

Population Viability Analysis for an Endangered Plant

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Abstract: Demographic modeling is used to understand the population viability of Furbish's lousewort, *Pedicularis furbishiae*, a perennial plant species endemic to the St. John River Valley in northern Maine. Environment-specific summaries of demographic parameters (survivorship, growth, and fecundity) over four years, organized into stage-based projection matrices, provide predictions of future population dynamics given a deterministic extension of past conditions. Stochastic modeling, using (1) empirically observed variation in demographic parameters, and (2) estimated natural catastrophes, leads to predictions of extinction probability.

P. furbishiae viability has varied widely over the study period. Viable populations with finite rates of increase >1 are found where cover is low, woody plants do not dominate, and disturbance does not occur. Rates of increase vary over time, suggesting that stochastic analyses would be realistic. Stochastic measures of population viability incorporating environmental variation suggest that early successional environments, especially wetter sites, can support viable populations in the absence of disturbance. However, observed rates of natural catastrophe dominate viability estimates of individual populations. Metapopulation dynamics feature extinction rates that are greater than recolonization rates, and may be affected by land use in the watershed. Species management needs to consider a large-scale view of the riverine corridor.

Resumen: En este trabajo se emplea el modelaje demográfico para esclarecer la viabilidad poblacional de la planta perenne *Pedicularis furbishiae*, (Furbish's lousewort), endémica al valle del río St. John, en el norte del estado de Maine. Los resúmenes de parámetros demográficos, (sobrevivencia, crecimiento, y fecundidad), de un periodo de cuatro años, específicos para cada tipo de ambiente, se organizaron en matrices de proyección por etapas, para predecir la futura dinámica poblacional en base a una extensión determinística de condiciones anteriores. Los modelos estocásticos, utilizando (1) variaciones en parámetros demográficos observadas en la práctica, y (2) índices estimados de catástrofes naturales, conducen a predicciones de probabilidades de extinción.

La viabilidad de *P. furbishiae* varió ampliamente durante el periodo de estudio. Se encuentran poblaciones viables (con λ mayor a 1) en áreas con poca cobertura, donde no dominan las plantas leñosas y no existe alteración. Las tasas de incremento varían con el tiempo, sugiriendo que los análisis estocásticos son realistas. Las medidas estocásticas de viabilidad poblacional que incorporan variaciones ambientales, sugieren que los ambientes en etapas de sucesión temprana, especialmente en los sitios más húmedos, podrían sostener poblaciones viables, si es que no existe alteración. Sin embargo, las estimaciones de viabilidad para poblaciones individuales, están dominadas por los porcentajes de catástrofes naturales. La dinámica de metapoblaciones presenta índices de extinción mayores que los índices de recolonización, y podrían ser afectadas por el uso de tierras en las áreas de las cuencas hidrográficas correspondientes. El manejo de especies necesita considerar el panorama a escala mayor del corredor fluvial.

Introduction

Furbish's lousewort, *Pedicularis furbishiae*, has been of interest to conservationists and scientists for some time. Once thought to be extinct, it became one of the first

plant species listed as federally endangered by the federal government (U.S. Fish and Wildlife Service 1978). Surveys by Richards (1980), Stirrett (1980), and Gawler (1983), documented the distribution of about 5,000 *P. furbishiae* plants in 28 colonies along a 140-mile stretch

of the St. John River in northern Maine and adjacent New Brunswick (Fig. 1). Some specific work on seedling requirements and pollination ecology were carried out by Macior (1978, 1980). Donald M. Waller, Susan C. Gawler, and I then collected baseline information on the species' distribution, life history, and genetics. Our goals were to assess population viability and understand human and natural threats to the long-term persistence of *P. furbishiae*.

P. furbishiae is a herbaceous perennial that produces erect reproductive stems (scapes) with spike-like inflorescences of bumblebee-pollinated flowers (Menges et al. 1986). Because vegetative plants consist only of basal rosettes and are susceptible to overtopping by competitors, this species is largely limited to periodically disturbed, north-facing riverbanks. *P. furbishiae* does not spread clonally, so establishment of new populations and expansion of existing populations occurs exclusively by sexual reproduction. Seeds lack sophisticated mechanisms for wind or animal dispersal, but their loose, reticulate seed coat allows them to float for sev-

eral days, perhaps accomplishing long-distance dispersal.

Any endemic may be threatened by its limited distribution, as local catastrophes can destroy large portions of its total population. *P. furbishiae* is an anomaly, an endemic in a region with notably low endemism and a recent biological history of less than 12,000 years (since the last glaciation). Speciation probably followed either isolated or long-distance dispersal (Macior 1982).

The restriction of *P. furbishiae* to the banks of a single river suggests that it has specific environmental requirements. However, the unique features of its habitat appear to be largely hydrologic. The St. John River, which drains one of the largest watersheds in the northeast, includes the longest free-flowing stretch of water in the northeast (Gawler 1983) but has relatively little headwater storage. Severe spring ice jams are well known, especially in the upstream, north-flowing stretches (Fig. 1). Dramatic seasonal and long-term fluctuations in water level (Menges & Gawler 1986) create the opportunity for great temporal variation in primary disturbance

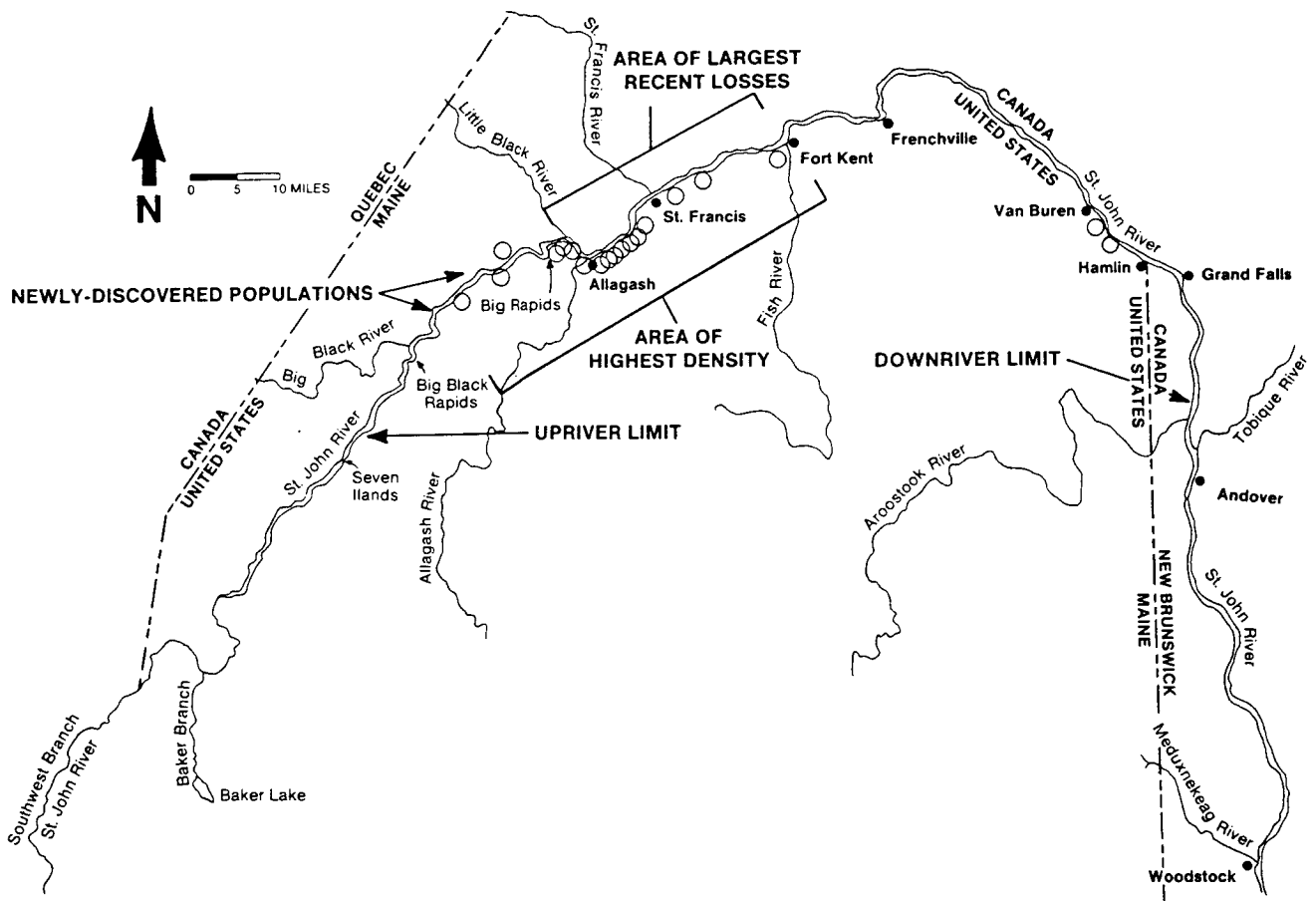


Figure 1. Map showing range of *Pedicularis furbishiae* and locations of populations studied in detail from 1983 to 1986 (open circles).

caused by ice scour, and for secondary disturbance by bank slumping and other erosional events along steep river banks. These disturbances also are distributed patchily in space on both large and small scales and, as will be described, dramatically affect *P. furbishiae* population dynamics.

A disturbance/successional niche for Furbish's lousewort is defined by river hydrology and vegetation response. Louseworts are largely confined to a shrub-dominated transition zone on the riverbank below undisturbed boreal forest and above a sparsely vegetated, frequently flooded cobble zone. This transition zone bears the brunt of ice scour, which prevents tree establishment and prunes above-ground shrub biomass. As time since disturbance increases, shrub height and cover increase. Nearby smaller rivers typified by infrequent disturbance are bordered by dense, older shrub thickets, lacking *P. furbishiae* and other species characteristic of the ice disturbance zone. The community patterns of zonation, disturbance, and competition have striking parallels with shoreline vegetation of lakes (Keddy 1983; Wilson & Keddy 1986).

Our research has confirmed that the dynamism of the St. John River is both a benefit and a problem for Furbish's lousewort populations, causing catastrophic mortality but also creating long-term, appropriate habitat by reversing successional changes that would doom lousewort populations. For assessing population viability means that single-time samples will not be representative, that dynamic behavior must be assessed, and that local equilibrium assumptions and models are invalid.

For *P. furbishiae*, population viability is modeled at multiple spatial and temporal scales, considering both within-population and metapopulation processes. Within individual populations, I modeled environmental stochasticity (population-wide variation in demographic parameters, May 1973; Sykes 1969 Model 3; Shaffer 1981) presumably due to environmental fluctuations. A second level of stochasticity affects the extinction and creation of entire populations by natural catastrophes, and creates metapopulation dynamics. I do not consider demographic stochasticity, which influences only very small populations (Keiding 1975; Shaffer 1987; Menges 1990). Genetic effects cannot be modeled because of the complete lack of genetic variation in *P. furbishiae* as detected by electrophoretic patterns (22 loci, 28 individuals, four populations) (Waller et al. 1988). Population viability analysis is in its infancy (Soulé & Simberloff 1986). To date, analysis of population viability of particular species has been limited to animals (e.g., Shaffer & Samson 1985; Knight & Eberhardt 1985; Nedelman et al. 1987; Belovsky 1987). By use of models incorporating individual population dynamics plus estimates of metapopulation dynamics,

the first assessment of population viability for a plant species is possible.

Methods

Demographic Parameters Within Individual Populations

To provide data on demographic parameters (annual rates of survival, growth or change among defined life history stages, and fecundity), over 6,000 individually marked and mapped plants were followed between 1983 and 1986. The parameters and their variation by population, year, and environment form the basis of population viability modeling. Environmental measurement included a visual estimate of vegetation cover (excluding overhanging trees), substrate type, substrate disturbance class, dominant vegetation, light (using canopy photographs), and soil water potential (using tensiometers). All but the latter two were quantified at the individual plant level; light and water were assessed by transect-level measurements (for details, see Menges 1988). Data were gathered from seven populations between 1983 and 1984 (three of which were destroyed in 1984) and 17 populations subsequently.

P. furbishiae survival, growth, and fecundity are clearly affected by the stage or size of plants (Gawler et al. 1987; Menges 1988), as in most plant species (e.g., Werner & Caswell 1977; Sarukhan et al. 1984; Lacy 1986). Therefore, stage classes based on reproductive status and size were used in modeling population dynamics. Two flowering size thresholds can be defined: one below which plants will not flower, and one above which plants will always flower. Therefore, I recognized six stages: (1) seedlings, (2) juveniles (below minimum flowering size), (3) vegetatives (above minimum flower size but not flowering), (4) flowering plants with one scape, (5) with two to four scapes, and (6) with more than four scapes. These stages differ markedly in demographic parameters (Menges 1988). Annual survival (from spring to spring) and growth for plants of particular populations, environments, life history stages, and years was calculated from sample sizes of seven plants or more; smaller samples were replaced by averages from larger groups.

Estimates of fecundity for transition matrix modeling need to consider the number of seedlings resulting from previous reproduction. In *P. furbishiae*, which lacks seed dormancy or a seed bank, seedling numbers in one year result from the previous year's reproduction. Two approaches can be taken to calculating fecundity: a mechanistic approach that attempts to understand all the components of fecundity using detailed data on reproductive effort, seed predation, herbivory, and field seed germination (Menges 1988), and an empirical approach that analyzes the relationship of seedlings cen-

sused in an area to total previous reproductive output (measured as inflorescence length) in the area. This paper reports the latter.

Modeling Population Viability

I use stage-based, transition matrix modeling based on demographic parameters (described above) to explore population viability for individual populations and environmental states. Matrix projection simulates the changes in a population with a given age or stage structure through time (Leslie 1945; Pollard 1966; Hubbell & Werner 1979; Caswell 1982*a, b*). In its simplest deterministic form, the elements of the matrix, which represent stage-specific demographic parameters, do not vary with time. Such a population will eventually grow exponentially at a fixed, finite rate of increase (λ), and will attain an equilibrium stage structure (Caswell 1982*a, b*). While it is unreasonable to assume such population growth could continue without change for long periods of time, calculations of λ and other derived values are useful to compare populations, environments, or stages (e.g., Werner & Caswell 1977; Schmidt & Levin 1985; Fiedler 1987).

Variations in population growth rate, driven by variation in demographic parameters, are crucial to understanding population persistence (Goodman 1987*b*). Therefore, a stochastic measure of population viability, low extinction probability, can be taken more literally than deterministic measures. I used a simulation model (POPPOJ; Menges 1986, 1990) to project *P. furbishiae* population growth, modeling environmental stochasticity by equal-probability sampling from the three observed transition matrices (1983–84, 1984–85, 1985–86). (A similar analysis limited to two matrices was used for *Arisaema triphyllum* by Bierzychudek [1982]). No density-dependence was assumed, as no clear evidence of it exists for *P. furbishiae*. For these simulations, populations of 500 individuals were followed for 100 years, with 100 replicate runs (more in a few cases to check extinction probabilities; they changed less than 5% [Harris et al. 1987; Maguire & Shaffer 1988]).

Metapopulation Data and Analysis

An understanding of metapopulation dynamics (metapopulation = a group of interacting populations) requires estimates of local population extinction, local population establishment, and spatial and temporal linkages among populations. These parameters are difficult to determine because they act on large spatial and temporal scales. For metapopulation parameters, I counted apparent extinctions and new foundings, based on repeat counts of numbers of flowering stems over the entire range of *P. furbishiae*, between 1980 and 1984 (Menges & Gawler 1986). Rates were expressed on an

annual percentage basis. These data need to be interpreted with caution because the disappearance of flowering stems or their new appearance may not be identical with patterns for vegetative plants.

Results and Discussion

Demographic Parameters

Demographic parameters for *Pedicularis furbishiae* vary from year to year and by environment and population. All parameters representing increases in stage were greater for 1984–85 than for either 1983–84 or 1985–86 (Table 1). Thus, the various matrix elements do not vary independently; a favorable year is favorable for all life history stages.

Favorable environments for individual survival and growth have low, herb-dominated vegetation cover (Table 2). Seedlings are particularly responsive to lower cover. In contrast, the effects of soil moisture vary with time. Wet soils favor growth, especially within dry growing seasons (e.g., 1984–85), but also are prone to spring disturbance (e.g., 1983–84), causing significant local mortality (Menges 1988).

Fecundity values vary by population (Table 3), with a mean of 0.41 seedlings produced per cm of inflorescence length (excluding one outlier). Multiplying by observed inflorescence length on individual plants gives fecundities, which also vary by population (Menges 1988). Demographic parameters can be conveniently summarized into transition matrices (e.g., Table 4), which are used in viability modeling.

Population Viability Analysis

Under unchanging conditions, λ (the equilibrium finite rate of increase) is a measure of population viability. For 1984–85, the calculated λ of 1.27 suggests rapid population growth under these favorable conditions. Under 1983–84 conditions ($\lambda = 0.77$), populations would decline rapidly. The 1985–86 rate ($\lambda = 1.02$) indicates nearly stable population size if conditions were to remain the same.

Individual *P. furbishiae* populations vary in the cal-

Table 1. Year-to-year variation in mean (and standard error) of demographic parameters representing survival and growth. Standard errors represent variation among populations (3 for 1983–84, 15 for other years).

From	To	Percentage From		
		1983–84	1984–85	1985–86
Seedling	Juvenile	33.3 (7.3)	39.0 (2.7)	30.6 (3.5)
Juvenile	Vegetative	12.3 (3.1)	21.1 (1.6)	15.6 (1.6)
Juvenile	Small repro.	6.4 (0.9)	10.9 (1.9)	3.4 (0.7)
Vegetative	Small repro.	35.6 (2.9)	45.1 (2.8)	35.2 (4.1)
Vegetative	Medium repro.	8.3 (1.0)	10.8 (1.9)	7.1 (1.8)
Small repro.	Medium repro.	8.0 (2.0)	21.3 (4.4)	16.3 (3.0)

Table 2. Effect of environment on advancement (vs status, regression, and mortality) from four life history stages, for three years.

Environmental factor	Years	Stage ^a	Chi square	Favorable environment
Cover	1983-84	S	34.0***	Low cover
		J	13.0*	
		V	8.8*	
		SR	3.2	
(3 Classes)	1984-85	S	30.9***	Low cover
		J	24.8***	
		V	2.4	
		SR	12.5***	
(2 df)	1985-86	S	34.5***	Low cover
		J	7.2*	
		V	17.0***	
		SR	0.8	
Dominant vegetation	1983-84	S	0.1	—
		J	1.8	
		V	2.6	
		SR	0.1	
(woody or not)	1984-86	S	0.0	Herbaceous dominant
		J	7.1**	
		V	0.4	
		SR	9.3**	
(1 df)	1985-86	S	6.4*	Herbaceous dominant
		J	14.5**	
		V	6.5*	
		SR	0.9	

^aSeedling, J = Juvenile, V = Vegetative, SR = Small Reproduc-

- * $P < 0.05$
 ** $P < 0.01$
 *** $P < 0.001$

culated lambdas, and rates also vary with time (Table 5). Based on lambdas, none of the three populations with 1983-84 data appear viable. However, all but 2 of 15 1984-85 populations have positive growth rates, with 3 having lambda > 1.5. About half of all populations have lambda > 1.0, based on 1985-86 data, with all but 4 populations clustered between 0.9 and 1.1. Thus, based on 1985-86 data, most undisturbed populations are predicted to remain fairly stable in size if these conditions continue.

Conditions do not remain constant, and variation in lambda over time demonstrates this. Only 7 of 15 populations have lambda > 1 for both 1984-85 and 1985-86 data. Four of 15 populations will decline based on at least two of the three study periods; these populations do not appear viable. For other populations, a viability assessment based on single lambdas would be misleading. While a relationship exists between population rank based on 1984-85 versus 1985-86 data, the ordering is imperfect (Table 5).

The variation of lambda among populations reflects, in large part, environmental conditions. Favorable conditions are low or medium vegetation cover and domi-

nance by nonwoody plants. Cover has important and consistent negative effects on population viability as measured by lambda (Fig. 2a). In all years, higher vegetation cover produces lower equilibrium population growth rates. However, in 1984, even populations consisting of plants under high cover have lambda > 1. In contrast, only low cover conditions promoted positive population growth in 1983. Dominant vegetation had a similar effect on lambda, with *P. furbishiae* in woody plant-dominated areas having lower lambdas in two of three years (Fig. 2b).

The effects of moisture were more variable with time (Fig. 2c). Dry soils generally supported less viable populations and promoted less population variation among years than wet soils. In 1984, only dry soils did not support growing populations, while in 1985 only saturated and wet soils were favorable. In 1983, moisture conditions had little overall effect. Saturated soils supported both highest growth and highest reproduction; however, plants growing on saturated and wet soils were particularly subject to partial disturbance by bank slumping between 1983 and 1984 (Menges 1988).

These results quantify the overall effects of different environments on population viability. Under dominance by woody plants with high cover, populations are not viable. These unfavorable conditions result from a lack of disturbance and resulting successional changes. Thus, too little disturbance sets demographic limits to *P. furbishiae*. Too much disturbance, however, may pose a threat by removing partial or entire populations.

Stochastic analyses, using alternative matrices representing different pairs of years, confirm conclusions based on deterministic analyses. Early successional environments with low vegetation cover not yet dominated by woody plants support viable *P. furbishiae* populations (Fig. 3). Such environments vary in soil moisture, but the driest sites do not maintain viable populations. These stochastic results include substantial environmental stochasticity, but not population destruction.

Metapopulation Analysis

The expectation of the previous analyses, that early-successional moist or mesic environments will support viable *P. furbishiae* populations, is based on viability analysis of individual populations not destroyed by catastrophic extinction events. However, population extinctions have been observed. Between 1983 and 1984, 3 of our 10 study populations were completely destroyed by ice scour and bank slumping, and none have been recolonized during the succeeding years. At Big Rapids, only two adult plants growing high on a riverbank were spared in 1983-84. Subsequently, a group of seedlings appeared below them, but perished due to further disturbance. Similar but more permanent local

Table 3. Fecundity estimated by field observations.^a

Population	Number seedlings			Seedlings/IL ^b		
	IL ^b —1983	1984	Seedlings/IL ^b	IL ^b —1984	1985	Seedlings/IL ^b
Gardner's Old	201	28	0.14	92	32	0.35
St. Francis	130	29	0.22	37	4	0.12
Fort Kent	191	54	0.28	271	244	0.90
Fox Brook South	NA	33	NA	627	343	0.55
Van Buren	NA	14	NA	50	51	1.02
Hamlin	NA	42	NA	186	78	0.42
Fox Brook Ledges	NA	NA	NA	50	44	0.88
Ferry Landing	NA	NA	NA	37	183	4.94
Jandreau	NA	NA	NA	1002	493	0.49
Wesley Ledges	NA	NA	NA	61	9	0.15
St. Paul	NA	NA	NA	377	188	0.50
Negro Brook	NA	NA	NA	489	213	0.44
Gardner's New	NA	NA	NA	196	113	0.58
Cone Burner	NA	NA	NA	894	225	0.25
Wesley Veratrum	NA	NA	NA	591	38	0.06
Wiggins	NA	NA	NA	21	1	0.05

NA No data available or not applicable.

^a Values are adjusted for missing inflorescence length data in a few reproductive plants.

^b IL = total inflorescence length in population (cm).

recolonizations have been inferred by seedling distributions without two other populations. Thus, populations driven to near-extinction may recover from a very few individuals, and such population bottlenecks could explain the apparent lack of genetic variation in surviving populations of *P. furbishiae*.

Metapopulation data provide estimates of extinction rates of 2% or 4–12%, depending on spatial scale (Table 6). Even these small annual probabilities of extinction translate to almost certain extinction over moderate periods of time. By raising annual survival rates to powers, long-term population survival rates were calculated. For example, the 100-year survival probability for 2% annual extinction risk is only 13%. Thus, the rates of catastrophic disturbance suggested by our study do not support the existence of viable individual populations (using 95% survival for 100 years as the usual, arbitrary criterion of population viability). One is forced to con-

clude that individual *P. furbishiae* populations are temporary features of the riverine ecosystem.

Catastrophic mortality dominates estimates of population viability, causing the majority of extinctions when added to within-population environmental stochasticity in simulations (Table 7). However, even under fairly severe (2%) catastrophic probabilities, favorable environments maintain an advantage (Table 7).

Catastrophic disturbance events vary with soil moisture of a given site, but their interaction with non-catastrophic processes does not favor *P. furbishiae*. For example, dry sites that may be least prone to bank slumping do not support viable populations, even in the absence of major disturbances (Fig. 2a), while wet sites favorable for growth and survival between disturbances suffer more frequent periodic extinction due to catastrophic disturbance. Mesic sites represent an intermediate case.

Table 4. Transition matrix, 1984–85, all populations ($\lambda = 1.27$). Values in parentheses are standard errors over 15 populations.

TO:	FROM:					
	Seedling	Juvenile	Vegetative	Small	Medium	Large
Seedling	—	—	—	2.45 (1.64)	7.48 (5.02)	29.93 (20.08)
Juvenile	0.39 (0.03)	0.47 (0.02)	0.14 (0.02)	0.09 (0.01)	0.04 (0.02)	—
Vegetative	0.01 (0.00)	0.21 (0.02)	0.24 (0.02)	0.24 (0.04)	0.16 (0.02)	0.01 (0.00)
Small repro.	—	0.11 (0.02)	0.45 (0.03)	0.36 (0.04)	0.26 (0.03)	0.00 (0.00)
Medium repro.	—	0.00 (0.01)	0.11 (0.02)	0.21 (0.04)	0.42 (0.03)	0.28 (0.00)
Large repro.	—	—	—	0.01 (0.01)	0.10 (0.03)	0.61 (0.00)

Table 5. Population viability (finite rate of increase, λ , at equilibrium), based on different years' data. *P. furbishiae* populations are ordered by λ based on 1984–85; note that ordering in other years.^a

Population	Finite rate of increase (λ), based on:		
	1983–84	1984–85	1985–86
Ferry Landing	—	1.81	1.67
Fox Brook South	—	1.71	1.00
Negro Brook	—	1.64	1.02
St. Paul	—	1.39	1.10
Jandreau	—	1.36	1.00
Fort Kent	0.68	1.27	0.94
Cone Burner	—	1.24	0.96
Fox Brook Ledges	—	1.16	1.18
Wesley Veratrum	—	1.05	0.88
Hamlin	—	1.05	1.12
Gardner's New	—	1.04	0.95
Gardner's Old	0.76	1.03	0.90
Wiggins	—	1.00	0.94
St. Francis	0.64	0.98	0.58
Wesley Ledges	—	0.92	0.92

^aNo analytical tests of significance are yet possible for λ , because it is a derived, multivariate value. The method of Lande (1988) assumes independently varying matrix elements, patently unreasonable for this species. The data were not collected in a way to allow jackknifing and bootstrapping methods (H. Caswell, personal communication).

Because individual populations appear to be short-lived, attention must be shifted to the founding of new populations. The annual founding rate has been 3% of extant populations (Table 4). Clearly, metapopulation viability in *P. furbishiae* depends on a positive balance between new populations and extinction due to all causes. The respective probabilities of these events (3% vs 2–12%) suggest a negative balance.

Conservation Considerations

Species such as *Pedicularis furbishiae* offer some distinct challenges to conservationists. The classic species conservation strategy of protecting the best individual populations while ignoring others will not necessarily ensure species persistence. The natural disturbance regime of the St. John River is destined to remove any given *P. furbishiae* population, making dispersal and establishment of new colonies a process essential to avoiding species extinction. The analysis of metapopulations is just starting for certain well-studied organisms (Ehrlich & Murphy 1987). Preliminary models, suggesting that in a stochastic environment, subdivided metapopulations are less likely to go extinct than single populations (Quinn & Hastings 1987; Goodman 1987a), depend on populations not being destroyed by the same disturbance events. Catastrophes that affect many populations at the same time, such as periodic ice damage, may threaten the *P. furbishiae* metapopulation. In addition,

high rates of population turnover can threaten metapopulations due to frequent demographic stochasticity and loss of genetic variation (Gilpin 1987).

A landscape-level view of biological diversity recognizes that populations shift spatially through time, which means that isolated small tracts may not protect species (e.g., Pickett & Thompson 1978; Henderson et al. 1985; Noss & Harris 1986). A viable metapopulation of *P. furbishiae* clearly depends on the availability of empty sites for new populations. Any preserve system that protects only extant populations may not provide such recolonization sites. Moist sites offer advantages

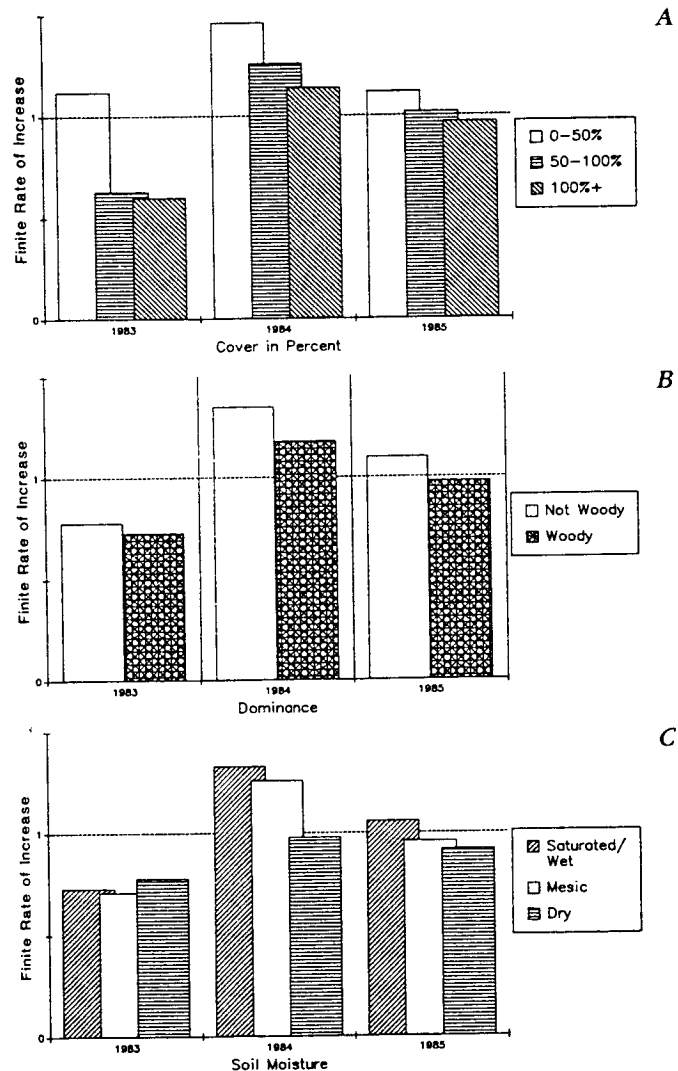


Figure 2. The effect of environmental state on equilibrium finite rate of increase (λ) over time. Each λ was calculated based on a transition matrix specific to the environmental state indicated, for the pair of years beginning with the year indicated.

A. Cover class

B. Woody plant dominance

C. Soil moisture class

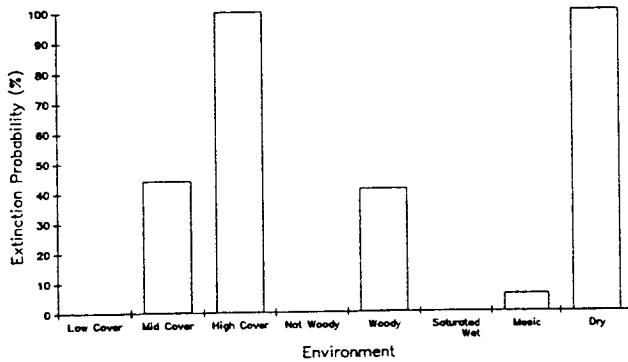


Figure 3. Extinction probability of lousewort populations as a function of environment. Extinction probability was simulated using the POPPROJ model and conditions described in the methods. Environmental states are those defined in Figure 2.

for colonization and population growth, but may be short-term habitats because of their instability. Mesic sites offer the highest viability in the presence of periodic disturbance. A range of edaphic conditions in potential sites will offer the greatest buffering from variations in disturbance intensity and frequency, as well as variation in other environmental conditions independent of the river hydrology. Little is now known of the mechanics of metapopulation processes for *P. furbishiae*. Still, an approach that will protect much of the St. John River corridor in its natural state would be a prudent one.

Too little disturbance clearly reduces the viability of *P. furbishiae* populations. Without ice scraping and bank slumping, cover of woody vegetation and litter depth both build up. These changes depress seedling recruitment, survivorship, growth, and reproductive output (Menges 1988). Clearly, any major hydroelectric project, by removing disturbance as a favor over a large portion of the St. John River, would threaten *P. furbishiae*.

Too frequent disturbance would also pose a problem, in that there might be insufficient time between disturbances for population establishment, expansion, and seed production for dispersal. How frequent is too frequent? Due to its hemiparasitism (Macior 1980), *P. furbishiae* cannot invade a recently disturbed area for at least 3 years. Individuals will not produce seeds until at least 3 years of age (Menges 1988). Therefore, a minimum time between disturbances allowing any population to contribute to the metapopulation is 6 years, and perhaps 10 years is more likely for a significant contribution. Some other modeling efforts have attempted to model population dynamics of individual populations within the context of disturbance frequency (e.g., Hanson & Tuckwell 1981; Manders 1987; Ewens et al. 1987).

Although the optimal disturbance regime for *P. furbishiae* (if it exists) cannot yet be quantified, catastrophic extinctions may currently be more frequent than would be ideal. The St. John River's recent increased variation in water level could explain spatial patterns of population trends (Menges & Gawler 1986). Most upriver populations were increasing while mid-river and downriver populations were, on the average, declining. Many factors, including weather and landscape factors, could explain these patterns. During the last decade, saw-timber volume in the county that includes the St. John River watershed has declined markedly (Powell & Dickson 1984). Runoff from recently cut areas will be more rapid, resulting in a flashier hydrology for the river and more frequent, severe disturbances, especially downstream. Peak river stage levels have indeed been increasing over the last several decades (Menges & Gawler 1986). If forests are allowed to recover, the frequency of catastrophic disturbance might decrease, allowing recovery of some midriver and downriver populations.

While disturbance and demographic change may be paramount in understanding short-term population via-

Table 6. Presumed rates of extinction and establishment of populations, inferred by stem count data.^a

First count	Second count	Portion of range surveyed	Relative size of areas	Number of areas with flowering stems			Raw extinction rate ^b	Extinction rate (per year) ^c
				1980	1981	1984		
1980	1984	Whole	Large	24	—	22	8.4%	2.1%
1980	1981	Part	Large	16	14	—	12.5%	12.5%
1981	1984	Part	Small	—	32	28	12.5%	4.2%
Establishment Rate per year ^d								
No. new populations appearing	Whole	Small	—	1	3			2.8%

^a Based on Table 3, Menges and Gawler (1986).

^b For number of years indicated.

^c Assuming independent distribution over time, calculated as n th root of $(1 - \text{raw extinction rate})$ where n is the number of years between observations.

^d Expressed as function of total number of populations.

Table 7. Probabilities of individual population survival (using model protocol described under methods), adding various probabilities of natural catastrophe, for three cover classes. Assumptions include within-population environmental stochasticity.

Conditions	Assumed annual probability of natural catastrophe				
	6%	2%	0.5%	0.1%	0%
1983–86, all	0.00	0.09	0.57	0.92	1.00
1985–86,					
Low cover	0.00	0.16	0.53	0.93	1.00
Intermediate cover	0.00	0.06	0.34	0.42	0.66
High cover	0.00	0.00	0.00	0.00	0.00

bility, genetic variation within populations and individual heterozygosity are generally seen as essential for long-term evolutionary potential (Wright 1948; Franklin 1980; Antonovics 1984). Ultimately, the lack of genetic variation in *P. furbishiae* (Waller et al. 1988) could inhibit its ability to adapt to changes in the environment. But even in the short run, species persistence appears to involve nonequilibrium metapopulation dynamics. To the extent that many species of this unique riverine ecosystem share similar ecological traits, *P. furbishiae* can be viewed as a sensitive indicator of the health of the St. John River ecosystem.

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