

A Preliminary Study of the Vegetation of Vernal Pools of Acadia National Park, Maine, U.S.A

Author(s) :Brett Ciccotelli, Tanner B. Harris, Bruce Connery, and Nishanta Rajakaruna

Source: Rhodora, 113(955):260-279. 2011.

Published By: The New England Botanical Club, Inc.

DOI:

URL: <http://www.bioone.org/doi/full/10.3119/0035-4902-113.955.260>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

A PRELIMINARY STUDY OF THE VEGETATION OF
VERNAL POOLS OF ACADIA NATIONAL PARK,
MAINE, U.S.A.

BRETT CICCOTELLI

College of the Atlantic, 105 Eden Street, Bar Harbor, ME 04609
Current Address: 3 Linden Court, Blackwood, NJ 08012

TANNER B. HARRIS

Department of Plant, Soil, and Insect Sciences, University of Massachusetts,
Fernald Hall, 270 Stockbridge Road, Amherst, MA 01003
Current Address: WRA, Inc. 2169-G East Francisco Blvd., San Rafael, CA 94901

BRUCE CONNERY

Acadia National Park, P.O. Box 177, Bar Harbor, ME 04609

NISHANTA RAJAKARUNA¹

Department of Biological Sciences, San José State University,
One Washington Square, San José, CA 95192

¹Author for Correspondence; Current Address: College of the Atlantic,
105 Eden Street, Bar Harbor, ME 04609
e-mail: nrajakaruna@gmail.com

ABSTRACT. We conducted a preliminary floristic study of six vernal pools in Acadia National Park on Mount Desert Island, Maine. Plant species were recorded on three sampling dates from April to October, 2008. Sixty-five vascular plant species from 26 families were recorded. Of these, 27 are considered occasional or uncommon in Acadia National Park. Thirteen species are new reports for vernal pools in the northeastern United States. This represents the first published study of the vernal pool flora of Acadia National Park.

Key Words: biogeography, edaphic islands, ephemeral wetlands, habitat conservation, insular ecology, isolated wetlands, plant-soil relations

Vernal pools have received much attention as they, like other edaphic islands (Rajakaruna and Boyd 2008), harbor distinct assemblages of plants and animals, including many rare and endangered species (Calhoun and deMaynadier 2008; Deil 2005; Gerhardt and Collinge 2003). Vernal pools are variously defined as seasonal or ephemeral wetlands that form in permanent basins

during the cooler or wetter part of the year and lack predatory fish populations (Sharitz and Pennings 2006; Tiner et al. 2002). In the United States, although more commonly associated with grasslands along the west coast (Kruckeberg 2006), woodland vernal pools occur throughout the Northeast (Sharitz and Pennings 2006; Tiner et al. 2002). Vernal pools are flooded each year in spring and fall, providing both a breeding habitat for a number of amphibians and invertebrates as well as a refuge for many native plant species (Barbour et al. 2005; Holland and Jain 1981; Zedler 2003). State and federal conservation efforts addressing vernal pools and isolated wetlands are limited. Existing efforts have been weakened in recent years by U.S. Supreme Court actions (Oscarson and Calhoun 2007; Zedler 2003), leaving nearly 29% of the United States' wetlands without protection (Cutko and Rawinski 2008). With little federal protection, many states are working to protect their biologically diverse vernal pools from development, poor land use practices, and climate change (Brooks 2009; Calhoun et al. 2003).

Vernal pools often contribute much to patterns of local and regional plant diversity (Barbour et al. 2005; Deil 2005; Schlisling and Sanders 1982). For example, in California, at least 43 plant species are restricted to vernal pools (Keeler-Wolf et al. 1998). Species that adapt to vernal pool conditions can experience reduced competition from invasive species and close relatives and become reproductively isolated, leading to further specialization and subsequent diversification (Barbour et al. 2005; Baskin 1994; Emery 2009; Linhart 1976). Cutko and Rawinski (2008) note that although there are no vernal pool endemics documented for northeastern North America, there have been no systematic assessments of rare plants associated with vernal pools in the region. Despite the lack of documented vernal pool endemics in the Northeast, numerous rare plant species are at least facultatively associated with vernal pools in the region, often well outside of their core distributions in eastern North America (Cutko and Rawinski 2008).

Despite much interest in the ecology and conservation of vernal pools in western North America (Barbour et al. 2007; Holland and Jain 1981; Lathrop et al. 2005; Oscarson and Calhoun 2007) there is limited knowledge of the flora that characterize vernal pools in eastern North America (Calhoun and deMaynadier 2008; Colburn 2004; Cutko and Rawinski 2008; Deil 2005; Keeley and Zedler

1998). Unlike many of the factors used to identify vernal pools in the Northeast, including animal indicator species, hydroperiod, and absence of fish species, floristic characteristics of vernal pools in the region are poorly documented (Maine Department of Environmental Protection 2009). References to plant life in vernal pools of the Northeast are generally based on single rather than multiple surveys throughout a growing season and are mentioned mostly in relation to studies on amphibians (Calhoun et al. 2003; Cutko and Rawinski 2008; Gahl and Calhoun 2008; Gahl et al. 2009).

In the northeastern United States, there are currently 422 plant species thought to be associated with vernal pools (Cutko and Rawinski 2008) with 92 of these identified as at risk, including at least six in Maine: *Clethra alnifolia* L. (Clethraceae), *Eleocharis nitida* Fernald (Cyperaceae), *Hottonia inflata* Elliott (Primulaceae), *Lindera benzoin* Blume (Lauraceae), *Platanthera leucophaea* (Nutt.) Lindl. (Orchidaceae), and *Rhynchospora macrostachya* Torr. ex A. Gray (Cyperaceae; Cutko 1997; Cutko and Rawinski 2008; Maine Natural Areas Program 2005; NatureServe 2009). Although it is also known to inhabit farm ponds and drainage ditches in the southern part of its range, *H. inflata* appears to be restricted to vernal pools in the northern part of its range in southern Maine, with a Maine state rank S1, global rank G4, and state status T (Maine Natural Areas Program 2005; NatureServe 2009).

While some attention has been given to rare plants of Maine's wetlands, including those of Acadia National Park (ANP) on Mt. Desert Island (MDI; Calhoun et al. 1994; Greene et al. 2005; Vaux et al. 2006), there are no published studies specific to vernal pool vegetation of ANP. Recent floristic treatments for ANP make no reference to vernal pool vegetation (Greene et al. 2005; Mittelhauser et al. 2010). Nearly 12% (133 taxa) of vascular plants in ANP have been designated locally-rare or state-listed (S1, S2, or S3) while approximately 25% of the plants (290 taxa) are considered exotic (Greene et al. 2005). It is unknown how many of these species are associated with ANP's vernal pools. We surveyed the vascular flora of six vernal pools in ANP in order to provide a useful comparison to the few available vernal pool studies from New England (Cutko 1997; Cutko and Rawinski 2008) and a baseline to compare coastal and inland, as well as mainland and island vernal pools of the Northeast. The objective of the study was to create a preliminary checklist of the vernal pool flora of ANP and to compare this checklist with previous vernal pool floras from the region.

MATERIALS AND METHODS

Study area. The primary land holdings of Acadia National Park are located on Mt. Desert Island (44°34'8"N, 68°34'4"W), a large (ca. 28,100 ha), coastal island in Hancock County, Maine, U.S.A. Mount Desert Island is roughly bisected into eastern and western halves by Somes Sound (Figure 1). Annually, MDI receives 140 cm of rain, 20 cm more than the rest of Maine (Nielsen and Kahl 2007), and 155 cm of snowfall (National Park Service 2009). Although precipitation falls throughout the year as both snow and rain, the majority of precipitation occurs from autumn through spring (National Park Service 2009); thus, most vernal pools dry out by mid- to late summer. This hydroperiod appears to be typical of woodland vernal pools throughout the Northeast (Tiner et al. 2002).

Estimates based on a compilation of ANP documents and field surveys put the number of vernal pools in ANP at over 80 (M. Gahl, Univ. New Brunswick, St. John, pers. comm.). Vernal pool selection for this study was based on a list of documented vernal pools in ANP (based on hydroperiod and the absence of fish populations), from which we eliminated any anthropogenically formed pools such as old gravel pits or cellars and pools with altered drainage. To avoid contaminating other pools, we also eliminated pools known to harbor, or to have previously harbored, amphibian diseases. From the remaining subset, we selected six pools of similar size and canopy cover (estimated visually in the field). Of the six pools, three each were located on the eastern (East 1–3) and western (West 1–3) sides of MDI (Figure 1). The three pools on the eastern side were located within areas dominated by deciduous tree species such as *Acer* sp. L., *Betula* sp. L., *Populus* sp. L., and *Quercus* sp. L., whereas the three on the western side were located in areas dominated by *Abies balsamea* (L.) Mill. (Pinaceae) and *Picea* spp. A. Dietr. All pools were located away from year-round roadways.

Five transects were established at each of the six pools between April 21–24, 2008. The transects radiated from the deepest point in each pool at a bearing of 0° (magnetic north), 72°, 144°, 216°, and 288°, and ended at the estimated 2008 spring high-water mark of each pool. The 2008 spring high-water mark was estimated based on the water level present at each pool at the height of the spring snow melt at the beginning of April and, where needed, adjusted at the beginning of the first sample period based on evidence of hydrology (a “bath-tub ring” of leaves and woody debris beyond the original

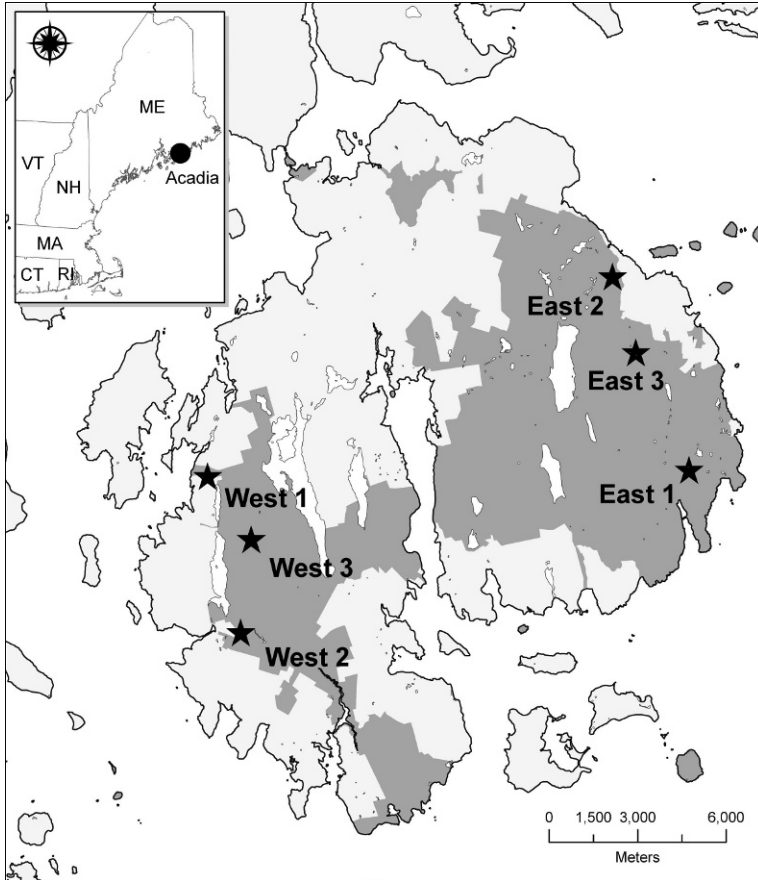


Figure 1. Locations of the six vernal pools selected for study in Acadia National Park, Mount Desert Island, Maine. Pools are labeled by location on the island and pool number and correspond to names given to each pool by Acadia National Park (East 1 = East Otter Creek, East 2 = Steve's, East 3 = Bill's Winterberry, West 1 = Long Pond, West 2 = Western Mountain Fire Road South, and West 3 = Western Mountain Trail). Shaded areas indicate Acadia National Park. Credit: Sarah Nelson.

high water estimate). Two \times two-meter-square quadrats were established at three-meter intervals along each transect. Vascular plant species were identified within each quadrat over three sampling periods during the growing season (28 April to 11 May; 29 June to 6 July; 18–30 September). Voucher specimens were collected only for

Table 1. Ecological characteristics and sampling specifications for the six vernal pools surveyed. Pools are labeled by location on Mount Desert Island (E = eastern side; W = western side) and pool number (1–3). See Figure 1 for locations and names of each pool. Pool areas are estimated based on polygons created from the lengths and bearings of the five transects in each pool. Pool depth is based on the deepest point in each pool as measured at the beginning of the season when water levels were highest. Transect lengths for the five transects (T1–T5) in each pool are given, as are the total number of quadrats surveyed in each pool.

	Pools					
	E1	E2	E3	W1	W2	W3
Pool Area (m ²)	881	235	221	393	325	171
Pool Depth (cm)	34	45	39	23	55	27
T1 (m)	36	3	3	12	6	3
T2 (m)	12	3	9	9	12	24
T3 (m)	15	9	9	12	12	6
T4 (m)	30	24	27	9	30	15
T5 (m)	12	9	3	24	3	3
Total Quadrats	35	16	17	22	23	17

those species not readily identifiable in the field. Transect lengths and the total number of quadrats surveyed for each pool, as well as pool depths and approximated areas, are listed in Table 1.

Plants were identified using Magee and Ahles (2007) and Haines and Vining (1998). Voucher specimens for those species not identified in the field are deposited at the College of the Atlantic Herbarium (HCOA). Nomenclature follows Haines (2010). To determine if species observed during the 2008 study period were new records for vernal pools in northeastern North America, we referred to the only two available floras for regional vernal pools: Cutko (1997) and Cutko and Rawinski (2008). Typical habitat preferences in Maine were determined from Haines and Vining (1998). We referred to Greene et al. (2005) and Vaux et al. (2006) to determine exotic species known to be invasive in Maine or New England. National Wetland Indicator Status for the Northeast Region (Region 1) was determined from (in order of precedence) Lichvar and Kartesz (2009), U.S. Fish and Wildlife Service (1988), and Tiner (2005).

RESULTS

Sixty-five vascular plant species from 26 families were identified in the six vernal pools studied (Table 2). The number of species

encountered in each pool was as follows: East 1 (32), East 2 (31), East 3 (15), West 1 (34), West 2 (16), and West 3 (29). The most species-rich families were Cyperaceae (14), Ericaceae (9), and Rosaceae (7). The largest portion of the species found (21) are considered obligate wetland species (OBL; 99% probability of occurring in wetlands) in the Northeast Region, whereas 14 species are considered facultative wetland species (FACW; 67–99% probability of occurring in wetlands), 12 are considered facultative species (FAC; 34–66% probability of occurring in wetlands), 14 are considered facultative upland species (FACU; 1–33% probability of occurring in wetlands), one species is considered an upland species (UPL; <1% probability of occurring in wetlands), and one species is rated as having insufficient information (NI; Table 2). The single species rated UPL, *Sibbaldiopsis tridentata*, does not occur on the National Wetland Plant List (Lichvar and Kartesz 2009; U.S. Fish and Wildlife Service 1988) and thus it was considered UPL by default; it has been suggested that this plant might be more accurately rated FAC or FACU (R. Lichvar, U.S. Army Corps of Engineers, pers. comm.).

Thirteen species had previously not been reported from vernal pools in the northeastern United States (Table 2; Cutko 1997; Cutko and Rawinski 2008). Of these 13 species, the largest portion (7) are rated FACU, whereas two are rated FAC, one is rated FACW, and three are rated OBL. No species listed as rare in Maine were observed (Brumback et al. 1996; Haines and Vining 1998; Maine Natural Areas Program 2005); however, 27 taxa were noted as occasional or uncommon for ANP by Greene et al. (2005; Table 2). We did not find any exotic invasive plant species, either terrestrial or aquatic, in the six vernal pools we studied (Greene et al. 2005; Vaux et al. 2006). We were unable to determine any obvious differences in species composition between pools based on their location on either the eastern or western sides of the island, despite differences in forest type.

DISCUSSION

Our study is the first to provide a survey of plant diversity for vernal pools in ANP and provides a baseline study from which to expand our knowledge of the vernal pool flora of the Park. Overall, the species compositions found in the six vernal pools visited in this study appear to be typical of vernal pools in the Northeast, being

Table 2. Vascular plant species found in six vernal pools in Acadia National Park (ANP). X = presence, plants encountered during one or more visits to each of six pools. Pools are labeled by their location on the island (E, east; W, west) and pool number (i.e., E1; see Figure 1 for pool locations and names). * = new reports for vernal pools in northeastern North America (Cutko 1997; Cutko and Rawinski 2008). ANP = frequency of occurrence in ANP; C = common, OC = occasional, UNC = uncommon; no plants considered rare in ANP were found (Greene et al. 2005). NWPL = wetland indicator status from the National Wetland Plant List for the Northeast Region (Region 1), listed for each species based on (in order of precedence) Lichvar and Kartesz (2009), U.S. Fish and Wildlife Service (1988), and Tiner (2005). Voucher specimens were collected only for those species not readily identifiable in the field; voucher numbers for those species are listed (all voucher numbers belong to the first author, B.C.). All vouchers were deposited at HCOA. Nomenclature follows Haines (2010).

Taxon	ANP	NWPL	Pools						Voucher #
			E1	E2	E3	W1	W2	W3	
ADOXACEAE									
<i>Viburnum nudum</i> L. var. <i>cassinoides</i> (L.) Torr. & A. Gray	C	FACW		X	X				X
APIACEAE									
<i>Aralia nudicaulis</i> L.	C	FACU	X	X					
AQUIFOLIACEAE									
<i>Ilex mucronata</i> (L.) M. Powell, Savol. & S. Andrews	OC	OBL	X			X	X		
<i>I. verticillata</i> A. Gray	C	FACW	X	X	X	X	X		X
ASTERACEAE									
* <i>Doellingeria umbellata</i> (Mill.) Nees var. <i>umbellata</i>	C	FACW	X						VPANP 6

Table 2. Continued.

Taxon	ANP	NWPL	Pools							Voucher #
			E1	E2	E3	W1	W2	W3		
BETULACEAE										
<i>Alnus incana</i> (L.) Moench subsp. <i>rugosa</i> (Du Roi) R. T. Clausen	C	FACW	X	X		X				
* <i>Betula papyrifera</i> Marshall	C	FACU	X	X	X					
<i>Betula populifolia</i> Marshall	C	FAC	X	X	X					
CORNACEAE										
<i>Chamaepericlymenum canadense</i> (L.) Asch. & Graebn.	C	FAC	X			X				
CUPRESSACEAE										
<i>Thuja occidentalis</i> L.	C	FACW				X				
CYPERACEAE										
<i>Carex atlantica</i> Sennen var. <i>capillacea</i> (L.H. Bailey) Cronquist	UNC	OBL	X			X				VPANP 26
<i>C. brunnescens</i> (Pers.) Poir. var. <i>brunnescens</i>	UNC	FACW		X		X		X		VPANP 22
<i>C. canescens</i> L. subsp. <i>disjuncta</i> (Fernald) H. Toivonen	OC	OBL							X	VPANP 25
<i>C. folliculata</i> L.	OC	OBL		X						VPANP 21

Table 2. Continued.

Taxon	ANP	NWPL	Pools							Voucher #
			E1	E2	E3	W1	W2	W3		
<i>C. debilis</i> Michx. var. <i>rudgei</i> L.H. Bailey	C	FAC				X			X	VPANP 24
<i>C. gynandra</i> Schwein.	C	OBL				X			X	VPANP 20
<i>C. lenticularis</i> Michx.	UNC	OBL	X							VPANP 15
<i>C. lurida</i> Wahlenb.	OC	OBL	X	X						VPANP 17
* <i>C. magellanica</i> Lam. subsp. <i>irrigua</i> (Wahlenb.) Hultén	OC	OBL				X			X	VPANP 13
<i>C. nigra</i> (L.) Reichard	OC	FACW				X			X	VPANP 19
<i>C. stricta</i> Lam.	OC	OBL	X						X	VPANP 14
<i>C. trisperma</i> Dewey	C	OBL				X	X		X	VPANP 23
<i>Eriophorum virginicum</i> L.	OC	OBL							X	VPANP 18
<i>Scirpus hattorianus</i> Makino	OC	NI	X	X		X			X	VPANP 12
DENNSTAEDTIACEAE										
* <i>Pteridium aquilinum</i> (L.) Kuhn	C	FACU		X		X				X
ERICACEAE										
<i>Chamaedaphne calyculata</i> (L.) Moench	C	OBL	X							X
<i>Gaultheria procumbens</i> L.	C	FACU		X						X
<i>Gaylussacia baccata</i> K. Koch	C	FACU	X			X			X	X
<i>Kalmia angustifolia</i> L.	C	FAC	X	X					X	X
<i>Rhododendron canadense</i> (L.) Torr.	C	FACW	X							X

Table 2. Continued.

Taxon	ANP	NWPL	Pools							Voucher #
			E1	E2	E3	W1	W2	W3		
* <i>Vaccinium angustifolium</i> Aiton	C	FACU	X	X	X	X	X	X	X	
<i>V. corymbosum</i> L.	OC	FACW	X		X	X	X			X
<i>V. macrocarpon</i> Aiton	C	OBL					X			
* <i>V. vitis-idaea</i> L. subsp. <i>minus</i> (Lodd., G. Lodd. & W. Lodd.) Hultén	C	FAC						X		
FAGACEAE										
<i>Quercus rubra</i> L.	C	FACU	X	X	X					
HYPERICACEAE										
<i>Triadenum</i> sp. Raf.	-	-		X			X			VPANP 1
IRIDACEAE										
<i>Iris versicolor</i> L.	C	OBL	X	X				X		
JUNCACEAE										
* <i>Juncus articulatus</i> L.	UNC	OBL		X						VPANP 10
<i>J. canadensis</i> J. Gay ex Laharpe	OC	OBL	X	X						VPANP 11
<i>J. effusus</i> L. subsp. <i>solutus</i> (Fernald & Wieg.) Hämet-Ahti	OC	FACW	X	X			X			VPANP 16

Table 2. Continued.

Taxon	ANP	NWPL	Pools							Voucher #	
			E1	E2	E3	W1	W2	W3			
LAMIACEAE											
<i>Lycopus uniflorus</i> Michx.	OC	OBL	X	X	X	X	X	X	X	X	VPANP 2
MYRICACEAE											
* <i>Morella carolinensis</i> (Mill.) Small	C	FAC	X			X				X	
MYRSINACEAE											
<i>Lysimachia borealis</i> (Raf.) U. Manns & Anderb.	C	FAC	X	X	X	X	X	X	X		VPANP 5
OSMUNDACEAE											
<i>Osmunda regalis</i> L. var. <i>spectabilis</i> (Willd.) A. Gray	OC	OBL		X			X				
PINACEAE											
<i>Abies balsamea</i> (L.) Mill.	C	FAC				X		X	X	X	
<i>Larix laricina</i> (Du Roi) K. Koch	OC	FACW						X		X	
* <i>Picea glauca</i> (Moench) Voss	C	FACU							X	X	
<i>P. mariana</i> Britton, Sterns & Poggenb.	OC	FACW				X		X	X	X	
<i>P. rubens</i> Sarg.	C	FACU		X		X		X	X	X	
<i>Pinus strobus</i> L.	C	FACU				X		X		X	

largely representative of the regional flora (Table 2; Calhoun et al. 2003; Cutko 1997; Cutko and Rawinski 2008). None of the 65 plant species we found are considered vernal pool obligates, although approximately 32% of the species found are considered obligate wetland species (Table 2; Lichvar and Kartez 2009; U.S. Fish and Wildlife Service 1988). Approximately 41% (27 species) of the taxa we recorded are considered occasional or uncommon in ANP; however, none are considered rare (Table 2; Greene et al. 2005).

Acadia National Park harbors a wide range of plant communities, including species of international, national, regional, and state significance (Greene et al. 2005; Vaux et al. 2006). Six plant species in ANP are listed as globally rare (Brumback et al. 1996). Fourteen taxa listed as being endangered or threatened in Maine (Maine Natural Areas Program 2005) have been documented in ANP (Greene et al. 2005). However, more recent data indicate that the number of threatened and endangered species in ANP is larger (Vaux et al. 2006). Despite the presence of a number of rare species in ANP, none were found in the vernal pools we studied. This suggests that, unlike vernal pools in western North America which are well known for their high number of rare and endemic plant species (Keeler-Wolf et al. 1998), vernal pools in eastern North America may not provide such a similar refuge for rare plants. This is supported by a general lack of vernal pool endemics in eastern North America and a mere 20 at-risk species associated with the region's isolated wetlands as a whole (Cutko and Rawinski 2008). Yet it is important to keep in mind that there have been no systematic surveys of rare plants associated with vernal pools in the Northeast (Cutko and Rawinski 2008) and thus the true number of rare, and possibly endemic, plant species associated with this type of wetland is unknown. The 13 species we found that have not previously been reported from vernal pools in northeastern North America (Table 2) demonstrate the importance of conducting region-specific biodiversity studies for unique habitats such as vernal pools (Cutko and Rawinski 2008).

Nearly all of the species we found were perennial, woody or herbaceous plants; only one annual species was found (*Persicaria hydropiper*). This is in strong contrast to the annual-dominated vernal pools of western North America (Keeler-Wolf et al. 1998; Kruckeberg 2006). Of the woody perennial species we found, 12 were rated OBL or FACW, whereas 19 were rated FAC or FACU. By contrast, 22 of the herbaceous perennial species we found were rated

OBL or FACW, eight were rated FAC or FACU, and only one was rated UPL. Despite these clear differences in growth habit and wetness preference or tolerance, we did not observe any strong patterns of zonation in the six pools we studied. A lack of strong patterns of zonation may be an indication of large variation in hydroperiod from year to year (Mitchell 2005). A more detailed study examining differences in water depth along sampling transects, as well as variations in hydroperiod from year to year, may be needed to determine the presence of vegetative zonation.

It is promising that we found no exotic, terrestrial or aquatic, invasive plant species (Vaux et al. 2006) in the pools we surveyed. Invasive, wetland-tolerant species such as purple loosestrife [*Lythrum salicaria* L. (Lythraceae)], shrubby St. Johnswort [*Hypericum prolificum* L. (Hypericaceae)], ninebark [*Physocarpus opulifolius* (L.) Maxim. (Rosaceae)], and forest woodrush [*Luzula luzuloides* (Lam.) Dandy & Wilmott (Juncaceae)] are found within and adjacent to basin wetlands within the Park but were absent from the vernal pools we visited. These species could expand their distributions, even into vernal pools, in response to further disturbance.

By expanding this study into other documented vernal pools in coastal and inland Maine, a more comprehensive species list for vernal pools could be developed for the State. Such detailed floristic information is currently lacking, a critical information gap in the efforts for conservation of Maine's vernal pools (Maine Vernal Pools Project 2010). It is yet unclear how distinct vernal pool vegetation may be from the vegetation of wetlands as a whole in eastern North America. Comparative floristic studies of permanent wetlands and ephemeral vernal pools in both coastal and inland habitats are needed. Such studies can better inform whether vernal pools harbor distinct species assemblages compared to those of permanent wetlands in New England. Given that their ecologies are distinct, especially with respect to hydroperiod, one would expect differences with respect to plant species assemblages, as are clearly reflected in differences between amphibian and invertebrate assemblages from vernal pools compared to permanent wetlands (Calhoun and deMaynadier 2008; Tiner et al. 2002). Treating vernal pools as separate ecological communities can better focus both management and research priorities of this under-explored habitat in New England.

ACKNOWLEDGMENTS. The authors thank David Manski of ANP for providing access to the Park's vernal pools and other resources

through National Park Service research permits; Megan Gahl for advice on site selection; Jill Weber, Fred Olday, and Luka Negoita for botanical advice and assistance with species identification; Chris Petersen, John Anderson, Steve Ressel, and Gordon Longworth for advice on field methods; Hazel Stark for assistance with tables; Sarah Nelson and José Perez-Orozco for the preparation of Figure 1; and two anonymous reviewers for providing useful comments. This study was supported with funds from the Maine Space Grant Consortium, Garden Club of America, and College of the Atlantic's Rothschild Research Grant for Faculty-Student Collaboration. The paper is based on the undergraduate thesis of the first author.

LITERATURE CITED

- BARBOUR, M. G., A. I. SOLOMESHCH, J. J. BUCK, R. F. HOLLAND, C. W. WITHAM, R. L. MACDONALD, S. L. STARR, AND K. A. LAZAR. 2007. Classification, ecological characterization, and presence of listed plant taxa of vernal pool associations in California. Final Report. U.S. Fish and Wildlife Service Agreement/Study No. 814205G238, Univ. California, Davis, CA.
- , ———, R. F. HOLLAND, C. W. WITHAM, R. L. MACDONALD, S. S. CILLIERS, J. A. MOLINA, J. J. BUCK, AND J. M. HILLMAN. 2005. Vernal pool vegetation of California: Communities of long-inundated deep habitats. *Phytocoenologia* 35: 177–200.
- BASKIN, Y. 1994. California's ephemeral vernal pools may be a good model for speciation. *BioScience* 44: 384–388.
- BROOKS, R. T. 2009. Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. *Climatic Change* 95: 469–483.
- BRUMBACK, W. E. AND L. J. MEHRHOFF ET AL. 1996. *Flora Conservanda: New England*. The New England Plant Conservation Program (NEPCoP) list of plants in need of conservation. *Rhodora* 98: 233–361.
- CALHOUN, A. J. K., J. E. CORMIER, R. B. OWEN JR., A. F. O'CONNELL JR., C. T. ROMAN, AND R. W. TINER JR. 1994. *The Wetlands of Acadia National Park and Vicinity*. Agricultural and Forest Experiment Station Miscellaneous Publication 721, Univ. Maine, Orono, ME.
- CALHOUN, A. J. K. AND P. G. DEMAYNADIER, eds. 2008. *Science and Conservation of Vernal Pools in Northeastern North America*. CRC Press, Boca Raton, FL.
- CALHOUN, A. J. K., T. E. WALLS, S. S. STOCKWELL, AND M. MCCOLLOUGH. 2003. Evaluating vernal pools as a basis for conservation strategies: A Maine case study. *Wetlands* 23: 70–81.
- COLBURN, E. A. 2004. *Vernal Pools: Natural History and Conservation*. McDonald & Woodward Publishing Company, Blacksburg, VA.

- CUTKO, A. 1997. A Botanical and Natural Community Assessment of Selected Vernal Pools in Maine. Maine Dept. Inland Fisheries and Wildlife and Maine Natural Areas Program, Augusta, ME.
- AND T. J. RAWINSKI. 2008. Flora of northeastern vernal pools, pp. 71–104. *In*: A. J. K. Calhoun and P. G. deMaynadier, eds., *Science and Conservation of Vernal Pools in Northeastern North America*. CRC Press, Boca Raton, FL.
- DEIL, U. 2005. A review of habitats, plant traits, and vegetation of ephemeral wetlands: A global perspective. *Phytocoenologia* 25: 533–705.
- EMERY, N. C. 2009. Ecological limits and fitness consequences of cross-gradient pollen movement in *Lasthenia fremontii*. *Amer. Naturalist* 174: 221–235.
- GAHL, M. K. AND A. J. K. CALHOUN. 2008. Landscape setting and risk of *Ranavirus* mortality events. *Biol. Conservation* 141: 2679–2789.
- , ———, AND R. GRAVES. 2009. Facultative use of seasonal pools by American bullfrogs (*Rana catesbeiana*). *Wetlands* 29: 697–703.
- GERHARDT, F. AND S. K. COLLINGE. 2003. Exotic plant invasions of vernal pools in the Central Valley of California, USA. *J. Biogeogr.* 30: 1043–1052.
- GREENE, C. W., L. L. GREGORY, G. H. MITTELHAUSER, S. C. ROONEY, AND J. E. WEBER. 2005. Vascular flora of the Acadia National Park region, Maine. *Rhodora* 107: 117–185.
- HAINES, A. 2010. *Flora Novae Angliae*. Delta Institute of Natural History, Canton, ME, Website: <http://www.arthurhaines.com/checklist.htm>. Most recently accessed Sep 2010.
- AND T. F. VINING. 1998. *Flora of Maine. A Manual for Identification of Native and Naturalized Vascular Plants of Maine*. V. F. Thomas Co., Bar Harbor, ME.
- HOLLAND, R. F. AND S. K. JAIN. 1981. Insular biogeography of vernal pools in the Central Valley of California. *Amer. Naturalist* 117: 24–37.
- KEELER-WOLF, T., D. R. ELAM, K. LEWIS, AND S. A. FLINT. 1998. California vernal pool assessment, preliminary report. The Resource Agency, Dept. Fish and Game, State of California, Sacramento, CA.
- KEELEY, J. E. AND P. H. ZEDLER. 1998. Characterization and global distribution of vernal pools, pp. 1–14. *In*: C. W. Witham, E. T. Bauder, D. Belk, W. R. Ferren Jr., and R. Ornduff, eds., *Conservation and Management of Vernal Pool Ecosystems. Proceedings from a 1996 Conference*, California Native Plant Society, Sacramento, CA.
- KRUCKEBERG, A. R. 2006. *Introduction to California Soils and Plants: Serpentine, Vernal Pools, and other Geobotanical Wonders*. Univ. California Press, Berkeley, CA.
- LATHROP, R. G., P. MONTESANO, J. TESAURO, AND B. ZARATE. 2005. Statewide mapping and assessment of vernal pools: A New Jersey case study. *J. Environm. Managem.* 76: 230–238.
- LICHVAR, R. W. AND J. T. KARTESZ. 2009. *North American Digital Flora: National wetland plant list, version 2.1.0*. U.S. Army Corps of Engineers, Engineer Research and Development Center, Cold Regions Research and Engineering Laboratory, Hanover, NH, and BONAP, Chapel Hill, NC. Website: https://wetland_plants.usace.army.mil. Most recently accessed Sep 2010.

- LINHART, Y. B. 1976. Evolutionary studies of plant populations in vernal pools, pp. 40–46. *In*: S. K. Jain, ed., *Vernal Pools: Their Ecology and Conservation*. Institute of Ecology, Univ. California, Davis, CA.
- MAGEE, D. W. AND H. E. AHLES. 2007. *Flora of the Northeast: A Manual of the Vascular Flora of New England and Adjacent New York*, 2nd ed. Univ. Massachusetts Press, Amherst, MA.
- MAINE DEPARTMENT OF ENVIRONMENTAL PROTECTION. 2009. Significant wildlife habitat: Significant vernal pool habitat. Bureau of Land and Water Quality, Augusta, ME. Website: <http://www.maine.gov/dep/blwq/docstand/nrpa/vernalpools/index.htm>. Most recently accessed Dec 2009.
- MAINE NATURAL AREAS PROGRAM. 2005. Rare, threatened, and endangered plant taxa. Maine Dept. Conservation, Augusta, ME. Website: <http://www.maine.gov/doc/nrimc/mnap/features/plantlist.htm>. Most recently accessed Sep 2010.
- MAINE VERNAL POOLS PROJECT. 2010. Maine municipal vernal pool mapping and assessment project. Dept. Wildlife Ecology, Univ. Maine, Orono, ME. Website: <http://www.umaine.edu/vernalpools/index.htm>. Most recently accessed Sep 2010.
- MITCHELL, J. 2005. Using plants as indicators of hydroperiod class and amphibian habitat suitability in Rhode Island seasonal ponds. M.S. thesis, Univ. Rhode Island, Kingston, RI.
- MITTELHAUSER, G. H., L. L. GREGORY, S. C. ROONEY, J. E. WEBER, M. LOVIT, AND D. KAUSEN. 2010. *Field Guide to the Plants of Acadia National Park*. Univ. Maine Press, Orono, ME.
- NATIONAL PARK SERVICE. 2009. Appendix A: General information. Acadia National Park, Bar Harbor, ME. Website: http://www.nps.gov/acad/parkmgmt/upload/gg_appA.pdf. Most recently accessed Sep 2010.
- NATURESERVE. 2009. NatureServe Explorer: An online encyclopedia of life, version 7.1. Association for Biodiversity Information, Arlington, VA. Website: <http://www.natureserve.org/explorer>. Most recently accessed Sep 2010.
- NEILSEN, M. G. AND J. S. KAHL. 2007. Nutrient export from watersheds on Mt. Desert Island, Maine, as a function of land use and fire history. *Environm. Monit. Assessm.* 126: 81–96.
- OSCARSON, D. B. AND A. J. K. CALHOUN. 2007. Developing vernal pool conservation plans at the local level using citizen-scientists. *Wetlands* 27: 80–95.
- RAJAKARUNA, N. AND R. S. BOYD. 2008. The edaphic factor, pp. 1201–1207. *In*: S. E. Jørgensen and B. Fath, eds., *The Encyclopedia of Ecology*, Vol. 2. Elsevier, Oxford, U.K.
- SCHLISING, R. A. AND E. L. SANDERS. 1982. Quantitative analysis of vegetation at the Richdale Vernal Pools, California. *Amer. J. Bot.* 69: 734–742.
- SHARITZ, R. R. AND S. C. PENNINGS. 2006. Development of wetland plant communities, pp. 177–241. *In*: D. P. Batzer and R. R. Sharitz, eds., *Ecology of Freshwater and Estuarine Wetlands*. Univ. California Press, Berkeley, CA.
- TINER, R. W. 2005. *Field Guide to Nontidal Wetland Identification*. Maryland Dept. Natural Resources, Annapolis, MD and U.S. Fish and Wildlife Service, Newton Corner, MA.

- , H. C. BERGQUIST, G. P. DEALESSIO, AND M. J. STARR. 2002. Geographically Isolated Wetlands: A Preliminary Assessment of their Characteristics and Status in Selected Areas of the United States. U.S. Dept. Interior, Fish and Wildlife Service, Northeast Region, Hadley, MA.
- U.S. FISH AND WILDLIFE SERVICE. 1988. National list of vascular plant species that occur in wetlands. Biol. Report 88, U.S. Fish and Wildlife Service, Washington, DC.
- VAUX, P. D., S. J. NELSON, N. RAJAKARUNA, G. MITTELHAUSER, K. BELL, B. KOPP, J. PECKENHAM, AND G. LONGSWORTH. 2006. Assessment of natural resources and watershed conditions in and adjacent to Acadia National Park. Natural Resource Tech. Report NPS/HTLN/NRTR—2006/001. National Park Service, Fort Collins, CO.
- ZEDLER, P. H. 2003. Vernal pools and the concept of isolated wetlands. *Wetlands* 23: 597–607.