Plant life history traits of rare versus frequent plant taxa of sandplains: Implications for research and management trials

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A B S T R A C T

I apply a comparative, functional group approach to coastal sandplain grassland taxa in order to examine whether rare plant species share certain aspects of rarity and life history characters that are distinct from their more common, co-occurring congeners in these habitats. I compiled a comparative data set containing 16 variables describing biogeographic distributions, level of imperilment, habitat specialization, vegetative versus sexual reproduction, seed dispersal, and dormancy of 27 closely-related pairs of plant species that contrast in their abundance (infrequent versus common) in coastal sandplain grasslands. Frequent and infrequent species were paired within genera (or closely related genera) and thus distributed equivalently across families to control for phylogenetic bias. Paired comparisons revealed that infrequent species were intrinsically rarer range-wide, and exhibited a narrower range and more habitat specialization than their common relatives. A classification tree distinguished infrequent species from common species on the basis of higher habitat specialization, larger seed size, smaller plant height, less reliance less on vegetative (colonial) reproduction, and tendency toward annual or biennial life history. Research and management steps to reduce competition from larger-satured, colonial, perennial species are recommended for these infrequent species. Basic research involving more species and more data on ecophysiological characters, demography, and competitive interactions are needed to identify critical life history traits that will influence responses to particular management regimes.

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1. Introduction

It is challenging to design effective management strategies that foster the survival of several rare species simultaneously (Groves, 2003; Pärtel et al., 2005). Taxa can differ widely in their apparent habitat "preferences," their vulnerability to competition and other threats, and fundamental aspects of their life histories; hence, they may respond in contrasting ways to management activities. However, the comparative method can be a useful approach for detecting commonalities and differences among species (Harvey and Pagel, 1993; Kunin and Gaston, 1997; Bevill and Louda, 1999). Using systematic

comparisons, species can be categorized conceptually into functional groups on the basis of shared traits and responses (Gitay and Noble, 1997). Suites of species can thus be identified that will respond predictably and similarly to particular types of environmental manipulation.

Likewise, large numbers of species can be grouped and studied separately based on the degree of rarity and severity of range restriction they exhibit. Globally-rare taxa may exhibit certain traits that consistently distinguish them from taxa that are regionally rare but globally secure (Kunin and Shmida, 1997; Pärtel et al., 2005). Several multi-species studies of national or regional floras identify and prioritize groups of

species based on range-wide versus localized rarity patterns (e.g., Schnittler and Günther, 1999). These are useful for pinpointing species that are intrinsically rare throughout their range ("naturally rare" in the parlance of Pärtel et al., 2005) and those that may be declining due to more local, usually human-imposed, causes that may be addressed with prudent management. However, consistent data that allow for in-depth comparisons of many autecological features across species are very scarce (Bevill and Louda, 1999). While some studies have identified certain reproductive or life-history traits that are associated with species of particular rarity types (e.g., Kunin and Shmida, 1997; Pilgrim et al., 2004), others have not discovered patterns that meaningfully inform management (Lozano et al., 2003).

In inland grassland ecosystems, the functional group concept has been useful for understanding species sorting and niche-partitioning along environmental gradients (Tilman and Wedin, 1991) and for predicting patterns of invasibility (Symstad, 2000). Functional group approaches also have been applied successfully in tailoring specific management regimes for particular groups of grassland plants, particularly in Europe (Kleyer, 1999; Cousins et al., 2003; Kühner, 2004) and Australia (McIntyre et al., 1995). Despite the demonstrated utility of these methods, these concepts have not been used to date to inform rare species research and conservation in North American coastal sandplain grasslands, which share similar ecological characteristics – including droughty soils and a propensity for burning – with other types of grasslands.

Instead, rare plant species of coastal sandplains typically have been studied singly, with careful autecological observations made about their life history and responses to disturbance (Lamont et al., 1988; Dunwiddie, 1990; Vickery, 2002; Martine et al., 2005). These are extremely valuable data, but do not by themselves necessarily yield insights into multi-species management. Only rarely have suites of rare species been studied together in order to detect commonalities in habitat preferences (Clarke and Patterson, this issue). From a different angle, phytosociological studies have revealed distinct species assemblages within coastal sandplain grasslands, their affinities with certain soil types, and their successional relationships (Harper, 1905; Conard, 1923; Wells and Shunk, 1931; Latham, 2003; Dunwiddie et al., 1996; Goebel et al., 2001; Jordan et al., 2003); these studies occasionally make reference to rare species, from which we can glean more information. Finally, there is a growing collection of published and unpublished studies about the generalized effects of particular management techniques (particularly grazing, mechanical clearing, fire, and the interaction between the three) on common and widespread species of grassland ecosystems (Niering and Dreyer, 1989; Dudley and Lajtha, 1993; Kimball et al., 1995; Vickery and Dunwiddie, 1997; Dunwiddie, 1998; Little, 1998). A few studies from coastal sandplains do group common species according to life form, and find telling differences in the responses of graminoids, forbs, and shrubs to mowing versus burning (Dunwiddie and Caljouw, 1990; Dunwiddie et al., 1996). Can we synthesize data from these varied studies to identify and compare functional groups of species that may respond favorably to particular management regimes?

In this review, I use multi-variate analyses of a data set that brings together information on biogeography, habitat breadth, rarity, and life history characters of 27 congeneric or closely-related pairs of "infrequent" and "common" species found primarily in coastal sandplain grassland habitats. I define "infrequent" plants in the context of this study as species that are targets of concerted conservation and management in the coastal sandplain grasslands of northeastern North America. Most of these species are typically noted as absent or very infrequent in botanical surveys of managed plots, despite the fact that management efforts are often designed in part to create amenable habitat for them (Patterson and Clarke, 2006; Beattie et al., this issue). By contrast, I define "common" species as native taxa that are frequently encountered in managed plots or sandplain grasslands generally (e.g., Dunwiddie, 1998; Patterson and Clarke, 2006; Lezberg et al., 2006). I ask first, what is the range-wide rarity status and habitat specificity of the infrequent species in northeastern sandplain grasslands? Second, are there suites of traits that are consistently exhibited by infrequent species that distinguish them from more common, closely related taxa? I examine the biogeographic distribution, reproductive modes, dispersal capacity, seedbanking, and architecture of these species – features related to fitness, colonization potential, and competitive ability. I also ask if these informative traits yield insights for designing research and management strategies, tailored to particular life histories.

2. Methods

I assembled a list of plant species (Table 1, nomenclature follows USDA, NRCS, 2006) reported from coastal sandplain grasslands, *sensu lato*, incorporating the set of multiple grassland types defined by Dunwiddie et al. (1996). Like Dunwiddie (1998), I focused on forb, graminoid, and shrub species, the predominant life forms of grasslands. I identified a set of 27 infrequent native species based on listing as Division I–III in the *Flora Conservanda*: New England (Brumback et al., 1996); state-listing by northeastern Natural Heritage Programs (NatureServe Explorer, 2006); the botanical studies of Bicknell from 1908 to 1919 on Nantucket Island, Massachusetts (summarized in Bicknell, 1919); floristic inventories and reviews (e.g., Olmsted, 1937; Stalter et al., 1986; Martha's Vineyard Sandplain Restoration Project, 1998; Dowhan and Rozsa, 1989; Sutton et al., 1990; Sorrie and Dunwiddie, 1996; Fairbrothers, 1998); Conservation and Research Plans recently completed by the New England Wild Flower Society (Farnsworth, 2003), in which the species were noted as declining or sporadic in occurrence; and personal communication with knowledgeable botanists.

I next developed a parallel list of 27 common native species, each paired to one closely related infrequent taxon (Table 1). Common species were defined as those that frequently occurred in botanical surveys of sandplain grasslands or were noted in the above sources as abundant. To avoid trait differences related to latitude (climatic contrasts), only species that overlapped substantially in range and predominant habitat type with the corresponding rare taxa were chosen. In most cases, these species were congeners of the corresponding infrequent taxon, and in all cases, only

Table 1 – Plant species used in the paired contrasts of infrequent and common coastal sandplain grassland species. Nomenclature follows USDA, NRCS, 2006

Infrequent species of grasslands	Common species of grasslands	Plant family
Asclepias purpurascens L.	*Asclepias amplexicaulis* J.E. Smith	Asclepiadaceae
Ageratina aromatica (L.) Spach	*Eupatorium hyssopifolium* L. var. *hyssopifolium*	Asteraceae
Gamochaeta purpurea (L.) Cabrera	*Gnaphalium obtusifolium* L.	Asteraceae
Liatris scariosa (L.) Willd. var. *novae-angliae* Lunell	*Liatris pilosa* (Ait.) Willd.	Asteraceae
Nabalus serpentarius Pursh	*Prenanthes trifoliata* (Cass.) Fern.	Asteraceae
Pityopsis falcata (Pursh) Nutt.	*Chrysopsis mariana* (L.) Elliott	Asteraceae
Symphyotrichum concolor (L.) Nesom	*Sericocarpus asteroides* (L.) B.S.P.	Asteraceae
Onosmodium virginianum (L.) A. DC	*Onosmodium molle* Michx.	Boraginaceae
Triosteum perfoliatum L.	*Triosteum angustifolium* L.	Caprifoliaceae
Helianthemum dumosum (E. Bickn.) Fern.	*Helianthum bicknellii* Fern.	Cistaceae
Helianthemum propinquum E. Bickn.	*Helianthemum canadense* (L.) Michx.	Cistaceae
Lechea pulchella Raf.	*Lechea minor* L.	Cistaceae
Scleria pauciflora Muhl. ex Willd. var. *caroliniana* Alph. Wood	*Scleria minor* W. Stone	Cyperaceae
Corema conradii Torr.	*Arctostaphylos uva-ursi* (L.) Sprengel.	Ericaceae
Chamaecrista fasciculata (Michx.) Greene	*Chamaecrista nictitans* (L.) Moench.	Fabaceae
Desmodium sessilifolium (Torr.) T.&G.	*Desmodium ciliare* (Muhl.) DC	Fabaceae
Lespedeza angustifolia (Pursh) Elliott	*Lespedeza capitata* Michx.	Fabaceae
Sisyrinchium fuscatum E. Bickn.	*Sisyrinchium atlanticum* Bickn.	Iridaceae
Juncus greenei Oakes & Tuckerman	*Juncus dichotomus* Ell.	Juncaceae
Linum intercursum E. Bickn.	*Linum virginianum* L.	Linaceae
Spiranthes vernalis Englm. & Gray	*Spiranthes lacera* (Raf.) Raf. var. *lacera*	Orchidaceae
Aristida purpurascens Poiret. Var. purpurascens	*Aristida dichotoma* Michx. var. *dichotoma*	Poaceae
Dichanthelium ovale var. *addisonii* (Nash) Gould & C.A. Clark	*Dicanthelium dichotomum* (L.) Gould var. *dichotomum*	Poaceae
Paspalum laeve Michx.	*Paspalum setaceum* Michx.	Poaceae
Polygala nuttallii T.&G.	*Polygala polygama* Walt.	Polygalaceae
Amelanchier nantucketensis E. Bickn.	*Amelanchier canadensis* (L.) Medikus	Rosaceae
Agalinis acuta Pennell	*Agalinis purpurea* var. *purpurea* (L.) Pennell	Scrophulariaceae

one congener or close relative was appropriate for selection by these stringent criteria. Where a qualifying congener could not be found, a closely-related species within the same family was chosen.

The 27 species pairs spanned 16 plant families. Endemic sandplain grassland species tend to fall into relatively few families (dominated by the Asteraceae, Poaceae, Fabaceae, and Cistaceae); thus, species are not statistically independent entities (Harvey and Pagel, 1993). The paired comparison employed here was specifically designed to control for phylogenetic bias by comparing between groups with parallel phylogenetic composition and patterns of relatedness.

For each species, I gathered data on 16 species-level traits. The variables chosen reflected a paucity of detailed data for many rare species, but formed a diverse subset of variables used by Kleyer (1999) and Kühner (2004) to describe European grassland functional types. The first four variables described aspects of the range-wide distribution and imperilment of each taxon, testing the hypothesis that infrequent sandplain species were intrinsically rarer throughout their range than common taxa (data from NatureServe Explorer, 2006):

(1) Total number of states and provinces from which the species was recorded.
(2) Proportion of states in which the taxon received an official listing of S1, S2, SH, or SX (as an index of rarity), values ranging from 0 to 1.
(3) A range code, describing the general distribution of the taxon in biogeographic regions, coded as follows: 1 = narrow coastal plain endemic; 2 = found west to

the Appalachian Mountains; 3 = found throughout the eastern half of North America; 4 = found throughout the east and west of the Rocky Mountains.
(4) G-rank, an index of global imperilment assigned by NatureServe, with values ranging from 1 (critically imperiled) to 5 (secure).
The next two variables tested the hypotheses that infrequent sandplain species were more restricted in habitat affinity than common species:
(5) "Other habitats" was coded as 1 if a species was described as occurring in a diversity of habitat types across their range and 0 if the species was recorded solely from dry–xeric sandplains or sparsely vegetated, graminoid-dominated glades (information from NatureServe Explorer, 2006; USDA, NRCS, 2006; and botanical references cited above).
(6) "Disturbance" was coded as 1 if all habitats occupied by a species were described in the original literature as "early successional," "fire-adapted," or "open-canopy" and 0 if closed canopy or later-successional habitats were reportedly occupied by the species.
The next set of five variables (data derived from Gleason and Cronquist, 1991; Holmgren, 1998; Magee and Ahles, 1999) described indices of plant size and growth strategy, and were used to test the hypothesis that plant commonness was correlated with competitive ability, drought tolerance, flexible allocation to vegetative versus sexual reproduction, and/or capacity to recover from disturbance (an important component of grassland ecology):

(7) Growth form was coded as "herbaceous/forb," "graminoid," or "shrub".

(8) Plant height (cm) was entered as the mean of the minimum and maximum stem height values published for each species.

(9) Leaf area (cm^2) of a single average leaf was calculated as an ellipse with the major axis determined from the mean of the minimum and maximum leaf lengths and the minor axis given by the mean of minimum and maximum leaf widths.

(10) Life history was coded "annual," "biennial," "monocarpic perennial," and "perennial".

(11) Clonality was coded "0" if no perennating organs such as rhizomes were described or if the species was classified as an annual; "0.5" if the species had short rhizomes, and "1" if "coloniality" was noted in published descriptions.

The next pair of variables characterized aspects of plant phenology, reproductive output, and, which I hypothesized would affect plant fitness (data from Gleason and Cronquist, 1991; Magee and Ahles, 1999):

(12) Flowering time was coded by number of the month corresponding to the peak of flowering time. For example, a plant known to flower between June and August was given a value of "7," corresponding to July, the seventh month of the year.

(13) Flowering duration was coded by the maximum number of days for which a species could flower, given the months of its flowering phenology.

Finally, I documented aspects of seed biology that would influence a species' capacity to disperse into new sites and to weather disturbance through dormancy in a soil seedbank:

(14) Seed size (mm) was given by the longest dimension of the species' seed as reported by Montgomery (1977) and Martin (1946).

(15) Capacity for long-distance dispersal was a composite variable that described the probability of a seed being transported > 100 m, based upon a combination of its size, morphology, and its mode(s) of dispersal. Values were "0" for locally-dispersed seeds (e.g., large, gravity-dispersed propagules); "0.5" for ant-dispersed or medium-sized seeds; and "1" for seeds with structures that would allow dispersal by wind or mobile animals.

(16) Dormancy was coded as "0" if a species was known to germinate immediately after dehiscence and was described as "nondormant"; "0.5" for seeds with "physical" or "nondeep morphophysiological" dormancy, and "1" for seeds with long-term dormancy or stratification requirements (all terms *sensu* Baskin and Baskin, 1998; other data from Matlack and Good, 1990; USDA, NRCS, 2006).

2.1. Statistical analyses

All analyses were computed using S-Plus 6.2 for Windows (Insightful Corporation; Crawley, 2002). All variables except plant height, leaf area, number of states, percent of states with listing, and seed size were categorical; the latter were continuous (or integer) values. To compare infrequent and common species, I used one-sided paired *t*-tests on the continuous variables, for which an *a priori* hypothesis of the sign of difference between was possible, and two-sided tests otherwise. Probabilities were assessed after Bonferroni correction (α/number of comparisons) for multiple comparisons. Wilcoxon signed-rank tests were performed on ranked variables (G-rank, Range Code, Peak Flowering Month) that were not normally distributed. Fisher's exact test was used for categorical variables for which frequencies approaching zero were observed (Other Habitats, Life History Code, Clonality, Dormancy), and Pearson's chi-square test was applied to other categorical variables.

Classification Trees (De'Ath and Fabricus, 2000) subsequently were constructed to detect which of the variables contributed to a maximally accurate classification of the 27 pairs of species into infrequent versus common, and to examine the topology and ordering by which these variables were used in prediction. Only the 13 life history variables were used in this analysis; degrees of range-wide rarity, range size, and range restriction were omitted. Classification trees were subjected to optimal recursive pruning. Classification trees repeatedly split the data into smaller categories, in which each split depends on a single variable. The splitting continues until no further improvement in the statistical fit of the model can be attained, and when each terminus is as homogeneous as possible. Homogeneity at each node is summarized by the misclassification error rate; predictive capacity of the model increases as the misclassification rate decreases.

3. Results

Infrequent species generally occurred in fewer states and provinces overall than common species, and were listed as imperiled or extirpated (S1/S2 or SH/SX) in a significantly higher proportion of their range than common species (Table 2). This result was observed even though the purported G-rank from NatureServe was higher on average (mean = 4.5; more secure) for infrequent species than for common species (3.0). Ten of the 27 infrequent species were narrow coastal plain endemics, whereas none of the 27 common species had constricted coastal ranges.

Examining habitat affinities in more detail, the common species were more likely to occur in a range of habitats beyond dry/xeric sandplain grasslands (Table 2). A higher proportion of infrequent species (59%) than of common species (41%) were exclusively associated with naturally disturbance-prone habitats in the heart of their range, but this difference was not statistically significant at the 0.05 level (Table 2). None of the other life history variables tested with paired comparisons differed significantly between infrequent and common species (Table 2).

The classification tree used five of the 14 uncorrelated variables to distinguish infrequent species from common species (Fig. 1). The first variable used by the tree at the first node to bifurcate the groups was the habitat specificity of the taxon. Thus, species of conservation concern in sandplain grasslands were far more likely to exhibit strict affinity for coastal sandplain grasslands. The remaining variables included: (1) the capacity for clonal reproduction (common species tended to exhibit coloniality); (2) seed size (rare species tended to

Table 2 – Paired comparisons of closely related infrequent and common species of coastal sandplain grasslands for the 16 variables describing rarity and aspects of life history

Variable	Infrequent species	Frequent species	Statistic, P-value
1. Total number of states in which species is found	Mean (SE) = 20.8 (2.1)	Mean (SE) = 30.3 (1.6)	One-sided paired t = 4.14, P = 0.0002
2. Percent of states in which species is listed as rare	Mean (SE) = 9.0 (5.2)	Mean (SE) = 15.3 (2.4)	One-sided paired t = 4.37, P = 0.0001
3. Range code (1 = narrow to 4 = cosmopolitan)	Mean (SE) = 2.0 (0.2)	Mean (SE) = 3.8 (0.1)	Wilcoxon Z = 5.89 P < 0.0001
4. G-rank (1 = imperiled to 5 = secure)	Mean (SE) = 4.5 (0.2)	Mean (SE) = 3.0 (0.2)	Wilcoxon Z = 5.03 P < 0.0001
5. Capacity to occupy habitats outside grasslands	Frequency: 61.5%	Frequency 96.2%	Fisher's exact test P = 0.0048
6. Requirement for disturbance	Frequency 59.3%	Frequency 40.7%	Pearson's χ^2 = 2.77, P = 0.095
7. Growth form (herb/forb, graminoid, shrub)	Frequencies 77.8%, 14.8%, 7.4% respectively	Frequencies 77.8%, 14.8%, 7.4% respectively	Identical frequencies
8. Height (m)	Mean (SE) = 0.50 (0.06)	Mean (SE) = 0.65 (0.14)	Two-sided paired t = 1.16, P = 0.26
9. Leaf area (cm^2)	Mean (SE) = 7.8 (2.4)	Mean (SE) = 7.1 (1.4)	Two-sided paired t = 0.43, P = 0.673
10. Life history code (annual, perennial, biennial/monocarpic)	Frequencies 11.1%, 81.4%, 7.5% respectively	Frequencies 11.1%, 85.2%, 3.7% respectively	Fisher's exact test P = 0.999
11. Capacity for clonal growth (none, partial, full)	Frequencies 74.1%, 14.8%, 11.1% respectively	Frequencies 70.4%, 3.7%, 25.9% respectively	Fisher's exact test P = 0.189
12. Flowering duration (days)	Mean (SE) = 84.6 (6.8)	Mean (SE) = 85.1 (5.9)	One-sided paired t = 0.081, P = 0.486
13. Peak flowering month	Mean (SE) = 7.6 (0.3)	Mean (SE) = 7.4 (0.2)	Wilcoxon Z = 0.413, P = 0.679
14. Seed size (mm)	Mean (SE) = 2.6 (0.4)	Mean (SE) = 2.5 (0.4)	Two-sided paired t = 0.387, P = 0.702
15. Capacity for long-distance dispersal (none, limited, strong)	Frequencies 29.6%, 25.9%, 44.5% respectively	Frequencies 22.2%, 22.2%, 55.6% respectively	Pearson's χ^2 = 0.69, P = 0.706
16. Longevity in seed bank (none, limited, long-term)	Frequencies 11.1%, 14.8%, 74.1% respectively	Frequencies 7.4%, 25.9%, 66.7% respectively	Fisher's exact test P = 0.673

Variables in boldface type differed significantly at P < 0.05 between groups.
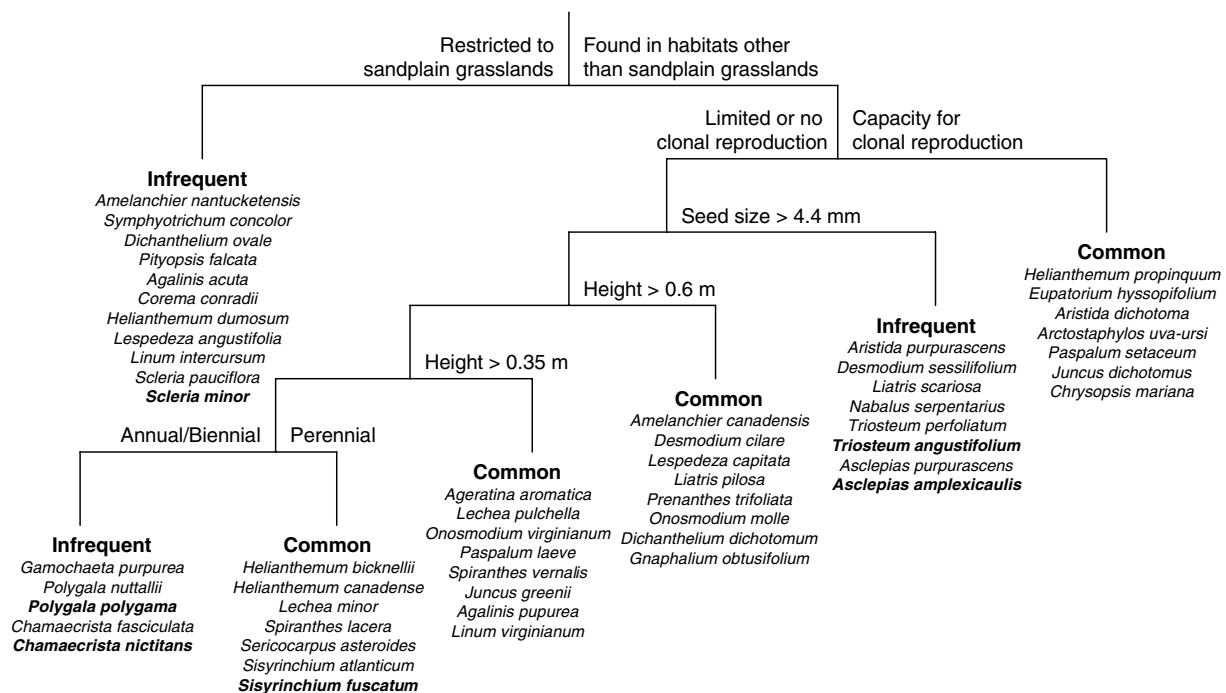
Fig. 1 – Classification tree for life history characters separating "infrequent" from "common" species. Misclassified species are shown in boldface type. Overall misclassification rate for the model was 0.185.

have seeds larger than 4.4 mm in diameter); (3) plant height (common species fell into a category of tall plants > 0.6 m and > 0.35 m tall); and (4) a perennial life history (observed more frequently among common species than infrequent taxa). Twenty-one (77.7%) of the species were correctly classified, and the overall misclassification rate for the model was

0.185 (Fig. 1). All of the six misclassified taxa were placed in groups with their congeners, indicating that phenotypic similarities due to phylogenetic relatedness contributed to errors in classification.

4. Discussion

Paired comparisons identify several characteristics that distinguish infrequent species from closely-related species that are more frequently observed (and documented as more abundant) in botanical surveys of coastal sandplain grasslands. Three indices of range-wide rarity – the proportion of states and provinces in which the species is listed, the number of states in which they occur, and the overall range size – differ significantly between the groups of infrequent and common species (Table 2). Counterintuitively, the global endangerment ranks (G-ranks) are somewhat higher on average among the infrequent species than among their closely-related counterparts (Table 2). This analysis points to a limitation of G-ranking methodology, which is derived at a first cut from a count of the total number of extant populations per species and secondarily from an assessment of other imperilment factors (NatureServe Explorer, 2006). It is possible for these species to have numerous populations, each of which are small and tenuous and/or that together occupy a limited range (Kunin and Shmida, 1997). Conversely, a few of the species of conservation concern, such as *Corema conradii* and *Pityopsis falcata* can attain high local abundances, for example (G. Motzkin, pers. comm.), but still occupy narrow ranges.

Indeed, the infrequent species studied here are more likely to exhibit a narrow range, being confined largely to coastal sandplains and areas northeast of the Appalachian Mountains. Infrequent species occupying a smaller area of extent tend to be state-listed as imperiled in a larger proportion of their range ($r^2 = 0.43$, $P = 0.0002$). The reasons for apparent range constraint are many and synergistic, likely including post-Hypsithermal climatic shifts, outright habitat destruction, and fire suppression (Vickery and Dunwiddie, 1997, and references therein). Range-wide botanical sampling needs to be intensified in order to understand the true geographical range of species and their attendant threats, especially for some of the less conspicuous or more difficult-to-identify taxa like *Scleria pauciflora* var. *caroliniana* (Zaremba, 2004). Likewise, much more data are needed on patterns of local abundance and precise population densities, both to understand the location and nature of species' strongholds and to develop a more complete picture and definition of "rarity" in the context of grassland species (Kunin and Gaston, 1997; Bevill and Louda, 1999). With more complete range-wide data on patterns of occurrence, large-scale analyses of threatened species can prove useful for understanding links between changes in land use, habitat availability, and species decline (Kerr and Cihlar, 2004).

The infrequent species studied here tend to show a more restricted affinity than the common species to xeric, sparsely vegetated, periodically disturbed habitats throughout their range (Table 2), and this apparent habitat specificity was the first explanatory variable in the classification tree (Fig. 1). Clarke and Patterson (this issue) also observed apparent habitat specialization among five rare plant species

inside and outside fire lanes; plants were largely restricted to microhabitats with a history of extensive disturbance, more bare soil, shallower litter layers, and lower percent cover of woody and herbaceous vegetation. Dunwiddie et al. (1996) reported that only four of 17 rare species they found in botanical surveys (and that I included in the present data set) occurred outside of sandplain grasslands (i.e., in heathlands). The actual extent of specialization on the part of these rare species must be demonstrated definitively in controlled experimental trials, such as common gardens, before we can draw definitive conclusions about their "congenital habitat pickiness" (*sensu* Rosensweig and Lomolino, 1997, p. 83).

It may seem at best obvious (and at worst tautological) that the first insight from this analysis is that "infrequent" species are intrinsically "rare". However, this finding accords with other comparative studies of rare species, which have found that restricted global distribution is a common shared characteristic of these taxa (Lozano et al., 2003; Pärtel et al., 2005). This finding confirms that this suite of species should be a focus of concern for conservationists throughout the species' ranges, and suggests that biologists should look at a large regional scale for insights into causes of rarity and habitat affinities. Overall, the data suggest that these infrequent species fit into the typology of the rarest of the rare identified by Rabinowitz (1981): constantly sparse to locally abundant in a specific habitat within a restricted range. Before managers throw up their hands in despair, however, it is important to acknowledge that rarity does not always reflect maladaptation (Rabinowitz et al., 1984); these and other very rare species of this ilk have persisted on the North American landscape for a very long time, and may prove quite resilient, albeit at low densities and frequencies, if basic processes driving their reproduction and dispersal can be sustained or promoted through management.

An investigation of life history traits can yield insight into how to facilitate these critical processes. The current study has identified certain features that distinguish infrequent species from common ones. For example, more common species of grasslands show a capacity for tillering or rhizomatous propagation (Fig. 1). Colonial grassland species can resort more flexibly to alternative modes of reproduction in times of scarce pollinators, can rapidly colonize newly-opened space, and can translocate nutrients and photosynthate belowground and to daughter ramets (McIntyre et al., 1995). Certain rhizomatous infrequent species, including *Amelanchier nantucketensis*, may establish more readily from nearby source populations in areas where local competition cannot be reduced. By contrast, non-colonial species such as *Asclepias purpurascens*, *Agalinis acuta*, or *Spiranthes vernalis* may require more intensive management to preclude competition with common rhizomatous forbs, foster sexual reproduction, and promote their dispersal and persistence in appropriate habitats.

Coincident with the lack of rhizomatous habit is the tendency of certain infrequent species to exhibit annual or biennial – rather than perennial – life histories (Fig. 1). Numerous ecological studies have established that shorter-lived species can compete or coexist with perennials, but usually do so more effectively when periodic disturbance creates new

opportunities for recruitment. In fact, infrequent sandplain grassland species show a marginally higher requirement for disturbance in their native habitats than their more common relatives (Table 1). Management to date in these systems has attempted, with varying success, to simulate disturbance through controlled burns and/or mowing. The analyses here also suggest that such disturbance may be important for persistence and that such management trials should be intensified.

It is also of interest that plant height distinguishes common species from infrequent species according to the classification tree (Fig. 1), a character that is likely indicative of competitive ability. Of the five rare plant species studied by Clarke and Patterson (this issue), for example, only *Nabalus serpentarius*, a relatively tall sandplain plant, occurred in later-successional sectors of fuelbreaks with considerable cover of other woody species. Other comparative studies have identified an association between short stature and rarity in regional floras (Pilgrim et al., 2004) and higher vulnerability of shorter plants to competitive exclusion and local extinction in grasslands (Leach and Givnish, 1996).

Seed size also helps to distinguish infrequent species from common taxa (Fig. 1). Seed size larger than 4.4 mm characterized a group of infrequent species in this sample; such seeds may be limited in their dispersal ability. There are frequently trade-offs between large seed size and the number of seeds produced per individual; more data are needed on whether these infrequent species are limited in seed output. Larger seed sizes are also associated with reduced longevity in the soil seedbank in European grassland species (Thompson et al., 1993) and in many other environments (Baskin and Baskin, 1998; Farnsworth, 2000). The composition of the coastal sandplain soil seedbank is very spatially variable, and rarely correlates with the distribution of species currently present aboveground (Matlack and Good, 1990). Systematic seedbank sampling is needed in more localities to understand the distribution of infrequent and common species in the soil (e.g., Thompson, 1986). Two recent, large land manipulation experiments designed to encourage sandplain grassland and grassland/shrubland mosaics were relatively unsuccessful in encouraging recruitment of relatively rare sandplain plants (Lezberg et al., 2006; Beattie et al., this issue). It is possible that these species are hindered in dispersal and need to be handintroduced into available habitat; but care needs to be taken to minimize risks of outbreeding depression that can accompany translocation of rare grassland species (Gravuer et al., 2005).

5.   Conclusions: what can life history tell us, and what do we still need to know?

Classification trees are useful exploratory tools for identifying suites of traits or environmental variables that distinguish functional groups of plants. The interpretation of these trees is only as reliable, however, as the data that are used to delimit character states. This preliminary analysis makes use of a small set of variables and species that could be coded with a high degree of confidence based on data availability. More sophisticated functional group models (e.g., Frappier and Eckert, 2003; Kühner, 2004) make use of

more variables for which data can be gathered for the relatively common species they address. Several variables I tested proved to be uninformative for distinguishing either of the two suites of species, including flowering time and duration, and life form (forb, shrub, graminoid; cf. Dunwiddie et al., 1996).

Among the obvious variables that were omitted from the present study due to lack of field data are the presence/absence of mycorrhizal associations; many grassland species have documented mycorrhizal associates (Harley and Harley, 1987). Such associations, along with other symbioses (such as the hemiparasitic life history of *A. acuta* or mycorrhizal orchids) may be critical for the survival of endemic grassland species, and need to be studied in more detail in coastal sandplain systems. One could also parameterize a spatially-explicit habitat use model using much higher-resolution data on microclimate, soil chemistry, moisture, spatial fragmentation, and land-use history (e.g., Kühner, 2004), but these data have only rarely been taken (Dunwiddie et al., 1996; Cousins et al., 2003; Eberhardt et al., 2003; Clarke and Patterson, this issue), and there are indications that differences in soil chemistry across the major vegetation types and land use histories are small (Neill et al., this issue).

Ultimately, there is no substitute for basic, controlled studies of the individual responses of multiple species to management regimes, in order to parameterize models, to characterize true functional groups, and to better predict the outcomes of management trials. Systematic botanical surveys of the aboveground and seedbank populations of rare species are sorely needed (Foster and Motzkin, 1999; Eberhardt et al., 2003); Clarke and Patterson (this issue) is a model study in this regard. Manipulative common garden experiments are also required to unambiguously establish germination requirements and tolerance limits for environmental conditions and competition. Demographic models are nonexistent and need to be developed for all of these species in order to identify life stages that are most vulnerable. Population genetic studies would reveal much about impediments to gene flow, degrees of adaptive population differentiation, and frequency of long-distance seed dispersal (e.g., Gravuer et al., 2003). Relatively simple, single-factor, controlled, well-replicated management trials, *potentially* assisted by augmentation from the *in situ* seedbank or judicious transplanting of rare plant progeny from nearby populations, are warranted once our ecological understanding of these species is sufficient to interpret results reliably.

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