Narragansett Bay
Research Reserve

Technical Report 2005:2

An Analysis of the Vegetative Composition of an Atlantic Coastal Pitch Pine Barren

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June 2005

Technical Report Series 2005:2

Abstract

Atlantic coastal pitch pine barrens are structurally diverse habitat mosaics that are maintained in early to mid-successional stages by regular fire disturbance. Because they are valuable to wildlife and enhance regional biodiversity, the barrens within the Narragansett Bay National Estuarine Research Reserve (NBNERR) are a priority for ecological maintenance and restoration. Evaluation of the composition of vegetation within and among the habitats of the mosaic will help NBNERR resource managers develop prudent management strategies, but to accomplish this, data collected by various methods according to each habitat's vegetative structure need to be standardized before analysis. Vegetation composition, structure, and relative cover were quantified using density-at-breast-height, line-intercept, and point-intercept methods in four habitat types along randomly located transects within the NBNERR mosaic. The habitat types sampled were pitch pine-oak forest (PO), a naturalized European larch plantation (LA), open grassland (OG), and shrub-dominated linear firebreaks (FB). All data were standardized to % total cover for each habitat type and for each of several habitat combinations. Community similarity, species richness, and species and structural heterogeneity were analyzed to determine the relative effects of each parameter on the alpha and beta diversities of the mosaic. PO areas managed by a single burn in 1996 versus areas unburned were dissimilar in crown cover by species and in understory by life form. PO habitat in total was dissimilar to LA habitat in crown cover by species and understory by species and life-form. Of the four habitat types sampled, PO was the most species rich, while OG was the most heterogeneous and contributed most to the beta diversity of the mosaic when added to PO. LA was the least species rich, least heterogeneous, and added the least to beta diversity. Standardization of the data worked well to evaluate the habitats and mosaic by indices of richness and heterogeneity. This study suggests that a single former burn was ineffective at properly maintaining the NBNERR pine barren mosaic, and that refined management strategies should be considered. In addition, restoration of LA to OG habitat would enhance the beta diversity and thus the ecological function of the mosaic.

Introduction

The Narragansett Bay National Estuarine Research Reserve (NBNERR) is a 1800 ha sanctuary of island properties located in the geographic center of Narragansett Bay, RI that is managed by the State of Rhode Island in partnership with the National Oceanic and Atmospheric Administration to promote coastal stewardship through research and education. The South Unit of the NBNERR contains 71 ha of Atlantic coastal pine barrens, a heterogeneous habitat mosaic consisting of oak-pine forest, pitch pine-oak forest, and adjacent grasslands and xeric shrublands. Pine barrens are early to mid-successional ecosystems that are generally maintained by fire. Without regular disturbance, Atlantic coastal barrens will normally progress into closed-canopy hardwood forests, such as oak-hickory or oak-maple, which are functionally distinct (Howard et al. 2005). Much of the NBNERR mosaic (30 ha) is covered by a continuous late-successional oak-pine forest, which is dominated by hardwoods and could not likely be reverted to a heterogeneous mosaic without clear-cutting. However, the balance of the mosaic currently exists in stages that could feasibly be maintained by selective cutting and regular burning. The containment of the mosaic within the reserve allows for the application of such controlled management practices. However, with the exception of a single controlled burn in 1996, manipulative management has not been employed and the functionality of the mosaic is threatened by ecological succession. The NBNERR pine barrens are also ecologically threatened by the continued naturalization and encroachment of an adjacent stand of European larch (*Larix decidua*) that was planted by the Navy during its occupation of the properties during WWII.

Pine barrens offer a unique set of environmental characteristics that support a wide range of specialized, unique, and rare plant and animal species, and are a significant contributor to regional and global biodiversity (Howard et al. 2005). Due to fire suppression and development, these habitats are regionally and nationally declining (Grand et al. 2003). The barrens are thus a priority for ecological maintenance and restoration at the NBNERR. Resource managers need to understand the dynamics of vegetative composition, and the effects of disturbance on that composition, to properly maintain or restore those characteristics that are of value to the ecological function of the pine barrens mosaic (Howard et al. 2005).

Valuation of habitat function is a process that resource managers pursue at numerous levels because no one attribute can fully characterize ecosystem value. Managers must rely on an integration of various weighted factors to help them make prudent decisions regarding resource management. Some quantifiable attributes of habitat value that have been employed for evaluating ecosystem function are species composition, species richness (number of species), species evenness (equitability among species), species heterogeneity (defined here as a function of richness and evenness, as opposed to diversity, defined here as either richness or heterogeneity), structural diversity of vegetation, and presence of rare species (Adamus 1995; Kinzig et al. 2002; Krebs 2001; Macarthur and Macarthur 1961; Heltshe and Forester 1983, respectively). Compositional vegetation inventories and indices of habitat diversity are especially useful because they quantify species composition dynamics. Species composition can act as a bio-indicator of habitat function because it is constantly affected by a multitude of environmental processes (Adamus 1995). Functions of species and structural diversity can be applied to help resource managers interpret compositional variability. High diversity within plant communities generally contributes to habitat stability and productivity (Tillman et al. 2001), and increases overall habitat function (Symstad et al. 2003). Diversity of vegetative structure has been found to partially determine the diversity of certain fauna (Macarthur and Macarthur 1961). Diversity across habitat types (beta diversity) is generally considered to spatially extend and enhance those attributes (Mueller-Dombois and Ellenberg 2002).

Comparing diversity among complete vegetation communities (including all strata) poses a challenge to resource managers. Communities may contain multiple structural strata, making them difficult to quantify due to inconsistencies in appropriate sampling methods depending on the community's structural makeup. Methods appropriate for censusing canopy data are not always appropriate for censusing shrub layer data or groundcover (Mueller-Dombois and Ellenberg 2002). Data variables must therefore be standardized to facilitate comparisons among complete vegetation communities.

This study will estimate vegetation community richness and heterogeneity, and develop simple methods of standardizing species and life form variables among various habitat types and strata, to evaluate the plant compositions of an Atlantic coastal pitch pine barren habitat mosaic. The specific objectives of this study are to establish a quantitative baseline for the vegetation, assess former management practices, explore the relationships of alpha (within habitat) and beta (across habitat) diversity, and compare the relative values of various habitats within the mosaic to help drive future management practices.

METHODS

Quantitative vegetation cover data were collected from vegetation communities in each of four habitat types within the pitch pine (*Pinus rigida*) barren habitat mosaic located in the South Reserve Unit of the NBNERR: pitch pine-oak forest (PO), larch forest (LA), open grassland (OG), and linear shrub dominated firebreaks (FB) (Fig. 1). Habitat types were initially characterized by tallest dominant vegetation species covering >30% of ground (Kutcher et al. 2004). Plant communities within each habitat were sampled using line-intercept (LI), point-intercept (PI), and belt transects, as was appropriate for the given structure of each habitat or stratum (Mueller-Dombois and Ellenberg 2002). Sampling effort was determined by plotting and interpreting species-area* curves with the data (Krebs 1989). For richness and heterogeneity comparisons, sampling effort was standardized among communities by finding the point on each species area curve where the rate equaled approximately one species gained per transect of extra effort, averaged from curves drawn from two random permutations of the data. Thus, the sampling effort was approximately equally adequate to characterize each community type by richness and heterogeneity indices of species diversity (Heltshe, personal communication).

PO and LA Analyses

Eighteen fixed transects were randomly selected by laying a numbered grid over the entire stand and selecting nine transect starting points from each treatment of formerly burned and non-burned pitch pine-oak forest. Six transects were likewise selected for the larch forest stand. Each transect was run 30m in a randomly selected direction. Continuous LI cover data were collected for all strata except tree cover. For trees, the basal area surrogate, density at breast height (DBH), was collected from a belt-transect that ran 3m to either side of each LI transect. Ground cover estimates for tree species data were derived assuming 100% canopy cover and direct proportionality between DBH and cover (Welch et al. 2000).

Nine samples each of formerly burned and non-burned pitch pine-oak habitat data were analyzed using PRIMER 4.0 (Plymouth Marine Laboratory) statistical software to determine dissimilarity between treatments (Analysis of Similarity, ANOSIM) and relative contribution to dissimilarity by similarity percentages (SIMPER). All data were transformed to the fourth root and run through 5000 permutations. The following parameters were compared between treatments: DBH of tree species, LI understory cover by species, and LI understory cover by vegetation life form (shrub, vine, grass, forb, seedling and moss). PO data in total were also compared to LA data and analyzed by tree DBH, understory cover by species, and understory cover by life form.

* Transect length was substituted for area

Richness and Heterogeneity Comparisons of Four Habitat Types

Point-intercept data were collected in OG and FB habitats using modified FIREMON methods (Lutes et al. 2004). One hundred points were sampled along each of six fixed 20-m transects per habitat type. Transects were randomly positioned in OG habitats, and positioned across FB habitats at fixed intervals with a randomly located starting point. A 3mm x 1m iron welding rod was dropped vertically from a stretched metric tape at 0.2-m intervals to estimate ground cover of all vegetation, accruing one percent cover (per transect) for each species contacting the rod per drop. These cover estimates, and those of the LI and DBH data of the PO and LA habitats, were used in species richness, and species and life-form heterogeneity analyses.

Nonparametric *jackknife* estimates of species richness were determined using the methods developed by Heltshe and Forrester (1983) for each the four habitats within the mosaic using the function:

$$\hat{S} = s + \left(\frac{n-1}{n}\right) k$$

Where: $\hat{S}$ = jackknife estimator of species richness
s = observed total number of species present in n transects
n = total number of transects sampled and
k = number of unique species

Shannon-Wiener indices of habitat heterogeneity (Krebs 2001) were calculated using the function:

$$H' = -\sum_{i=1}^{S} (p_i)\,(\log_2 p_i)$$

Where: H' = index of species heterogeneity
S = number of species and
p_i = proportion of total sample belonging to the *i* th species

Species richness estimates ($\hat{S}$) and heterogeneity indices (H') were calculated for each of the four habitat types, and for the following combined datasets: PO+FB, PO+OG, PO+LA, PO+FB+OG, and PO+FB+OG+LA, to determine how the addition of associated pine barrens habitats to PO habitats affected the overall diversity of the mosaic. For $\hat{S}$ calculations, species for all habitats and mosaics were determined as present or absent for each transect. For H' calculations, all species data variables for habitats were standardized to a proportion of total vegetation cover. For forested habitats, multiple steps were used to standardize data from various strata. First, canopy variables (DBH) were standardized to a proportion of an assumed 100% total canopy coverage. The resulting values were then added directly to actual cover (as proportion) values of understory species. Finally, summed, combined data from both strata were re-standardized to a proportion of total cover as follows:

$$H'_{tot} = -\sum_{i=1}^{S} (p_i)(\log_2 p_i)$$

Where: H'_{tot} = index of species heterogeneity for total strata in forested habitats
S = number of species
p_i = proportion of total sample belonging to the i th species and
$i = \Sigma(c + u)$ where:
c = canopy cover values of each species derived from DBH assuming 100% cover and direct proportionality, and
u = actual understory cover values of each species from line intercept sampling

For combined mosaics, each standardized habitat was given equal weight and variables were again combined, summed, and re-standardized to a proportion of total cover within the mosaic as follows.

$$H'_{m} = -\sum_{i=1}^{S} (p_i)(\log_2 p_i)$$

Where: H'_m = index of species heterogeneity for each mosaic
S = number of species
p_i = proportion of total sample belonging to the i th species and
$i = (\Sigma(c + u) + h) / n_m$ where:
c = canopy cover values of each species derived from DBH assuming 100% cover and direct proportionality, and
u = actual understory cover values of each species from line intercept sampling
h = actual understory cover values of each species from line intercept or point intercept sampling of additional habitats, and
n_m = number of habitats in the mosaic

RESULTS

Pitch Pine-oak Forest (PO)

Pitch pine-oak forest habitat is the spatially dominant and keystone feature of the study area. Data were collected to characterize 15.0 ha of pitch pine-oak forest which is fragmented into five discontinuous adjacent segments by 20m wide firebreaks, two of which constitute the FB study area. The canopy is dominated by pitch pine and black oak (*Quercus velutina*), with twelve tree species observed (Table 1). The understory is dominated by highbush blueberry (*Vaccinium corymbosum*), northern bayberry (*Myrica pensylvanica*), and greenbrier (*Smilax rotundifolia*) with 28 species observed (Table 2). Overall 35 species were observed in all PO strata.

The composition of the PO canopy differed significantly between formerly burned and unburned areas ($R = 0.28$, $p = 0.002$). Based on SIMPER analysis, black oak contributed 11.4% to the dissimilarity, followed by Scotch pine (*Pinus sylvestris*) 11.1%, and bear oak (*Quercus illicifolia*) 11.0%. In the unburned areas the ratio of pine to oak canopy species was 99% greater, while overall stem density was 11% greater than in formerly burned areas.

Although understory species composition was not dissimilar between the treatments ($R = 0.06$, $p = 0.19$), life-form composition of understory vegetation was ($R = 0.20$, $p = 0.02$). Grasses contributed 24.0% to the dissimilarity of understory life forms, followed by mosses (22.9%), and shrubs (20.4%) (Table 3). Total understory cover was 95% greater in formerly burned areas.

Total richness ($\hat{S}$) was estimated to be 50 species in all strata of the entire PO habitat, with 42 in the understory and 14 in the canopy. The Shannon-Wiener index of heterogeneity (H') was calculated to be 1.80 for the canopy, 2.60 for the understory (3.04 for previously burned and 2.28 for unburned), and 2.77 for all strata.

Table 1. Stem density (DBH) of trees in the South Prudence PO habitat (m^2ha^{-1})

Species	Unburned	Burned	Mean	% Total
Pinus rigida	13.20	11.91	12.55	52.73
Quercus velutina	5.29	9.57	7.43	31.22
Pinus sylvestris	4.02	0.00	2.01	8.45
Quercus illicifolia	0.97	0.10	0.53	2.23
Quercus alba	0.80	0.03	0.42	1.76
Populus grandidentata	0.30	0.24	0.27	1.13
Quercus coccinea	0.00	0.45	0.23	0.97
Acer rubrum	0.02	0.28	0.15	0.63
Quercus rubra	0.22	0.00	0.11	0.46
Quercus palustris	0.11	0.00	0.06	0.25
Betula populifolia	0.06	0.00	0.03	0.13
Sassafras albidum	0.04	0.00	0.02	0.08
Total	25.02	22.58	23.80	100.00
DBH by Genus				
Pinus sp.	17.22	11.91	14.56	61.17
Quercus sp.	7.39	10.16	8.77	36.84
Pinus:Quercus	2.33	1.17	1.66	

Table 2. Percent cover of understory species of South Prudence PO habitats

Species	Unburned	Burned	Mean
Vaccinium corymbosum	11.07	12.40	11.74
Myrica pensylvanica	2.26	9.26	5.76
Smilax rotundifolia	2.89	7.17	5.03
Gaylussacia baccada	0.46	8.38	4.42
Festuca sp.	1.71	2.07	1.89
Polytrichum juniperinum	1.85	0.26	1.06

Euthamia tennuifolia	0.00	1.46	0.73
Kalmia angustifolia	0.17	0.27	0.22
Pinus rigida seedling	0.04	0.26	0.15
Smilax glauca	0.24	0.03	0.14
Lyonia ligustrina	0.22	0.00	0.11
Panicum virgatum	0.00	0.16	0.08
Sphagnum sp.	0.08	0.00	0.04
Chimaphila maculata	0.02	0.03	0.03
Needle-leaved seedling*	0.00	0.06	0.03
Celastrus orbiculatus	0.00	0.05	0.03
Broad-leaved herb*	0.00	0.05	0.02
Toxicodendron radicans	0.04	0.00	0.02
Quercus alba	0.00	0.04	0.02
Cerastium vulgatum	0.00	0.01	0.01
Acer rubrum seedling	0.01	0.00	0.00
Polygonum scandens	0.00	0.01	0.00
Potentilla canadensis	0.01	0.00	0.00
Rumex acetosella	0.00	0.01	0.00
Betula populifolia seedling	0.00	0.00	0.00
Broad-leaved seedling*	0.00	0.00	0.00
Veronica officinalis	0.17	0.00	0.09
Total	21.24	41.34	31.79

** unidentified*

Table 3. Percent cover of understory life-forms of South Prudence PO habitats

Life Form	Unburned	Burned	Mean
Shrub	16.88	37.30	27.09
Grass	1.71	2.29	2.00
Moss	1.93	0.27	1.10
Herb	0.20	1.56	0.88
Seedling	0.48	0.87	0.67
Vine	0.04	0.06	0.05
Total	21.24	42.34	31.79

Larch Forest (LA)

A stand of European larch covers 9.7 Ha of land directly adjacent to the PO habitats, sharing the same Poquonnock soil type. The canopy is dominated by European larch with eight species observed (Table 4). The Understory is dominated by greenbrier and highbush blueberry with 15 species comprising five life-forms (Table 5, Table 6). Overall 20 species were observed in all LA strata.

Total species richness was estimated to be 26 in all strata of the LA habitat, while species heterogeneity (H') was calculated to be 0.69 for the canopy, 1.15 for the understory, and 1.64 for all strata.

Table 4. Stem density (DBH) of trees in the South Prudence LA habitat (m^2ha^{-1})

Species	Transects

	L1	L10	L2	L4	L8	L9	Mean	% Total
Larix decidua	25.63	6.41	41.97	20.65	25.97	20.46	23.52	89.74
Quercus velutina	2.41	2.73	0.00	3.80	0.00	0.00	1.49	5.69
Juniperus virginiana	1.98	0.00	0.00	0.00	0.00	0.00	0.33	1.26
Nyssa sylvatica	0.91	1.02	0.00	0.00	0.00	0.00	0.32	1.23
Acer rubrum	1.47	0.00	0.00	0.00	0.00	0.00	0.25	0.93
Prunus serotina	0.68	0.00	0.00	0.21	0.00	0.00	0.15	0.57
Sassafras albidum	0.00	0.53	0.00	0.00	0.00	0.00	0.09	0.34
Quercus illicifolia	0.00	0.00	0.39	0.00	0.00	0.00	0.07	0.25
Total	33.08	10.69	42.36	24.66	25.97	20.46	26.20	100.00

Table 5. Percent cover of understory species of the LA habitat of the NBNERR

Species	Transects						
	L1	L10	L2	L4	L8	L9	Mean
Smilax rotundifolia	11.67	58.30	23.80	24.63	21.83	54.03	32.38
Vaccinium corymbosum	0.00	0.00	0.00	13.10	0.33	20.73	5.69
Larix decidua	0.00	0.00	0.00	0.00	0.00	4.50	0.75
Viburnum dentatum	0.00	0.00	0.00	0.00	2.67	0.50	0.53
Myrica pensylvanica	0.00	0.00	0.00	0.00	2.60	0.00	0.43
Vitus labrusca	0.00	0.00	0.00	0.00	0.00	1.83	0.31
Rubus flagellaris	0.00	0.00	0.00	0.00	0.33	1.20	0.26
Festuca sp	0.00	0.00	0.00	0.00	0.83	0.67	0.25
Panicum virgatum	0.00	0.00	0.00	0.00	0.10	1.00	0.18
Prunus serotina	0.00	0.00	0.00	0.00	0.00	0.40	0.07
BLD Shrub*	0.00	0.00	0.00	0.00	0.20	0.00	0.03
Acer rubrum	0.00	0.00	0.00	0.00	0.00	0.17	0.03
Quercus alba	0.00	0.00	0.00	0.00	0.17	0.00	0.03
Panicum clandestinum	0.00	0.00	0.00	0.00	0.13	0.00	0.02
Polytrichium juniperus	0.00	0.00	0.00	0.00	0.13	0.00	0.02
Total	11.67	58.30	23.80	37.73	29.33	85.03	40.98

** unidentified*

Table 6. Percent cover of understory life-forms of the South Prudence LA habitat

Life Form	Transects						Mean
	L1	L10	L2	L4	L8	L9	
Shrub	11.67	58.30	23.80	37.73	27.97	80.97	40.07
Grass	0.00	0.00	0.00	0.00	1.07	1.67	0.46
Vine	0.00	0.00	0.00	0.00	0.00	1.83	0.31
Seedling	0.00	0.00	0.00	0.00	0.17	0.57	0.12
Moss	0.00	0.00	0.00	0.00	0.13	0.00	0.02
Total	11.67	58.30	23.80	37.73	29.33	85.03	40.98

Open Grassland (OG)

The open grassland habitat covers 2.6 ha of land directly adjacent to the PO habitats. OG habitat is dominated by the grasses little blue-stem (*Schizachyrium scoparium*), early ticklegrass (*Agrostis hyemalis*), tall fescue (*Festuca pratensis*), and switchgrass (*Panicum virgatum*) (Table 7). Grasses account for over 90% of total cover (Table 8). Overall 30 species were observed.

Total species richness was estimated to be 45 in OG habitat, while the Shannon-Wiener index of community heterogeneity was calculated to be 3.49.

Table 7. Percent cover for species in the South Prudence OG habitat

Species	G1	G2	G3	G4	G5	G6	Mean
Schizachyrium scoparium	29	2	1	17	71	32	25.33
Agrostis hyemalis	71	21	32	14	4	0	23.67
Festuca pratensis	27	69	5	28	0	0	21.50
Panicum virgatum	0	29	31	2	5	1	11.33
Solidago nemoralis	3	33	0	10	0	0	7.67
Paspalum setaceum	0	18	2	10	0	1	5.17
Centauria nigra	2	17	0	7	0	0	4.33
Prunus serotina	20	0	0	0	0	0	3.33
Smilax rotundifolia	16	0	0	0	0	0	2.67
Cladonia sp	0	0	0	0	0	14	2.33
Pinus rigida	0	0	0	0	0	13	2.17
Polytrichium sp	0	0	0	0	0	8	1.33
Trifolium arvense	0	0	0	7	0	0	1.17
Hypericum gentianoides	0	0	6	0	0	0	1.00
Juncus greenei	4	1	0	0	1	0	1.00
Panicum lanuginosum	0	2	3	1	0	0	1.00
Digitaria sanguinalis	0	0	4	1	0	0	0.83
Panicum dichotomiflorum	0	5	0	0	0	0	0.83
Toxicodendron radicans	5	0	0	0	0	0	0.83
Trifolium pratense	0	1	0	4	0	0	0.83
Hudsonia tomentosa	0	0	0	0	0	4	0.67
Plantago lanceolata	0	1	0	2	0	0	0.50
Euthamia tenuifolia	0	2	0	0	0	0	0.33
Vaccinium corymbosum	0	0	0	0	0	2	0.33
Celastrus orbiculatus	1	0	0	0	0	0	0.17
Hieracium gronovii	0	0	0	0	0	1	0.17
Hypochoeris radicata	0	0	0	0	1	0	0.17
Juniperus virginiana	0	0	0	1	0	0	0.17
Oxalis stricta	0	1	0	0	0	0	0.17
Unknown forb	0	0	0	0	0	1	0.17
Total	178	202	84	104	82	77	121.17

Table 8. Percent cover for life forms in the South Prudence OG habitat

Life form	G1	G2	G3	G4	G5	G6	Mean
Grass	131	147	78	73	81	34	90.67
Herb	5	55	6	30	1	2	16.50
Shrub	39	0	0	1	0	18	9.67
Lichen	0	0	0	0	0	14	2.33
Moss	0	0	0	0	0	8	1.33
Seedling	3	0	0	0	0	1	0.67
Total	178	202	84	104	82	77	121.17

Firebreaks (FB)

The Firebreaks study area is a pair of linear 20m wide re-grown clear-cuts running through the PO habitats and covering 1.3 ha of land. Historic topsoils have apparently been mostly stripped from these cuts. FB habitat is dominated by shrubs and grasses, including stunted, prostrate pitch pine scrub, little blue-stem, highbush blueberry, and northern bayberry (Table 9). Overall 24 species were observed comprising five life-forms (Table 10).

Total species richness was estimated to be 32 in FB habitats, while the Shannon-Wiener index of community heterogeneity was calculated to be 3.00.

Table 9. Mean percent cover by species in North and South FB habitats of South Prudence

Species	Transect		Mean
	North	South	
Pinus rigida	17.33	23.00	20.17
Schizachyrium scoparium	20.33	19.33	19.83
Vaccinium corymbosum	8.33	18.33	13.33
Myrica pensylvanica	12.67	11.67	12.17
Panicum virgatum	1.00	7.67	4.33
Polytrichum juniperinum	4.33	0.33	2.33
Festuca pratensis	3.00	0.00	1.50
Hudsonia tomentosa	2.67	0.00	1.33
Gaylussacia baccata	1.00	1.33	1.17
Euthamia tenuifolia	0.67	0.67	0.67
Digitaria sanguinalis	1.00	0.00	0.50
Juncus greenei	1.00	0.00	0.50
Lechea tenuifolia	0.67	0.33	0.50
Unidentified herb	1.00	0.00	0.50
Agrostis perennans	0.67	0.00	0.33
Betula populifolia	0.33	0.33	0.33
Danthonia spicata	0.67	0.00	0.33
Hieracium lachenalii	0.67	0.00	0.33
Populus grandidentata	0.67	0.00	0.33
Quercus alba	0.67	0.00	0.33
Hypericum gentianoides	0.00	0.33	0.17
Panicum lanuginosum	0.33	0.00	0.17
Polygonum aviculare	0.33	0.00	0.17

Solidago rugosa	0.33	0.00	0.17
Total	79.66	83.33	81.51

Table 10. Mean percent cover by life form in the South Prudence FB habitats

Life Form	Transect		Mean
	North	South	
Shrub	36.33	51.00	43.67
Grass	28.33	27.00	27.67
Seedling	4.67	3.67	4.17
Herb	6.00	1.33	3.67
Moss	4.33	0.33	2.33
Total	79.66	83.33	81.51

PO Versus LA

Canopy species differed significantly between PO and LA habitats ($R = 0.95$, $p < 0.001$), with the following relative contributions to dissimilarity: European larch 26.3%, pitch pine 21.1%, and black oak 11.7% (Tables 1 and 4).

Understory species also differed between PO and LA habitats ($R = 0.70$, $p < 0.001$), including the following relative contributions to dissimilarity: highbush blueberry 16.7%, greenbrier 15.7%, and northern bayberry 13.0% (Tables 2 and 5). Life forms of understory vegetation were also dissimilar ($R = 0.17$, $p = 0.05$). Relative contributions to dissimilarity of understory life forms were as follows: grasses 22.5%, seedlings 22.4%, shrubs 19.9%, and mosses 18.8% (Tables 3 and 6).

Richness and Heterogeneity of Habitat Groupings

LA, OG, and FB habitats data were added, singly and in combination, to PO data to determine how each addition affected overall species richness and heterogeneity of the habitat mosaic (Table 11). For heterogeneity determinations it was assumed that habitat areas added to PO habitat were equal in area to the areas in the study sites.

Both richness and heterogeneity were highest for a grouping of all habitats and lowest for LA habitat. PO habitats were highest in estimated species richness, while OG habitat was highest in species heterogeneity. LA was the only habitat less heterogeneous than PO. The addition of OG habitat enhanced both the richness and heterogeneity of the mosaic more dramatically than other habitats. The further additions of FB and LA to PO+OG habitats increased the mosaic species richness, but had a negligible effect on heterogeneity (Table 11).

Table 11. A comparison of jackknife estimates of richness ($\hat{S}$) and Shannon-Wiener indices of heterogeneity (H') for habitats and habitat mosaics of the South Prudence pitch pine mosaic.

Habitat / Mosaic	$\hat{S}$	H'	$\hat{S}$ %>PO	H' %>PO
PO	50	2.77	0	0

FB	32	3.00	-35	8
OG	45	3.49	-10	26
LA	26	1.64	-49	-41
PO+FB	69	3.34	38	20
PO+OG	80	4.03	60	46
PO+LA	59	2.97	18	7
PO+FB+OG	90	4.02	80	45
PO+FB+OG+LA	95	4.06	90	47

DISCUSSION

Standardization of Data

Data collected by three methods and in various strata were standardized to characterize each habitat or mosaic by overall community heterogeneity. The described methods of standardization are conceptually justified in the assumption that each species exploits the total resources of light, air, and soil, to a relative degree that can be characterized by the proportion of total vegetation cover in the habitat or mosaic. Discounted for canopy values is leaf area index, which adjusts exploitation for overlap of leaves of a single species, which reflects resource use efficiency. However, since DBH was used as a surrogate for actual cover in the canopy, relative cover here is derived from basal area, which for trees is a direct relative measure of resource use (Mueller-Dombois and Ellenberg 2002).

Effectiveness of characterization using the described standardization methods can be demonstrated through a conceptual analysis of the resulting data. For example, the heterogeneity indices for understory data were H' = 2.60 for PO and H' = 1.15 for LA. These are considerably less heterogeneous than the richer, more even FB (H' = 3.00) and OG (H' = 3.49) habitats as well as somewhat less heterogeneous than total-strata indices for PO (H' = 2.77) and LA (H' = 1.64). Note that the addition of standardized relatively-less-rich canopy data (resulting in total-strata) has a small, but consequential positive effect on H' values for PO and LA, which suggests that it positively accounts for minor additional richness, without overwhelming the parameter of evenness built into the function, which would have caused a negative change in the value (conceptually, adding another stratum to a habitat *should* make it somewhat more heterogeneous).

Because they quantify species composition and relative indices of habitat quality in a standardized, logically relative and replicable way, these methods facilitate the application of these data as a baseline for future study and management both within and across habitats. The multivariate analysis of formerly burned versus unburned PO habitats can be temporally expanded to quantify changes in response to future management efforts such as more rigorous prescribed burning or selective cutting. The richness and heterogeneity analyses, as well as associated species lists, can be applied to long-term compositional studies such as those relating to successional change, influences of exotic species, or response to changes in herbivore pressure due to management.

Direct Management Implications

Study values for mean stem density in the previously burned PO habitat areas were 11% less than in unburned areas, mean understory cover values were double, and understory heterogeneity was greater. This suggests that the single burn of the NBNERR pine barren may have temporarily opened the canopy and thus allowed higher production and diversity of understory vegetation, which is a desirable effect of prescribed burning in maintaining PO habitats (Welch et al. 2000). However, this study also indicates that the burn may not have met another basic objective of maintaining the pitch pine forest, which is the reduction of hardwoods with the promotion of pitch pine propagation (Howard et al. 2005). The DBH data show that previously burned areas of the PO habitat contain half the pine:oak ratio of unburned habitats. If ratios were similar between treatments pre-burn (which is unknown), this would challenge the standard assumption that burning within pitch pine forest will raise pine:oak ratios. Carey (1992) suggests that while regular burning increased pitch pine relative to oak, occasional burning may actually decrease the pine:oak ratio, which would concur with our findings. Welch et al. (2000) found that while prescribed burning top killed mostly hardwoods, burning would not top kill trees with stems greater than 25cm, and shading due to the lack of regular top-kill reduced pitch pine recruitment and selected for shade tolerant (hardwood) species. Although the previous management history of the area is unclear, the data still suggest that the NBNERR burn was not appropriately timed to reduce hardwoods and promote pitch pine domination (i.e. the hardwoods were allowed to grow too large for effective maintenance). At this point, selective cutting followed by a regular burning schedule may be the most appropriate action to restore and maintain the pine-oak forest.

The comparative analyses of habitat groupings to assess richness and heterogeneity changes as habitats were added to the PO habitat reveal information that will guide other future management practices within the pine-barrens mosaic. This study suggests that LA habitat is not contributing appreciably to the beta diversity of the mosaic. LA contributes a near mono-cultural nonnative canopy of European larch, which has naturalized outside of the original plantation and into other pitch pine habitats. Values of $\hat{S}$ and H’ for LA canopy, understory and overall were lower than those for PO, and were lowest compared to all other habitats in the mosaic. PO+LA H’ values were only 7% higher than those of PO alone, and adding LA to the PO+FB+OG habitat mosaic only raised the H’ value by 1%. OG habitats have the highest $\hat{S}$ and H’ values and contribute the most to the beta diversity of the mosaic. Adding OG to the mosaic increases H’ values 46% over PO alone and 35% over PO+FB.

Interpretation of beta diversity is an effective way to guide appropriate management strategies for the pitch pine mosaic in South Prudence. Firstly, under the premise that vegetation communities with higher species diversity are generally more productive and valuable to habitat function than are less diverse communities (Symstad et al. 2003), maintaining or expanding the highly diverse OG habitats would enhance the ecological productivity and value of the mosaic and should thus be considered for management. Secondly, restoration of the LA habitat to grasslands may be a prudent management action for the NBNERR because small open grasslands are declining regionally (Massachusetts Audubon Society 2005), LA habitat contributes little to the beta diversity of the pine barrens mosaic, and non-native species (such as European larch) can threaten the functionality of native ecosystems (e.g. Fike and Niering 1999).

ACKNOWLEDGEMENTS

Thanks to Keith Killingbeck at URI for his guidance and review of this manuscript and to Jim Heltshe for his statistical guidance. Research was conducted under an award from the Estuarine Reserves Division, Office of Ocean and Coastal Resource Management, National Ocean Service, National Oceanic and Atmospheric Administration.

The Narragansett Bay National Estuarine Research Reserve is part of the National Estuarine Research Reserve System (NERRS), established by Section 315 of the Coastal Zone Management Act, as amended. Additional information about the system can be obtained from the Estuarine Reserves Division, Office of Ocean and Coastal Resource Management, National Oceanic and Atmospheric Administration, US Department of Commerce, 1305 East West Highway - N/ORM5, Silver Spring, MD 20910.

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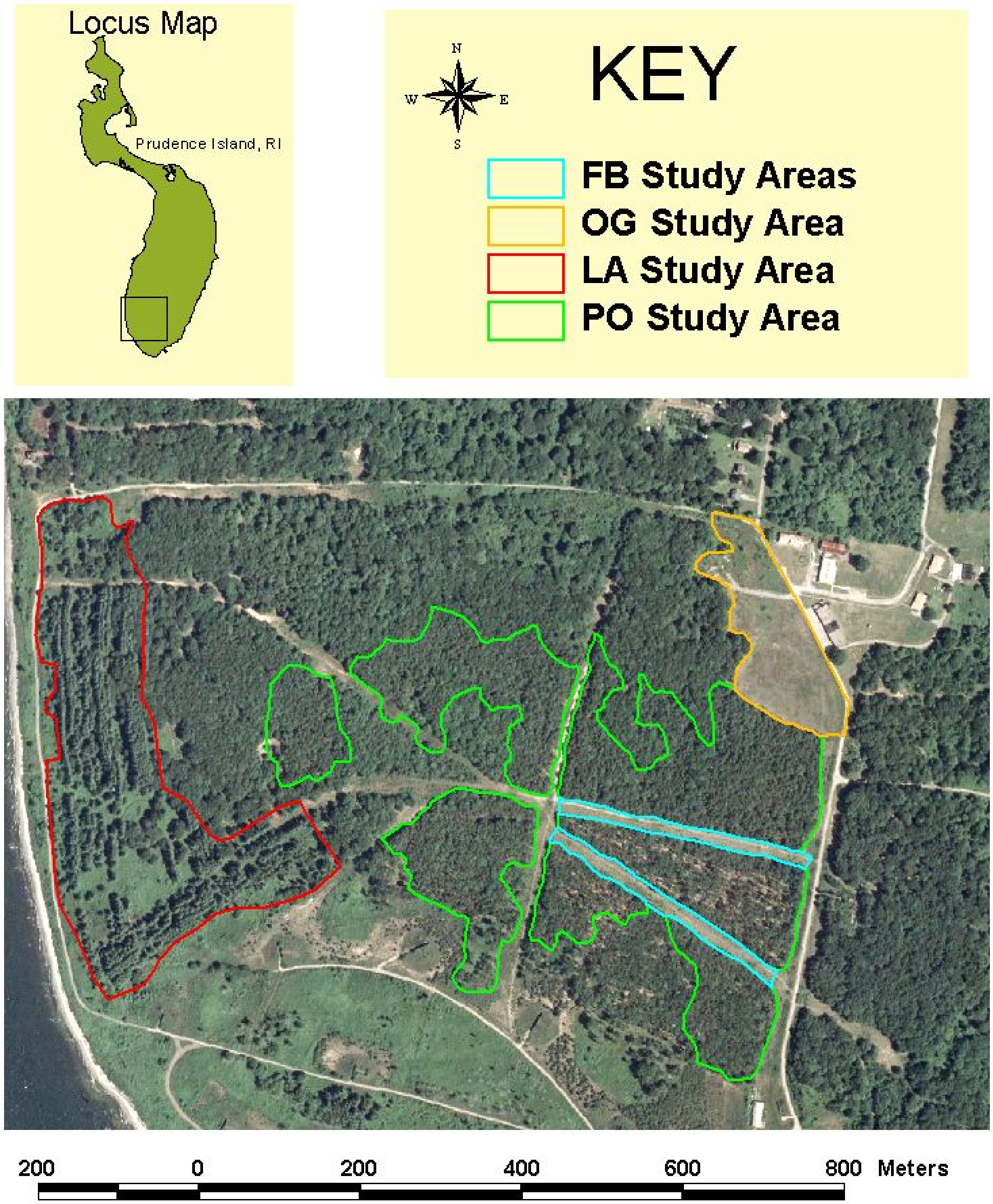

Figure 1. Firebreak (FB), open grassland (OG), larch forest (LA), and pitch pine-oak forest (PO) habitats of the South Prudence Unit of the NBNERR.