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PREDICTION OF RARE-PLANT OCCURRENCE: A SOUTHERN APPALACHIAN EXAMPLE

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Abstract. Ecologically sound efforts to manage or reintroduce populations of rare species require detailed knowledge of species habitat requirements. However, the fact that such species are rare implies that the data needed for habitat characterization are sparse and that species might well be absent from favorable sites due to chance aspects of dispersal or mortality. We use four rare plant species endemic to southern Appalachian high-elevation rock outcrops, to illustrate how nonparametric and parametric logistic regression can yield predictive models of the probability that a species will occur, given certain site conditions. Models were constructed for each species at two scales: 100-m² plots and 1-m² subplots. At the 100-m² plot scale, absences beyond the current geographic range were excluded. At the 1-m² subplot scale, absences from subplots were only included if the species occurred elsewhere on the 100-m² plot.

Six significant models resulted; no significant model could be constructed for *Solidago spithamea* or *Calamagrostis cainii* on 1-m² subplots. For 100-m² plots, the most valuable predictors were potential solar radiation, a soils gradient related to available soil iron, boron, and copper, and coarse-scale rock surface texture, although *Geum radiatum* occurrences were difficult to predict at this scale. For 1-m² subplots the best predictors were available soil cations, potential solar radiation, the proportion of exposed bedrock, and vegetation height. Along individual gradients response curves were often similar, but no two species were predicted by identical sets of site parameters. Beyond current range limits, existence of suitable habitat on 100-m² plots was demonstrated for *Solidago spithamea*, supporting a view that the range limits of this species are not necessarily set by availability of suitable habitat. Habitat-based models have numerous management applications (such as to guide restoration and reintroduction efforts as well as to direct searches for additional populations) and provide a framework for future work on species-specific physiological requirements.

Key words: *Calamagrostis cainii*; endemic; generalized additive models; *Geum radiatum*; habitat characterization; *Houstonia purpurea* var. *montana*; logistic regression; rare plants; rock outcrops; *Solidago spithamea*; southern Appalachian Mountains (USA).

INTRODUCTION

Effective management of rare plant species requires an understanding of their ecology. Knowledge of which habitat parameters most accurately predict the occurrence of a rare plant species, and the likelihood that species will occur given specific site conditions, is fundamental (Simberloff 1988, Brussard 1991, Falk and Olwell 1992). The development of analytical approaches to predict the occurrence of plant species from environment has received considerable attention (e.g., Austin et al. 1984, Nicholls 1989, Yee and Mitchell 1991), but has generally been applied to common species at broad geographic scales. Such approaches ap-

plied to rare species at a site-by-site scale can be used by managers to (1) guide searches for unknown populations, (2) indicate site suitability for restoration or reintroduction, (3) predict impacts of habitat degradation and (4) provide a framework for further research on specific physiological requirements.

In the southern Appalachian Mountains, high-elevation rock outcrops constitute a rare habitat, and many of the inhabitants grow in few, if any, other habitats in the region. Forty outcrop species are regionally rare, including twelve that are either southern Appalachian endemics or species disjunct from alpine, arctic, and other treeless habitats far to the north. These species are noteworthy in that they are considered relicts of a Pleistocene alpine flora in a region where no alpine environment currently exists (White et al. 1984, Schafale and Weakley 1990). Beyond the observation that they are restricted to outcrops above 1200 m, little

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about their distribution relative to environment has been published. Implicit in earlier publications is the assumption that these species persist because conditions peculiar to certain high-elevation outcrops, such as moist north-facing slopes, closely resemble past alpine conditions. Within these macrosites, the species may be expected to follow the general pattern observed for other outcrop endemics of the Southeastern United States and occur on shallow-soiled microsites where competition and shading from other species is low (Baskin and Baskin 1988).

In this paper, nonparametric and parametric logistic regression are used to determine the utility of a range of physical site parameters in predicting four of the twelve rare, Pleistocene-relict outcrop species at two spatial scales. The following questions are addressed for these four species. (1) At the scale of the 100-m² plot, which environmental factors best predict species occurrence? Are these relicts predicted to occur at the highest elevations and coolest (i.e., lowest potential solar radiation) sites? (2) At the scale of the 1-m² subplots, which environmental factors best predict species occurrence? Are soil depth and shading important? (3) Do the models predict species to occur on mountain ranges where they are absent, which would suggest non-environmental control of distribution across mountain ranges? We conclude by examining the strengths and weaknesses of habitat-based models for conservation applications.

METHODS

Study species

Predictive models were constructed for four rare, high-elevation rock-outcrop endemics: *Geum radiatum* Michx. (Rosaceae), *Solidago spithamea* M. A. Curtis (Asteraceae), *Calamagrostis cainii* A. S. Hitchcock (Poaceae), and *Houstonia purpurea* L. var. *montana* (Small) Terrell (Rubiaceae) (hereafter *Geum*, *Solidago*, *Calamagrostis* and *Houstonia*, respectively; botanical nomenclature follows Kartesz 1994). All four are ranked as critically imperiled globally (G1) by the Nature Conservancy and are listed, or proposed for listing, as either threatened or endangered by the U.S. Fish and Wildlife Service (Murdock and Sutter 1987, Murdock 1993, Saunders 1996). These species were chosen for study because they are globally rare, and also because they occurred with sufficient frequency in the study area to allow adequate sampling. In the typology of Rabinowitz (1981:210), these species have small geographic ranges and narrow habitat requirements (relative to the landscape as a whole), and are "classic rarities in the sense of restricted endemics." Local population sizes vary from a few dozen individuals to hundreds. Life-history characteristics (which are mostly poorly understood) and population data have been assembled for *Geum*, *Solidago*, and *Houstonia* by the U.S. Fish and Wildlife Service (Murdock and Sutter

1987, Murdock 1993, Saunders 1996). All four species are perennials. The limited data on seed dispersal suggest that most dispersal is passive by wind, gravity, or overland flow. Birds and rodents are frequent on the outcrops, but their role in seed dispersal is unknown and probably minimal. Propagation by rhizomes has been observed in *Geum* and *Houstonia*. Only *Calamagrostis* has been observed to colonize disturbed sites, and this was adjacent to a pre-existing population (S. K. Wiser, *personal observation*). Herbarium records suggest that these species have been present at most of their current sites for at least a century. Field observations suggest recent population declines in *Solidago*, *Geum*, and *Houstonia*, whereas insufficient data are available to assess population trends in *Calamagrostis* (N. Murdock [U.S. Fish and Wildlife Service, Asheville, North Carolina, USA], *personal communication*).

Study area

All populations of the four study species occur exclusively on outcrop sites above 1200 m and south of the Virginia–North Carolina border (Fig. 1). These outcrops are widely scattered and primarily occur in seven mountain ranges, each range 25–60 km from the nearest range. Compositional differences in vegetation among outcrops relate to differences in elevation, geology, potential solar radiation, and soil chemistry (Wiser et al. 1996). Wiser et al. (1996) provide a detailed description of the study area and dominant compositional and environmental gradients.

Data collection

As part of a larger study on outcrop vegetation, presence/absence of the four study species was recorded in 154 10 × 10 m (100-m²) plots distributed among 42 peaks in western North Carolina and eastern Tennessee. Plots were located to include all possible combinations of major site parameters such as elevation, slope, aspect, geology, and topographic position. All known populations of the four target species were included. Within each 100-m² plot, two to seven 1 × 1 m (1-m²) subplots were sampled, depending on the internal heterogeneity of the larger plot. For 100-m² plots, the following site parameters were determined: latitude, elevation, slope percentage, aspect, bedrock type, presence of perennial seepage, percentage of exposed bedrock, and degree of fracturing (using an index such that nearly smooth outcrops containing ledges and cracks <0.3 m wide were classified as "1," and highly fractured and angular outcrops containing ledges and cracks >0.3 m wide were classified as "3"). The average topographic position of each plot was recorded as an index from 0 to 10 with 1 being the base of the outcrop, and 10 being the top. Outcrops were classified into one of five height classes (1 = <5 m high, 2 = 5–16 m, 3 = >16–32 m, 4 = >32–64 m, 5 = >64

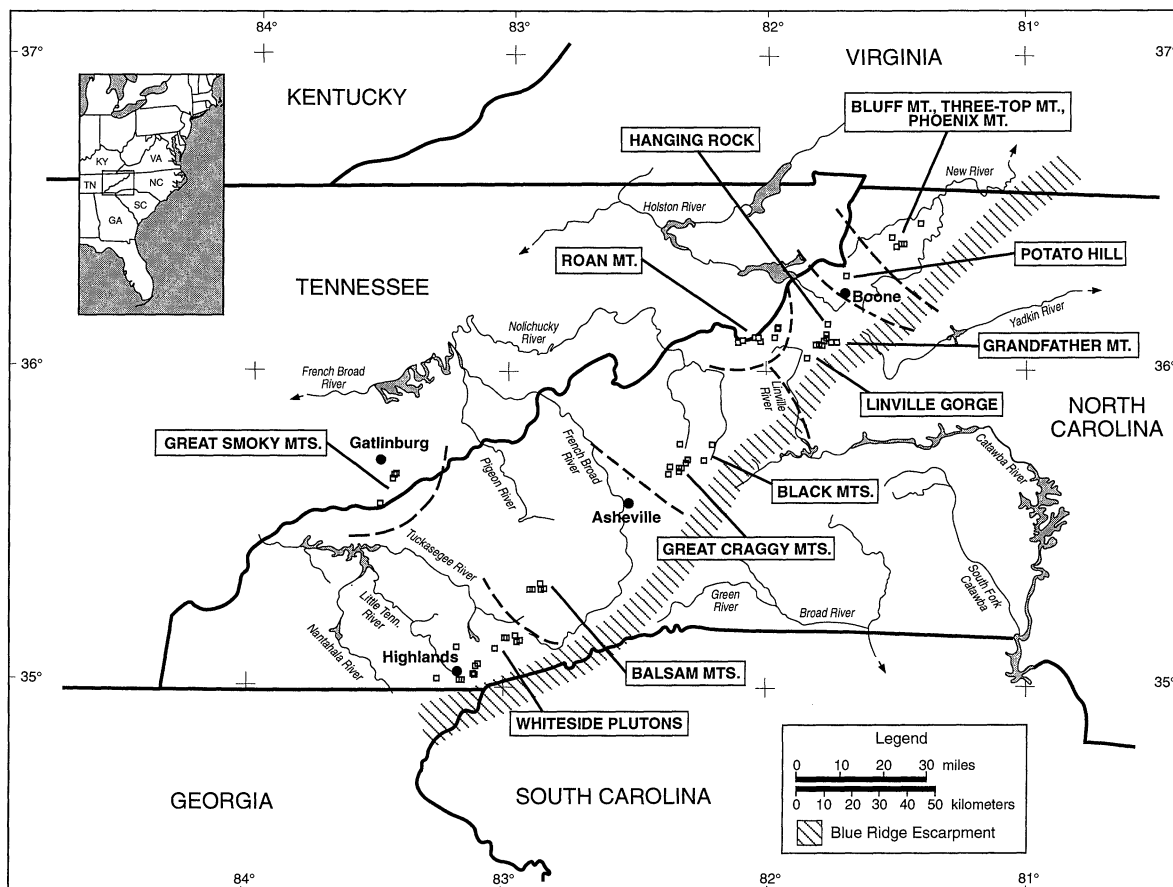


FIG. 1. Map of southern Appalachian Mountain (USA) study area showing 100-m² plot locations (small squares) and major peaks. Dashed lines separate mountain ranges. Reprinted from Wiser et al. (1996) with permission from the *Journal of Vegetation Science*.

m), and into one of six area classes (based on measurements from orthophoto quadrangle maps: 1 = not visible, 2 = visible, <0.25 ha; 3 = 0.25–1 ha; 4 = >1–9 ha; 5 = >9–25 ha; 6 = >25 ha).

Soil parameters (pH; percentage organic matter; percentage water holding capacity; available calcium, magnesium, potassium, manganese, phosphorus, sulfate, sodium, aluminum, iron, boron, and copper) were averaged across individual samples taken in each 1-m² subplot. Soils were analyzed by Brookside Farms Laboratory Association (New Knoxville, Ohio, USA). Available nutrients were extracted using the Mehlich 3 method (Mehlich 1984). Percentage organic matter was determined by loss-on-ignition. Variation in soil parameters was reduced to five major components using principal components analysis with varimax rotation to reduce collinearity as a preparation for later analysis (Duntelman 1989). The name assigned each axis derives from the soil parameters with the highest loadings (Table 1).

Potential solar-beam irradiation was calculated based on slope, aspect, and latitude using the equations of

Frank and Lee (1966). Results are reported as an index that is the ratio of total annual radiation to annual maximum potential insolation (Frank and Lee 1966).

Exposure at each of four 90° bearings (towards, opposite from, and both perpendiculars to the direction of maximum exposure) was quantified with a 1-to-5 scale ("1," or totally protected, when the height of neighboring landforms or vegetation was >10 times the distance to the plot; "3" when nearby structures were intermediate in height relative to distance to the plot; and "5," or totally exposed, when the height of such structures was <0.1 times the distance to the plot). These four values were averaged to produce a composite site-exposure index.

On 1-m² subplots the mean soil depth (based on 16 measurements on an equally spaced grid), source of moisture (surface runoff, drip from ledges and overhangs above, direct precipitation, and perennial seepage), percentage shading, percentage bare soil, percentage moss cover, and maximum vegetation height were also assessed. Determinations of slope, potential solar radiation, exposure, and percentage exposed bed-

TABLE 1. Factor loadings of individual soil parameters on the first five varimax-rotated principal component axes for (A) 100-m² plots (*N* = 154) and (B) 1-m² subplots (*N* = 577).

Parameter	Soil cations axis	Soil moisture axis	Soil iron axis	Soil pH axis	Soil sulfate axis
A) 100-m ² plots					
pH	0.15	-0.27	0.13	<i>0.82</i>	-0.13
Boron	0.39	0.05	<i>0.71</i>	0.20	0.03
Aluminum	-0.32	-0.02	0.06	<i>0.61</i>	0.50
SQRT(iron) [†]	-0.29	0.04	<i>0.76</i>	-0.03	-0.08
SQRT(potassium)	0.51	<i>0.62</i>	0.03	0.19	0.19
ln(calcium)	<i>0.91</i>	0.08	-0.05	-0.13	-0.04
ln(copper)	0.11	-0.22	<i>0.67</i>	0.04	0.14
ln(magnesium)	0.85	0.09	0.03	0.18	-0.21
ln(manganese)	<i>0.72</i>	0.17	0.23	0.16	0.06
ln(sodium)	0.00	0.42	-0.02	<i>0.71</i>	-0.17
ln(organic matter)	0.21	<i>0.92</i>	0.01	-0.12	-0.07
ln(phosphorus)	0.15	-0.30	-0.27	-0.19	<i>0.72</i>
ln(sulfate)	-0.12	-0.06	0.43	-0.05	<i>0.78</i>
ln(water-holding capacity)	0.05	<i>0.83</i>	-0.07	0.09	-0.20
ln(zinc)	<i>0.81</i>	0.22	-0.13	-0.27	0.07
Cumulative variance explained (%)	28.8	44.6	58.7	68.5	76.6
B) 1-m ² subplots					
pH	0.21	-0.20	-0.02	<i>0.86</i>	0.01
ln(boron)	0.41	0.04	<i>0.68</i>	0.19	0.28
Aluminum	-0.46	0.03	-0.06	0.46	<i>0.48</i>
Iron	-0.22	-0.03	<i>0.85</i>	-0.15	0.11
SQRT(potassium)	0.46	<i>0.68</i>	0.07	0.08	0.21
ln(calcium)	<i>0.92</i>	0.12	-0.10	-0.01	-0.08
ln(copper)	0.15	-0.21	0.25	0.17	<i>0.54</i>
ln(magnesium)	<i>0.86</i>	0.17	0.07	0.19	-0.11
ln(manganese)	<i>0.76</i>	0.17	0.06	0.20	0.10
ln(sodium)	0.04	0.43	0.10	<i>0.62</i>	-0.14
ln(organic matter)	0.24	<i>0.90</i>	0.09	-0.06	-0.06
ln(phosphorus)	0.14	-0.12	-0.53	-0.31	<i>0.57</i>
ln(sulfate)	-0.20	0.04	0.15	-0.16	<i>0.86</i>
ln(water-holding capacity)	0.03	<i>0.73</i>	-0.07	0.06	-0.06
ln(zinc)	<i>0.80</i>	0.32	-0.15	-0.16	-0.04
Cumulative variance explained (%)	29.8	42.9	51.1	61.5	73.8

Notes: The highest loading for each soil parameter is italicized. Original units for all variables are "ppm" (parts per million), i.e., mg/kg, except pH, organic matter (percentage), and water-holding capacity (percentage dry mass).

[†] SQRT = square root.

rock were determined at the smaller scale as well. Wiser et al. (1996) provide further details on data collection and treatment of site parameters prior to analysis.

Data analysis

Predictive models were initially developed using a nonparametric analogue of logistic regression. Logistic regression is a statistical technique used to predict the probability of event occurrence (P_e) and has been applied to predict the probability that a plant species will occur, given certain site conditions (e.g., Austin et al. 1984, ter Braak and Looman 1986, Margules and Stein 1989, Nicholls 1989). Since probability values must lie between 0 and 1, they cannot be modeled directly from linear predictors. A logit link function transforms the value fitted from linear predictors (which can range

from $-\infty$ to ∞) into a probability value lying between 0 and 1. The deviation of the observed responses from the fitted responses is measured by the residual deviance ($-2 \log L$ where L = maximum likelihood).

A chi-square test is used to assess the significance of the difference in residual deviance when a parameter is included in a model vs. when it is not (df = the number of parameters being tested). Use of polynomial or other transformations of the predictive variables can allow for responses that are nonlinear, such as the use of a quadratic term to allow for unimodal responses (ter Braak and Looman 1986, Jongman et al. 1987).

Generalized additive models (GAMs) relax the assumption of a parametrically defined relationship between the predictor variables and the fitted values. This is of considerable use in developing models of plant

response to environmental gradients, as numerous response-curve shapes are plausible and the actual shape is usually unknown prior to analysis. GAMs use a spline smoothing function to determine the fitted model that best fits the predictor variables; hence the models are data driven, rather than model driven as in logistic regression and other generalized linear models (Yee and Mitchell 1991). Using GAMs, a binomial model with a logit link function is analogous to parametric logistic regression. If there are no interactions with other variables, graphs of the fitted function and residuals can be examined to determine the general shape of the response. In GAMs, the degrees of freedom of the predictor variable reflect the complexity of the smoothed fitted function. Chi-square tests (as described above) can be applied to determine which level of complexity results in the most significant decrease in deviance. Estimates of total deviance explained are often used as an overall goodness-of-fit measure in regression modeling. Unfortunately, for presence/absence and other binomially distributed data, such estimates are not valid (Austin et al. 1984), so goodness of fit cannot be compared between unrelated models.

To reduce the influence of absences resulting from non-environmental causes, only absences within mountain ranges where the species is known to occur were included at the model-building stage. This was done since non-environmental influences (e.g., failure to disperse) were suspected to be of increased importance in mountain ranges where the species was absent, and could distort the model. Similarly, for those models based on the 1-m² subplots, only absences recorded within 100-m² plots where the species was present were included so resulting models would reflect microsite features rather than phenomena influencing occurrence at the larger scale.

For each species, the best combination of predictor variables was chosen using forward selection in a procedure analogous to that outlined by Nicholls (1989), where (1) all parameters are tested individually, (2) the one that results in the largest change of deviance given the degrees of freedom (assessed by the chi-square test) is added to the model, and (3) the procedure is repeated with all remaining predictor variables until addition of another variable does not result in a change in deviance significant at the 0.05 level. The significance of interactions between significant parameters was tested by the addition of individual interaction terms to the models.

Although nonparametric logistic regression is useful in the development of predictive models, parametric models are more desirable if they fit the data adequately (Yee and Mitchell 1991). Response curves were examined to determine the appropriate parametric model (e.g., linear, polynomial, etc.). To assess whether the parametric model predicted P_o as adequately as the nonparametric model, the total deviances of the two models

were compared. Three types of residual diagnostics were examined on the parametric models as suggested by Nicholls (1989). If a parameter estimate was found to be highly influenced by a single observation, that parameter was dropped from the final model.

Because sample sizes were small in comparison to the number of predictor variables tested, there was a danger of the forward selection procedure overfitting the data. This could result in a final model that selects random environmental variables and has no biological meaning. To test whether the final models differed from random expectations, the following approach was used. For each species, at each scale, 100 data sets were generated such that the original presences and absences were randomly assigned to each set of site environmental variables. Each random data set was then fit with a forward-selection logistic regression using linear predictors only. While it would be optimal to conduct this test using either nonparametric or polynomial logistic regression as previously outlined, both of these approaches required interactive computing and are not practicable for randomization tests. This resulted in a conservative test when nonlinear responses considerably improved the model (i.e., lowered the deviance substantially). The original model was judged to be significant if its final deviance (based on linear predictors only) was less than that of at least 95 of the 100 random models for that species and plot size.

For the final model $P_o = 0.7$ was arbitrarily chosen as a level above which occurrence was considered highly probable; above $P_o = 0.5$ occurrence was considered moderately probable. Within the known range of a species, on 100-m² plots where the species was absent but was predicted to occur, 1-m² subplots were examined for site suitability. To determine whether plots and subplots beyond the current ranges were appropriate for the species, an initial requirement was that they have site conditions within the limits of site conditions used to generate the original model. This prevented extrapolation beyond the bounds of the original model. P_o was then calculated for both plot sizes.

Generalized additive models were computed using GAIM (Tibshirani Enterprises 1991). Other statistical analyses were performed using SAS (SAS Institute 1989).

RESULTS

Predictive value of specific site parameters

Six of the eight final models (all four species on 100-m² plots and *Geum* and *Houstonia* on 1-m² subplots) had significantly lower final deviances than expected at random and so reflect biological effects rather than statistical artifacts, despite small sample sizes relative to the number of predictor variables (Tables 2 and 3). On 100-m² plots (Table 3, Figs. 2–4), potential solar radiation (three species), the soil iron axis (three species) and the fracturing index (*Geum*) were significant

TABLE 2. Numbers of presences and absences on 100-m² plots and 1-m² subplots included in models for each of four plant species endemic to southern Appalachian high-elevation outcrops.

Species	No. of ranges where present	100-m ² plots		1-m ² subplots	
		Present	Absent	Present	Absent
<i>Calamagrostis cainii</i>	2	14	29	34	21
<i>Geum radiatum</i>	6	23	101	34	62
<i>Houstonia purpurea</i> var. <i>montana</i>	3	21	50	27	65
<i>Solidago spithamea</i>	2	10	32	12	26

Note: Only absences on mountain ranges where the species is known to occur were included in the models.

predictors. *Geum*, *Houstonia*, and *Solidago* all have their lowest P_0 at the highest annual potential solar radiation levels (Fig. 3). This suggests intolerance of the higher temperatures associated with increased potential solar radiation as expected for such alpine relicts. On the iron axis the response curves are similar to each other (Fig. 2) with the lowest P_0 predicted for all three species at soil axis scores <0.0 (typically with boron <0.55 mg/kg, copper <2.3 mg/kg and iron <400 mg/kg) and optimal predictions at soil axis scores >1.2 where levels of these micronutrients are higher. The truncated response of *Houstonia*, as contrasted with those of the other species, reflects the smaller gradient sampled in mountain ranges where it occurs.

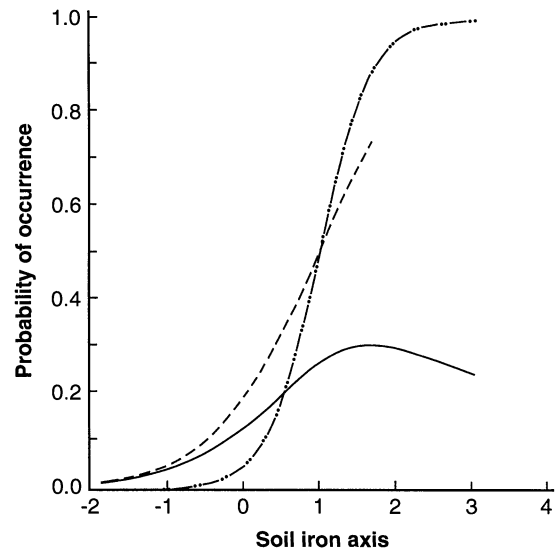


FIG. 2. Probability response curves for *Geum radiatum* (—), *Houstonia purpurea* var. *montana* (---), and *Calamagrostis cainii* (-.-.-), along the iron axis; 100-m² plots. Curves are based on nonparametric generalized-additive-model (GAM) fits, although linear fits (*Calamagrostis* and *Houstonia*) are, in fact, parametric.

For 1-m² subplots the soil cations axis (*Geum* and *Houstonia*), potential solar radiation (*Geum*), percentage exposed rock (*Geum*), and vegetation height (*Houstonia*) were all significant predictors. *Geum* and *Hous-*

TABLE 3. Summaries of predictive models for the four rare plant species. For linear responses the nature of the relationship (+ or -) is indicated. Final deviance is compared between nonparametric and parametric models, with degrees of freedom for each in parentheses.

Species	Significant environmental parameters†	Response	Final deviance			
			GAMS model	Parametric model	Linear terms only	Randomization <i>P</i> value‡
A) 100-m ² plots						
<i>Calamagrostis cainii</i>	iron axis	linear (+)	27.83 (2)	27.83 (2)	27.83 (2)	<0.01
<i>Geum radiatum</i>	fracture	linear (+)				
	iron axis	unimodal				
	p.s.r.	linear (−)	91.20 (4.9)	91.5 (4)	94.43 (4)	0.01
<i>Houstonia purpurea</i> var. <i>montana</i>	iron axis	linear (+)				
	p.s.r.	bimodal	57.30 (4.8)	60.64 (5)	63.87 (3)	0.01
<i>Solidago spithamea</i>	p.s.r.	linear (−)	29.67 (2)	29.67 (2)	29.67 (2)	0.02
B) 1-m ² subplots						
<i>Calamagrostis cainii</i>	p.s.r.	bimodal				
	pH	linear (+)	46.82 (4.8)	47.86 (4)	59.71 (3)	0.08
<i>Geum radiatum</i>	% exp. rock	linear (+)				
	p.s.r.	linear (−)				
	cations axis	sigmoidal	95.10 (4.9)	94.75 (5)	97.41 (4)	<0.01
<i>Houstonia purpurea</i> var. <i>montana</i>	veg. ht.	linear (−)				
	cations axis	linear (+)				
	veg. ht. × cations	linear (−)	90.61 (4)	90.61 (4)	90.61 (4)	0.01
<i>Solidago spithamea</i>	moss	linear (+)				
	cations axis	bimodal?	33.38 (5.7)	33.49 (5)	43.87 (3)	1.0

† Fracture = rock fracture index; p.s.r. = potential solar radiation; % exp. rock = percentage exposed bedrock; veg. ht. = vegetation height.

‡ The percentage of 100 random models having final deviance less than that of the linear terms only of the final models.

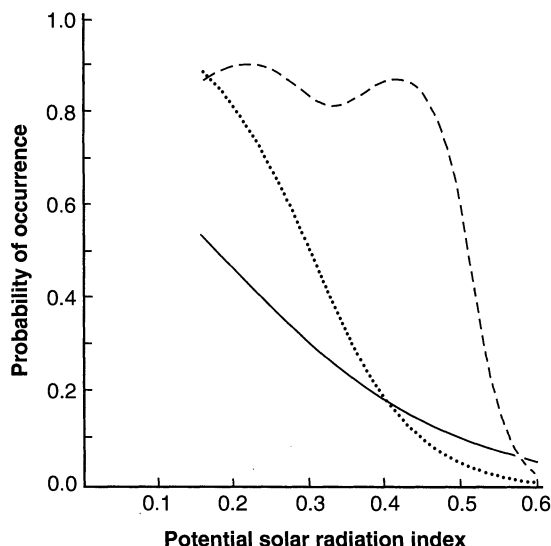


FIG. 3. Probability response curves for *Geum radiatum* (—), *Houstonia purpurea* var. *montana* (---), and *Solidago spithamea* (.....) along the potential solar-radiation gradient; 100-m² plots. Curves are based on nonparametric GAM fits, although linear fits (*Geum* and *Solidago*) are, in fact, parametric.

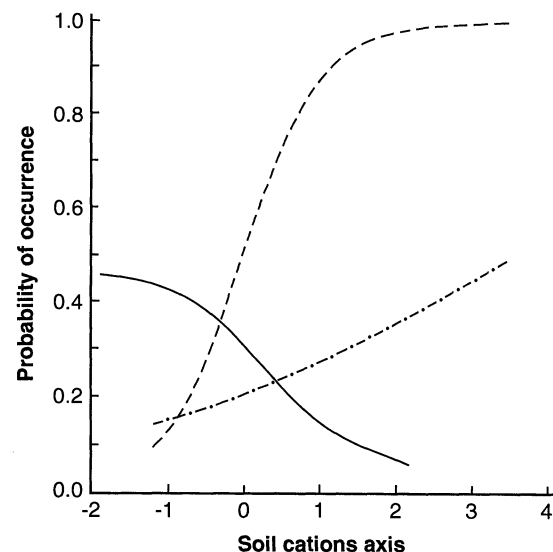


FIG. 4. Probability response curves for *Geum radiatum* (—), *Houstonia purpurea* var. *montana* with 5 cm vegetation (---), and *H. purpurea* var. *montana* with 40-cm vegetation (-.-.-) along the soil cations axis; 1-m² subplots. The curve for *Geum* is the nonparametric GAM fit. The parametric fit of *Houstonia* is shown to illustrate the interaction between cations and vegetation height.

tonia showed different responses to the soil cations axis (Fig. 4).

For *Geum* and *Houstonia*, predictors tended to be different at the two plot sizes. For example, for both species the iron axis was predictive on 100-m² plots whereas the cations axis was predictive on 1-m² subplots.

Response-curve shapes were highly variable (Table 3, Figs. 2–4) and included linear, unimodal, sigmoidal, and bimodal responses. Complex responses were parametrically approximated with quadratic, cubic, and sine functions. Interaction terms were significant in only one of the six significant models (*Houstonia* on 1-m² subplots). Parametric models provided close approximations of nonparametric models except for *Houstonia* on 100-m² plots. An example of the model-building process is provided for *Geum* on 100-m² plots (Table 4).

Calamagrostis cainii

As 10 of the 14 occurrences of *Calamagrostis* in 100-m² plots were sampled from Mount LeConte in the Great Smoky Mountains, the macroscale model primarily distinguished plots on Mount LeConte from all others. Anakeesta sulfite slate, the bedrock at Mount LeConte, is iron rich and produces soils with scores above 1.1 on the soil iron axis (iron range: 464–972 mg/kg; boron levels are also higher than average), and P_o increases with increased iron-axis score (Table 3, Fig. 2). Occurrences on Mount LeConte are well predicted (P_o : 0.59–0.99), but three of the four occurrences

beyond the Smoky Mountains are only poorly predicted (P_o : 0.11–0.17).

Two 100-m² plots without *Calamagrostis* had $P_o > 0.76$ (one on Mount LeConte, one in the Craggy Mountains). As the 1-m² subplot model was insignificant, no assessment of microhabitat suitability could be made.

Geum radiatum

On 100-m² plots, presence of *Geum* was difficult to predict; only 30% of the plots containing *Geum* had $P_o > 0.50$. Occurrences towards the northeastern part of the study area were the most successfully predicted, those toward the southwest the most poorly predicted. Three 100-m² plots lacking *Geum* had $P_o > 0.5$ (range: 0.58–0.63). All of these plots had at least one 1-m² subplot where P_o of *Geum* exceeded 0.7. One of these sites is remote (>100 m) from current populations, so absence may be a consequence of past extinction or current dispersal limitation. The remaining two plots are within 75 m of extant populations.

Houstonia purpurea var. *montana*

On 100-m² plots over 75% of the occurrences of *Houstonia* were accurately predicted with $P_o > 0.50$. The importance of the iron axis for prediction of *Houstonia* (Table 3, Fig. 2) is a reflection of the strong relationship between this soil axis and bedrock type. Among the mountain ranges where this taxon occurs, iron-axis scores distinguish mafic from felsic bedrock, with soils on mafic rock being higher in both boron and copper than those on felsic rock. *Houstonia* occurs

TABLE 4. (A) Stages of the forward-selection nonparametric logistic regression procedure in fitting the model for *Geum radiatum* for 100-m² plots. (B) Coefficients and standard errors for the complete parametric model that best approximates the nonparametric model.

A)	Model	Residual deviance	df	Change in deviance	df of added predictor	P
	Intercept	118.94	123.0	...	1	...
	Intercept + x_1	104.70	122.0	14.24	1	<0.001
	Intercept + $x_1 + x_2$	95.54	120.12	9.16	1.88	0.009
	Intercept + $x_1 + x_2 + x_3$	91.20	119.12	4.34	1	0.037
	Parametric model	91.5	120.0		4†	
B)	Site parameter	Parameter estimate	1 SE			
	Intercept	-3.89	2.15			
	Rock-fracturing index	1.38	0.62			
	Sin(iron axis)	1.22	0.45			
	Potential solar radiation	-4.39	2.14			

Notes: (A) At the first stage, rock-fracturing index (x_1) was the best predictor and was linearly related ($df = 1$) to the logit of occurrence probability (P_o); P_o increased with increased degree of rock fracturing. At the second stage adding the iron axis (x_2) with $df = 1.88$ resulted in the most significant change in deviance; P_o showed a unimodal response to iron-axis score. At the third stage adding potential solar radiation (x_3) with $df = 1$ resulted in the most significant change in deviance; P_o decreased with increased solar radiation. No additional predictor variables resulted in a change of deviance with a probability < 0.05 (assessed with a chi-square test). (B) Only predictors with $df > 1$ require a parametric approximation, as $df = 1$ indicates a linear response. The function sin(iron axis) best approximated the nonparametric relationship between P_o and the iron axis.

† Degrees of freedom of the full model.

only on mafic bedrock or on felsic bedrock where mafic minerals occur in nearby pockets or veins. On 1-m² subplots there is a significant interaction between maximum vegetation height and soil cations (Table 3, Fig. 4). The rate of increased P_o with increasing cations declines as vegetation gets taller. When vegetation height exceeds 50 cm, P_o is always below 0.5, regardless of cation level.

Five 100-m² plots lacking *Houstonia* were predicted as appropriate (P_o range: 0.52–0.80), but only two of the five plots had appropriate 1-m² subplots (i.e., vegetation of short stature and high soil cations). One of these plots is within 20 m of an extant population of *Houstonia*; the other is within 100 m of an extant colony. The former is in an area undergoing aberrant mass wasting of soil resulting from building construction above, and may be a site where *Houstonia* occurred in the past.

Solidago spithamea

Of the ten occurrences of *Solidago* on 100-m² plots, six are well predicted (P_o range: 0.52–0.88). One plot where *Solidago* occurs is predicted particularly poorly ($P_o = 0.05$); it has a northwest-facing aspect (324°), but the slope is nearly flat, resulting in relatively high potential solar radiation (0.349 J·m⁻²·s⁻¹).

All 100-m² plots with a $P_o > 0.7$ contain *Solidago*. Only one plot lacking *Solidago* has a $P_o > 0.5$. Suitability at the 1-m² subplot scale cannot be assessed as the model was not significant. The closest known population is 150 m away.

Predictions for mountain ranges where a species is absent

No 100-m² plots lacking either *Geum* or *Calamagrostis* had $P_o > 0.5$. *Geum* occurs on all ranges sampled except the Whiteside Plutons. While 24 100-m² plots in the Whiteside region fall within the original model's site limits, none had $P_o > 0.04$. These plots have rock surfaces that are generally smoother with shallower fractures and crevices than plots where *Geum* occurs, have high potential solar radiation as a result of generally south-facing aspects, and have low iron-axis scores (range from -1.94 to 0.22). Because the model for *Calamagrostis* is strongly influenced by the unique soil conditions on Anakeesta Slate, the inability of the model to predict occurrence on mountain ranges with different soil conditions may be misleading. For *Houstonia*, two plots had $P_o > 0.5$, but neither had appropriate subplots.

The only species for which a case for the existence of suitable habitat beyond contemporary range limits can be made is *Solidago*. Four 100-m² plots had $P_o > 0.7$; three additional plots had $P_o > 0.5$. Unfortunately, the lack of a significant subplot model means microsite suitability cannot be determined.

DISCUSSION

A prerequisite to developing a strategy for the conservation of rare plant species, is an understanding of the habitats in which populations of the species occur. Numerous studies have focused on life history or site

factors that may limit populations of rare species (e.g., Meagher et al. 1978, Ward 1981, Preston and Whitehouse 1986, Pavlik 1993), but predictive models based on habitat parameters are uncommon (see Gehlbach and Polly [1982], Prober and Austin [1990] for examples). Habitat parameters have been used to predict rare species richness (Nillson et al. 1988, Hill and Keddy 1992), but such models do not make predictions about individual species. Further, many studies of rare species describe the habitat where a species is found, but not where it is absent (e.g., Prince and Hare 1981, Demauro 1994, Pavlovic 1994, but see Lesica 1992, Menges 1992, and Boyd and Hilton 1994). Unless habitats where it is absent are also examined, models predicting occurrence cannot be constructed.

Predictive value of specific site parameters

The four alpine relict species examined were expected to occur on the cooler, moister outcrops studied. Potential solar radiation was used as an indicator of this. At a macroscale (100-m² plots), potential solar radiation was an important predictor for all species but *Calamagrostis*, and at a microscale (1-m² subplots) it predicted *Geum*. Other important predictors on 100-m² plots, specifically the fracturing index and iron axis, are significantly related to either primary or secondary gradients of vegetation composition (Wiser et al. 1996). However, elevation, the site parameter most strongly related to composition at this scale, was not a good predictor for the species.

For 1-m² subplots, neither soil depth nor percentage shading were good predictors for the species studied, although *Geum* was predicted in part by percentage exposed bedrock, which is usually correlated with soil depth (Wiser et al. 1996). Soil depth and shading are important to the distribution of outcrop endemics elsewhere (Baskin and Baskin 1988), and soil depth is strongly related to subplot composition on the high-elevation outcrops (Wiser et al. 1996). That soil depth was not predictive may reflect measurement scale—soil depth measurements were averaged over the 1-m² subplot rather than made at the individual plant scale. Also, both soil depth and shading may be important in making the outcrops suitable habitat in contrast to surrounding forests, but may be less important in influencing distributions within the outcrops where they show less variation. Two predictors, the cations axis and vegetation height are strongly related to secondary vegetation-composition gradients on the outcrop subplots, but potential solar radiation was not strongly related to compositional gradients at this scale (Wiser et al. 1996).

That response curves had a range of shapes underscores the importance of testing for higher order relationships between site parameters and species presence/absence. Often *t* tests are used to compare site characteristics where a species is present to those where

it is absent (e.g., Lesica 1992, Menges 1992), but this test is only appropriate if the relationship is monotonic. Bimodal curves may indicate that the species is out-competed at its physiological optimum, but is superior at coping with site conditions that are less favorable (Jongman et al. 1987). This may be especially important for rare species, as low competitive ability is often suggested as a cause of rarity (e.g., Griggs 1940, Harper 1981). Caution must be exercised in making such an interpretation however, as bimodal curves may arise from problems in sampling, analysis, or interpretation (Austin et al. 1984). For *Houstonia* five of the ten 100-m² plots with moderate potential solar radiation were on felsic rock where the species is usually absent, and two of the remaining five plots were highly disturbed. The observed bimodal response may result from these other influences, and illustrates a difficulty of working with rare species in uncommon habitats.

Importance of plot size

The finding that for *Geum* and *Houstonia* occurrence was best predicted by different sets of site parameters for each of the two plot sizes underscores the importance of attention to spatial scale in the development, interpretation, and application of such models. Here, this partly reflects the analytical approach; by restricting the 1-m²-subplot analysis to those 100-m² plots where the species occurs, the source of variation that predicts occurrence for 100-m² plots is effectively removed, allowing predictions to more definitively reflect microsite differences. Attention to scale is also essential to judge whether an unoccupied site is suitable for a species—predictors at one scale must be used in combination with predictors at another. Suitability at one spatial scale will not guarantee suitability at another.

Prediction of occurrence on mountain ranges where a species is absent

A definitive statement that unoccupied habitat beyond current range limits is unsuitable should not be based on distributional information alone. Determination of outcrop suitability for a species necessitates transplant experiments. Ideally, a study such as this would also be accompanied by complementary research on the physiological tolerances of the species (Hodgson 1986). Determination of habitat suitability based on distributional data alone (cf. Prince and Hare 1981) will result in a conservative assessment. However, one can judge whether there is likely to be suitable habitat that is unoccupied, which suggests a non-environmental mechanism for the absence, such as dispersal limitation (cf. Quinn et al. 1994), past extinction events (cf. White et al. 1984, White and Miller 1988), or competition. The evidence presented here suggests that *Solidago* may be absent from certain mountain ranges for reasons other than unsuitability of environment alone.

Conservation applications

Co-occurrence of rare species in unusual habitats is a frequently observed phenomenon (e.g., Griggs 1940, Ogle 1980, Hodgson 1986), and is characteristic of Southern Appalachian high-elevation outcrops. Hill and Keddy (1992) suggest that habitats shared by rare species may imply shared life-history strategies, which would enable management to be enacted at a group level rather than integrating multiple management strategies for individual species. On the outcrops no two species exhibited the same distribution patterns across mountain ranges or among plots and subplots within a mountain range, and each species is predicted by a different combination of site parameters (Tables 2 and 3). The suitability of a site for a particular suite of rare species depends on both its position along major site gradients and the combination of different site parameters that it provides. The unique responses to habitat imply that management strategies need to account for differences among species. Analogous observations that co-occurring rare species have different life-history strategies (Bradshaw and Doody 1978) and different reasons for their rarity (Fiedler and Ahouse 1992) lend further support to this view.

One of the more compelling motivations to predict rare-species occurrence from habitat parameters is to determine site suitability for restoration or reintroduction of rare species, actions that may play increasingly important roles in rare-plant conservation in the future (Maunder 1992, Pavlik et al. 1993, Demauro 1994, Johnson 1996). For severely degraded sites, records on species occurrence may be non-existent, and the ability to determine the probability that a site may have supported a particular rare species becomes a valuable tool. For restoration of particularly rare habitats such as the high-elevation cliffs, roadcuts and other anthropogenically created outcrops could be assessed for suitability and used as test locations to refine restoration and reintroduction techniques (e.g., Johnson 1996), and to serve as reservoirs for genetic material of rare species.

That our knowledge of the distribution of populations of rare plants is woefully incomplete is exemplified by the nearly continuous discoveries of previously unknown populations in areas frequented by botanists for many years. Surveys of all potential sites for a species are usually not feasible (Margules and Stein 1989, Nicholls 1989). Exhaustive surveys are especially problematic for inaccessible habitats such as high-elevation outcrops. Habitat-based models can be used to evaluate the likelihood that undiscovered populations exist and to guide rare-plant searches, thus reducing field time. This approach would be most fruitful for species that are predicted from parameters that can be known prior to visiting a site, such as elevation, slope, potential solar radiation, or geology. Unfortunately for the outcrop species, soil parameters are important predictors (as indicated by their inclusion in

five of the six models), yet cannot be known prior to visiting a site and can only be roughly inferred from geology.

Limitations of habitat-based models

Although there is potentially great utility in predicting rare-plant occurrences from environment, researchers and managers should be aware of the limitations of these models. These limitations are especially relevant for species with small populations that are isolated from one another. Problems may arise from (1) small sample sizes combined with uneven occurrence frequency in different mountain ranges, (2) confounding influences, and (3) genetic differentiation of populations between mountain ranges.

Because the species studied are rare, prediction may be hampered by the reduced statistical power of small sample sizes, the increased chance of model instability, and the possibility that models are statistical artifacts, as demonstrated here for *Solidago* and *Calamagrostis* on 1-m² subplots. Highly uneven frequencies in different areas can distort models due to spatial autocorrelation of environment, as happened here for *Calamagrostis* on 100-m² plots. In such instances, models will be highly influenced by the site characteristics of areas where the species is frequent; absences in these areas will be difficult to predict. Conversely, in areas where a species occurs but is infrequent, models will be highly influenced by where the species is recorded as absent; infrequent occurrences will be difficult to predict.

At the spatial scales studied here, prediction of species occurrence is complicated by influences of competition, predation, dispersal limitation, extinction, and random events. These may be especially pronounced in rare species since all of these mechanisms have been proposed as ultimate causes of rarity (Griggs 1940, Stebbins 1942, Proctor and Woodell 1975, Harper 1981). The observed absences of *Geum* and *Houstonia* at sites near conspecifics and with suitable environment implies non-environmental influences on distribution.

Genetic adaptation to local conditions may further reduce our ability to make models that are predictive across a species' entire geographic range, particularly if populations are highly isolated. In the Southern Appalachians, populations on different mountain ranges have likely been genetically isolated since soon after the onset of postglacial warming, if not before. *Geum* in the Great Smoky Mountains exhibits several minor morphological differences from the other Southern Appalachian populations (Bratton and White 1980), and may have different physiological tolerance as well.

The best test of the predictive models presented here would be experimental field verification by attempting to establish plants from seed at sites both where the species is predicted to occur and where it is not (Kruckeberg and Rabinowitz 1985). This could determine if

current distributions (at all scales) are limited by environment or not. Long time periods are necessary for such experiments as it may be conditions of extreme years rather than average years that determine distribution. When conducting verification studies with rare plants, however, the side effects of such experiments must be carefully considered. The required disturbance may not be appropriate given the fragile nature and small extent of many rare habitats. In atypical habitats, selection may favor genetic characteristics that are disadvantageous to the original plant population (Pavlik et al. 1993). Further, in the United States the U.S. Fish and Wildlife Service currently does not support reintroductions of rare species outside of their historic range (Falk and Olwell 1992). So while field verification is scientifically desirable, care must be taken to ensure that this does not harm the same rare species one is trying to understand.

Prediction of rare-species occurrence from environment shows that certain site parameters are better predictors than others and adds to our understanding of the distribution and site requirements of species under present-day conditions. Increased understanding of controls on distribution serves to focus experimentation and further research on causal mechanisms. It must be kept in mind, however, that environments are not static, particularly over long time spans. Habitat-based models also provide a focus for questions related to natural and anthropogenically induced environmental change. In this study, soil cations were important predictors for two species. Will soils with different levels of cations react differentially to acidic precipitation on the southern Appalachian high peaks? Will this result in differential impact on different populations? Similarly, occurrence of all four species was significantly related to potential solar radiation. Would changes in average or maximum summer temperatures change their distributions along this gradient? More generally, will analogues of current habitats exist in the future, and will human intervention be required to allow rare plant species to persist? Habitat-based models represent a necessary step in efforts to understand current distribution patterns and to predict future distributions of plants in a changing environment.

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