CONSERVATION ISSUES

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Disturbance and Scale Effects on Southern Old-Growth Forests (USA): The Sand Pine Example

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ABSTRACT: Sand pine *(Pinus clausa* [Chapm. ex Engelm.] Vasey ex Sarg.), often a monotypic dominant of the Florida (USA) scrub assemblage, is an early successional tree species that is small in size, short-lived, and disturbance dependent. It does not conform to traditional images of old-growth forest. Nevertheless, to implement old-growth policy, the U.S. Forest Service has published stand-scale quantitative guidelines for recognizing old-growth sand pine (Outcalt 1997). Although the policy is well intentioned, we question the conceptual basis and management perspective implicit in developing a stand-scale definition of old-growth sand pine. Our principal concerns involve matters of scale and disturbance suppression. A stand-scale perspective on management of old-growth sand pine is doomed to failure: if fires are allowed to burn, older forests will be consumed; if fires are suppressed, sand pine will likely be replaced by shade-tolerant associates. A landscape-level management framework is essential to allow for a spatiotemporally shifting pattern of mature sand pine patches embedded within a matrix of younger scrub. Moreover, we caution that modern scrub vegetation in wilderness areas occurs on a small scale and is dramatically altered by fire suppression; therefore, it is imprudent to use wilderness areas as a standard for judging the character of a sand pine scrub landscape in pre-European-contact conditions.

Index terms: Florida, old growth, *Pinus clausa,* sand pine scrub, scale effects

DIFFERING IMAGES OF OLD GROWTH

Images of old-growth forest in the American Southeast are varied. For many, the mixed mesophytic cove forests of the southern Appalachians, with large tulip-popiar *(Liriodendron tulipifera* L.) trees, lichen-covered tree bark, humid air, and high arborescent diversity is the epitome of old-growth forest (Braun 1950, Whit-taker 1956, Martin 1992). Others might select a cypress swamp as an image of old-growth forest, typified by massive, old baldcypress *(Taxodium distichum [L.]* Richar3) trees, branches festooned with Spanish moss *(Tillandsia usneoides L.),* and standing water punctuated by cypress knees (Stable et al. 1988). Still others may be partial to an old-growth image of the longleaf pine *(Pinus palustris* Miller) savannas of the upland Coastal Plain, with scattered large, several-hundred-year-old long. eaf pine trees amidst a wiregrass *(Aristida beyrichiana* Trin. and Rupr.) under-story historically maintained by regular surface fires (Platt et al. 1988, Glitzenstein et al. 1995). Finally, there are those who argue for recognition of the old-growth character of post oak *(Quercus stellata* Wangenh.)/ blackjack oak *(Q. marilandica* Muenchh.) woodlands of the Ozark Plateau, with open, stunted, aged trees on windswept, rocky ridges and south-facing slopes characterized by thin, sandy soils (Stahle and Chaney 1994).

Collectively, these images capture many different dimensions of the old-growth forest concept. They range across a continuum of moisture regimes, from hydric swamps to xeric ridges. They span a structural range from dense forests of large trees to savannas and open woodlands of stunted trees. They represent a variety of relationships with disturbance, from cove forests presumably maintained by individual treefall and canopy gap regeneration (Runkle 1990) to savannas frequented by surface fires several times per decade. Among this constellation of features, a few basic elements of an old-growth forest concept emerge: oldness, naturalness, structural complexity, and, perhaps, stability.

Surprisingly, the literal oldness of trees on a site is rarely stressed as an important trait in old-growth forest recognition, although David Stahle and other dendrochronologists have championed its importance (Stahle and Chaney 1994). This lack of attention presumably is rooted in the logistical difficulty of extracting tree cores during rapid stand inventories. Nonetheless, some might argue that the literal age of individual trees in a stand is of less significance to old-growth character than the oldness of the stand itself, that is, the amount of time it has remained free of catastrophic disturbance (Whitney 1987).

Much attention has been paid to the notion of naturalness in grappling with definitions of old-growth forests. Most conceptual definitions of old growth express or imply a relative absence of human modification (Hunter 1989, Hunter and White 1997). Generally, this attention is focused on technological activities of modern culture (such as logging, grazing, or land clearing), al-though the notion of naturalness opens a Pandora's box when viewed from the historical perspective of the interaction of indigenous cultures with their landscape (Denevan 1992, Vale 1998), or treated in light of the philosophical debate on humans as part of nature (Gomez-Pampa and Kaus 1992, Cronon 1995). Regardless of debates over the meaning of "natural," the obviousness of direct human modification of a setting plays a key role in the evaluation of its old-growth character.

Structural complexity is the cornerstone of practical, quantitative definitions of old-growth forest stands. Many authors have established size-structural criteria for old-growth recognition, such as the density of trees exceeding a given diameter at breast height (dbh), or a minimum value for bas-al area (Martin 1992, Hardt and Swank 1997). A complex vertical profile with multiple tree layers is indicative of old-growth structure in some practical definitions, although this implies a strong role for localized tree-fall and within-stand mortality agents. Another prominent element of structural complexity in practical old-growth definitions is evidence of on-going mortality in the stand, usually in the form of a critical concentration of snags, downed logs, or other coarse woody debris (Martin 1992, Hardt and Swank 1997). Although structural complexity has been touted as a key trait in old-growth forests, it varies spatially within forest types and regionally among forest types, so that few quantitative criteria could be universally applied with satisfactory results. Hence, quantitative definitions must be tailored to specific forest types and ecological regions (U. S. Forest Service 1997).

Earlier views accepted stability as a common feature of old-growth forests (Bormann and Likens 1979, Whitney 1987), envisioning stands in which populations maintain a dynamic equilibrium over time stimulated by fine-scale patterns of mortality and recruitment. In recent decades, a range of views has been expressed regarding the role of natural stand-destroying agents in old-growth forests. Some have insisted that recently catastrophically disturbed sites lose their old-growth status (Whitney 1987). Others have embraced events such as crown fires and blowdowns as a part of the texture of old-growth images (Sprugel 1991, Kaufmann et al. 1992, Trombulak 1996). The balance of opinion has shifted so that stability is no longer widely regarded as a typical condition of old-growth forest ecosystems.

BRIEF BACKGROUND ON OLD-GROWTH FOREST POLICY

As part of the reaction to the spotted owl *(Strix occidentalis* [Xantus de Vesey]) controversy in the Pacific Northwest during the 1980s, the U.S. Forest Service (USFS) formally recognized old growth as a critical forest resource and implemented a policy to identify tracts of old-growth forest that remain under the Forest Service's jurisdiction. As an aid to stand recognition and mapping, the Old-Growth Task Force for the combined Eastern and Southern Regions mandated that specific, quantitative definitions of old-growth forest be established for each forest type formally recognized by the Society of American Foresters (SAF) (Eyre 1980). Balanced against other priorities, appropriate examples of old-growth forest from each forest type were to be included as set-aside areas (i.e., areas "permanently" excluded from timber sales) in the plans developed for each national forest. (See Tyrrell 1996 for a more detailed treatment of the history of USFS old-growth policy.)

Several difficulties have emerged in the implementation of this policy, chief among which are practical problems presented by the prevalence of early successional dominants in SAF forest types and their linkage to catastrophic disturbance agents, as well as related conceptual concerns over the spatial scale at which management for old growth should be focused. In this pa-per, we highlight these difficulties by contemplating the definition and management of a single SAF example: old-growth sand pine *(Pinus clausa* [Chapm. ex Engelm.] Vasey ex Sarg.) forests.

SAND PINE FORESTS

Sand pine forests (SAF cover type 69, Eyre 1980) are not among the gallery of southern old-growth forest images with which we opened this paper. Sand pine is an early successional species that displays most of the traits that typify this seral status; it is generally short-lived, rapid growing, early maturing, and small in stature compared to most pines and dominant species of other southern forests. Sand pine occasionally exceeds 100 years of age in some stands, and maximum stem diameters are less than 50 cm dbh. Sand pine is the nearly monotypic, overstory dominant of the Florida scrub (Myers 1990). The scrub assemblage comprises an understory of evergreen shrubs and small trees, including myrtle oak *(Quercus myrtifolia* Willd.), sand live oak *(Q. geminata* Small), Chapman's oak *(Q. chapmanii* Sargent), saw palmetto *(Serenoa repens* [Bartram] Small), scrub palmetto *(Sabal etonia* Swingle ex Nash), rusty lyonia *(Lyonia ferruginea* [Walter] Nuttall), and Florida rosemary *(Ceratiola ericoides* Michaux). In addition, Florida scrub is habitat for a number of federally threatened or endangered plant and animal species, including gopher tortoises *(Gopherus polyphemus* [Daudin]) and scrub jays *(Aphelocoma coerulescens* [Bost.]) (Flather et al. 1994).

Despite the ample precipitation that characterizes Florida, scrub sites are edaphically dry and nutrient poor, occurring on virtually pure quartz sand (Evans et al. 1996) associated with the modem coastal strand as well as paleo-dunes in the interior of the Florida peninsula.

Sand pine has been taxonomically partitioned into two varieties, based on geographic disjunction and expression of cone serotiny. Ocala sand pine *(Pinus clausa* var. *clausa* D.B. Ward) is limited in distribution to the Florida peninsula and exhibits a high degree of cone serotiny in many populations. Choctawhatchee sand pine (P. c. var. *immuginata* D.B. Ward) occurs primarily on the Florida panhandle (one population occupies a barrier island in coastal Alabama), and cone serotiny is rare in this variety. These two varieties differ substantially in response to disturbance (Myers 1990). Ocala sand pine, the serotinous variety, is a fire-resilient taxon (McCune 1988); historically, stands were consumed by crown fires at 40- to 60-year intervals. Populations are even-aged, with large patches established following stand-destroying fires. With the advent of effective fire suppression following World War II, many extant sand pine forests have developed canopy gaps from root rot and contain many trees of relatively old age (60–70 years) (Parker et al. 1997b). By contrast, Choctawhatchee sand pine shows little imprint of crown fires; rather, episodic wind events, such as hurricanes, prune the existing canopy and permit regeneration in small patches. Hence, forests are more uneven-aged and Choctawhatchee sand pine is persistent without the intervention of stand-destroying disturbance events (Myers 1990).

Given its small stature, short life span, and dependence on disturbance (either fire or wind) for regeneration, sand pine seems to be an unlikely candidate for consideration as an exemplar of old-growth forest. But because it constitutes an SAF cover type, the USFS has published an empirical definition of old-growth sand pine forest (Outcalt 1997). Should sand pine have been excluded from the southern region's characterization of old-growth forests, or should our image of old-growth be re-molded to fit the character of the region and its flora?

STAND-SCALE DEFINITIONS OF OLD-GROWTH SAND PINE FORESTS

Ot.r prior experience in sampling sand pine forests for other purposes lends itself to an appraisal of Outcalt's (1997) stand-scale definition of old-growth sand pine forests. In 1994 we mapped small plots (0.16–0.36 ha) from mature sand pine forests in six locations, three of each sand pine variety (Table 1). We recorded diameters and extracted cores from each sand pine individual exceeding 5 cm dbh to determine age. Hence, we have reasonably good demographic characterizations for representative sites. Moreover, we have sampled a broader range of sand pine forests (12 Ocala sand pine stands, 9 Choctawhatchee sand pine stands) for the purposes of characterizing genetic structure within and between varieties (Parker and Hamrick 1996, Parker et al. 1997a).

Ocala Sand Pine

The stands used by Outcalt (1997) to develop quantitative measures of old-growth conditions for Ocala sand pine averaged 55 years of age, based on a small sample of cores from the largest trees (Table 2). Our mature Ocala sand pine stands, based on a complete collection of tree cores, were 60–70 years old. Maximum stem diameters were similar for both studies, approximately 43–44 cm dbh for the largest trees. The most striking contrast was evident for mean stand basal areas, roughly twice as great in our data as in Outcalt's (1997). In general, Ocala sand pine is neither old nor massive. Myers (1990) indicated that the oldest known Ocala sand pine trees are about 80 years of age. Even the former champion tree from Wekiwa Springs State Park was smaller than 50 cm dbh and less than 50 years old when it was felled by a windstorm.

Outcalt (1997) emphasized that Ocala sand pine stands exceeding 40 years of age of-ten succumb to root rot, so that a few snags and canopy gaps are found in old-growth stands. Our data provide comparable measures of snag density. Whether this is historically representative of mature sand pine stands is debatable. Prior to the advent of fire suppression around the 1940s, snags would have been more readily consumed by crown fires; indeed, median stand age would have likely been lower, so that Ocala sand pine forests old enough to experience initiation of gap-phase mortality were probably uncommon. In any event, today's older sand pine forests are not very structurally diverse, nor are they laden with snags and downed wood. Without human intervention into the natural fire regime,

Table 1. Location of Florida sand pine stands investigated for this study.

Site Name	County	Latitude	Longitude	Plot Size (m)
Choctawhatchee Sand Pine *(Pinus clausa* var. *immuginata)*				
Eglin Air Force Base, Scrub Hill Site	Walton	30°34'N	86°09'W	50 x 50
St. Joseph Peninsula State Park	Gulf	29°48'N	85°25'W	40 x 40
Gulf Islands National Seashore, Naval Live Oaks	Santa Rosa	30°22'N	87°08'W	40 x 40
Ocala Sand Pine *(Pinus clausa* var. *clausa)*				
Highlands Hammock State Park	Highlands	27°29'N	81°31'W	50 x 50
Jonathan Dickinson State Park	Martin	27°01'N	80°07'W	60 x 60
Rock Springs Run State Reserve	Orange	28°46'N	81°27'W	40 x 40

Table 2. Comparison of quantitative attributes between Outcalt's (1997) examples of old-growth sand pine stands and our examples of mature sand pine forests. Values from Outcalt occupy the top line of each entry; values from our sampling occupy the bottom line.

	Choctawhatchee Sand Pine		Ocala Sand Pine	
Attribute	**Range**	**Mean**	**Range**	**Mean**
Age of largest tree (years)	60-113	83	45-70	55
	66-89	79	53-61	57
Age of oldest tree (years)	N/A	N/A	N/A	N/A
	72-132	107	59-71	63
Maximum diameter (cm)	32.5-47.9	39.2	26-43	35.0
	26.1-37.1	33.4	31.1-44.3	38.5
Stand basal area	11.2-19.2	16.1	8.4-9.0	8.6
(m^2/ha of trees > 10 cm dbh)	5.6-15.4	10.3	9.9-26.6	17.6
Tree density (#/ha > 10 cm dbh)	247-450	354	160-300	194
	260-362	295	289-556	418
Snag density (#/ha >10 cm dbh)	7-47	22	13-73	47
	20-38	28	24-88	53

most dead wood, along with the dense understory shrub layer, would be readily consumed in crown fires.

Choctawhatchee Sand Pine

Outcalt's (1997) representative old-growth stands of Choctawhatchee sand pine aver-aged about 80 years of age for the largest trees, with larger individuals approaching 48 cm dbh in one stand (Table 2). Our stands were generally older, with the oldest trees ranging from 72 to 132 years. Our largest tree diameters were substantially smaller than those reported by Outcalt for Choctawhatchee sand pine, as were our stand basal area values. The densities of trees and snags were comparable between studies. In general, Choctawhatchee sand pine stands display an uneven-aged structure, possessing both old, large trees as well as seedlings and saplings within the same stand. Like Ocala sand pine, Choctawhatchee sand pine trees are neither very large nor very old by traditional old-growth standards. Indeed, the oldest Choctawhatehee sand pine trees that we sampled (up to 132 years) were stunted, twisted individuals found growing on the back dunes at St. Joseph Peninsula State Park. This diminutive coastal morphology de-parts widely from traditional images of old-growth forest, but it does occupy the kind of ecophysiologically stressed setting that typifies truly old trees (Stahle and Chaney 1994, Abrams and Orwig 1995).

Hurricanes and other windstorms are prev-alent along the coast of the Florida pan-handle (Wilkinson et al. 1978). They serve as an important disturbance stimulus by opening canopy gaps and triggering ongoing recruitment in mature Choctawhatchee sand pine forests. Crown fires are not important in stand dynamics, presumably because many sites along the Gulf Coast have historically been isolated from more flammable surrounding vegetation by open water. In the absence of crown fires, wind damage helps maintain persistent populations of this early successional taxon. Between the two varieties, Choctawhatchee sand pine more closely approaches the common expectation of a self-replicating population in an old-growth forest stand.

When compared against the usual stan-dards by which old-growth forests are eval-uated, sand pine forests demonstrate little old-growth character. Sand pine trees do not attain venerable ages. Modern scrub remnants are often small, highly fragment-ed, and, for Ocala sand pine, suffer from fire suppression policies that have altered the structure and dynamics of most re-maining sites. Hence, they do not convey a pristine image of natural forest, one un-modified by modern human technologies. Sand pine trees are not massive in size, their forests are not particularly structural-ly complex, nor are dead stems common, even on mature sites. By these structural standards, sand pine forests do not ap-proach old-growth character. Finally, like other early successional taxa, sand pine populations are not stable or self-replicat-ing in the absence of disturbance (although Choctawhatchee sand pine comes closer to this ideal than Ocala sand pine).

LANDSCAPE-SCALE PERSPECTIVES ON OLD-GROWTH SAND PINE FORESTS

Tyrrell (1996) advocated a landscape-level perspective for U.S. Forest Service old-growth planning, and Trombulak (1996) explored the ramifications of this idea in some detail. Trombulak observed that a stand-scale focus, such as that of Outcalt (1997) for sand pine, does not address scale-dependent processes such as disturbance, recovery, and population persistence. He suggested several guidelines for old-growth policy implementation, among which the following are germane to the sand pine scrub: employ flexible management goals, recognizing that the location of old-growth forests may change in response to episodic patterns of disturbance and recovery; accept that history matters in vegetation development—that is, the details of initial conditions and subsequent history leave a lasting legacy on the vege-tation cover; and accept that restoration efforts probably will be a necessary com-ponent of old-growth maintenance. The emphasis here should be on retaining or reintroducing stresses that shape the site (such as fire or native herbivores), rather than recreating a specific, idealized com-position or forest structure.

Outcalt (1997) wisely pointed out the management conundrum involved in pre-serving old-growth Ocala sand pine stands by noting that lack of regeneration in the absence of crown fires hastens conversion to oak cover. He suggested that prescribed natural wildfires be allowed in nonharvest zones (i.e., wilderness areas). Management focus on wilderness areas for old-growth sand pine is understandable but potentially misleading. A wilderness area from which crown fires have been suppressed for most of the typical life-span of the overstory dominant will comprise a much higher percentage of mature sand pine stands ("old growth") than would be evident if fires had been allowed to carry through scrub terrain without human intercession. As a result, we must be cautious in adopting the relatively small wilderness area in Ocala National Forest as a standard or control that reflects how sand pine scrub landscapes might have been configured in the past. Such a standard almost certainly overestimates the natural prevalence of older sand pine stands. In any event, a self-replicating population of Ocala sand pine trees within an undisturbed stand is a virtual impossibility. If crown fires are allowed to burn, older tracts of Ocala sand pine would eventually be consumed. If disturbance suppression continues, Ocala sand pine probably will eventually be replaced by more tolerant associates in most of the scrub habitats where it dominates today (Abrahamson and Abrahamson 1996).

From a conservation perspective, reintroduction of fire to Florida peninsular scrub is crucial to management of its rich concentration of endemic plants and animals, a number of which are federally threatened and endangered species (Flather et al. 1994). Unlike spotted owls, scrub jays and gopher tortoises inhabit young, recently burned scrub sites (Woolfenden and Fitzpatrick 1984:36-42, Diemer 1986). In this century, large tracts of former scrub have been converted to citrus orchards, rangelands, and human settlements. The remaining scrub habitat is largely protected from fire by management directive or simply because it is no longer adjacent to more flammable plant assemblages (Christensen 1993). Hence, we find some examples of mature Ocala sand pine scrub, but few that preserve the character of a former scrubland in which wildfires sculpted a landscape of open scrub with small enclaves of older sand pine that temporarily evaded wildfire. In presettlement Florida, large tracts of scrub with mature sand pine overstory were probably rare. Most scrub would likely have been young, having been burned every few decades, given the seasonality of the precipitation regime, the prevalence of thunderstorms over the Florida peninsula, and the interdigitation of scrub with more flammable longleaf pine savannas. Ironically, through fire suppression activities, we have fostered the development of larger tracts of mature sand pine forests than are likely to have existed otherwise.

Organisms dependent on open sand pine scrub are in peril. The conservation value of preserving uncharacteristically old sand pine stands that owe their development to over a half-century of fire suppression is dubious. To ensure preservation of scrub endemics, management should be redirected from putative old-growth sand pine stands to preserving a dynamic scrub landscape that experiences episodic crown fires. Such an Ocala sand pine scrub landscape would have patches of scrub intermixed with longleaf pine savanna, and the scrub patches themselves would represent a range of ages/stages of development.

Young, open scrub on recently burned sites would be areally dominant, given the short fire rotation typical of scrub (30–60 years). Scattered patches of mature scrub (old growth by USFS standards) would be evideat in this landscape on long-unburned sites, but these could be expected to shift spatially over multi-decadal time periods.

Of course, there are substantial impediments to instituting landscape-scale old growth policies for Ocala sand pine (or most other fire-dependent taxa). The fragmented collection of private and public lands scattered across Florida that support remnants of sand pine scrub restricts pollen flow, seed exchange, animal movement, and fire propagation among extant populations; the economic pressures to con".inue harvesting sand pine do not favor reintroduction of crown fires into the largest remaining tract of sand pine forest on federal lands (Ocala National Forest); and the specter of potential property damage and legal liability stymies efforts to em-ploy prescribed crown fires, even on smaller, isolated scrub remnants. Perhaps the public resolve to maintain a dynamic sand pine scrub is, at present, insufficient to address these impediments. Even so, we should not be misled into thinking that a stand-scale management plan, like that of the USFS, will be adequate to create a lasting network of representative mature sand pine scrub forests. A landscape that perpetuates mature stands of Ocala sand pine scrub must incorporate crown fires that occasionally raze scrub, destroy stands of older trees, and permit the seeds of future mature sand pine to be sown. Pre-scribed crown fires might be feasible in a few locales, such as at Rock Springs Run State Reserve near Orlando, Lake Arbuckle State Park near Avon Park, or, with substantially modified priorities, on the heavily cutover Big Scrub of Ocala National Forest.

Should a crown fire management program be instituted for scrub landscapes, we would caution that it is ecologically unrealistic to expect that "old-growth" sand pine (or any other stand age class) would occupy a fixed percentage of area, even if we had the luxury of an extensive scrub landscape in which disturbances were permitted to operate without suppression. The vagaries of stand development, meteorology, and burn pattern will not yield a tidy, steady-state landscape mosaic of young and old scrub in dynamic equilibrium (Baker 1989, Wu and Loucks 1995).

Ironically, the effect of fire suppression in the Florida panhandle has been to facilitate invasion of nonserotinous Choctawhatchee sand pine into former longleaf pine savanna (McCay 1998). The result is a dramatic inland invasion of sand pine along the near coastal zone of Eglin Air Force Base, where sandy substrates are available. Although this suggests that sand pine is doing well in this region, it is misleading in so far as these are overstory populations of sand pine that virtually lack an understory scrub layer. In this case, identification of historical scrub sites from which the modern populations of Choctawhatchee sand pine have invaded remains an important conservation initiative. From a stand-scale management perspective, protection of Choctawhatchee sand pine scrub sites up to several kilometers inland from the Gulf coastal strand represents our best hope for maintaining mature sand pine scrub of presettlement character, simply because wind damage is not readily sup-pressed and the local scale of wind effects provides ongoing regeneration opportunities within the small pockets of scrub that remain on public lands in the Florida pan-handle. None of this land is currently ad-ministered by the USFS.

The current USFS policy to identify and preserve representative stands of old-growth forest from different cover types is not universally appropriate. It is, without question, well-intentioned, and may well be an effective vehicle for preserving natural, structurally complex, old forests in regions where disturbance regimes permit their development, such as in parts of the southern Appalachians. However, implementation of a stand-scale old-growth policy suffers from a museum-piece mentality in which change is unanticipated and unwanted. Any long-term success in old-growth forest management that involves early successional species necessitates a reversal of this attitude, so that change is embraced as normal. We should not be surprised when our best modern examples of old-growth forest succumb to disturbance agents (see Pollan 1991 re: Cathedral Pines in Connecticut), nor should we be surprised as younger forests of today mature into an old-growth status that is structurally or compositionally different from present-day examples. Land management policies need to recognize the dynamic nature of vegetation cover and embrace disturbance as a crucial element in the fabric of most landscapes (Attiwill 1994). In cases such as Florida sand pine scrub, devotion to preserving a single condition, such as old growth, obscures the larger need for a flexible plan that values all stages of stand development. This need becomes especially acute in circumstances where rarer elements of the biota are concentrated in disturbed settings, as is the case for sand pine scrub.

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LITERATURE CITED

Abrahamson, W.G. and J.R. Abrahamson. 1996. Effects of a low-intensiity winter fire on long-unburned Florida sand pine scrub. Natural Areas Journal 16:171-183.

Abrams, M.D. and D.A. Orwig. 1995. Structure, radial growth dynamics and recent climatic variations of a 320-year-old *Pinus rigida* rock outcrop community. Oecologia 101:353-360.

Attiwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservation management. Forest Ecology and Management 63:247-300.

Baker, W.L. 1989. Landscape ecology and nature reserve design in the Boundary Waters Canoe Area, Minnesota. Ecology 70:23-35.

Bormann, F.H. and G.E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. American Scientist 67:660-669.

Braun, E.L. 1950. Deciduous Forests of East-ern North America. Hafner Publishing Company, New York. 596 pp.

Christensen, N.L. 1993. Fire regimes and ecosystem dynamics. Pp. 233-244 *in* P.J. Crutzen and J.G. Goldammer, eds., Fire in the Environment: The Ecological, Atmospheric, and Climatic Importance of Vegetation Fires. John Wiley and Sons, New York.

Cronon, W. 1995. The trouble with wilderness, or, getting back to the wrong nature. Pp. 69-90 *in* W. Cronon, ed., Uncommon Ground: Toward Reinventing Nature. W.W. Norton, New York.

Denevan, W. M. 1992. The pristine myth: the landscape of the Americas in 1492. Annals of the Association of American Geographers 82:369-385.

Diemer, J.A. 1986. The ecology and management of the gopher tortoise in the southeast-ern United States. Herpetologica 42:125-133.

Evans, J.K., A.J. Parker, K.C. Parker, and D.S. Leigh. 1996. Edaphic properties and foliar elemental concentrations from sand pine *(Pinus clausa)* populations throughout Florida. Physical Geography 17:219-241.

Eyre, F.H. (ed.). 1980. Forest cover types of the United States and Canada. Society of American Foresters, Washington, D.C. 148 pp.

Rather, C.H., L.A. Joyce, and C.A. Bloomgarden. 1994. Species endangerment patterns in the United States. General Technical Report RM-241, U.S. Department of Agri-culture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 42 pp.

Glitzenstein, J.S., W.J. Platt, and D.R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs 65:441-476.

Gomez-Pampa, A. and A. Kaus. 1992. Taming the wilderness myth. BioScience 42:271-279.

Hardt, R.A. and W.T. Swank. 1997. A comparison of structural and compositional characteristics of southern Appalachian young second-growth, maturing second-growth, and old-growth stands. Natural Areas Journal 17:42-52.

Hunter, M.L., Jr. 1989. What constitutes an old-growth stand? Journal of Forestry 87:33-35.

Hunter, M.L., Jr. and A.S. White. 1997. Ecological thresholds and the definition of old-growth forest stands. Natural Areas Journal 17:292-296.

Kaufmann, M.R., W.H. Moir, and W.W. Covington. 1992. Old-growth forests: What do we know about their ecology and management in the Southwest and Rocky Mountain regions? Pp. 1-11 in M.R. Kaufmann, W.H. Moir, and R.L. Bassett, eds., Old-growth forests in the Southwest and Rocky Mountain regions: proceedings of a workshop. General Technical Report RM-213, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Martin, W.H. 1992. Characteristics of old-growth mixed mesophytic forests. Natural Areas Journal 12:127-135.

McCay, D.H. 1998. Vegetation dynamics, landscape change, and land use history in north-ern Florida. Ph.D. diss., University of Georgia, Athens. 127 pp.

McCune, B. 1988. Ecological diversity in North American pines. American Journal of Botany 75:353-368.

Myers, R.L. 1990. Scrub and high pine. Pp. 150-193 *in R.* L. Myers and J. J. Ewel, eds., Ecosystems of Florida. University of Central Florida Press, Orlando.

Outcalt, K. W. 1997. An old-growth definition for sand pine forests. General Technical Report SRS-12, U.S. Department of Agri-culture, Forest Service, Southern Research Station, Asheville, N.C. 8 pp.

Parker, K.C. and J.L. Hamrick. 1996. Genetic variation in sand pine *(Pinus* clausa). Canadian Journal of Forest Research 26:244-254.

Parker, K.C., J.L. Hamrick, A.J. Parker, and E.A. Stacy. 1997a. Allozyme diversity in *Pinus virginiana* (Pinaceae): intraspecific and interspecific comparisons. American Journal of Botany 84:1372-1382.

Parker, K.C., A.J. Parker, R.M. Beaty, M.M. Fuller, and T.D. Faust. 1997b. Population structure and spatial pattern of two coastal populations of Ocala sand pine *(Pinus clausa* [Chapm. ex Engelm.] Vasey ex Sarg. var. *clausa* D. B. Ward). Journal of the Torrey Botanical Society 124:22-33.

Platt, W.J., J.W. Evans, and S.L. Rathbun. 1988. The population dynamics of a long-lived conifer *(Pinus palustris).* American Naturalist 131:491-525.

Pollan, M. 1991. Second Nature: A Gardener's Education. Dell Publishing, New York. 304 pp.

Runkle, J. R. 1990. Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. Canadian Journal of Forest Research 20:632-641.

Spiegel, D.G. 1991. Disturbance, equilibrium, and environmental variability: What is "natural" vegetation in a changing environment? Biological Conservation 58:1-18.

Stahle, D.W. and P.L. Chaney. 1994. A predictive model for the location of ancient forests. Natural Areas Journal 14:151-158.

Stahle, D.W., M.K. Cleaveland, and J. G. Hehr. 1988. North Carolina climate changes re-constructed from tree rings: A.D. 372 to 1985. Science 240:1517-1519.

Trombulak, S.C. 1996. The restoration of old growth: why and how? Pp. 305-320 *in* M.B. Davis, ed., Eastern Old-growth Forests: Prospects for Rediscovery and Recovery. Island Press, Washington, D.C.

Tyrrell, L.E. 1996. National forests in the East-ern Region: land allocation and planning for old growth. Pp. 245-273 *in* M.B. Davis, ed., Eastern Old-growth Forests: Prospects for Rediscovery and Recovery. Island Press, Washington, D.C.

U.S. Forest Service. 1997. Guidance for con-serving and restoring old-growth forest communities on national forests in the Southern Region. Forestry Report R8-FR 62, U.S. Department of Agriculture, Forest Service, Southern Region, Atlanta, Ga.

Vale, T. R. 1998. The myth of the humanized landscape: an example from Yosemite National Park. Natural Areas Journal 18:231-236.

Whitney, G.G. 1987. Some reflections on the value of old-growth forests, scientific and otherwise. Natural Areas Journal 7:92-99.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.

Wilkinson, R.C., R.W. Britt, E.A. Spence, and S.M. Seiber. 1978. Hurricane-tornado dam-age, mortality, and insect infestation of slash pine. Southern Journal of Applied Forestry 2:132-134.

Woolfenden, G.E. and J.W. Fitzpatrick. 1984. The Florida Scrub Jay: Demography of a Cooperative-breeding Bird. Monographs in Population Biology 20. Princeton University Press, Princeton, N.J. 406 pp.

Wu, J. and O.L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quarterly Re-view of Biology 70:439-466.