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Arctic and Alpine Rare Plant Population Dynamics at Isle Royale National Park

Response to Changing Lake Levels

Natural Resource Report NPS/GLKN/NRR—2022/2350

ON THE COVER
Clockwise from top left: Crowberry, *Empetrum nigrum* (NPS); three-toothed saxifrage, *Saxifraga tricuspidata* (NPS); American parsley fern, or American rockbrake, *Cryptogramma acrostichoides* (NPS); encrusted saxifrage, *Saxifraga paniculata* (NPS).

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Suzanne Sanders[1], Jessica Kirschbaum[1], and Sarah E. Johnson[2]

[1] National Park Service
Great Lakes Inventory and Monitoring Network
2800 Lake Shore Drive East
Ashland, Wisconsin 54806

[2] Northland College
Department of Natural Resources
1411 Ellis Avenue
Ashland, Wisconsin 54806

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Abstract

Arctic and alpine rare plant species populate wave-splashed rocky shorelines of Isle Royale National Park, where summer temperatures are moderated by Lake Superior. Using data from the mid-1990s and resurvey data from 1998, 2003, and 2016, we examined trajectories of change in occurrence for 25 species at 28 sites coincident with rising lake levels that followed a period of sustained low levels. We analyzed changes in site occupancy of species individually and by functional, geographic, and microhabitat groupings. We also assessed change in population structure for four focal species: *Saxifraga paniculata*, *S. tricuspidata*, *Pinguicula vulgaris*, and *Vaccinium uliginosum*. Of the 25 species, site occupancy increased for 13 and remained steady for six, declining in another six. Site occupancy did not change over time within functional, geographic, and microhabitat groupings. The four focal species showed similar dynamic and systematically changing populations, responding to similar ecological exposures. We hypothesize that the moderating influence of Lake Superior on air temperature benefits these populations despite warming temperatures and a 15-year sustained low water period. This work contributes to our understanding of the responses of at-risk species to extreme climate events.

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We thank L. Potvin, M. Romanski, and other natural resource staff at Isle Royale National Park for arranging logistics during our field work. We are indebted to Dr. E. Judziewicz for his impressively expansive floristic surveys on Isle Royale National Park in the 1990s and early 2000s, and for having the foresight to identify permanent monitoring sites for tracking populations of numerous rare species. We are grateful to A. Reznicek for providing natural history insight for *Carex* spp. Finally, we appreciate the assistance of R. Key for her database savvy and data management insight.

Introduction

The cold, upwelling waters of Lake Superior provide refugia for small suites of both Arctic and alpine disjunct plant species (Given and Soper 1981). Populations of these species are found in a limited number of rocky shoreline habitats on islands and along the north shore of the lake (Soper and Maycock 1963, Marr et al. 2009, Zlonis and Gross 2018) (Table 1). Perhaps most notably, Isle Royale National Park ("Isle Royale" or the "Park"), located in northwest Lake Superior, is host to several dozen rare species with distributions more common at higher latitudes and higher altitudes.

On Isle Royale and elsewhere around Lake Superior, many of these species opportunistically grow in narrow veins of soil that form in rock cracks, or on thin cryptobiotic crusts. Some species occur at the margins of rock pool wetlands that have formed in rock depressions (Judziewicz 1999). Isle Royale's rocky headlands, which dominate both the northeast coast of the main island and numerous barrier islands, are directly exposed to the wind and wave action of the open lake (Figure 1). As a result, changes in lake level and storm events affect the availability of water to plants via the height of wave splash and rock pool recharge.

Lake Superior water levels are dynamic and are largely influenced by the regional climate (Stow et al. 2008). The Lake Superior region experienced warming temperatures, increased evaporation, and intermittent declines in precipitation from the late 1990s to the early 2010s due to a strong El Niño event, such that Lake Superior levels dropped (Assel et al. 2004, Gronewold and Stow 2014). Water levels remained below the 100-year mean from 1998 to 2013, the longest such period (15 years) since 1918, when the collection of long-term data begins (USACE 2020) (Figure 2).

Coincident with this extreme low water period, three censuses of the distribution and abundance of Isle Royale's rocky shoreline rare plant communities were made in 1993–1994, 1998, and 2003 (Judziewicz 1995, 1999, 2004). Subsequent to the 2003 census, the height of Lake Superior dropped to its lowest level in 85 years before rising to levels above the 100-year mean in 2014

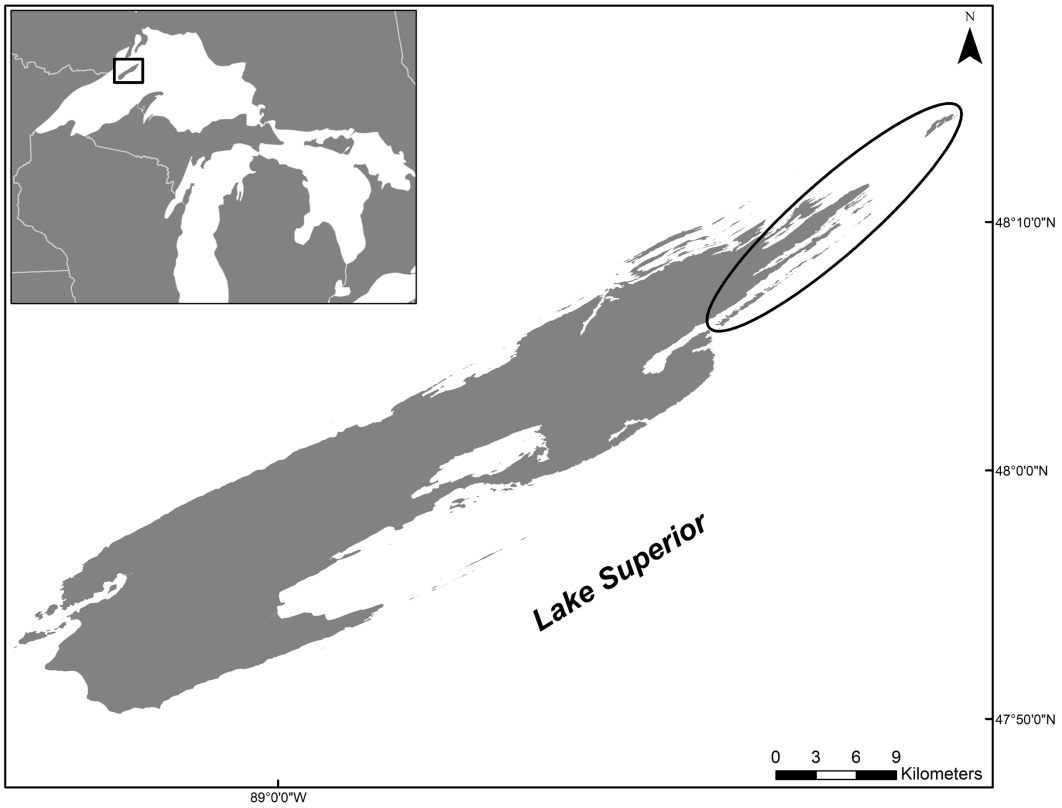

Figure 1. Isle Royale with the study area shown circled on the northeast end of the island. *Inset:* Location of Isle Royale National Park in Lake Superior and the Great Lakes (ESRI Basemap 2019).

Table 1. Michigan state conservation status of the 25 species in this study, and their NatureServe status in bordering states, USA, and Canada.

		NatureServe Status[2]						
Scientific Name and Authority	**MI Status[1]**	***Michigan***	***Minnesota***	***Wisconsin***	***Ontario***	***USA***	***Canada***	***Global***
Allium schoenoprasum L.	T	S2	S2	unranked	S4	N3N5	N5	G5
Bistorta vivipara (L.) Delarbre	T	S1S2	S3	not present	S5	unranked	N5	G5
Carex atratiformis Britton	T	S2	not present	not present	S2	unranked	N4N5	G5
Carex gynocrates Wormsk. ex Drejer	not listed	unranked	unranked	S4	S5	unranked	N5	G5
Carex media R.Br.	T	S2S3	unranked	S2	S4S5	unranked	N5	G5T5
Castilleja septentrionalis Lindl.	T	S2S3	S1	not present	S5	unranked	N5	G5
Cryptogramma acrostichoides R.Br.	T	S2	not present	not present	S2S3	unranked	N5	G5
Draba arabisans Michx.	SC	S3	S3	S2	S4	unranked	N4N5	G4
Drosera anglica Huds.	SC	S3	S3	S1	S5	unranked	N5	G5
Empetrum nigrum L.	T	S2	S1	not present	S5	N5	N5	G5
Euphrasia hudsoniana Fernald & Wiegand	T	S1	S3	not present	S4?	unranked	N4N5	G5?
Huperzia selago (L.) Bernh. ex Schrank & Mart.	SC	S3	unranked	S1S2	S4	unranked	N5	G5
Lonicera involucrata (Richardson) Banks ex Spreng.	T	S2†	not present	S1	S5	unranked	N5	G5T4T5
Packera indecora (Greene) A. Löve & D. Löve	T	S1	S3	S1	S5	unranked	N5	G5
Parnassia palustris L.	T	unranked	unranked	unranked	unranked	unranked	N5	G5
Pinguicula vulgaris L.	SC	S3	S3	S1	S5	unranked	N5	G5
Poa alpina L.	T	S1S2	unranked	not present	S4	unranked	N5	G5
Sagina nodosa (L.) Fenzl	T	S2	S1	not present	S4	N3N4	N5	G5
Saxifraga paniculata Mill.	T	S1	S2	not present	S4	N2	N4N5	G5
Saxifraga tricuspidata Rottb.	T	S2	not present	not present	S4	unranked	N5	G5
Tofieldia pusilla (Michx.) Pers.	T	S2	S1	not present	S5	unranked	N5	G5
Triantha glutinosa Baker	not listed	unranked	S4S5	S2S3	S4?	unranked	N5	G5
Trisetum spicatum (L.) K. Richt.	SC	S2S3	S4S5	S2	S4	unranked	N5	G5
Vaccinium uliginosum L.	T	S2	S2	not present	S5	unranked	N5	G5
Vaccinium vitis-idaea L.	E	S1	unranked	S1S2†	S5	unranked	N5	G5T5

[1] Michigan legal status: E, endangered; T, threatened; SC, special concern (Michigan Natural Features Inventory 2017).

[2] NatureServe Conservation Status Rank (NatureServe 2017):
S, state; N, national; G, global.
1, critically imperiled; 2, imperiled; 3, vulnerable; 4, apparently secure; 5, secure.
?, inexact or uncertain; a rank range, N#N# or S#S#, indicates uncertainty about the status; a T# following the G indicates the status of subspecies or varieties; † indicates a value for subspecies or variety was used.

(Figure 2), setting a record for the most rapid rise in levels over a 2-year period (Gronewold et al. 2016). Water levels were still above the long-term average in 2016, coinciding with our most recent plant recensus, as reported in this paper.

Many of the rare rocky outcrop species at Isle Royale National Park are at or near their distribution limits; as such, conditions may already be marginal for them (Lawton 1993, Curnutt et al. 1996) and any additional stresses brought on by low lake levels could lead to losses of populations and extirpation from the Park.

We undertook the present work to examine changes in populations of rare Arctic and alpine species of Lake Superior rocky shorelines on Isle Royale, concurrent with long-term low lake levels. We examined site-level trajectories of change in occurrence for 25 species, individually and in functional and microhabitat groupings based on pollination mechanism, dispersal distance, degree of clonality, vertical distribution above the lake, and geographic range position. These groupings were selected because they may inform the ability of species to persist and spread in response to warming and future lake level variation. We also tested for differences in measures of abundance of four focal species between the initial and final censuses: *Saxifraga paniculata*, *S. tricuspidata*, *Pinguicula vulgaris*, and *Vaccinium uliginosum*. These four species were chosen, because they are generally more apparent and widespread across the survey area than the other species in this study. Understanding their responses on Isle Royale could provide information to managers, conservationists, and researchers that is applicable across the broader distributions of these species.

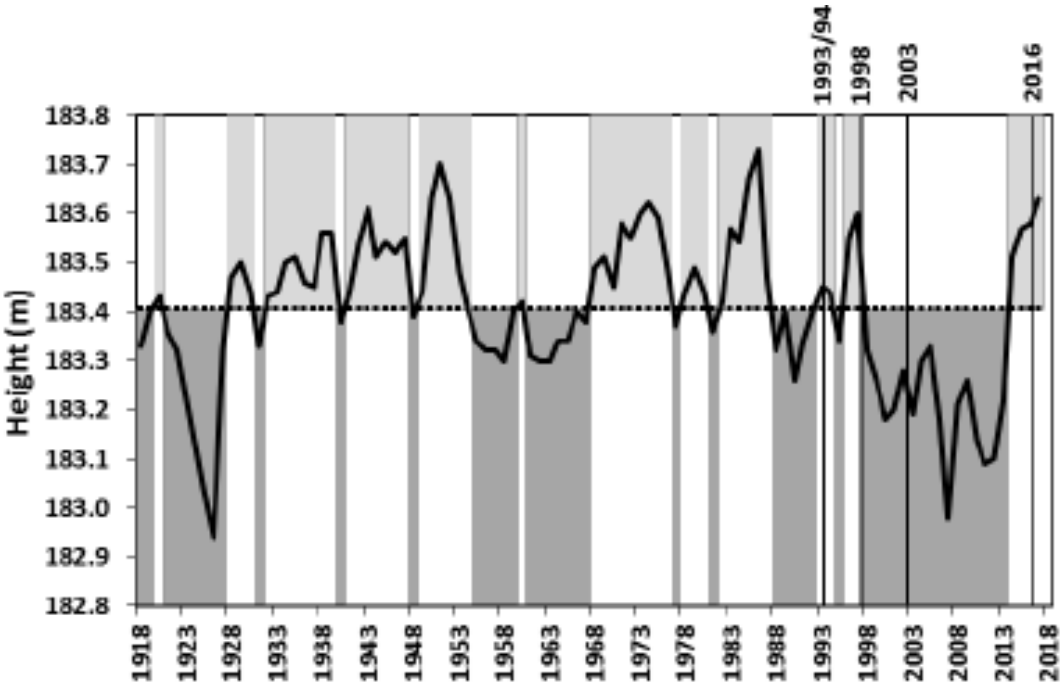

Figure 2. Lake Superior water levels, expressed as meters above sea level, during the period from 1918 to 2018 (USACE 2020). The horizontal dashed line represents the 100-year mean; the vertical solid lines represent the four sampling events. Gray bars highlight the duration of periods above and below the long-term mean water level.

Methods

Study Area

Isle Royale National Park, Michigan (see Figure 1) is an archipelago in Lake Superior composed of one large island (72 km long, 14 km wide) and more than 400 smaller barrier islands. Their general orientation is a northeast-southwest direction with parallel, erosion-resistant basalt ridges (Thornberry-Erlich 2008). Jurisdictionally, the Park is a part of Keweenaw County, Michigan.

Many of the Park's rare plant species are located on the exposed rocky headlands and cliffs of the main island and the barrier islands at the northeast end of the park (Slavic and Janke 1987; see Figure 1). These headlands provide sunny microhabitats exposed to the temperature-moderating effects of Lake Superior (Given and Soper 1981), water recharge from the lake, and shelter from prevailing west winds due to the land mass of the main island (Judziewicz 1995). Soil formation is negligible here and is restricted to cracks, crevices, and other low depressions. Cryptobiotic crusts provide thin organic surfaces, which are often colonized by a suite of more widespread species (e.g., *Campanula rotundifolia* L., *Achillea millefolium* L., and *Solidago hispida* Muhl. ex Willd.) that are adapted to the stresses of sun exposure, ice heaving, and relatively low nutrient availability.

Xeric species occupy the most exposed faces of these rocky headlands, while hydrophytes occupy rock pools that form in crevices and depressions. The most xeric microhabitats support species dependent on occasional wave splash, precipitation, and probably fog (Larson et al. 2000, Fischer et al. 2009, Marr et al. 2009), such as *Saxifraga paniculata* and *Trisetum spicatum*. Rock pools within most headland areas provide habitat for *Sphagnum* spp. and wetland species such as *Trichophorum cespistosum* (L.) Hartm., *Drosera rotundifolia* L., and *Pinguicula vulgaris* (Slavik and Janke 1987). Due to the heterogeneity among rock pool locations, the water budgets of these rock pools vary in their hydrologic input sources (Smith 1983). Some pools are precipitation-dominated via snowmelt and rainfall, some are exposed to Lake Superior wave splash, some receive runoff inputs from higher points on the island, some are in groundwater seepage areas, and some are influenced by multiple hydrologic inputs (Egan et al. 2015). Water levels are the most consistent in seepage area pools and in pools at lower elevations relative to Lake Superior.

While some species in the rocky shoreline community of Isle Royale have distributions well south of Lake Superior, several have broad northerly distributions and are circum-Arctic or circumboreal. Some taxa represent disjunct populations of Arctic or alpine species at the far southern extent of their range (Table 2), while others are disjunct from western or northwestern North America populations. Climate-driven glaciation and glacial retreats during the Quaternary period facilitated disjunctions in some species (Comes and Kadereit 1998). For example, research indicates that two of our focal species, *Vaccinium uliginosum* (Alsos et al. 2005) and *Saxifraga paniculata* (Reisch 2008), expanded post-glaciation northward into the Arctic via dispersal from refuge sites they occupied during glaciation. Be it due to dispersal events after glaciation or to refuge sites that remained after range contractions during glaciation, the timing and causes of disjunction should not be assumed to be the same among all taxa in our study (Thorne 1972).

Plant Censuses

Judziewicz (1995) conducted baseline field censuses for 102 rare plant species in 1993 and 1994. He chose locations based on known occurrences of rare plant species from earlier botanical surveys, known habitat preferences, and interpretation of aerial imagery. These area-wide censuses were conducted in both early and late season; thus, his data encompass the fruiting and flowering periods for most of the target species.

Judziewicz's approach to quantifying abundance depended on the species and its growth habitat. For example, both *Saxifraga*

Table 2. Rare species included in our study and their functional groups for three plant traits, microhabitat type, and range position.

Species	Pollination	Dispersal Distance	Clonality	Microhabitat Type	Range Position[1]
Allium schoenoprasum	Biotic	Local	Short distance	Splash zone	Northern
Bistorta vivipara	Biotic	Local	Short distance	Splash zone	Southern
Carex atratiformis	Abiotic	Widespread	Not clonal	Splash zone	Southern
Carex gynocrates	Abiotic	Widespread	Long distance	Peaty shore	Southern
Carex media	Abiotic	Widespread	Not clonal	Rock pool	Southern
Castilleja septentrionalis	Biotic	Local	Not clonal	Forest edge	Central
Cryptogramma acrostichoides	Abiotic	Widespread	Not clonal	Lichen zone	–
Draba arabisans	Biotic	Widespread	Long distance	Lichen zone	Central
Drosera anglica	Biotic	Widespread	Short distance	Rock pool	Central
Empetrum nigrum	Abiotic	Widespread	Long distance	Lichen zone	Southern
Euphrasia hudsoniana	Biotic	Local	Not clonal	Rock pool	Southern
Huperzia selago	Abiotic	Widespread	Short distance	Lichen zone	Southern
Lonicera involucrata	Biotic	Widespread	Not clonal	Forest edge	Central
Packera indecora	Biotic	Widespread	Not clonal	Lichen zone	Central
Parnassia palustris	Biotic	Widespread	Not clonal	Peaty shore	Central
Pinguicula vulgaris	Biotic	Widespread	Long distance	Rock pool	Southern
Poa alpina	Abiotic	Widespread	Not clonal	Forest edge	Southern
Sagina nodosa	Biotic	Widespread	Clonal	Splash zone	Central
Saxifraga paniculata	Biotic	Local	Short distance	Lichen zone	Southern
Saxifraga tricuspidata	Biotic	Local	Not clonal	Lichen zone	Southern
Tofieldia pusilla	Biotic	Local	Short distance	Rock pool	Southern
Triantha glutinosa	Biotic	Local	Not clonal	Rock pool	Central
Trisetum spicatum	Abiotic	Widespread	Not clonal	Lichen zone	Southern
Vaccinium uliginosum	Biotic	Widespread	Long distance	Rock pool	Southern
Vaccinium vitis-idaea	Biotic	Widespread	Long distance	Lichen zone	Southern

[1] Range values denote where the Isle Royale populations fall, with respect to the overall species range. See text below Figure 3 for a detailed explanation. We did not assign a range location to *Cryptogramma acrostichoides*, as Isle Royale is the only documented location within the study's range criteria.

paniculata and *S. tricuspidata* form cushions composed of multiple rosettes (McGuire and Armbruster 1991, Reisch 2008, Medeiros et al. 2012). While uncertainty about genetic identity of individual rosettes exists (McGuire and Armbruster 1991), Judziewicz (2004) followed Reisch et al. (2003) and recognized cushions as genetically unique individuals, or "genets", and the rosettes comprising these cushions as clones of one another, or "ramets" (Dr. E. Judziewicz, personal communication, 17 May 2016). In these instances, data include counts of both ramets and genets, as well as reproductive stems. In the case of *Pinguicula vulgaris*, vegetative reproduction is prolific, and there is no visual method to discern genetic differences. In this instance, all rosettes were considered ramets. For other species that have a prostrate or spreading growth habit (e.g., *Empetrum nigrum*, *Vaccinium uliginosum*), he made visual estimates of the area occupied in square meters. In several instances, Judziewicz noted only presence or absence.

In collaboration with the National Park Service, he established and permanently marked 28 locations where he found target rare species. Sites were loosely defined as areas supporting rare plants and located on separate islands from one another, or on the mainland, separated by at least 300 meters. The sizes of the sites varied to include the entirety of the rare plants present, in most cases, unless he noted a constrained census area. He revisited and collected similar data at these 28 plots in 1998 (Judziewicz 1999) and 2003 (Judziewicz 2004).

We resampled the 28 permanent plots between 6 July and 1 August 2016 to maximize the probability that plants were flowering or fruiting. We applied area-wide census searches to count or measure all individuals present for any of the 25 target species (see Table 2). Search techniques varied by plot; since these were typically no more than 30 meters in radius, searchers could cover the entire area, easily keeping track of where they had looked. We *a priori* chose four focal species for more intensive population metrics: *Saxifraga paniculata*, *S. tricuspidata*, *Pinguicula vulgaris*, and *Vaccinium uliginosum*. Judziewicz's surveys in 1998 and 2003 most consistently included demographic data across all sites for these four species, which are generally more abundant and apparent than the others. Applying similar methods as Judziewicz, we counted the number of ramets (rosettes), genets (cushions), and reproductive stems of *Saxifraga paniculata* and *S. tricuspidata* at all sites where they were located. For *Pinguicula vulgaris*, a highly clonal species, we recorded the total number of ramets (rosettes). We estimated areal coverage for *Vaccinium uliginosum*.

Data Summaries and Analyses

The availability of quantitative data from the earlier surveys varies among species, years, and sites. In some instances, only presence is noted, while in others, detailed counts of both reproductive and non-reproductive individuals were recorded. However, site occupancy data (i.e., whether a species is present at a site) are standard and comparable among years and species in the long-term data set. For each of the 25 target species, we summed the number of sites occupied by each species during each census and examined the magnitude and direction of change in site occupancy between the initial and final censuses.

We then identified five broad, functional, geographic, and microhabitat groups that could potentially further explain site occupancy: pollination mechanism, dispersal distance, degree of clonality, vertical distribution above Lake Superior, and geographic range position (see Table 2). Some levels within these categorical groups (e.g., abiotic and biotic pollination or long- and short-distance dispersal; see below) may indicate species traits that contribute to the persistence, expansion, or contraction of a population over time. Using literature searches and our knowledge of the species' biology, we classified species into levels for each group (see Table 2). For each of the five groups of interest, we summed site occupancy (the number of sites where a given species was present) across species within each level. In each group, we then compared these sums across the four censuses, the three by Judziewicz in 1993–1994, 1998, and 2003, and our sampling in 2016.

To group species by pollination mechanism, we classified species as biotically pollinated if they contained any specialized attractants, such as colorful flowers. Otherwise, species were classified as abiotically pollinated. For dispersal distance, we considered species to be capable of widespread dispersal if the fruits have adaptations for wind, water, fur, or animal gut dispersal. Otherwise, dispersal was considered local. We categorized the degree of clonality as short distance if the species is capable of vegetative reproduction with only a very limited distance from the parent plant (e.g., adventitious buds). We categorized some taxa as having long distance clonality if there are adaptations for further spread (e.g., rhizomes, stolons, bulbils). Species were considered not clonal if they were capable of only sexual reproduction.

Most of the species here occupy distinct zones within the rocky shorelines (Figure 3), so we categorized species by their microhabitat or vertical position and relative influence by Lake Superior (see Table 2). For example, among our target species, *Sagina nodosa* is largely limited to rock cervices in the lowest elevation habitat <4 meters (slope distance) from the calm weather waterline, which we categorized as the "splash zone" of Lake Superior. Other species also growing near the waterline but in isolated pockets of perpetually wet soil were placed in the "peaty shore" microhabitat. *Pinguicula vulgaris* and *Drosera anglica* are largely confined to the edges of small

Figure 3. Four habitats included in this study. *Clockwise from top left:* splash zone, forest edge, lichen zone, and rock pool. Note: peaty shore habitat not included in this figure.

rock pools. For these and other species occupying a similar niche, we designated the microhabitat as "rock pool." Some species, such as *Trisetum spicatum*, occupy cracks in the basalt in more upland microhabitats that receive less frequent splash from Lake Superior. These upland areas of exposed rock are lichen-covered and soil formation is minimal, so we refer to this microhabitat as the "lichen zone." Finally, the lichen zone transitions to a shrub (i.e., *Juniperus communis* L.) and forested zone, and species such as *Saxifraga tricuspidata* occupy this transition zone, which we refer to as the "forest edge."

To categorize species within their broader geographical ranges, we determined whether the Isle Royale populations were in the southern, central, or northern third of the species ranges in eastern North America (see Table 2). Using the online data portals of Canadensys (2017), Consortium of Midwestern Herbaria (2017), and Consortium of Northeastern Herbaria (2017), we recorded the most northern and southern records for each species. Because populations in mainland Europe and western North America are subject to vastly different temperature patterns from those in central and eastern North America and Greenland, we considered only North American records east of the 100° meridian west and in Greenland. We computed range thirds from UTM northing values of the northernmost and southernmost record for each species. In some instances, herbarium reports at the southern end suggest adventive individuals (e.g., a record of *Lonicera involucrata* in the city of Washington D.C., "near fence gate"). These were not included. We also did not include *Cryptogramma acrostichoides* in this classification, because the Isle Royale populations, which are disjunct from the main range of this species in western North America, were the only ones within the study area.

For the four focal species with complete abundance records, we evaluated the change in abundance from prior to the 15-year drop in lake level (1990s) to 2016 after the lake level rose again. Our goal here is to test for changes in species abundance, concurrent with changing lake levels. For *Saxifraga* spp., we assessed the abundance of ramets, genets, and reproductive stems, while for *Pinguicula vulgaris*, we assessed only the abundance of ramets due to limited data on reproductive status in the historical records. For *Vaccinium uliginosum*, we tested for change in areal coverage. We computed the annual percentage change for most metrics using the formula

[(2016 value–1993 value)/(1993 value * 100)] / 22 years

In some cases, 1994 was the baseline year. We applied non-parametric permutation tests (R, coin package, symmetry_test) to test for differences in abundances between years. This is a non-parametric resampling technique that tests whether values of paired data are symmetrical. These tests do not require assumptions of equal variance between groups and normality of errors; as such, they are applicable here, where sample sizes are small and assumptions of parametric tests cannot be met. In most instances, the baseline time period was from the 1993–1994 census. However, in three instances where earlier data were not available, once for *P. vulgaris* and twice for *V. uliginosum*, we instead used 1998 as the baseline year. The number of site-census year pairs tested for each species was eight (*Saxifraga paniculata*), nine (*S. tricuspidata*), nine (*P. vulgaris*), and 14 (*V. uliginosum*). Continued persistence of these populations is of management significance, so detecting any potential decline is paramount, and we are less concerned about making a Type I error (concluding that population decline exists even when it does not) than a Type II error (concluding that there is no change in abundance when, in fact, change has occurred). For this reason, we considered significance as $P \leq 0.1$.

Results

The 25 rare plant species surveyed in 2016 were dispersed over the 28 monitoring sites (n=3.4 rare species/site). Site occupancy increased for 13 species and remained steady for six species. Six species underwent losses in the number of sites occupied (Table 3). In most cases, functional, microhabitat, and geographic groupings of taxa showed little change in site occupancy between the censuses (Figure 4). Biotically pollinated species composed over two-thirds of the site occupancy, regardless of year (Figure 4a). Likewise, species with widespread dispersal represented nearly two-thirds of the species-site combinations for all years (Figure 4b). During all censuses, non-clonal species were slightly more common at sites than species capable of either long- or short-distance clonality (Figure 4c). The lichen zone and rock pools are more frequently occupied by rare species than other microhabitats within sites (Figure 4d). Throughout all sample periods, most of the rare species occurrences were of species in the southern third of their ranges (Figure 4e).

While change over time was not linear, basal rosette (ramet) numbers for the three herbaceous focal species increased between the early 1990s and 2016 (Figure 5, Table 4) at an annual growth rate ranging from 9.8% (*Saxifraga paniculata*) to almost 14%

Table 3. The number of sites in Isle Royale National Park where rare species were observed in 1993–1994 and their site occupancy in those same sites in subsequent years. Numbers in parentheses indicate the total site occupancy among the 28 sites, including additional sites, where those species were not recorded as observed in previous censuses. "Direction" indicates direction of change between the first and last sampling event, including any additional sites (NNC = no net change).

	Sample Period				
Species	*1993–1994*	*1998*	*2003*	*2016*	Direction[1]
Allium schoenoprasum	1	1	1	1(3)	Gain
Bistorta vivipara	3	2	2	2	Loss
Carex atratiformis	2	1	3	2	NNC
Carex gynocrates	1	0	0	0	Loss
Carex media	3	1	1	2(4)	Gain
Castilleja septentrionalis	3	3	1	3(5)	Gain
Cryptogramma acrostichoides	2	1	2	2	NNC
Draba arabisans	2	2	3(4)	4(5)	Gain
Drosera anglica	1	1	1	1	NNC
Empetrum nigrum	8	8	8	8(10)	Gain
Euphrasia hudsoniana	2	1	0	0(1)	Loss
Huperzia selago	2	2	1(2)	1(3)	Gain
Lonicera involucrata	1	1	1	1	NNC
Packera indecora	4	2	2	3	Loss
Parnassia palustris	2	2	0	0	Loss
Pinguicula vulgaris	11	9	12(15)	11(16)	Gain
Poa alpina	4	2	2	2(3)	Loss
Sagina nodosa	2	2(3)	2	2(4)	Gain
Saxifraga paniculata	6	7	7	8(9)	Gain
Saxifraga tricuspidata	9	7	10	9	NNC
Tofieldia pusilla	3	3	2	1(3)	NNC
Triantha glutinosa	2	3	3	5(9)	Gain
Trisetum spicatum	8	6(8)	7(12)	12(19)	Gain
Vaccinium uliginosum	13	12	14	13(16)	Gain
Vaccinium vitis-idaea	1	1	1	1(2)	Gain

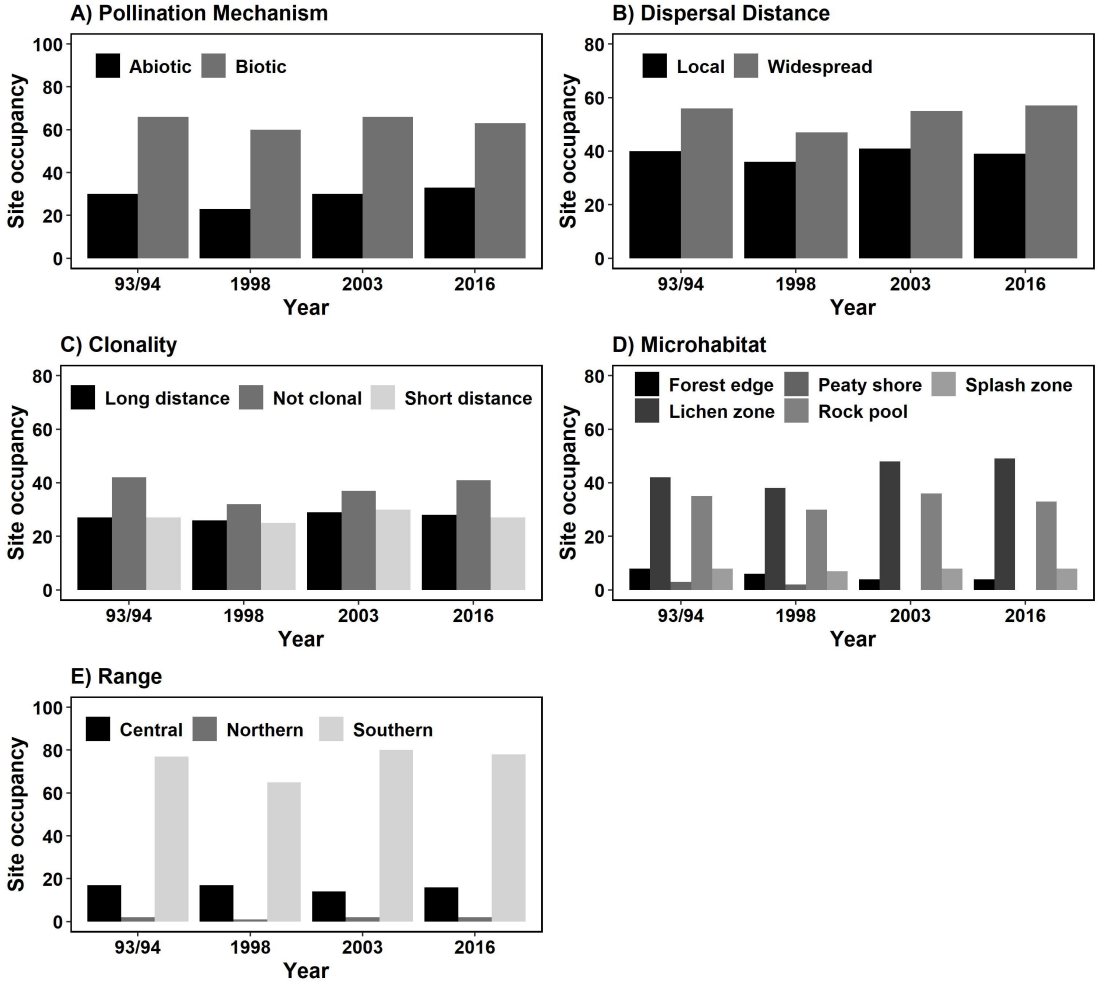

Figure 4. Site occupancy across sample years, grouped by life history traits (*panels a–c*), their local habitat niches (*panel d*), and geographic range position at Isle Royale National Park (*panel e*). Y-axis represents the number of sites where a given species was located, summed across all species within that level-year combination. *Cryptogramma acrostichoides* is not included in range location since it is the only location of this species within the study area.

(*Saxifraga tricuspidata* and *Pinguicula vulgaris*). Despite four times as many total ramets observed for *S. tricuspidata* in 2016 compared to the early 1990s (Figure 5, Table 4), mean ramet number among sites was not statistically greater (Table 5). The only decline in abundance that occurred during the low water period (2003) was in the areal coverage of *Vaccinium uliginosum* (Figure 5, Table 4), but this species had an overall increasing trend with an 8% annual growth rate from the early 1990s to 2016. While average areal coverage of *Vaccinium uliginosum* was 2 m^2 greater in 2016 than in 1993–1994, high variability among populations precluded significant differences (Figure 5, Table 5). The mean plant population size (number of genets) of the lichen zone species *S. paniculata* was five times larger in 2016 than was observed in 1993–1994 (Figure 5, Table 4), representing a 21.4% annual growth rate. Similarly, the average number of reproductive stems was almost five times greater in 2016 for *S. paniculata* (Figure 5, Table 4), but less than 10% of all ramets were reproductive. The forest edge species *S. tricuspidata* had greater variability among populations in some years, so increases observed in average ramet number, genets, and counts of reproductive stems in 2016 were not statistically greater than baseline numbers (Figure 5, Table 5).

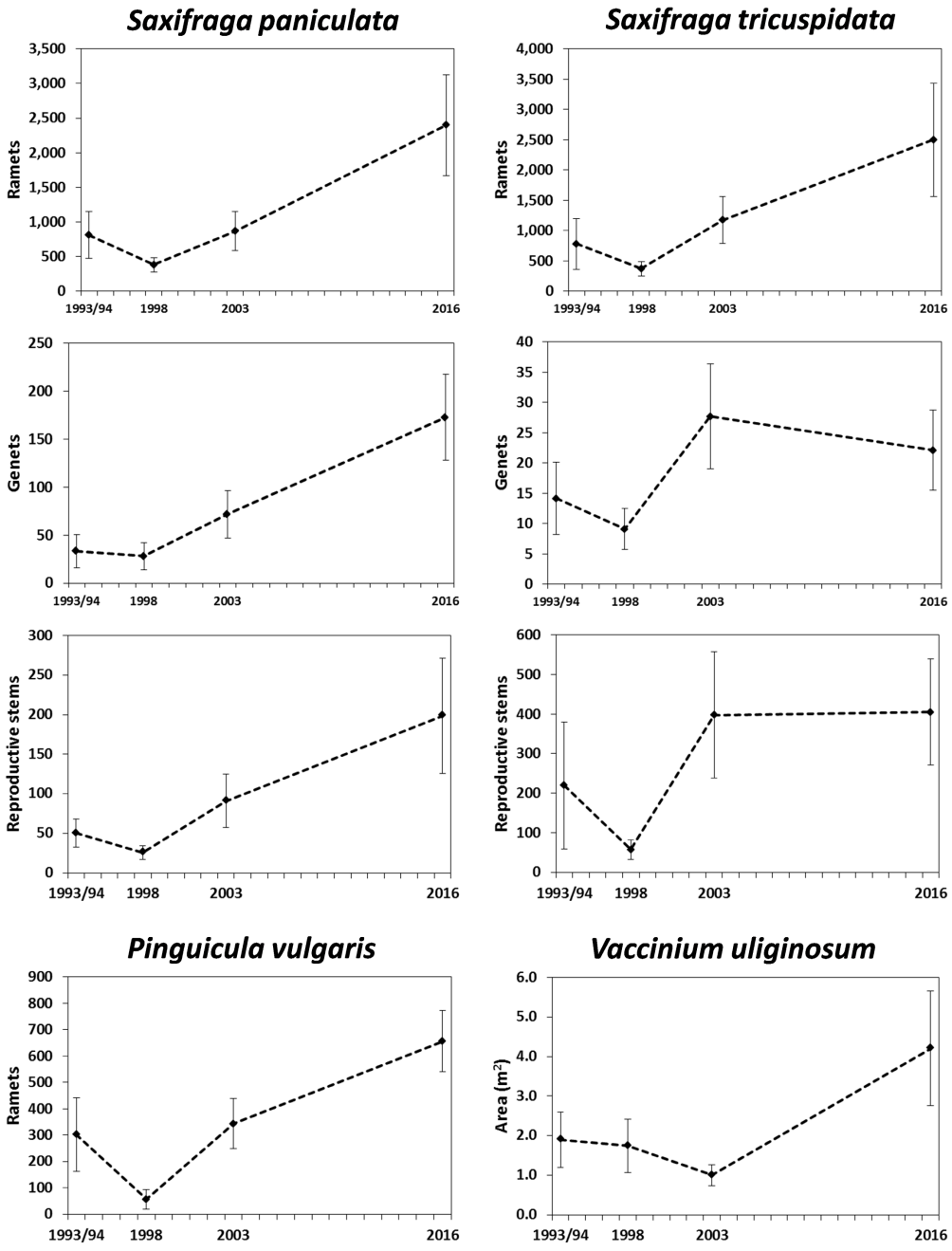

Figure 5. Mean values of ramets, genets, reproductive stems, and/or area occupied for sites of the four focal species across all study years in Isle Royale National Park. Error bars represent ±1 s.e. Permutation tests compared only one pre-low water level time (typically 1993–1994) against the 2016 value.

Table 4. Population metrics across all sites in Isle Royale National Park during each sample period for four focal species for which consistent quantitative abundance data were available.

Species	Sample Period	Total Areal Coverage (m^2)	Total Number of Ramets	Total Number of Genets	Number of Reproductive Stems	Percentage of Reproductive Stems
Saxifraga paniculata	1993–1994	n/a	4,757	186	263	5.53
	1998	n/a	2,807	190	170	6.06
	2003	n/a	5,642	450	610	10.81
	2016	n/a	15,009	1,060	1,230	8.2
Saxifraga tricuspidata	1993–1994	n/a	6,245	113	1,755	28.1
	1998	n/a	3,346	82	515	15.39
	2003	n/a	11,714	277	3,977	33.95
	2016	n/a	24,977	221	4,046	16.2
Pinguicula vulgaris	1993–1994	n/a	2,417	n/a	n/a	9.18
	1998	n/a	506	n/a	n/a	32.41
	2003	n/a	4,799	n/a	n/a	27.76
	2016	n/a	9,829	n/a	n/a	28.38
Vaccinium uliginosum	1993–1994	22.75	n/a	n/a	n/a	n/a
	1998	24.4	n/a	n/a	n/a	n/a
	2003	13.97	n/a	n/a	n/a	n/a
	2016	63.07	n/a	n/a	n/a	n/a

Table 5. P-values for permutation tests for site-year pairs by species. All tests compared the first and last censuses. An asterisk indicates significance at alpha = 0.1.

Species	Ramets	Genets	Reproductive Stems	Area
Saxifraga paniculata	0.0551*	0.0324*	0.0781*	–
Saxifraga tricuspidata	0.1380	0.330	0.4010	–
Pinguicula vulgaris	0.0230*	–	–	–
Vaccinium uliginosum	–	–	–	0.131

Discussion

Our work detailing the population trends of rare species on Isle Royale shows that the majority of these species (19 of 25) are either remaining stable or experiencing expanding population structure. This must be interpreted cautiously, as the number of individuals and sites supporting each of these species remains small. The more detailed data on population structures that we collected on the four focal species tend to support the idea of modest growth. While permutation tests showed changes (increases) in only four of the eight species-metric measures of abundance, we recognize that the small number of these populations can limit statistical power to detect change. Actual values of site occupancy and abundance are generally of more interest to managers; in our case, we observed sizeable increases in all measures of abundance for all four focal species. Across all 25 species, the success of the majority of species we observed in 2016 after a 13-year sampling hiatus was surprising given a 15-year low water level concomitant with rising air temperature, increased evaporation, and intermittently lower precipitation regionally (Gronewold et al. 2016, Zhong et al. 2016), coupled with the fact that these species generally grow farther north or at higher altitudes than Isle Royale. Air and water temperatures have both risen over the 25 years of this monitoring, with lake temperatures warming faster (Austin and Colman 2008). Nonetheless, temperature moderation of coastal habitats by Lake Superior may be limiting the effects of warming temperatures.

Lake Superior hydrology could be playing a role in regulating the occurrence and population sizes of these rare species via changes in lake levels. Water levels are determined by a number of natural inputs and outputs (precipitation, stream input, groundwater, surface water runoff, and evaporation) (Gronewold et al. 2016), as well as limited water level regulation, which is managed by the International Joint Commission and currently follows the Lake Superior Regulation Plan 2012 (International Joint Commission 2012). Lake Superior water level fluctuation has been recorded since 1918, with an average water height of 183.4 m above sea level. These levels were below average from 1998 through 2013, after which levels rose to above-average heights (see Figure 2). While the difference between the 1986 high (183.73 m) and the most recent low (182.98 in 2007) is only 0.75 m, this can significantly impact the amount of bedrock either exposed or submerged, as these headlands are low and with gradual slopes into the lake. The increase in lake level and increases in precipitation between 2013 and 2016 (Gronewold et al. 2016) could explain the relatively successful response of species in 2016, as long-established populations are once again in closer proximity to water recharge and to the temperature-moderating influence of moister coastal conditions.

Rocky shoreline species, while presumably weak competitors, generally possess physiological and anatomical adaptations that confer tolerance against stress (Maestre et al. 2009, Pellissier et al. 2010). *Saxifraga paniculata* (Figure 6), in particular, displays a number of these traits associated with water stress, including leaf cupping (Neuner et al. 2008) and a thick cuticle (Hegi 1975). This species also displays leaf hydathodes, an adaptation to, among other things, high summer temperatures often present on limestone substrates (Andrei and Paraschivoiu 2008). This adaptation creates a cooler, more humid atmosphere around the plant (Andrei and Paraschivoiu 2008), but also allows direct uptake of snowmelt (see Hacker and Neuner 2006) and possibly rainwater and moisture from fog.

Figure 6. *Saxifraga paniculata*, showing white calcium-containing crystals. A calcium solution is exuded through the hydathodes; the water evaporates, leaving the calcium-rich residue.

The ability to absorb moisture from the air may also exist in *Pinguicula* (Figure 7), a genus of carnivorous species with specialized glands on the lower leaf surfaces (Lloyd 1942, Adlassnig et al. 2005), but we do not know if this has been demonstrated. The favorable performance of *P. vulgaris* may be more a function of its dispersal mechanism. Like most carnivorous plants, *P. vulgaris* possesses only a weak root system (Adlassnig et al. 2005); in autumn, a winter bud (hybernaculum) is produced with several gemmae around the base (Heslop-Harrison 2004). Running water or, in the case of Isle Royale, wave action can dislodge gemmae, allowing them to disperse to and colonize new rock pools (Legendre 2000). The 0.75-m rise in water level may have allowed wave action to reach extant colonies that had experienced either limited or no high velocity wave action for several years. Expanded rock pool habitat may also have occurred with increased water levels.

Despite the numerous positive changes, six species experienced overall losses in the number of sites occupied (population contraction) over the entirety of the study period. It is likely that several factors contributed to changes for each species. One of the declining species, *Bistorta vivipara* (Figure 8), is known to have a low seed set

Figure 7. *Pinguicula vulgaris* (light green basal rosettes) growing in a small pool.

Figure 8. *Bistorta vivipara* showing reddish bulbils on the lower part of the inflorescence.

and slow and conservative growth (Diggle 1997); five growing seasons are required between leaf and inflorescence initiation to reach functional maturity. As a consequence, the current season's above-ground appearance reflects environmental conditions of the previous four years; likewise, poor environmental conditions during one year could impact five years of plant performance. Reproduction is primarily asexual, by bulbils, and successful fruit set has only rarely been reported in the literature (see Diggle et al. 2002 for citations). In North America, fruit set in the subalpine environment has been reported only in Wyoming (Bliss 1958). Reasons for the low fruit set include low pollen viability (Engell 1978, Diggle et al. 2002) and high rates of embryo abortion, possibly due to genetic abnormalities (Diggle et al. 2002). Reproduction by bulbils may be adaptive in cold environments (Billings and Mooney 1968) by reducing reliance on pollinators and allowing dispersion of successful genotypes away from the parent plant. Like many of the species in this study, however, Isle Royale populations are highly isolated from other populations outside of the Park, and often even from one another within the archipelago. Lack of genetic recombination on a regular basis would limit the ability of *Bistorta vivipara* to adapt at the southern

edge of its distribution, where conditions are likely sub-optimal (Reed and Frankham 2003, Spielman et al. 2004).

Like *Bistorta vivipara*, *Poa alpina* also reproduces by both bulbils and seed and also experienced a decline over the 24-year study period, with two of the four sites extirpated. Research in North America (Hermesh and Acharya 1987) has demonstrated temperature-specific adaptation for a number of reproductive characteristics, including the number of florets per panicle. In an alpine environment in Europe, Steiner et al. (2012) found plastic responses of *P. alpina* in response to transplantations across elevations. Although we are unaware of the relative proportion of seed vs. bulbil production for Isle Royale populations, collectively, these suggest *Poa alpina* should be able to either adapt or acclimate to environmental conditions there.

The ability to adapt may be greater for annual species, as a result of more frequent genetic recombination, although distances between populations could also be prohibiting this. One of the species that fared the poorest over the 24-year study period is *Euphrasia hudsoniana* (Figure 9), originally present at two locations. This appears to have been extirpated from the sites where it was originally known, although it was subsequently found in 2016 at a site not previously occupied by this species. Zlonis and Gross (2018) examined the genetic structure of this species on the rocky shoreline of Lake Superior in northern Minnesota. They demonstrated a high degree of heterozygosity within populations, which may be a result of its tetraploid genome (Meirmans and Van Tienderen 2013). While this level of heterozygosity should promote population persistence, the distances separating known populations will inhibit, or even prevent, gene flow between them. Additionally, the small population size will also limit the ability to mate successfully (Hackney and McGraw 2001). Ultimately, such isolation may be rendering this species unable to adapt to changing environmental conditions.

Of the species that performed well, two—

Figure 9. *Euphrasia hudsoniana* on one of the Isle Royale barrier islands.

Sagina nodosa (Figure 10) and *Trisetum spicatum* (Figure 11)—were particularly surprising to us. *Sagina nodosa* grows just above the waterline and typically occupies the lowest niche on the rocks. Because of this, we may have anticipated a downward migration of existing populations over the low water period, followed by a loss of these populations as the water level rose to above-average levels after 2013. Instead, we found a net increase in populations. In addition, although abundance data are not available for all sites at all time periods, where data are available, we found marked increases in the number of stems in total, as well as those that were reproductive (data not shown). *Sagina nodosa* produces vegetative buds on the stem that disarticulate; these float and are carried by wind and water to potential new colonization sites (Wright 1953). This form of reproduction and dispersal is highly adaptive in this environment and will likely serve this species well in the face of future potential fluctuating water levels.

The grass species *Trisetum spicatum* is also performing well in the Park. While we do not have abundance data for all sites and censuses, the abundance of both genets and reproductive stems generally increased ten-fold at sites where data are available (data not shown). In addition, we often

Figure 10. *Sagina nodosa* showing proximity to water.

noticed this species growing in several areas along the rocky coastlines outside of established sampling sites. Unfortunately, little is known about the biology of this species that could inform us of the causes for this increase.

Piecing together the biological basis for change in rare species can be challenging, and rare species sampling efforts themselves also present unique challenges. In the absence of aerial imagery, maps were often hand drawn in earlier sampling efforts, and GPS was often either unavailable or unreliable, making relocation inexact, although, Judziewicz's (1999) maps and notations about sample locations were quite detailed. Differences between observers also introduces uncertainty (Alexander et al. 2012, Morrison and Young 2016); these differences can be between sampling events or from within the same event. Finally, a species population in some locations could be comprised of large numbers of genets or ramets, which also introduces some degree of error in complete census counts, especially when, as in some instances, hundreds of ramets are present. For the current work, we acknowledge a degree of uncertainty when counting ramets and assessing areal coverage, including for all four focal species. However, counts of genets and reproductive stems were much more straightforward, since these were fewer and more clearly defined. We note here that the relative patterns of abundance of both genets and reproductive stems

Figure 11. *Trisetum spicatum* on rocks.

largely mirror those of ramet abundance for the first three time periods of this study, a small dip in abundance in 1998 followed by a sizeable increase in 2003 (see Figure 5). In our current census (2016), we see a similar pattern, where marked increases in ramets are concordant with more genets and reproductive stems, providing further assurance that the large increases we observed in 2016 are genuine. Finally, the three earlier censuses were completed by Judziewicz (1995, 1999, 2004), who one of us (S. Johnson) assisted elsewhere to monitor rare plants using similar methods. Because Johnson was at all sampling locations and times in 2016, we have assurance that techniques and practices of the 2016 event were fairly consistent with those of earlier censuses.

We recognize that factors besides lake level may be playing into species performance, particularly locally. Unfortunately, we lack site-level data on temperature and solar radiation; likewise, the record for precipitation at the Park is incomplete. Because of these shortfalls, we are unable to test for correlations of these metrics with population response. However, what this work does show is that, despite a 16-year

record of low water, the majority of these species are as abundant, or even more abundant, than prior to the drop in water level. Our work here, which represents only a relatively short period of time, suggests that these species possess a degree of resilience to ecosystem stressors that we had, perhaps, not anticipated. The continued fate of these populations, of course, remains uncertain.

Research Needs and Management Recommendations

For the majority of species studied here, we lack detailed information on basic biology (Godefroid et al. 2011). Understanding the breeding system, population genetic structure, anatomy (as it relates to growth and development), and physiology (responses to temperature and solar irradiation) would help guide any future management action and/or development of restoration plans. Thorough, updated inventories of all potentially suitable habitat is also desired.

At this point in time, we urge park managers to explore seedbanking for some of these species. Retaining seed not only conserves genetic material, but provides sources for *ex-situ* research, as suggested above. We also suggest that Isle Royale managers initiate a dialogue with their counterparts at other parks around Lake Superior that support these species. For populations with limited genetic diversity, reciprocal outplanting of seed (or vegetative material) between them may be required to avoid local extinction.

While the idea of working to preserve these species is noble, in reality, options to manage these species will be limited in the face of continuing climate change. By and large, these species are adapted to cooler, moist conditions with less solar irradiation, concomitant with northern latitudes. They have most likely persisted due to the moderating effects of Lake Superior and available rocky shoreline habitat. As air and water temperatures continue to rise, suitable habitat within the Park may cease to exist. Managing foot traffic in high visitor use areas (e.g., Scoville Point on the main island) could limit trampling of species such as *Saxifraga tricuspidata* and *Empetrum nigrum*.

Removing non-native wetland species (*Typha angustifolia* L. and its hybrid with the native *T. latifolia* L.) from rock pools may serve to protect habitat for rare species such as *Carex media* R.Br. At the upper edge of their habitat, succession to shrubs and forest may overcome habitat for populations of species such as *S. tricuspidata* and *E. nigrum*, so maintaining more open conditions in some sites is an option to retain regenerating populations of these rare species.

Managing for other species is not as clear-cut. While we have every interest in preserving natural resources within the National Park System, one may question the prudence of this, given the current climate forecasts, the difficulties encountered during rare species reintroductions, and the fiscal demands of such efforts (Godefroid et al. 2011). Nonetheless, what we propose here is still of value. Several of these species have widespread distributions and documenting their changes in occurrence on Isle Royale may signal species-scale distributional shifts related to climate change. Documenting changes in rare species may cue managers of the risk of deeper ecosystem changes. Knowledge gained of breeding systems, physiology, and genetic structure of these species could be applied not only to managers on Isle Royale, but to practicing conservationists elsewhere.

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National Park Service
U.S. Department of the Interior

Natural Resource Stewardship and Science
1201 Oak Ridge Drive, Suite 150
Fort Collins, Colorado 80525