Roadside Soils: A Corridor for Invasion of Xeric Scrub by Nonindigenous Plants

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ABSTRACT: Invasion of ecosystems by nonindigenous species threatens native biodiversity by altering species composition and site characteristics, and by potentially impacting endangered species. We compared plant communities and soil characteristics along clay, limerock, and unmodified sand roadsides, and in adjacent clearcuts in xeric Florida sand pine scrub to test our hypothesis that modified soils used in constructing roadways provide a roadside corridor for invasion by nonindigenous species and species that are uncharacteristic of xeric scrub. Clay and limerock roadsides had more clay and less sand than sand roadsides or clearcuts. Soil pH and levels of several nutrients differed significantly in limerock roadsides relative to the other substrates. In general, sand roadsides and clearcuts had higher characteristic but lower uncharacteristic and nonindigenous plant cover and number of species than modified roadside substrates. This suggests that xeric scrub may be somewhat resistant to invasion where native soils are present, even if disturbed. However, presence of nonindigenous species suggests that roadways facilitate the transport of source propagules to otherwise remote sites. Especially where roadside and native soil characteristics differ markedly, conditions may be enhanced for invasion by nonindigenous and uncharacteristic plants.

Index terms: exotic plants, invasive plants, roadside soils, roadside vegetation, scrub

INTRODUCTION

Invasive, nonindigenous species are taxa that have been introduced, intentionally or not, into a novel habitat and successfully establish and reproduce (sexually or asexually) in that new location (U.S. Office of Technology Assessment 1993). Invasion of ecosystems by nonindigenous species (NIS) directly threatens native biodiversity by altering species composition and ecosystem structure and function (Elton 1958, Mooney and Drake 1986, Vitousek 1986). NIS may cause indirect adverse effects by disrupting ecosystem processes such as nutrient cycling and retention, hydrology and water flux, soil erosion and fertility, and disturbance regime (Vitousek et al. 1987; D'Antonio and Vitousek 1992; Gordon 1993; Gordon, in press).

In the United States, billions of dollars have been spent on purchasing lands for protection of native biodiversity even as they are being invaded and degraded by NIS (Anonymous 1993). NIS have caused over $97 billion in economic loss since 1906 (Office of Technology Assessment 1993). In Florida, over 25% of all plant species living in the wild are NIS (Ward 1990). Because of the subtropical climate, multiple entry routes and modes, deliberate introductions and trade of NIS, and habitat degradation due to increasing population growth and urbanization, Florida's ecosystems are among those at highest risk for invasion by NIS (Anonymous 1993, Office of Technology Assessment 1993, Florida Department of Environmental Protection 1994). A better understanding of conditions facilitating the establishment of NIS plants will enhance efforts to control of their spread.

Disturbance may enable NIS to gain a foothold in ecosystems by reducing competition, affecting surface texture and microclimate, and changing the availability of resources such as nutrients, water, and light (Fox and Fox 1986, Orians 1986, Hobbs and Huenneke 1992, McIntyre and Lavorel 1994). A "disturbance" in this context may be defined as a deviation from the natural processes that cause resource releases in a given ecosystem. Modification of an "endogenous" disturbance regime, or regime under which the plant community evolved (Denslow 1985), may increase the vulnerability of a community to invasion by NIS (Fox and Fox 1986; Hobbs and Huenneke 1992). Hence, the removal of grazers from grazing-adapted ecosystems (Hobbs and Huenneke 1992), or fire suppression in "fire-climax" communities (Abrahamson and Hartnett 1990, Myers 1990), constitutes a disturbance insofar as the endogenous disturbance regime is disrupted. Similarly, the introduction of novel, or "exogenous" disturbance types may increase community invasibility (Westman 1985).

Roadsides provide optimal conditions for invasion by NIS. Vehicle tires, imported road-building materials, and people provide source propagules (Wace 1977, Willard et al. 1990). Substrate used in road construction may modify soil properties such as pH, particle size, texture, nutrient levels, and water-holding capacity (Fox and Fox 1986). Removal of native vegetation, soil disturbance, and increased runoff from road surfaces may further enhance conditions for invasion by NIS and reduce the ability of native species to compete. This effect may be most pronounced where native soils differ markedly from modified soils used in roadway construction.

We hypothesized that the addition of clay and limerock substrates used in constructing permanent unpaved roads and temporary logging roads in the xeric, infertile sandy soil of the Ocala National Forest provides a roadside corridor for invasion by NIS and other plant species that are not generally found in the sand pine scrub ecosystem.

METHODS AND MATERIALS

Study Area

The Ocala National Forest covers approximately 180,000 ha in Marion, Lake, and Putnam Counties in central Florida. The national forest is bounded by the Ocklawaha River to the west and north, the St. John's River to the east, and extensive wetlands to the south. Elevations range from 2 to 49 m above mean sea level. The sand pine scrub community occupies over half of the national forest area.

Sand pine scrub is a sclerophyllous shrub-dominated ecosystem occurring on infertile, xeric sands. Soils supporting sand pine scrub are excessively drained aeolian or marine sands, classified as hyperthermic, uncoated families of spodic (Paola series) and Typic Quartzipsamments (Astatula series). This area receives approximately 1,300 mm of rainfall annually, with over half falling between June and September. Average temperatures range from 20° to 32° between April and October, and from 11° to 23° C between November and March (U.S. Soil Conservation Service 1975).

Sand pine, *Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg., is managed for pulpwood production in the Ocala National Forest. Stand management and harvest, public access, and fire lanes all require the creation of roads in the forest. Three types of secondary (unpaved) roads occur in the Ocala National Forest. Limerock-based roads are constructed using a layer of limerock several centimeters thick, overlain by several centimeters of clay. Clay-based roads are constructed by logging companies to gain access for heavy equipment to forest stands. Clay is placed on sand roads in patches, as needed to prevent machinery from becoming stuck in sand. Clay for both types is obtained from local claypits within the national forest, and the percentage clay present may vary among claypits. Sand roads are constructed simply by clearing vegetation from sandy soil. Sand roads grid the forest as section boundary lines; plow lines around forest stands are also occasionally used as roads.

Field Measurements

To test our hypotheses in the field we compared plant communities and soils of sand (SAND), clay (CLAY), and limerock-clay (LIME) roadsides within the scrub community to adjacent disturbed stand interiors that had been clearcut and site-prepared for planting (either roller-chopped or "bracke-seeded" by creating 8-cm-high mounds of soil) 1–5 years prior to sampling (CLEARCUT). By including sand roadsides and scrub clearcuts we controlled for disturbance alone as the primary factor in facilitating establishment by NIS and species not commonly found in intact scrub communities, hereafter referred to as "uncharacteristic species," along roadsides.

Percentage cover of each plant species was measured in 15 replicate sites for SAND, CLAY, and LIME substrates, and paired (adjacent) CLEARCUT substrate using the line-intercept method along a single 15-m line transect. Transects parallel to roads were randomly located along roadsides. Parallel transects were laid in adjacent CLEARCUTS within a randomly selected distance between 10 and 130 m toward the site interior from the roadside transect. If two roadside types bordering the same clearcut were sampled, paired CLEARCUT transects did not overlap.

The top 5 cm of soil were sampled for particle size and nutrient analyses every 2.5 m along each transect (six subsamples). The subsamples were combined to make one composite sample per transect.

Laboratory Measurements (Soils)

Soil samples were oven dried at 40°C, passed through a 2-mm sieve, and thoroughly mixed. Standard analyses (Soil Survey Staff 1992) were used in the following procedures: particle-size distribution (sand, silt, and clay percentages) was determined by the pipette analysis, organic carbon content was determined by acid-dichromate digestion, soil pH was measured in distilled water at a 1:1 ratio, and ammonium nitrogen (NH_4^+–N) and nitrate nitrogen (NO_4^-–N) were determined using the micro Keljdahl procedure in a 2:1 water to soil ratio.

Exchangeable bases (potassium, calcium, and magnesium), extractable phosphorus, and aluminum were determined using the Mehlich-I procedure (Hanlon et al. 1994). Potassium, calcium, magnesium and aluminum were analyzed by inductively coupled argon plasma (ICAP) spectroscopy at the IFAS Analytical Research Laboratory at the University of Florida in Gainesville. Phosphorus was determined colorimetrically by a procedure designed to analyze the Mehlich-I extractable phosphorus (Hanlon et al. 1994).

Data Analysis

Each species was categorized as "characteristic," "nonindigenous" (NIS), or "uncharacteristic." Categories were based on extensive vegetation sampling of xeric sand pine scrub at Ocala National Forest in a prior study (Greenberg 1993); all category assignments were verified by botanist Daniel Ward (Department of Botany, University of Florida, pers. com.).

We selected a random subsample of the 45 CLEARCUT transects to create a balanced statistical design for comparing species richness (number of species) and percentage cover of characteristic, uncharacteristic, and NIS plant species as well as soil characteristics among the four substrates (n=15 each) using ANOVA (SAS Institute 1989). Data were log transformed or (for proportional data only) arcsine square-root transformed (Zar 1984) where required to correct for nonnormality or heteroscedasticity. If percentage plant cover exceeded 100% we assigned it a 100% cover value for arcsine square-root transformation. Pairwise contrasts between least squares means were performed when there was a significant treatment effect (SAS Institute 1989).

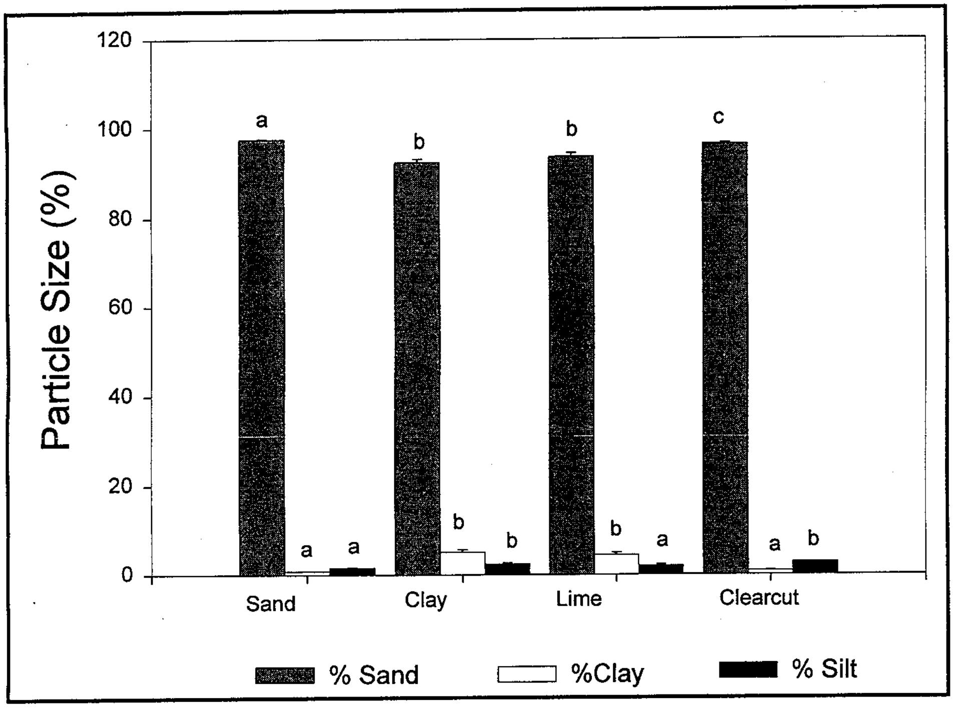

Figure 1. Mean (± SE) particle size distribution of sand-, clay-, and limerock-based roadside soils and in adjacent clearcuts, Ocala National Forest, Florida. Significant differences in percentage sand, silt, or limerock were determined by pairwise contrasts between least squares means (SAS Institute 1989) and are denoted by different letters among treatments.

RESULTS

Particle Size Analysis

SAND and CLEARCUT substrates had significantly more sand (SAND having slightly but significantly more sand than CLEARCUT) (F=23.78, df=3, *P*=0.0001) and less clay (F=64.88, df=3, *P*=0.0001) than CLAY or LIME substrates (Figure 1). Percentage silt was lowest in SAND and LIME substrates followed by CLAY and CLEARCUT substrates (F=6.83, df=3, *P*=0.0005).

Soil Chemical Analysis

Soil pH was significantly lower in SAND and CLEARCUT substrates than in other substrates, and was significantly higher in LIME than in others (F=80.6, df=3, *P*=0.0001). Percentage organic carbon was significantly higher in SAND and CLEARCUT substrates than in CLAY or LIME substrates (F=6.68, df=3, *P*=0.0006) (Table 1).

Soil nutrient levels varied among substrates (Table 1). The aluminum level was significantly lower (F = 38.76, df=3, *P*=0.0001) and calcium (F=5659, df=3, *P*=0.0001) and phosphorus (F=3.8, df=3, *P*=0.0149) levels were significantly higher in LIME than in other substrates. Potassium levels were significantly lower in SAND than in other substrates (F=6.93, df=3, *P*=0.0005). Magnesium levels also were significantly

Table 1. Mean ± SE soil chemical properties of sand-, clay-, and limerock-based roadsides and adjacent clearcuts, Ocala National Forest, Florida.

	Roadside Substrates[a]			
Chemical Properties	**Sand**	**Clay**	**Lime**	**Clearcut**
pH	4.85[a]±0.08	5.38[b]±0.18	8.14[c]±0.08	4.68[a]±0.1
Organic carbon (%)	1.05[a]±0.09	0.77[b]±0.1	0.72[b]±0.12	1.24[a]±0.06
Aluminum (mg/kg)	53.33[a]±4.21	53.96[a]±4.6	4.9[b]±2.93	43.95[a]±2.84
Calcium (mg/kg)	62.65[a]±19.08	121.16[a]±29.22	6270.67[b]±55.77	93.96[a]±20.24
Potassium (mg/kg)	3.37[a]±0.25	5.34[b]±0.56	5.73[b]±0.55	5.93[b]±0.34
Magnesium (mg/kg)	4.91[a]±0.59	9.74[b]±1.22	38.34[c]±1.41	11.04[b]±1.27
Nitrate nitrogen (mg/kg)	0.63±0.16	0.3±0.07	0.5±0.1	0.53±0.1
Ammonium nitrogen (mg/kg)	0.2±0.14	0.06±0.04	0.23±0.66	0.4±0.21
Phosphorus (mg/kg)	1.43[a]±0.12	1.57[a]±0.19	8.36[b]±3.49	1.62[a]±0.09

[a] Different letters within a row denote significant differences among treatments (*P* < 0.001).

lower in SAND and significantly higher in LIME than in CLAY or CLEARCUT substrates (F=168.45, df=3, *P*=0.0001). Levels of ammonium nitrogen and nitrate nitrogen did not significantly differ among substrates.

Roadside Plant Associations

We recorded a total of 62 characteristic, 27 uncharacteristic, and 7 NIS species in SAND, CLAY, LIME, and CLEARCUT substrates combined (Table 2). Most species occurred infrequently and were patchy in their distribution.

CLEARCUT substrates had significantly higher percentage cover of characteristic plant species (F=11.19, df=3, *P*=0.0001) than other treatments; SAND had significantly more characteristic species than CLAY but not LIME (Figure 2). SAND and CLEARCUT had significantly lower percentage cover of NIS species than CLAY or LIME substrates (F=5.31, df=3, *P*=0.0027). SAND and CLEARCUT substrates also had significantly lower percentage cover of uncharacteristic species than CLAY or LIME substrates, but LIME had significantly higher percentage cover of uncharacteristic species than all other substrates (F=26.61, df=3, *P*=0.0001).

Richness of characteristic plant species along the transects was significantly higher in SAND and CLEARCUT substrates than in CLAY or LIME, but was significantly lower in LIME than in CLAY (F=14.53, df=3, *P*=0.0001) (Figure 3). Uncharacteristic species richness was significantly lower in SAND and CLEARCUT substrates than in CLAY or LIME, and was significantly higher in LIME than in CLAY (F=54.07, df=3, *P*=0.0001). Species richness of NIS was lowest in SAND and CLEARCUT substrates, followed by LIME, which differed significantly only from CLEARCUT substrate. CLAY had significantly higher NIS species richness than SAND and CLEARCUT substrates (F=9.03, df=3, *P*=0.0001).

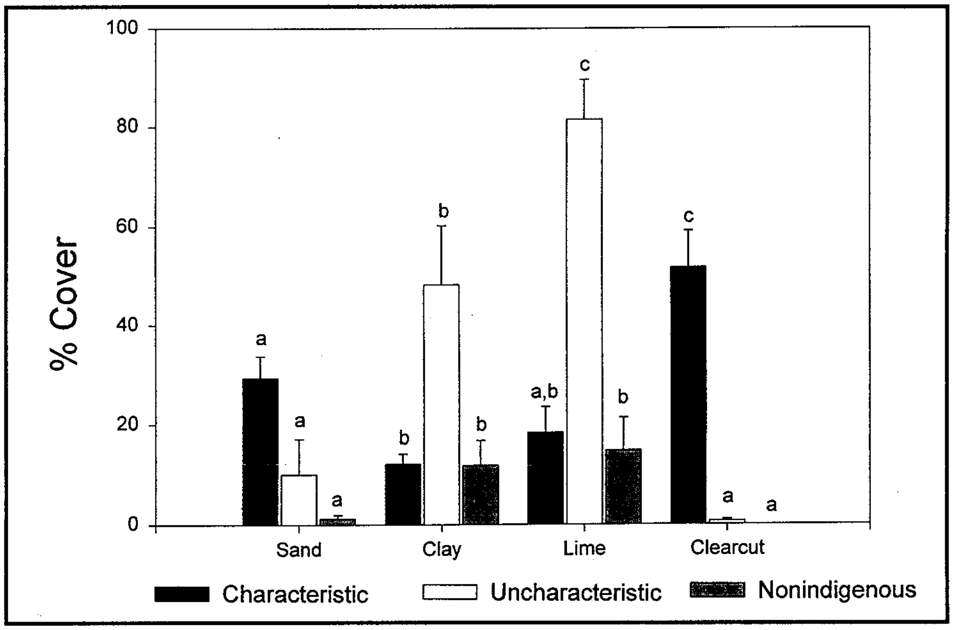

Figure 2. Mean (± SE) percentage cover of characteristic, uncharacteristic, and nonindigenous plant species along sand-, clay-, and limerock-based roadsides and in adjacent clearcuts, Ocala National Forest, Florida. Significant differences in percentage cover of each category were determined by pairwise contrasts between least squares means (SAS Institute 1989) and are denoted by different letters among treatments.

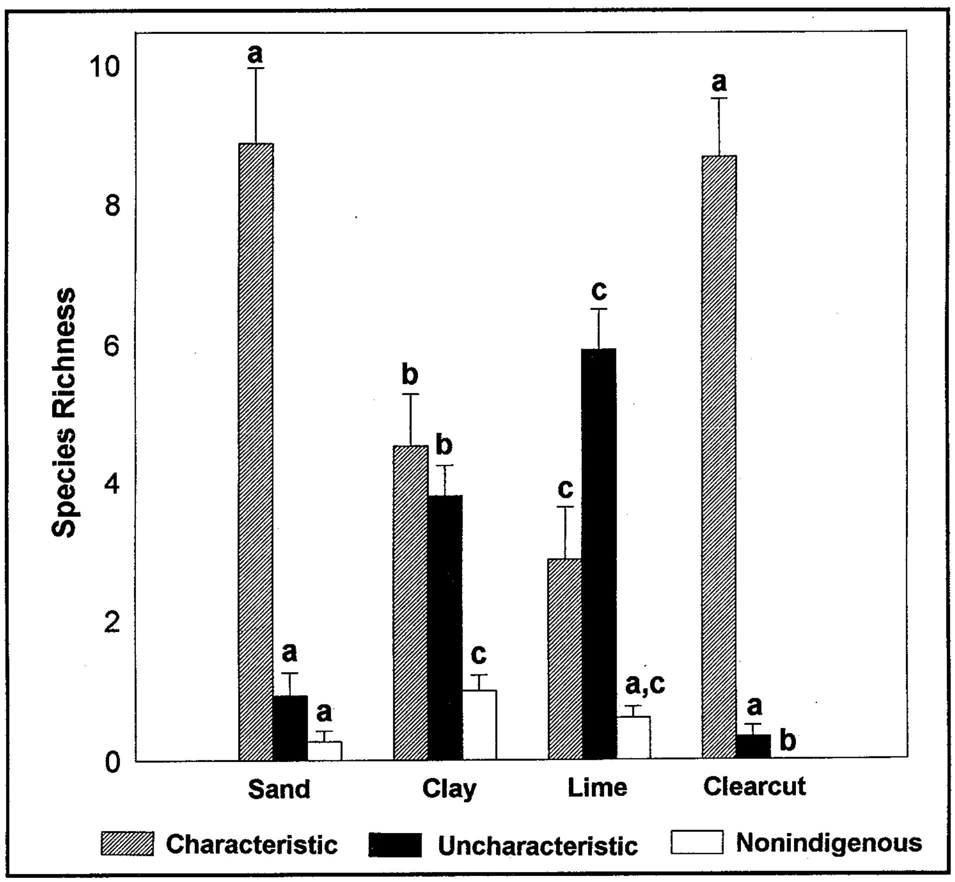

Figure 3. Mean (± SE) species richness (number of species) of characteristic, uncharacteristic, and nonindigenous plants along sand-, clay-, and limerock-based roadsides and in adjacent clearcuts, Ocala National Forest, Florida. Significant differences in species richness within each category were determined by pairwise contrasts between least squares means (SAS Institute 1989) and are denoted by different letters among treatments.

DISCUSSION

Proportional differences in characteristic, NIS, and uncharacteristic species among

Table 2. Mean percent cover[a] ± SE and frequency (in parentheses) by transect of uncharacteristic, nonindigenous, and characteristic scrub plant species along sand-, clay-, and limerock-based roadsides and in adjacent clearcuts, Ocala National Forest, Florida.

Species	Roadside Substrates[a]			
	Sand	Clay	Lime	Clearcut
UNCHARACTERISTIC SPECIES				
Ambrosia artemisiifolia L.	0.00 (0.00)	0.12±0.12 (6.67)	3.38±1.98 (46.67)	0.00 (0.00)
Bidens albs (L.) DC.	0.00 (0.00)	0.00 (0.00)	0.82±0.73 (13.33)	0.00 (0.00)
Cassia nictitans L.	0.00 (0.00)	0.14±0.10 (0.00)	30.50±7.61 (6.67)	0.16±0.16 (0.00)
Cenchrus incertus M.A. Curtis	0.00 (0.00)	0.00 (20.00)	0.007±0.07 (86.67)	0.00 (6.67)
Chamaesyce cordifolia (Ell.) Small	0.00 (0.00)	0.20±0.20 (6.67)	0.00 (0.00)	0.00 (0.00)
C. maculata (L.) Small	0.00 (0.00)	0.70±0.70 (6.67)	0.00 (0.00)	0.00 (0.00)
C. hyssopifolia (L.) Small	0.00 (0.00)	0.00 (0.00)	0.02±0.02 (6.67)	0.00 (0.00)
Cirsium horridulum Michx.	0.00 (0.00)	0.00 (0.00)	x (6.67)	0.00 (0.00)
Conyza canadensis (L.) Cronq.	0.00 (0.00)	0.01±0.01 (6.67)	4.99±1.51 (73.3)	0.00 (0.00)
Desmodium incanum DC.	0.00 (0.00)	0.00 (0.00)	0.04±0.04 (6.67)	0.00 (0.00)
Digitaria ciliaris (Retz.) Koel.	0.00 (0.00)	6.51±4.32 (33.30)	2.30±1.25 (40.00)	0.00 (0.00)
D. villosa (Walt.) Pers.	2.37±1.43 (20.00)	5.37±2.41 (53.30)	0.09±0.09 (6.67)	0.02±0.02 (6.67)
Dioda teres Walt.	0.48±0.38 (0.00)	11.80±3.47 (0.00)	1.16±1.16 (6.67)	0.00 (0.00)
Eragrostis hirsuta (Michx.) Nees	0.00 (0.00)	0.27±0.27 (6.67)	6.82±4.75 (33.33)	0.00 (0.00)
E. refracta (Muhl.) Scribn.	0.04±0.04 (6.67)	0.04±0.04 (6.67)	11.91±5.66 (53.33)	0.31±0.31 (6.67)
E. spectabilis (Pursh) Steud.	0.00 (0.00)	2.74±1.43 (33.33)	11.40±7.69 (33.33)	0.00 (0.00)
Eustachys petraea (Sw.) Desv.	0.00 (0.00)	0.00 (0.00)	6.12±2.15 (80.00)	0.00 (0.00)
Gaura angustifolia Michx.	0.00 (0.00)	0.00 (0.00)	0.01±0.01 (6.67)	0.00 (0.00)
Gnaphalium obtusifolium L.	0.04±0.04 (6.67)	0.00 (0.00)	0.00 (0.00)	0.02±0.02 (6.67)
Hypericum gentianoides (L.) BSP.	0.00 (0.00)	0.00 (0.00)	0.01±0.01 (6.67)	0.00 (0.00)
Linaria floridana Chapm.	0.01±0.01 (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Lippia nodiflora (L.) Michx.	0.00 (0.00)	0.00 (0.00)	0.31±0.31 (6.67)	0.00 (0.00)
Oxalis stricta L.	0.00 (0.00)	0.00 (0.00)	0.05±0.05 (6.67)	0.00 (0.00)
Paspalum setaceum Michx.	0.00 (0.00)	0.27±0.27 (6.67)	0.31±0.23 (13.33)	0.00 (0.00)

Table 2, continued

Species	Roadside Substrates[a]			
	Sand	Clay	Lime	Clearcut
Setaria geniculata (Lam.) Beauv.	0.00 (6.67)	0.07±0.07 (13.33)	0.21±0.21 (13.33)	0.00 (0.00)
Solidago chapmanii Torr. & Gray	0.00 (0.00)	0.07±0.07 (6.67)	0.21±0.21 (6.67)	0.00 (0.00)
Triplasis purpurea (Walt.) Chapm.	7.09±6.20 (33.33)	16.87±7.71 (86.67)	0.58±0.31 (26.67)	0.13±0.13 (6.67)
Nonindigenous Species				
Eremochloa ophiuroides (Munro) Hack.	0.00 (0.00)	0.26±0.26 (13.33)	11.22±6.67 (26.67)	0.00 (0.00)
Mitracarpus hirtus (L.) DC.	1.11±0.71 (26.67)	7.86±3.90 (53.33)	0.00 (0.00)	0.00 (0.00)
Paspalum notatum Fluegge	0.00 (0.00)	0.00 (0.00)	2.60±1.98 (13.33)	0.00 (0.00)
P. urvillei Steud.	0.00 (0.00)	0.01±0.00 (13.33)	0.84±0.75 (13.33)	0.00 (0.00)
Rhynchelytrum repens (Willd.) C.E. Hubb.	0.00 (0.00)	0.19±0.16 (13.33)	0.00 (0.00)	0.00 (0.00)
Richardia brasiliensis (Moq.) Gomez	0.05±0.05 (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Sporobolus indicus (L.) R. Br.	0.00 (0.00)	0.84±0.84 (6.67)	0.09±0.09 (6.67)	0.00 (0.00)
Characteristic Species				
Andropogon floridanus Scribn.	0.01±0.01 (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
A. ternarius Michx.	0.56±0.47 (13.33)	0.18±0.18 (13.33)	0.81±0.54 (13.33)	0.18±0.14 (13.33)
A. virginicus L.	0.19±0.09 (26.67)	0.14±0.10 (13.33)	4.69±2.47 (40.00)	0.85±0.84 (13.33)
Aristida gyrans Chapm.	1.55±1.55 (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
A. purpurascens Poir.	1.24±0.51 (60.00)	0.53±0.41 (20.00)	0.00 (0.00)	0.23±0.16 (13.33)
Asimina obovata (Willd.) Nash	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.05±0.04 (6.67)
Balduina angustifolia (Pursh) Robins.	0.11±0.11 (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Baptisia lecontei Torr. & Gray	0.00 (0.00)	0.13±0.13 (6.67)	0.00 (0.00)	0.00 (0.00)
Bonamia grandiflora (A. Gray) Heller	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.06±0.04 (13.33)
Bulbostylis ciliatifolia (Ell.) Fern.	0.60±0.19 (53.33)	0.46±0.33 (13.33)	0.04±0.04 (6.67)	0.56±0.51 (130.33)
Ceratiola ericoides Michx.	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.06±0.05 (13.33)
Chapmania floridana Torr. & Gray	0.20±0.11 (26.67)	0.01±0.01 (13.33)	0.00 (0.00)	0.00 (0.00)
Clitoria mariana L.	0.00 (0.00)	0.04±0.04 (6.67)	0.00 (0.00)	0.05±0.04 (0.00)

Table 2, continued

Species	Roadside Substrates[a]			
	Sand	Clay	Lime	Clearcut
Cnidoscolus stimulosus (Michx.) Engelm. & Gray	0.02±0.02 (6.67)	x (0.00)	0.00 (0.00)	0.00 (0.00)
Commelina erecta L.	0.00 (0.00)	x (6.67)	0.00 (0.00)	0.00 (0.00)
Crotonopsis linearis Michx.	5.24±3.30 (46.67)	1.96±0.76 (46.67)	0.00 (0.00)	0.00 (0.00)
Cyperus nashii Britt.	2.73±1.41 (66.67)	0.60±0.31 (46.67)	x (6.67)	3.56±1.50 (53.33)
Dalea feayi (Chapm.) Barneby	0.37±0.22 (26.67)	0.02±0.02 (6.67)	0.00 (0.00)	0.01±0.01 (6.67)
Dicanthelium ovale (Ell.) Gould & Clark	x (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
D. sabulorum (Lam.) Gould & Clark	0.16±0.16 (13.33)	1.18±0.11 (20.00)	0.00 (0.00)	2.07±1.28 (33.33)
Eupatorium compositifolium Walt.	0.40±0.22 (26.67)	0.80±0.07 (13.33)	0.18±0.18 (93.33)	0.49±0.26 (20.00)
Galactica elliottii Nutt.	0.02±0.02 (6.67)	1.27±1.22 (13.33)	0.04±0.04 (6.67)	0.58±0.58 (6.67)
G. volubilis Britt.	0.75±0.29 (60.00)	0.60±0.39 (20.00)	0.00 (0.00)	0.75±0.36 (33.33)
Garberia heterophylla Bartr. Merr. & Harp.	0.69±0.57 (26.67)	0.00 (0.00)	0.22±0.22 (6.67)	0.95±0.62 (26.67)
Hypericum hypericoides (L.) Crantz	0.16±0.16 (6.67)	0.00 (0.00)	0.07±0.07 (6.67)	0.20±0.20 (6.67)
Lactuca graminifolia Michx.	0.00 (0.00)	0.00 (0.00)	0.14±0.07 (26.67)	0.00 (0.00)
Lechea deckertii Small	0.12±0.11 (13.33)	0.05±0.04 (13.33)	0.00 (0.00)	0.00 (0.00)
Liatris tenuifolia Nutt.	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01±0.01 (6.67)
Licania michauxii Prance	0.43±0.43 (6.67)	0.00 (0.00)	0.00 (0.00)	1.00±0.59 (20.00)
Lupinus diffusus Nutt.	0.00 (0.0)	0.00 (0.00)	0.00 (0.00)	0.22±0.22 (6.67)
Lyonia ferruginea (Walt.) Nutt.	0.36±0.36 (6.67)	0.00 (0.00)	0.00 (0.00)	0.67±0.62 (13.33)
Opuntia humifusa (Raf.) Raf.	0.02±0.02 (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Palafoxia feayi A. Gray	0.00 (0.00)	0.01±0.01 (6.67)	0.00 (0.00)	0.00 (0.00)
Panicum sp.	0.01±0.00 (6.67)	0.67±0.67 (6.67)	0.00 (0.00)	0.01±0.00 (6.67)
Paronychia patula Shinners	3.59±1.89 (26.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Persea humilis Nash	0.00 (0.00)	0.04±0.04 (6.67)	0.00 (0.00)	0.00 (0.00)
Physalis arenicola Kearny	x (6.67)	0.00 (0.00)	0.02±0.02 (6.67)	0.00 (0.00)
Pinus clausa (Chapm. ex Engelm.) Vasey ex Sarg.	0.08±0.05 (20.00)	0.11±0.11 (6.67)	0.00 (0.00)	2.76±1.57 (53.33)

Table 2, continued

Species	Roadside Substrates[a]			
	Sand	Clay	Lime	Clearcut
Pityopsis graminifolia (Michx.) Nutt.	1.04±1.00 (20.00)	0.02±0.02 (6.67)	0.00 (0.00)	0.21±0.20 (6.67)
Polanisia tenuifolia Torr. & Gray	x (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Polygonella gracilis (Nutt.) Meisn.	0.19±0.18 (20.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Quercus chapmanii Sarg.	1.87±1.13 (20.00)	0.68±0.26 (26.67)	0.09±0.09 (6.67)	1.65±0.59 (40.00)
Q. geminata Small	0.96±0.63 (33.33)	0.00 (26.67)	0.36±0.28 (13.33)	6.97±2.08 (0.00)
Q. laevis Walt.	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.13±0.10 (13.33)
Q. myrtifolia Willd.	0.69±0.62 (20.00)	0.64±0.37 (20.00)	0.67±0.67 (6.67)	17.95±5.06 (86.67)
Rhynchosia cineria Nash	0.03±0.03 (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
R. megalocarpa A. Gray	0.80±0.41 (33.33)	0.11±0.11 (6.67)	0.00 (0.00)	1.45±0.40 (60.00)
Sabal etonia Swingle ex Nash	3.32±0.93 (66.67)	1.92±0.67 (40.00)	0.53±0.53 (6.67)	6.23±1.63 (80.00)
Scleria triglomerata Michx.	0.07±0.07 (6.67)	0.00 (0.00)	0.00 (0.00)	0.29±0.29 (6.67)
Selaginella arenicola Underw.	0.02±0.02 (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Serenoa repens (Bartr.) Small	0.09±0.09 (6.67)	0.00 (0.00)	0.05±0.04 (13.33)	0.62±0.38 (33.33)
Smilax auriculata Walt.	0.00 (0.00)	0.01±0.01 (6.67)	0.10±0.10 (6.67)	0.01±0.01 (33.33)
S. pumila Walt.	0.02±0.02 (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Stillingia sylvatica L.	0.00 (0.00)	0.11±0.11 (6.67)	0.00 (0.00)	0.00 (0.00)
Stipulicida setacea Michx.	0.13±0.13 (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Tephrosia chrysophylla Pursh	0.19±0.14 (20.00)	0.04±0.04 (6.67)	0.01±0.01 (6.67)	0.13±0.13 (6.67)
Tragia urens L.	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.06±0.06 (6.67)
Trichostema dichotomum L.	0.18±0.18 (6.67)	0.00 (0.00)	0.04±0.04 (6.67)	0.00 (0.00)
Triplasis americana Beauv.	0.04±0.04 (6.67)	0.42±0.42 (6.67)	0.00 (0.00)	0.00 (0.00)
V. myrsinites Lam.	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.62±0.39 (26.67)
V. stamineum L.	0.12±0.12 (6.67)	0.00 (0.00)	0.00 (0.00)	0.16±0.13 (13.33)
Zamia pumila L.	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01±0.01 (6.67)

[a] An "x" denotes cover <0.01 percent.

substrates were closely related to differences in soil properties. Despite soil disturbance to SAND and CLEARCUT substrates, richness and percentage cover of uncharacteristic and NIS species were significantly lower, and richness and percentage cover of characteristic species were significantly higher, than for substrates with introduced soils having different properties. These relationships suggest that clay and limerock substrates used in roadway construction permit uncharacteristic and NIS species to establish and persist in an ecosystem that is otherwise inhospitable to their survival.

Nutrient enrichment of low-fertility soils can promote invasion by NIS, often with a corresponding decrease in native species richness (Heddle and Specht 1975, Clements 1983, Huenneke et al. 1990). Several studies suggest that nitrogen and phosphorus have the greatest effects. Hobbs et al. (1988) reported that invasion by nonindigenous grasses appears to be especially enhanced by fertilization (N compounds, P and K) to the detriment of native broadleaved plants. Hobbs and Atkins (1988) reported higher establishment rates of NIS in disturbed soils, and higher growth rates in fertilized (N compounds, P and K) soils, with a combination of disturbance and fertilizer resulting in the highest biomass of NIS. Heddle and Specht (1975) reported a decrease in native species and an increase in nonindigenous herbaceous species on phosphorus-enhanced plots in Australian heath. Cale and Hobbs (1991) reported that roadside soils contained significantly higher levels of soil phosphorus and NO_3 than off-road soils. In their study, percentage cover of both native and exotic plants was significantly positively correlated with soil phosphorus and (less so) NH_4, and diversity of exotic plants was positively correlated with soil phosphorus levels.

Soil pH is directly linked to nutrient availability. As reflected in the LIME versus other substrates, increased pH results in decreased Al and increased Mg and Ca levels (Brady 1974). Phosphorus increases with pH as well, but at about pH > 7 phosphorus availability is reduced by formation of complex insoluble calcium phosphates. In addition, Ca may hinder absorption and use of P by plants. Hence changes in soil pH may affect invasibility directly or indirectly by altering nutrient availability (Buchanan et al. 1975). Soil pH also may directly or indirectly affect plant species composition, because each species has an optimum pH range (Buchanan et al. 1975, Johnson and Burns 1985, Stephenson and Recheigl 1991). We suggest that reduced cover and richness of characteristic native scrub species and higher cover and richness of uncharacteristic species and NIS along CLAY and LIME roadsides are associated with modified soil properties and nutrient availability that favor different species. The observation that percentage cover and species richness of uncharacteristic species were higher along LIME than along CLAY roadsides could be related to higher phosphorus levels in LIME.

Potentially higher soil moisture levels along CLAY and LIME roadsides, a result of increased runoff from compact road surfaces and/or higher clay content (hence water-holding capacity), also may contribute to higher incidence of uncharacteristic species and NIS species. Amor and Stevens (1975) suggested that higher disturbance, light, and moisture availability along roads accounted for higher frequency of NIS along roads and decreasing frequency with distance from the road. McIntyre and Lavorel (1994) found fewer native plant species and more NIS along disturbed roadsides receiving increased road runoff than in undisturbed sites.

An additional explanation for the greater abundance of uncharacteristic species and NIS along roads with stabilizing substrate additions is that these roads likely receive greater use by vehicles. If propagules are transported on vehicles (e.g., Wace 1977), introduction probability is higher on these road surfaces. However, no parallel higher colonization rates were observed on CLEARCUT soils adjacent to LIME or CLAY roadsides, nor on (albeit less travelled) SAND roads. As a result, we suggest that modification to soil properties is the dominant factor in the species composition changes.

Ecosystems vary in their susceptibility to invasion by NIS (Hobbs and Atkins 1988, Hobbs and Huenneke 1992). Early successional, floristically simple, anthropogenically disturbed communities on mesic, fertile soils may be especially vulnerable (Ewel 1986, Fox and Fox 1986, Orians 1986, Hobbs and Huenneke 1992, Lodge 1993, McIntyre and Lavorel 1994). Invaded habitats also may have climate, soils, and plant life forms resembling those of the nonindigenous species' habitat of origin (McIntyre and Lavorel 1994).

Invasion-resistant ecosystems tend to have dense, closed vegetation or stressful abiotic features that require specialized adaptations (Baker 1986). Communities that evolved under pressure from grazers, predators, or fire may be more resistant to invasion by NIS intolerant of those conditions (Lodge 1993). Hence, xeric habitats such as warm deserts and semideserts have lower numbers of NIS (MacDonald et al. 1989). Similarly, Hobbs and Atkins (1988) reported low invasibility of Australian heath. Forcella and Harvey (1983) reported high NIS invasion in lower-elevation mountains of Montana, whereas invasions were limited to clearcuts in mid-montane forests, presumably because of suboptimal climatic conditions.

The presence of few NIS and/or uncharacteristic species along sand roadsides and in clearcuts suggests that xeric scrub may be somewhat resistant to invasion where native soils are present, even if disturbed. Austin et al. (1977) noted that some exotic trees can nearly eliminate native plants in scrub sites that are recently disturbed or are continually disturbed, such as along roadsides, but not in sites where the disturbance is a one-time event and happened in the distant past.

We suggest that the xeric, infertile soils and low frequency, high intensity wildfire regime under which Florida scrub plants evolved may preadapt them to exogenous disturbances that mimic the natural disturbance regime (Abrahamson 1984a, 1984b; Fox and Fox 1986; Hobbs and Atkins 1991; McIntyre and Lavorel 1994; Greenberg et al. 1995). However, the presence of NIS and uncharacteristic species along sand roadsides and in clearcuts emphasizes the role of roads in facilitating transport of source propagules to otherwise remote sites.

Although sand pine scrub may be more resistant to NIS invasions than many Florida ecosystems, clearly it is not invasion-proof. One motivation for initiation of this study was our observation of species like *Rhynchelytrum repens* (Willd.) C.E. Hubb. and *Imperata cylindrica* (L.) Beauv. in both roadside and clearcut scrub vegetation. Some NIS may be "preadapted" or sufficiently plastic to invade the local environment (Baker 1986). Others may undergo genetic change in response to selection pressure once they are established, enabling them to spread into hitherto inhospitable edaphic conditions (Baker 1967). Because genetic adjustment may require a lag time, the threat to intact ecosystems may not be immediately apparent (Bazzaz 1986).

CONCLUSIONS

Modified soils used in road construction appear to facilitate the spread of NIS and uncharacteristic plant species along roadside corridors. This invasion may be especially pronounced where roadside soil properties differ markedly from those of native soils (as in xeric scrub), because conditions governing competition and survival of native versus introduced species are altered. The presence of some NIS and uncharacteristic species in SAND and CLEARCUT substrates suggests that roadways facilitate the transport of source propagules to otherwise remote sites. Our data suggest that land managers should exercise caution when making decisions on if, where, and how roads must be constructed through natural areas.

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