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ECOSYSTEMS

The Role of Soil Classification in Geographic Information System Modeling of Habitat Pattern: Threatened Calcareous Ecosystems

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ABSTRACT

Maps of potential habitat distribution are needed for regional population models of rare species, but reliable information from ground surveys is not always available. Existing data sources from disciplines other than ecological research often are underused. In this article, we discuss the development of a geographic information system (GIS) model that predicts potential habitats from ecosystem information contained in the US soil classification and soil survey. Soil classification and survey were used in the GIS model in an earlier study on the US Department of Energy's Oak Ridge Reservation, Tennessee, to predict threatened calcareous habitats. The model predicts potential habitats from the combination of (a) soil taxon as an indication of long-term ecosystem processes; (b) geologic parent material; and (c) slope class. Satellite imagery was added to indicate current successional state. In this study, we tested the model's predictive ability by using data from the Cedar Creek Slope Glades Preserve at the 44,000-ha US Department of Defense Fort Knox Military Reservation, Kentucky. We then used the model to predict occurrences of potential suitable habitat on the remainder of the Fort Knox reservation, including heavily impacted ordnance and tank training areas that are unsafe for public access. The soil component of the model also was applied to a 1.2×10^6–km^2 region of the US, by using the US Department of Agriculture–National Resources Conservation Service (USDA-NRCS) State Soil Geographic Database (STATSGO) combined with official soil series descriptions. Soil taxa from the USDA-NRCS Soil Taxonomy were demonstrated to be associated with threatened calcareous habitats of rare plant species. These soil taxa were lithic mollisols (rendolls and udolls; Food and Agriculture Organization of the United Nations (FAO) rendzinas and chernozems) and alfisols (udalfs; FAO luvisols). The combined soil/geology/slope GIS approach has potential for prediction of rare ecosystems with narrow edaphic constraints. The approach would be useful in long-term planning for conservation management and restoration, especially where intensive ground surveys are expensive and/or impractical and where disturbance history obscures patterns of historical distribution.

Key words: calcareous; glades; barrens; GIS; Department of Defense; conservation; mollisol; soil taxonomy; threatened and endangered species.

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INTRODUCTION

Regional or metapopulation dynamics are important in the management and recovery of threatened and endangered species (Lande 1988; Akçakaya and Atwood 1997). Models that predict landscape responses of populations of threatened and endangered species benefit from cost-effective methods to produce spatial input of historical, existing, and potential habitat. Producing suitable map input for demographic models often is hindered by the lack of ground reconnaissance data (Dale and others 1998; Ives and others 1998), and researchers have acknowledged the need for greater use of existing ecological data resources in biological conservation strategies (Bunce and others 1996; Austin 1998). In spite of many well-documented links between organisms and edaphic characteristics, soil genesis, soil classification, and existing standardized soil survey maps rarely are used as a basis for predicting potential habitat distribution (for example, Sperduto and Congalton 1996).

This article explores the potential for developing habitat maps for demographic models by combining features of soil genesis and classification with traditional methods of landscape ecology. Specifically, we discuss our ability to use existing data sources and soil taxonomy to map critical habitats and the usefulness of such an approach. For the approach to be useful, diagnostic characteristics used in soil classification must be explicitly related to properties of ecosystems and supporting digital data, and literature must be readily available. In this article, we test the hypotheses (a) that soil classification can be used to predict the potential distribution of ecosystems; and (b) that such predictions are applicable at multiple scales. Furthermore, we demonstrate that such predictions are possible by using readily available sources of information concerning soil genesis, survey, and classification. To test the hypotheses, we use soil classification to predict the presence of suitable habitat by applying a geographic information system (GIS) model to a specific ecosystem example of conservation concern.

Studies of rare species and threatened habitats often use GIS models that incorporate landscape characteristics, such as land cover or vegetation type (for example, Lowell and Astroth 1989; Lauver and Whistler 1993; Sperduto and Congalton 1996; Scott and Csuti 19973. Such models have the potential for accurately predicting the locations of rare species and habitats with a minimum of costly field sampling (Dale and others 1998). GIS models often use vegetation types and patterns as ecosystem analogs because they integrate many physical factors, such as moisture regime, aspect, elevation, and temperature (Bunce and others 1996; Scott and Csuti 1997; Austin 1998). The presence of specific vegetation types, including mature forest, however, can result from relatively recent land use (Dale and others 1990; Foster and others 1998); thus, current vegetation does not always indicate long-term or potential spatial pattern of ecosystems.

In contrast, soil diagnostic characteristics can result from processes or events that are of Pleistocene origin or older, and soil characteristics at various levels in the soil profile can indicate interactions with climate and land cover for hundreds or thousands of years. Such diagnostic characteristics are the basis of the soil classification system used by the US National Resources Conservation Service (NRCS) Soil Survey (USDA-SCS 1975; SSSA 1994; USDA-NRCS 1998). The soil survey also incorporates remote imagery in preparation of county soil survey maps, interpreting spatial relationships between soil characteristics and land use, topography, hydrology, and landscape context (SSSA 1994; Buol and others 1997). The resultant soil map cannot make a prediction of ecosystem distribution that is independent of current and historic vegetation or land cover. However, soil maps inherently contain ecosystem information (including long-term history of land cover) that can be used to predict the distribution of potential core habitat. The complex relationships among soil-forming factors are not well understood and often involve circularity in definition as a result of complex feedback mechanisms (for example, vegetation influences soil characteristics and vice versa). Nevertheless, soil classification is applied uniformly, is based on known ecological processes and theoretical relationships relevant to the formation of the diagnostic characteristics, and is not explicitly linked to current land cover or successional state. The relationships between ecosystem types and diagnostic characteristics are only partially known, and soil classification is applied to ecosystem research in relatively few published studies. Most previous studies use point data aggregated by soil classes to predict processes or dynamics at the landscape (soil catena) or watershed scale (see Kachanoski 1988). For rare ecosystems, quantitative sample data often do not exist, but qualitative characterization of diagnostic characteristics are readily available in soil surveys.

In this article, diagnostic characteristics of soil classification are used to predict critical habitat, by using the example of calcareous ecosystems in the eastern US. The threatened status of calcareous ecosystems included in our analyses is documented by the presence of threatened and endangered or limestone-endemic plants. We show that the GIS model previously developed to predict the distribution of threatened calcareous habitat on the US Department of Energy (DOE) Oak Ridge Reservation (ORR), Oak Ridge, Tennessee (Dale and others 1998) is applicable to other sites. In developing our model, published descriptions of soil and geologic characteristics, climate, and history of threatened calcareous habitats were used to select appropriate soil taxonomic classes. Characteristics of current vegetation indicated successional state. In this article, we evaluate a test application of the model at the Cedar Creek Slope Glades Preserve (referred to as the Cedar Creek Preserve in this article) at the US Department of Defense (DoD) Fort Knox Military Reservation, Kentucky and then use the model to predict occurrences of potential suitable habitat on the rest of the reservation, including impact areas used for ordnance and tank training. A limited field survey of the accuracy of the model was conducted at Fort Knox for areas outside the impact areas. To further evaluate the approach, we also applied the soil component of the model to a 1.2 × 10^6–km^2 region by using the State Soil Geographic Database (STATSGO; USDA-NRCS 1994), and the results are compared with the distribution of limestone glade–endemic vascular plant species (Baskin and Baskin 1986). We evaluate the suitability of our predicted habitat maps as input to regional population models by comparing the dispersal and persistence characteristics of species of conservation concern with the scale of predicted habitat patches. We conclude that current US soil classification can be used to predict the spatial distribution of threatened calcareous ecosystems and that this approach has potential for other ecosystems with edaphic constraints.

CALCAREOUS ECOSYSTEMS AND THE STUDY SITES

Threatened calcareous habitats containing rare (threatened and endangered) or limestone-endemic plants (referred to as TCH/RP in this article) occur throughout the eastern US (Somers and others 1986; Baskin and Baskin 1986; DeSelm 1993; Mann and others 1996), but knowledge of their distribution and dynamics is not currently adequate for population models (DeSelm and Murdock 1993; Quarterman and others 1993; Thomas 1996), and no theoretical basis was found for predicting soil types of such habitats before our work (Dale and others 1998). In the literature, the terms “barren” and “glade” components of TCH/RP often overlap or are contradictory; recent use consistently refers to barrens and glades as having perennial, warm-season grass cover of greater than 50% and less than 50%, respectively (Quarterman and others 1993; DeSelm and Murdock 1993). Our definition of TCH/RP in this article includes bare calcareous rock (Baskin and Baskin 1986; Quarterman and others 1993), gravelly sites of weathered limestone or dolomite and accumulated soil [for example, gravel glades of Quarterman (1950)], cedar barrens (DeSelm and others 1969; DeSelm 1993), xeric limestone prairie (Baskin and others 1994), limestone barrens (TNC 1995), and limestone slope glades (White and others 1994). Species composition in such habitats differs across the eastern US, but threatened and endangered species often are present (Baskin and Baskin 1986; Bridges and Orzell 1986). Open xeric woodland containing eastern red-cedar (*Juniperus virginiana*), several species of oaks (*Quercus* spp.), and pines (*Pinus* spp.) forms the matrix for calcareous openings and provides additional habitat for rare species [for example, Appalachian endemic tall larkspur (*Delphinium exaltatum*)]. In the absence of disturbance, woodland canopy gradually develops in all but the largest, rockiest environments.

Differences and similarities of TCH/RP in the eastern US have been documented extensively (Quarterman 1950; Baskin and Baskin 1985, 1986; Bridges and Orzell 1986; Delcourt and others 1986; Somers and others 1986; Quarterman and others 1993; DeSelm 1993). Although species assemblages vary across the region, our soil-based model assumes that soils of TCH/RP have developed in response to similar spatial and long-term temporal gradients of edaphic conditions and land-cover types.

Study sites included calcareous ecosystems on the ORR and Fort Knox reservations. The ORR in eastern Tennessee, used in the original development of our model, is described in detail elsewhere (Mann and others 1996; Dale and others 1998). Threatened and endangered vascular plant species (Table 1) occur in eight registered State Natural Areas containing calcareous habitat on the ORR and adjacent land (Mann and others 1996; TNC 1995). Perennial warm-season grasses are abundant in TCH/RP of the ORR (DeSelm and others 1969; DeSelm and Murdock 1993), but small areas are dominated by annual grasses and forbs. Slopes are characteristically less than 25%, and Midwestern prairie species are frequent. Wildfires have not been documented in calcareous habitats. Chickamauga limestone, often associated with glades and barrens elsewhere (DeSelm 1993), occurs on the ORR (Figure 1) in parallel valleys.

Fort Knox occupies 44,150 ha in north-central Kentucky (Figure 1). The Fort Knox Reservation is divided northwest to southeast by a steep escarpment drained by several tributaries. The Cedar Creek Preserve of Fort Knox is a relatively intact 900-ha tract of TCH/RP (White and others 1994) on the edge of this escarpment that contains several threatened and endangered species (Table 1). Most of Fort Knox is forested. Nonforested areas include (a) the munitions testing area; (b) tank or tracked vehicle training areas; and (c) the cantonment. As is true of other DoD reservations, frequent fire from ordnance testing and soil disturbance from training activities has contributed to the development and persistence of existing land-cover types.

Limestone formations at Fort Knox are primarily of Upper Mississippian age. The Ste. Genevieve and St. Louis Limestone formations are usually under deeply weathered red clay (McDowell 1986) but can outcrop in erosional areas, such as in the vicinity of the Cedar Creek Preserve (White and others 1994). The Salem and Harrodsburg formations weather into flaggy, gravelly surface soil similar in appearance and physical characteristics to that found on the Chickamauga limestone of the ORR and in gravel glades of the Central Basin of Tennessee (McDowell 1986). All four geologic layers outcrop in the dissected region of the escarpment in the area of the Cedar Creek Preserve. Only the part of Fort Knox outside the training impact zone has been surveyed for rare species and habitat boundaries. However, potential TCH/RP is thought to be relatively extensive in the southern part of the reservation, which contains a mixture of highly disturbed and eroded areas resulting from military vehicle use and logging operations, grazing, and fire (White and others 1994).

METHODS

An overview of the GIS model is shown in Table 2. The GIS model combines soil taxonomic, geologic parent material, and rock fragment characteristics to predict patches of potential habitat. In the site-specific model, soil slope classes refine the model, and land-cover classes identify woodland openings that provide optimal habitat for TCH/RP plant species. The model is based on a combination of (a) experience with calcareous ecosystems of the ORR (Mann and others 1996; Dale and others 1998); (b) familiarity with the US soil classification (Mann and Kitchings 1982; Mann 1985); (c) existing literature about calcareous barrens, glades, and woodlands, especially of the Ridge and Valley and the Central Basin (Quarterman 1950; DeSelm and others 1969; Quarterman and others 1993; Baskin and Baskin 1986; DeSelm 1993); and (d) soil classification and soil series descriptions from the on-line Internet information system of the USDA-NRCS and supporting literature (USDA-SCS 1975; SSSA 1994; Buol and others 1997; USDA-NRCS 1998). Decision rules for the site-specific and regional model application, sources of data, the theoretical basis for selecting soils associated with potential core and other habitat, and tests of the success of the model applications are discussed in the following sections. Intensive field studies were beyond the scope of this research, which focuses on the use of existing data sources.

Floristics

Whether or not to include a site as TCH/RP was determined from the presence of threatened and endangered or limestone glade–endemic vascular plant species (Table 1). Floristic data for the Oak Ridge area came from Mann and Shugart (1983) and previously unpublished species lists and ongoing surveys. Floristic data for the Cedar Creek Preserve of Fort Knox came from White and others (1994). Similarity of floristic composition was determined by using Sørenson's index of similarity {100% × number of species common to both sites ÷ [½ (total species at ORR + total species at Fort Knox)]} (Mueller-Dombois and Ellenberg 1974). All plants from the complex of known openings and surrounding xeric open-woodland matrix were included. Floristic data for the regional application of the soil-based model and comparisons of the ORR, Fort Knox, and the Central Basin of Tennessee were from Baskin and Baskin (1986) and from Somers and others (1986). Sources of species characteristics for evaluation of dispersal characteristics in relation to habitat prediction are given in Table 1.

Theoretical Basis of Soil Components

Working with conservation of biodiversity in Australia, Austin (1998) has pointed out the need for a theoretical basis for determining the potential distribution on the landscape rather than depending on species presence alone. The soil component of our model used the current US soil classification and taxonomy (SSSA 1994; Buol and others 1997; USDA-NRCS 1998) that provided the theoretical framework for predicting potential habitat. The taxonomy is hierarchical, with higher levels related to dominant characteristics that result from interactions of vegetation, climate, and relative topographic position over time. Although classes are not always comparable at all levels of the classification, modifiers at lower levels of the hierarchy include those related to temperature and moisture regime, depth to parent rock, and drainage. Diagnostic characteristics include the development of distinc-

Table 1. Vascular Plants of TCH/RP in the Eastern United States and Their Characteristics

	Status[a]						
Species	Federal	State (TN and KY)	ORR	Ft. Knox	Longevity	Characteristics of Dispersal Unit[b]	Likely Dispersal Mode
Agalinis auriculata	S	TN-E	X		Annual	Reticulated, small	Wind/water
Astragalus tennesseensis		TN-T			Perennial	None, small	Gravity
Allium cernuum[c]			X	X	Perennial	Bulbs, seeds small	Gravity
Arenaria patula[c]			X		Annual	Small	Gravity/wind
Aristida longespica[c]					Annual	Bristles, large	Gravity/animal
Carex crawei[c]		TN-S, KY-S			Perennial	Resin dotted, large	Gravity/animal
Croton capitatus[c]					Annual	Flattened, large	Gravity
C. monanthogynus[c]			X	X	Annual	Large	Gravity
Dalea foliosa	E	TN-E			Perennial	Indehiscent pod, large	Water/gravity
D. gattingeri[c]					Perennial	Winged, large	Water/gravity
D. alabamicum					Perennial	Large	Water/gravity
Delphinium exaltatum		TN-E	X		Perennial	Ridged, large	Water/gravity
Diodia teres[c]			X		Annual	Toothed, large	Gravity/animal
Echinacea tennesseensis	E	TN-E			Perennial	Ridged, large	Water/gravity/ animal
Erigeron strigosus[c]			X		Annual or biennial	Pappus, large	Wind/animal
Euphorbia dentata[c]			X		Annual	Lumpy, large	Gravity
Hedyotis nigricans[c]			X		Perennial	Small	Gravity/wind
Heliotropium tenellum[c]				X	Annual	Large	Gravity
Hypericum dolabriforme			X	X	Perennial	Small	Gravity/wind
H. sphaerocarpum[c]			X	X	Perennial	Small	Gravity/wind
Isanthus brachiatus[c]			X		Annual	Large	Gravity
Leavenworthia alabamica					Annual	Winged, large	Gravity
L. crassa vars.					Annual	Winged, large	Gravity
L. exigua vars.[c]	S	TN-T and E, KY-T			Annual	Winged, large	Gravity
L. stylosa[c]					Annual	Winged, large	Gravity
L. torulosa		TN-T, KY-T			Annual	Winged, large	Gravity
L. uniflora					Annual	Winged, large	Gravity
Lesquerella lyrata					Annual	Inflated silicles, large	Water
Liatris cylindracea		TN-E, KY-T	X	X	Perennial	Pappus, large	Wind
Lobelia appendiculata var. *gattingeri*		KY-E			Perennial	Small	Wind/water
Manfreda virginica[c]			X	X	Perennial	Fleshy, large	Gravity/animal
Nothoscordum bivalve[c]					Perennial	Bulbs, seeds large	Gravity
Onosmodium molle		TN-E, KY-E			Perennial	Pitted, large	Gravity
Oxalis priceae		KY-H			Perennial	Explosive, large	Gravity
Panicum capillare[c]			X		Annual	Tumbleweed, large	Wind/gravity/ animal
Panicum flexile[c]			X		Annual	Large	Gravity/animal
Penstemon tenuiflorus					Perennial	Small	Gravity
Phacelia dubia					Annual	Reticulate or pitted	Gravity
Psoralea subacaulis[c]					Perennial	Large	Gravity
Psoralea stipulatum					Perennial	Large	Gravity
Rudbeckia triloba[c]					Annual/ biennial	Large	Gravity/animal
Ruellia humilis[c]			X	X	Perennial	Small	Gravity
Satureja glabella[c]					Perennial	Reticulate, large	Gravity
Schizachyrium scoparium[c]			X	X	Perennial	Spikelet, hairs, large	Wind/animal
Scutellaria parvula[c]			X		Perennial	Bumpy, large	Gravity
Sedum pulchellum[c]			X		Annual	Small	Gravity/wind

Table 1. (Continued)

Species	Status[a]						
	Federal	State (TN and KY)	ORR	Ft. Knox	Longevity	Characteristics of Dispersal Unit[b]	Likely Dispersal Mode
Senecio anonymus[c]			X		Perennial	Hairs, large	Wind
Silphium terebinthinaceum			X	X	Perennial	Toothed, large	Gravity/animal
S. laciniatum		TN-T, KY-T		X	Perennial	Toothed, large	Gravity/animal
Solidago gattingeri		TN-E			Perennial	Pappus, large	Wind/animal
S. ptarmicoides		TN-E	X		Perennial	Pappus, large	Wind/animal
S. shortii	E	KY-E			Perennial	Pappus, large	Wind/animal
Spiranthes magnicamporum[c]		KY-T		X	Perennial	Small	Wind/gravity
Sporobolus vaginiflorus[c]			X	X	Annual	Large	Gravity/animal
Talinum calcaricum[c]		TN-T, KY-E			Perennial	Rough, large	Gravity
Verbena simplex[c]			X	X	Perennial	Reticulate, large	Gravity
Viola egglestonii		KY-S		X	Perennial	Eliasome, large	Ants, gravity

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[a] *E, endangered; T, threatened; S, special concern; H, historic records, presumed extirpated (Kentucky State Nature Preserves Commission 1994; Nordman 1996).*

[b] *Characteristics of seeds or other propagules. From Baskin and Baskin (1985) and references cited therein or derived from Fernald (1970), Gleason (1952), or unpublished data for similar genera. Small, <0.5 mm; large, >0.5 mm.*

[c] *Characteristic, most frequent limestone glade endemics of the Central Basin, Tennessee (Somers and others 1986).*

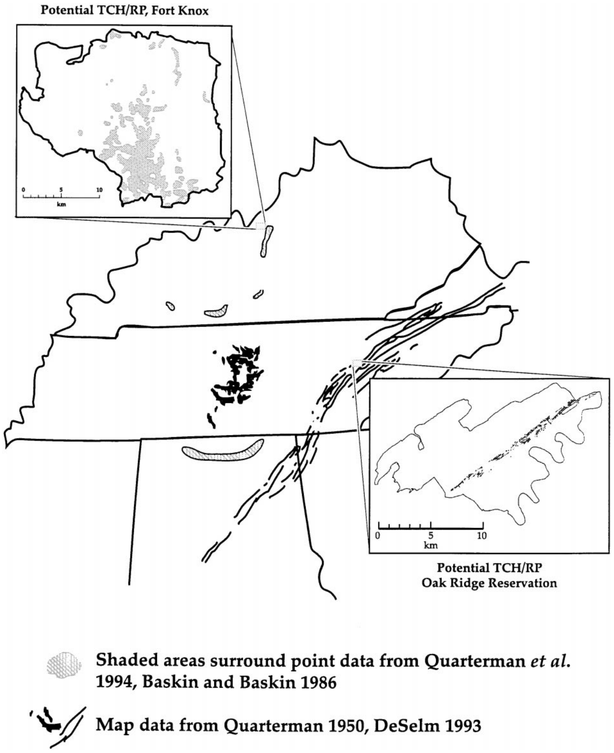

Figure 1. Location of the DOE Oak Ridge and the DoD Fort Knox reservations. Reprinted with permission.

tive layers or horizons as long-term responses to vegetation influences on organic matter and geochemistry and to movement of water through the soil profile. The lowest level of the hierarchy is the soil series. In this taxonomic system, mollisols are fertile, neutral soils, characterized by a diagnostic horizon called the mollic epipedon, which is a relatively homogeneous, highly organic layer near the surface. The high level of organic matter in this soil layer is attributed to hundreds of years of high levels of input of organic carbon from fine root turnover, primarily from grasses and forbs, and is retained in the soil profile by interactions with clays and divalent cations, especially calcium, in neutral to alkaline soils (Oades 1988; Jastrow 1996; Buol and others 1997).

We hypothesize that shallow, rocky mollisols are "core" areas of TCH/RP and that they indicate the long-term presence of herbaceous vegetation cover in both openings and part of the areas currently occupied by oak–red-cedar woodlands. Such herbaceous vegetation is maintained in TCH/RP in the eastern US by disturbances that periodically remove woodland canopy (Lowell and Astroth 1989; Quarterman and others 1993; DeSelm and Murdock 1993). The udoll suborder of soils (freely drained mollisols of humid continental climates in midlatitudes) and the rendoll suborder (mollisols that have formed from highly calcareous parent materials in primarily forested regions) are the two suborders that develop in humid temperate regions. Such soils develop on parent material with high levels of cations, either from relatively young surface deposits of loess or from calcareous minerals near the surface, and are thought to have high rates of input of organic carbon from fine roots of herbaceous

Table 2. Matrix of Decision Rules for the GIS Model[a]

	Soil Components				
	Soil Taxa	Geologic Parent Material	Soil Slope	Other Soil Parameters	Land-Cover Components
Potential core habitat					
Site specific	Lithic[b] mollisols[c] (NRCS soil survey)	Limestone (data layer)	<25% (data layer)	Presence of small flat stone fragments; rock outcrops (soil series descriptions)	Urban, barren, grass, transitional (data layer)
Regional	Same	Limestone or dolomite (soil series descriptions)	Not used	Same	Not used
Other potential habitat					
Site specific	Other mollisols, alfisols[d] (NRCS soil survey)	Limestone (data layer)	<25% (data layer)	Same	Urban, barren, grass, transitional (data layer)
Regional	Not used	Limestone or dolomite (soil series description)	Not used	Same	Not used

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[a] *Data source given in parentheses. See Tables 3 and 4 for additional information on data and sources.*

[b] *Lithic, soils less than 50 cm deep.*

[c] *Mollisols, soils with characteristic layer high in organic matter near the soil surface due to high cation levels and high rates of organic matter input, usually from herbaceous vegetation (Buol and others 1997).*

[d] *Alfisols, soils with slightly lower cation levels than mollisols, often formed under forest or in forest/prairie transition (Buol and others 1997).*

plants for long periods of time (Buol and others 1997). We also speculate that alfisols would be part of TCH/RP, being intermediate in soil characteristics between mollisols and highly leached ultisols more typical of the southeastern US. Alfisols contain less organic matter than mollisols and generally have moderate base content. Other soil types were not included because they did not have diagnostic characteristics related to the long-term presence of TCH/RP.

The model is restricted to lithic mollisols, defined as less than 50 cm to solid rock, assuming that deeper mollisols would be more likely to be associated with "true" prairie (Buol and others 1997). Soils mapped as lithic mollisols often include areas of rock outcrop. Therefore, although bare rock is not soil, such outcrops were included in the soil component of the model.

The soil-geologic parent material component of the model is limestone or dolomite occurring in thin- to medium-bedding planes separated by calcareous shale. The parent material weathers into the typical "flags" or small bits of flat, gravelly rock. This rock is characteristic of the gravel glades of the Central Basin and TCH/RP on the ORR. The limestone rock is either at the surface or is covered with shallow soil, and it contributes to high pH, high calcium content, and poor water-holding capacity. The presence of flat, gravelly rock was determined from Official Soil Series Descriptions by using the NRCS Internet website query system (USDA-NRCS 1998).

No documentation of a definitive relationship between slope angle and the occurrence of TCH/RP was found. Most TCH/RP sites are moderately sloping to level and on the ORR, slopes are less than 25%. Therefore, slope class was set at less than 25%.

Site-Specific Model

The model predicted locations of TCH/RP at Fort Knox from soil type, geologic parent material, slope-class, and land-cover GIS data layers and base maps of standard features (Table 2). Predictions were the

Table 3. Summary of Spatial Data[a]

Theme	Fort Knox Data Sources
Land cover	1992 Landsat TM, 1081 rows × 1290 columns from EOSAT corporation. Resampled to 20 m.
Terrain, including slope	Digital terrain model from aerial photographs (Aerometric, Inc., Sheboygan, WI, and Construction Engineering Research Laboratory, Champaign, IL, USA, 1985). Supplemented from DEM data (USGS 7.5-min quadrangle maps).
Geology	7.5-min, 1:24,000 maps (McDowell 1986)
Soil	Soil series (Arms and others 1979; Whitaker and Waters 1986; unpublished Meade County soil survey)
Protected natural areas	Manual map overlay (White and others 1994)

[a] *ORR spatial data are described in detail in Dale and others (1998).*

product of positive intersections of lithic mollisols (FAO rendzinas or chernozems) or alfisols (FAO luvisols); transitional, barren, urban, or grass land cover; flaggy limestone or dolomite geology; and slopes less than 25%. The application of the model was considered successful if the boundaries of TCH/RP openings delineated by White and others (1994) were contained within or coincident with a predicted patch.

Data used in the model development and application were from several sources (Table 3). Technical details of the ORR GIS data layers are reported in Dale and others (1998). For Fort Knox, the soil data layer was derived from existing county soil survey maps (Table 3) and supplemented with soil series descriptive information, and the geology layer was derived from a digitized version of 7.5-min 1:24,000 maps from the 1985 Kentucky Geologic Survey.

To determine slope at Fort Knox, we used a digital terrain model that was developed by Aerometric, Inc., Sheboygan, Wisconsin from aerial photographs taken in 1985 (1:24,000 scale, 12,000-ft altitude) and rectified by the Construction Engineering Research Laboratory, Champaign, Illinois (horizontal resolution, 10 m; vertical resolution, 0.1 m). Slope data were patched in for a small portion of the reservation from 30-m digital elevation model (DEM) data available from the US Geological Survey. The terrain model was then spline-smoothed within this lower-resolution section to 10-m horizontal resolution, by using the GRASS program s.surf.2d (Mitasova and Hofierka 1993).

The land-cover component of the model was determined from satellite imagery to provide "snapshot" surrogates for current successional status. Suitable habitats selected in the development of the model of TCH/RP were (a) urban (mimics bare rock); (b) barren, (c) grassland, and (d) transitional (young forest and open eastern red-cedar–hardwood woodlands) (Dale and others 1998). The land-cover data layer at Fort Knox was derived from a thematic mapper (TM) image [Earth Observation Satellites (EOSAT) Corporation] and from Fort Knox Land Condition Trend Analysis (LCTA) vegetation data. The September 1992 TM image had an original resolution of 30 m for the entire reservation, which was georegistered and resampled to 20-m resolution by staff at Fort Knox, who also provided data layers of standard features, such as roads and rivers. The LCTA data, collected from 1991 to 1994 on 100-m–long transects, provided spectral signatures for a supervised land-cover classification of the TM image. Lakes and major rivers, as well as primary roads, were used from preexisting GIS layers to provide spectral signature sites for water and urban categories with the outermost cells discarded to improve the spectral signatures for these classes. The urban and water signatures and the 152 LCTA plots with GPS locations (converted to North American Datum 27 for proper registration) were unambiguously grouped into eight categories inside the boundaries of Fort Knox: urban, barren, grass, transitional, evergreen forest, mixed forest, deciduous forest, and water. An iterative maximum-likelihood discriminant-function algorithm was used to classify each cell in the image (i.maxlik program, GRASS 4.1 1993).

Regional Model

The model predicted TCH/RP in the 1.2 × 10^6–km^2 region from soil type and geologic parent material (Table 2). Data sources were STATSGO (USDA-NRCS 1994) and other components of the public access USDA-NRCS Internet information system (USDA-NRCS 1998). STATSGO soil associations are named for the three primary soil series present, and minor soil types are identified by taxonomic class only. The STATSGO database contains 133 soil associations that contain mesic (mean annual soil temperature, 8–15°C) or thermic (mean annual soil temperature, 15–22°C) lithic mollisols (rendolls and udolls). Of the 20 lithic mollisol soil series geographically associated with these 133 soil associations, 11 soil series were eliminated because they are too

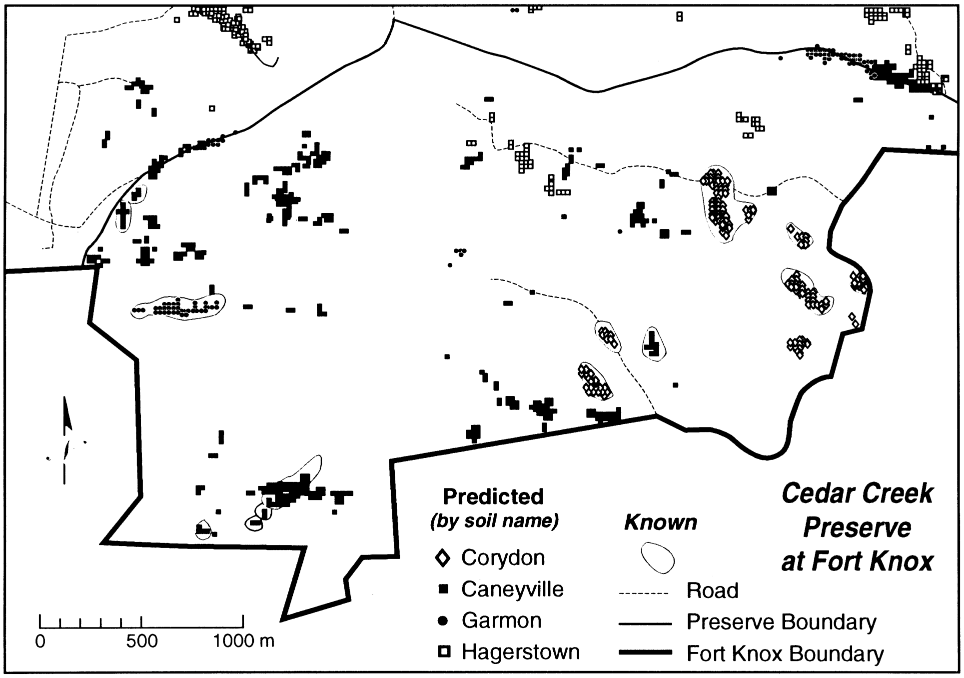

Figure 2. Predicted and known rare plant habitat locations in the Cedar Creek Preserve at Fort Knox showing the distribution of soils predicted by the model.

acidic, lack limestone or dolomite fragments, or are not derived from calcareous parent material. The nine remaining soil series (Gladeville, Balltown, Barfield, Corydon, Fairmount, Gasconade, Knobby, Moko, and Swink) were considered appropriate because they contain rock fragments indicative of thin-bedded limestone parent material and have slightly acid to slightly alkaline pH (USDA-NRCS 1998). All soil series were hapludolls except for Gladeville (Rendoll) and Corydon (Argiudoll). These nine soil series occur in 41 of the 133 soil associations. Therefore, map pixels that contain those 41 soil associations were identified as containing potential "core" TCH/RP.

The map of the 41 soil associations, generated from the STATSGO analysis, then was evaluated by comparing it with the county-level distribution of known limestone glade–endemic species (Baskin and Baskin 1986). The success of the model was determined by means of a chi-square test (Sokal and Rohlf 1969) of co-occurrence of (a) counties containing predicted calcareous habitat; and (b) counties actually containing records of threatened and endangered or limestone-endemic species.

Field Survey

A limited field test of the model was conducted at Fort Knox by randomly selecting 142 pixells in locations outside the impact zone. Before sampling, field crews developed a search image of potential TCH/RP by viewing known TCH/RP sites in the preserve. Each sample pixell was visited by a two-person field team equipped with a portable global position system (GPS) receiver. Sites were evaluated for presence or absence of potential TCH/RP and were photographed. The model was considered successful if it included all sample sites visually identified as potential TCH/RP.

RESULTS

Floristics

Our review of previous and ongoing vegetation surveys revealed that seven state or federally listed species occur in the calcareous natural areas on the ORR and Cedar Creek Preserve of Fort Knox (Table 1); thus, the areas meet the criterion as TCH/RP. Sørenson's index of similarity for the two sites was 30%, indicating that the ORR and Fort Knox TCH/RP contained many of the same species: 62 species were common to both sites, including eight of 33 species that were the most frequent taxa of Central Basin glades (Somers and others 1986).

Site-Specific Model

Our model accurately predicted the locations of the habitat patches that contain TCH/RP in the Cedar Creek Preserve at Fort Knox. The model initially predicted all but one of the 10 sites reported by White and others (1994) as containing TCH/RP within the Cedar Creek Preserve boundary (Figure 2) and subsequently predicted the remaining site after further analysis of soil survey information and

Table 4. Suitable Substrates for Threatened Calcareous Habitats at Fort Knox and the ORR

Soil Order	Soil Suborder	Soil Series ORR[a]	Geologic Substrate Fort Knox
Mollisols: characteristic organic layer (mollic epipedon) and high cation exchange capacity. Primarily formed under prairie	Lithic rendolls: shallow (<50 cm), well drained, rocky soils developed on carbonate bedrock under calcareous, open woodland in temperate climate	Gladeville	None present
	Lithic argiudolls: shallow (<50 cm), well drained, rocky soils developing a clay layer, containing carbonates	Not identified by series name	Corydon: mapped as rock outcrop—Corydon complex
Alfisols: moderate cation exchange, with a defining clay layer. Forest soils also formed in transitional areas between prairie and forest in moist, temperate climates	Hapludalfs: well-drained soils developed in moist, temperate climate	Carbo Upshur variant[b] Capshaw	Caneyville: mapped as Caneyville rock outcrop complex and Garmon[c] Caneyville: mapped as Hagerstown[d] Hagerstown
	Thin layers of limestone resistant to weathering	Chickamauga	Salem, Harrodsburg

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[a] *Soil suborders of the ORR are from the Hatcher and others (1992) geologic survey and data base (this source did not use soil series names); soil series names are from the Anderson County Soil Survey (Moneymaker 1981).*

[b] *Soil mapped as Upshur variant also contain areas of lithic hapludalfs.*

[c] *Soil mapped as Garmon (dystric Eutrochrept) contains thin bands of Caneyville rock outcrop complex.*

[d] *Soil mapped as Hagerstown also contains small areas of shallower Caneyville.*

geologic data layers. From existing soil surveys, we determined that mollisols at Fort Knox were lithic argiudolls (Corydon series; Table 4; Arms and others 1979; Whitaker and Waters 1986). The map unit of rock outcrop complex containing lithic mollisols in the soil surveys consists of approximately 40% rock outcrop, 30% Corydon soil, and 30% other soil (Arms and others 1979). In the model prediction, only 15 ha was mapped as this rock outcrop complex, or less than 2% of the total Cedar Creek Preserve (Fort Knox 1995). Other predicted locations of TCH/RP contained alfisols mapped in complex with rock outcrops (Hapludalf Caneyville rock outcrop complex; Figure 2), consisting of approximately 20% rock outcrop and 65% Hapludalf, and all 10 known locations of TCH/RP in the Cedar Creek Preserve were associated with Salem limestone. Although White and others (1994) previously reported Ste. Genevieve and St. Louis limestone as substrate for the Cedar Creek Preserve, neither type of limestone fit the required physical characteristics of the model. Instead, the model successfully used Salem and Harrodsburg limestone as the geologic indicator of TCH/RP. The GIS analysis showed that approximately 75–88% of Corydon, Caneyville and Hagerstown soil series was associated with Salem and Harrodsburg limestones, with the remainder primarily Ste. Genevieve and St. Louis limestones. The Hardin County Soil Survey includes additional thin bands of Hapludalf Caneyville rock outcrop complex within the Garmon soil map unit. The prediction was modified to add areas of Garmon soil series that were coincident with Salem limestone (possibly the Caneyville component), thus successfully identifying the two remaining known locations of TCH/RP in the Cedar Creek Preserve.

The model predicted approximately 7500 ha of potential TCH/RP at Fort Knox (Figure 1). Discussions with staff at Fort Knox indicated that the overall predicted potential habitat distribution, most of which occurs inside the impact zone, appears to be accurate but more extensive than they expected. Approximately 30% of the predicted potential habitat at Fort Knox occurs on Hagerstown soil series, but none of the predicted areas of this soil type coincided with known TCH/RP openings in the Cedar Creek Preserve (Figure 2). Less than 10% of areas mapped as Hagerstown soil series contain intermingled areas of shallower Caneyville soil series (Arms and others 1979), but we were unable to refine the prediction to identify possible Caneyville components.

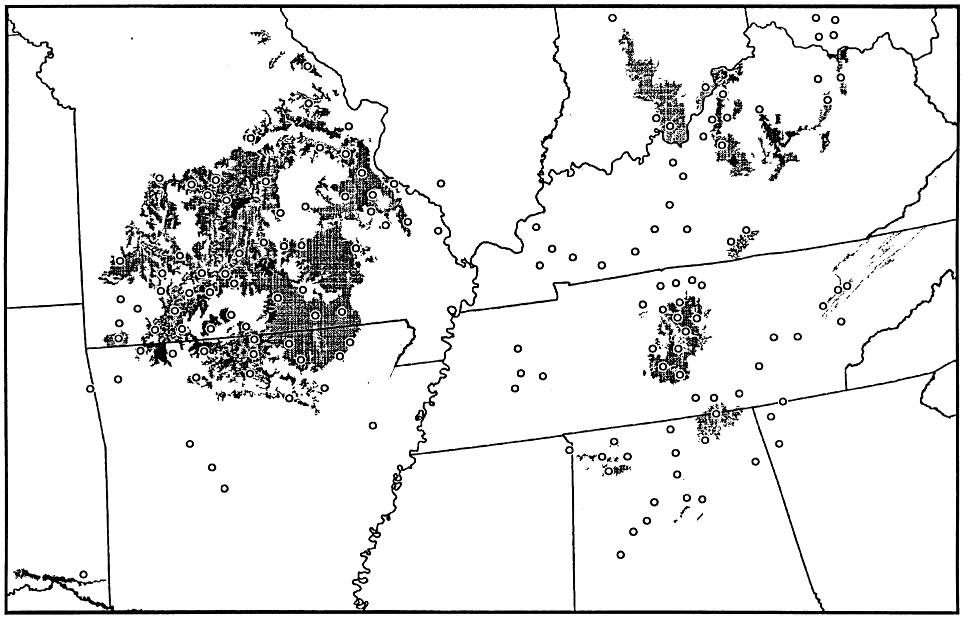

Figure 3. Distribution of predicted soils (lithic Rendolls and Udolls) in the eastern US (USDA-NRCS 1994) and county occurrences of limestone glade endemics (Baskin and Baskin 1986). Soil data is at 1-km^2 resolution.

Regional Model

In the regional application of the model by using STATSGO, TCH/RP was predicted in 159 of 562 counties (Figure 3). Moreover, the soil component of the model was coincident with the location of 99 of 158 county occurrences of limestone/dolomite glade–endemic species listed by Baskin and Baskin (1986). Thus, the coincidence of the model with the Baskin and Baskin (1986) survey was 63%; expected coincidence was 28% if the distribution of species were independent of predicted habitat within the study area ($\chi^2 = 91$, $P \leq 0.005$; Figure 3).

Field Survey

In the field test, none of the randomly selected pixells occurred within the preserve. Of the 142 sampled pixells, our model correctly predicted that 123 would not be potential habitat. Our model also predicted that the remaining 19 pixells were potential habitat. Of these 19 predicted potential habitat pixells, seven were not potential habitat.

DISCUSSION

Our model accurately predicted the location of TCH/RP on the ORR (see Dale and others 1998) and at Fort Knox, and it predicted the pattern of distribution of limestone glade–endemic plants throughout the eastern US (Figure 1). The presence of 62 species at both the ORR and Fort Knox indicates similarities in edaphic conditions and potential similarities in soil development, in spite of the regional differences in species composition that we found and that have been reported in previous studies.

Results of this study demonstrate that soil classification can be used to predict TCH/RP at multiple scales. Diagnostic characteristics of soil classification that proved applicable to our predictions included (a) mesic or thermic temperature regime; (b) presence of a mollic epipedon; and (c) lithic contact at less than 50 cm. The mesic or thermic temperature regime restrict the model to temperate climates. We speculate that the mollic epipedon, or organic layer, in TCH/RP results from the long-term occupation of calcareous sites by herbaceous vegetation. Fire and other disturbances that contribute to removal of woodland canopy and expansion of herbaceous land cover from areas of bare rock or gravelly openings have been documented as important factors in the persistence of optimal habitat for calcareous glade–endemic species (Lowell and Astroth 1989; Thomas 1996). Lithic (shallow) soils are drought prone, thus contributing to high potential fire frequency and intensity in TCH/RP.

Although soil classification was important in identifying TCH/RP, it was not sufficient to identify potentially suitable soil types. Soil series descriptions or a GIS geologic data layer was needed to determine geochemistry and physical characteristics of rock fragments.

Most previous studies have reported the presence of TCH/RP on either mollisols or alfisols (Table 5). However, Garmon soil (a dystric eutrochrept) is reported by Baskin and others (1994) as the primary soil type on which xeric limestone prairies occur in the Fort Knox area. Mollisols may have only developed where herbaceous vegetation has been present for long time periods on relatively stable soil sur-

Table 5. Soils of Previous Studies of TCH/RP

Location	Soils (Soil Order)	Geographically Associated Lithic Mollisols[a]
Tennessee (Quarterman 1950)	Gladeville series (mollisol)	Gladeville (Tennessee)
Missouri (Lowell and Astroth 1989)	Gasconade series (mollisol)	Gasconade (Missouri, Arkansas)
Alabama, Tennessee, Kentucky (Quarterman and others 1993)	Mollisol order	Gladeville, Barfield (Tennessee, Alabama, Kentucky), Corydon (Indiana, Kentucky, Virginia), Fairmount (Kentucky, Indiana, Ohio)
Alabama, Tennessee, Kentucky (Quarterman and others 1993)	Ultisol order	None; possibly includes Gladeville, Barfield, Corydon, Fairmount
Alabama, Georgia, Tennessee, Virginia (DeSelm 1993)	Colbert association (alfisol and other)	Barfield, Gladeville
	Conasauga series (alfisol)	None found; associated with Colbert (hence possibly Barfield and Gladeville)
	Talbott association (alfisol and other)	Barfield, Gladeville
Kentucky, Tennessee (Baskin and others 1994)	Caneyville series (alfisol)	Corydon
	Colbert series (alfisol)	Barfield, Gladeville
	Fredonia series (alfisol)	None found
	Garmon series (inceptisol)	None found; associated with Caneyville (hence Corydon)
	Hagerstown series (alfisol)	None found; associated with Caneyville (hence Corydon)
	Talbot series (alfisol)	Barfield, Gladeville

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[a] *From USDA-NRCS (1998) official soil series descriptions.*

faces. Alfisols were associated with the TCH/RP woodland matrix at Fort Knox and may have been part of larger openings throughout the region during extensive drought, such as between 9000 and 4000 BP (Delcourt and others 1986).

In the regional analysis, the model did not predict TCH/RP in some areas in which occurrences of TCH/RP have been reported in the literature. Areas of underprediction may be due to coarse resolution of data or may be alfisols or other soil types not considered characteristic of "core" TCH/RP in the regional application. The model also predicted extensive areas of TCH/RP in the western part of the study region, where only one of five predicted soil series is reported in the TCH/RP literature (Lowell and Astroth 1989).

More than 80% of the 46 native species at both Fort Knox and the ORR are characteristically found in both open woodlands and openings (Fernald 1970; Somers and others 1986; Quarterman and others 1993). Thus, many species of TCH/RP are well adapted to persist in woodlands with at least partially closed canopy from which populations may rapidly expand into nearby, recently disturbed areas. For example, military tank training and establishment of powerline rights-of-way in woodlands provided a disturbance regime that was compatible with the persistence of several state-listed endangered TCH/RP species on the ORR (Mann and others 1996). Similarly, Terletzky and Van Auken (1996) reported that approximately one-third of glade species of the Edwards Plateau in Texas were found in both woodlands and openings. Such habitat heterogeneity may be important to long-term persistence in the harsh and unpredictable environment of limestone glades (Thomas 1996) but also may create dispersal barriers. Previous studies have found that species whose seeds are dispersed mainly by gravity, such as *Leavenworthia* spp. (Table 1), are particularly poorly adapted to crossing unsuitable habitat gaps more than 100-m wide (Primack and Miao 1992; Dale and others 1998). Very small, light seeds, such as those of *Hypericum dolabriforme,* and wind-dispersed seeds, such as those of *Liatris cylindracea,* could potentially be moved farther distances in windy periods (Howe and Smallwood 1982) but might not move beyond intervening woodlands (Table 1). Therefore, the spatial configuration of openings and woodlands may be critical for dispersal and establishment of TCH/RP species.

We conclude that current county soil survey data can provide data at a scale appropriate to the occurrence and distribution of TCH/RP patches on the landscape and suitable for evaluating potential barriers to dispersal. Recent US NRCS county soil survey maps have a typical minimum resolution of approximately 40 m, and features as small as 16 m are delineated in some surveys. This level of resolution is compatible with species of poorest dispersal capability (see Figure 2). Gaps between suitable habitat patches that would result from ordnance testing and tank training on military reservations, for which the model was originally developed, would typically be greater than the grain size of the habitat patches predicted by the model by using county soil survey data. In contrast to the county soil surveys, the model predictions by using STATSGO are coarser at 1-km^2 resolution than the distribution of TCH/RP on the landscape and would not be suitable for regional population models of TCH/RP species.

In this article, we take advantage of the pedogenic theory that underlies the use of soil properties for classification. The arcane-sounding language of US soil classification may deter researchers unfamiliar with the terminology, but the diagnostic criteria used in each level of the classification hierarchy capture components of the long-term history of ecosystem development. Having perhaps pushed the predictive capability of the soil classification system to its limit in this example, we conclude that results of our analysis add to the understanding of the spatial and temporal characteristics of soils of TCH/RP.

The approach also shows promise for prediction of the potential distribution of other ecosystems. For example, at another US military training facility, we successfully used a soil taxonomic approach to predict the Karner blue butterfly habitat in oak savannahs at Fort McCoy in Wisconsin. Predicting potential habitat distribution of other threatened and endangered species and ecosystems with narrow edaphic constraints also might be compatible with this approach if suitable data bases are available. Possible examples in the US include serpentine barrens (Kruckeberg 1984) and Silurian limestone and dolomite wetlands supporting Hine's Emerald dragonfly (*Somatochlora hineana*) and Lakeside Daisy (*Hymenoxys herbaceae;* USDA-FWS 1997). Additional potential examples from other countries include the northern bettong (*Bettongia tropica*) in Queensland on rich basaltic or alluvial soils (Laurance 1997); *Gentianella germanica* on nutrient-poor calcareous grasslands in central Europe (Fischer and Matthies 1998); and *Aster kantoensis,* on the gravelly river floodplains of Japan (Washitani and others 1997).

CONCLUSIONS

The application of soil taxonomy to traditional GIS modeling demonstrates that diagnostic characteristics used in the soil classification are related to the presence and potential distribution of an example ecosystem. Several diagnostic characteristics from the current US soil classification system proved applicable to our prediction, including (a) presence of a mollic epipedon; (b) lithic contact at greater than 50 cm; and (c) mesic or thermic temperature regime. Additional characteristics from geologic data layers or soil series descriptions that were needed for prediction were (a) calcareous parent material; and (b) the presence of small, flat, calcareous rock fragments. Land-cover classification identified optimal habitat for TCH/RP species.

The approach of defining habitats on the basis of soil classification and other spatial information should be effective for other habitats that have strong edaphic constraints. In ecosystems such as old-growth forest or native grassland, in which edaphic constraints are less important than other factors, such as land-use history, additional data coverage would be needed to attain similar accuracy. Disturbance history, such as fire exclusion or grazing, often obscures patterns of historical or optimal habitat distribution. In such instances, and in areas of multiple private ownership with differing histories and uneven sampling of species and habitats, our approach may be particularly useful for conservation planning.

ACKNOWLEDGMENTS

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Appendix 1 Internet websites of the USDA-NRCS used in the research reported in this manuscript:

National Soil Survey Center (links to nsdaf)
  http://www.statlab.iastate.edu/soils/nssc/
National Soil Data Facility
  http://www.statlab.iastate.edu/soils/nsdaf/
  contains links to:
    Soil Survey Data (MUIR)
    http://www.statlab.iastate.edu/soils/muir/
    Official Soil Series Descriptions (OSD)
    http://www.statlab.iastate.edu/soils/osd/
    Soil Series Classification (SC)
    http://www.statlab.iastate.edu/soils/scl
    National Soil Characterization Database (NSSL)
    http://www.statlab.iastate.edu/soils/ssl/
    Published Soil Surveys of the United States
    http://www.statlab.iastate.edu/soils/soildiv/sslistsl
  Soil Geographic Databases (STATSGO)
  http://www.ftw.nrcs.usda.gov/stat_data.html
Keys to Soil Taxonomy
http://www.statlab.iastate.edu/soils/keytax/