Impacts of endangered Key deer herbivory on imperiled pine rockland vegetation: a conservation dilemma?

M. A. Barrett & P. Stiling

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Abstract

Impacts of endangered Key deer herbivory on imperiled pine rockland vegetation: a conservation dilemma?— In the lower Florida Keys, endangered Key deer (*Odocoileus virginianus clavium*) herbivory, along with fire, can affect pine rocklands, an endangered plant community. We compared pineland vegetation from three studies over approximately 50 years on four islands with either high or low deer density (historical analysis). We also compared extant vegetation samples between two islands with high or low deer density, which contained pinelands burned 10 years and 14 years prior to sampling and control areas (unburned for > 50 yr). In addition, experimental deer exclosures and control plots established in pineland were prescribe burned and analyzed for deer effects on an island with high density of Key deer. The historical analysis suggests that, over time, deer–preferred plant species declined while less–preferred species increased, regardless of fire history on islands. The extant vegetation analysis suggests that fire and Key deer herbivory both reduce hardwood plant density and growth. Densities of deer–preferred woody species were higher on an island with low deer density than on an island with high deer density in burn treatments, but relatively similar in control areas. On the high deer density island, a fire effect was evident in that the control area had higher densities of woody species than burned areas, and herbaceous species richness was higher in the control area, indicating a possible refuge from deer herbivory. In deer exclosures, preferred woody species and herbaceous species tended to increase after fire, but decrease in adjacent open plots. Results suggest that Key deer herbivory, along with fire, shapes pine rockland plant communities, and that overbrowsing might have substantial impacts on preferred herbaceous and woody species in pinelands. Therefore, efforts could be confounded in managing both the endangered Key deer and the endangered pine rocklands that they affect.

Key bwords: Browsing, Exclosure, Fire–deer interactions, Fire history, Island, *Odocoileus virginianus clavium.*

Resumen

Impactos del pastoreo del ciervo de los cayos, una especie en peligro de extinción, sobre el también amenazado pinar rupícola: ¿un dilema conservativo?— En los cayos del sur de Florida, el pastoreo del ciervo de los cayos (*Odocoileus virginianus clavium*), junto con los incendios, pueden afectar a los pinares rupícolas, una comunidad vegetal en peligro. Hemos comparado la vegetación de los pinares de tres estudios llevados a cabo durante aproximadamente 50 años en cuatro islas con densidades de ciervos altas o bajas (análisis histórico). También comparamos muestras de vegetación existentes en dos islas con una densidad alta y baja de ciervos, que contenían pinares quemados 10 y 14 años antes del muestreo con áreas de control (sin incendiar durante más de 50 años). Además, se incendiaron intencionadamente y se analizaron parcelas experimentales con exclusión de ciervos y de control, para conocer los efectos de los ciervos en una isla con una gran densidad de éstos de los cayos. El análisis histórico sugirió que, con los años, las especies de plantas preferidas por los ciervos decayeron, mientras que las menos preferidas proliferaron, independientemente de los incendios sufridos. El análisis de la vegetación existente sugiere que tanto los incendios como la alimentación de los ciervos reducen la densidad y el crecimiento de la vegetación leñosa. Las densidades de las especies leñosas preferidas por los ciervos eran mayores en la isla con una densidad baja de ciervos, que en la isla con una densidad alta de ciervos tras los incendios,

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pero eran relativamente similares en las áreas de control. En la isla con una mayor densidad de ciervos, los efectos del fuego eran evidentes, ya que el área de control poseía mayores densidades de especies leñosas que las áreas incendiadas, y la riqueza de especies herbáceas era mayor en la zona de control, lo que indicaba que se trataba posiblemente de un refugio ante los ciervos. En las zonas cerradas a los ciervos, las especies herbáceas y las leñosas preferidas por los ciervos tendían a aumentar tras el incendio, pero disminuían en las áreas abiertas adyacentes. Los resultados sugieren que el pastoreo del ciervo de los cayos, junto con el fuego, dan forma a las comunidades vegetales rupícolas, y que el sobrepastoreo puede tener un impacto sustancial sobre las especies herbáceas leñosas preferidas de los pinares. Por lo tanto, los esfuerzos para la gestión, tanto del amenazado ciervo de los cayos como de los pinares rupícolas afectados por éste, también en peligro, podrían ser contradictorios.

Palabras clave: Pastoreo, Exclusión, Interacciones fuego–ciervos, Historial de incendios, Isla, *Odocoileus virginianus clavium.*

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Mark A. Barrett & Peter Stiling, Dept. of Biology, Univ. of South Florida, 4202 E Fowler Ave, SCA110, Tampa, FL 33620, USA.

Corresponding author: M. A. Barrett. Present address: U.S. Fish and Wildlife Service, Arthur R. Marshall Loxahatchee National Wildlife Refuge, 10216 Lee Road, Boynton Beach, FL 33437 USA. E–mail: mark_barrett@fws.gov

Introduction

There is much impetus for conservation biologists to protect both endangered animals and imperiled plant communities, though measures to protect these two entities are not always mutually exclusive. That is, protecting an endangered animal species could result in unintentional impacts on an endangered plant community. This could complicate management and conservation efforts to concomitantly protect both animal species and plant communities. Such a scenario could be occurring in the National Key Deer Refuge (NKDR) where protection of federally endangered Key deer (*Odocoileus virginianus clavium*), a diminutive subspecies of white–tailed deer, has led to increased deer densities on certain islands. This, in turn, has subsequently caused strong browsing pressure on tropical plant communities, e.g., hardwood hammock, buttonwood transition, and mangrove wetland (Barrett, 2004; Barrett & Stiling, 2006a; Barrett et al., 2006). In this paper, we investigate whether elevated densities of Key deer might also impact pine rockland (hereafter pineland), a globally endangered plant community (Florida Natural Areas Inventory, 1990) found in the NKDR.

Habitat loss and over–hunting of Key deer galvanized the establishment of the NKDR in 1957. Furthermore, extensive development in the Florida Keys prompted conservationists to begin land acquisition efforts to protect both endangered Key deer and plant communities. The refuge, and federal protection of Key deer in 1967, allowed the deer population to increase from 25–80 animals in the 1950s to 300–400 in the 1990s and 500–700 by 2000 (Klimstra, 1990; Lopez, 2001). Despite a potential range of 26 islands, approximately 75% of the Key deer population resides on Big Pine and No Name keys, resulting in high deer densities on these islands (Lopez et al., 2004a).

Because Key deer prefer pinelands as an important habitat for foraging (Dickson, 1955; Klimstra et al., 1974; Silvy, 1975; Klimstra & Dooley, 1990; Carlson et al., 1993; Lopez et al., 2004b), it is anticipated that the increased densities of Key deer would result in strong browsing pressure that could affect the fundamental composition of pineland plant communities. Pinelands in the NKDR may also be affected by fire, which can accelerate, decelerate, or stabilize community succession (Abrahamson, 1984a, 1984b). Pineland is considered a fire–climax system in the lower Florida Keys. In the absence of fire, pinelands may ultimately succeed into hardwood hammock, which may occur within 2 to 3 decades on the Florida mainland (Alexander, 1967) but may take longer (> 100 years) in the lower Florida Keys (Carlson et al., 1993). For example, Folk (1991) generally found higher densities of hardwood tree species in lower Key's pinelands subject to less–frequent burns (possibly > 50 yrs), though ultimate succession to hardwood hammock was incomplete.

Browsing pressure by Key deer could also impact pinelands, as heavy herbivory by white–tailed deer has been noted to influence species composition, successional pathways, and regeneration of plant communities (e.g., Russel et al., 2001; Rooney & Waller, 2003). Deer browsing can affect plant communities associated with fire by reducing plant growth in relatively short–time periods after fire (e.g., Davis, 1967; Huffman & Moore, 2004). Fire in pinelands benefits Key deer by increasing plant availability and quality, and consequently Key deer more frequently browse certain woody and herbaceous plant species in recently burned pinelands (Carlson et al., 1993; U.S. Fish and Wildlife Service, 1999).

To determine if increased densities of endangered Key deer, along with fire, are impacting pineland communities, this study investigated the effects of browsing pressure and fire on pinelands between islands with high and low densities of deer. The study tested the null hypotheses that (1) plant species differentially preferred by deer show no difference in relative density over a long–term period (approximately 50 years) on islands with contrasting deer densities regardless of fire history, (2) there is no difference in vegetative cover or density between islands with high and low deer density in areas with identifiable fire history, and (3) deer exclusion along with fire has no impact on pineland vegetation.

Methods

Study area

In the lower Florida Keys, the mean annual temperature is ~25.2°C and mean annual rainfall is ~1,000 mm. The climate is subtropical with evident wet (May–October) and dry (November–April) seasons. Many lower keys have vegetation types ranging from inundated wetlands and transitional zones to uplands (Dickson, 1955; Folk, 1991), though pinelands (totaling < 1000 ha) are predominately found on only five islands within the NKDR boundaries (24° 36´ N – 81° 18´ W to 81° 34´ W). For each island, percent pineland area of the total island area was as follows: Big Pine (28%), Little Pine (17%), No Name (11%), Sugarloaf (5%), and Cudjoe (5%), with relic stands on Howe (<1%) and Knockemdown keys (< 1%) (Lopez, 2001).

Pineland occurs 2 m or more above sea level and has the highest elevation among plant communities in the lower Keys (Folk, 1991). The soil is very shallow, underlain by oolitic limestone (exposed in many areas), which is continuous with Miami Oolite of mainland Florida (Dickson, 1955). Vegetation is primarily of West Indian origin (Stern & Brizicky, 1957). The monotypic canopy is dominated by the only pine species in the lower Keys, slash pine (*Pinus elliottii* var. *densa*), while the mid–story includes silver–palm (*Coccothrinax argentata*), Key thatch palm (*Thrinax morrisii*) and black–bead (*Pithocellobium keyense*). Though pinelands may contain a high diversity of shrubs and herbaceous species (Snyder et al., 1990), characterization of the understory depends on successional stage and fire history. Plant nomenclature throughout the paper follows Scurlock (1987) for woody species and Wunderlin (1998) for herbaceous species.

Key deer densities

Key deer densities were estimated by various methods for each sampling period. Dickson (1955) and Folk (1991) employed less rigorous methods, such as deer pellet counts, track counts, and informal census (i.e., casual sightings) to assign a relative use index of Key deer per island. Dickson (1955) only provided a qualitative account of deer incidence. Folk (1991), however, used the information of deer observations to create a quantitative index (e.g., 0 representing no use and 10 representing maximum use) that was used to coarsely estimate a range of deer abundance per island (Folk 1991 in Klimstra, 1990) —we used the midpoint of this range to present deer density per island in the present study. Between 1999 and 2000, infrared—triggered cameras placed near areas frequented by Key deer were used to estimate Key deer abundance on most islands (Lopez, 2001) following protocol of Jacobson et al. (1997) by using 1 camera/50 ha for periods > 3 months. On Big Pine and No Name keys, deer numbers were estimated via census and radio–telemetry (Lopez, 2001; Lopez et al., 2004a). Estimates of deer abundance from the Folk (1991) and Lopez (2001) studies were divided by island size (km^2) to conservatively calculate Key deer densities (deer/km^2) (table 1).

Fire history

Though fire history is limited in the lower Keys, Bergh & Wisby (1996) mapped occurrences (but not intensities) of controlled burns and wildfires between 1960 and 1996 within the NKDR. Big Pine experienced periodic fires in certain pineland areas (some areas were burned repeatedly) occurring in 1966, 1977, 1987, 1990, 1991 and 1994 whereas other areas have not been burned in > 50 years. Frequent fires likely occurred on Big Pine before the 1950s as well (Dickson, 1955; Alexander & Dickson, 1970). Pinelands on Sugarloaf were burned in 1987, 1990, and 1991 and also contained areas unburned in > 50 years. All pineland areas were burned on Little Pine, Cudjoe, and No Name in various years between 1960–1996, whereas no fires have occurred on Howe for at least 50 years.

Deer selectivity among plant species

Key deer preference among woody plant species (based on foliage consumption) were established from feeding trials (Barrett & Stiling, 2006a), rumen analyses (Klimstra & Dooley, 1990), and direct or indirect observations of Key deer browse (Dickson, 1955; Klimstra et al., 1974; personal observations). Woody plant species were grouped by deer preference as follows: (1) preferred species were *Bursera simaruba, Erithalis fruticosa, Bumelia celastrina, Jacquinia keyensis, Guapira discolor, Pithecellobium keyense*, and *Morinda royoc* and (2) less–preferred species were all other species besides those in the final category and (3) other species were fruit suppliers (three palm species and *Byrsonima lucida*) of which Key deer mainly consume the fruits (impact of Key deer frugivory on recruitment of plant species is uncertain). The following classification of deer preference was used for herbaceous species based on Dooley (1975), Folk (1991) and personal observations: (1) preferred species were notably grazed including *Chiococca pinetorum*, *Smilax havanensis*, and *Chamaecrista aspera*, (2) less–preferred species were the remaining species besides grasses and (3) other species were all grass species of which Key deer mainly consume the seeds.

Historical analysis

Pineland vegetation was analyzed on islands with high (Big Pine and No Name) and low (Cudjoe and Sugarloaf) deer densities over a long–term period of approximately 50 years. Three studies were used for temporal comparison including Dickson (1955), Folk (1991) and the present study, conducted in 2001. The historical analysis was utilized to track overall pineland condition as deer densities have increased, regardless of fire history. However, pineland on Sugarloaf was not sampled in the 1955 study.

For vegetation sampling protocol, densities (ha^{-1}) of woody plant species were estimated by counting individual plants in 1 x 30.5 m rectangular quadrats in the 1955 and 1991 study and a 1 x 50 m rectangular quadrat for the 2001 study. Woody seedlings < 30.5 cm tall were sampled in 1 m^2 quadrats ($n = 3$ per rectangular quadrat) nested within the larger quadrat in the 1991 study, whereas the 1955 and 2001 studies quantified woody seedlings in the entire larger quadrat. The same number of larger quadrats was used for each island ($n = 10$) among studies. Densities of woody plant species were summarized to height classes: < 1.2 m tall (within Key deer reach) and > 1.2 m tall (midstory / canopy). The former height class was examined for changes in understory vegetation that can be directly attributable to browsing effects, and the latter height class was examined for any changes in midstory / canopy species composition, potentially caused by lack of regeneration or stunted plant growth following deer herbivory. Key deer herbivory can be distinguished from other herbivory types as the petiole is left intact after browsing the leaf / leaflet.

Standardized relative densities (species density / $\sum$ all species densities) of plant species

Table 1. Estimates of Key deer densities or incidence on four islands in 1955, 1991 and 2001. For 1955, estimates are of deer incidence via observational analyses, and for 1991 and 2001, Key deer densities were calculated by dividing the estimated number of deer per study year by island size. The estimated population size represents the predicted size of the entire Key deer population throughout its range in the NKDR during each study year.

Tabla 1. Estimas de las densidades o presencia del ciervo de los cayos en cuatro islas, en 1955, 1991 y 2001. Para el año 1955, las estimas de la presencia de ciervos se hicieron mediante análisis de observación, y para 1991 y 2001, las densidades del ciervo de los cayos se calcularon dividiendo el número estimado de ciervos por año de estudio por el tamaño de la isla. El tamaño estimado de la población representa el tamaño predicho de la población total del ciervo de los cayos en todo su hábitat de distribución en el Refugio Nacional del ciervo de los cayos (NKDR) durante cada año de estudio.

	Island size	Deer incidence	Key deer km^{-2}	
Island name	km^2	1995	1991	2001
Big Pine	25.03	Extensive evidence	7.39	17.74
No name	4.91	Extensive evidence	13.75	21.59
Cudjoe	14.35	Very little evidence	0.21	0.35
Sugarloaf	8.06	No evidence	0.50	0.62
Estimated population size		25–80	300–400	500–700

were statistically evaluated per sampling period to alleviate effects of variation in quadrat size among studies on absolute plant densities. The relative densities of plant species, categorized by preferred, less–preferred and other species, were compared between each year (1955 vs.1991, 1955 vs. 2001, and 1991 vs. 2001) employing a similar analysis used by Whitney (1984) by testing the equality of two percentages (Sokal & Rohlf, 1969). This test compares the relative density, or percentage, between two samples (i.e., study years) by analyzing the sample proportions and the total sample size using the formula:

$$ts = \frac{\arcsin \sqrt{p1} - \arcsin \sqrt{p2}}{\sqrt{(820.8 \times (1/n_1 + 1/n_2)}}$$

where p1 and p2 are the proportions of each sample (e.g., relative density of preferred species in a study year), n_1 and n_2 are the representative sample size (i.e., total density of preferred species in a study year), and 820.8 is a constant representing the parametric variance of the distribution of arcsine transformations of proportions.

Variation in vegetation quadrat sizes between the studies also likely influenced estimates of plant species richness. This concern was minimized by passively sampling species richness (all height classes combined) from 2001 samples by equilibrating vegetation quadrat areas between studies following the formula (Gotelli & Graves, 1996):

$$E(S_j) = \sum_{i=1}^{S} 1 - (1 - a_j / A_T)^{n_i}$$

where a_j is the area of the *j*th subsample (i.e. the smaller 1991 quadrat), A_T is the area of the larger sample (i.e. the larger 2001 quadrat), n_i is the abundance of species *i* per island, and $E(S_j)$ equals the expected number of species in the 2002 sample. We qualitatively compared plant species richness from the 2001 passive sample to species richness from 1955 and 1991.

Analysis of deer–fire effects

Due to limitations in equivalent fire history among all islands, pineland communities were compared on two islands with contrasting deer densities, Big Pine and Sugarloaf, each containing areas with similar burn years and unburned areas. Deer densities were high on Big Pine and low on Sugarloaf, and fire history on both islands included areas burned in 1991 and 1987, and unburned areas. Therefore, data collected in 2001 (present study) are referred to as 10 years after fire (YAF), 14 YAF, and Control (unburned), respectively.

Vegetation in pinelands was sampled during the dry season from January to May of 2001. Digital habitat maps (MacAuley et al., 1994) were used in conjunction with maps from Bergh & Wisby (1996) to determine sample units for fire treatments on Big Pine and Sugarloaf keys. In the designated pineland

Table 2. Relative densities of woody plant species < and > 1.2 m tall categorized by deer preference, and plant species richness (S) of both height classes combined on islands with high and low deer densities. Plant measures were from three studies in pinelands from 1955, 1991, and 2001. Different letters among years within an island indicate significant difference (equality of percentages test —see Methods for explanation).

Tabla 2. Densidades relatives de las especies vegetales leñosas < y > de 1,2 m de altura, clasificadas según la preferencia de los ciervos, y riqueza de especies vegetales (S) de ambos grupos de alturas combinados en islas con densidades grandes y pequeñas de ciervos. Las mediciones de plantas proceden de tres estudios de pinares de 1955, 1991 y 2001. Las distintas letras entre los años dentro de una isla indican diferencias significativas (tests de igualdad de porcentajes —véase Methods para la explicación).

		Less–preferred relative density			Preferred relative density			Other relative density		
Island	Year	< 1.2 m	> 1.2 m	S	< 1.2 m	> 1.2 m	S	< 1.2 m	> 1.2 m	S
High deer density										
Big Pine	1995	35.6 a	69.8 a	10	27.4 a	17.0 a	5	37.1 a	13.2 a	3
	1991	67.2 b	76.2 a	15	22.7 a	8.2 a	6	10.1 b	115.6 a	3
	2001	63.4 b	70.2 a	17	14.8 b	11,9 a	6	21.5 c	17.9 a	3
No name	1995	19.0 a	19.6 a	17	68.1 a	67.6 a	5	12.9 a	12.8 a	3
	1991	54.3 b	74.2 b	19	41.4 b	18.0 b	4	4.3 b	7.7 a	3
	2001	62.8 b	73.4 b	20	28.6 c	18.3 b	3	8.6 ab	8.3 a	3
Low deer density										
Cudjoe	1995	38.8 a	40.4 a	18	47.1 a	45..7 a	5	14.1 a	13.9 a	4
	1991	43.2 a	46.3 ab	16	45.2 a	45.3a	4	11.6 a	8.4 a	3
	2001	46.4a	57.2 b	20	43.7 a	33.7 a	6	9.9 a	14.1 a	4
Sugarloaf	1995	–	–	–	–	–	–	–	–	–
	1991	72.2 a	47.1 a	23	22.1 a	29.8 a	5.7 a	23.1 a	2	
	2001	65.5 a	56.7 a	23	28.2 a	24.5 a	7	6.3 a	18.9 a	5

areas, a total of 43 vegetation rectangular quadrats (n = 5–13 quadrats per burn treatment per island) were randomly located and sampled. Rectangular 1 x 50 m quadrats were used to sample woody plant species that were assigned to height classes: < 1.2 m and > 1.2 m. Plant species that branched underground were considered individuals if the protruding stems were separated. Herbaceous ground cover was estimated at five circular plots (1 m^2) placed every 10 m along the 1 x 50 m quadrat using percentage cover classes described by Daubenmire (1969) as follows: < 1, 1–5, 6–25, 26–50, 51–75, and > 75. Canopy cover (5 samples per quadrat) was measured with a concave densiometer (Forest Densiometers, Bartlesville, Oklahoma) on a tripod (45 cm high) placed every 10 m along the 1 x 50 m quadrat. Methodology for recording densiometer readings was according to Lemmon (1957). Data were summarized for each burn treatment per island.

For quadrat data, density of woody plants (all species combined within each < 1.2 m tall and > 1.2 m tall classes), species richness, herbaceous % cover, and canopy % cover were each analyzed separately within each island of low (Sugarloaf) or high (Big Pine) levels of deer density using 1–way ANOVA with burn treatment (10YAF, 14YAF, Control) as the main effect. Bonferonni post hoc tests were used to compare differences among means. To meet normality assumptions as analyzed with Lillifor's test, data for plant density (both < 1.2 m and > 1.2 m class) were each log + 1 transformed. Jaccard similarity was used to compare species composition among burn treatments per island. Furthermore, each preferred woody species (< 1.2 m tall and > 1.2 m tall) was analyzed separately using nonparametric Mann–Whitney U tests comparing densities between Sugarloaf and Big Pine within each burn treatment (10YAF, 14YAF, Control).

Table 3. Mean (± SE) percent canopy cover, density of woody species (< and > 1.2 m tall) and percent cover of herbaceous species on islands with high deer density (Big Pine) and low deer density (Sugarloaf). Burn year treatments were 10YAF, 14YAF, and Control; Cc. Canopy cover; Ch. Cover of herbaceous species.

Tabla 3. Porcentaje medio (± EE) de la cobertura del dosel forestal, densidad de especies leñosas (< y > de 1,2 m de altura) y porcentaje de cobertura de especies herbáceas en islas con densidades de ciervos alta (Big Pine) y baja (Sugarloaf). Los incendios intencionados tuvieron lugar 10 años tras el fuego (YAF), 14YAF, y Control (C). Cc. Cobertura arbórea; Ch. Cobertura de especies herbáceas.

			Density woody species					
	% Cc		< 1.2 m tall		> 1.2 m tall		% Ch	
Treatment	X	± SE	X	± SE	X	± SE	X	± SE
High deer density								
10 YAF	51.6	5.7	14000	741.1	1550	320.2	16.0	2.8
14 YAF	47.1	3.3	14235	1891.1	2625	517.5	12.9	1.9
Control	59.6	5.9	22762	3099.1	4723	770.5	12.7	1.3
Lower deer density								
10 YAF	71.4	5.4	23400	1398.6	6480	804.0	9.5	1.2
14 YAF	68.8	4.4	34450	4952.3	11975	1570.7	8.8	2.0
Control	80.7	7.9	28040	5805.0	10240	1497.2	7.0	0.6

Due to pseudoreplication (Hurlbert, 1984), with only one area per burn treatment on each island, data were analyzed assuming that sampling error represented the experimental error (Webster, 1992). Pseudoreplicated designs for many fire studies are problematic but can be somewhat moderated (Mantgem et al., 2001). For example, because our study design did not allow burn treatments to be independently applied (i.e., vegetation quadrats were considered the independent units within each burn treatment per island), inferences derived from the analyses only include the study islands. However, because Key deer use is mainly confined to Big Pine and No Name, the limited inference space of this study still has valuable applicability for management of Key deer and their habitat.

Deer exclosures

In August 2001, two square 37 m^2 deer exclosures were constructed that were randomly located in pinelands on No Name Key. Control plots were non–randomly selected within 10 m of exclosure plots that had a relatively similar composition of plant species. Chain–linked fencing 1.8 m high was erected for exclosure plots to exclude Key deer, but was raised 15 cm above the ground to allow access by other species including the lower Keys marsh rabbit (*Sylvilagus palustris hefneri*), raccoon (*Procyon lotor*) and the Florida box turtle (*Terrapene carolina bauri*).

Data were collected every 6 months from August 2001 to July 2004. In June 2003 a prescribed fire burned > 95% of the area in both exclosures and their adjacent open plots. To examine deer–fire effects on plant composition and structure, the plots were sampled directly after the burn, then in August 2003, January 2004 and July 2004 (1 year post–burn). Woody species were quantified over the entire plot. Mean percent cover of herbaceous species was quantified from 9 circular subplots (1 m^2), and percent frequency of herbs was determined from the 18 subplots summarized over treatment replicates. To limit edge effects, data were not recorded in a buffer zone (0.3 mW x 2.1 mH) within the plot perimeters.

To separate potential deer effects from fire effects in the deer exclosure study, statistics were employed separately for data collected pre–fire (August 2001 to January 2003) and post–fire (June 2003 to July 2004). Plant abundances were summarized per treatment (open / exclosure) within each species group (i.e., preferred, etc.) for each replicate plot from the first sample date and last sample date for each pre–fire and post–fire event. The difference in plant abundance per species per replicate plot between the two times (abundance of last sample–abundance of first sample) was then calculated and averaged within treatment. Data (mean difference between first and last sampling dates) were tested using a two sample *t*–test for each plant category (e.g., pre-

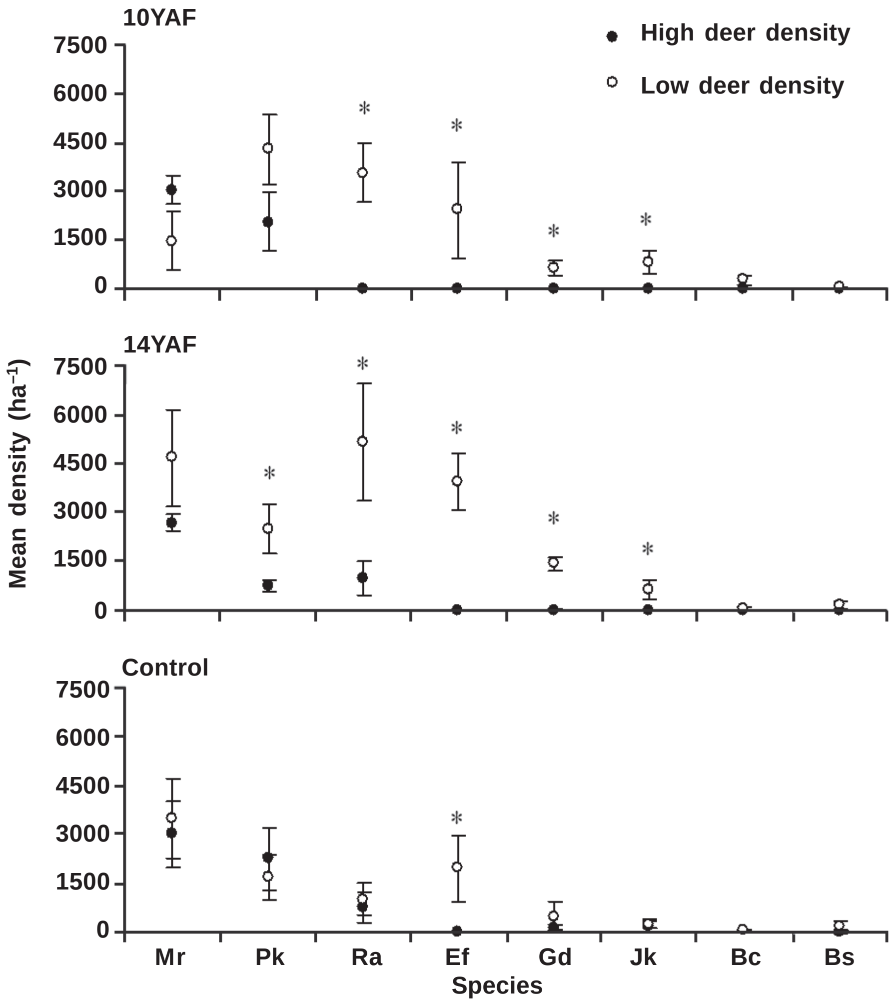

Fig. 1. Mean (± SE) densities of preferred woody plant species < 1.2 m tall in pinelands on islands with high deer density (Big Pine) and low deer density (Sugarloaf). Burn year treatments were 10YAF, 14YAF, and Control (unburned). Asterisks indicate significant differences ($P < 0.05$) based on Mann–Whitney U tests. Species: Mr. *M. royoc*; Pk. *P. keyense*; Ra. *R. aculeata*; Ef. *E. fructicosa*; Gd. *G. discolor*; Jk. *J. keyensis*; Bc. *B. celastrina*; Bs. *B. simaruba.*

*Fig. 1. Densidades medias (± DE) de las especies leñosas preferidas < 1,2 m en pinares en islas con una densidad de ciervos alta (Big Pine) y baja (Sugarloaf). Los incendios intencionados fueron 10YAF, 14YAF y Control (sin incendio). Los asteriscos indican diferencias significativas (*P *< 0,05), basándose en los test U de Mann–Whitney. (Para las abreviaturas, ver arriba.)*

ferred, etc.) for woody abundance and herb percent cover. Herb percent cover was arcsine square root transformed prior to analysis to meet normality assumptions. All statistical analyses were tested at the $P = 0.05$ significance level. For data analyses, SYSTAT® (1998) was used for conventional statistics (e.g., ANOVA, *t*–tests) and Microsoft® Excel (Microsoft, 1997) was used to set up and perform analyses that were not readily available (e.g., equality of percentages test, passive sampling).

Results

Historical analysis

Regardless of fire history, relative plant densities < 1.2 m tall of deer–preferred species significantly declined while less–preferred species increased on islands with high deer density (table 2). Relative densities of preferred species in the > 1.2 m height class also tended to decline on islands with high density of deer. Comparatively, islands

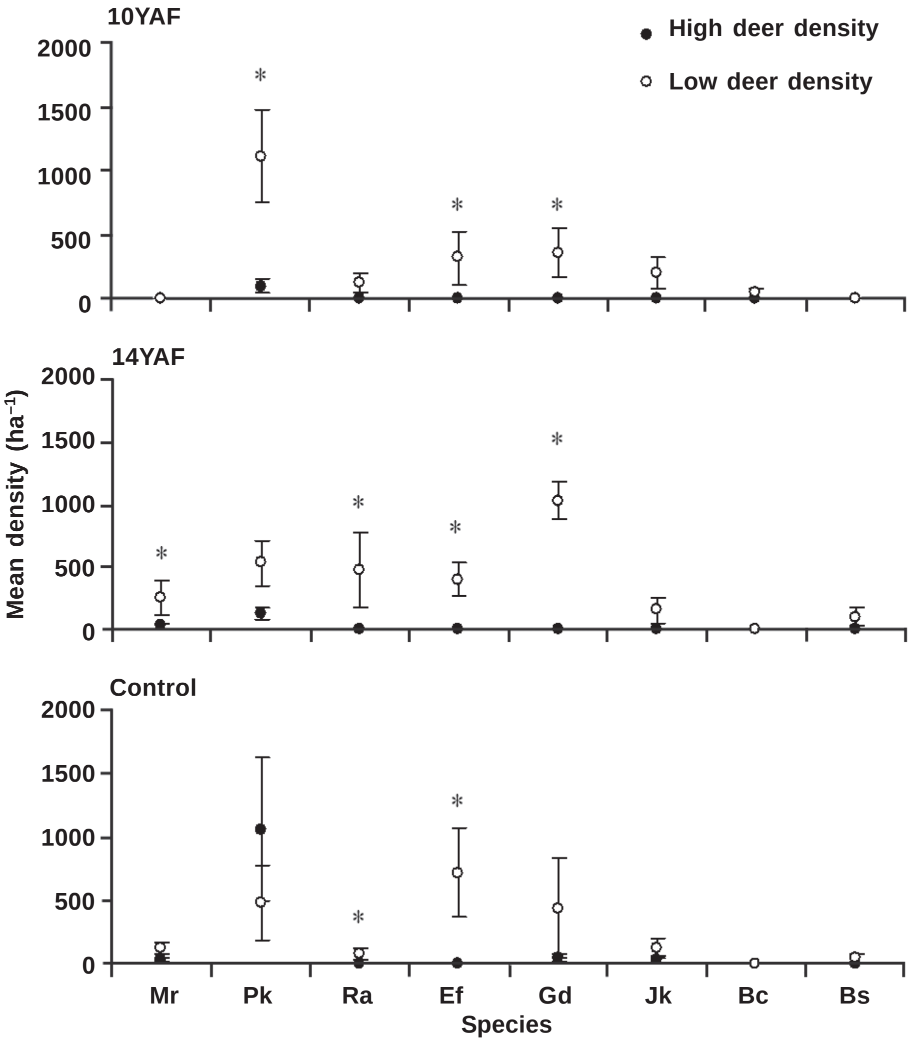

Fig. 2. Mean (± SE) densities of preferred woody plant species > 1.2 m tall in pinelands on islands with high deer density (Big Pine) and low deer density (Sugarloaf). Burn year treatments were 10YAF, 14YAF, and Control (unburned). Asterisks indicate significant differences ($P < 0.05$) based on Mann–Whitney U tests. (For abbreviations of species see figure 1.)

*Fig. 2. Densidades medias (± EE) de las especies leñosas preferidas > 1,2 m en pinares en islas con una densidad de ciervos alta (Big Pine) y baja (Sugarloaf). Los incendios intencionados fueron 10YAF, 14YAF y Control (sin incendio). Los asteriscos indican diferencias significativas (*P *< 0,05), basándose en los test U de Mann–Whitney. (Para las abreviaturas de las especies ver la figura 1.)*

with low deer density showed little change in relative density of plant species regardless of deer preference (table 2). Observed changes in species richness were predominately found on islands with many deer, especially increases in less–preferred species.

Deer–fire effects on vegetation

Among burn treatments in pinelands, percent canopy cover was similar on both Sugarloaf ($F_{2, 15} = 0.21$, $P = 0.813$) and Big Pine ($F_{2, 22} = 2.64$, $P = 0.093$) (table 3). Mean densities of woody plant species < 1.2 m tall were similar on Sugarloaf ($F_{2, 15} = 1.64$, $P = 0.227$) but marginally differed on Big Pine ($F_{2, 22} = 3.38$, $P = 0.053$) (table 3). Mean densities of woody plants for the > 1.2 m tall class were significantly different among burn treatments on Sugarloaf and on Big Pine (both $P < 0.009$), with densities in the 10YAF less than Control (Bonferonni post–hoc: $P = 0.062$ (marginal significance) for Sugarloaf and $P = 0.007$ for Big Pine) (table 3). Mean woody

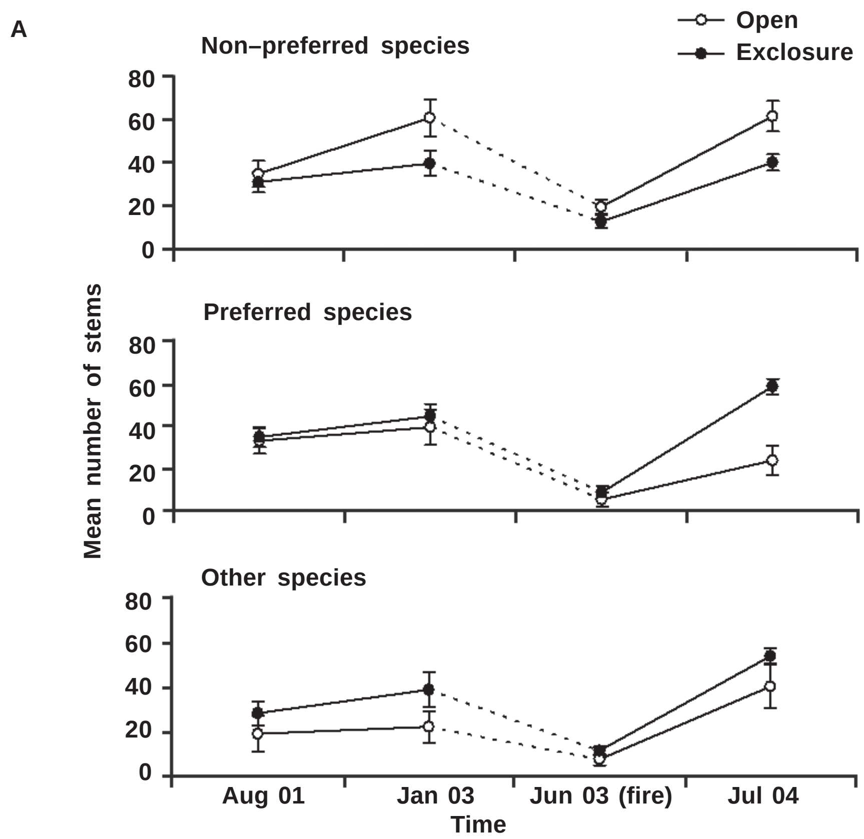

Fig. 3. Mean (± SE) abundance (number of stems) of woody species (A) and % cover of herbaceous species (B) in exclosure and open plots in pinelands on No Name. A fire occurred in June 2003. For woody species, plant abundances were all height classes combined for each category of deer preference, and plant species are categorized as preferred, non–preferred, and other (*Palm* spp. and *Byrsonima lucida*). Herbaceous species are categorized as preferred, less–preferred and grass species (other).

species richness was similar on Sugarloaf among 10YAF, 14YAF, and Control plots with 29, 33, and 30 species respectively ($F_{2, 15}$ = 0.88, P = 0.430), compared to Big Pine's 18, 27 and 30 species respectively ($F_{2, 22}$ = 6.13, P = 0.011) where 10YAF differed from 14YAF and Control (Bonferonni post hoc: P < 0.017). Differences were mainly caused by absence of deer–preferred (hammock associated) species in 10YAF. Jaccard similarity indices indicated that plant species composition among burn treatments on Big Pine were all < 69%, whereas similarities were > 89% among burn treatments on Sugarloaf.

Compared to Sugarloaf, Big Pine had lower densities of most preferred woody plant species < 1.2 m tall (Mann–Whitney U tests; fig. 1). The species highly preferred by Key deer that were absent or virtually absent from Big Pine pinelands were *Bursera simaruba, Erithalis fruticosa, Jacquinia keyensis, Guapira discolor* and *Bumelia celastrina*, which are all mainly associated with hardwood hammock. As time from last burn increased, a pattern of increasing density and number of preferred species was evident on Big Pine, suggesting that unburned pinelands support more deer–preferred woody species on this island. Similar trends also occurred for densities of preferred plant species > 1.2 m tall (fig. 2).

Mean percent cover of herbaceous species was similar among burn treatments on Sugarloaf ($F_{2, 15}$ = 0.39, P = 0.681) and on Big Pine ($F_{2, 22}$ = 0.30, P = 0.744) (table 3), though control plots tended to have the lowest cover values on both islands. For 10YAF, 14YAF, and Control areas, herb species richness significantly differed on Big Pine with 15, 16, and 25, respectively ($F_{2, 22}$ = 5.23, P = 0.015) with Control having the highest richness (Bonferonni post hoc: P < 0.025), but did not differ on Sugarloaf ($F_{2, 15}$ = 0.78, P = 0.476) with of 6, 9, and 7, species respectively.

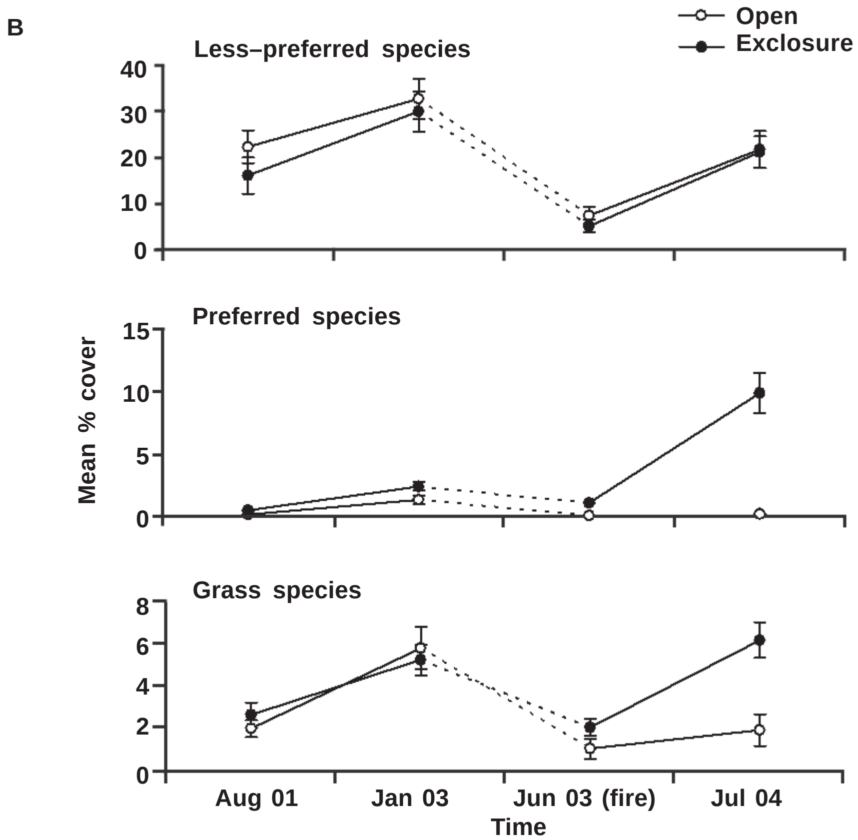

Fig. 3. Abundancia media (número de tallos) (± DE) de especies leñosas (A) y % de cobertura de especies herbáceas (B) en áreas cerradas y abiertas en los pinares de No Name. Hubo un incendio en junio del 2003. Para las especies leñosas, las abundancias son el resultado de la combinación de todas las clases de altura para cada categoría de preferencia de los ciervos, y las plantas se clasificaron en preferidas, menos preferidas y otras (especies de palmáceas y Byrsonima lucida*). Las especies herbáceas se clasificaron como preferidas, menos preferidas y especies de hierbas (otras).*

Deer exclosures and fire

For both exclosures and open plots, some woody individuals (e.g., *P. keyense* and *Myrsine floridana*), that were burned and appeared dead re–flushed within two months after the fire. Though differences between time periods in abundance or percent cover were analyzed for plant data, raw data are presented in figures 3A and 3B. For the pre–fire analysis, the difference in abundance of less–preferred woody species was significantly higher in open plots than exclosure plots (t = 10.82, P = 0.008) (fig. 3A). However, the difference in woody plant abundance did not significantly differ between treatments for preferred (t = 1.37, P = 0.304) or other species (t = 3.13, P = 0.089). For post–fire analysis, the difference in abundance of less–preferred woody plant species was higher in open plots than exclosure plots (t = 6.60, P = 0.022) (fig. 3A). Difference in abundance of preferred plant species was significantly higher in exclosures than control plots after fire (t = 8.49, P = 0.014) (fig. 3A). Palm species and *Byrsonima lucida* increased in both open and exclosure plots but the difference in abundance did not vary between treatments (t = 3.09, P = 0.091) (fig. 3A). Woody species richness increased inside exclosures from 15 pre–fire to 18 post–fire, but declined in open plots from 14 pre–fire to 12 post–fire.

For the pre–fire analysis, the difference in percent cover was similar between exclosure and open plots for less–preferred herbaceous species (t = 0.60, P = 0.609), preferred species (t = 4.13, P = 0.054) and grasses (t = 1.89, P = 0.198) (fig. 3B), though preferred species showed a marginal trend in difference. For post–fire analysis, the difference in percent cover of less–preferred herb species was not significant (t = 0.987, P = 0.428). The difference in percent cover did significantly vary for grasses (t = 0.753, P = 0.017) and preferred species (t = 12.33, P = 0.007). The trend of all preferred herb species was driven by *Chamaecrista aspera,* which continually increased in cover (from 1% to 12%) and frequency (from 22% to 83%) from Aug 2001 to Jul 2004. Herb species richness increased by 2 inside exclosures and decreased by 2 in open plots from pre–fire to post–fire. Though not quantified, many herb species were observed (post–fire) flowering inside exclosures compared to open plots, and certain species were observably (post–fire) taller inside exclosures compared to open plots.

Discussion

Imperiled pineland plant communities on certain islands in the NKDR are being impacted by high densities of endangered Key deer. Although Key deer densities are not directly comparable between studies (historical versus present) due to different methodologies, Big Pine and No Name have had relatively higher deer densities or incidence compared to other islands, and thus browsing impacts are presently pronounced on these two islands. Whether this impact is negative, however, remains to be seen. For example, although deer browsing is causing preferred plant species to decline in pinelands, many of these are hardwoods that are mainly associated with hammock communities. This may aid in retarding succession and maintaining open pinelands, a natural landscape pattern on Big Pine (Snyder et al., 2005) and deter heavy fuel buildup that could cause damaging fires. Also, Key deer frugivory may aid in dispersing the seeds of certain plant species, such as palms, via endozoochory. Contrarily, Key deer herbivory may have detrimental impacts on the herbaceous layer causing certain pineland associated species to remain depleted, e.g., *C. aspera* incidence on No Name. Our results indicate that strong browsing pressure may outweigh the benefits of fire on pineland communities, a pattern found in other herbivore–fire studies (e.g., Romme et al., 1995; Hessl, 2002).

On Big Pine and No Name, Key deer herbivory appears to have longer–term impacts on composition of woody plant species, compared to fire, as strong browsing pressure deters the establishment and growth of preferred hardwood species, while less–preferred species increase. These results negate the first null hypothesis regarding a deer effect on vegetation, regardless of fire history, over a long–term period on islands with contrasting deer densities. Though it is certainly not the rule, a lack of a fire effect on plant species composition can occur (e.g., Dix, 1960; Daubenmire, 1969; Abrahamson, 1984a). For example, in pinelands on Sugarloaf (low deer density), Folk (1991) found a relatively short–term effect (2–3 years) of fire on composition of woody plant species, though the effect of fire is lacking in the long term (> 10 YAF) as indicated in the present study. However, fire could revitalize some herbaceous species that notably suffer from heavy browsing by Key deer as evidenced from the deer exclosure study on No Name. Herbaceous species tend to recover slowly after release from browsing pressure by white–tailed deer (Balgooyen & Waller, 1995), yet fire often aids in the recovery (Lay, 1956; Snyder, 1986). For example, mean cover of *C. aspera* increased only slightly inside exclosures, relieved of Key deer herbivory for a 2–year period, until fire impacts caused mean cover and frequency of *C. aspera* to considerably increase within 2 months post–burn and remain elevated by 1 year post–burn. Yet, even after fire on No Name, mean % cover of *C. aspera* and other deer–favored species remained very low outside deer exclosures. These results contradict null hypothesis 3 regarding deer exclosures. Further evidence for fire–deer effects on herb species was observed on Big Pine in unburned pinelands, which had the highest herb species richness compared to other areas, thus negating null hypothesis 2. Because white–tailed deer tend to forage on herbaceous species more in burned areas (McCulloch, 1969) and Key deer frequently browse burned areas (Carlson et al., 1993; Snyder et al., 2005), unburned pinelands where Key deer browsing is not prevalent could offer a "refuge" for some herb species. On Sugarloaf, where browsing pressure is relatively much lower, however, substantial canopy cover likely limits the establishment of herbaceous species indicating that a complex interaction of fire and deer herbivory likely determines herbaceous composition and richness in NKDR pinelands.

Our study suffered from un–replicated fire treatments among islands, so our results should be viewed with caution and interpretations should mainly be limited to the three islands of study (Big Pine, Sugarloaf and No Name). However, Big Pine and No Name contain the majority of the Key deer population and the only other island with relatively extensive pineland is Little Pine, so our study does provide valuable information for NKDR biologists regarding Key deer and fire management. Furthermore, our results were consistent with other pineland vegetation studies in the NKDR. For example, Snyder et al. (2005) found that stem length, cover and richness of pineland plant species was higher in small exclosures (1 m^2) compared to open plots 1 year post–burn on Big Pine. Furthermore, we found more preferred woody species in unburned pinelands on Big Pine (again negating hypothesis 2). This result is comparable to previous vegetation surveys on Big Pine that found deer–preferred woody species in unburned pinelands (Dickson, 1955; Alexander & Dickson, 1970). However, Key deer densities on Big Pine were much lower during the studies in the 1950s and 1970s, which resulted in the presence of certain deer–preferred plant species (seedlings and trees) that are lacking from the present study, such as *E. fruticosa* and *J. keyensis*, both of which are state–listed threatened species. Impacts from high densities of Key deer on preferred species in pineland are comparable to effects on the same preferred species in other plant communities on

Big Pine and No Name (Barrett & Stiling, 2006a; Barrett et al., 2006), suggesting that the herbivore effects are not spurious. Furthermore, impacts from other herbivores are not likely as marsh rabbit populations are very small on islands they occupy and are generally not found in pinelands or near the deer exclosures on No Name (Faulhaber 2003); also insect herbivory is not considerable in pinelands (personal observation) or in other communities in the NKDR (Barrett & Stiling, 2006b).

A simple solution to managing Key deer and pinelands is likely not possible. Instead, a more comprehensive and complicated approach is required that takes into account deer–fire interactions on plant communities, species–specific responses of plants to fire, selective deer herbivory, and fire effects on deer population dynamics. Perhaps burning pinelands in small tracts of 20–40 ha when possible could (1) allow unburned areas to serve as refuges from heavy deer herbivory, (2) provide a mosaic of successional stages to potentially increase plant species diversity over the landscape, and (3) gradually establish small areas with quality food plants for deer, but (4) deter large–scale nutrient inputs that could substantially augment Key deer populations. Undoubtedly, striking a careful balance of adaptive deer management and controlled burn regimes is required in the NKDR to alleviate a potential conservation dilemma of protecting both the endangered Key deer and endangered pine rocklands.

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