands, woodlands still host the highest overall number of exclusive taxa (16), even though only 22% of the taxa are exclusive. Woodlands frequently include rock outcroppings, and half of the taxa exclusive to the woodland type are rock specialists.

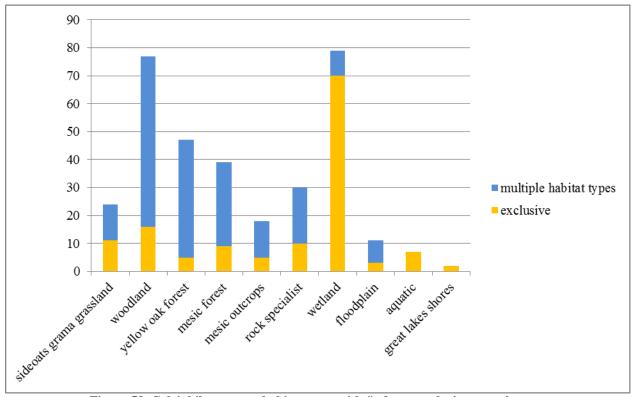


Figure 58. Calciphile taxa per habitat type, with # of taxa exclusive to each type.

Table 22. Hab	itat types of	calciping	e species.							
Habitat type	Calcareous	Wood-	Dry	Mesic	Mesic	Rock	Wetland	Flood	Aquatic	Great
	grassland	land	forest	forest	outcrops	specialist		plain		lakes
										shores
# taxa	24	77	47	39	18	30	79	12	7	2
Taxa only in habitat	11	16	5	9	5	10	70	3	7	2
%exclusive	46%	22%	11%	23%	28%	33%	89%	25%	100%	100%

Table 22. Habitat types of calciphile species.

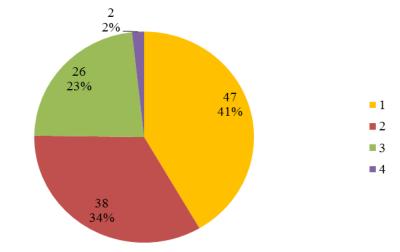


Figure 59. Number of habitat types occupied by terrestrial calciphile taxa.

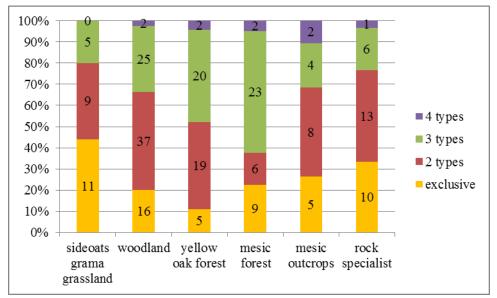


Figure 60. Habitat specificity of terrestrial calciphiles, by habitat type.

Floristic Quality Assessment

As a group, limestone species have a much higher average coefficient of conservatism than the Pennsylvania flora as a whole (Table 23). The taxa with the most habitat specificity have the highest C averages; exclusive calciphiles at 8.9, and calcium / diabase species at 7.2. Strong calciphile species are less distinct from the statewide average. The high C averages suggest that this group of taxa tends to require fairly intact natural habitats. Such habitats may experience and even require natural disturbances such as fire or grazing, but they are distinguished by not having experienced the kinds of major postsettlement anthropogenic disturbances that remove the seed bank, fundamentally alter soil structure, or otherwise remove such a large portion of the vegetation that it cannot recover close to its original species composition. This indicates that the large proportion of Pennsylvania's calcareous lands that have experienced disturbances such as soil tillage, surface mining, or residential/urban development may be permanently inaccessible to most calciphile species without restoration efforts.

While the average conservatism of all calciphile taxa has broad implications for the conservation of this group of plants, differences in conservatism were also observed between different types of habitats. These are best understood in the context of the ecological factors that shape these habitats.

The wetland taxa as a group are extremely conservative, with an average C of 9.0; the northern species are even more conservative, with an average C of 9.7.

Our field data show that calciphile taxa are not always a large proportion of the flora even at calcareous sites. Most of the field sites analyzed in this study were over limestone geology and with high pH soils, but the percentage of calciphiles in the flora ranged from 3% to 25%. The percentage of calciphile species at a site is positively correlated with the mean native C value for the site (r square = .23, F = .005). However, additional ecological factors are also important to understanding patterns in the number of calciphile species per site and in the mean C values for the site.

Analysis of the plot data shows that mean C and C' values are correlated with community type and with physiognomic type (Table 25, Table 26). The correlation is significant for both, but stronger for community type than for physiognomic type. Mesic outcrops have the highest mean C, while sideoats grama grasslands have the lowest. Total number of calciphile species and number of strict calciphile species (002) per plot are also significantly correlated with community type (Table 27, Table 28). Several other studies have also found that FQI indices vary by community type (Andreas, Mack, and McCormac 2004; Malik, Shinwari, and Waheed 2012; Rooney and Rodgers 2002).

However, the average numbers of calciphiles per community type does not increase with mean C. Figure 61 shows that different patterns are found across community types for mean C, total calciphile species, and strict calciphile species.

Plots taken at woodland and dry yellow oak forest community types had, on average, the highest numbers of calciphiles. These field results are consistent with the expert rating of calciphile species' habitat types, which suggested that woodland habitats host the highest number of PA's terrestrial calciphile species (Table 22).

Grasslands and unclassified forests have the lowest average number of calciphile species. Although the sample size for unclassified forests (27) was three times the size of any of the defined community types, the variation in mean C, total calciphile species, and strict calciphile species for plots in this group was comparable to or even lower than for the defined community types. Despite the variation in species composition, this broad group is fairly consistent in having medium-high C values, but very few calciphiles. The dry yellow oak forest group has similar mean C values, but a higher number of calciphiles.

In general, the community types found in more xeric settings had more calciphiles than those found in mesic settings (forests and mesic outcrops). There is a weakly positive correlation between hydrological regime category and soil moisture categories and total number of calciphiles, with the most xeric category averaging the highest number of calciphiles. However, xeric conditions as experienced by plants at sites are not summarized easily by a single variable; topographic position, aspect, soil texture, soil drainage, and physiognomy all interact. Soil moisture has been documented to influence pH and nutrient availability; although pH tends to increase with soil moisture, most of the nutrients that are typically limited in limestone soils are more available at higher soil moisture levels (Misra and Tyler 1999). It is possible that the nutrient limitations of calcareous soils are more extreme at dry sites, creating an environment that differentially favors species adapted to deal with those conditions, while at mesic sites, species with more general tolerances compete more successfully with calciphiles.

The average number of strict calciphile species per community type follows yet a different pattern than mean C or total calciphiles. Red oak woodlands host notably more strict calciphiles than any other type, even when variation is considered. This type is characterized by a wide range in canopy cover and bedrock; outcrops did not separate from woodlands and were lumped into a single type. Yellow oak woodlands have the next highest average, followed by yellow oak forest and mesic outcrops. Mesic outcrops have relatively few total calciphiles, but a relatively high number of strict calciphiles. The southwestern yellow oak woodland type averaged relatively few strict calciphiles, even though those sites had comparable average of total calciphiles to the other woodland types.

As a group, grasslands have the lowest mean C value, while mesic outcrops have the highest mean C value; forests and woodlands fall in between. Grasslands are the most disturbance-dependent of the community types, while mesic outcrops are likely to be disturbance intolerant, dependent on specific microclimate conditions maintained in part by forest canopy. Furthermore, many sites with grasslands present also had a high percentage of non-native species in the flora; this may be in part because the open physiognomy facilitates establishment of exotic species, and in part because grasslands tend to be located in highly fragmented landscapes. Mesic outcrops had a low percentage of invasive species; invasive establishment may be limited by full forest canopy and the more intact landscape setting of some of these sites.

The mean C values for community types indicate both the degree of conservatism of the habitat, and its vulnerability to disturbance. Community averages have important implications for appropriate conservation management for that habitat type. While grasslands may depend on disturbance, mesic outcrops may be very sensitive to disturbance.

If mean C values are used in assessing conservation value for sites, it is best to do so within groups of similar habitats. Although grasslands have low mean C values, they clearly have high conservation value because of their unique floras including species with geographic disjunct populations. Furthermore, mean C values should be only one of several metrics used to assess conservation value, depending on conservation goals. In the case of the terrestrial calcareous sites evaluated in this study, the habitat value for calciphile species appears to be uncorrelated with mean C and dependent on environmental factors.

Table 25. Average coefficients of conservatism for care	iplines compared to an I A native species.
Category	Average C value
Exclusive calciphiles (002)	8.9
Strong calciphiles (012)	6.7
Calcium and diabase species (022 d)	7.2
All calciphile categories	8.1
All native species in PA	6.3

Table 23. Average coefficients of conservatism for calciphiles compared to all PA native species.

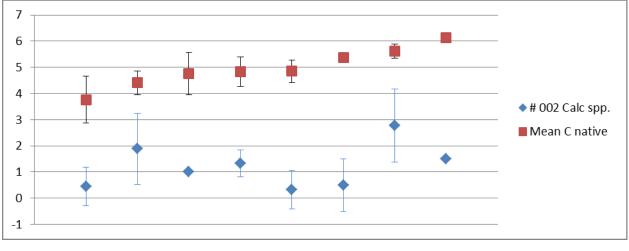
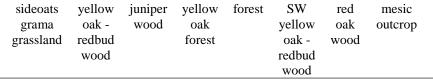
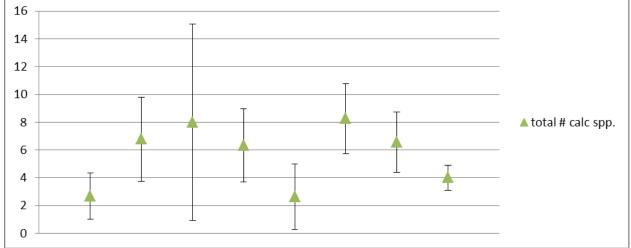


Figure 61. Mean C, # exclusive calciphiles, and total # of calciphiles per plot, averaged for each community type (with standard deviation error bars).





Community Type	Count	Average	Variance
Juniper woodland	2	4.8	0.659
mesic outcrop	6	6.1	0.615
red oak woodland	9	5.6	0.073
sideoats grama grassland	9	3.8	0.808
SW yellow oak - redbud woodland	4	5.4	0.037
yellow oak forest	6	4.4	0.308
yellow oak - redbud woodland	9	4.8	0.212

Table 24. Single-factor ANOVA results for mean C and plot community type.

ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	27.9	6	4.65	12.51	9.76452E-08	2.35
Within Groups	14.1	38	0.37			
Total	42.0	44				

Table 25. Single factor ANOVA results for mean C' and plot community type.

Community Type	Count	Average	Variance
Juniper woodland	2	3.8	1.125
mesic outcrop	6	5.9	0.657
red oak woodland	9	5.3	0.277
sideoats grama grassland	9	3.8	0.808
SW yellow oak - redbud woodland	4	5.1	0.018
yellow oak forest	9	4.8	0.212
yellow oak - redbud woodland	6	4.4	0.308

ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	23.12	6	3.854	8.94	0.000004	2.35
Within Groups	16.39	38	0.431			
Total	39.51	44				

Physiognomy	Count	Average	Variance
sparse	11	5.9	0.43
herb	9	4.6	0.50
shrub	2	5.6	0.01
woodland	16	5.3	0.17
forest	7	5.0	0.11

Table 26. Single factor ANOVA results for mean C and plot physiognomy.

ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	9.5	4	2.36	8.25	0.00006	2.61
Within Groups	11.5	40	0.29			
Total	20.9	44				

Table 27. Single factor ANOVA results for community type and # calciphiles per plot.

Groups	Count	Average	Variance	Stdev	
Juniper woodland	2	8.0	50.0	7.1	
mesic outcrop	6	4.0	0.8	0.9	
red oak woodland	9	6.6	4.8	2.2	
sideoats grama grassland	9	2.7	2.8	1.7	
SW yellow oak - redbud woodland	4	8.3	6.3	2.5	
yellow oak forest	9	6.8	9.2	3.0	
yellow oak - redbud woodland	6	6.3	7.1	2.7	
forest	27	2.6	5.5	2.3	

ANOVA

SS	df	MS	F	P-value	F crit
311.8	7.0	44.5	7.4	0.000002	2.2
384.2	64.0	6.0			
695.9	71.0				
	311.8 384.2	311.8 7.0 384.2 64.0	311.8 7.0 44.5 384.2 64.0 6.0	311.8 7.0 44.5 7.4 384.2 64.0 6.0	311.8 7.0 44.5 7.4 0.000002 384.2 64.0 6.0

Groups	Count	Average	Variance	Stdev	
juniper woodland	2	1.0	0.0	0.0	
mesic outcrop	6	1.5	0.7	0.8	
red oak woodland	9	2.8	1.9	1.4	
sideoats grama grassland	9	0.4	0.5	0.7	
SW yellow oak - redbud woodland	4	0.5	1.0	1.0	
yellow oak - redbud woodland	9	1.9	1.9	1.4	
yellow oak forest	6	1.3	0.3	0.5	
forest	27	0.3	0.5	0.7	
ANOVA					
Source of Variation	SS	df	MS	F	P-value
Between Groups	53.3	7.0	7.6	8.62	0.0000002
Within Groups	56.5	64.0	0.9		
Total	109.8	71			

F crit 2.16

Table 28. Single factor ANOVA results for strict calciphiles (002) and community type.

Climate Change Vulnerability Assessment

All calcareous wetland species with northern distributions that were assessed through the Climate Change Vulnerability Assessment tool were found to be "Extremely Vulnerable" or "Highly Vulnerable" (Table 29). Several factors were influential in these ratings: these species have limited available habitat at present because calcareous wetlands are uncommon on the landscape; they are sensitive to changes in temperature as well as hydrological regimes, both of which are likely to result from anthropogenic climate change; and many also had limited dispersal capacity.

Terrestrial calciphiles display much more variation in biogeographic patterns than do wetland calciphiles, which almost all have northern distributions. As with wetland taxa, the vulnerability of terrestrial taxa to climate change appears to depend primarily on whether the taxon is at the southern edge of its range, but dispersal capacity and environmental specificity are also important.

We assessed several upland calciphile taxa with northern distributions. The slender cliff-brake (*Cryptogramma stelleri*), which reaches the southern edge of its range in central Pennsylvania, was rated extremely vulnerable. This species has a very limited dispersal capacity (Peck, Peck, and Farrar 1990).

Several of these species show contraction of their range in the state over the past century; a common pattern is failure to relocate records from the eastern or central parts of the state, while some populations persist in the northwestern part of the state (see Appendix 3: Calcareous Wetland Taxa With Range Contractions, p. 150). It is not within the scope of this study to definitively assess the cause of these range contractions, which may have resulted from land use changes or site degradation as well as from climate changes.

Ricegrass (*Piptatherum racemosum*) was rated moderately vulnerable. This species is moderately widespread in calcareous portions of Pennsylvania and reaches the southern edge of its range in West Virginia, where it has a noticeable affinity for cooler microclimates. Ebony sedge (*Carex eburnea*) and snowberry (*Symphoricarpos albus var. albus*), species that are near the southern edge of their range in Pennsylvania and sparse in the state, although they do extend into West Virginia, were also rated moderately vulnerable. James' sedge (*Carex jamesii*), a species with a Midwestern forest distribution that reaches its northern limit in New York, was rated moderately vulnerable as well. All of these species had common traits of some level of dispersal limitation, and a state distribution with a slightly smaller than normal range of variation in historical precipitation.

Most upland calciphiles that were not at the southern edge of their range were rated "presumed stable" or "increase likely" (*Galium boreale*, Table 29; *Arabis patens, Bouteloua curtipendula, Delphinium exaltatum, Liatris scariosa, Amelanchier sanguinea, Thalictrum coriaceum, Paxistima canbyi* - Morton and Speedy 2012). The exceptions to this pattern were all species that were judged to be extremely limited in dispersal capacity (*Lithospermum canescens, Euphorbia purpurea;* Morton and Speedy 2012).

These results suggest that the vulnerability of northern upland species in Pennsylvania depends upon the ecology of the species, and how close to the edge of the range Pennsylvania's populations are. Species with limited dispersal capability and more specialized habitats appear to be vulnerable to the impacts of climate change even if they are not near the edge of their range.

Most of the terrestrial calciphiles with northern distributions are found in woodlands (8 taxa of 11 total). Nine of these eleven taxa are rock specialists. However, most woodland calciphiles do not have northern distributions; southern distributions are more common. While calcareous wetland habitat specialists are almost all affiliated with northern distributions, terrestrial habitat types host calciphile taxa with a mixture of biogeographic patterns. For terrestrial calciphiles, conservation measures related to climate change are best oriented around taxa rather than habitat type.

State Rank	Scientific Name	calc. 12	calc. 22	calc 002	dry outcrop	wet outcrop	open herb/ shrub	dry forest	mesic forest	Wood land	Wet land	CoC value	CCVI rank	confidence
	WETLAND SPECIES													
S 1	Carex bebbii			1							X	10	Extremely vulnerable	Very High
S2	Carex flava			1							X	10	Extremely vulnerable	Very High
SNR	Carex interior			1							X	10	Highly vulnerable	Very High
S2	Carex prairea			1							X	10	Extremely vulnerable	Very High
S 1	Carex pseudocyperus	1									X	10	Highly vulnerable	Very High
S 1	Carex schweinitzii			1							X	10	Extremely vulnerable	Very High
S1	Conioselinum chinense			1							x	10	Extremely vulnerable	low
S2	Eleocharis elliptica	1									X	10	Extremely vulnerable	Very High
S 1	Equisetum variegatum			1							х	10	Extremely vulnerable	Very High
S2	Eriophorum viridicarnatum			1							x	10	Extremely vulnerable	Very High
S1	Galium labradoricum			1							х	10	Extremely vulnerable	Very High
SNR	Geum rivale			1							x	10	Extremely vulnerable	Very High
S 1	Lobelia kalmii			1							X	10	Highly vulnerable	Very High
S 1	Malaxis monophyllos var. brachypoda			1							X	10	Extremely vulnerable	Very High

Table 29. Climate Change Vulnerability Index results for selected calciphile species in PA/

State Rank	Scientific Name	calc. 12	calc. 22	calc 002	dry outcrop	wet outcrop	open herb/ shrub	dry forest	mesic forest	Wood land	Wet land	CoC value	CCVI rank	confidence
S4	Mitella nuda			1							х	10	Extremely vulnerable	Very High
S 1	Platanthera dilatata var. dilatata			1							X	10	Extremely vulnerable	Very High
S2	Ribes triste			1							X	10	Extremely vulnerable	Very High
S 1	Symphyotrichum boreale			1							X	10	Highly vulnerable	Very High
	UPLAND SPECIES													
S 1	Carex eburnea				X							9	moderately vulnerable	Very High
S 4	Carex jamesii		1					X	X			8	moderately vulnerable	Very High
S 1	Cryptogramma stelleri			1		X						10	Extremely vulnerable	Very High
SNR	Galium boreale		1					X				8	not vulnerable	Very High
S5	Piptatherum racemosum	1						X	X			9	moderately vulnerable	Very High
S2S4	Symphoricarpos albus var. albus						1			x		8	moderately vulnerable	Very High

Summary of Conservation Significance

Analysis of the pH categorization for Pennsylvania's vascular flora (Section I), shows that calcareous habitats harbor a disproportionately large share of the state's overall native vascular plant biodiversity. While calcareous bedrock underlies only 8% of the state's land area, and an even smaller fraction of this area still contains viable habitat, a third of Pennsylvania's extant native vascular plant taxa utilize calcareous habitat. Ten percent, 197 taxa, are habitat specialists that are mainly or only found in calcareous habitat. Furthermore, most (57%) of these are rare in the state (Table 2). There 31 globally rare calciphile taxa (ranked G2-G4G5). Twenty-three percent of all rare vascular plant taxa in the state are calciphiles.

For many of the state's calciphile taxa, the populations found in Pennsylvania are at the edge of their range, or are disjunct from the major portion of the range. This includes northern species reaching the southern edge of their range, southern and Appalachian mountain species reaching the northern edge of their range, and prairie/Midwestern species with disjunct eastern populations. These disjunct and edge of range populations are considered to have particular conservation significance, even when the species itself is not rare at the state or global level. Because these populations exist in different environmental conditions than the major portion of the range, they may harbor genetic differences as well. If climate change scenarios continue as predicted, genetically unique populations may be important to the taxon's ability to adapt to changing conditions.

Three-quarters of Pennsylvania's calcareous wetland species are rare in the state. This habitat type is also extremely limited in extent. Furthermore, most calcareous wetland species have northerly distributions and are at the southern edge of their range in Pennsylvania. Calcareous wetlands are the exclusive habitat of a significant portion of the state's vascular plant biodiversity: 79 taxa that make up 4% of all native taxa found in PA.

Terrestrial calcareous habitats also harbor biodiversity significance disproportionate to their size. They host a large number of rare taxa, many of which are additionally significant because they are edge-of-range populations. For each habitat type identified in the report, there is a group of calciphile taxa that are found exclusively on that type. Woodlands harbor the greatest number of calciphile taxa. Grasslands host a group of prairie taxa whose Pennsylvania populations are disjunct from the major portion of the range; many of these taxa are found only in this habitat type.

Calcareous habitats of all types have been greatly reduced due to land use changes; the capacity to support the calciphile component of plant biodiversity in the state rests with the small fraction of habitat remaining in natural condition. Individual sites are valuable for the taxa and communities they support, and also for their place in a geographic network that ideally supports gene flow between sites and healthy metapopulations of calciphile taxa. Because at the present time calcareous habitats mostly exist as small and isolated fragments, it is likely this network is effectively discontiguous for many taxa. If climate change proceeds, this geographic network is also the landscape that species taxa must navigate if they must to shift their range in order to find environmentally suitable conditions.

Conservation Needs of Calcareous Vascular Plants and Their Habitats

This section synthesizes the results of the various sections of this report to address the overall conservation needs of Pennsylvania's calcareous flora and plant communities. We begin with discussion of conservation issues of general relevance, and then we address the specific conservation needs of the major calcareous habitat types.

Habitat Isolation and Fragmentation

For both wetlands and uplands, most of the calcareous habitat remaining in the state occurs in isolated small patches. This situation has serious conservation implications, because habitat fragmentation is correlated with strongly negative effects on genetic diversity and reproductive success in plants (Aguilar et al. 2008; Aguilar et al. 2006). If a species does not have a mechanism for long-distance dispersal, populations in widely separated habitats are essentially isolated. Gene flow does not occur between populations, and over time small populations can develop inbreeding effects; if this happens in many populations, the overall fitness of the species is reduced. Furthermore, isolated small populations are vulnerable to extinction from chance events such as a tornado or other large disturbance.

For some species, their specific habitat requirements and their low capacity for dispersal are the most likely causes of their present rarity. The calciphile fern slender cliffbrake (*Cryptogramma stelleri*) requires cool, moist calcareous rock faces, an uncommon habitat, and has extremely low ability for long-distance dispersal because it is heterosporous (requiring two spores to create a new individual) and its spores have low viability (Peck, Peck, and Farrar 1990). Even in a pristine landscape, this species would likely be rare. However, for many other species, it is almost certain that human modification of the landscape has reduced the contiguity of habitat and the ability of species to traverse the landscape. Conversion of matrix forest habitat to other land uses reduces the mobility of animal dispersal agents and pollinators, which not only reduces plant species' ability to migrate between patches, but over time leads to diminished reproductive success within a population (Aguilar et al. 2006). The effects of dispersal limitation on isolated habitats can already been seen in the lack of regeneration of many animal-dispersed species after disturbances (Honnay et al. 2005; Matlack 1994).

Small size of habitat patches can present additional problems for some species. In general, the long-term viability of forest species in isolated patches of 100 acres or smaller is very low (S. M. Pearson, Smith, and Turner 1998). Species are vulnerable to habitat degradation from edge effects, including altered light and temperature levels, and enhanced ability of invasive species to colonize (Honnay et al. 2005). While some types of calcareous habitats naturally occur in small patches, such as outcrops or woodlands on steep slopes, these habitats have historically been embedded in natural forest cover, which provides some safeguard against edge effects. At present, the impacts of small patch size on long-term viability are of great concern to Pennsylvania's calcareous habitats, as over 50% of the remaining forest cover on calcareous geology occurs in fragments of less than 100 acres (Table 24).

Because many forest species are long-lived perennials or clonal species, negative effects of habitat fragmentation on species diversity may be delayed by decades; researchers have coined the term "extinction debt" to describe this phenomenon (Honnay et al. 2005). Over the long-term, species of calcareous habitats may face a serious crisis in viability if landscape and habitat contiguity is not restored.

The GIS analysis in Section III demonstrates that a large proportion of the state's terrestrial limestone habitat has been converted to other land uses, and provides an estimate in acres of how much remains in each physiographic province. The actual amount of natural habitat available for most terrestrial calciphile

species is almost certainly lower, as this estimate cannot incorporate habitat quality factors such as past disturbance, age of forest stand, or presence of invasive species, and some portion of the habitat in this estimate will have been rendered unsuitable due to these factors.

The species and community habitat models further demonstrate that for individual calciphiles, many of which have habitat requirements with a more specific set of environmental conditions that the general estimate described above, the available habitat in the state is extremely limited in area. This underscores the importance of known high-quality sites.

There are significant geographical differences across the state in the density, distribution, and condition of calcareous habitats. These should be considered when setting conservation goals for species and for regions.

Over half of all locations for rare calcareous wetland plant taxa occur in the glaciated northwestern part of the state. In most of Pennsylvania, calcareous wetlands are relatively few and scattered, and should be considered particularly vulnerable to effects of fragmentation and isolation.

For upland habitats, the southwestern (Pittsburgh Low Plateau / Waynesburg Hills) and Ridge and Valley regions have the largest amount of remaining calcareous habitat. These are the only regions with any remaining habitat 500 acres or greater in size (Figure 23, pg. 46). It should also be noted that the southwestern region and the Ridge and Valley are not entirely equivalent in terms of the habitat they provide because of regional variations in the flora; there are many taxa for which one or the other of these regions should be considered the only available habitat in the state. The habitats in these regions with good quality landscape context should be protection priorities. In the Piedmont and the Great Valley portion of the Ridge and Valley, the only remaining calcareous habitat occurs in small patches; the long-term viability of the diversity found in these patches may depend on restoration of habitat contiguity and migration potential.

Regionally, there is a substantial north-south gap between Pennsylvania's Ridge and Valley and New York's lake region calcareous areas. Populations of northern species in Pennsylvania may not be able to move across this gap if climate change renders their present locations unsuitable. In a species like *Symphoricarpos albus var. albus* (Figure 39, pg. 71), where the Pennsylvania populations are near the southern edge of the range, if the habitat becomes unsuitable and the plants cannot migrate across the large gap between the next suitable habitat to the north, the genetic material in the Pennsylvania populations may be lost to extinction.

Land Protection

Calcareous habitats are disproportionately lacking from Pennsylvania's protected land system. Although 8% of the state's land area is calcareous geology and 9% is moderately calcareous geology, less than 1% of all protected lands in the state are on calcareous geology, and only 7% are on moderately calcareous geology. While other minority geology categories in the state are proportionately represented in protected lands, calcareous geology is very much underrepresented in protected lands (Table 11, p 64).

Fewer than half of the known calcareous wetland sites in Pennsylvania are on protected lands (Table 12, p 65). The glaciated northwestern region has the most sites, and also has a relatively high proportion of protected sites. Within the lakeplain area (the Central Lowlands physiographic province), however, only a small fraction of the numerous sites in this small region are protected (Figure 35). The Ridge and Valley physiographic province also has a significant number of calcareous wetlands, but a lower proportion of these are protected, only 15 of 74.

A large majority of the state's remaining calcareous habitat area is currently in private ownership with unknown protection status. Protection for these habitats may involve working with landowners to develop conservation easements or conservation management plans, or pursuing transfer of ownership to a conservation-oriented public or private agency.

In general, education efforts are needed to raise awareness about the significance of calcareous habitats to the state's biodiversity. Outreach to landowners of the state's remaining significant calcareous sites is important to raise awareness of the biodiversity elements present on these properties and its larger significance to regional conservation. Conservation of calcareous habitats should be a focus of land protection activities by state and private conservation agencies, planners and development professionals, and private landowners.

Conservation efforts should focus on the relatively few remaining sites that are in good condition and are found within a matrix of predominately natural landscape, especially where a high proportion of the natural landscape context occurs on calcareous bedrock. For uplands, these sites occur in the Ridge and Valley and Pittsburgh Low Plateau regions; for wetlands, the Northwest contains the most pristine sites. Within regions where such sites no longer exist, protection should focus on highly diverse sites and those that include particularly unique plants or communities, and include efforts to improve prospects for long-term ecological viability by restoring habitat quality, as well as improving connection with other natural landscapes.

Invasive species

Certain invasive species have been documented to be especially successful in terrestrial calcareous habitats (Silveri, Dunwiddie, and Michaels 2001; Forrest Meekins and McCarthy 2001). Furthermore, several of the rare terrestrial calcareous community types have relatively open canopies, which enhances the ability of invasive species to colonize. This problem is shared by wetland habitats with herbaceous physiognomy. Among the sites surveyed for this study, several provide examples of the potential of calcareous habitats to be severely degraded by invasive species. Many sites, especially woodland sites, currently host a diverse native flora but also have small populations of invasive species, which may be the beginning stages of larger-scale invasions that will displace native flora. Sites in Eastern Pennsylvania, such as Williamson Park and Dale's Ridge, have extremely extensive cover of invasive species, with quality habitat for native species remaining only in small patches. Many invasive species established first in the eastern part of the state and have been spreading west; similar problems are likely to develop in time at central and western sites that presently have lower populations of invasives.

Furthermore, invasive species pose a serious challenge to regeneration of calcareous communities. Centre County's Spring Creek Valley is a large area including a variety of terrestrial calcareous habitats that has been studied extensively. A PNHP study including community mapping, completed in 2006, showed that areas which regenerated naturally before the 1960s developed into high-quality natural communities, while areas which have regenerated since then contain thickets of invasive species (McPherson and Bier 2006). These include some previously farmed areas, but also many slopes which were cleared but never tilled. Even in a landscape where interspersed native plant communities provided seed source for native species, the path of natural community recovery from disturbance before the introduction of invasive species such as oriental bittersweet, Morrow's honeysuckle, and multiflora rose was dramatically different than the results observed after these species have become widely established in the region. Although this is a single case study, the problem is likely applicable in many regions where invasive species have now become pervasively established. Restoration of calcareous communities is

clearly necessary to remediate the problems that habitat fragmentation poses to long-term viability of existing calcareous communities, but techniques must be developed to surmount the challenge of invasive species.

Climate Change

As climate change proceeds, the geographical distribution of calcareous habitats in Pennsylvania and surrounding regions poses a problem for the ability of taxa to migrate across the landscape to suitable habitat. For terrestrial taxa, most of Pennsylvania's major calcareous regions occur in the southern half of the state, with adjacent calcareous regions to the south, but large distances between the next major calcareous region to the north (regions with northern terminus in Pennsylvania are the Waynesburg Hills, the Allegheny Mountain Sections of the Appalachian Plateaus Province, and the Appalachian Mountain Section of the Ridge and Valley Province). For wetland taxa, the populations in the central and eastern portion of the state may be especially vulnerable, because the climate in these regions is warmer than the glaciated northwest ("USDA Plant Hardiness Zone Map" 2012), and because the calcareous wetlands in these regions are geographically isolated by large distances from the next available habitats northwards. Furthermore, water-dispersed taxa may be limited in their ability to migrate northwards because almost all of Pennsylvania's calcareous wetlands are situated in south-flowing watersheds.

If climatic zones shift northwards, we may also expect migration of new species into Pennsylvania's calcareous habitats. Invasive species now concentrated in the south, such as kudzu (*Pueraria lobata*), empress tree (*Paulownia tomentosa*), and others, may increase in our area. Some species migrate easily, dispersed by birds or wind, but others move much more slowly. Furthermore, a species' ability to migrate depends not only on how fast and far it can disperse, but on whether it can disperse to habitat suitable for successful establishment. Because Pennsylvania's calcareous flora is quite conservative on average, especially the wetland taxa, many taxa have limited dispersal ability and/or require specific habitat conditions to establish; for these taxa, migration is not a naturally fast process. For taxa that naturally move slowly and require specific habitats that are uncommon or widely spaced in the landscape, such as calcareous wetlands, woodlands, or outcrops, migration may not even be possible. If climate change renders their habitat unsuitable more quickly than they can migrate, populations will go extinct and their genetic material will be lost.

Furthermore, the other threats that calcareous ecosystems are experiencing simultaneously, such as small patch size, fragmentation, and invasive species, may lower the resiliency of these systems to the impacts of climate change.

Wetlands

Forty percent (79 taxa) of all calciphiles are wetland species (Table 22, Figure 58). There is little overlap between species of terrestrial and wetland habitats, with only three taxa found in both. Sixty-eight percent (41 of 60) of the wetland taxa have northerly distributions, with Pennsylvania at or near the southern edge of their range. Pennsylvania is situated between northern and Midwestern regions where calcareous wetlands are more common; the predominance of northern species in our calcareous flora, however, suggests that our calcareous wetlands are primarily northern-influenced habitats. Most calcareous wetlands are at low-lying topographic positions and fed by groundwater seepage, which may create local conditions with a cool microclimate where northern species can survive.

The wetland taxa as a group are extremely conservative, with an average C of 9.0; the northern species are even more conservative, with an average C of 9.7. All calcareous wetland species with northern distributions that were assessed through the Climate Change Vulnerability Assessment tool were found to be "Extremely Vulnerable" or "Highly Vulnerable" (Table 29). Several factors were influential in these ratings: these species have limited available habitat at present because calcareous wetlands are uncommon on the landscape; they are sensitive to changes in temperature as well as hydrological regimes, both of which are likely to result from anthropogenic climate change; and many also had limited dispersal capacity.

Among the northern wetland calciphile taxa, half appear to be calciphiles throughout their range, while 1/3-1/2 appear to occupy a broader span of habitats in regions more central within their geographic range (Table 15). Although these data are based on qualitative descriptions in published manuals and field experience, rather than empirical testing, they suggest that some species have greater habitat specialization at the edge of their range. This may result from competition, environmental specialization, or both. The taxa may be specialized to function better at higher pH, and in marginal environmental conditions are able to survive only at optimal pH conditions. Marginal environmental conditions may also put these taxa at competitive disadvantage, and because few species are adapted to function well in high pH environments, these are the only settings in which they remain competitive. Because edge-of-range populations inhabit environmental conditions distinct from the majority of the range, these populations may also be genetically distinct and therefore of particular conservation value.

Calcareous wetlands are of high value to biodiversity because they are the exclusive habitat for a large number of rare taxa, some of which may also be genetically unique. These habitats are also highly sensitive, because they exist in a narrow environmental setting, and the calciphile taxa are highly conservative. Some calcareous wetland habitats are also threatened by the lack of historically present disturbances, and by alterations in hydrological regime.

The term "fen" is used to describe wetlands fed by calcareous groundwater, often with peat accumulation. They often include substantial open herbaceous portions. This type of wetland, considered broadly, is the single habitat type that hosts the largest number of Pennsylvania's calciphile taxa. Fens may require active management to maintain open herbaceous areas. Recent research suggests that fens in Europe and in North America have been maintained by traditional agricultural processes such as grazing and mowing, and are now in decline because they are either abandoned (in which case they succeed to forest) or agricultural practices have intensified such that they no longer support biodiversity (Diggelen et al. 2006; Middleton, Holsten, and Van Diggelen 2006). Mowing, low-intensity grazing, and burning have all been used to mimic the past disturbance regime and maintain herbaceous diversity in fens.

However, relatively little work has been done to date to develop best management practices for fens in our region. A recent study of the globally rare species American globeflower (*Trollius laxus*), whose limited global range includes Pennsylvania, documents the importance of active management to the species' persistence, but also the complexity of successful management and the importance of evaluating the impacts of management on individual conservation targets (Scanga and Leopold 2010; Scanga and Leopold 2012). The study found that the globeflower requires conditions of medium- to high-light but low competition; it therefore responded best to the creation of small canopy gaps in areas with high water levels. Larger canopy gaps or gaps with lower water levels facilitated dense herbaceous growth that outcrowded the globeflower, while shaded conditions created low competition but also caused the plant to decline due to lack of light. More such work is needed to test different methods of management and their impacts on calcareous wetland taxa in our region.

Calcareous wetland communities are also threatened by land use activities in surrounding areas that alter the hydrological flows feeding the wetland, such as groundwater abstraction, drainage, and groundwater irrigation. Even when these activities occur at significant distances from the fen, the wetland can be impacted (Diggelen et al. 2006). Compared to other wetland types, fens are especially sensitive to hydrological alteration, because they depend not only on the total amount of water but on the nutrient and mineral inputs. Changes may not be observable in the water table, but if groundwater is being removed from the system, surface water becomes relatively more important, and this can lead to acidification (Wassen et al. 1996; Grootjans et al. 2006). The process can take several decades (Diggelen, Molenaar, and Kooijman 2009; Hoek and Sỳkora 2006).

When the water table is lowered, nutrient balances can change in the wetland, including increased nitrogen mineralization and shifts in which nutrients are limiting to plants (Wassen and Olde Venterink 2006; Higgins, Colleran, and Raine 2006; Belle et al. 2006). This leads to changes in the wetland's plant community, such as increased productivity and shifts in species dominance (Kotowski et al. 2009).

As in the case of active management, research in other regions suggests this threat may be relevant to our calcareous wetland ecosystems, but little research has been done locally. Most of the regions in Pennsylvania where calcareous wetlands occur (the glaciated Northwest, the valleys of the Ridge and Valley) have also been extensively developed for agriculture, and drainage modifications are common, especially in the glaciated Northwest. Few studies have been conducted on the hydrology of our wetland habitats; it is likely that at many sites, alterations have taken place from historical conditions, but at present there is little documentation of the extent of such modifications or the impact on plant communities. ("USDA Plant Hardiness Zone Map" 2012)

Climate change is also likely to impact hydrological regimes at these sites.

Grasslands

A substantial portion of Pennsylvania's terrestrial calciphile species depend on open grassland, shrubland, or woodland habitats. In Pennsylvania's temperate, high-rainfall climate, these habitats require periodic disturbance, especially fire, in order to persist. In the absence of disturbance, open habitats succeed to forest. Many grassland or woodland species require high light levels to persist or reproduce. Some require mineral soil to germinate (Vickery 2002). As canopy cover and leaf litter increases, these species decline and eventually are lost from the habitat.

Grassland habitats are especially threatened by succession, as has been documented by other authors already (R. Latham and Thorne 2007; Laughlin 2004a; Baskin and Baskin 2000). There are very few calcareous grasslands remaining in the state, and over the course of the past century, their extent has diminished greatly through succession to forest. These habitats host disjunct populations of species whose major range is further west, and this unique genetic material may be lost if these habitats continue to succeed to forest. Calcareous grasslands appear to require fire in order to persist, and under current fire management practices wildfires are far less common than previous centuries. Although it is likely that fire is the optimal management tool for Pennsylvania's sites, we know of no examples where it has been tried in recent times. Grazing may have also historically played a role in maintaining these sites, and should be evaluated as a management technique.

Mechanical and chemical management has been tried at three sites, Westfall Ridge Prairie, Rupert Cave, and Big Hollow. We are not aware of any quantitative monitoring associated with these cases, but we can report the techniques used based on discussion with the practitioners, and some qualitative observations on the effects.

At Westfall Ridge, one grassland area has been mown annually or semi-annually over the past decade, and shrubs have been cut from the edges. The vegetation remains herbaceous in character, but old-field species such as Canada goldenrod are more prevalent than at some other sites. The shrub border around the grassland is very dense, suggesting that cutting may have stimulated growth to some degree.

At Rupert Cave, one portion of the top of a ridge has been mown semi-annually to maintain a wide path. The mown area is densely covered in sideoats grama grass, while adjacent areas have much more shrub growth and a lower density of sideoats grama. Grassland species are present throughout, although obviously less abundant in areas with more canopy cover. The impact of mowing on species besides the sideoats grama was not clear from casual observation.

At Big Hollow, shrubs and trees have been removed in the past two years on a small scale from grassland areas through mechanical and chemical techniques. The areas previously occupied by woody growth currently have sparse vegetation.

Although anecdotal and preliminary, these cases suggest that the success of mowing may depend to some degree on the edaphic factors at a site. At more mesic sites, it may encourage old field vegetation, while at more xeric, exposed sites, it may encourage more typical calcareous grassland vegetation.

Because these grassland habitats are few in number, small in extent, and host species of conservation concern, it is recommended to develop management techniques through well-planned experimental research including the following steps:

- Identify important conservation features and management goals at site(s).
- Design and implement baseline data collection based on conservation features and goals.
- Test different active management techniques on a small scale.
- Design and implement monitoring studies to evaluate the results in relation to the conservation features and goals.

It may also be possible to restore areas that were previously grassland and have now succeeded to forest, through active management and/or reintroduction of native species from local seed source. Such areas can be identified by historical records, early aerial photos, and herbarium records for grassland indicator taxa.

Woodlands

Calcareous woodlands provide habitat for a very large number of the state's calciphile taxa, almost as many as wetlands. This group of taxa is somewhat diverse in its ecological requirements and biogeographical patterns. It includes some taxa that are rock specialists, and some that require higher light levels and mineral soils for germination; these are often also found on grasslands (i.e., *Liatris scariosa*). The majority of taxa have southern distributions, but some northern and Midwestern species are also found in woodlands.

Calcareous woodlands may depend on disturbance to maintain their open character. However, there are no examples where active management has been attempted among the sites considered in this study. The origins and disturbance history of calcareous woodlands are not nearly as well documented as that of grasslands, and a clearer understanding of these factors is important to designing ecologically appropriate management techniques. Edaphic factors may place a role in slowing or preventing entirely the establishment of full forest canopy at woodland sites. Many woodlands are located on steep, west- or south- facing slopes. However, some are also known from steep slopes with other aspects. Some

woodlands occur at extremely steep and rocky sites, others at moderately steep and less rocky sites. Some sites are known to have persisted many decades, while others have clearly developed after a fairly recent disturbance. Studies of past land use and disturbance history at these sites could greatly inform our understanding of their ecology and management needs.

Similar studies have been conducted for acidic barrens, and revealed that most barrens resulted from postsettlement disturbances, and succeed to forest within decades when disturbances cease (Copenheaver, White, and William A. Patterson III 2000; Kurczewski 1999; Leimanis 1993; Milne 1985; Russell 1996; G. Motzkin and Foster 2002; G. Motzkin et al. 2002; G. Motzkin et al. 2008; G. Motzkin, Patterson Iii, and Foster 1999). In a few cases, barrens have been shown to be older than European settlement, either in extremely harsh settings (G. D. Motzkin, Orwig, and Foster 2003; Abrams and Orwig 1995), or in areas that Native Americans likely managed with fire, and post-colonization disturbances maintained subsequently (Russell 1996). Roger Latham examined shrubland communities throughout northeastern North America, and found that those hosting rare plants are older, while those with more recent origins tend not to include rare plants (R. E. Latham 2003). Land use and disturbance history studies also revealed that fire was the single most important disturbance type for maintaining barrens, and showed the frequency which it had occurred in the past.

Investigations into open-physiognomy limestone communities in other regions have found that the origins, age, and disturbance history of these communities are variable. Alvar communities in Michigan date from before European settlement, but have also been created more recently through fire. However, in many cases fire is infrequent, and is not the primary factor maintaining open physiognomy. Grazing by native ungulates is an important factor (Jones and Reschke 2005). Open-physiognomy limestone communities in the Midwest and in the Ozarks have been shown to succeed to forest in the absence of fire or disturbance, and it is likely that they have shifted back and forth between forest and grassland over the course of centuries (Baskin and Baskin 2000). However, at steeper woodland sites in West Virginia, observation of drought stress on vegetation suggests this may be a major factor in preventing the establishment of forest (Bartgis 1993).

Based on our field observations, it seems likely that calcareous woodlands in Pennsylvania have variable origins and disturbance regimes; those on eastern and northern slopes that are less rocky may be of more recent origin from cutting, burning, or grazing; while extremely rocky slopes, especially south- and west-facing, may be older and more strongly maintained by edaphic factors. However, many theories about community origins have been proven wrong by historical ecology investigations. The results of such investigations done in other regions can provide valuable guidance, but because there is clearly a wide range of regional variation in the origin and disturbance processes of limestone communities, it is important to conduct local investigations as well.

It is likely that if disturbance is required to maintain woodlands, it is needed far less frequently than is required to maintain grasslands. Sites that are on steep slopes are also vulnerable to erosion and destabilization. Research on other savannah and woodland communities shows that edaphic factors also influence the frequency and severity of disturbance required to maintain open physiognomy, with harsher sites requiring less disturbance. In addition to the afore-mentioned need for guidance from historical investigations, these factors should be considered when designing trials of active management techniques on woodlands.

While preservation and maintenance of woodland calcareous habitats is key to the conservation of a large group of calciphile taxa, it is also important to understand the taxa on an individual basis because it is a diverse group with variable ecology. Northern-distribution taxa may respond differently than southern-distribution taxa under climate change. Site conservation plans should consider the calciphile taxa present and their individual ecological requirements. While statewide there are 77 calciphile taxa known

to occur on woodlands, most of the sites visited in this study had 4-10 calciphile species present. The small number of taxa per site increases the feasibility of tailoring conservation efforts to their needs, but also emphasizes a need for conservation of many examples of these habitats throughout the limestone regions the state.

Mesic Outcrops

Mesic outcrops harbor a relatively small group of taxa, but many of these are found exclusively in this habitat. These habitats are small and located in particular environmental settings, usually north-facing and lower-slope positions. They are mostly forested, sometimes with near complete canopy cover from surrounding trees. Because the taxa depend on a mesic setting, these habitats may be particularly sensitive to disturbances that alter the local microclimate, such as timber clearance in adjacent areas. Conservation of these habitats should include conservation of a forested buffer surrounding the outcrop. These habitats have high bryophyte cover, and more work is needed to inventory these taxa.

Forests

In Pennsylvania, forests are typically viewed as matrix ecosystems, because the majority of the landscape reverts to forest in absence of disturbance. However, calcareous forests largely cannot provide the ecosystem functions of matrix forest, due to the extremely fragmented state of these ecosystems. Dry calcareous forests (the "Yellow oak redbud forest" type) require specific environmental settings that are somewhat uncommon; steep slopes, south- or west- facing aspect, upper slope or hilltop locations over calcareous geology. It is likely that these forests have always been small-patch communities, because the appropriate setting occurs in small patches. However, in pre-European settlement times, patches of dry calcareous forest were probably in most cases embedded within mesic calcareous forest or other forest types. As with all calcareous systems, the long-term viability of many examples of dry calcareous forest is seriously threatened by fragmentation (see further discussion under "Habitat Isolation and Fragmentation," p 100).

Dry calcareous forests may also benefit from periodic fire. However, the ecology of the calcareous taxa present should be considered individually at a given site in designing a fire management program. Additionally, there is no research on historical fire frequency that is specific to dry calcareous forests in Pennsylvania, although research on other dry forests may be relevant.

It is likely that in pre-European settlement times, mesic calcareous forests occurred in larger patches and occupied more of the landscape than dry calcareous forests; today, the vast majority of the land area that would have hosted such forests, the flat or gently sloped valleys of the Ridge and Valley and Piedmont, has been converted other uses. It is somewhat uncertain, however, how much of this landscape would have contained forests with high soil pH, and how much value these forests have for calcareous plant taxa. In Pennsylvania's climate, limestone-derived soils on flat or gently sloping surfaces typically undergo leaching that lowers the pH. Because many of the valley areas have been converted to agriculture and had lime added to the soils for many years, it is now difficult to assess the original character of the soil. In our study, mesic forest plots had the lowest number of calciphiles per plot, even though these plots were larger than woodland or grassland plots. Calciphiles may be favored by dry conditions because these exacerbate the nutrient limitations of calcareous soils to which calciphiles are physiologically adapted (see "Plants and Substratum Chemistry", p 8). However, rocky portions of mesic forests may host mesic outcrop calciphile species. Although our study did not identify many calcareous

indicator species in mesic forests over calcareous bedrock, these sites should be investigated further and compared with a larger dataset of forest plots on a variety of bedrock settings.

Several larger sites considered in this study provide examples of a variety of calcareous community types embedded within a context of natural landscape: Spring Creek Valley (Centre County), Enlow Fork (Greene/Washington Counties), and Canoe Creek State Park (Blair County). At these sites, forest is the dominant cover type in unmaintained areas, including patches of calcareous dry forest in appropriate settings as well as a variety of calcareous and non-calcareous mesic forest types. Woodlands and grasslands are also present as very small patches embedded in the forested matrix. These examples are particularly valuable because individual small-patch communities are protected from the negative impacts of fragmentation, and population viability may be enhanced by the presence of multiple potential habitat sites within the natural landscape block.

Future Study Needs

Dispersal capacity of calciphiles, habitat fragmentation, & long term viability of species.

Because many calcareous habitats, both wetland and upland, now occur in small, isolated patches, it is important to understand the dispersal mechanisms and capacity of the plant taxa that are found mainly or exclusively in these habitats. Strategies for habitat connectively cannot be effectively devised without understanding dispersal biology. Many ant-dispersed forest species, for example, are transported only very short distances per dispersal event and do not move through non-forest landscapes. Species dispersed by deer may be effectively transported across agricultural lands, but less effectively across developed lands. Wetland species that can be transported by water can move between habitats if there is a hydrological connection even when intervening land use is non-natural, while wind-dispersed wetland plants will cross non-natural landscapes less successfully.

Planning for dispersal corridors across the landscape is especially important in the context of adaptation to climate change.

Lepidoptera inventory

Many calciphiles are host plants for rare lepidopteron species. Lepidoptera inventories have been conducted at a few calcareous habitat sites, such as Spring Creek (Centre County), which produce high species diversity and several rare taxa. However, many calcareous habitats have not yet been inventoried for Lepidoptera, and there has been no comprehensive assessment of the importance of these habitats to Lepidoptera diversity in Pennsylvania.

Historical Ecology Studies

Studies of past land use and disturbance history can provide essential guidance for active management at woodlands and fens.

Literature Cited

- "7.5 Minute Digital Elevation Models (DEM) for Pennsylvania (30 M)." 2000. U.S. Geological Survey.
- "A Study of Calcareous Fen Communities in Pennsylvania." 1995. Pittsburgh, PA: Western Pennsylvania Conservancy and The Nature Conservancy.
- "A Study of Seepage Wetlands in Pennsylvania." 1998. Pittsburgh: Western Pennsylvania Conservancy and The Nature Conservancy.
- Abrams, M. D., and D. A. Orwig. 1995. "Structure, Radial Growth Dynamics and Recent Climatic Variations of a 320-Year-Old Pinus Rigida Rock Outcrop Community." *Oecologia* 101 (3): 353–360.
- Aguilar, Ramiro, Lorena Ashworth, Leonardo Galetto, and Marcelo Adrián Aizen. 2006. "Plant Reproductive Susceptibility to Habitat Fragmentation: Review and Synthesis through a Metaanalysis." *Ecology Letters* 9 (8): 968–980.
- Aguilar, Ramiro, Mauricio Quesada, Lorena Ashworth, Yvonne Herrerias-Diego, and Jorge Lobo. 2008. "Genetic Consequences of Habitat Fragmentation in Plant Populations: Susceptible Signals in Plant Traits and Methodological Approaches." *Molecular Ecology* 17 (24): 5177–5188.
- Anderson, Mark G., and Charles E. Ferree. 2010. "Conserving the Stage: Climate Change and the Geophysical Underpinnings of Species Diversity." *PLoS ONE* 5 (7) (July 14): e11554. doi:10.1371/journal.pone.0011554.
- Andreas, Barbara K., John J. Mack, and James S. McCormac. 2004. *Floristic Quality Assessment Index* (*FQAI*) for Vascular Plants and Mosses for the State of Ohio. Ohio EPA. http://johnsilvius.cedarville.org/research/floristicquality.pdf.
- Balme, O. E. 1953. "Edaphic and Vegetational Zoning on the Carboniferous Limestone of the Derbyshire Dales." *Journal of Ecology* 41 (2) (August 1): 331–344. doi:10.2307/2257045.
- Bartgis, Rodney L. 1993. "The Limestone Glades and Barrens of West Virginia." *Castanea* 58 (2) (June 1): 69–89. doi:10.2307/4033660.
- Baskin, Jerry M., and Carol C. Baskin. 2000. "Vegetation of Limestone and Dolomite Glades in the Ozarks and Midwest Regions of the United States." *Annals of the Missouri Botanical Garden* 87 (2) (April 1): 286–294. doi:10.2307/2666165.
- Belle, J., A. Barendregt, P. P. Schot, and M. J. Wassen. 2006. "The Effects of Groundwater Discharge, Mowing and Eutrophication on Fen Vegetation Evaluated over Half a Century." *Applied Vegetation Science* 9 (2): 195–204.
- Bennie, Jonathan, Mark O. Hill, Robert Baxter, and Brian Huntley. 2006. "Influence of Slope and Aspect on Long-term Vegetation Change in British Chalk Grasslands." *Journal of Ecology* 94 (2): 355– 368. doi:10.1111/j.1365-2745.2006.01104.x.
- Berg, T.M, W.E. Edmunds, A.R. Geyer, and and others. 1980. "Geologic Map of Pennsylvania." 4th Ser., Map 1. Pennsylvania Geological Survey.

http://www.dcnr.state.pa.us/topogeo/publications/pgspub/map/map1/index.htm.

- Blumberg, Betsie, and Robert L. Cunningham. 1982. "An Introduction to Soils of Pennsylvania". AGDEX 512. Teacher Education Series. The Pennsylvania State University. http://www.envirothonpa.org/documents/AnIntrotoSoilsofPA_000.pdf.
- Bourdaghs, Michael, Carol A. Johnston, and Ronald R. Regal. 2006. "Properties and Performance of the Floristic Quality Index in Great Lakes Coastal Wetlands." *Wetlands* 26 (3): 718–735.
- Brady, Nyle C. 1990. *The Nature and Properties of Soils*. Tenth. New York: MacMillan Publishing Company.
- Chamberlain, S.J., and H.M. Ingram. 2012. "Developing Coefficients of Conservatism to Advance Floristic Quality Assessment in the mid-Atlantic Region." *Journal of the Torrey Botanical Society* 139 (4): 416–427.

Ciolkosz, Edward J., Richard C. Cronce, William D. Sevon, and William J. Waltman. 1995. "Genesis of Pennsylvania's Limestone Soils". 135. Agronomy Series. Penn State College of Agricultural Sciences. http://agris.fao.org/agris-

search/search/display.do?f=1997/US/US97022.xml;US9715741.

- "Classification, Assessment and Protection of Forested Floodplain Wetlands of the Susquehanna Drainage." 2002. US EPA Wetlands Protection State Development Grant CD-993731. Pennsylvania Natural Heritage Program.
- "Classification, Assessment and Protection of Non-Forested Floodplain Wetlands of the Susquehanna Drainage." 2004. US EPA Wetlands Protection State Development Grant CD-98337501. Pennsylvania Natural Heritage Program.
- Copenheaver, Carolyn A., Alan S. White, and William A. Patterson III. 2000. "Vegetation Development in a Southern Maine Pitch Pine-Scrub Oak Barren." *Journal of the Torrey Botanical Society* 127 (1) (March): 19–32.
- Diggelen, R., B. Middleton, J. Bakker, A. Grootjans, and M. Wassen. 2006. "Fens and Floodplains of the Temperate Zone: Present Status, Threats, Conservation and Restoration." *Applied Vegetation Science* 9 (2): 157–162.
- Diggelen, R., W. J. Molenaar, and A. M. Kooijman. 2009. "Vegetation Succession in a Floating Mire in Relation to Management and Hydrology." *Journal of Vegetation Science* 7 (6): 809–820.
- Dufrene, M., and P. Legendre. 1997. "Species Assemblages and Indicator Species: The Needs for a Flexible Asymmetrical Approach." *Ecological Monographs* 67 (3): 345–366.
- Ellenberg, H. 1979. "Zeigerwerte Der Gefasspflanzen Mitteleuropas." Scripta Geobotánica 9: 1-122.
- Ellenberg, H. H. 1988. Vegetation Ecology of Central Europe. Cambridge University Press.
- Ellenberg, H., H.E. Weber, R. Dull, V. Wirth, W. Werner, and D. Paulissen. 1991. "Zeigerwerte von Pflanzen in Mitteleuropa." *Scripta Geobotánica* 18: 1–248.
- Fernald, M. L. 1907. "The Soil Preferences of Certain Alpine and Subalpine Plants." *Rhodora* 9 (105) (September 1): 149–193. doi:10.2307/23296509.
- Flora of North America Editorial Committee, eds. 1993. *Flora of North America North of Mexico*. New York and Oxford.
- Forrest Meekins, J., and Brian C. McCarthy. 2001. "Effect of Environmental Variation on the Invasive Success of a Nonindigenous Forest Herb." *Ecological Applications* 11 (5): 1336–1348.
- Fry, J., G. Xian, S. Jin, J Dewitz, L. Yang, C. Barnes, N. Herold, and J. Wickham. 2011. "Completion of the 2006 National Land Cover Dataset for the Coterminous United States." *PE&RS* 77 (9): 858– 864.
- Gignac, L.D., R. Gauthier, L. Rochefort, and J. Bubier. 2004. "Distribution and Habitat Niches of 37 Peatland Cyperaceae Species Across a Broad Geographic Range in Canada." *Canadian Journal* of Botany 82: 1292–1313.
- Girvetz, Evan H., Chris Zganjar, George T. Raber, Edwin P. Maurer, Peter Kareiva, and Joshua J. Lawler. 2009. "Applied Climate-Change Analysis: The Climate Wizard Tool." *PLoS ONE* 4 (12) (December 15): e8320. doi:10.1371/journal.pone.0008320.
- Grootjans, A. P., E. B. Adema, W. Bleuten, H. Joosten, M. Madaras, and M. Janáková. 2006. "Hydrological Landscape Settings of Base-rich Fen Mires and Fen Meadows: An Overview." *Applied Vegetation Science* 9 (2): 175–184.
- Higgins, T., E. Colleran, and R. Raine. 2006. "Transition from P-to N-limited Phytoplankton Growth in an Artificial Lake on Flooded Cutaway Peatland in Ireland." *Applied Vegetation Science* 9 (2): 223–230.
- Hill, Mark O., J. O. Mountford, D. B. Roy, and R. G. H. Bunce. 1999. Ellenberg's Indicator Values for British Plants. ECOFACT Volume 2 Technical Annex. Vol. 2. Institute of Terrestrial Ecology. http://nora.nerc.ac.uk/6411/1/ECOFACT2a.pdf.
- Hill, Steven R. 1992. "Calciphiles and Calcareous Habitats of South Carolina." *Castanea* 57 (1) (March 1): 25–33. doi:10.2307/4033847.

- Hoek, D., and K. V. Sýkora. 2006. "Fen-meadow Succession in Relation to Spatial and Temporal Differences in Hydrological and Soil Conditions." *Applied Vegetation Science* 9 (2): 185–194.
- Honnay, Olivier, Hans Jacquemyn, Beatrijs Bossuyt, and Martin Hermy. 2005. "Forest Fragmentation Effects on Patch Occupancy and Population Viability of Herbaceous Plant Species." *New Phytologist* 166 (3): 723–736. doi:10.1111/j.1469-8137.2005.01352.x.
- Jones, Judith, and Carol Reschke. 2005. "The Role of Fire in Great Lakes Alvar Landscapes." *The Michigan Botanist* 44 (1). http://hdl.handle.net/2027/spo.0497763.0044.105.
- Keener, Carl S., and Marilyn M. Park. 1986. "An Overview of the Vascular Plant Geography of Pennsylvania." In *Engandered and Threatened Species Programs in Pennsylvania and Other States: Causes, Issues and Management.* Phillipsburg, NJ: Pennsylvania Academy of Science.
- Kotowski, W., W. Thörig, R. Diggelen, and M. J. Wassen. 2009. "Competition as a Factor Structuring Species Zonation in Riparian Fens-a Transplantation Experiment." *Applied Vegetation Science* 9 (2): 231–240.
- Kurczewski, Frank E. 1999. "Historic and Prehistoric Changes in the Rome, New York Pine Barrens." Northeastern Naturalist 6 (4): 327–340.
- Landolt, Elias. 1977. Ökologische Zeigerwerte Zur Schweizer Flora. Geobotan. Inst.
- Latham, Roger Earl. 2003. "Shrubland Longevity and Rare Plant Species in the Northeastern United States." *Forest Ecology and Management* 185 (1-2) (November 3): 21–39. doi:10.1016/S0378-1127(03)00244-5.
- Latham, Roger, and J. F. Thorne. 2007. "Keystone Grasslands: Restoration and Reclamation of Native Grasslands, Meadows, and Savannas in Pennsylvania State Parks and State Game Lands." Harris: Wild Resources Conservation Program, Pennsylvania Department of Natural Resources. http://www.continentalconservation.us/Roger%20Latham/Roger%20Latham%20publications.htm l.
- Laughlin, D.C. 2003a. "Geographic Distribution and Dispersal Mechanismsof Bouteloua Curtipendula in the Appalachian Mountains." *The American Midland Naturalist* 149 (2): 268–281.
- ———. 2003b. "Lack of Native Propagules in a Pennsylvania, USA, Limestone Prairie Seed Bank: Futile Hopes for a Role in Ecological Restoration." *Natural Areas Journal* 23 (2) (April). http://www.naturalarea.org/journaltoc.aspx?p=28.
- ———. 2004a. "Woody Plant Invasion and the Importance of Anthropogenic Disturbance Within Xeric Limestone Prairies." *J PA Acad Sci* 78 (1): 12–28.
 - . 2004b. "Did Tallgrass Prairie Extend into Pennsylvania?" Prairie Naturalist 36 (1): 11–22.
- Laughlin, D.C., and C.F. Uhl. 2003. "The Xeric Limestone Prairies of Pennsylvania." *Castanea* 68 (4) (December 1): 300–316.
- Lawesson, Jonas Erik. 2003. "pH Optima for Danish Forest Species Compared with Ellenberg Reaction Values." *Folia Geobotanica* 38 (4) (December 1): 403–418.
- Leimanis, A. 1993. "Vegetation and Fire History of the Rome Sand Plains". Central and Western New York Chapter of The Nature Conservancy.
- Malik, Riffat Naseem, Zabta Khan Shinwari, and Hinna Waheed. 2012. "Linkages Between Spatial Variations in Riparian Vegetation and Floristic Quality to the Environmental Heterogeneity: a Case Study of River Soan and Its Associated Streams, Pakistan." *Pakistan Journal of Botany* 44: 187–197.
- Matlack, G. R. 1994. "Plant Species Migration in a Mixed-history Forest Landscape in Eastern North America." *Ecology* 75 (5): 1491–1502.
- Matthews, Jeffrey W., Paul A. Tessene, Scott M. Wiesbrook, and Bradley W. Zercher. 2005. "Effect of Area and Isolation on Species Richness and Indices of Floristic Quality in Illinois, USA Wetlands." *Wetlands* 25 (3): 607–615.
- McPherson, Jessica, and Charles Bier. 2006. "Spring Creek Valley Ecological Assessment Report". Prepared for Benner Township: Western Pennsylvania Conservancy. benner.centreconnect.org/Canyon/Spring%20Creek%20Valley%20Ecological%20Assessment.pd f.

- Middleton, B.A., B. Holsten, and R. Van Diggelen. 2006. "Biodiversity Management of Fens and Fen Meadows by Grazing, Cutting and Burning." *Applied Vegetation Science* 9 (2): 10.
- Miller, S. J., and D. H. Wardrop. 2006. "Adapting the Floristic Quality Assessment Index to Indicate Anthropogenic Disturbance in Central Pennsylvania Wetlands." *Ecological Indicators* 6 (2): 313–326.
- Milne, Bruce T. 1985. "Upland Vegetational Gradients and Post-Fire Succession in the Albany Pine Bush, New York." *Bulletin of the Torrey Botanical Club* 112 (1) (March): 21–34.
- Minnesota Department of Natural Resources. 2012. "Rare Species Guide." http://www.dnr.state.mn.us/rsg/index.html.
- Misra, Aparna, and Germund Tyler. 1999. "Influence of Soil Moisture on Soil Solution Chemistry and Concentrations of Minerals in the Calcicoles Phleum Phleoides and Veronica Spicata Grown on a Limestone Soil." *Annals of Botany* 84 (3): 401–410.
- Motzkin, G., R. Eberhardt, B. Hall, D. R Foster, J. Harrod, and D. MacDonald. 2002. "Vegetation Variation Across Cape Cod, Massachusetts: Environmental and Historical Determinants." *Journal of Biogeography* 29 (10-11): 1439–1454.
- Motzkin, G., D. Foster, A. Allen, J. Harrod, and R. Boone. 2008. "Controlling Site to Evaluate History: Vegetation Patterns of a New England Sand Plain." http://academics.smcvt.edu/sburks/out.pdf.
- Motzkin, G., and D. R Foster. 2002. "Grasslands, Heathlands and Shrublands in Coastal New England: Historical Interpretations and Approaches to Conservation." *Journal of Biogeography* 29 (10-11): 1569–1590.
- Motzkin, G., W. A. Patterson Iii, and D. R. Foster. 1999. "A Historical Perspective on Pitch Pine–scrub Oak Communities in the Connecticut Valley of Massachusetts." *Ecosystems* 2 (3): 255–273.
- Motzkin, Glenn D., David A. Orwig, and David R. Foster. 2003. "Vegetation and Disturbance History of a Rare Dwarf Pitch Pine Community in Western New England, USA." *Journal of Biogeography* 29 (10-11) (December): 1455–1467.
- Mueller-Dombois, D., and H. Ellenberg. 1974. *Aims and Methods of Vegetation Ecology*. New York: Wiley.
- Nichols, J. D., J. E. Perry, and D. A. DeBerry. 2006. "Using a Floristic Quality Assessment Technique to Evaluate Plant Community Integrity of Forested Wetlands in Southeastern Virginia." *Natural Areas Journal* 26 (4): 360–369.
- PA DCNR. 1990. "Limestone and Dolomite Distribution in Pennsylvania". Bureau of Topographic and Geologic Survey.

http://www.dcnr.state.pa.us/cs/groups/public/documents/document/dcnr_016201.pdf.

PA DCNR, Bureau of Topgraphic and Geologic Survey. 2013. "Glacial Geology in Pennsylvania." *Geology of Pennsylvania*. Accessed June 16. http://www.dcnr.state.pa.us/topogeo/field/glacial/index.htm.

- Pearson, Richard G., Christopher J. Raxworthy, Miguel Nakamura, and A. Townsend Peterson. 2007. "Predicting Species Distributions from Small Numbers of Occurrence Records: a Test Case Using Cryptic Geckos in Madagascar." *Journal of Biogeography* 34 (1): 102–117. doi:10.1111/j.1365-2699.2006.01594.x.
- Pearson, Scott M., Alan B. Smith, and Monica G. Turner. 1998. "Forest Patch Size, Land Use, and Mesic Forest Herbs in the French Broad River Basin, North Carolina." *Castanea*: 382–395.
- Peck, James H., Carol J. Peck, and Donald R. Farrar. 1990. "Influences of Life History Attributes on Formation of Local and Distant Fern Populations." *American Fern Journal* 80 (4) (October 1): 126–142. doi:10.2307/1547200.
- Phillips, Steven J., Robert P. Anderson, and Robert E. Schapire. 2006. "Maximum Entropy Modeling of Species Geographic Distributions." *Ecological Modelling* 190: 231–259.
- Reznicek, A.A., E.G. Voss, and B. S. Walters. 2011. "Michigan Flora Online". University of Michigan.
- Rooney, T.P., and D.A. Rodgers. 2002. "The Modified Floristic Quality Index." *Natural Areas Journal* 22 (4): 340–344.

- Russell, E. W. B. 1996. "Six Thousand Years of Forest and Fire History in the Rome Sand Plains". Central New York Chapter of The Nature Conservancy.
- Scanga, S. E., and D. J. Leopold. 2010. "Population Vigor of a Rare, Wetland, Understory Herb in Relation to Light and Hydrology 1." *The Journal of the Torrey Botanical Society* 137 (2): 297– 311.
 - ———. 2012. "Managing Wetland Plant Populations: Lessons Learned in Europe May Apply to North American Fens." *Biological Conservation*. http://www.sciencedirect.com.navigatorstlib.passhe.edu/science/article/pii/S0006320712000742.
- Schaffers, A. P., and K. V. Sykora. 2000. "Reliability of Ellenberg Indicator Values for Moisture, Nitrogen and Soil Reaction: a Comparison with Field Measurements." *Journal of Vegetation Science* 11 (2): 225–244.
- Schimper, Andreas Franz Wilhelm. 1898. *Pflanzen-geographie auf physiologischer Grundlage*. G. Fischer.
- Schultz, A. P. 1999. "The Geology of Pennsylvania." PA, Pennsylvania Geological Survey: 888.
- Sevon, W. D. 2000. "Physiographic Provinces of Pennsylvania". Pennsylvania Geological Survey.
- Sevon, William D., Gary M. Fleeger, and Vincent C. Shepps. 1999. "Pennsylvania and the Ice Age". Pennsylvania Geological Survey.
 - http://www.dcnr.state.pa.us/cs/groups/public/documents/document/dcnr_014595.pdf.
- Shepps, Vincent C., G.W. White, J.B. Droste, and R.F. Sitler. 1959. *Glacial Geology of Northwestern Pennsylvania*. 4th Bull. G 32. Pennsylvania Geological Survey. http://www.dcnr.state.pa.us/topogeo/publications/pgspub/map/index.htm#Map59.
- Silveri, Ann, Peter W. Dunwiddie, and Helen J. Michaels. 2001. "Logging and Edaphic Factors in the Invasion of an Asian Woody Vine in a Mesic North American Forest." *Biological Invasions* 3 (4): 379–389.
- Steele, B. 1955. "Soil pH and Base Status as Factors in the Distribution of Calcicoles." *Journal of Ecology* 43 (1) (January 1): 120–132. doi:10.2307/2257125.
- Strakosch-Walz, K., ed. 2001. "Instruction Manual on Heritage Field Methodology: Documenting Ecological Communities". New Jersey Natural Heritage Program.
- Ström, Lena. 1997. "Root Exudation of Organic Acids: Importance to Nutrient Availability and the Calcifuge and Calcicole Behaviour of Plants." *Oikos* 80 (3) (December 1): 459–466. doi:10.2307/3546618.
- Swink, F., and G. Wilhelm. 1994. *Plants of the Chicago Region*. 4th ed. Indianapolis, IN: Indiana Academy of Science.
- Tansley, A. G. 1917. "On Competition Between Galium Saxatile L. (G. Hercynicum Weig.) and Galium Sylvestre Poll. (G. Asperum Schreb.) On Different Types of Soil." *Journal of Ecology* 5 (3/4) (December 1): 173–179. doi:10.2307/2255655.
- "Terrestrial and Palustrine Plant Communities of Pennsylvania, 2nd Edition." 2012. Harri: Pennsylvania Natural Heritage Program. http://www.naturalheritage.state.pa.us/Communities.aspx.
- "USDA Plant Hardiness Zone Map." 2012. Agricultural Research Service, U.S. Department of Agriculture. http://planthardiness.ars.usda.gov.
- Veblen, Kari E., and Truman P. Young. 2009. "A California Grasslands Alkali Specialist, Hemizonia Pungens Ssp. Pungens, Prefers Non-alkali Soil." *Journal of Vegetation Science* 20 (1): 170–176.
- Vickery, Peter. 2002. "Effects of Prescribed Fire on the Reproductive Ecology of Northern Blazing Star Liatris Scariosa Var. Novae-Angliae." *American Midland Naturalist* 148 (1) (July): 20–27.
- Voss, Edward G. 1972. *Michigan Flora a Guide to the Identification and Occurrence of the Native and and Naturalized Seed-Plants of the State*. Cranbrook Instit. of Science.
- Ware, Donna M. E., and Stewart Ware. 1992. "An Acer barbatum-Rich Ravine Forest Community in the Virginia Coastal Plain." *Castanea* 57 (2) (June 1): 110–122. doi:10.2307/4033717.
- Wassen, M. J., R. Diggelen, L. Wolejko, and J. T. A. Verhoeven. 1996. "A Comparison of Fens in Natural and Artificial Landscapes." *Plant Ecology* 126 (1): 5–26.

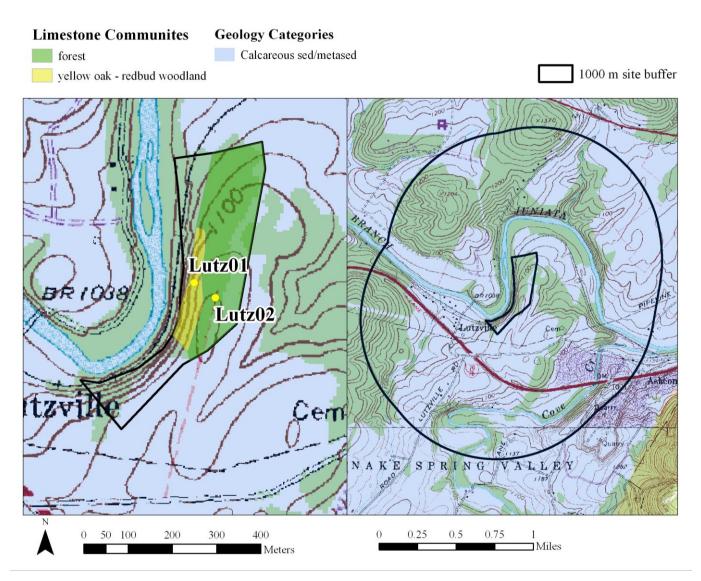
- Wassen, M. J., and H. Olde Venterink. 2006. "Comparison of Nitrogen and Phosphorus Fluxes in Some European Fens and Floodplains." *Applied Vegetation Science* 9 (2): 213–222.
- Weakley, Alan. 2012. *Flora of the Southern and Mid-Atlantic States*. Working Draft. University of North Carolina.
- Weldy, Troy, and David Werier. 2012. "New York Flora Atlas." http://newyork.plantatlas.usf.edu/Default.aspx.
- Wherry, Edgar T. 1927. "Divergent Soil Reaction Preferences of Related Plants." *Ecology* 8 (2): 197–206.
- Wisconsin State Herbarium. 2012. "Wisflora: Wisconsin Vascular Plant Species." http://www.botany.wisc.edu/wisflora/.
- WPC, and TNC. 2007. "Pennsylvania Forest Conservation Analysis". Western Pennsylvania Conservancy & The Nature Conservancy; unpublished.
- Young, Bruce, Elizabeth A. Byers, Kelly Gravuer, Kim Hall, Geoff Hammerson, and Alan Redder. 2011. "Guidelines for Using the NatureServe Climate Change Vulnerability Index". NatureServe. www.natureserve.org/prodServices/climatechange/pdfs/Guidelines_NatureServeClimateChangeV ulnerabilityIndex_r2.1_Apr2011.pdf.
- Zimmerman, Ephraim, and Greg Podniesinski. 2008. "Classification, Assessment, and Protection of Floodplain Wetlands of the Ohio Drainage." US EPA Wetlands Protection State Development Grant CD-973081-01-0. Pennsylvania Natural Heritage Program, Western Pennsylvania Conservancy.
- Zohlen, Angelika, and Germund Tyler. 2004. "Soluble Inorganic Tissue Phosphorus and Calcicole– Calcifuge Behaviour of Plants." *Annals of Botany* 94 (3) (September 1): 427–432. doi:10.1093/aob/mch162.

Appendix 1: Study Site Profiles

Site name: LutzvillePhysiographic setting: Ridge and Valley province, Appalachian Mountain section.County: BedfordGeology: strongly calcareous (Nittany and Stonehenge / Larke formations, undivided)

The site has a yellow oak - redbud woodland on the steep slope above the Raystown Branch Juniata River, with second-growth forest at the summit. It is surrounded by younger forest and non-forest land uses. It has low cover of invasive species. WPC is conducting removal efforts for Oriental bittersweet (*Celastrus orbiculatus*) to protect the globally rare Canby's mountain lover (*Paxistima canbyi*) population, which is vulnerable to a scale hosted by Oriental bittersweet.

mean	mean C						total	%	protection	calc002	calc012 sp
С	native	Ν	А	Ι	I'	% exotic	sp.	native	status	sp count	count
5.2	5.7	103	11.0	58.2	49.4	11%	114.0	90%	Private	6	9



Site name: Martin Mountain Physiographic setting: Ridge and Valley province, Appalachian Mountain section. County: Bedford Geology: strongly calcareous (Keyser and Tonoloway formations, undivided)

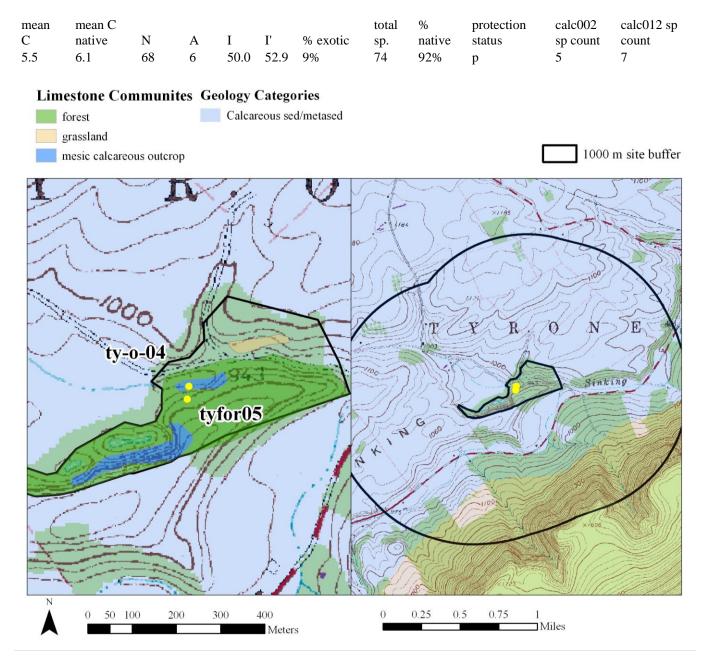
The site has a red oak – sugar maple woodland on a north-east facing, convex upper slope of Martin Mountain. It has very low cover of invasive species, and is surrounded by forest. The species diversity is exceptionally higher and more calcareously influenced at this site than other areas surveyed. Much of the mountain does have high-pH soils, but the forests have low diversity and few to no calcareous indicators. Local landowners report that deer were extremely abundant for many decades, although recently more hunting has reduced populations. Gypsy moth outbreaks reduced oak cover. Some timbering has also occurred.

mean C 5.2	mean C native 5.6	N 87	A 6	I 52.3	I' 50.5	% exotic 7%	total sp. 93	% native 94%	protection status np	calc002 sp count 3	calc012 sp count 5
	estone Cor ed oak - sugar			(Calcareo	ntegories ous sed/metased ely calcareous		sed	[1000	m site buffer
				NIO3	400						
				12	Meter	s			N	files	

Site name: Tytoona CavePhysiographic setting: Ridge and Valley province, Appalachian Mountain section.County: BlairGeology: strongly calcareous (Bellefonte and Axeman formations, undivided; Coburn through Loysburg

formations, undivided)

The site has two north-facing mesic calcareous outcrops, with a small patch of forest adjacent to the outcrops. The upland portion of the forest includes few calcareous indicators and has lower soil pH than the lower areas at the north edge of the site. There is also a grassland along a right-of-way where sideoats grama grass has been documented; however, it also includes significant exotic cover and species composition was not well documented enough to assign a community type. The surrounding land use is agriculture.

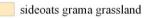


Site name: Big Hollow Physiographic setting: Ridge and Valley province, Appalachian Mountain section. County: Centre Geology: strongly calcareous (Mines member of the Gatesburg formation)

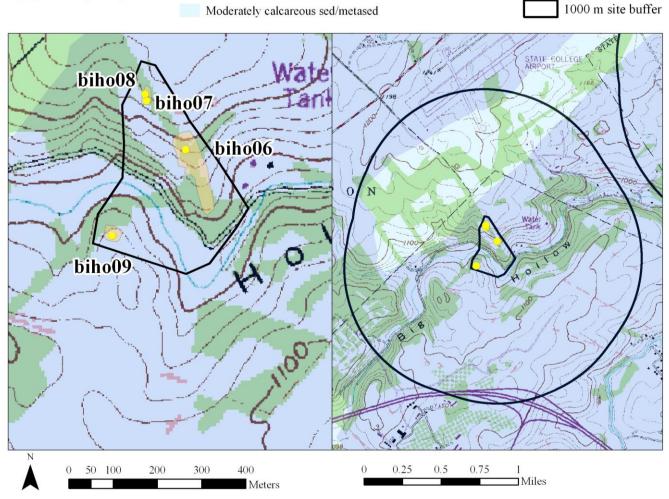
The site has several patches of sideoats grama grassland community, hosting a significant number of rare grassland indicator species. Aerial photographs from the 1930s show that much more of the area used to be in grassland than what presently remains. The grassland areas are surrounded by early successional forest and shrublands, with high cover of invasive shrub species. The grassland at biho09 has more big bluestem cover than the other areas, and may be more mesic in character. The area is owned by Penn State; surrounding land is used for agricultural research or left fallow.

mean C	mean C native	N	А	Ι	I'	% exotic		protection status		1
3.4						29%	-		2	2

Limestone Communites Geology Categories



Calcareous sed/metased Moderately calcareous sed/metased



Site name: Westfall Ridge Physiographic setting: Ridge and Valley province, Susquehanna Lowlands section. County: Juniata Geology: strongly calcareous (Keyser and Tonoloway formations undivided)

The site has several patches of sideoats grama grassland community, hosting several rare grassland indicator species. Aerial photographs from the 1930s show that much more of the area used to be in grassland than what presently remains. The grassland areas are surrounded by early successional forest and shrublands, with high cover of invasive shrub species. The western grassland patch has been maintained by The Nature Conservancy through mowing; this has preserved the open character of the site, although more mesic old field species such as goldenrods are present at this location than at the eastern location. Some invasive species have established in this area. The southern patch is densely covered in Japanese stiltgrass with few grassland indicators remaining. The eastern patch of grassland appears drier in character, with very high sideoats grama grass cover and very little invasive cover.

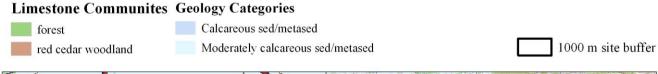
mean	mean C						total	%	protection	calc002	calc012 sp
С	native	Ν	А	Ι	Ι'	% exotic	sp.	native	status	sp count	count
4.1	5.1	44	9	33.5	37.7	20%	53	83%	Р	0	4

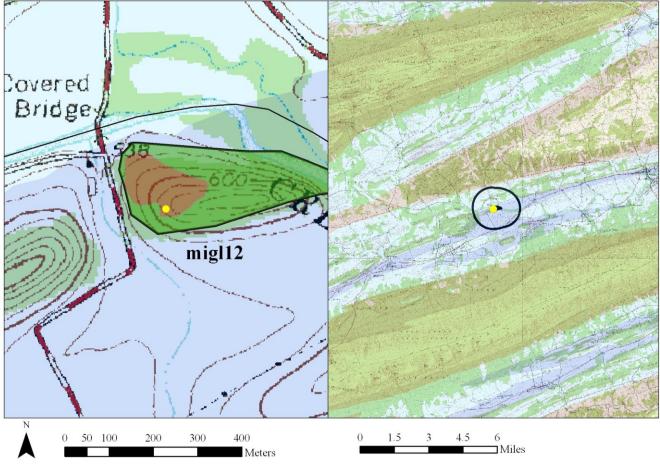
Limestone Communites Geology Categories sideoats grama grassland Calcareous sed/metased 1000 m site buffer Moderately calcareous sed/metased westp11 westp10 EM 774 G O 400 0.25 0.75 50 100 200 300 0.5 Miles Meters

Site name: Missionary Glade Physiographic setting: Ridge and Valley province, Appalachian Mountain section. County: Snyder Geology: strongly calcareous (Keyser and Tonoloway formation)

This site is a small hill with calcareous forest on its north face, invasive shrub on its south face, and a red cedar woodland on the dry west-facing portion of the hill. At the most exposed point, the woodland includes a number of grassland indicators such as sideoats grama grass (*Bouteloua curtipendula*), grooved yellow flax (*Linum sulcatum*), and green milkweed (*Asclepias viridiflora*). These species are very sparse now, as shrub cover has increased in this area over the past few decades, reducing the open herbaceous habitat.

mean	mean C						total	%	protection	calc002	calc012 sp
С	native	Ν	А	Ι	Ι'	% exotic	sp.	native	status	sp count	count
3.6	4.6	51	13	32.7	31.7	25%	64	80%	np	1	4



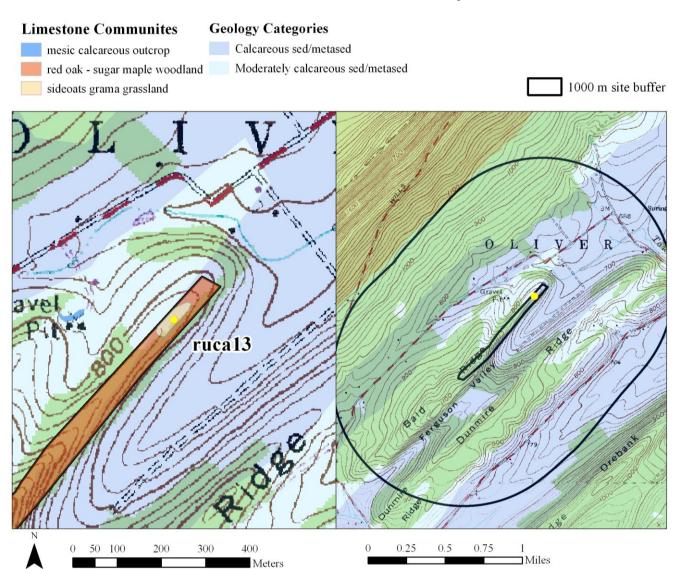


Site name: Rupert Cave Physiographic setting: Ridge and Valley province, Appalachian Mountain section. County: Mifflin Geology: moderately calcareous (Onondaga and Old Port formations, undivided) and stro

Geology: moderately calcareous (Onondaga and Old Port formations, undivided) and strongly calcareous (Keyser and Tonoloway formations, undivided).

The site includes a cave entrance with some mesic outcroppings surrounding it, and a narrow ridge with forest on the sides and dry woodland & grassland communities at the summit. The northern end of the ridge is mown in the center to maintain a path, which has also maintained a sideoats grama grassland. The area surrounding the grassland has many grassland indicator species, but is also succeeding to juniper shrub and oaks. Further south along the ridgetop, the woodland character changes, with no juniper and more oak. The species diversity is very high here, with many calcareous indicators. Some invasive species are present at the northern end of the ridge, but south of the grassland they are very uncommon.

mean	mean C						total	%	protection	calc002	calc012 sp
С	native	Ν	А	Ι	Ι'	% exotic	sp.	native	status	sp count	count
4.0	4.9	187	42	67.3	36.3	22%	229	82%	р	5	15



Site name: Braddock Trail Park Physiographic setting: Appalachian Plateaus province, Waynesburg Hills section. County: Westmoreland Geology: strongly calcareous (Monongahela formation)

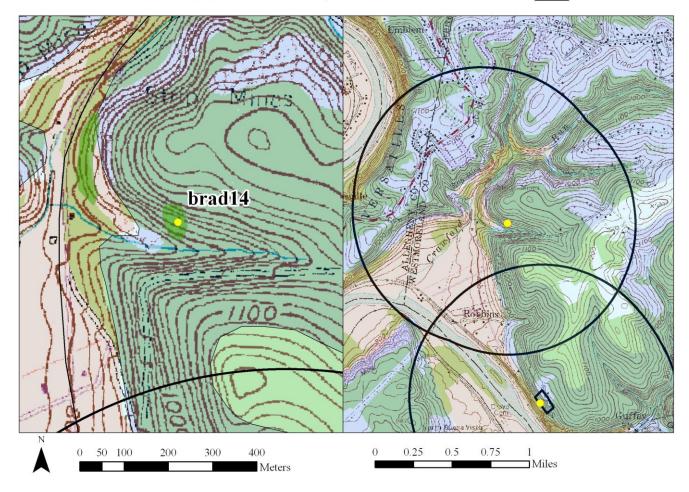
This site has mesic forest, with soil pH ranging from 5-7.5. The vernal flora is very diverse, and limestone indicators such as snow trillium *Trillium nivale*), bulblet fern (*Cystopteris bulbifera*), and harbinger-of-spring (*Erigenia bulbosa*) are found in patches where the pH is higher. Sugar maple dominates on the lower and more mesic areas, while beech and oak are common in drier sections with lower soil pH.

mean	mean C						total	%	protection	calc002	calc012 sp
С	native	Ν	А	Ι	Ι'	% exotic	sp.	native	status	sp count	count
5.0	5.6	62	7	44.1	47.7	11%	69	90%	р	2	2

Limestone Communites Geology Categories

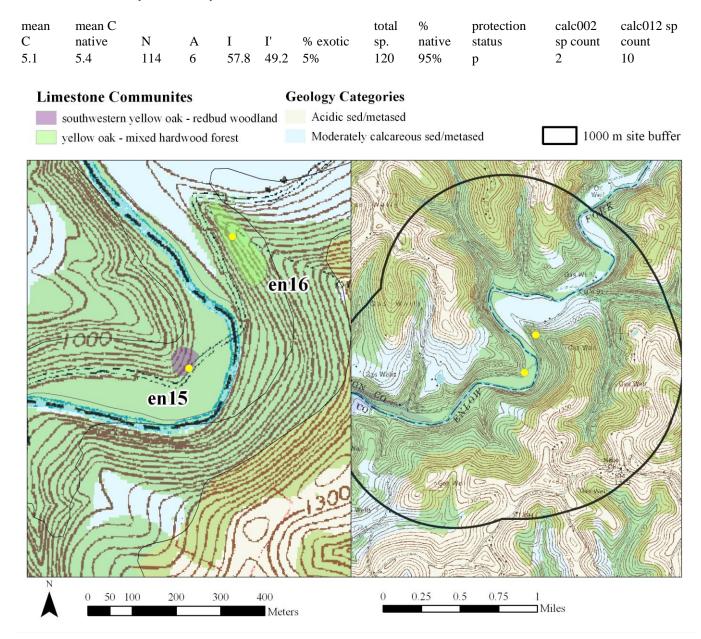






Site name: Enlow Fork Physiographic setting: Appalachian Plateaus province, Waynesburg Hills section. County: Washington Geology: moderately calcareous (Washington Formation)

The site has a very rich flora, including many southern species that are at the northern edge of their range. It includes floodplain forests with pH 6.5-7.5, dominated by sycamore and sugar maple; and slope forests with substantial areas of calcareous influence. Plots were taken at a steep nose with yellow oak – redbud woodland vegetation, and a steep slope with yellow oak – mixed hardwood forest. Calcareous communities occur elsewhere at the site but were not mapped comprehensively. Surrounding land use is forest, with agriculture, previously mined lands, and residential development higher on the slopes. Invasive species are present, especially along paths, but still low in density at the study communities.



Site name: Finnegan's Ledges Physiographic setting: Appalachian Plateau province, Allegheny Mountain section. County: Fayette Geology: moderately calcareous (Mauch Chunk formation)

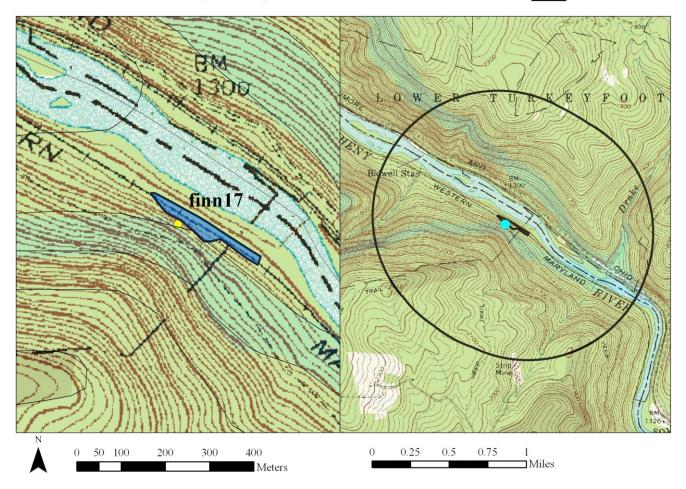
This site has a large mesic calcareous outcrop, on Mauch Chunk limestone just above the rails-to-trails path along the Youghiogheny river. Weathering on the rock faces indicates the outcrops are natural, and not the result of blasting. Invasive species cover is very low, and the surrounding land use is forest.

mean	mean C						total	%	protection	calc002	calc012 sp
С	native	Ν	А	Ι	I'	% exotic	sp.	native	status	sp count	count
5.7	6.2	36	2	37.2	55.6	6%	38	95%	р	1	5

Limestone Communites Geology Categories

mesic calcareous outcrop Acidic sed/metased Acidic shale Moderately calcareous sed/metased

1000 m site buffer



Site name: Williamson Park Physiographic setting: Piedmont province, Piedmont Lowland section. County: Lancaster Geology: strongly calcareous (Conestoga Formation)

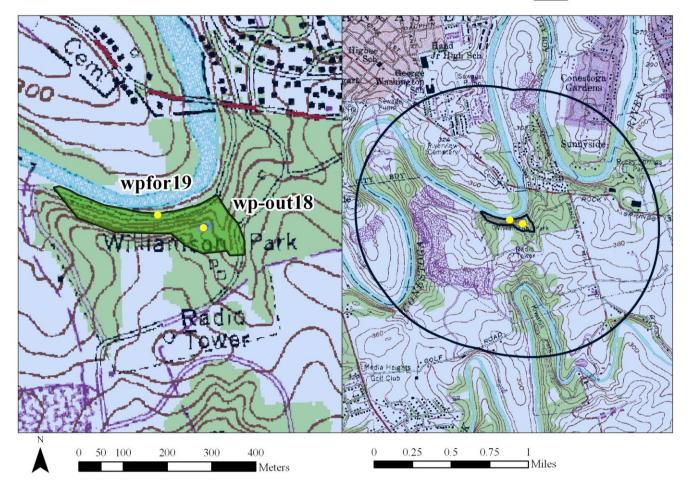
This is the eastern-most site in our study area, and our only Lancaster County site. Two plots were taken on a steep north-facing forested slope with mesic outcrops near the summit. The forested area is very small. The western and southern edges have dense invasive species cover, although the center remains mainly native. Surrounding land is developed for recreational use and residential development.

mean	mean C						total	%	protection	calc002	calc012 sp
С	native	Ν	А	Ι	Ι'	% exotic	sp.	native	status	sp count	count
4.8	5.7	70	10	47.5	45.1	14%	80	88%	р	6	7

Limestone Communites Geology Categories



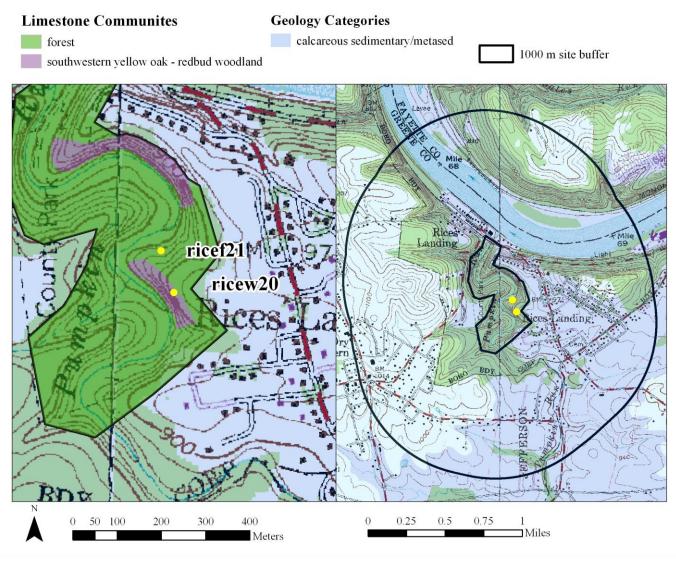
1000 m site buffer



Site name: Rice's Landing Physiographic setting: Appalachian Plateau province, Waynesburg Hills section. County: Greene Geology: strongly calcareous (Monongahela formation)

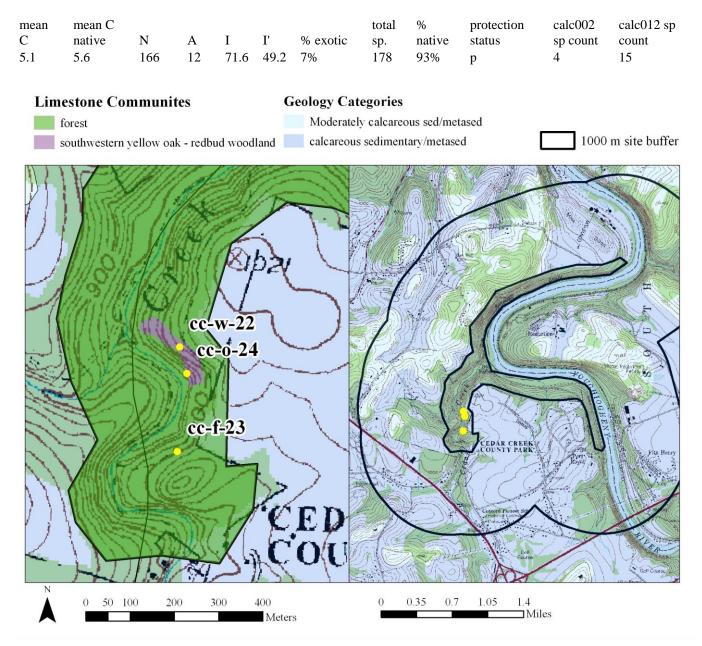
This site is a forested county park along Pumpkin Run, a tributary to the Monongahela River. It includes a variety of landforms and aspects. There is calcareous floodplain forest along the stream, yellow oak – redbud woodland on very steep south and west facing slopes, and forest that is variably mesic to dry-mesic in other portions. Plot 20 is in a steep woodland area, while plot 21 is a dry-mesic forest. The soil pH is quite high on the steeper slopes, and ranges from 6.0-7.0 on the gentler slopes and floodplains.

mean C 4.1							sp.	native	protection status P	sp count	count	
------------------	--	--	--	--	--	--	-----	--------	---------------------------	----------	-------	--



Site name: Cedar Creek Physiographic setting: Appalachian Plateaus province, Pittsburgh Low Plateau section. County: Westmoreland Geology: strongly calcareous (Monongahela Formation)

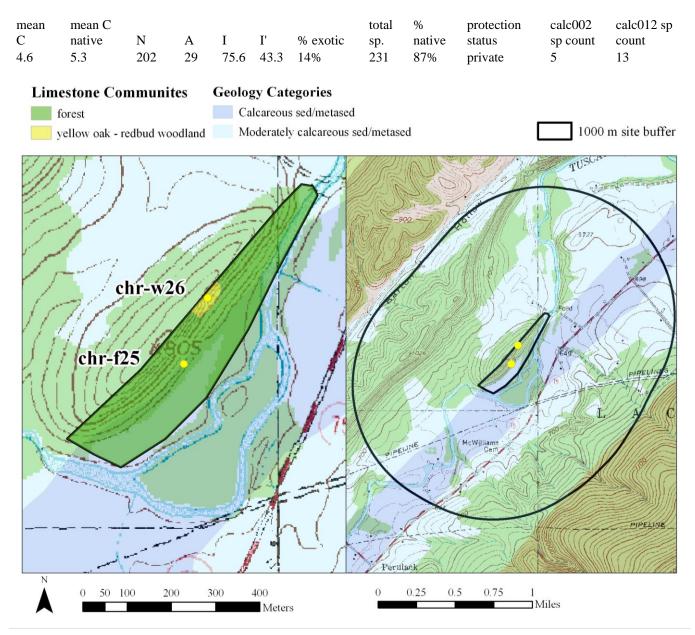
The site is a county park with forested slopes along Cedar Creek and the Youghiogheny River. Much of the area is calcareously influenced. With a variety of landforms and aspects in a small area, it includes floodplain, mesic forest community, and dry forest and woodland. The woodlands occur in small patches on very steep upper slopes, south or west facing. A few small calcareous outcroppings are present, including a tufa formation by the stream. Invasive species have low cover. Surrounding land use is farmland, residential development, and previously mined lands.



Site name: Christian Retreat Physiographic setting: Ridge and Valley province, Appalachian Mountain section. County: Juniata

Geology: moderately calcareous (Onondaga and Old Port formations, undivided) and strongly calcareous (Keyser and Tonoloway formations, undivided).

This site includes a small patch of forest on a small, steep hill. The northwestern slope of the hill is more acidic in character, while the southeastern slope is calcareous. The summit includes small areas of yellow oak – redbud woodland with rock outcroppings; the slope is mesic forest with a number of calcareous indicators, including green violet (*Hybanthus concolor*) and a sedge (*Carex careyana*). Invasive shrub and herb species are dense in portions of the slope. Surrounding land use is forest and farmland.



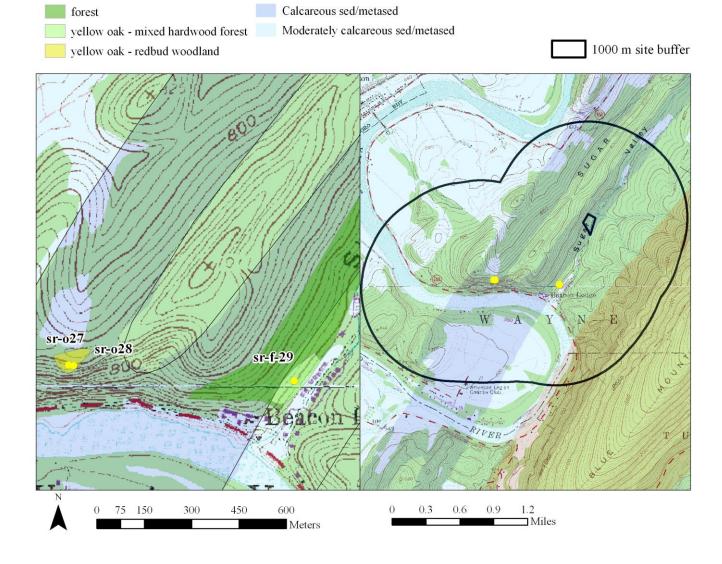
Site name: Sugar Ridge Physiographic setting: Ridge and Valley province, Appalachian Mountain section. County: Mifflin Geology: strongly calcareous (Keyser and Tonoloway formations, undivided).

Limestone Communites

The sampled areas at this site are part of a large forested ridge, Sugar Ridge. The surface geology is strongly calcareous along the lower slopes of the ridge, and limestone outcrops also occur at the summit of the water gap cut by the Juniata River. Two plots were taken in this area, one on rock outcroppings and one plot in a sloped woodland just above the outcroppings at the summit of the slope. The species composition is similar, and the entire area was classified as yellow oak – redbud woodland. Plot 29 is a dry portion of the lower slope forest, classified as yellow oak – mixed hardwood forest. Other more mesic calcareous forests are also present along the lower slopes of the ridge but were not sampled. Invasive species are very dense at the eastern end of the woodland area, but the western end is still predominately native.

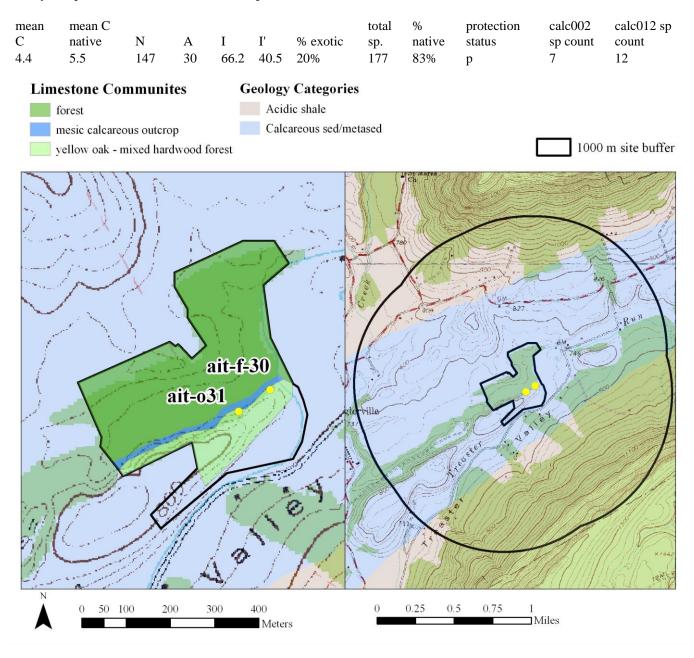
mean	mean C						total	%	protection	calc002	calc012 sp
С	native	Ν	А	Ι	I'	% exotic	sp.	native	status	sp count	count
4.5	5.4	209	41	78.5	40.9	20%	250	84%	np	5	15

Geology Categories



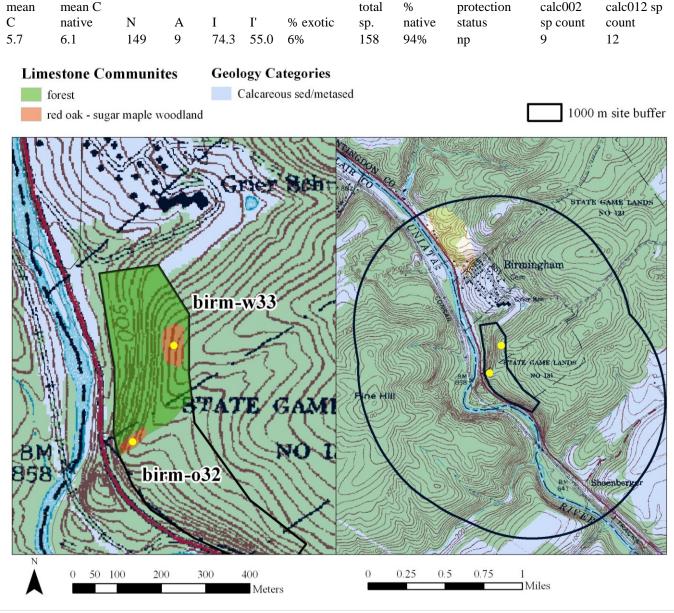
Site name: Aitkins Cave Physiographic setting: Ridge and Valley province, Appalachian Mountain section. County: Mifflin Geology: strongly calcareous (Coburn through Nealmont formations, undivided).

This site is a small patch of lowland calcareous forest surrounding a cave entrance. The northern portion is young sugar maple forest with low diversity, but high cover of the calcareous indicator Carex jamesii. The central portion of the site has high soil pH (7.0-8.0), but very few indicators are present. Hemlock is prominent in the canopy, and there are many sinkholes and wet areas; invasive species are moderately dense. The ridge at the southern edge is drier, with yellow oak – mixed hardwood forest, including many calcareous indicator species. The northern slope is very steep with mesic calcareous outcrops.



Site name: Birmingham Physiographic setting: Ridge and Valley province, Appalachian Mountain section. County: Huntingdon Geology: strongly calcareous (Gatesburg formation)

This site is a calcareous slope above the Juniata River. Although it is mainly forested, much of the slope has rocky scree; the rock appears to be calcareous sandstone. The soils are correspondingly much sandier at this site than most other sites, which tend to have clay soils. The lower slope includes mesic species such as bladdernut (*Staphylea trifolia*), green violet (*Hybanthus concolor*), and bulblet fern (*Cystopteris bulbifera*). The upper slope is much drier, with woodland indicators such as (*Polygala senega*), (*Arabis patens*), and (*Aureolaria flava*). Near the summit the canopy is stunted and somewhat sparse, with about 70% cover; this area was classified as red oak – sugar maple woodland. The southern end forms a nose with substantial rock outcroppings; plot 32 was taken in this area. Although outcrop obligates such as (*Asplenium trichomanes*) were present in this location, the overall species composition did not differ significantly from plot 33, and both are classified as woodlands.



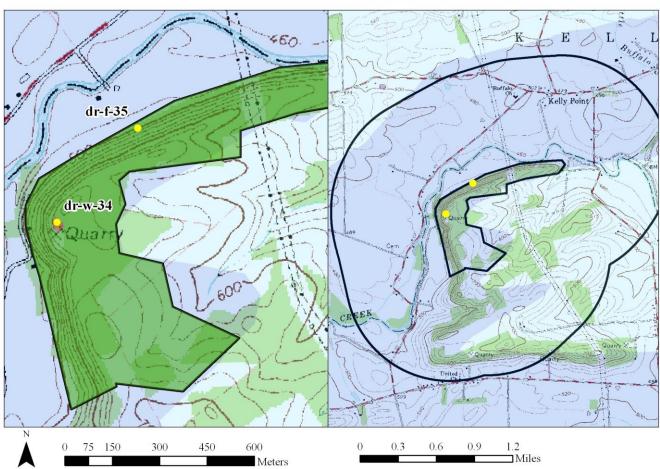
Site name: Dale's Ridge Physiographic setting: Ridge and Valley province, Susquehanna Lowland section. County: Union Geology: strongly calcareous (Keyser and Tonoloway formations, undivided).

This site is a narrow forested ridge surrounded by farmland. Most of the ridge is heavily dominated by invasive species, including shrub honeysuckles (*Lonicera spp.*) and Norway maple (*Acer platanoides*). Some areas, however, including the portions sampled, are still relatively invasive free. Plot 34 is in a small area of woodland with natural outcroppings at the summit of the slope. It is adjacent to a quarry, and may have been cleared in the past. Plot 35 is in a mesic lower-slope forest.

mean	mean C						total	%	protection	calc002	calc012 sp
С	native	Ν	А	Ι	Ι'	% exotic	sp.	native	status	sp count	count
4.6	5.6	129	26	63.8	42.0	20%	155	83%	р	2	13

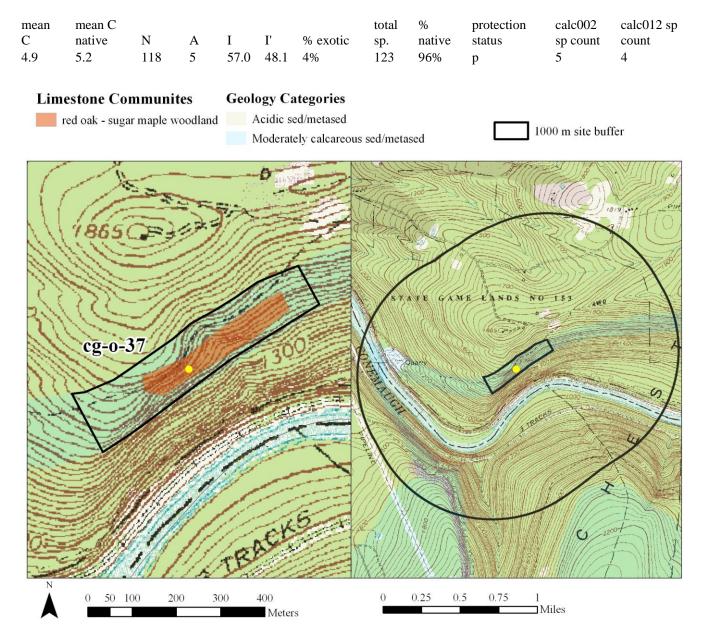
Limestone Communites Geology Categories

forest	Calcareous sed/metased	
red cedar woodland	Moderately calcareous sed/metased	1000 m site buffer



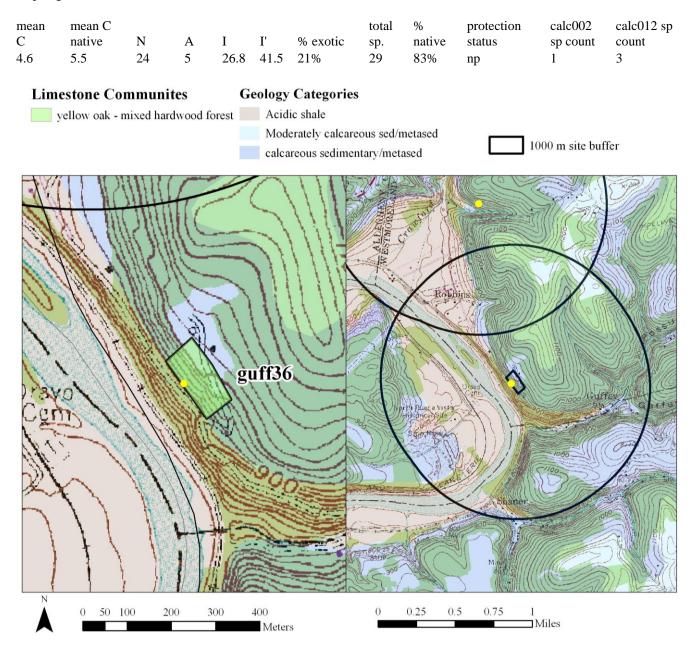
Site name: Conemaugh Gap Physiographic setting: Appalachian Plateaus province, Allegheny Mountain section. County: Indiana Geology: moderately calcareous (Mauch Chunk formation).

This site is a steep outcropping of the Loyalhanna limestone in a gap cut by the Conemaugh River. The surrounding land use is forested, generally with acidic soil and species composition. The outcrop is quite dry in character, with sparse woody vegetation. Yellow oak and redbud were absent or very sparse at the site, which grouped in ordination and cluster analysis with the red oak – sugar maple woodland type. It also has an unusually high number of limestone indicator species compared with other Loyalhanna outcroppings, which may also have contributed to its placement in a group whose other sites are located in the Ridge and Valley province.



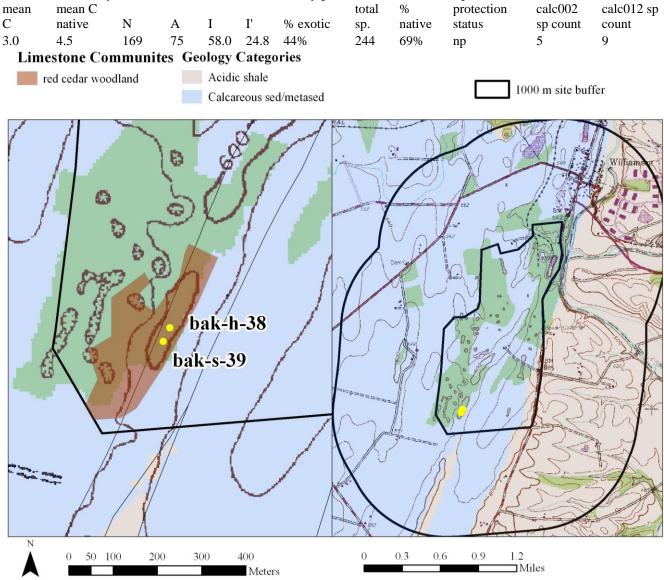
Site name: Guffey Railroad Slope Physiographic setting: Appalachian Plateaus province, Waynesburg Hills section. County: Westmoreland Geology: strongly calcareous (Monongahela formation).

Plot 36 was sampled in a small patch of forest on a steep southwest-facing slope above the Monongahela River. The slope is bisected by a road and a railroad track, with the sample location in between these corridors. It is somewhat disturbed, with invasive shrub species moderately common. The dominant species at the site are calcareous indicators - yellow oak (*Quercus muhlenbergii*), bladdernut (*Staphylea trifolia*), and twinleaf (*Jeffersonia diphylla*). However, overall species diversity was lower; this may be a factor of the late date of sampling, or the disturbed character of the site.



Site name: Baker Quarry Physiographic setting: Ridge and Valley province, Great Valley section. County: Franklin Geology: strongly calcareous (St. Paul group and Chambersburg formation).

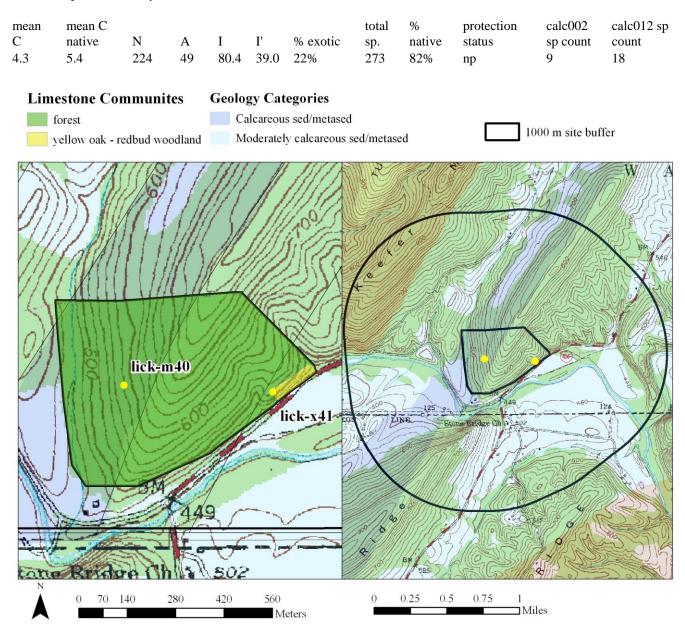
Plots 38 and 39 were sampled in the southern end of a large complex of shrublands, grasslands, and early successional forest on limestone geology. It is one of only a few calcareous sites remaining in natural cover in the Great Valley section of the Ridge and Valley province, and hosts a number of species that reach their northern limit in Franklin County. The land is owned by a mining company, and some portions may have been mined or timbered; the forest cover is all relatively young, and earlier reports indicate that herbaceous areas have been reduced in recent decades. The area sampled was a red cedar woodland with small patches of more open grassland and shrubland. One herbaceous plot and one woodland plot were collected (39). Although there were clearly observable differences in the cover of grassland species and of red cedar (*Juniperus virginiana*) between the two plots, these were not sufficient to merit segregation into separate types. Invasive species are quite dense in some portions of the early successional forest, but minimally present in the areas sampled.



Site name: Licking Creek Physiographic setting: Ridge and Valley province, Great Valley section. County: Franklin

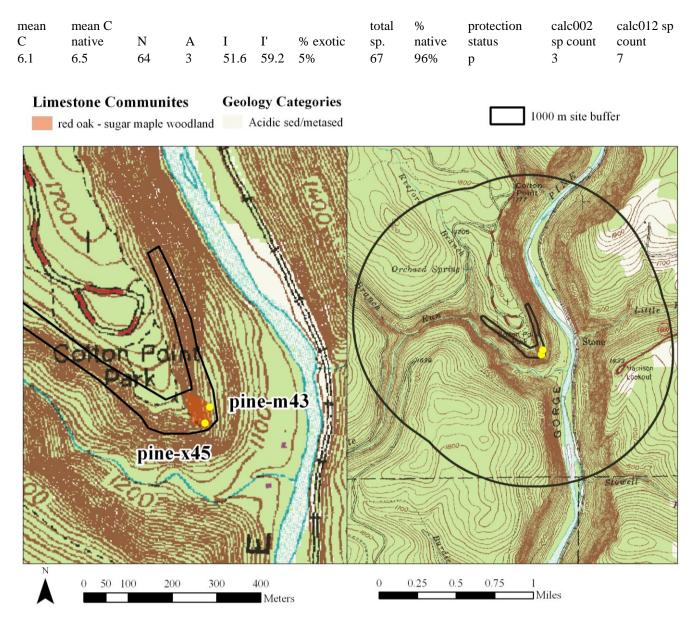
Geology: moderately calcareous (Onondaga and Old Port formations, undivided) and strongly calcareous (Keyser and Tonoloway formations, undivided).

Plots 40 and 41 were collected on the southern end of a forested ridge, with limestone surface geology. Plot 40 is more mesic, although a slightly drier and more exposed subsite than the forest immediately surrounding it. Plot 41 was in a small patch of yellow oak – redbud woodland on a steep slope. Invasive species cover was low at both sample locations, although fairly dense in some areas on the slopes between the two sample points. Surrounding land use is predominantly forest, with some farmland.



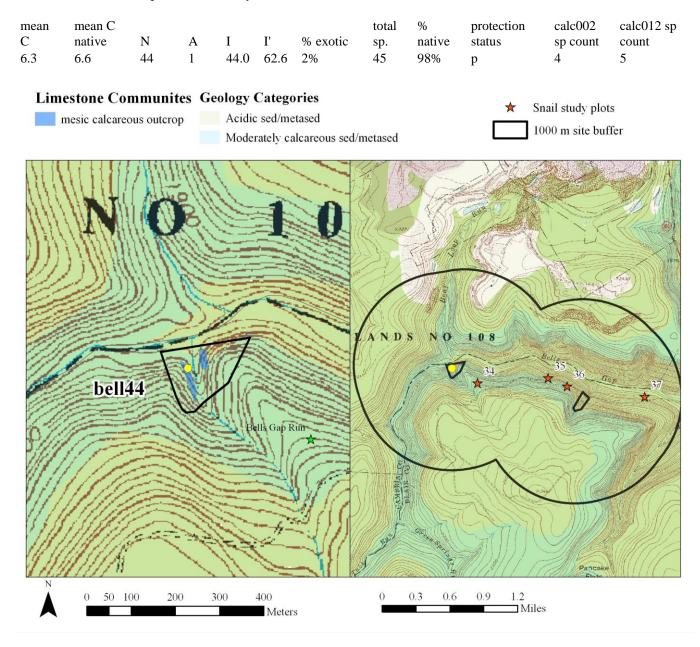
Site name: Pine Creek Gorge Physiographic setting: Ridge and Valley province, Deep Valleys section. County: Tioga Geology: Catskill formation

Plots 43 and 45 were collected at outcroppings along the upper slope of the Pine Creek Gorge canyon. These are the northern-most sites in the study. Calcareous shale or sandstone geology is exposed in a relatively narrow strip along much of the canyon slopes, on both sides; many locations similar to the sample points have been documented in the canyon. The surrounding area is forest, predominantly acidic in character. Plot 45 was more xeric and had much less canopy cover than plot 43. However, both plots were included in the red oak – sugar maple grouping. Yellow oak and redbud are absent from these sites.



Site name: Bell's Gap Run Physiographic setting: Appalachian Plateaus province, Allegheny Front section. County: Blair Geology: moderately calcareous (Mauch Chunk formation).

Bell's Gap Run is a forested stream valley with seams of Mauch Chunk geology on both slopes. The Loyalhanna limestone outcrops along the southern slope and on either side of a small tributary, where plot 44 was sampled. The tributary outcroppings are in a cold air drainage, and noticeably cooler in temperature than surrounding areas, with several northern species present such as American yew (*Taxus americana*). The forest surrounding the outcroppings is acidic in character, with pH 4.5-5.5. Another drainage channel along the southern slope is also calcareously influenced, with a large population of glade fern (*Diplazium pycnocarpon*). The surrounding land use is forest, and invasive species are mainly absent.



Site name: Chestnut Ridge Physiographic setting: Appalachian Plateau province, Allegheny Mountain section. County: Fayette Geology: moderately calcareous (Mauch Chunk formation)

This site has two mid-sized mesic calcareous outcrops of Mauch Chunk limestone mid-slope along Chestnut Ridge, surrounded by more acidic geology. Invasive cover is very low, and the surrounding land use is forest.

mean	mean C						total	%	protection	calc002	calc012 sp
С	native	Ν	А	Ι	Ι'	% exotic	sp.	native	status	sp count	count
5.8	5.8	50	0	41.0	57.9	0%	50	100%	р	1	5

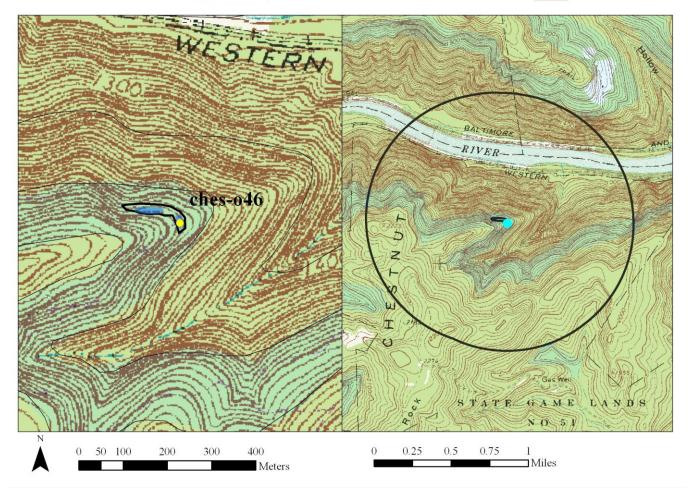
Limestone Communites Geology Categories

mesic calcareous outcrop

Acidic sed/metased

Moderately calcareous sed/metased

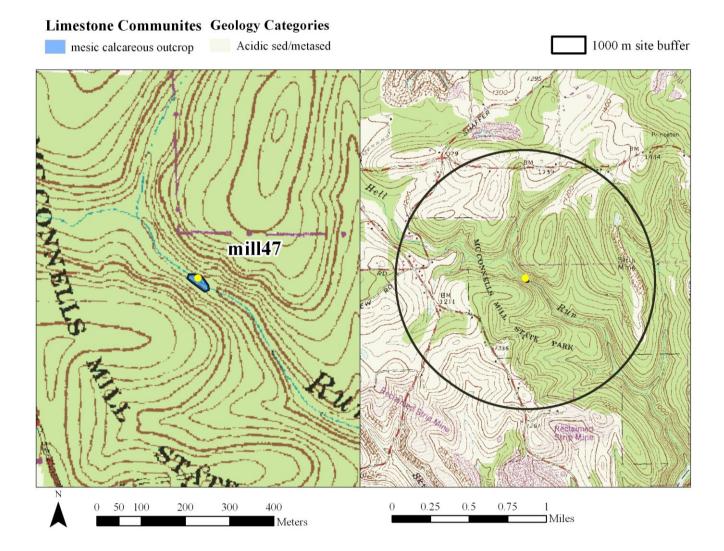
1000 m site buffer



Site name: McConnell's Mills OutcropPhysiographic setting: Appalachian Plateaus province, Pittsburgh Low Plateau section.County: LawrenceGeology: outcropping of Van Port limestone of Allegheny Formation. Surrounded by acidic geology.

This site has a mesic calcareous outcrop on Van Port limestone. It is our only study site on this geology. The outcrop community includes some calcareous indicators, but is relatively small and low-diversity. The surrounding land use is forest, which is mainly more acidic in soil pH and species composition.

mean	mean C						total	%	protection	calc002	calc012 sp
С	native	Ν	А	Ι	I'	% exotic	sp.	native	status	sp count	count
4.7	5.0	33	2	28.9	45.8	6%	35	94%	р	1	2



Appendix 2: Calciphile Taxa Habitat Preferences

Expert assessment of habitats used by each taxon is shown with "x"s. Where plot data is available for a taxon, it is shown in a separate row indicating the number of plots with the taxon in each habitat. For taxa with plot data, the presence/absence rows were amended to match plot data; presence was indicated if the taxon was found in more than one plot for a habitat type, while presence was removed if the taxon was not found in any plots of a habitat type.

Terrestrial and wetland taxa are placed in separate tables. Taxa with asterisks are found in both tables.

Terrestrial habitat types match the community types identified in Section III except that all woodland types are combined, and all mesic forests are considered one habitat type.

Ratings are based on field experience and consultation of published literature, including flora habitat descriptions and U.S. Fish and Wildlife Service wetland codes. Taxa were assigned more than one category where appropriate.

The "rock specialist" category is used to indicate whether a species grows mainly or exclusively on rock outcroppings. "Fac-r" is assigned to taxa which are often but not exclusively found on rock outcroppings, while "obl" is assigned to species that only occur on rocks. This category was added because rock outcroppings vary in size, and many rock specialists can be found on small rock piles in forested landscapes in addition to larger outcroppings.

	sideoats grama grassland	wood- land	yellow oak forest	mesic forest	mesic outcrop	rock specialist	unclassified forest	total plots
Amelanchier humilis*		Х				fac-r		
Amelanchier sanguinea*		1		1		fac-r		2
Amelanchier sanguinea*		Х				fac-r		
Anemone acutiloba		7	1	7	3			18
Anemone acutiloba		х	Х	х	х			
Anemone cylindrica	Х							
Aquilegia canadensis		13		6	3	obl		22
Aquilegia canadensis		х		х	х	obl		
Arabis hirsuta var. adpressipilis		х				fac-r		
Arabis hirsuta var. pycnocarpa		х				fac-r		
Arabis patens		1				fac-r		1
Arabis patens		х	Х			fac-r		
Arabis shortii var. shortii				х				
Arnoglossum atriplicifolium			Х	х				
Aruncus dioicus				х				
Asplenium resiliens		?			?	obl		
Asplenium rhizophyllum		1		3	4	obl		8
Asplenium rhizophyllum				х	х	obl		
Asplenium ruta-muraria		2				obl		2
Asplenium ruta-muraria var. cryp	otolepis				Х	obl		
Asplenium trichomanes		3		1	2	obl		6
Asplenium trichomanes ssp. quad	rivalens	х			Х	obl		
Astragalus canadensis	Х	х						
Astragalus neglectus*		х	140			fac-r		

Terrestrial Taxa Habitat Preferences

Scientific Name	sideoats grama grassland	wood- land	yellow oak forest	mesic forest	mesic outcrop	rock specialist	unclassified forest	total plots
Aureolaria flava var. flava		Х	Х					
Bouteloua curtipendula	7	2						9
Bouteloua curtipendula	х	Х						
Brickellia eupatorioides	2							2
Brickellia eupatorioides	х							
Bromus kalmii	1							1
Bromus kalmii	Х							
Campanula americana		1	1	1				3
Campanula americana		х	Х	х				
Carex albursina		3	3	10				16
Carex albursina		Х	Х	Х				
Carex careyana*			1					1
Carex careyana*		Х		Х				
Carex eburnea		Х			х	fac-r		
Carex formosa				х				
Carex geyeri		х						
Carex granularis			1					1
Carex hitchcockiana			1	1				2
Carex hitchcockiana		х	х	х				
Carex jamesii		2	4					6
Carex jamesii		х	х					
Carex leavenworthii	х							
Carex oligocarpa		1	1					2
Carex oligocarpa		х	х					
Carex woodii				х				
Celastrus scandens		3		4				7
Celastrus scandens		X		х				
Chrysogonum virginianum		?						
Cirsium altissimum*	1							1
Cirsium altissimum*	X		Х	х				
Clematis occidentalis		х		X	х	fac-r		
Clematis viorna	х	X						
Corallorhiza wisteriana				?				
Cornus rugosa		Х	Х					
Cryptogramma stelleri					1	obl		1
Cryptogramma stelleri					x	obl		-
Cypripedium parviflorum var.	pubescens		Х					
Cystopteris bulbifera	r	1	28	2	6	obl		9
Cystopteris bulbifera		•		X	x	obl		
Cystopteris laurentiana					X	0.01		
Cystopteris tennesseensis					X			
Delphinium exaltatum		4			~			4
Delphinium exaltatum		X						
Dichanthelium oligosanthes	3	Λ						3
Dichanthelium oligosanthes	X							5
Diplazium pycnocarpon	Λ			х				
Dodecatheon amethystinum		1		Λ		fac-r		1
Dodecatheon amethystinum						fac-r		1
Dodecatheon meadia		Х	1			fac-r		1
			1			lat-1		1

Scientific Name	sideoats grama grassland	wood- land	yellow oak forest	mesic forest	mesic outcrop	rock specialist	unclassified forest	total plots
Dodecatheon meadia		Х			Х	fac-r		
Erigeron pulchellus		5						5
Erigeron pulchellus		х						
Euonymus atropurpureus			Х	Х				
Eupatorium altissimum		2						2
Eupatorium altissimum	х	х						
Euphorbia commutata		х	Х	Х				
Fragaria vesca ssp. americana		Х	Х			fac-r		
Galium boreale		1						1
Galium boreale		Х	Х					
Galium concinnum		1	2					3
Galium concinnum		Х	Х					
Geranium robertianum	Х							
Helianthus strumosus*	2	1						3
Helianthus strumosus*	х	х	х					
Hybanthus concolor		5		2				7
Hybanthus concolor		х	х	х				
Hydrastis canadensis		1		1				2
Hydrastis canadensis		х	х	х				
Jeffersonia diphylla		2	3					5
Jeffersonia diphylla		х	х	х				
Lithospermum canescens	3	2						5
Lithospermum canescens	х	х						
Maianthemum stellatum*		2						2
Maianthemum stellatum*		х						
Melica nitens		Х	Х	х				
Muhlenbergia glomerata		X	X					
Muhlenbergia sobolifera		2	1					3
Muhlenbergia sobolifera		X				obl		
Myosotis laxa				1				1
Obolaria virginica				X				
Onosmodium molle var.								
hispidissimum	х							
Ophioglossum engelmannii		1						1
Ophioglossum engelmannii	?	?						
Oxalis grandis		2	2					4
Oxalis grandis		х	х	х				
Paxistima canbyi		1				obl	1	1
Paxistima canbyi		х				obl		
Pellaea atropurpurea		10		1		obl		11
Pellaea atropurpurea		х				obl		
Pellaea glabella		х			Х	obl		
Piptatherum racemosum		10	1	4		fac-r		15
Piptatherum racemosum		X	X	X		fac-r		
Poa cuspidata			X					
Polygala senega		8						8
Polygala senega var. latifolia		X						
Polygala senega var. senega		X						
Prunus alleghaniensis	Х	X	Х					

	sideoats grama grassland	wood- land	yellow oak forest	mesic forest	mesic outcrop	rock specialist	unclassified forest	total plots
Quercus muehlenbergii		16	5	6				27
Quercus muhlenbergii		х	Х	х				
Ranunculus allegheniensis				х				
Ranunculus fascicularis	Х	х						
Ratibida pinnata	Х	Х						
Rhamnus lanceolata			Х					
Rhus aromatica var.								
aromatica		6					2	6
Rhus aromatica var. aromatica		Х	Х					
Ribes americanum*				1				1
Ribes hirtellum*		Х						
Ruellia caroliniensis		Х	Х	Х				
Ruellia humilis	1	1						2
Ruellia humilis	Х	Х						
Ruellia strepens		Х		х	Х	fac-r		
Shepherdia canadensis	х							
Silphium asteriscus var. trifoliatur	n	3		1	4			4
Silphium asteriscus var. trifoliatus	п	Х	Х					
Solidago flexicaulis		6	1	10	4	fac-r		21
Solidago flexicaulis		Х		х	х	fac-r		
Solidago rigida	Х							
Solidago squarrosa	х							
Sporobolus neglectus	х							
Symphoricarpos albus var. albus		Х						
Symphyotrichum ericoides ssp. er	icoides	х			х	fac-r		
Symphyotrichum laeve var. laeve		Х	Х					
Symphyotrichum lowrieanum		2		2				4
Symphyotrichum lowrieanum		х	х	х				
Symphyotrichum oblongifolium		х	Х			fac-r		
Symphyotrichum patens	Х	Х		х				
Symphyotrichum phlogifolium		2						2
Symphyotrichum phlogifolium	х	х	х					
Symphyotrichum shortii		5	1	5				11
Symphyotrichum shortii		х	Х	х				
Symphyotrichum urophyllum		5				fac-r		5
Symphyotrichum urophyllum		X				fac-r		-
Taenidia integerrima	1	12	1	1				15
Taenidia integerrima		X	X	-				
Thalictrum coriaceum		X	X					
Thalictrum dioicum		9	4	5	1	fac-r	2	19
Thalictrum dioicum		X	X	x	•	fac-r		.,
Trillium flexipes		~	21	X		1		
Trillium nivale		х	х	2 x				
Triosteum aurantiacum		3	1				2	4
Triosteum aurantiacum		X	X				2	т
Triosteum perfoliatum		Λ	X					
Valerianella chenopodiifolia*		1	1					2
Valerianella chenopodiifolia*		-		х				- 2
Veratrum latifolium		Х	X X	Λ				

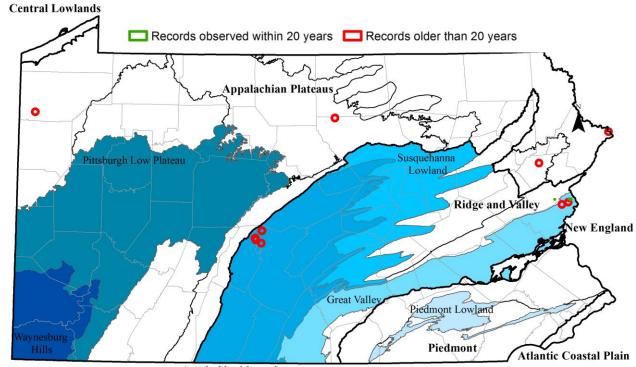
Scientific Name	sideoats grama grassland	wood- land	yellow oak forest	mesic forest	mesic outcrop	rock specialist	unclassified forest	total plots
Zanthoxylum americanum		3		2			1	5
Zanthoxylum americanum		Х	х	х				
Zigadenus glaucus					Х			
Zizia aptera		7	1	2		fac-r		10
Zizia aptera		х	Х	Х	х	fac-r		
total # taxa in habitat								
type	16	53	36	24	10	26		

Wetland Taxa Habitat Preferences

Amelanchier humilis*			
	Х		
Amelanchier sanguinea*	Х		
Astragalus neglectus*		Х	
Cardamine pratensis var. palustris	Х		
Carex alata	Х		
Carex aurea	Х		
Carex bebbii	Х		
Carex careyana*		Х	
Carex comosa	Х		
Carex crawfordii	Х		
Carex cryptolepis	Х		
Carex disperma	Х		
Carex flava	Х		
Carex garberi	Х		
Carex granularis var. haleana	Х		
Carex hystericina	Х		
Carex interior	Х		
Carex mitchelliana	Х		
Carex pellita	Х		
Carex prairea	Х		
Carex pseudocyperus	Х		
Carex retrorsa	Х	Х	
Carex schweinitzii	Х		
Carex shortiana	Х	Х	
Carex sterilis	Х		
Carex tetanica	Х		
Carex typhina	х	Х	
Carex viridula	х		
Cirsium altissimum*		Х	
Conioselinum chinense	Х		
Cyperus diandrus	Х		
Cypripedium parviflorum var. mokasen	х		
Cypripedium reginae	Х		
Eleocharis elliptica	Х		
Eleocharis intermedia	х		
Eleocharis rostellata	х		
Equisetum scirpoides	Х		
Equisetum variegatum	х		
Eriophorum gracile	х		

Scientific name	Wetland	Floodplain	Aquatic
Eriophorum viridicarinatum	х		
Euphorbia purpurea	Х		
Filipendula rubra	Х		
Galium labradoricum	Х		
Gentianopsis crinita	Х		
Gentianopsis virgata	Х		
Geum rivale	Х		
Helianthus strumosus*		Х	
Hierochloe hirta	Х		
Juncus alpinoarticulatus ssp. nodulosus	Х		
Juncus arcticus var. littoralis	Х		
Juncus brachycarpus	Х		
Juncus brachycephalus	Х		
Juncus dudleyi	Х	Х	
Juncus nodosus	Х		
Lathyrus palustris	?		
Liparis loeselii	Х		
Lobelia kalmii	Х		
Lobelia siphilitica	Х		
Maianthemum stellatum	Х		
Malaxis monophyllos var. brachypoda	Х		
Mitella nuda	Х		
Myosotis laxa	Х		
Myriophyllum verticillatum			Х
Parnassia glauca	Х		
Pedicularis lanceolata	Х		
Persicaria setacea	Х		
Phragmites australis ssp. americanus	Х		
Pilea fontana	Х		
Platanthera aquilonis	Х		
Platanthera dilatata var. dilatata	Х		
Potamogeton filiformis var. borealis			Х
Potamogeton friesii			Х
Potamogeton gramineus			Х
Potamogeton hillii			Х
Potamogeton praelongus			Х
Potamogeton richardsonii			Х
Potentilla fruticosa	х		
Ptelea trifoliata		Х	
Rhamnus alnifolia	х		
Rhynchospora capillacea	?		

Scientific name	Wetland	Floodplain	Aquatic
Ribes americanum	Х		
Ribes hirtellum	Х		
Ribes triste	Х		
Salix candida	?		
Salix serissima	Х		
Schoenoplectus acutus	Х		
Scirpus pendulus	Х		
Scleria verticillata	Х		
Spiranthes lucida	Х	Х	
Spiranthes romanzoffiana	Х		
Symphyotrichum boreale	Х		
Triadenum walteri	Х		
Trollius laxus	Х		
Valerianella chenopodiifolia*		Х	
Viburnum trilobum	Х		



Appendix 3: Calcareous Wetland Taxa With Range Contractions

Appalachian Mountain

Figure 62. State distribution of Conioselinum chinense.

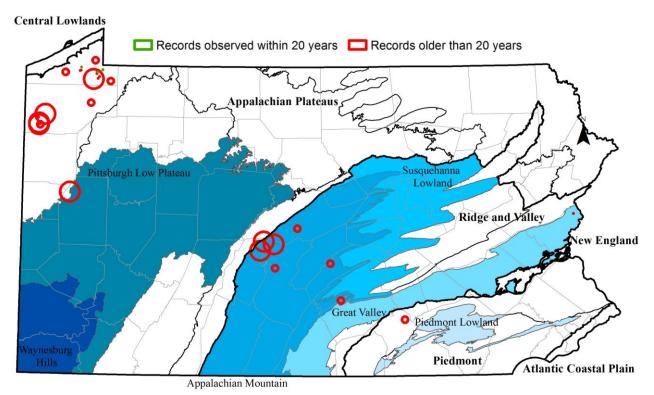
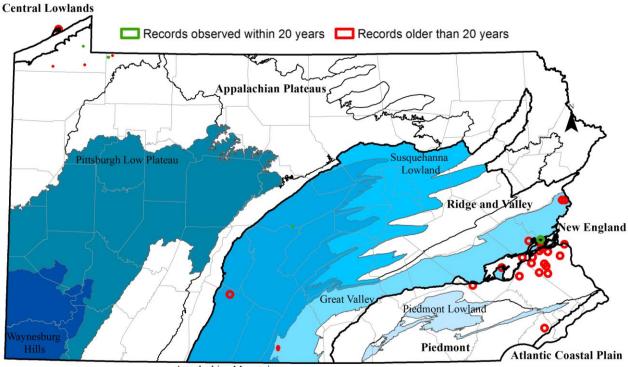


Figure 63. State distribution of Cypripedium reginae.



Appalachian Mountain

Figure 64. Statewide distribution of *Eriophorum gracile*.

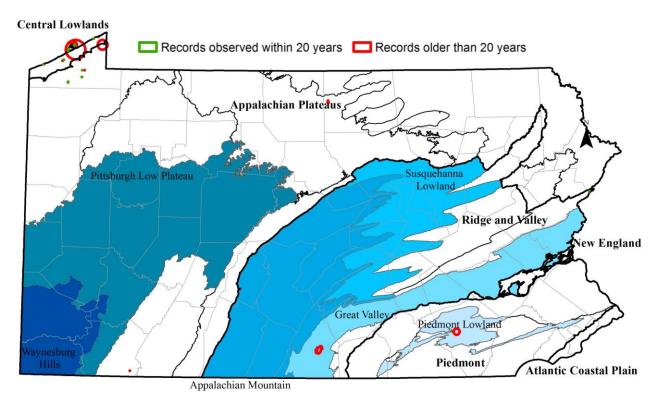
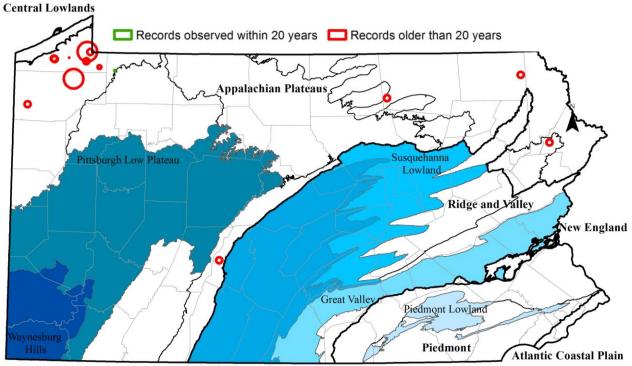
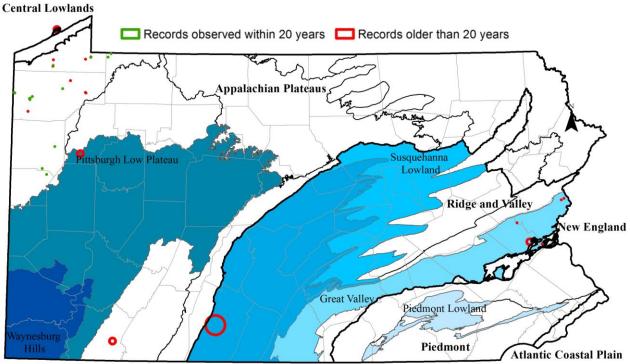


Figure 65. Statewide distribution for Juncus brachycephalus.



Appalachian Mountain

Figure 66. Statewide distribution for Malaxis monophyllos.



Appalachian Mountain

Figure 67. Statewide distribution for Salix serissima.