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Avian Species Richness in Different-Aged Stands of Riparian Forest Along the Middle Rio Grande, New Mexico

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Abstract: *Riparian forests are important for maintaining vertebrate species richness in the southwestern United States, but they have become restricted in distribution due to both historical and current management practices. In order to counteract continued loss of this habitat, several mitigation programs were developed in the middle Rio Grande Valley of New Mexico. Three areas ranging from 50 to 140 ha were revegetated with native trees using pole planting and cattle*

Riqueza específica de aves en sitios de distinta edad en bosques ribereños a lo largo del valle medio del Río Grande, Nuevo México

Resumen: *Los bosques ribereños son importantes para el mantenimiento de la riqueza de especies de vertebrados en el sudoeste de los Estados Unidos, pero su distribución ha sido reducida debido a prácticas de manejo tanto pasadas como presentes. Varios programas de mitigación fueron desarrollados en el valle medio del Río Grande de Nuevo México, a*

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exclosures, and changes in vegetation structure were quantified after 2, 3, and 5 years of growth. As expected, the older site contained the most heterogeneous mix of plant species and the greatest structural diversity. We compared year-round avian use of the revegetated sites with a mature cottonwood forest site of approximately 30 years of age. As the revegetated sites matured and salient habitat features changed, the population dynamics of individual avian species and patterns of guild structure varied. The older revegetated sites showed a greater similarity to the mature cottonwood site, suggesting that reclamation efforts established quality riparian habitats for birds in as little as 5 years. The revegetated sites appeared especially important for Neotropical-migrant birds. We suggest that a mosaic of riparian woodlands containing mixtures of native tree and shrub species of different size classes is necessary to maintain avian species richness in the middle Río Grande drainage, and probably throughout the southwestern United States.

efecto de poder contrarrestar la contínua pérdida de este hábitat. Tres áreas que abarcan de 50 a 140 ha fueron reforestadas con árboles nativos utilizando estacas en la plantación y cercos de exclusión de ganado. Los cambios en la estructura vegetativa fueron cuantificados después de 2, 3 y 5 años de crecimiento. Como se esperaba, el sitio más antiguo contenía la mezcla más heterogénea de especies de plantas y la mayor diversidad de estructura. Comparamos a lo largo de todo un año el uso de los sitios reforestados por las aves con aquel de un bosque maduro de álamos de aproximadamente 30 años de edad. La dinámica poblacional de las especies de aves y los patrones de la estructura de la comunidad variaron, a medida que los sitios reforestados maduraron y las caracertísticas más importantes cambiaron. Los sitios reforestados más antiguos mostraron una mayor similitud con el sitio de álamos maduro, sugiriendo que los esfuerzos de restauración permitieron establecer hábitats ribereños de calidad para las aves, en un plazo de sólo 5 años. Los sitios revegetados parecieron ser especialmente importantes para aves migratorios Neotropicales. Sugerimos que se necesita un mosaico de áreas boscosas ribereñas, que contenya una mezcla de árboles nativos y especies de arbustos de diferentes tamaños de clases, en or den de mantener la riqueza de especies avícolas en el valle medio del Río Grande y probablemente a través de todo el sudoeste de los Estados Unidos.

Introduction

Riparian flood plains in the southwestern United States support some of the highest concentrations of breeding bird species in temperate North America in terms of both abundance and diversity (Hubbard 1971; Carothers et al. 1974; Johnson et al. 1977; Szaro 1980; Rice et al. 1983). The presence of foliage in various height classes, the diversity of plant species and forms, the heterogeneous mix of open and densely vegetated areas, and the relatively high frequency of nesting cavities all combine to form a complex association that can support a variety of avian species. These corridors of woody vegetation also appear to be important for migrant landbirds, including both species that overwinter in the Neotropics and short-distance migrants that usually winter in the southern United States and northern Mexico (Stevens et al. 1977; Stamp 1978; Knopf et al. 1988). Riparian habitat in this region is confined to zones with regular flooding or a high water table, and it currently covers less than 1% of the land area of the western United States (Knopf et al. 1988). Prior to modern human development of the flood plain, riparian forest was more widely distributed and probably historically supported an even greater density and diversity of bird populations. The restricted distribution and high species richness of this habitat has led to conservation and management concerns, not only in North America but elsewhere in the world (see Decamps et al. 1987).

Most avian species are closely associated with particular habitats (see Cody 1985) and, despite their ability to move over relatively large geographic areas, will consistently be found in localities that meet their specific ecological requirements. Removal of critical vegetation can have dramatic effects on bird populations, as in the case of stopover sites for long-distance migrants (Finch 1991; Moore et al. 1993) or species with restricted breeding habitats such as the Red-cockaded Woodpecker (*Picoides borealis;* Walters 1991) and Least Bell's Vireo (*Vireo bellii pusillus;* Goldwasser et al. 1980). Once a specific vegetation type is eliminated from a region, the associated avifauna often disappears as well.

Various agencies have been involved in vegetation restoration efforts in the Rio Grande Valley of New Mexico in an attempt to replicate natural successional processes. Avian responses to restored vegetation in southwestern riparian areas has been largely unstudied (Hunter et al. 1989). This study describes the differences in vegetative structure on three sites of riparian restoration and quantifies concomitant patterns of avian use among sites of different age. We compare these

revegetated sites to a nearby mature riparian forest to quantify similarities among bird communities.

History of Study Area

The Rio Grande Valley of central New Mexico contains one of the most extensive riparian gallery forests or *bosques* dominated by Rio Grande cottonwood (*Populus fremontii* var *wislizeni*) in the southwestern United States (Howe & Knopf 1991). Associated with cottonwood are a variety of trees and shrubs, including Goodding willow (*Salix gooddingii*), coyote willow (*Salix exigua*), New Mexico olive (*Forestiera neomexicana*), seepwillow (*Baccharis glutinosa*), wolfberry (*Lycium* sp.), and screwbean mesquite (*Prosopis pubescens*); together these characterize the floodplain-plains riparian vegetation type of Dick-Peddie (1993).

Within the last two centuries, the middle Rio Grande has been subjected to a variety of human-induced changes that have permanently altered its hydrology and ecology (Bullard & Wells 1992). Although the river flood plain was farmed for centuries prior to settlement by Europeans, extensive modifications of the riparian ecosystem were not evident until the 1800s, when livestock grazing and timber and firewood harvesting reduced much of the existing forest and understory vegetation (Scurlock 1988). The construction of riverside drains, levees, and irrigation works during the early 1900s lowered the water table, drained much of the riverside wetlands, and allowed further agricultural development of the flood plain (Van Cleave 1935).

Channelization and dam construction on the Rio Grande were implemented during the early 1900s to limit seasonal flooding and increase the efficiency of water deliveries. The control of yearly flooding has suppressed the regeneration of flood-dependent native species, particularly cottonwoods, while nonnative species such as salt cedar (*Tamarix chinensis*) and Russian-olive (*Elaeagnus angustifolia*) have become widely established (Dick-Peddie 1993). Salt cedar is now common throughout much of the central and southern Rio Grande Valley, where it frequently occurs to the exclusion of native woody vegetation.

Methods

The Study Sites

Studies were conducted at four sites in the Rio Grande Valley in southcentral New Mexico, three at the Bosque del Apache National Wildlife Refuge, Socorro County, and one near Las Palomas at the north end of Caballo Reservoir, Sierra County. Despite their substantially different histories, the four sites provided examples of different successional stages in the maturation of a riparian forest after complete deforestation (Fig. 1).

Young Cottonwood Sites (two sites, Bosque del Apache). In 1989 the U.S. Fish and Wildlife Service initiated a program for the restoration of native vegetation in several management units of the refuge containing dense monotypic stands of salt cedar. These areas were cleared by root-plowing and burning and were replanted with native trees and shrubs, including cottonwood (*Populus fremontii* and hybrid forms), Goodding willow, squawbush (*Rhus trilobata*), wolfberry, and New Mexico olive. Cottonwoods and willows were established as pole-plantings, whereas other species were nursery-stock seedlings.

Two management units included in the revegetation project were used as young cottonwood sites for our study. Replanting was completed on a 50–ha site in spring 1989 (3-year site) and a second 50–ha site early in 1990 (2-year site). Trees were planted in evenly spaced rows, resulting in an open woodland plantation. A small natural grove of mature cottonwoods near the revegetation area on the 2-year site was left intact during clearing; otherwise both units were devoid of woody vegetation other than the plantings and a few volunteer shrubs. Cleared areas between the planting rows on both sites had become well vegetated with annuals by early 1992. There is no livestock grazing on the refuge.

Medium-aged Cottonwood Site (one site, Caballo Reservoir). The 5-year site (140 ha) was located at the head of Caballo Reservoir within an area subject to periodic inundation by the reservoir. The site was downriver from a large dam and reservoir project (Elephant Butte) and thus was within a highly managed riparian area, subject to a range of man-made hydrologic conditions. Much of the area is presently used for livestock grazing, and the major woody plant present is salt cedar.

Between 1985 and 1988, unusually high water levels in Caballo Reservoir flooded much of the study area, drowning most vegetation. After the reservoir was lowered in early 1988, a 140-ha fenced livestock exclosure was established at the upper end of the flood zone. Natural regrowth within the exclosure established a complex vegetation community of cottonwood, willows, salt cedar, screwbean mesquite, and native shrubs. Elements of the sand-scrub vegetation community located outside of the flood plain were also represented in the exclosure. Intermixed with native vegetation was a small number of preexisting pole-planted cottonwoods and shrubs that survived inundation in the late 1980s.

Mature Cottonwood Site (one site, Bosque del Apache). The 42–ha mature site (30-year site) was in an undisturbed mixed cottonwood forest on the refuge that had been protected from major flooding and burning since about 1941. Woody vegetation included a well-developed canopy of cottonwoods 8–15 meters in height, a large number of salt cedar and Goodding willow, and an understory of seepwillow, New Mexico olive, and various shrubs. Similarly sized cottonwoods at a

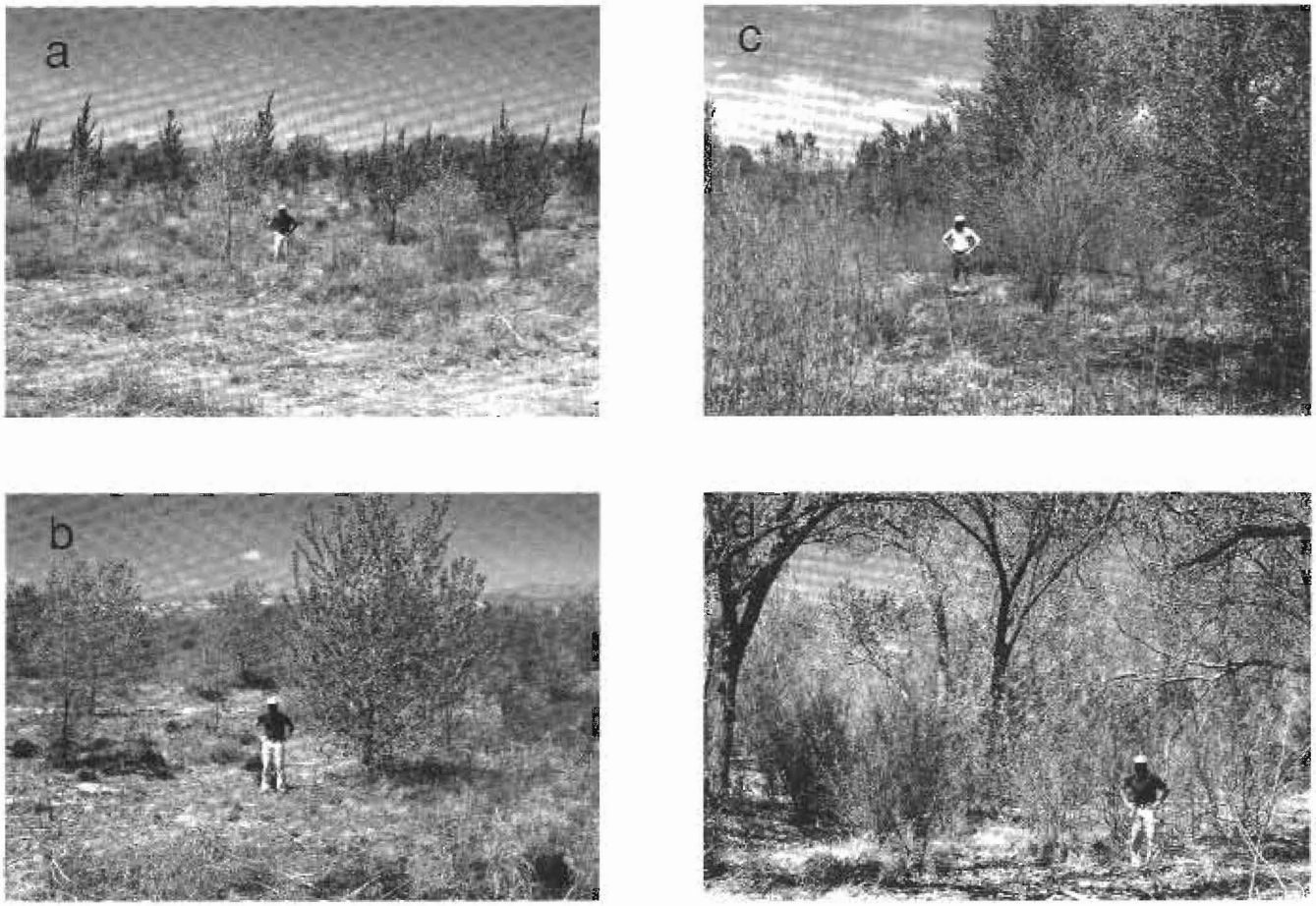

Figure 1. Revegetated and mature cottonwood study sites in the middle Rio Grande Valley of central New Mexico, photographed in June 1993: (a) 2-year site, (b) 3-year site, (c) 5-year site, and (d) 30-year site.

nearby site on the refuge had been aged to between 30 and 40 years old (Ritter 1993).

Census Methods

VEGETATION SURVEYS

We characterized the complexity and maturity of the woody vegetation communities at the four study sites by estimating the individual and cumulative densities of the woody plant species present and by constructing height-frequency profiles for each of the most common species.

Surveys of the revegetated sites were conducted in July 1992 and the mature cottonwood site in January 1993. At each site we established two perpendicular transect lines that intersected near the geographic center of the site. All trees and shrubs more than 0.5 meters tall within 10 meters of either side of the line were counted. Densities for individual species (plants/ha) were calculated and then totaled to provide an overall density estimate for woody vegetation on each site.

BIRD SURVEYS

Transect and point-count surveys were used to determine avian species composition within the sites (Verner & Ritter 1985; Hutto et al. 1986). The lengths of the transects and the number of count stations varied according to the size and complexity of each site. The transect at the 2-year site was 550 meters long with three point-count stations separated by 250 meters, and the 3-year site transect was 1300 meters with six point-count stations 250 meters apart. The 5-year site transect was 1800 meters long and had eight point-count stations, each 250 meters apart. At the 30-year site, two transects of 600 meters were established through the forest interior, each with three point-count stations 200 meters apart. Surveys began within one half hour before sunrise and ended within three hours of sunrise during spring, summer, and fall. Winter surveys began approximately one hour after sunrise and ended within three hours of that time. Transects were walked slowly, and all birds seen or heard within the boundaries of the study site were recorded. At each point-count station, the observer counted all birds seen or heard within a 100-

meter radius during a period of 10 minutes (30-year site) or 8 minutes (all other sites). Birds detected during point counts were recorded separately from transect surveys. No effort was made to record detection distances, and therefore no density estimates could be made. Surveys began in Winter 1991 and continued seasonally through Fall 1992. Winter surveys were conducted in mid- to late December and February. Spring surveys were conducted in late April and mid-May. Summer surveys were conduced in late May and early June. Fall surveys were conducted in early to mid-September. A complete list of bird species detected by season for each site is provided by Farley et al. (1994).

Data for transect and point-count surveys were combined within seasons for each site and for the two transects in the 30-year site. Species richness was calculated as the total number of species detected during both survey types during each season. Although transect lengths and the uumber of count stations were not identical, we believe they were similar enough to allow a reliable estimate of the avian species present. The 2-year site was the smallest and therefore had the shortest transect and fewest count stations. This site was also the most open, and birds were easily detected; thus we are confident that the numbers of species and individuals were accurately recorded and were not artificially low due to a reduced sampling effort.

Similarity of species composition between each revegetated site and the mature site was calculated for each season using Whittaker's Coefficient of Community (CC): $CC = 2S_{ab}/(S_a + S_b)$, where S_{ab} is the number of species in common between the two habitats, and S_a and S_b are the numbers of species in each of the two habitats, respectively (Whittaker 1975).

Results

Vegetation Surveys

Vegetation structure showed a general pattern of increasing complexity, plant density, and overall species richness with age. The height profiles of the woody plant species on the revegetated sites indicated greater structural diversity with age (Fig. 2). The 5-year site contained the largest number of species and had the greatest overall plant density (Table 1). Species richness and total plant density were greater at this site than at the 30-year site. These sites differed in number of particular shrub species. The 2- and 3-year sites were similar to each other in vegetative composition and structure; their height profiles (Fig. 2) and shrub species (Table 1) differed from those of the two oldest sites. The youngest two sites had the fewest woody plaut species.

Bird Surveys

The maximum number of bird species detected in any season was 28, which we counted on the 3-year site in fall and the 30-year site in spring (Fig. 3). The 3-year site had an influx of migrants during fall; migrants were also primarily responsible for the increase in species richness in spring on the 30-year site (Fig. 3). During fall and winter, the 3-year site contained the most species, followed by the 5-year and 30-year locales. These rankings are consistent despite turnover of individual species. Second, the number of breeding species, which includes individuals detected during both the spring and summer censuses, increased with site age. The single exception was the 2-year site in summer. Many species detected on the 2-year site during the summer were foraging in the planted area while nesting in the nearby mature woodland—for example, Rufous-sided Towhee (*Pipilo erythrophthalmus*) and Northern Oriole (*Icterus galbula*). If these species are removed, the number of species present during the summer at the 2-year site is reduced to seven, and the pattern of relative species richness among sites is consistent between spring and summer.

There was a striking difference among sites in the number of unique species, defined as species detected at only a single site, particularly in spring and summer (Fig. 3). The 30-year site supported more species that were not using the younger-aged stands during spring and summer, while the 2-year site had no unique species during those seasons. The distribution of species was more uniform during fall and winter, because relatively small numbers of species were found on only a single site. Values ranged from 2 to 8 and reflected the presence of migrant and overwintering species with relatively broad ecological and geographic distributions. These results are consistent with the Coefficients of Community comparing the avian assemblage from the 30-year site with each of the revegetated sites (Table 2). The similarity in species composition between revegetated sites and the mature forest increased with site age. Similarity was greatest in the fall and winter, while revegetated sites shared fewer species with the 30-year forest in the spring and summer.

Ground-searching foragers were predominant on all sites, particularly in winter—for example, Chipping (*Spizella passerina*) and White-crowned (*Zonotrichia leucophrys*) Sparrows (Farley et al. 1994). During the remaining seasons the proportion of ground foragers was greater on the two younger sites—for example, Vesper (*Pooecetes gramineus*) and Lark (*Chondestes grammacus*) Sparrows—reflecting the higher proportion of bare ground relative to vegetation. Timber-foliage searching species were detected on all sites: Bewick's Wren (*Thryomanes bewickii*) and Ruby-crowned King-

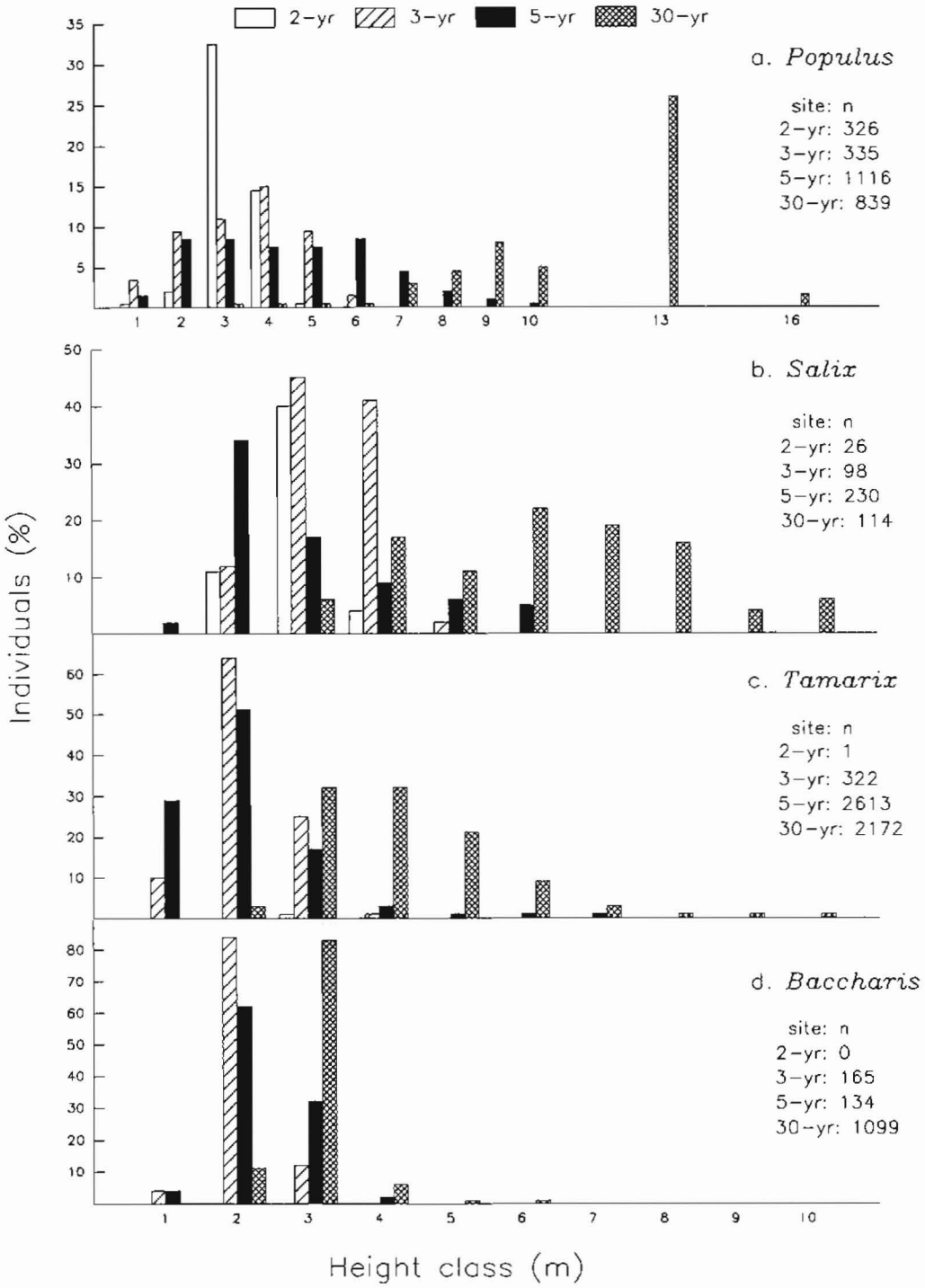

Figure 2. Height class distribution of individuals of the four most common woody plant species at revegetated and mature cottonwood sites: (a) Populus fremontii, (b) Salix gooddingii, (c) Tamarix chinensis, (d) Baccharis glutinosa.

let (*Regulus calendula*) were present on the 5- and 30-year sites in winter, Yellow-breasted Chat (*Icteria virens*) and Summer Tanager (*Piranga rubra*) were on the mature site in spring, and Blue Grosbeaks (*Guiraca caerulea*) were common on all sites in summer. In the fall, a variety of insectivorous neotropical migrants, such as Orange-crowned (*Vermivora celata*) MacGillivray's (*Oporornis tolmei*) and Wilson's (*Wilsonia pusilla*) Warblers, moved through the well-vegetated 5- and 30-year sites.

Table 1. Estimated densities of woody plant species present at revegetated and mature cottonwood sites.

		Study Sites			
		2-year	*3-year*	*5-year*	*30-year*
Total Area (ha)		*50*	*50*	*140*	*42*
Area Sampled (ha)		*1.6*	*3.1*	*4.9*	*3.1*
Woody Plant Species	*Plant Type*[a]	*Plants/ha*[b]			
Rio Grande Cottonwood, *Populus fremontii*	T	204	108	228	271
Salt Cedar, *Tamarix chinensis*	T	2	104	533	701
Goodding Willow, *Salix gooddingii*	T	16	32	47	37
Seepwillow, *Baccharis glutinosa*	S	—	53	27	355
Coyote Willow, *Salix exigua*	S	—	8	589	—
New Mexico Olive, *Forestiera neomexicana*	T	—	2	—	209
Screwbean Mesquite, *Prosopis pubescens*	T	—	—	66	2
Wolfberry, *Lycium* sp.	S	—	—	8	2
False Indigo, *Amorpha fruticosa*	S	—	—	1	+
Arrowweed, *Pluchea sericea*	S	—	—	178	—
Broom Dalea, *Dalea scoparia*	S	—	—	70	—
Honey Mesquite, *Prosopis juliflora*	S	—	—	4	—
Russian Olive, *Elaeagnus angustifolia*	T	—	—	—	2
Velvet Ash, *Fraxinus cuspidata*	T	—	—	3	—
Squawbush, *Rhus trilobata*	S	—	1	—	—
Four-Winged Saltbush, *Atriplex canescens*	S	—	+	—	—
Total Plants/ha		222	308	1754	1579

[a] *Plant type: T = tree, S = woody shrub.*
[b] *Number of individual plants indicated; — = species absent in survey; + = species present but less than 1 plant/ha.*

Discussion

Disturbance plays an important role in the establishment and development of the riparian plant community in the middle Rio Grande Valley of New Mexico (Szaro 1989). Historically this ecosystem was maintained in a state of dynamic equilibrium through the effects of periodic destructive floods and more frequent smaller floods (Crawford et al. 1993), which promoted recruitment of riparian plant species. The localized effects of flood events resulted in a mosaic of vegetation of various ages, structures, and species compositions.

Our revegetated study sites were chosen to approximate different successional stages in this ecosystem. The 2- and 3-year sites generally had an even distribution of small trees with a poorly developed perennial understory (Fig. 2). Young, naturally occurring *bosque* is characterized by a plant species mix that includes a small shrub component of coyote willow and seepwillow, and small cottonwood and willow trees. On our sites, this homogeneous distribution of a few species of similar age resulted from selective planting and the clearing methods used prior to revegetation; it resembled early successional growth of many riparian communities following major floods.

The 5-year site contained a mixture of cottonwood, willow, and screwbean mesquite trees, in addition to various shrub elements such as arrowweed (*Pluchea sericea*) and broom dalea (*Dalea scoparia*), which typifies riparian vegetation in the southern Rio Grande area (Table 1; Dick-Peddie 1993). The 5-year site was most comparable to mature riparian forest, such as the 30-year site, which had a similar species mix but a taller canopy and less dense understory.

Avian assemblages varied among our riparian woodland sites of different ages, a pattern consistent with observations at other riparian sites in southwestern states (Hubbard 1971; Szaro 1980; Anderson et al. 1989; Rosenberg et al. 1991). The pattern accentuates the relatively inflexible relation between many bird species and salient habitat features. Vegetation structure appears in part to determine the bird species that use the different-aged stands. The youngest sites (most open) contained predominantly ground-searching species in most seasons. Timber-foliage searching species were present on all sites but were consistently more common in the older two sites and peaked at the 30-year site in spring. The mature sites also contained bird species in several foraging guilds, all timber specialists, that were never detected on the recently revegetated sites.

Insectivorous species passing through the riparian corridor in spring contributed to the high species richness in the 30-year site (Fig. 3). An equal value was recorded on the 3-year site in fall, where both insectivorous and granivorous migrants were detected. The two older sites also contained the greatest number of unique species (Fig. 3), particularly during the breeding season. These data suggest that the complexity of the bird as-

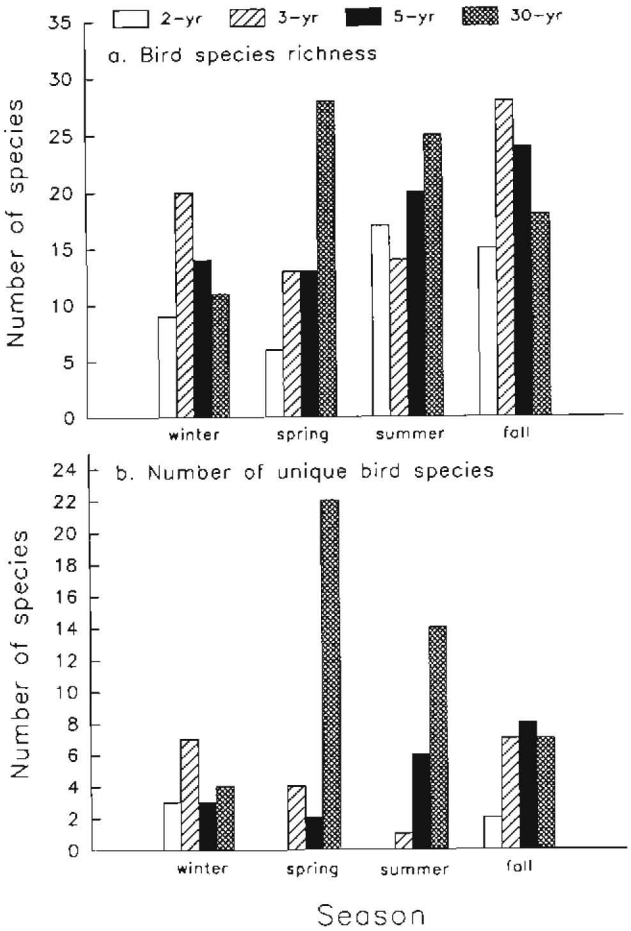

Figure 3. Estimates for revegetated and mature cottonwood sites: (a) bird species richness includes the total number of bird species detected at each site during each season and (b) number of unique bird species indicates the number of species at each site not present at other sites during that season.

Table 2. Whittaker's Coefficient of Community for avian species at revegetated and mature cottonwood sites.[a]

	Coefficient of community		
Season	*2-year*	*3-year*	*5-year*
Winter	0.30	0.32	0.40
Spring	0.06	0.15	0.20
Summer	0.16[b]	0.21	0.31
Fall	0.36	0.35	0.43

[a] *Values show the proportion of overlap in species between each revegetated site compared with the 30-year site. Coefficient of community* = $2S_{ab}/(S_a + S_b)$, *where* S_{ab} = *the number of species in common between the two sites,* S_a = *the number of species in a revegetated site, and* S_b = *the richness of the 30-yr site.*

[b] *This value equals 0.38 when species nesting in the mature cottonwood island are included.*

Table 3. Distribution of species (n = 31) of Neotropical migrant (NM) birds using revegetated and mature cottonwood sites in the middle Rio Grande Valley.*

	Season			*Number of NM Species per Site*
Site	*Spring*	*Summer*	*Fall*	
2-year	3	7	6	12
3-year	4	6	10	15
5-year	8	13	13	20
30-year	11	13	8	19
Number of NM Species per Season	16	21	20	

* *Individual species may be included in more than one cell.*

semblage generally increases with the age of the site. A similar pattern has been observed in other locations in the Southwest (Stamp 1978; but see Knopf 1985) and elsewhere in the temperate zone (Lanyon 1981).

As the riparian plant community matures, a larger number of height classes, structural forms, and plant species occur, producing a more heterogeneous plant environment (Table 1). A positive relationship between foliage-height diversity and bird community structure is a long-standing and much debated issue (MacArthur & MacArthur 1961; Willson 1974; Karr & Roth 1971), and results vary both regionally and seasonally (Stamp 1978; Knopf 1985). Although the number of niches is likely to increase with vegetative complexity, the actual relationship appears to be more complex.

For example, plant species composition, local variation in habitat structure and topography, and abiotic conditions can profoundly affect bird species composition in a particular locality (Karr & Roth 1971). In our study, these factors together increased local habitat heterogeneity, which appeared to correlate positively with bird species diversity on our sites. The avian assemblage on the 5-year site was more similar to that of the 30-year site for most seasons than to that of the younger sites (Farley et al. 1994). This pattern documents the rapidity by which a revegetated plot can become suitable for many segments of the bird community.

Concern has been expressed about apparent decline in populations of birds that breed in the United States and winter in the Neotropics (Robbins et al. 1989; Askins et al. 1990; Finch 1991; Hagen & Johnston 1992; Finch & Stangel 1993. The riparian *bosque* is important to these birds during both migration and the breeding season. Thirty-one species of neotropical migrants were recorded on our sites (Farley et al. 1994); older sites supported greater numbers of these species (Table 3). Revegetation plots rapidly became acceptable to many species of neotropical migrants; the 5-year old site was used by as many species as the 30-year site (Table 3).

High stem density and leaf cover provided increased

foraging substrate and appeared to be important determinants of Neotropical migrant use. Fewer species were present during spring migration when some trees were leafless than in fall when trees still had leaves. The movement of migrants through the 3- and 5-year revegetation plots in fall may also reflect a preference by many of these species for habitats with high stem density. Some recent studies show that many Neotropical migrant species select second-growth and previously disturbed habitats, possibly because of the high vegetation density (Hutto 1989, 1992; Kricher & Davis 1992; Petit et al. 1992); dense deciduous vegetation occurs primarily in riparian corridors in much of the southwestern United States. This may explain the greater concentration of many Neotropical migrants in this habitat type (Stevens et al. 1977) compared to adjacent nonriparian areas (Knopf 1985; Farley, unpublished data). Although riparian zones may provide corridors for the movement of species through otherwise unsuitable habitat (see Mackintosh 1989), corridors may be distinct habitats themselves for a variety of organisms and not merely bridges between areas of more extensive habitat (Simberloff et al. 1992; Knopf & Samson 1994).

Our observations emphasize the importance of maintaining stands of riparian vegetation of different ages in the middle Rio Grande Valley. Species diversity has been defined at three levels of complexity: (1) alpha diversity, the assemblage of species within a given habitat; (2) beta diversity, the change in species assemblages along an ecological gradient; and (3) gamma diversity, the combination of various habitats and their associated species on a regional scale (Whittaker 1972; Samson & Knopf 1982; Pimm & Gittleman 1992). In our study the alpha diversity at any single site never contained more than two-thirds of the total number of species present on all sites (beta diversity, Fig. 3). The number of species was maximized by the simultaneous availability of vegetation of different ages. When all stages of different age and size are considered together for the middle Rio Grande Valley, overall gamma diversity is further increased. For this diversity to be maintained, ongoing regeneration of the flood plain vegetation community is necessary.

Unfortunately, the hydrologic processes necessary for the maintenance of habitat variability in the Rio Grande Valley have been irrevocably altered by human activities. Flood control and the establishment of exotic species are rapidly eliminating the historical heterogeneity of this ecosystem. Knopf (1989) and Howe and Knopf (1991) proposed that, without human intervention to control the spread of nonnative species and enhance recruitment of native species, a near-complete replacement of the native plant community in the Rio Grande Valley could take place within the next century. We believe that a concordant reduction in avian beta and gamma diversity would be a likely result. Presently, localized revegetation efforts, such as livestock exclusion and planting native species, appear to mitigate the detrimental effects of riparian habitat loss and may be a useful method of maintaining avian richness in this ecosystem.

Acknowledgments

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