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BIOGEOGRAPHY AND DECLINE OF RARE PLANTS IN NEW ENGLAND: HISTORICAL EVIDENCE AND CONTEMPORARY MONITORING

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Abstract. Detecting range shifts and contractions is critical for determining the conservation priority of rare and declining taxa. However, data on rare species occurrences frequently lack precise information on locations and habitats and may present a biased picture of biogeographic distributions and presumed habitat preferences. Herbarium or museum specimen data, which otherwise could be useful proxies for detecting temporal trends and spatial patterns in species distributions, pose particular challenges. Using data from herbaria and Natural Heritage Programs on numbers of occurrences within individual municipalities (towns, cities, or townships), we quantified temporal changes in the estimated distributions of 110 rare plant species in the six New England (USA) states. We used the partial Solow equation and a nonparametric test to estimate the probability of observing multiple absences (gaps in the collection record) if a given population was actually still extant. Bayes' Theorem was used to estimate the probability that occurrences were misclassified as extinct. Using the probabilities obtained from these three methods, we eliminated taxa with high probabilities of pseudo-absence (that would yield an inaccurate profile of species distributions), narrowing the set for final analysis to 71 taxa. We then expressed occurrences as centroids of town polygons and estimated current and historical range areas (extents of occurrence as defined by α-hulls inscribing occurrences), mean distances between occurrences, and latitudinal and longitudinal range boundaries. Using a geographic information system, we modeled first, second, and third circular standard deviational polygons around the mean center of the historical range. Examining the distribution of current occurrences within each standard deviational polygon, we asked whether ranges were collapsing to a center, expanding, fragmenting, or contracting to a margin of the former range. Extant ranges of the species were, on average, almost 67% smaller than their historical ranges, and distances among occurrences decreased. Five New England hotspots were observed to contain >35% of rare plant populations. Extant occurrences were more frequently marginalized at the periphery of the historical range than would be expected by chance. Coarse-grained data on current and historical occurrences can be used to examine large suites of species to prioritize taxa and sites for conservation.

Key words: biogeography; distribution dynamics; GIS; herbarium records; historical plant collections; marginal populations; New England, USA; rare plants; rarity; species range.

INTRODUCTION

It is imperative to understand the current status and distribution of populations of rare species in order to design efficient, large-scale conservation strategies that successfully target the most extinction-prone taxa. To evaluate extinction probabilities of a species, it is also important to gain a sense of how many of its constituent populations have declined or disappeared and how its geographic range may have shifted spatially over time. Great strides have been made recently in developing methodologies for estimating species ranges, particularly GIS-based methods that examine correlations between the known spatial array of populations on a landscape and specific habitat variables that may be predictive of the presence of other, as-yet-undetected occurrences (Scott et al. 2002, Gaston 2003, Rushton et al. 2004). These approaches can be used to generate spatially explicit habitat models based on apparent tolerances and specialization of species. These detailed models have successfully predicted where new species occurrences might be found (Scott et al. 2002, Edwards et al. 2005), have permitted an assessment of bias in former sampling that is manifest in museum and herbarium collections (Ponder et al. 2001, Stockwell and Peterson 2002), and have enabled ecologists to assign confidence levels and assess variance in their estimation of range envelopes (Engler et al. 2004).

However, GIS-based modeling methods depend on the availability of precise and up-to-date locality data for populations, data that are not widely available for many rare species due to both confidentiality issues and

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limitations in field sampling. Such intensive methods are most amenable to analyses of one or a few species at a time. Because the precision of data collection varies markedly among taxa, it is often difficult to examine correlations in distributions among groups of taxa that share either phylogenetic affinities (i.e., clades) or ecological characteristics (i.e., functional groups or "guilds").

Much information on the distribution of species also follows artificial political boundaries; in the United States and Canada, for example, data on specific populations are maintained by state and provincial Natural Heritage Programs and Conservation Data Centres, respectively. Regional or range-wide analyses are constrained and complicated by cross-boundary differences in the quality and intensity of data collection and maintenance (Rodrigues and Gaston 2002).

Likewise, modeling methods are predicated on an assumption that the locations and habitat variables associated with current populations reflect species' inherent habitat preferences, rather than an ecologically more realistic concept that populations are frequently marginalized and thus found in areas that do not represent their adaptive optima. Arguably, rare (regionally or globally listed) species are more frequently confined to suboptimal habitats than are common species (Husband and Barrett 1996, Dorrough and Ash 1999, Lennon et al. 2002). A paucity of autecological and ecophysiological field studies also limits our understanding of the actual factors that limit establishment and persistence (Fertig and Reiners 2002). In addition, these models can be influenced by sampling bias, i.e., roadside surveys (Kadmon et al. 2004) and poor detectability of taxa (G. E. Garrard, S. A. Bekessy, B. A. Wintle, W. T. Langford, and N. A. Baran, *unpublished manuscript*). The reality of the situation is that, for most rare species, we possess scarce data, mostly in atlas form, reflecting imperfect, sporadic, and spatially biased sampling, that describe ranges in a coarse-grained way. Can these data be adapted to enable detection of trends across multiple species?

The present study had three goals. The first objective was to identify a suite of regionally rare plant species in New England (USA) with sufficient town-level occurrence data to permit spatial analyses of their ranges, given a lack of precise locational and habitat information. Using three approaches, one adapted from Bayesian analysis and the others building on methods of Solow (1993), Burgman et al. (1995), McCarthy (1998), Ungricht et al. (2005), and van der Ree and McCarthy (2005), we assessed the level of uncertainty inherent in predicting whether historical occurrences are still extant (given a low frequency of targeted searches for these occurrences). Together, this information allowed us to identify a group of species appropriate for reliably characterizing changes in the estimated distribution of occurrences over time.

Our second objective was to develop a set of GIS-based methods by which to quantify spatial envelopes that broadly described the present and past distributions of extant and "historical" populations (defined by Natural Heritage Programs as occurrences documented in herbarium collections only through 1975) of rare species, respectively. We used both α-hulls (Burgman and Fox 2003) and standard deviational polygons to describe and compare the biogeographic distributions of extant and historical occurrences.

Third, we applied these methods to an analysis of a group of 71 taxa. We asked whether the ranges of the majority of these rare species were contracting to a few central or marginal populations within the region, exploring the potential importance of protecting marginal populations (Lesica and Allendorf 1995, Channell and Lomolino 2000*a*, *b*). We identified regional "hotspots" of threatened species richness (sensu Orme et al. 2005) of extant occurrences of rare plants and examined temporal changes in the locations and fragmentation of these hotspots.

New England is an excellent region in which to conduct these analyses due to: (1) a long history of intensive botanical collection (among the longest and most comprehensive in North America; Mehrhoff [2000]); (2) the existence of a regional network (the New England Plant Conservation Program [NEPCoP]; Farnsworth [2004]) that coordinates ongoing botanical surveys and population monitoring by both professional botanists and trained volunteers; and (3) the recent completion of a project that produced detailed, peer-reviewed Conservation and Research Plans for rare plant species (Brumback et al. 1996, Farnsworth 2003), each of which described town-based presences and absences and moderately detailed information regarding species life history and population status. Although these data are particularly amenable to these types of analyses, we contend that such methods could be widely applied to a variety of data sets, floras, and atlases, as long as the history of collections of, and searches for, particular occurrences is known (Shaffer et al. 1998, Weldy and Werier 2005).

METHODS

The species

The plant species selected for analysis (Table 1) formed a subset of a group of 110 taxa, listed in one or more New England states, and for which a NEPCoP Conservation and Research Plan had been completed between 2001 and 2004 (abridged Plans with extensive background information on each taxon, current to 2004, are *available online*).[4] The Conservation Plan taxa, in turn, had been chosen from the full group of 479 taxa identified in the *Flora Conservanda*: New England (Brumback et al. 1996) as either "state-Endangered/

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[4] ⟨http://www.newfs.org/conserve/plans.htm⟩

Threatened" (337 taxa) or "Rare" (recorded from <20 towns in New England and/or state-listed as Special Concern or S1–S3 using NatureServe [2005] rarity criteria. The project focused on the regionally rarest taxa (*Flora Conservanda* Division 1 or 2, globally or regionally rare; Brumback et al. [1996]).

The set of 110 taxa was further narrowed to 71 to eliminate bias (see *Methods: Sampling bias and the selection of species for analysis*). The 71 taxa belonged to 34 plant families. Of the 34 families, 28 (82%) contained only one or two species, indicating quite even distribution of species among families. The most speciose families analyzed included the Cyperaceae (with 10 species), the Asteraceae (7 species), and the Orchidaceae (7 species). Habitat affinities and ecological affiliations varied widely among species within these clades. When we removed the most speciose clades of related species from the analyses, all trends and statistical significance remained unchanged. Therefore, we concluded that minimal phylogenetic bias was present in the data, and for the purposes of this analysis, we treated taxa as phylogenetically independent units (Harvey and Pagel 1993).

These taxa ranged across an average of 26.6 states and provinces (data compiled from NatureServe 2005), with a mean approximate range area in North America (calculated from state and provincial areas) of 5.8×10^6 km^2 ($\pm 4.5 \times 10^5$ SE). They were recorded as extirpated (ranked SX or SH via NatureServe criteria) in an average of 2.1 states and provinces (a mean of 8.2% of total range). They were listed as critically imperiled (S1 or S2) in an average of 7.8 states and provinces (33.7% of total range). These taxa received the majority of "secure" rankings (S5) in the Midwestern and Appalachian states (Illinois, Michigan, Indiana, Kentucky, Wisconsin, Ohio, Minnesota, Missouri, Virginia, Tennessee, Georgia, Iowa, West Virginia, Arkansas, Pennsylvania) and Ontario. A majority of the species reached either the northern (44.2% of taxa) or southern (26.9% of taxa) boundary of their North American range in New England. Collectively, this suite of species consisted of taxa that were "sparse" (characterized by small populations in a limited number of habitats throughout the range), "endemic" (locally abundant or sparse in a narrow range of habitats and a geographically restricted range), or "predictable" (specialized to a particular habitat throughout the range) in the classification developed by Rabinowitz (1981).

Data on the town-level location of each known extant and historical occurrence of each species (current to 2004) were made available by the Natural Heritage Programs of all six New England states and by the Herbarium Recovery Project of the New England Wild Flower Society (an exhaustive review of all New England herbarium records for all *Flora Conservanda* taxa). For each occurrence, we analyzed the following information: (1) year(s) in which the occurrence was observed or searched for, and (2) town(s) in which the occurrence was located. Because these elementary data are available for many species in atlas form, we sought to develop analytical methods that could be applied to a range of taxa in the future.

Sampling bias and the selection of species for analysis

The final group of 71 species was selected using probabilities calculated from the partial Solow equation (sensu McCarthy [1998]). Solow's equation (Solow [1993]; as modified by Burgman et al. [1995]) estimates the probability that an observed run of absences would be obtained if a given population were still extant. In other words, the original Solow equation estimates how "overdue" the collection of a specimen is for a taxon; if collections are highly "overdue" relative to past collection patterns, a high degree of threat or probability of extinction of the taxon is inferred (McCarthy 1998, Ungricht et al. 2005). The equation is based on the frequency of museum/herbarium records collected between the first and most recent observations of a species. However, because collection effort usually is not constant over time, the partial Solow equation accounts for periods of time in which records are absent due to sampling bias. Let the number of collections in any given time interval, i (in this case, in units of years), be e_i. The probability that a taxon is still present at a locality is given as

$$P = \left(\sum_{i=1}^{t} e_i \Big/ \sum_{i=1}^{T} e_i \right)^n$$

where a taxon has been recorded n times between the start of the assessment period (year of first observation of the occurrence) and t, the time at which the occurrence was last recorded; T marks the year of last observation of the taxon as a whole. If the taxon has been positively recorded in the most recent assessment year, $P = 1$; P approaches 0 if every occurrence has been confirmed as extirpated. Conversely, small values of P indicate a low probability that the observed pattern of zeroes (years with no collections) would be seen if a population were still extant. Although the partial Solow equation typically has been applied to estimate extinction probability of taxa, we applied it to assess the probability of redetecting a particular occurrence of a taxon, given a known collection effort for the taxon as a whole in New England. This enabled us to estimate the probability of observing a pattern of absences if any given "historical" occurrence (usually ranked "H" by the relevant state's Natural Heritage Program) were actually still extant.

Solow and Roberts (2003) provide an alternative nonparametric test that does not make assumptions about collection effort. P is calculated as the ratio of the time interval between the most recent sighting (t, as previously defined) and the second-most recent sighting (t_{n-1}), to the time interval between the most recent

TABLE 1. List of 71 New England rare plant taxa analyzed.

Species	Family	Solow probability of pseudo-absence	Total occurrences lost (%)
Agastache scrophulariifolia (Willd.) Kuntze	Lamiaceae	0.34	94.4
Ageratina aromatica (L.) Spach	Asteraceae	0.21	87.5
Amerorchis rotundifolia Banks	Orchidaceae	0.05	50.0
Aplectrum hyemale (Muhl.) Torr.	Orchidaceae	0.29	84.8
Aristolochia serpentaria L.	Aristolochiaceae	0.12	52.0
Asclepias purpurascens L.	Asclepiadaceae	0.43	94.2
Bouteloua curtipendula (Michx.) Torr.	Poaceae	0.11	42.9
Calystegia spithamaea (L.) Pursh	Convolvulaceae	0.27	83.2
Carex davisii Schwein. & Torr.	Cyperaceae	0.22	55.6
Carex garberi Fern.	Cyperaceae	0.09	18.4
Carex lupuliformis Sartwell	Cyperaceae	0.09	16.2
Carex polymorpha Muhl.	Cyperaceae	0.19	50.0
Carex wiegandii Mackenzie	Cyperaceae	0.15	36.4
Castilleja coccinea (L.) Sprengl.	Scrophulariaceae	0.42	91.9
Chamaelirium luteum (L.) A. Gray	Liliaceae	0.19	74.4
Cynoglossum virginianum L. var. *boreale* (Fern.) Cooperrider	Boraginaceae	0.39	79.5
Cyperus houghtonii Torr.	Cyperaceae	0.06	51.5
Desmodium cuspidatum (Muhl.) Loudon	Fabaceae	0.27	90.2
Doellingeria infirma (Michx.) Greene	Asteraceae	0.12	85.0
Draba reptans (Lam.) Fern.	Brassicaceae	0.23	69.6
Eriocaulon parkeri Robinson	Eriocaulaceae	0.06	28.8
Floerkea proserpinacoides Willd.	Limnanthaceae	0.03	54.5
Goodyera oblongifolia Raf.	Orchidaceae	0.06	33.3
Hackelia deflexa (Wahlenb.) Opiz var. *americana* (A. Gray) Fern.	Boraginaceae	0.06	17.4
Hydrastis canadensis L.	Ranunculaceae	0.15	50.0
Hydrophyllum canadense L.	Hydrophyllaceae	0.28	37.5
Hypericum adpressum Barton	Clusiaceae	0.22	36.4
Juncus torreyi Cov.	Juncaceae	0.12	31.3
Juncus vaseyi Engelman.	Juncaceae	0.30	57.1
Liatris scariosa (L.) Willd. var. *novae-angliae* Lunell	Asteraceae	0.17	57.5
Liparis liliifolia Rich.	Orchidaceae	0.16	83.2
Listera auriculata Wieg.	Orchidaceae	0.21	64.9
Ludwigia polycarpa Short & Peter	Onagraceae	0.11	43.8
Ludwigia sphaerocarpa Elliott	Onagraceae	0.16	50.0
Lycopodiella alopecuroides (L.) Cranfill	Lycopodiaceae	0.17	63.2
Mimulus moschatus Douglas	Scrophulariaceae	0.11	27.3
Nabalus racemosus (Michx.) Hook.	Asteraceae	0.02	11.1
Nabalus serpentarius Pursh	Asteraceae	0.23	86.7
Neobeckia aquatica (Eaton) Greene	Brassicaceae	0.12	66.7
Nymphaea leibergii Morong	Nymphaceae	0.00	10.0
Oligoneuron rigidum (L.) Small var. *rigidum*	Asteraceae	0.13	86.0
Oxalis violacea L.	Oxalidaceae	0.14	66.7
Oxytropis campestris (L.) DC var. *johannensis* Fern.	Fabaceae	0.13	50.0
Paronychia argyrocoma (Michx.) Nutt.	Caryophyllaceae	0.14	9.1
Pedicularis lanceolata Michx.	Scrophulariaceae	0.32	87.5
Piptatherum canadense (Poir.) Dorn.	Poaceae	0.24	54.5
Platanthera ciliaris (L.) Lindl.	Orchidaceae	0.19	72.9
Polymnia canadensis L.	Asteraceae	0.00	75.0
Populus heterophylla L.	Salicaceae	0.25	77.4
Potamogeton ogdenii Hellquist & Hilton	Potamogetonaceae	0.05	58.8
Potamogeton strictifolius Ar. Benn.	Potamogetonaceae	0.07	22.9
Pterospora andromedea Nutt.	Pyrolaceae	0.13	70.0
Rhynchospora capillacea Torr.	Cyperaceae	0.07	33.3
Rhynchospora inundata (Oakes) Fern.	Cyperaceae	0.01	7.7
Rosa acicularis Lindley ssp. *sayi* (Schwein.) W. H. Lewis	Rosaceae	0.35	45.5
Rotala ramosior (L.) Koehne	Lythraceae	0.11	64.0
Sabatia stellaris Pursh.	Gentianaceae	0.18	58.8
Salix myricoides (Muhl.) J. Carey	Salicaceae	0.00	25.0
Saururus cernuus L.	Saururaceae	0.00	78.9
Scirpus longii Fern.	Cyperaceae	0.01	13.2
Scleria triglomerata Michx.	Cyperaceae	0.09	81.6
Senna hebecarpa (Fern.) Irwin & Barneby	Fabaceae	0.38	92.8
Silene stellata (L.) Aiton f.	Caryophyllaceae	0.45	94.1
Sphenopholis nitida (Biehler) Scribn.	Poaceae	0.29	85.5

TABLE 1. Continued.

Species	Family	Solow probability of pseudo-absence	Total occurrences lost (%)
Sporobolus compositus (Poir.) Merr. var. *compositus*	Poaceae	0.19	40.5
Sporobolus heterolepis A. Gray	Poaceae	0.00	20.0
Taenidia integerrima (L.) Drude	Apiaceae	0.25	60.0
Triphora trianthophora (Swartz) Rydb.	Orchidaceae	0.16	41.0
Valeriana uliginosa (T. & G.) Rydb.	Valerianaceae	0.09	22.2
Verbena simplex Lehm.	Verbenaceae	0.43	92.3
Zizia aptera (A. Gray) Fern.	Apiaceae	0.18	62.5

Notes: Techniques for calculating Solow probabilities are described in *Methods: Sampling bias and the selection of species for analysis*. The percentage of total occurrences lost is calculated from the ratio of the number of confirmed, extant occurrences over the total number of separate occurrences ever documented in the region.

sighting and the end of data collection (T as previously defined), namely,

$$P = (t - t_{n-1})/(T - t_{n-1}).$$

The partial Solow and nonparametric probabilities gave similar results, although the nonparametric equation returned probabilities that were consistently lower for each species than the partial Solow probabilities (the latter are reported in Table 1). The P given by the partial Solow was 0.16 ± 0.01 (mean ± CV; range 0–0.454, skewness 0.61; $N = 71$ taxa). The P for the subset of 61 species for which the nonparametric P could be calculated was 0.096 ± 0.01 (mean ± CV). Van der Ree and McCarthy (2005) also use a Bayesian method to calculate the posterior probability of an occurrence still being extant. The P values that we calculated using this metric were significantly correlated with the P values obtained from the other two methods ($0.38 < r^2 < 0.56$; $0.0000031 < P < 0.003$) and gave an overall mean < 0.5. However, for our purposes, this method was found to be insensitive when total collections for a species were below 100 (the case for several of the taxa studied here).

Taxa for which the set of "historical" occurrences had a mean $P > 0.5$ (a 50% probability of being rediscovered) were viewed as potentially subject to high bias in our estimates of current and historical ranges. Because these taxa had potentially high percentages of "pseudo-absences" sensu Engler et al. (2004), we could not be confident that their so-called "historical" occurrences could be considered as truly nonextant. On this quantitative basis, as well as prior knowledge of poor collection history or taxonomic uncertainty in certain taxa (noted in the Conservation and Research Plans), we eliminated 39 of the original 110 taxa, leaving a total species sample size of 71. For this subset of species, neither the partial Solow probability nor the nonparametric probability was correlated with the response variables that we tested (range area, percentage loss of occurrences, and distance between occurrences).

We also used Bayes' Theorem to refine our estimate of uncertainty in the distribution of extant occurrences of the 71 chosen taxa. Let H be the event that a town contains an historical record of a rare taxon and C the event that a town contains an extant occurrence corresponding to that record (their complements, whereby a town contains no historical record or no extant occurrence, are denoted H^c and C^c, respectively). We sought to calculate $P(C|H)$, the probability that a town still has an extant occurrence, given the existence of an historical record. Bayes' Theorem stipulates that:

$$P(C|H) = \frac{P(H|C) \times P(C)}{P(H|C) \times P(C) + P(H|C^c) \times P(C^c)}.$$

We calculated the following probabilities (Sokal and Rohlf 1995): (1) "sensitivity," $P(H|C)$, the probability that an historical (1975 or earlier) record exists, given an extant population; (2) "prevalence," $P(C)$, the proportion of all New England towns with one or more extant rare plant occurrences; (3) the number of "false positives" $P(H|C^c)$, i.e., historical records that erroneously identified species as extant in towns when in fact they were not; (4) the remaining term, $P(C^c) = 1 - P(C)$.

From Conservation Plans and data compiled from the Herbarium Recovery Project (N = 16 834 records examined), we calculated the following maxima for these probabilities as: (1) sensitivity = 0.188 (18.8% of extant occurrences are associated with a pre-1975 record); (2) prevalence = 0.005 (each rare taxon occupies, on average, 0.5% of the 1984 New England towns); (3) false positives = 0.068 (1145 of 16 834 records (6.8%) had been previously misidentified by the collector.

Using these estimates in Bayes' Theorem, we calculated the probabilities that all botanical searches (whether targeted or not) would yield an extant occurrence, given the existence of an historical record. The maximum probability of an occurrence being extant, given an historical record, was 0.013. This estimate accorded in order of magnitude with a probability of rediscovery calculated simply from the number of searches made by trained botanists for "historical" occurrences in New England (120) and the number of successful rediscoveries (3) documented in the element occurrence data for the 71 species: 0.025. Thus, all methods returned very small probabilities of pseudo-absences, increasing our confidence that we had an accurate account of the distribution of extant occurrences.

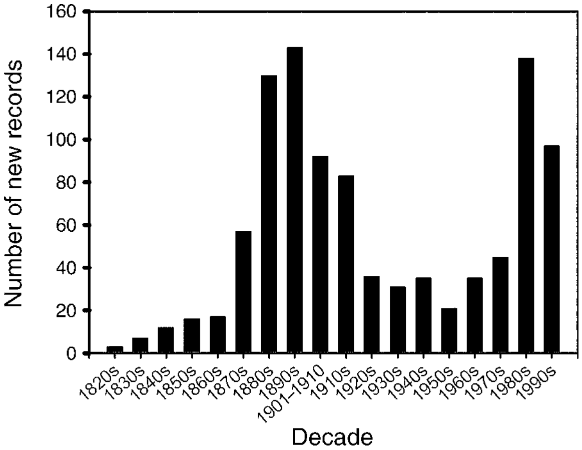

FIG. 1. Temporal trends in collections documenting newly discovered populations of the 110 rare plant species covered in the NEPCoP (New England Plant Conservation Program) Conservation and Research Plans. Data are based on year of "first observation" of an occurrence, as recorded in Natural Heritage Program databases.

Botanical collection has been intensive throughout New England since the early 1800s (Mehrhoff 2000) and herbarium records have been used with success to detect phenological and biogeographic trends (Primack et al. 2004), with distinct peaks in detection of "new" plant occurrences during the Victorian era and in the 1980s following the formation of the Natural Heritage Program network (events that spurred both searches for previously documented populations and new botanical inventories; Fig. 1). These temporal patterns of collection have been nearly identical in all six New England states ($0.616 < r < 0.965$ for correlations among all possible pairs of states of collections per decade from 1820 to 2000), indicating minimal latitudinal or longitudinal bias in sampling intensity.

Estimating historical and current ranges

Town- and township-level occurrences were recorded for each species on a base map of the six New England states (data layer obtained from MassGIS, *available online*).[5] The occurrences were georeferenced in the Massachusetts State Plane coordinate system, Mainland zone (FIPSzone 2001), and were tied to the North American datum of 1983 (NAD83) using ArcGIS 9 software (ESRI 2002). All units were in meters. Centroids were generated for each New England town, corresponding to the geometric center of the polygon inscribing the town boundary. With the coordinates of centroids corresponding to each occurrence, we created contour plots of threatened species richness across the New England landscape using SigmaPlot 9.0 (SigmaPlot 2005); we employed nearest neighbor smoothing to estimate contours. We computed Euclidean distances (Crawley 2002) among all possible pairs of centroids within sets of historical and extant occurrences within species, and compared the mean distance among historical occurrences with the mean distance among extant occurrences. A polygon corresponding to the α-hull of the centroid distribution (sensu Burgman and Fox 2003) was constructed using a script in S-Plus kindly provided by M. A. Burgman. This polygon was used as a proxy for range area of each taxon within New England, and has been demonstrated to more conservatively and successfully estimate a species' range than conventional convex polygons (e.g., Kaluzny et al. 1996). Occasionally, this method can exclude outlying occurrences and thus underestimate a range (Getz and Wilmers 2004); however, this was not the case with the taxa that we studied. Although such polygons were likely to overestimate the actual land area occupied by each species (because populations do not occupy all points in space and insufficient habitat-specific information existed to refine the exact range boundaries), they served as relative measures for comparing extant and historical ranges within taxa.

Using the spatial distribution of historical occurrences, we calculated the location of the weighted mean center (ESRI 2002) of each species' range: namely, the point that corresponded to the average x-coordinates and the average y-coordinates of all occurrences of each species. This weighted measure of the spatial central tendency of the species' distribution accounted for multiple as well as single occurrences in each town. Employing the standard distribution tool in the ArcGIS ArcToolbox, we then generated circular standard deviational circular polygons around each species' historical mean center. One standard deviational radius covered >60% of the centroids in the cluster, the second encompassed >95% of the centroids, and the third captured >99% of the centroids (ESRI 2002). We overlaid the set of extant occurrences on this background setting of historical range and determined how many extant occurrences currently fell in the first, second, and third standard deviational shells of the historical range. This analysis enabled us to detect what percentage of species had extant populations that occurred in the center or the margin of the former range. This method built quantitatively on the Index of Centrality computed by Channell and Lomolino (2000*a*, *b*) for 245 rare species, but incorporated spatial weighting of clustered historical occurrences in characterizing the former range.

RESULTS

Changes in numbers of occurrences and ranges over time

The majority of the 71 species comprised fewer extant occurrences now than had been historically documented, indicating a significant loss of populations over time (Tables 1 and 2; Wilcoxon signed-rank test; $Z = 3.23$; $P = 0.0012$). On average, each rare taxon had 13 extant occurrences region-wide, compared to a mean of 26

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[5] ⟨http://www.massgis.com⟩

TABLE 2. Summary of variables (mean with SE in parentheses), including occurrences, range size, distance between occurrences, and losses for 71 rare plant species in New England, comparing historical (pre-1975) and extant (confirmed since 1976) distributions.

Variable	Extant	Historical
Number of occurrences recorded per taxon	13.0 (1.5)*	26.2 (3.3)
Range size (km^2) (area of α-hull inscribing centroids)	15 985 (2624)*	24 845 (3157)
Distance between occurrences (km)	97.4 (6.6)*	109.1 (6.5)
Percentage of historical occurrences lost	55.9 (3.1)	
Percentage loss of range area	66.9 (3.4)	
Latitude of mean center of range (MA State Plane)	983251 (22631)*	964317 (21970)
Position of northernmost latitude (MA State Plane)	1078509 (25653)	1078648 (22796)
Position of southernmost latitude (MA State Plane)	881109 (15628)	867366 (19264)

Notes: Asterisks indicate significant differences between extant and historical response variables at $P < 0.05$ (see *Results* for statistical analyses). Data registered to the Massachusetts State Plane Coordinate System are in Mainland Zone meters (FIPSzone 2001): projection, Lambert conformal conic; spheroid, GRS 80; central meridian –71.5; reference latitude 41; standard parallel 1, 41.71667; standard parallel 2, 42.68333; false easting 200000; false northing 750000.

separate populations recorded from herbaria (Table 2). These differences were significant even when the number of extant populations was recalculated conservatively to include all possible pseudo-absences using the partial Solow probabilities obtained for each species (Wilcoxon signed-rank test; $Z = 2.04$; $P = 0.041$). The percentage of occurrences lost in New England states was positively correlated with the number of state-level extinctions (SH rankings) reported throughout the range ($r^2 = 0.16$; $P = 0.0006$, $N = 71$ species), indicating that regional rarity was loosely associated with range-wide imperilment. Similarly, across New England, 585 towns reported historical occurrences of taxa, whereas only 425 (73%) reported extant occurrences.

Range area estimated from α-hulls was positively correlated with numbers of occurrences ($r^2 = 0.212$, $P < 0.0001$), and thus followed a similar temporal trend; the range area covered by extant occurrences was significantly (66.9% ± 3.4%, mean ± SE; Table 1) smaller than that of the historical range area (Table 2; paired *t* test by taxon on square-root transformed values of range area, $t_{70} = 4.38$, $P < 0.0001$).

The number of extant occurrences was positively correlated with the number of occurrences recorded historically ($r^2 = 0.55$, $P < 0.0001$), and the extant range area was correlated with the historical range area ($r^2 = 0.34$, $P < 0.0001$). Thus, the species that historically exhibited comparatively large ranges and numbers of populations continued to do so relative to taxa with smaller ranges and numbers of populations.

The mean linear distance separating all occurrences within each taxon decreased significantly over time; that is, extant occurrences were separated by smaller distances than historical occurrences (Table 2; paired *t* test on log-transformed distance in kilometers, $t_{70} = 2.79$, $P = 0.007$).

Clusters of extant occurrences were largely restricted to a handful of species-rich centers, namely the Berkshire Highlands, Lake Champlain valley, Cape Cod, Rhode Island south shore and the islands, St. John and Allagash River valleys, and the White Mountains (Fig. 2). These "hotspots" (sensu Flather et al. 1998, Orme et al. 2005) also historically encompassed high richness of rare species. However, richness historically was more evenly distributed throughout a larger percentage of the region; thus connectivity among hotspots was higher than it is today (Fig. 2). Together, the five current hotspots encompassed ~37% of extant occurrences in New England (analysis of 926 occurrences).

The mean centers of the New England ranges of the 71 taxa showed significant temporal shifts in latitude, but not longitude (Table 2). The mean centers of extant occurrences were located significantly farther north than those of historical occurrences (paired *t* test on normally distributed latitude coordinates, $t_{70} = 2.46$, $P = 0.017$). The maximum (northernmost) latitude did not differ significantly among historical and extant distributions (by paired *t* test on log-transformed data; Table 2), indicating that extant occurrences were not occupying higher latitudes than historical occurrences. Because northernmost occurrences could extend into Canada, for which we had no data on distributions, we circumscribed the data set to include only 16 species with no known occurrences north of New England; we obtained the same nonsignificant result ($t_{15} = 1.21$, $P = 0.24$). In contrast, the southernmost extant occurrences were located north of the southernmost historical occurrences, indicating a disproportionate loss of populations at the southern latitudes of New England. Although these latitudinal differences were not significant at the $P = 0.05$ level (Table 2; paired *t* test on log-transformed data, $t_{70} = 1.89$, $P = 0.0625$), 46 of 71 taxa showed a northward shift of the southernmost occurrence, a proportion greater than that expected by chance (exact binomial test, $P = 0.017$). Across all taxa, mean center locations shifted an average of 68 ± 7 km (mean ± SE), with 80% of the taxa having shifted <100 km. Connecticut hosted the largest number of extant mean centers (23 of 71 species), followed by Massachusetts (15 species) and Maine (12 species), closely paralleling the distribution of historical mean centers.

Analyses of the placement of extant occurrences relative to the first, second, and third circular standard deviational polygons inscribing the historical mean center indicated that a significantly larger percentage of extant occurrences now occupied the third standard

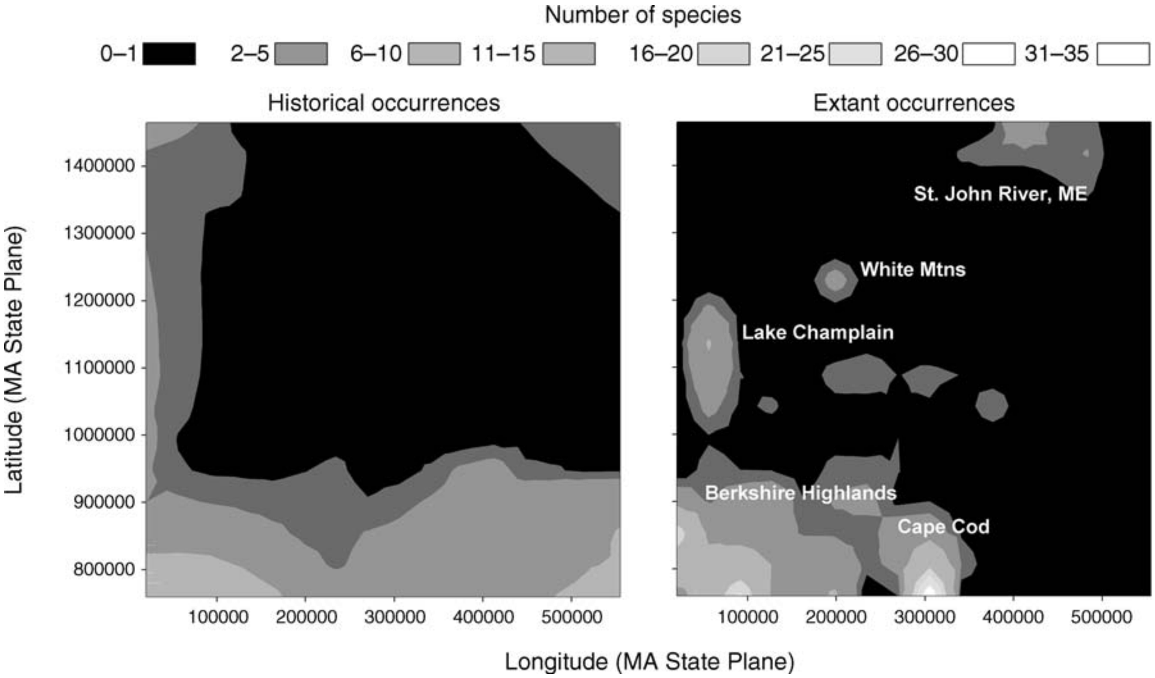

FIG. 2. Contour plot of species richness across New England. Contour shades correspond to the number of species, smoothed in one-species intervals across MA (Massachusetts) State Plane coordinates (units are meters; see the MassGIS web site ⟨http://www.mass.gov/mgis/dd-over.htm⟩). Particularly diverse geographic localities in New England are labeled in the right panel.

deviational polygon (Fig. 3; $t_{70} = 3.17$, $P = 0.0023$). Conversely, a significantly smaller percentage of extant occurrences were found within the first standard deviational radius inscribing the historical range (Fig. 3; paired *t* test on normally distributed data; $t_{70} = 3.06$, $P = 0.0031$). Together, these findings indicated that a large number of occurrences were now occupying the margins of the former species ranges. Of the 50 taxa exhibiting shifts toward the range margin, six (*Bouteloua curtipendula, Liparis liliifolia, Paronychia argyrocoma, Potamogeton strictifolius, Saururus cernuus*, and *Sporobolus compositus*) were undergoing true fragmentation, that is, splitting into two or more clusters with higher than expected numbers of occurrences in both the first and third standard deviational polygons.

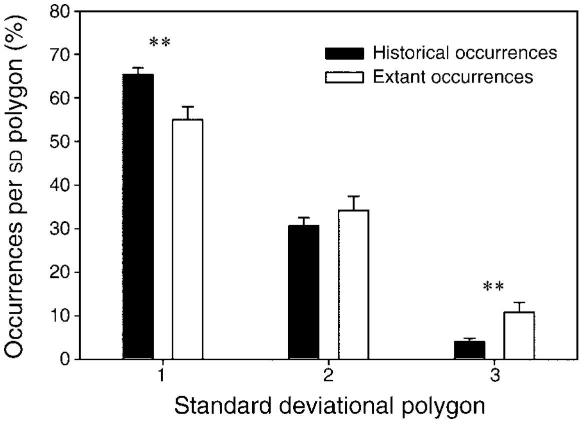

FIG. 3. Comparison of the placement of extant and historical occurrences relative to the circular standard deviational polygons around the historical mean center. Shown are mean (+SE) percentages of historical and extant occurrences per taxon falling within each standard deviational shell. Asterisks indicate significant differences between the percentage of extant and historical occurrences in each shell (paired *t* tests on normally distributed data within taxa and shells, $P < 0.004$ for shells 1 and 3).

DISCUSSION

Data on multiple species made available by recent thorough herbarium searches (Fig. 1) and field monitoring coordinated through the New England Plant Conservation Program (Farnsworth 2004) are useful for understanding the dynamics of the regional flora of northeastern North America. Furthermore, our low estimated probabilities of pseudo-absence indicate that we have a reliable, relatively unbiased estimation of the actual geographic distribution of these taxa in New England. We were able to sensitively detect shrinkage, broad latitudinal shifts, and fragmentation of species' ranges. Such methods could be applied to analogous data sets with coarse-grained information on search histories and localities of taxa available from atlases and Natural Heritage databases. Our findings help to identify several species in the region that merit urgent conservation attention and to direct land managers to focus their efforts in the remaining hotspots of New England. Furthermore, because New England shares many of these rare species with other biomes of North

America (Crins 1997, NatureServe 2005), these results have implications for conservation practices throughout a broad geographical area.

We caution that town-level coverages of species occurrences cannot provide a precise estimate of the actual distribution of plants on the landscape. Populations, especially those of rare species, are arrayed patchily in space, and their past and present biogeography is shaped by habitat preferences, manipulation of ecosystems by humans, dispersal constraints, and random events. Polygons and standard deviational polygons are simplified means of characterizing complex distributional patterns, but represent some of the only analytical tools available in the absence of fine-scale data on occurrences. Thus, we must interpret our comparisons of extant and historical range envelopes ("extents of occurrence" sensu Kunin and Gaston [1997]) as relative, rather than absolute, measures.

Four major patterns emerge from these analyses. First, the New England ranges of the 71 taxa have significantly contracted (by an average of 67%) and the number of extant occurrences per taxon is approximately one-half the number of historical occurrences (Tables 1 and 2). This finding underscores the magnitude of the decline in New England and the urgent need for conservation measures to stem further losses (Brumback et al. 1996). Several species (including *Agastache scrophulariifolia, Asclepias purpurascens, Silene stellata, Senna hebecarpa, Verbena simplex, Castilleja coccinea*, and *Desmodium cuspidatum*) have lost >90% of their historical populations, and the majority (46 species) have lost >50% (Table 1). Quantifying losses across these species enables them to be ranked more precisely in terms of their need for region-wide conservation action.

Second, the mean distances separating extant occurrences are now smaller than those that formerly separated historical occurrences (Table 2), indicating that current populations within species are now more tightly clustered than they once were. As a consequence, clusters of occurrences may be vulnerable to stressors or disturbances that operate on small-to-intermediate spatial scales. Related to this pattern, occurrences now occupy a limited set of recognizable hotspots in New England (Fig. 2), punctuated by regions with few rare species. These hotspots have long attracted the attention of both botanists and regional conservation organizations in planning for surveys and for land protection (e.g., Mehrhoff 1989, Sorrie 1989, Vickery et al. 1989). They include the calcareous marble valleys and pre-Cambrian schist uplands of the Berkshire/Taconic region and Lake Champlain valley; the subalpine and alpine elevations of the White Mountains; the coastal outwash plains and terminal moraines of southern New England; and the St. John and Allagash watersheds of northern Maine. These hotspots have, until recently, remained relatively remote from human development, although the southern coastal plain and western border of New England are increasingly at risk of alteration. Many of these hotspots afford relictual habitat for species that were once more common following on the heels of Pleistocene deglaciation and during the Hypsithermal warming interval (Miller 1989, Spear et al. 1994). The fact that these hotspots now contain over one-third of the known extant populations of the rare plants studied confirms that conservation efforts should continue to focus on these botanically rich and unusual areas.

Third, significantly higher percentages of rare plant occurrences now occupy the margin of their former ranges, in this case expressed as the third standard deviational polygon around the historical mean center of each species (Fig. 3). This pattern accords with previous observations by Channell and Lomolino (2000*a*, *b*) that many rare species are becoming confined to the periphery of their historical ranges, and highlights the importance of range margins as potential refugia for declining species and harbors of genetic diversity (Lesica and Allendorf 1995, Lomolino and Channel 1998). An examination of the taxa undergoing marginalization indicates that the process appears to be driven by two main phenomena: (1) the loss of populations from heavily populated New England towns, particularly in the south, due to habitat conversion (e.g., *Asclepias purpurascens, Castilleja coccinea, Desmodium cuspidatum, Polymnia canadensis, Saururus cernuus, Liparis liliifolia, Lycopodiella alopecuroides*); and (2) the appearance of new populations (or at least new collections) of a taxon that lie on the fringes of the former range (e.g., *Carex davisii, Mimulus moschatus, Scirpus longii, Valeriana uliginosa, Populus heterophylla, Lycopodiella alopecuroides*). (Likewise, a few other species, confined to large, discrete river systems such as the Connecticut River or the St. John, are inherently likely to show disjunct distributions.) Note that these processes are not mutually exclusive within a given taxon. Thus, the pattern of marginalization does not necessarily indicate greater persistence or potential resilience of outlying populations; rather it may reflect that existing populations have (to date) escaped anthropogenic threats and/or that populations are actively colonizing new sites. Outlying populations may be disproportionately vulnerable to extinction due to their relative isolation and occupancy of suboptimal habitats (Lawton and May 1995, Nathan et al. 1996, Rosenzweig and Lomolino 1997, Lennon et al. 2002); nevertheless, these peripheral populations now represent a tenuous, but critical, foothold for these species in New England.

A fourth and related pattern is apparent in the northward shift in the mean centers of the majority of taxa. This phenomenon occurs in species that reach their northern or southern range limits in New England, as well as those with the heart of their range in northeastern North America. This shift does not appear to be attributable to a northward colonization of new populations at the northern edge of the species' ranges (Table 2), as might be expected under current conditions of warming climate in New England (New England Regional Assessment 2001, Walther et al. 2002). Although it is possible that Canadian occurrences are showing northward shifts that we could not detect, northward shifts were not observed among species reaching the northern edge of their range in New England. Rather, the mean center shift is due primarily to high losses of populations that once occupied southern New England. Connecticut, Massachusetts, and Rhode Island have undergone intense urbanization and habitat conversion, and, on average, support >10 times the human population density (people per square kilometer) of Maine, New Hampshire, and Vermont (U.S. Census Bureau data, *available online*).[6] Thus, local extirpation of plant occurrences has been frequent and largely permanent. Although the northern latitudes of New England have been subject to widespread logging and landscape manipulation, they are important refugia for the rare plant species that once extended throughout the region and warrant increased attention for conservation and prudent land management. However, it is important to recognize that the remaining southern populations could form essential "rear guards" of genetic diversity with possible temperature tolerances that may become increasingly adaptive as climatic change proceeds (Hampe and Petit 2005).

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