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Floristic composition, beta diversity, and nestedness of reference sites for restoration of xeroriparian areas

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Abstract. In restoration ecology, reference sites serve as models for areas to be restored and can provide a standard of comparison for restoration project outcomes. When reference sites are located a relatively long distance from associated restoration projects, differences in climate, disturbance history, and biogeography can increase beta diversity and may decrease the relevance of reference sites. Variation in factors at the scale of individual reference sites such as patch size, microclimate, barriers to dispersal, or soil chemistry can result in reference site species composition that is a nested subset of the regional species pool. In the western United States, restoration of riparian areas, particularly those occupied by *Tamarix* spp., has become a priority; however, little is known about suitable native replacement vegetation communities for relatively dry and saline riparian terraces that comprise many of the sites where *Tamarix* is removed prior to restoration activities. We studied plant communities on riparian terraces along five rivers in New Mexico, USA, to (1) determine whether the floristic composition of reference sites can be predicted by easily measured soil variables such as pH, salinity (electric conductivity), and texture; (2) examine the extent of distance decay in the compositional similarity of xeroriparian plant communities in the southwestern United States; and (3) determine the degree of nestedness in xeroriparian plant communities in relationship to soil variables. We found that sites clustered into groups based largely on variation in soil salinity and texture. Vegetation across all sites was highly nested with dominant, salt-tolerant species found on most soil groups and salt-intolerant subordinate species restricted to low-salinity soils. The identity of subordinate species was largely site dependent, causing all sites to have the same low degree of similarity regardless of the distance between them. We conclude that, when planning restoration projects on dry and saline riparian sites, soil salinity and texture are good predictors of which species will be most suited to the area being restored, but a candidate species pool should be developed from the nearest possible reference sites, particularly for subordinate species.

Key words: beta diversity; distance decay; nestedness; reference site; restoration; riparian; Tamarix.

INTRODUCTION

Ecosystem or habitat restoration efforts often rely on the use of reference sites, which are locations that serve as models for areas to be restored. These sites are crucial for determining the suitability of species for a particular restoration site, defining restoration goals or targets, and measuring the success of restoration efforts (Pickett and Parker 1994, White and Walker 1997, Harris 1999, SER International Science and Policy Working Group 2004, Goebel et al. 2005). The challenge of selecting appropriate reference sites can be exacerbated by issues related to the spatial context of available sites (White and Walker 1997). Reference sites containing target community types may only exist a relatively long distance (tens to hundreds of kilometers) from restoration project locations due to widespread land use impacts (White and Walker 1997). This is problematic because, as geographic distance from the project site increases, the relevance of a reference site can decrease due to differences in climate, disturbance history, species biogeography, and other factors that alter the context in which a community occurs.

The spatial correlation among biotic, environmental, and historical factors (White and Walker 1997) causes beta diversity (species turnover or distance decay) to increase with distance (Nekola and White 1999, Soininen et al. 2007). Beta diversity can vary widely among different taxonomic groups, among different locations such as along elevational gradients or biome boundaries vs. relatively homogenous terrain (McKnight et al. 2007), and among different functional groups such as between herbs and trees, large-seeded and small-seeded plants, and common and rare taxa (Nekola and White

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1999). Understanding beta diversity patterns for the plant community of interest can help restoration practitioners select suitable reference sites.

Reference site relevance can also be altered by patterns of community nestedness, which may affect particularly small sites, isolated sites, or sites with stressful conditions. Understanding the structure of communities in small vs. large patches or between harsh sites (conditions that only a few species can tolerate) and more amenable sites (conditions that many species can tolerate) can also inform restoration efforts. In some cases, such as with small patches or harsh sites, a restoration or reference site may only be able to support a subset of species found in larger patches or more amenable habitats. This causes a nested pattern of community composition that typically occurs when taxa inhabiting species-poor sites are also found at progressively richer sites (Patterson 1987). Nestedness can occur in communities containing a diverse group of species with similar ecological tolerances, ecological requirements, and biogeographic histories (Patterson and Brown 1991) and can arise due to differences in species extinction probabilities or colonization abilities, or due to nested habitat requirements. The first two mechanisms are most common in island environments, while the third mechanism has been seen in studies of continental species where "generalists" are found in most habitats, and "specialist" species will only occur in a subset of areas where limiting requirements are met (Patterson and Brown 1991, Worthen 1996, Honnay et al. 1999, Stromberg et al. 2009*b*). Conversely, harsh or small sites may contain an entirely different set of species from those found in other areas, resulting in a non-nested pattern. Understanding sources and patterns of variation in ecological communities is an important part of selecting appropriate reference sites, and ecological concepts related to spatial patterns of diversity can aid applied restoration endeavors.

In recent years, conservation and restoration of riparian ecosystems has become a global priority (Postel and Richter 2003, Palmer et al. 2005, Lake et al. 2007, Richardson et al. 2007). Riparian ecosystems are notable for supporting high levels of biodiversity, yet they are also subject to high levels of degradation from a variety of sources such as land clearing for agriculture, road building, sand and gravel mining, and exotic species invasion (Naiman et al. 2005, Tockner et al. 2010). Due to the multiple stressors on riparian areas, they are now considered one of the most imperiled ecosystems on Earth (Sala et al. 2000), and efforts to restore their structure and function are common (Peterken and Hughes 1995, Webb and Erskine 2003, Holmes et al. 2005, Shafroth et al. 2008, Bunn et al. 2010).

In western USA, programs to control invasive trees and shrubs in the genus *Tamarix* (Gaskin and Schaal 2002) on floodplains have become the impetus for numerous restoration efforts (Hart et al. 2005, Bay and Sher 2008). *Tamarix* spp. are now among the most frequent and abundant woody riparian plants in western USA (Friedman et al. 2005, Ringold et al. 2008), occupying several hundred thousand hectares, and have been associated with losses of biodiversity and ecosystem services (Brock 1994, Di Tomaso 1998, but see also Shafroth et al. 2005, Stromberg et al. 2009*a*). Restoration of floodplains following *Tamarix* removal can prove difficult, particularly at sites where water tables are deep and soils are salinized (hereafter referred to as xeroriparian or dry riparian sites) due to elimination of overbank flooding from operation of upstream dams (Shafroth et al. 2008, Nagler et al. 2009). Sites that no longer flood are often unsuitable for native, mesic riparian taxa such as *Populus* and *Salix* (Glenn and Nagler 2005, Stromberg et al. 2007, Nagler et al. 2009, Merritt and Poff 2010); however, little is known about the composition of plant communities that occupy dry riparian sites or the tolerances of many candidate restoration species to edaphic conditions that characterize such sites (but see Shafroth et al. 2008, Beauchamp et al. 2009). Removal of large stands of *Tamarix* often leaves broad swaths of bare soil with little or no remnant native vegetation to provide clues as to appropriate targets for restoration (Taylor and McDaniel 1998, McDaniel and Taylor 2003, Lair 2006).

In light of the difficulty in identifying appropriate native species for revegetation after *Tamarix* removal, a major objective of our study was to determine whether the composition of xeroriparian plant communities at reference sites could be predicted based primarily on simple and inexpensive soil tests accessible to restoration ecologists. We also wanted to understand the degree to which xeroriaprian plant communities differ as geographic distance (and presumably topography and climate) between them increases (Nekola and White 1999). Our specific objectives were to: (1) investigate relationships between plant community composition and soil variables including salinity (electric condictivity), texture, and organic matter; (2) determine whether distance decay (beta diversity) of xeroriparian vegetation communities was significant over the scale of multiple watersheds within our study region (Sieben and Reinecke 2008); and (3) examine whether the distribution of plant species in xeroriparian communities exhibits a nested pattern, or whether the species composition on sites with stressful soil conditions (high salinity or coarse texture) was unique compared to sites with low salinity or finer textured soils.

To address these objectives, we sampled native grassland, shrubland, and savanna vegetation communities and associated soils occupying riparian terraces and abandoned floodplains in New Mexico, USA. Like *Tamarix*-dominated areas, these xeroriparian areas typically have alluvial-derived soils, but because of natural channel downcutting, channel migration, or flood control (via flow regulation or levees), they rarely flood, have relatively deep water tables, and in some

areas have highly saline soils (Lair 2006, Hupp and Rinaldi 2007, Nagler et al. 2009).

We expect our results to be applicable in the context of selecting appropriate species and communities for restoration following *Tamarix* control, where information on soil texture, salinity, and distance to a reference site may be the only information readily available to restoration ecologists. We also expect our results to have general applications to reference site selection in many ecosystems (Nekola and White 2002) and to theoretical studies of distance decay, beta diversity, and nestedness in ecological communities (Worthen 1996).

Methods

Study area

This study included five sites in New Mexico situated on five rivers in three watersheds separated by 50 to 380 km (Fig. 1, Table 1). Because our aim was to characterize xeroriparian reference sites that have received minimal recent and historic disturbance and where the land use history was relatively well known; most of our study areas were located on lands managed for habitat conservation. Study sites were located on abandoned river terraces or floodplains and supported native xeroriparian vegetation. Vegetation at these sites is dominated by *Prosopis pubescens* Benth, *P. glandulosa* Torr., *Sporobolus airoides* (Torr.) Torr., *S. cryptandrus* (Torr.) A. Gray, *Distichlis spicata* (L.) Greene, *Suaeda suffrutescens* S. Watson, *Allenrolfea* occidentalis (S. Watson) Kuntze, *Atriplex canescens* (Pursh) Nutt., *Bouteloua barbata* Lag., *Isocoma pluriflora* (Torr. & A. Gray) Greene and *Erigeron bellidiastrum* Nutt., and most closely resembles the Floodplain-Riparian Mesquite series and the Arroyo Riparian Saltbush and Mesquite series described in Dick-Peddie (1993).

From north to south, study sites were located on the Rio Puerco (PUR), the Rio Salado (SAL), the Rio Grande (RG), the Pecos River (PECOS), and on the Gila River (GILA). The sites ranged in elevation from 1000 m above sea level (asl) at PECOS to 1500 m asl at PUR and GILA, and fall within three of the six ecoregions defined for New Mexico (Bailey 1995). PECOS is located in the Southwest Plateau and Plains Dry Steppe and Shrub Province, RG and GILA are located in the Chihuahuan Semi-Desert Province, and SAL and PUR are in the Arizona–New Mexico Semi-Desert Province. Sites in the Rio Grande Valley (RG, PUR, SAL) receive less rainfall on an annual basis than PECOS and GILA, while the average maximum temperature is higher at RG and PECOS when compared to the other sites (Table 2). Sites differed in land use history, with PUR currently grazed, GILA grazed until 1993, and the sites at Sevilleta (SAL), Bosque del Apache (RG), and Bitter Lake (PECOS) National Wildlife Refuges grazed until they became wildlife refuges in 1973, 1939, and 1937, respectively. Essentially all sites in the Rio Grande Valleyand other areas in New Mexico have at some point been impacted by anthropogenic disturbance due to the long history of human occupation and extensive farming and ranching.

Data collection

Between 6 and 15 vegetation patches at each site were sampled within patch types that were representative of each study site. Sampled vegetation patches did not appear to have been recently disturbed. In each vegetation patch, stem density and basal area of trees (*Celtis laevigata* Willd., *Chilopsis linearis* (Cav.) Sweet, *Elaeagnus angustifolia* L., *Fraxinus* spp., *Juniperus* spp., *Pinus edulis* Engelm., *Platanus wrightii* S. Watson, *Prosopis* spp., *Quercus* spp., *Salix gooddingii* C.R. Ball and *Tamarix* spp.) were measured in a 10 × 50 m area within dense stands or a 20 × 50 m area within sparse stands. Tree species were sampled in May 2006.

Sampling of herbaceous vegetation and shrubs took place in September 2006 and May 2007 to capture both the warm- and cool-season floras that are typical of the Chihuahuan Desert region (Guo et al. 2002). Herbaceous and shrub species richness varied widely between patches (range of 5–65 species per patch). As our objective was to identify the majority of species in each vegetation patch rather than quantify richness or diversity in a fixed area, the area within a patch sampled for herbaceous and shrub species was adjusted based on the rate of accumulation of new species. Herbs and shrubs were sampled along belt transects that were 2 m wide and from 50 to 150 m long. These transects were centered within each area previously sampled for tree density and basal area. As transects were walked, the occurrence of new species was recorded in 5-m increments. At a random point within every 10-m interval through the first 100 m of each transect, a 2-m^2 herbaceous/shrub plot was centered on the transect line and cover by species was recorded using modified Daubenmire cover classes (Daubenmire 1959). After 50 m, transects were extended in 5-m segments until either (1) no new species had been encountered in the previous 20 m and no more than two new species were encountered in the previous 40 m, or (2) the transect was 150 m long. Once one of these two criteria had been met, the entire transect was walked in a 5 m wide belt on each side and all new species were recorded. Total area sampled on each transect ranged from 500 m^2 to 1500 m^2. Plant species were identified using *Flora of New Mexico* (Martin and Hutchins 1981) and *Flora of Arizona* (Kearney and Peebles 1960). Nomenclature follows the USDA PLANTS database (*available online*).[4]

In September 2006, ~1570 cm^3 soil was collected (10 cm diameter × 20 cm deep core) from each of the first five herbaceous cover plots on each transect and composited into a single sample for each transect.

[4] ⟨http:/plants.usda.gov⟩

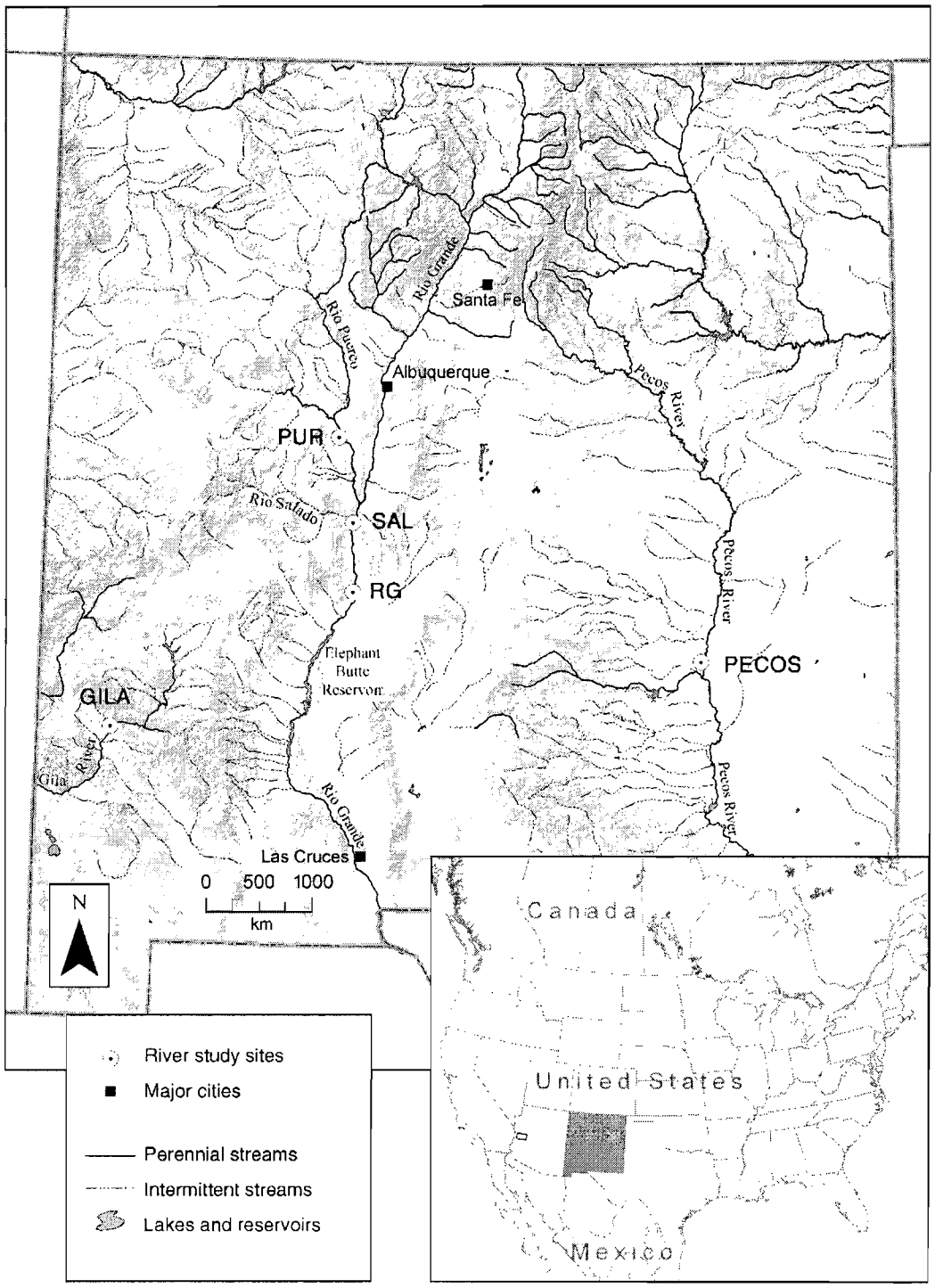

FIG. 1. Locations of xeroriparian study sites in New Mexico, USA.

Soils were analyzed by Brookside Laboratories (New Knoxville, Ohio, USA) for pH (1:1 extract in water; McLean 1982), percentage of organic matter (OM; loss on ignition at 360 degrees C; Schulte and Hopkins 1996), electrical conductivity (EC; soluble salts 1:2 (V:V) soil : water extract; Gavlak et al. 2003), and sand, silt, and clay fractions (hydrometer method; ASTM International 2002).

Soil sampling and testing were designed to be relatively simple and inexpensive, so that they would be accessible to restoration practitioners. Shallow (20 cm) soil samples require minimal time and equipment to

TABLE 1. Distances (in kilometers) between xeroriparian study sites along five rivers in New Mexico, USA.

Site	SAL	PUR	PECOS	GILA
RG	53	101	235	174
SAL		53	254	202
PUR			282	238
PECOS				386

Note: Abbreviations are: RG, Rio Grande (Bosque del Apache National Wildlife Refuge); SAL, Rio Salado (Sevilleta National Wildlife Refuge); PUR, Rio Puerco (Pueblo of Isleta Indian Nation); PECOS, Pecos River (Bitter Lake National Wildlife Refuge); and GILA, Gila River (Nature Conservancy Gila River Preserve; USDA Forest Service). Sites within the Rio Grande watershed are RG, SAL, and PUR.

collect, and tests for soil pH, electrical conductivity, and soil texture can be conducted in-house with minimal expense, equipment, and expertise (Brady 1990). We also included organic matter in our analysis, although this test requires more technical equipment and expertise. Soil organic matter can influence the water-holding capacity of the soil and is a major source for phosphorus, sulfur, and nitrogen and for soil microorganisms, which are major drivers of soil biochemical activity (Wedin and Pastor 1993, Evans et al. 2001). Due to its influence over a wide range of soil properties and processes, we included soil organic matter as a surrogate for more extensive and expensive testing of water holding capacity, nutrient levels, and biochemical activity.

Data analysis

Environmental variables were used to define soil groups within the 57 study sites. Values for soil variables (pH, OM, EC, and texture) were relativized with a general relativization (McCune and Grace 2002) to standardize variables with different scales, and then all variables except pH were arcsine square-root transformed to decrease skewness before analysis. Cluster analysis was performed in PC-ORD (version 5) using a Euclidian distance measure and Ward's Method for group linkage (McCune and Grace 2002). To create ecologically meaningful groups, the resulting dendrogram was pruned until Wishart's objective function indicated that ~80% of information remained in the dendrogram and all groups contained at least five plots. To determine the best soil variables for discriminating between groups, a stepwise discriminant approach (SAS PROC STEPDISC) with the FORWARD selection method and a 15% significance level ($P \leq 0.15$) was used (SAS Version 9.1; SAS Institute 2003). The same relativized, arcsine square-root transformed data set for the cluster analysis was also used for the discriminant analysis. A graphical representation of the groups was created by nonmetric multidimensional scaling (NMS) using the significant variables from the stepwise discriminant analysis (PC-ORD version 5). The correlation coefficients between the original variables and axis scores provided a biological interpretation of the axes and allowed for characterization of the groups. ANOVA (PROC GLM) with Fisher's LSD test used for post hoc pairwise comparisons (SAS Institute 2003) was used to examine differences in soil variables between the groups (Bonferroni corrected $P < 0.003$).

The average maximum cover and frequency for each species over the two sampling seasons were used to characterize vegetation composition. Average maximum cover was calculated by averaging the cover of each species over all 2-m^2 plots within a patch for each season and then choosing the maximum value for each species within that patch over both seasons. Average maximum frequency was calculated in a similar manner based on the number of 2-m^2 plots in which a species was present in each patch during each season. This ensures that the cover and frequency values reported reflect the seasonal peak for each species, as this can differ between spring (May) and summer (September).

Using these average maximum cover and frequency data, a plant community profile was developed for each soil group by averaging the cover and frequency of grass, herb, and shrub species across all patches within each group. Stem density and basal area of trees were calculated for each patch and also averaged across all patches in each soil group. Importance values were calculated for all non-tree species within each soil group by ranking relative average cover and relative average frequency for each species, summing these values, and re-scaling these ranks so that the species with the greatest importance is given a value of 1. Species found in the vegetation patch but not encountered in any of the 2-m^2 plots within the patch were ranked as having the lowest importance. Importance values for trees were calculated in a similar manner using the relative basal area and relative stem density for each species in each soil group. Importance values for tree species are reported separately from those for herbaceous and shrub species. While importance values are typically

TABLE 2. Mean temperatures and rainfall for National Climatic Data Center (NCDC) gauges nearest to study sites.

Site	NCDC number	Period of record	Annual maximum temperature (°C)	Annual minimum temperature (°C)	Annual precipitation (cm)
RG	291138	1894–2008	24.6	4.4	21.7
PUR	290846	1971–2000	22.6	4.0	25.7
SAL	290915	1933–2008	23.6	3.2	20.3
PECOS	290992	1950–2008	25.3	5.4	32.4
GILA	291910	1937–2008	23.6	3.1	36.5

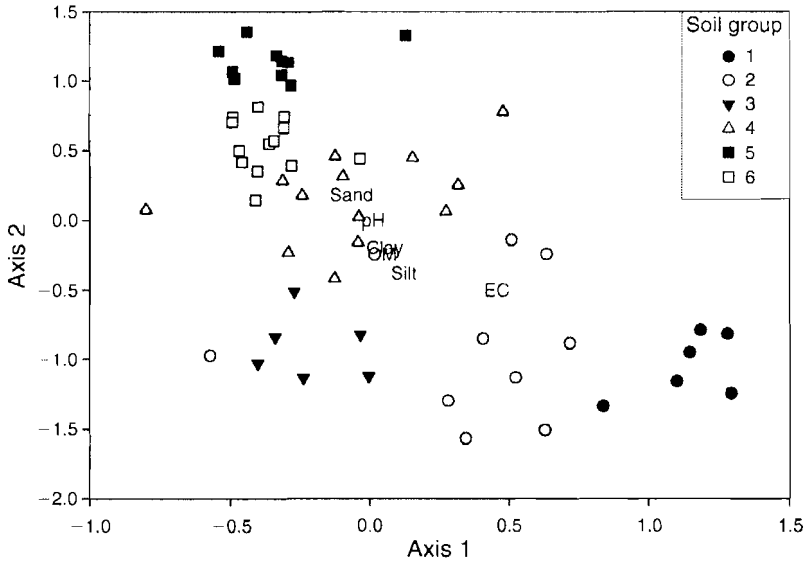

FIG. 2. Scatter plot of the first and second axes of a nonmetric multidimensional scaling (NMS) analysis to discriminate vegetation patches based on soil variables. Soil groups were defined from soil properties using cluster analysis. Soil variable centroids are labeled with the variable name. Abbreviations are: EC, electrical conductivity; and OM, organic matter.

expressed as the sum of relative productivity, density and frequency (Curtis and McIntosh 1951), our herbaceous and shrub data collection combined information on productivity and density as species cover, and our tree data did not include frequency, given that only one large plot per patch was sampled. To determine whether the groups of patches defined in the soil variable cluster analysis also corresponded to distinct plant communities, these data were analyzed using a multiple response permutation procedure (MRPP) with a Sorenson distance measure (McCune and Grace 2002) based on the average maximum cover of each species in a patch. Additionally, Sorenson similarity coefficients ($C = 2j/(a + b)$) were calculated to compare species composition between study sites across multiple soil groups and between plant communities on the same soil groups within and across watersheds. To examine the magnitude of distance decay between sites within soil groups, Sorenson similarity was regressed (SAS PROC REG) against between-site distances using the full set of species encountered. Because these data are not independent, a Mantel test with 9999 replications (PC-ORD version 5) was used to determine the significance of this relationship (Nekola and White 1999).

The nestedness of the full species data set was analyzed using the BINMATEST algorithm on a matrix consisting of presence–absence data for all species by study patch. This algorithm yields a nestedness temperature score ranging from 0 to 100 with the score increasing as disorder (lack of nestedness) in the matrix increases (Rodriguez-Girones and Santamaria 2006). Spearman rank-order correlations were calculated between the nested rank-order of patches and soil variables (Stiles and Scheiner 2008).

RESULTS

Cluster analysis with soil variables (pH, OM, EC, and fractions of sand, silt, and clay) produced seven groups when pruned with 80% information remaining in Wishart's objective function; however, one of the groups contained only two patches and consequently was joined with its sister group (Appendix A). Stepwise discriminant analysis indicated that all soil variables contributed to the differentiation of these groups ($P \leq 0.15$). NMS revealed two significant axes, accounting for 39% and 58% of the variation (Fig. 2). Soil EC was highly positively correlated with the first axis. Sand fraction was highly positively correlated, and silt fraction and OM were highly negatively correlated with the second axis (two-dimensional solution, 8.012 final stress; 0.000 final instability after 78 iterations). Pairwise comparisons of soil variables between soil groups indicated that groups 1, 2, and 3 were dominated by silt and clay, while groups 4, 5, and 6 were sand-dominated; soil EC was higher in groups 1 and 2 when compared to all other groups; soil group 1 was significantly more alkaline than soil group 6; and OM was highest in soil group 2 (ANOVA results; Table 3).

Of the 14 forb, grass, or shrub species found in all six soil groups, *S. airoides*, *A. canescens*, and *B. barbata* had the greatest importance across all groups (ranks closest to 1; Table 4). Along with *S. airoides* and *A. canescens*, *D. spicata* and *I. pluriflora* dominated the soil groups with the highest EC (groups 1 and 2); these species, along with *E. bellidastrum* and *B. barbata*, were common in patches with fine-textured soils (groups 1–3); *E. bellidastrum*, *I. pluriflora*, *Gutterizia* spp., *S. cryptandus*, *and B. barbata* dominated patches with coarse-textured soils (groups 4–6). *P. pubescens* and *P. glandulosa* were

TABLE 3. Mean (±SE) soil properties and ANOVA P values for soil groups defined by cluster analysis.

	Soil variable						
Soil group	pH	EC (dS/m)	OM (%)	Sand (%)	Silt (%)	Clay (%)	Categories
1 (n = 6)	$8.7^{a} \pm 0.37$	$9.4^{a} \pm 0.8$	$0.96^{a} \pm 0.21$	$32^{a} \pm 4.0$	$46^{a} \pm 4.2$	$23^{ac} \pm 1.7$	silt loam, loam, sandy clay loam
2 (n = 9)	$8.2^{ab} \pm 0.04$	$3.0^{b} \pm 0.41$	$2.3^{b} \pm 0.43$	$43^{a} \pm 6.1$	$40^{a} \pm 5.0$	$18^{a} \pm 3.3$	clay loam, sandy loam, silt loam, loam, sandy clay loam, silty clay loam
3 (n = 6)	$8.4^{ab} \pm 0.47$	$0.47^{c} \pm 0.15$	$1.4^{ab} \pm 0.15$	$32^{a} \pm 4.2$	$37^{a} \pm 4.1$	$31^{c} \pm 3.3$	clay, loam, clay loam, silt loam
4 (n = 13)	$8.3^{ab} \pm 0.09$	$0.66^{c} \pm 0.16$	$0.74^{a} \pm 0.09$	$70^{b} \pm 2.6$	$20^{c} \pm 2.3$	$10^{b} \pm 0.9$	sandy loam, loamy sand
5 (n = 10)	$8.5^{ab} \pm 0.06$	$0.17^{c} \pm 0.04$	$0.32^{a} \pm 0.03$	$90^{c} \pm 0.8$	$2^{b} \pm 0.5$	$8^{b} \pm 0.6$	sand, loamy sand
6 (n = 13)	$7.9^{b} \pm 0.21$	$0.15^{c} \pm 0.02$	$0.77^{a} \pm 0.05$	$82^{bc} \pm 1.3$	$9^{b} \pm 0.7$	$9^{b} \pm 1.0$	loamy sand, sandy loam, sand
ANOVA P	0.023	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	

Notes: The table presents results of ANOVA for soil variables ($P \leq 0.05$). Different superscript letters designate significant differences (Fisher's LSD, Bonferroni corrected $P \leq 0.003$) between soil groups. The categories section lists the soil texture categories associated with patches in each soil group. Abbreviations are: EC, electrical conductivity; OM, organic matter.

the dominant tree species in most soil groups (Appendix B).

Across all sites, when the average maximum cover of each species in each patch was examined between soil groups, MRPP analysis showed significant, but somewhat small differences in vegetation communities among the groups formed by soil variables ($T = -5.84$, $A = 0.067$, $P < 0.001$). Groups are more different as T becomes more negative, and a value of $A = 1$ indicates all items are identical within groups. Comparison of similarity coefficients for vegetation communities between soil groups showed that plant communities became more dissimilar as soil sand fraction increased and EC decreased (communities on group 1 and 2 soils compared to all other soil groups; Table 5). Soil groups 1 and 2 are characterized by relatively high EC and low sand content and appear to contain a core set of species that are also found in most other groups. All species found in group 1 were found in at least one other soil group, and 61% of species found in group 1 and 48% of species found in group 2 were also found in at least four other groups, but species dominance changed as soil properties changed (Table 4). Alpha richness of groups also increased as soils became sandier and less saline. While some species were found at several sites, the majority of species within each soil group were found at only one site (Group 1, 68% of species found at only one site; Group 2, 90%; Group 3, 73%; Group 4, 65%; Group 5, 64%; Group 6, 70%).

Analysis of nestedness calculated a nestedness temperature score of 7.69 ($P < 0.0001$), indicating that the species data set is highly nested (Rodriguez-Girones and Santamaria 2006). Spearman correlations showed that EC and soil texture (percentages of sand, silt, and clay) were significantly related to the nested rank-order of plots, meaning that species in patches with high EC and fine-textured soils were a nested subset of those in patches with lower EC and coarse-textured soils (EC $r = 0.71$, $P < 0.0001$; sand $r = -0.49$, $P < 0.0001$; silt $r = 0.51$, $P < 0.0001$; clay $r = 0.38$, $P = 0.004$).

When Sorenson similarity coefficients were compared between different soil groups at the same site and within the same soil groups across sites (within and between watersheds), the highest similarities occurred between soil groups within an individual site. The majority of these comparisons had similarity coefficients of 0.50 or greater (76% of comparisons; Table 6). Plant communities tended to be more similar within watersheds on the same soil group than between watersheds, but this difference was not very pronounced (Table 7). Within the Rio Grande watershed, plant communities were more similar between PUR and SAL than between RG and either PUR or SAL. Between watersheds, no comparisons had similarity coefficients higher than 0.50 and most were below 0.35. A Mantel test showed that there was no significant relationship between geographic distance (distance between sites) and Sorenson similarity between sites within soil groups.

DISCUSSION

Selection of appropriate reference sites is critical for determining what vegetation to plant at a specific restoration site and for evaluating the success of restoration projects. In restoring *Tamarix*-dominated areas, reference site selection can be particularly difficult, as site hydrology has often been altered to the point that the plant species best adapted to the current edaphic conditions may be novel to the site (Lair 2006, Shafroth et al. 2008). In some cases, the *Tamarix* clearing process leaves little remnant native vegetation to guide restoration efforts. Examination of the soils and vegetation in 57 vegetation patches across five rivers in New Mexico revealed that soil salinity, pH, OM, and texture alone are good predictors of vegetation commu-

TABLE 4. Importance value of core species found in soil group 1 or 2 and in at least four other soil groups.

Species	Soil group 1	2	3	4	5	6
Herbaceous and shrub species						
Allionia incarnata		47	26	66	80	15
Aphanostephus ramosissimus	23	47	7	22	21	56
Atriplex canescens	5	7	6	2	2	8
Bassia scoparia	7	2	9	6	19	108
Bouteloua barbata	14	13	4	13	8	2
Bouteloua gracilis		35	42	8	20	82
Chamaesyce serpyllifolia		47	2	10	6	6
Chenopodium leptophyllum		15	76	52	53	49
Conyza canadensis	13	15	29	20	43	48
Cryptantha crassisepala		42	23	21	11	10
Descurainia pinnata	10	11	13	12	29	44
Dimorphocarpa wislizeni		47	22	16	5	13
Distichlis spicata	1	3	58	100	101	
Eragrostis cilianensis		47	50	66	101	21
Erigeron bellidiastrum	15	21	2	3	18	124
Gaillardia pulchella		47	26	42	14	37
***Gutierrezia* spp.**	19	47	10	9	3	12
Halogeton glomeratus		36	67	28	35	169
Helianthus annuus		23	57	31	40	174
Hoffmannseggia glauca	23	25	12	32	101	
Isocoma pluriflora	5	6	8	4	15	69
Kallstroemia parviflora		26	16	27	24	3
Laennecia coulteri	23	38	16	36	101	174
Machaeranthera gracilis		47	31	40	22	13
Machaeranthera tanacetifolia		47	28	22	62	7
Malacothrix fendleri		47	76	79	101	138
Melampodium leucanthum		47	76	93	101	174
Nama hispidum		47	24	19	11	27
Pectis angustifolia		38	30	48	65	98
Phacelia integrifolia		47	51	26	11	97
Portulaca oleracea	17	8	45	7		28
Portulaca suffrutescens		47	67	15	98	138
Proboscidea parviflora		47	45	79	82	16
Salsola kali	15	17	5	5	10	4
Solanum elaeagnifolium	17	18	18	16	16	9
Sporobolus airoides	1	1	1	1	1	1
Sporobolus cryptandrus	23	47	40	10	4	4
Tidestromia lanuginosa		14	67	13	28	38
Tree species						
Prosopis glandulosa	1	3	1	1	1	1

Notes: Species occurring in all soil groups are in boldface. Importance values are calculated as a combination of plot cover and frequency of occurrence and are scaled such that the most abundant/frequently encountered species in a soil group has an importance value of 1.

nity composition, suggesting that plant species on sites where these soil variables are similar to the project site likely will be well suited to the project site. One caveat is that these results pertain to soil conditions in the top 20 cm of the soil profile. While shallow soil conditions explained a substantial amount of the variation in xeroriparian plant communities (NMS combined axes 97%) and are very relevant to plant establishment,

TABLE 5. Sorenson similarity coefficient for comparison of species composition among soil groups.

Soil group	Soil group 1	2	3	4	5	6
1	*28*	0.44	0.32	0.27	0.26	0.14
2		*80*	**0.56**	0.48	0.44	0.38
3			*109*	**0.64**	**0.57**	0.47
4				*127*	**0.75**	**0.52**
5					*128*	**0.52**
6						*216*

Notes: Coefficients with values of 0.50 or greater are in boldface. Italicized numbers are species richness (number of species) for each soil group.

TABLE 6. Sorenson similarity coefficients for comparisons between soil groups within study sites.

Soil group comparisons	Site			
	RG	PECOS	PUR	SAL
1 and 2	0.47	**0.50**		
1 and 3	**0.55**	0.29		
1 and 4	**0.63**	0.20		
1 and 5		0.23		
2 and 3	**0.50**	**0.52**		
2 and 4	**0.52**	**0.41**		
2 and 5		**0.47**		
3 and 4	**0.54**	**0.59**		**0.65**
3 and 5		**0.50**		**0.58**
3 and 6				**0.67**
4 and 5		**0.81**	**0.61**	**0.70**
4 and 6			**0.75**	**0.69**
5 and 6			**0.72**	**0.72**

Notes: Coefficients with values of 0.50 or greater are in boldface. All patches at GILA fall into soil group 6.

phreatophytes and other deep-rooted species could eventually encounter different soil conditions in buried soil horizons or in the aquifer.

While soil variables are helpful in identifying reference plant communities, this study also found that nestedness and beta diversity are important factors in structuring xeroriparian plant communities. Vegetation encountered in our sample patches was significantly nested, with the plant communities of highly saline and fine-textured sites a nested subset of the vegetation communities of low-salinity, sandy sites. In xeroriparian communities, the plant species capable of tolerating high salinity are "generalists" and are also found on most other xeroriparian soil groups, while "specialist" species are restricted to less saline locations (Patterson and Brown 1991, Worthen 1996, Honnay et al. 1999).

Nested subset structure can occur when communities are assembled from a common species pool and differences in extinction probability, colonization ability, or environmental tolerances result in some species being restricted to a subset of all possible sites (Patterson and Brown 1991, Honnay et al. 1999, Stiles and Scheiner 2008). The strong correlations of the nested rank order of plots with soil variables suggest that environmental tolerances rather than differences in colonization or extinction probabilities are the major mechanisms creating a nested subset structure in xeroriparian vegetation. Additionally, the topography of xeroriparian areas makes it unlikely that differential colonization or extinction would have a large effect on community structure in these communities. The majority of patches surveyed for this study were situated on open terraces with few barriers to dispersal, either along the riparian corridor or from the surrounding uplands (Gregory et al. 1991), an arrangement that could allow species to recolonize a site relatively easily if they were to undergo local extinction (Honnay et al. 1999, Honnay and Hermy 2000).

While xeroriparian vegetation exhibited a nested community structure, the degree of difference in vegetation patches on the same soil group was not significantly related to the distance between patches. Distance decay of similarity can be caused by increased climatic differences with distance, narrow niche breadths, or limits to dispersal of certain species (Nekola and White 1999). Nekola and White (1999) found that in *Picea–Abies* forests, herbaceous (non-woody vascular) plants experienced more loss of similarity with distance than other physiognomic groups. Because the majority of our xeroriparian study sites were dominated by forb and grass species (with some co-dominated by shrubs such as *A. canescens*), and because they were distributed over five rivers in southern New Mexico, separated by up to 386 km and located in three different ecoregions (Bailey 1995), we expected to see a strong decay of community similarity between sites within each soil group. Instead, we observed that the dominant species at xeroriparian sites in New Mexico (*S. airoides*, *A. canescens*, *B. barbata*, *I. pluriflora*, *E. bellidastrum*, and *S. cryptandus*) were often the same regardless of site or soil type. This wide niche-breadth indicates that these species are likely superior competitors across a broad range of edaphic, physiographic, and climatic conditions (Nekola and White 1999).

Unlike dominant species, subordinate species composition varied across rivers. The identity of subordinate

TABLE 7. Sorenson similarity coefficients for comparisons within soil groups between study sites.

Level and site	Soil group					
	1	2	3	4	5	6
Within Rio Grande watershed						
RG/PUR				0.42		
RG/SAL			0.30	0.40		
PUR/SAL					**0.69**	0.47
Between watersheds						
RG/PECOS	0.49	0.18	0.25	0.31		
PECOS/PUR				**0.50**	0.38	
PECOS/SAL			0.33	0.40	0.44	
PUR/GILA						0.24
SAL/GILA						0.34

Note: Coefficients with values of 0.50 or greater are in boldface.

species that are added as plots become sandier and less saline is largely site dependent and is likely associated with local or watershed-level climate and topography and small differences in soil chemistry due to local geology. As a result, communities were more similar across soil groups within a site than to communities at other sites on the same soil groups (Sieben and Reinecke 2008). This is true even for sites in relatively close proximity, such as SAL, PUR, and RG, which are only separated by ~50 km. Distance decay of similarity is not very strong for xeroriparian vegetation at the scale studied because the dominant species are similar between most sites, while the subordinate species are different between most sites, causing all sites to have similar beta diversity regardless of the distance between them (i.e., the "core" and "satellite" species of Hanski 1982). Similar situations have been found in other communities or taxa where common or broadly distributed species had a lower rate of distance decay than less frequently encountered or more locally distributed species (Nekola and White 1999, Buckley and Jetz 2008).

Restoration projects often seek to restore native species cover and diversity (SER 2004). If nonnative weed propagule pressure at a site is high, success of restoration efforts in xeroriparian or other habitat types may be increased by focusing first on restoring competitive species that are tolerant of most conditions and more likely to outcompete nonnative species emerging from the seed bank or dispersing in from other areas (Lym and Tober 1997, Di Tomaso 2000, Masters and Sheley 2001, Lair 2006). Once the dominant native species have become established, then efforts could switch to establishing subordinate species. These species appear to be much more sensitive to small regional differences in climate, soils, and topography; thus, it would be important to choose them using information from reference sites that match the soil conditions at the project site and are in close proximity to the project site (<50 km away and within the same watershed if possible). It is also possible that subordinate species may be able to disperse into the site from nearby areas. In cases where active revegetation is necessary, using locally collected seed or stock whenever possible would help to preserve region-specific genetic diversity (Burton and Burton 2002, McKay et al. 2005).

An understanding of the influence of edaphic factors on vegetation composition and the degree of distance decay and nestedness of plant communities used as reference sites in restoration projects can help inform choices regarding target species for project sites. Choosing appropriate target species for revegetation can increase project success, reduce costs (Shafroth et al. 2008), and help preserve local-level diversity (Burton and Burton 2002, McKay et al. 2005, Sieben and Reinecke 2008). This paper examined beta diversity of xeroriparian areas across five watersheds separated by nearly 400 km; however, the region currently affected by *Tamarix* covers 470 000–650 000 ha (Zavaleta 2000) and stretches over several biomes, including the plains grasslands and the Chihuahuan, Sonoran, Mojave, and Great Basin Deserts. As efforts such as biological control aimed at removing *Tamarix* over large areas are implemented (Hudgeons et al. 2007, Tracy and Robbins 2009), more information on reference sites will be needed in other subregions of the western United States to determine the general applicability of these results and the communities identified.

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APPENDIX A

Dendrogram created by hierarchical cluster analysis using soil variables (*Ecological Archives* A021-027-A1).

APPENDIX B

Species composition and importance values for each site by soil group (*Ecological Archives* A021-027-A2).