FLORISTICS AND PHYSIOGNOMY DETERMINE MIGRANT LANDBIRD RESPONSE TO TAMARISK (*TAMARIX RAMOSISSIMA*) INVASION IN RIPARIAN AREAS

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Abstract.—I investigated the relative importance of floristics and physiognomy in determining community organization of autumn-migrating landbirds in a riparian corridor in New Mexico invaded by Tamarisk (*Tamarix ramosissima*). All six avian measures were associated with floristics, physiognomy, or both. However, usefulness in predicting migrant parameters differed between floristics and physiognomy, and depended on the vegetation measures used (direct measures vs. plant community-structure indices) and the scale investigated (micro- vs. macrohabitat). Using direct vegetation measures, migrant abundance, energy consumption, and evenness were more strongly associated with floristics than with physiognomy at all scales. Contrastingly, migrant species richness and diversity were more strongly associated with physiognomy than with floristics at the microhabitat scale, and appeared to be unrelated to vegetation measures at the macrohabitat scale. Migrant species composition was similar among floristically similar macrohabitats, but it was equally correlated with floristics and physiognomy at the microhabitat scale. Using plant community-structure indices, migrant species composition and evenness remained strongly associated with the floristic measure (plant species diversity). However, floristic diversity was most important in predicting migrant abundance and diversity, whereas both floristic and physiognomic (horizontal structure) diversity were important in predicting migrant energy consumption. Migrant species richness was not associated with plant community structure. Respective relationships of floristics and physiognomy to food resources and foraging substrates might explain observed bird–vegetation associations. The results indicated that floristics and physiognomy are both useful in predicting avian community organization in exotic vegetation, and such information can guide conservation and management strategies that seek to control *Tamarix* while protecting migrant landbirds and their stopover habitats. *Received 30 January 2007, accepted 3 November 2007.*

Key words: community organization, exotic, floristics, migrants, physiognomy, riparian, *Tamarix*.

Las Características Florísticas y la Fisonomía Determinan la Respuesta de las Aves Terrestres Migratorias a la Invasión de *Tamarix ramosissima* en Áreas Ribereñas

Resumen.—Investigué la importancia relativa de las características florísticas y de la fisonomía en determinar la organización comunitaria de las aves terrestres migratorias de otoño en un corredor ribereño invadido por *Tamarix ramosissima* en Nuevo México. Las seis medidas recolectadas de las aves estuvieron asociadas con las características florísticas, la fisonomía, o ambas. Sin embargo, la utilidad en predecir los parámetros migratorios difirió entre las variables florísticas y las fisonómicas, y dependió de los tipos de medidas de vegetación utilizadas (medidas directas vs. índices de estructura de la comunidad) y de la escala investigada (micro- vs. macro-hábitats). Utilicé medidas directas de la vegetación y comprobé que la abundancia de aves migratorias, el consumo de energía y la equidad estuvieron más fuertemente asociadas con la florística que con la fisonomía a todas las escalas. En contraste, la riqueza y la diversidad de las especies migratorias estuvieron más fuertemente asociadas con la fisonomía que con la florística a escala de micro-hábitat, y parecieron no estar relacionadas con las medidas de la vegetación a la escala de macro-hábitat. La composición de especies migratorias fue similar entre macro-hábitats con características florísticas similares, pero estuvo igualmente correlacionada con las condiciones florísticas y la fisonomía a la escala de micro-hábitat. Utilizando los índices de estructura de la comunidad vegetal, la composición y la equidad de las especies migratorias permanecieron fuertemente asociadas con la medida florística (diversidad de especies de plantas). Sin embargo, la diversidad florística fue más importante en predecir la abundancia y la diversidad de aves migratorias, mientras que la diversidad florística y fisonómica (estructura horizontal) fueron importantes en predecir el consumo de energía de las aves migratorias. La riqueza de especies migratorias no estuvo asociada con la estructura de la comunidad vegetal. Las relaciones respectivas de las características florísticas y fisonómicas con los recursos alimenticios y con los sustratos de forrajeo podrían explicar las asociaciones observadas entre las aves y la vegetación. Los resultados indicaron que las características florísticas y la fisonomía son ambas útiles en predecir la organización de la comunidad de aves en la vegetación exótica. Esta información puede guiar las estrategias de conservación y manejo que buscan controlar a *Tamarix* y al mismo tiempo proteger a las aves migratorias terrestres y los hábitats donde éstas hacen sus escalas migratorias.

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Plant taxonomic composition (floristics) and vegetation structure (physiognomy) are important predictors of distributions and abundances of birds because they either directly provide or are strong correlates of environmental factors necessary for birds to fulfill their life-history requirements. Floristics and physiognomy influence the types and availability of (1) food resources, (2) foraging and nesting substrates, and (3) shelters from predators and physiological stress (Cody 1985). Although both floristics and physiognomy influence avian habitat occupancy, physiognomy has been considered more useful than floristics in predicting avian community parameters. Avian species composition, abundance, richness, and diversity all have been found to be strongly correlated with various measures of vegetation structure, such as foliage height diversity (MacArthur 1964, MacArthur et al. 1966, Recher 1969, Karr and Roth 1971, Willson 1974, Rotenberry and Wiens 1980) and horizontal patchiness (Roth 1976, Rotenberry and Wiens 1980). This paradigm is partly an artifact of the greater number of papers investigating avian-physiognomy relationships, inspired by MacArthur and MacArthur's (1961) seminal paper that showed that, because of covariation between floristics and physiognomy, consideration of floristic diversity did not improve power in predicting avian diversity over consideration of foliage height diversity alone. Recent evidence suggests that floristics also can be an important determinant of avian community parameters, particularly of avian species composition (Rice et al. 1983, 1984; Rotenberry 1985; Rodewald and Abrams 2002; Fleishman et al. 2003). However, few studies have employed a rigorous experimental design to quantify the relative roles of floristics and physiognomy in influencing avian species composition and community structure (but see Mac Nally 1990b, Fleishman et al. 2003).

Identifying environmental correlates useful for predicting broad patterns in migrant bird communities is increasingly relevant to federal, state, tribal, and private land managers as stopover areas where migrating (*en route*) landbirds replenish fat, nutrient, and water stores depleted by migratory flight become lost or degraded as a result of land clearing, habitat fragmentation, and the spread of invasive exotic plant species (Coblentz 1990, Soulé 1990, Moore and Simons 1992, Vitousek et al. 1996, Yong and Finch 1997, Moore 2000, Palumbi 2001). *En route* migrant landbirds are generally underrepresented in avian habitat-use studies (Petit 2000), and little information exists on how anthropogenic changes in floristics and physiognomy influence *en route* migrant species composition and community structure. In particular, there are large gaps in our knowledge regarding how the increasing dominance of exotic plants in native ecosystems effects changes in the organization of migrant bird communities by altering local floristics and physiognomy.

In the arid and semiarid southwestern United States, the widespread establishment of exotic tamarisks (*Tamarix* spp.; often referred to as "saltcedars") in native riparian ecosystems, which support high concentrations of migratory passerines *en route* to their wintering or breeding grounds, has the potential to influence stopover ecology of migrant landbirds and to negatively affect migratory bird populations (Yong and Finch 1997, Yong et al. 1998, DeLoach et al. 2000, Kelly et al. 2000). Several species of these long-lived (50–100 years), deciduous trees native to arid regions of the Eastern Hemisphere were first introduced into the United States in the early 1800s, and Tamarisk (*Tamarix*

ramosissima) is now the dominant plant species in many southwestern riparian ecosystems at elevations <1,500 m. Tamarisk often forms large monotypic stands to the exclusion of native plants, but both the vegetation structure and plant species composition of Tamarisk-dominated vegetation are variable across the Southwest (DeLoach et al. 2000). The structure of individual Tamarisk plants can vary from thin-stemmed shrubs to multi-trunked trees and from groundcover seedlings to trees ≥10 m in height (Brotherson et al. 1984). In addition, Tamarisk-dominated vegetation can vary from mixtures of native and exotic plant species to stands consisting solely of Tamarisk. The variability of Tamarisk-infested vegetation provides a unique situation in which to examine the roles of floristics and physiognomy in influencing avian community organization, and I used this opportunity to explore the relative importance of floristics and physiognomy in determining the community organization of *en route* migrant landbirds in a desert riparian corridor during the fall migratory period.

Methods

Study area.—The study area was located on 746 ha along the Rio Grande where the river bends around a volcanic formation called Mesa del Contadero in San Marcial, Socorro County, New Mexico (33°40′N, 107°00′W). The study area was chosen because it supported large numbers of migrating birds during fall and spring, as well as large patches of both native and exotic riparian vegetation. Like other riparian ecosystems in the Southwest, the study area has experienced major alterations since the early 1900s because of such human activities as (1) removal of native riparian vegetation (e.g., phreatophyte control); (2) urban and suburban development; (3) groundwater pumping; and (4) river damming, diversion, and channelization. In addition, exotic plants were introduced into the ecosystem and, by the 1950s, Tamarisk had become well established. Despite anthropogenic changes to the natural ecosystem, the study area experienced high river flows over the past two decades and several large overbank floods (breaching the levees) over the past five decades, which sustained successional patches of native Rio Grande Cottonwood (*Populus deltoides* ssp. *wislizeni*), Coyote Willow (*Salix exigua*), Seepwillow (*Baccharis salicifolia*), and Goodding's Willow (*S. gooddingii*) (U.S. Department of Interior Bureau of Reclamation unpubl. data).

I examined bird–vegetation associations from 1999 through 2002 within 24 plots (0.2 ha each) established either adjacent to the Rio Grande or ~500 m west of the Rio Grande near a conveyance channel. Plot size corresponded well to that of patches of riparian vegetation and, thus, best captured the relationships among floristics, physiognomy, and avian community parameters. Plots of similar size have been used in numerous other avian habitat-use studies, particularly those employing mist nets (e.g., James and Shugart 1970; Blake and Hoppes 1986; Mac Nally 1990a, b; Winker et al. 1992). Vegetation gradients among plots formed a continuum over a range in floristics and physiognomy. Tamarisk, Coyote Willow, Rio Grande Cottonwood, Seepwillow, Goodding's Willow, and the exotic Russian-olive (*Elaeagnus angustifolia*) were all found in the shrub, subcanopy, or canopy of plots, but presence of the more widespread Tamarisk, Coyote Willow, and Rio Grande Cottonwood was most useful in characterizing plots according to floristics. Plots varied from monocultures of Tamarisk to various

mixtures of native Coyote Willow and Rio Grande Cottonwood. Structure of plots was also variable, with overstories ranging from open to closed and understories ranging from open to dense. In addition, though absent in plots dominated by native vegetation, percent groundcover varied from 0 to 23% in Tamarisk-dominated plots.

To ensure detection of avian responses to floristic and physiognomic gradients and to isolate floristic and physiognomic effects, I grouped study plots (six each) into four broadly defined vegetation types paired according to floristics (native and exotic) and physiognomy (low and tall growth form) based on a 2 × 2 factorial design: low willow (native, low), tall cottonwood–willow (native, tall), low tamarisk (exotic, low), and tall tamarisk (exotic, tall). The two native vegetation types were floristically unique: low willow was dominated by dense Coyote Willow shrubs interspersed with Rio Grande Cottonwood and Goodding's Willow saplings, whereas tall cottonwood–willow was characterized by a Coyote Willow-dominated understory and a closed to semiclosed overstory of middle-aged Rio Grande Cottonwood. Nonetheless, the native vegetation types were floristically more similar to each other than to the two exotic vegetation types, which were both dominated by Tamarisk. Furthermore, although all vegetation types were structurally unique and supported unique foliage profiles (Fig. 1), physiognomy was generally more similar within physiognomic vegetation types. Overall, in contrast to the low vegetation types, the tall vegetation types tended to be characterized by a lower density of shrubs and saplings and by higher live-tree density, live-foliage density, number of vertical layers of live foliage, and vegetation height (mean height of low willow and low tamarisk = 4.76 m and 3.74 m, respectively, whereas mean height of tall cottonwood–willow and tall tamarisk = 9.36 m and 6.52 m, respectively).

Bird sampling.—I used mist nests to sample *en route* migrant landbirds (landbird species that only migrated through the study area; hereafter "migrants") at the 24 plots during the months corresponding with peaks in fall migration (3 September–22 October 1999, 30 August–13 October 2000, 22 August–12 October 2001, and 15 August–16 October 2002). In the 1999 field season, avian data were collected only in plots within low willow and low tamarisk because of logistical constraints resulting from flooding of the Rio Grande. A mist net (12 m long × 2.6 m high, 4 shelves, 30-mm mesh) was set up in the center of each of the 24 plots. Nets were placed ≥30 m apart and ≥12 m from the vegetation edge. Nets were opened ~20 min before sunrise and run for 6 h day^{-1}, five days a week. To compensate for possible time-of-day effects on capture rates, the opening sequence of nets was reversed daily within each vegetation type. Nets were checked at 20- to 30-min intervals, depending on weather conditions (e.g., nets were checked more frequently during extreme cold or heat that might have been stressful to netted birds).

Using initial-capture data (i.e., excluding data on recaptured individuals) of migrants, I tallied abundances per species, and I calculated five avian community-structure variables for each of the 24 plots averaged over all years: (1) total avian abundance,
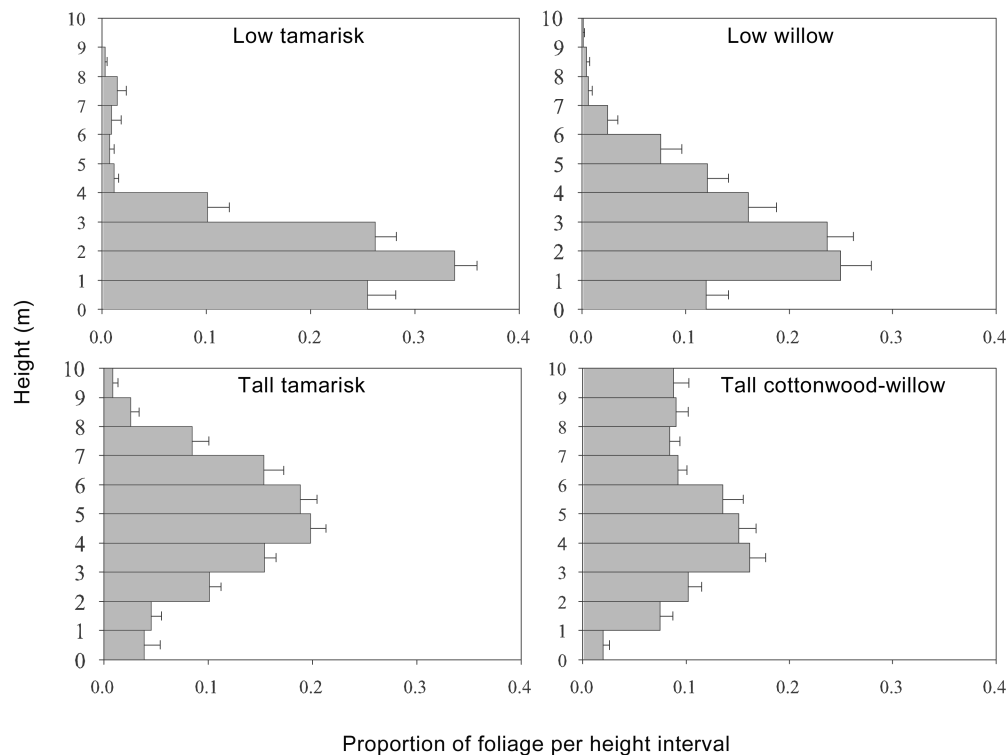

FIG. 1. Vertical-foliage height profiles showing the vertical distribution of proportional live-vertical-foliage density (mean ± SE) within low tamarisk, low willow, tall cottonwood–willow, and tall tamarisk vegetation types (see text) along the middle Rio Grande, Socorro County, New Mexico, during the fall migrations of 1999–2002. Each vegetation type supported unique foliage profiles (multi-response permutation procedures, $P < 0.001$).

(2) avian species richness, (3) avian species diversity, (4) avian species evenness, and (5) total avian energy consumption. To compare relative abundances and account for differences in mist-netting effort, abundance data were divided by the total number of net hours (1 net hour [Nh] = one mist net operated for 1 hour) in each plot. I computed the yearly mean avian species diversity for each plot by averaging yearly measures of the Shannon-Wiener Index (H'), which were calculated according to Shannon (1948) and Nur et al. (1999). Evenness was computed using the diversity values ($E = H'/\ln S$) for each plot each year and then was averaged over all years (Nur et al. 1999). I computed the final avian community-structure variable, an estimate of avian energy consumption, by averaging yearly measures of total avian energy consumption for each plot calculated according to Ernest and Brown (2001):

$$C_{tot} = \sum_{i=1}^{S} a N_i M_i^b \quad i = 1, 2, \ldots S \quad (1)$$

where S was the number of species captured in each plot each year, N_i was the abundance per 200 Nh of the ith species in each plot each year, and M_i was the mean mass of the ith species in each plot each season from mist-net data collected in the present study. The values for a and b were derived from Anderson and Jetz (2005) and were 1.02 and 0.68, respectively. Only primarily insectivorous migrants (after Ehrlich et al. 1988) were considered in calculations of avian energy consumption.

Vegetation sampling.—Because both floristics and physiognomy can be measured in numerous ways, I chose to examine features of floristics and physiognomy found to be relevant to birds (Table 1), including both direct vegetation measures and diversity indices measuring plant community structure. Vegetation data were collected at the end of each field season

after completion of avian data collection but before vegetation senescence (28 October–5 November 1999, 19–26 October 2000, 18 October–2 November 2001, and 18–31 October 2002). As with bird sampling, vegetation data in tall tamarisk and tall cottonwood–willow plots were not collected in 1999 because of logistical constraints. Further logistical constraints prevented collection of vegetation data in plots in the low vegetation types in 2000.

Vegetation data were collected in 11.3-m-radius (0.04-ha) circular plots centered on mist nets. Given that a lane ~1 m wide was manually cleared of vegetation for placement of the mist net, the circular plots actually comprised two semicircles separated by 2 m to remove mist-net lanes from consideration (Winker et al. 1992). Four transects were established within each plot, aligned either parallel or perpendicular to the mist-net lane. Data collected within each plot included (1) live-tree density per plant species, (2) shrub and sapling stem density per plant species, (3) live vertical foliage density, (4) canopy height, (5) percent canopy cover, and (6) percent live groundcover (Table 1). Live-tree density within each plot was measured by tallying all live trees per plant species, defined as woody plants with trunk diameter >7.6 cm at 1.4 m above ground (diameter at breast height [DBH]). Shrub and sapling stem density was estimated by counting all woody stems per species along the four transects that were (1) within 0.5 m of each transect, (2) ≥1.4 m tall, and (3) <7.6 cm DBH (James and Shugart 1970). Live-vertical-foliage density was measured at points 0, 2, 4, 6, 8, and 10 m along each transect by counting the number of contacts of live foliage with a vertically raised fiberglass telescoping measuring rod that was marked at 1-m vertical height intervals (from 0 m to 10 m). Canopy height (measured with the measuring rod) and percent canopy cover (measured with a densiometer) were measured at points 0, 5, and 10 m along each transect. Percent live groundcover was measured in 1-m quadrats centered

Table 1. Floristic and physiognomic variables measured within exotic *Tamarix ramosissima* and native vegetation along the middle Rio Grande, Socorro County, New Mexico, during the fall migrations of 1999–2002.

Variable	
Physiognomy	
Total number of all live trees with DBH > 7.6 cm	TREE_{tot}
Mean density of shrub and sapling stems	SHRUB
Mean live-foliage density within each 1-m vertical height increment between 0 and 10 m	FD0-1, FD1-2 … **FD9-10**
*Mean total live-vertical-foliage density in four vertical layers (0–1 m, 1–3 m, 3–7 m, 7–10 m)	FD0-1, FD1-3, FD3-7, FD7-10
*[A]Mean total live-vertical-foliage density between 0 and 4 m	FD0-4
*[B]Mean total live-vertical-foliage density between 4 and 10 m	FD4-10
*Mean number of 1-m-increment vertical layers with live foliage	LAYERS
Mean canopy height	CH
Mean percent canopy cover	CC
Mean percent live groundcover	GC
*Diversity of live-foliage density among four vertical layers (0–1 m, 1–3 m, 3–7 m, 7–10 m)	FHD_4
*Coefficient of horizontal variation in percent canopy cover	HCV_{cc}
Floristics	
*Total number of trees of each plant species with DBH > 7.6 cm	$\text{TREE}_{tot i}$ for ith species
*[C]Proportion of total trees of each plant species with DBH > 7.6 cm	$\text{PTREE}_{tot i}$ for ith species
Density of shrub and sapling stems of each plant species	SHRUB_i for ith species
*[D]Proportion of shrub and sapling stems of each plant species	PSHRUB_i for ith species
*Coverage per species calculated using A, B, C, and D above	CVR_i for ith species
*Plant species coverage diversity	CVRD

DBH = diameter at breast height (1.4 m above ground)
*Indicates derived variables.

at points 0, 5, and 10 m along each transect and included all living woody vegetation <0.5 m in height, as well as all living nonwoody vegetation (e.g., grasses, forbs) of any height.

I extracted information on floristics from the vegetation data by averaging over all years the following coverage measure calculated each year for each shrub and tree species found in each plot:

$$CVR_i = (x ps_i) + (z pt_i) \qquad (2)$$

where x was the mean proportion of live vertical foliage between 0 and 4 m (FD0-4), ps_i was the proportion of all shrub and sapling stems of the ith species, z was the mean proportion of live vertical foliage between 4 and 10 m (FD4-10), and pt_i was the proportion of all live trees of the ith species. The coverage measure provided an index of the distribution (dominance) of plant species in vertical and horizontal space, and the height of 4 m was employed because it delineated shrub and sapling plant species from those that were generally present as mature trees. In addition to the direct floristic measures of plant species coverages, an index of floristic diversity, the Shannon-Wiener index of diversity of plant species coverage (CVRD), was computed for each plot averaged over all years.

I compiled 16 direct measures of physiognomy (hereafter "direct physiognomic variables") for each plot averaged over all years: (1) total number of live trees ($TREE_{tot}$), (2) mean shrub and sapling stem density (SHRUB), (3) mean live-vertical-foliage density within each of the ten 1-m vertical height increments (FD0-1, FD1-2,…FD9-10; 10 variables), (4) mean number of vertical layers with hits of live foliage (LAYERS), (5) mean canopy height (CH), (6) mean percent canopy cover (CC), and (7) mean percent live groundcover (GC) (Table 1). Next, I collapsed direct physiognomic variables into two physiognomic indices, calculated for each plot averaged over all years: (1) the Shannon-Wiener index of diversity of live-foliage density among four vertical layers that comprised the ground (0–1 m), shrub (1–3 m), subcanopy (3–7 m), and canopy (7–10 m) layers (FHD_4); and (2) the coefficient of horizontal variation in percent canopy cover (HCV_{cc}). The first index provided a measure of variation in vertical structure. The second index provided a measure of horizontal "patchiness" within each plot and was computed by dividing the standard deviation of percent canopy cover by mean percent canopy cover. Though measured differently, FHD_4 was analogous to foliage height diversity (FHD) of MacArthur and MacArthur (1961), MacArthur (1964), MacArthur et al. (1966), and others; HCV_{cc} was analogous to the index of heterogeneity of Roth (1976).

Data analyses.—I analyzed the data to determine whether floristics or physiognomy was a better predictor of migrant community organization, and whether the influences of floristics and physiognomy on migrant species composition and community structure were evident (1) when considering direct and indirect measures (diversity indices) of floristics and physiognomy and (2) at both the microhabitat (among-plot) and macrohabitat (among-vegetation-type) scales. Before I conducted statistical tests, I tested data for normality and homogeneous variances of studentized residuals by computing Shapiro-Wilk and Levene statistics, respectively. Where possible, data that did not meet assumptions of normality and homogeneous variances were transformed using the natural logarithmic, arcsine square root, or square-root transformations. Because several variables did not fit and could not be transformed to fit normality and homogeneity of variance

assumptions, primarily nonparametric univariate and multivariate tests were computed to establish relationships among floristics, physiognomy, and avian community parameters.

I first examined the migrant data to determine whether the influences of floristics and physiognomy were evident from the avian species composition patterns among plots. Specifically, I used nonmetric multidimensional scaling (NMS) with Bray-Curtis distances, a nonparametric technique found to be successful in ordinating avian communities (Mac Nally 1990a), to graphically visualize rank similarities in avian species compositions among all 24 plots (Kruskal 1964, Mather 1976). Before the NMS analyses were computed, avian species composition data were square-root transformed to down-weight the importance of abundant species, thereby avoiding pitfalls associated with basing similarity on the presence of substantially more-abundant species (Clarke and Warwick 2001, McCune and Grace 2002). The NMS ordination was run in PC-ORD for Windows, version 4.10 (see Acknowledgments), using a random start, 200 runs with real data, and 400 iterations. The final NMS ordination solution was chosen on the basis of (1) the optimal number of axes determined by a Monte Carlo test computed with 100 randomized runs, (2) a minimal stress determined from a plot of the final stress versus the number of dimensions (a scree plot), and (3) a stable solution (McCune and Mefford 1999).

After ordinating the avian species-composition data to qualitatively assess species-similarity patterns among plots, I computed Mantel tests (Mantel 1967, Douglas and Endler 1982) with Bray-Curtis distances in PC-ORD to formally test for correlations between a matrix containing the direct measure of floristics (plant species coverages) and a matrix containing the 16 direct physiognomic variables, as well as for correlations of both of these matrices with the six avian matrices: (1) avian species composition (square-root transformed), (2) total avian abundance, (3) avian species richness, (4) avian species diversity, (5) evenness, and (6) total avian energy consumption. Before Mantel tests were computed, the direct physiognomic variables were subjected to the following relativization transformation that placed variables on the same unit scale:

$$b_{ij} = x_{ij} / x \max_j \qquad (3)$$

where rows (i) were samples, columns (j) were direct physiognomic variables, and $x \max_j$ was the largest value in the matrix for variable j. In addition, before testing for correlations between avian variables and physiognomy, I used the BIOENV analyses in PRIMER 5 for Windows, version 5.2.9 (PRIMER-E, Plymouth, United Kingdom), to select the subset of direct physiognomic variables that had the highest rank correlation with each avian variable, because inclusion of direct physiognomic variables that differed greatly among the plots but had no effect on avian patterns will degrade the strength of correlations among similarity matrices (Clarke and Ainsworth 1993). Once the subsets of direct physiognomy variables best explaining avian variables (P_b) were determined, Mantel tests were conducted to determine significance of correlations between avian variables and P_b. The Bonferroni correction was used to set the level of significance of all Mantel tests at $\alpha = 0.025$ ($n = 2$).

I further explored the avian relationships with floristics and physiognomy by testing for correlations of avian species composition (square-root transformed) with the three plant community-structure indices (CVRD, FHD_4, HCV_{cc}) by running

Table 2. The subsets (P_b) of the full set ($n = 16$) of direct physiognomic variables measured within exotic *Tamarix ramosissima* and native vegetation along the middle Rio Grande, Socorro County, New Mexico, during the fall migrations of 1999–2002 that "best explained" avian variables determined by BIOENV analyses run in PRIMER 5 for Windows, version 5.2.9.

Avian variable	P_b
Avian species composition	SHRUB, FD0-1, FD2-3, FD9-10
Total avian abundance	SHRUB, CC, GC
Total avian energy consumption	SHRUB, CC, GC
Evenness	FD0-1, FD1-2, FD9-10
Avian species richness	SHRUB, FD5-6
Avian species diversity	SHRUB, FD2-3, FD5-6, FD6-7

Mantel tests with Bray-Curtis distances in PC-ORD. Similarly, I conducted two-tailed bivariate correlation analyses in SPSS, version 13.0, to test for correlations of the five avian community-structure variables with CVRD, FHD_4, HCV_{cc}. The Bonferroni correction was used to set the level of significance of all tests at $\alpha = 0.0083$ ($n = 6$).

To determine whether the influences of floristics and physiognomy on avian species composition and community structure were evident at the macrohabitat level, I examined whether migrant patterns were more similar between floristically similar vegetation types (i.e., between native vegetation types or between exotic vegetation types) or between structurally similar vegetation types (i.e., between low vegetation types or between tall vegetation types). I computed multi-response permutation procedures (MRPP; Zimmerman et al. 1985) with Bray-Curtis distances in PC-ORD to test for differences among the four vegetation types in migrant species compositions. Analysis of variance (ANOVA) or Kruskal-Wallis *H* (with Mann-Whitney *U* multiple comparisons) tests were conducted, where appropriate, in SPSS to test for differences among the four vegetation types in the avian community-structure variables. Where ANOVA gave statistically significant ($P < 0.05$) differences, Tukey HSD was used as a *post hoc* test when the assumption of homogeneous variances of studentized residuals was met, and Dunnett's T3 was used when this assumption was not met.

After examining the strength of associations between avian and vegetation variables, tests were performed to determine to

what extent avian species composition and community structure were associated with floristics and physiognomy after eliminating the confounding effects of covariation between floristics and physiognomy. Partial Mantel tests were computed in Microsoft Office EXCEL 2003 using XLSTAT-PRO, version 7.5 (Addinsoft, New York), to determine to what extent avian species composition and community structure were associated with the direct measures of floristics (plant species coverages) and physiognomy (the 16 direct physiognomic variables) after controlling for covariation between floristics and physiognomy. Partial correlations were calculated in SPSS to determine to what extent avian species composition and community structure were associated with CVRD, FHD_4, and HCV_{cc} after controlling for covariation among the three plant community-structure indices. The Bonferroni correction was used to set the level of significance of all partial-correlation tests at $\alpha = 0.025$ ($n = 2$).

Results

Excluding hummingbirds, 1,027 new individuals (initial captures) and 26 species of *en route* migrant landbirds were captured in mist nets over four years (11,617 Nh). All 26 species of captured migrants, except Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*, a short-distance migrant), were Neotropical migrants (Sauer et al. 2003). In addition, all migrant species were primarily insectivorous, except the granivorous Clay-colored Sparrow (*Spizella pallida*) and Brewer's Sparrow (*S. breweri*) (Ehrlich et al. 1988). Parulids dominated, especially Wilson's Warbler (*Wilsonia pusilla*), which was, on average, 9× more abundant than the next three most common species: MacGillivray's Warbler (*Oporornis tolmiei*), Dusky Flycatcher (*Empidonax oberholseri*), and Orange-crowned Warbler (*Vermivora celata*). Captured migrants were primarily of three foraging guilds: foliage-glean, hawking, and ground-glean (Ehrlich et al. 1988). Members of the foliage-glean guild were mainly parulids and, thus, this was the most common foraging guild. Members of the hawking guild were all tyrannids, and emberizids dominated the ground-glean guild.

All measures of avian community organization were significantly correlated with plant species coverages or the subset of direct physiognomic variables identified by the BIOENV analyses, or both (Tables 2 and 3). All subsets of direct physiognomic variables identified by the BIOENV analyses were not significantly

Table 3. Correlations (Mantel's *r* statistics) of avian species composition and community-structure variables with (1) floristics (plant species coverages), (2) the full set of direct physiognomic variables measured (P), and (3) subsets of direct physiognomic variables that "best explained" the avian variables (P_b). Partial Mantel statistics, which measure the partial linear correlation between two variables after controlling for the linear effect of a third, were also computed. All data were collected within exotic *Tamarix ramosissima* and native vegetation along the middle Rio Grande, Socorro County, New Mexico, during the fall migrations of 1999–2002.

Avian variable	Floristics	P	P_b	Floristics (P_b = covariate)	P_b (floristics = covariate)
Avian species composition	$r = 0.54$**	$r = 0.23$**	$r = 0.39$**	$r = 0.36$***	$r = 0.38$***
Total avian abundance	$r = 0.27$**	$r = 0.00^{NS}$	$r = 0.23^{NS}$	$r = 0.29$**	$r = 0.22^{NS}$
Total avian energy consumption	$r = 0.31$**	$r = -0.02^{NS}$	$r = 0.20^{NS}$	$r = 0.32$**	$r = 0.22^{NS}$
Avian species richness	$r = -0.05^{NS}$	$r = 0.10^{NS}$	$r = 0.28$**	$r = -0.05^{NS}$	$r = 0.28$**
Evenness	$r = 0.42$**	$r = 0.07^{NS}$	$r = 0.24$*	$r = 0.42$***	$r = 0.23$*
Avian species diversity	$r = 0.18$*	$r = 0.09^{NS}$	$r = 0.26$**	$r = 0.18$*	$r = 0.26$**

Significance of correlation set at $\alpha = 0.0083$ ($n = 6$) by Bonferroni correction.
^{NS} Not significant, *$P < 0.025$, **$P < 0.01$, and ***$P < 0.001$.

correlated (Mantel, $P > 0.05$) with plant species coverages and, thus, these correlations remained significant when the confounding effects of covariation between floristics and physiognomy were eliminated (Table 3). Only a slightly greater number of avian variables was significantly correlated with plant species coverages than with P_b (5 vs. 4 of 6). However, avian species composition and community structure were differentially associated with plant species coverages and P_b. Several associations delineated at the microhabitat (among-plot) scale were also evident at the macrohabitat (among-vegetation-type) scale, but not all were parallel at both scales.

Which migrant species were present and their abundances were more similar among plots and vegetation types that supported similar plant species coverages. Avian species composition was significantly correlated (partial Mantel, $P < 0.025$) with both P_b and plant species coverages, before and after controlling for covariation (Table 3). However, avian species compositions differed significantly (MRPP, $P < 0.001$) between the native and exotic vegetation types, and the NMS ordination of avian species-composition data grouped floristically similar plots closer in ordination space (Fig. 2), primarily because native-dominated plots supported relatively higher abundances of hawking insectivores (e.g., Dusky Flycatcher), whereas exotic-dominated plots supported relatively higher abundances of both foliage- and ground-gleaning insectivores (e.g., Wilson's Warbler and Mountain White-crowned Sparrow, respectively). As with avian species composition, measures of avian abundance were more similar among plots and vegetation types that supported similar plant species coverages (Table 3 and Fig. 3). Total avian abundance and total avian energy consumption were both significantly correlated with plant species coverages but not P_b, before and after controlling for covariation (Table 3). In addition, how evenly the abundance data were distributed among species was more strongly correlated with plant species coverages than with P_b, before and after controlling for covariation (Table 3). Furthermore, all three abundance variables tended to differ among floristic, rather than physiognomic, vegetation types, with total avian abundance and total avian energy consumption averaging higher in the exotic vegetation types, and evenness averaging higher in the native vegetation types (Fig. 3).

Compared to plant species coverages, P_b was a stronger correlate of the number and diversity of avian species. When species richness was examined over the 24 plots, avian species richness was significantly correlated with P_b but not plant species coverages, before and after controlling for covariation (Table 3). Similarly, though avian diversity was significantly correlated with both plant species coverages and P_b, most of the variation in avian diversity among the plots before and after controlling for covariation was predicted by P_b (Table 3). The microhabitat species-richness and diversity patterns were not evident at the macrohabitat level. Not only did overall avian species richness not differ significantly between physiognomic vegetation types, it did not differ significantly among any of the vegetation types (Fig. 4). Furthermore, avian species diversity was significantly higher in tall cottonwood–willow than in the two exotic vegetation types (Dunnett's T3: low tamarisk, $P = 0.01$; tall tamarisk, $P = 0.02$), which indicated neither a floristic nor a physiognomic association (Fig. 4).
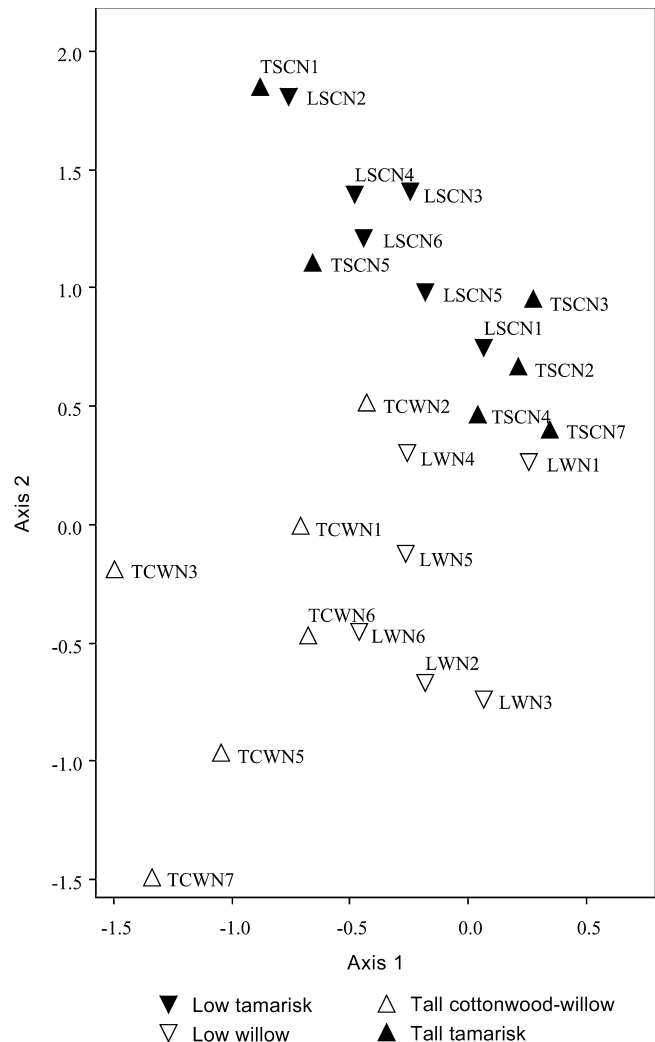

Fig. 2. Ordination from nonmetric multidimensional scaling run with Bray-Curtis distances on the species compositions of *en route* migrant landbirds captured in mist nets during fall migrations of 1999–2002 within 24 plots located within exotic *Tamarix ramosissima* and native vegetation along the middle Rio Grande, Socorro County, New Mexico. The final solution was a two-dimensional ordination (Monte Carlo test, $P = 0.01$) with a stress of 9.29. Approximately 93% of the variation in the resultant ordination space was accounted for by the first two dimensions (R^2 value for first axis = 0.81, R^2 value for second axis = 0.12). Avian species compositions were similar among floristically similar plots and differed significantly between the native and exotic vegetation types (multi-response permutation procedures, $P < 0.001$).

When floristic data were collapsed into an index of floristic diversity and direct physiognomic variables were collapsed into indices of vertical and horizontal structural diversity, floristics and physiognomy remained significant correlates of avian species composition and community structure. All the avian species-composition and community-structure variables could be predicted by one or more of the three plant community-structure indices when alpha was set at 0.05 (Table 4). However, on the
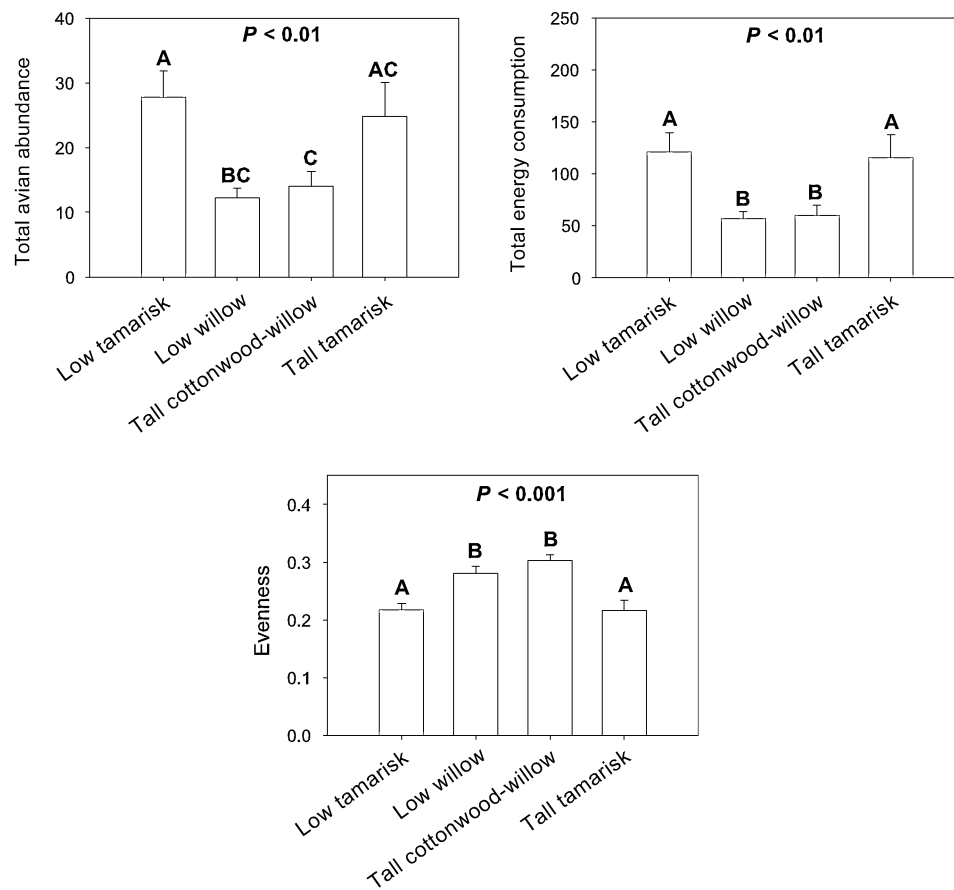
FIG. 3. Patterns in total abundance per 200 mist-net hours, evenness, and total avian energy consumption (mean ± SE) of *en route* migrant landbirds captured in mist nets during fall migrations of 1999–2002 within exotic *Tamarix ramosissima* and native vegetation along the middle Rio Grande, Socorro County, New Mexico. *P* value from ANOVA. Vegetation types with the same letter were not significantly different (*P* > 0.05), as determined by Tukey HSD multiple comparisons.
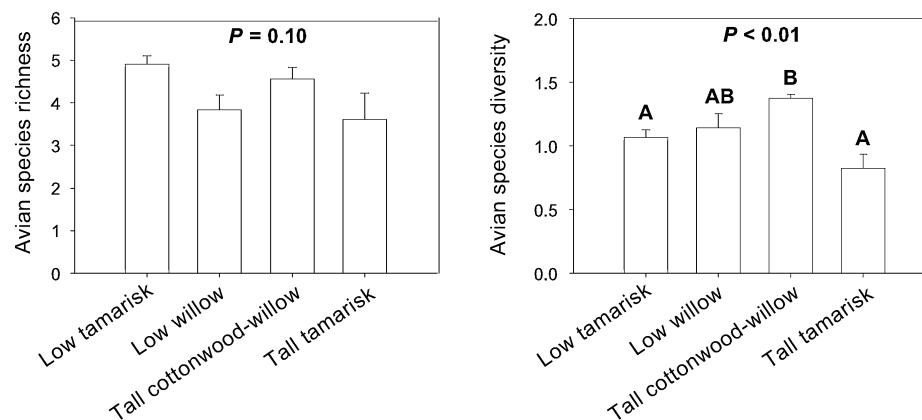

FIG. 4. Avian species richness and diversity (mean ± SE) patterns of *en route* migrant landbirds captured in mist nets during fall migrations of 1999–2002 within exotic *Tamarix ramosissima* and native vegetation along the middle Rio Grande, Socorro County, New Mexico. *P* values from ANOVA. Vegetation types with the same letter were not significantly different (*P* > 0.05), as determined by Dunnett's T3 multiple comparisons.

Table 4. Correlations (*P* value) of avian species composition (Mantel's *r* statistics) and community structure (Pearson product-moment correlations) with three indices of plant community structure: (1) the Shannon-Wiener index of floristic diversity (CVRD); (2) the Shannon-Wiener index of diversity of live-foliage density among four vertical layers that approximate the ground, shrub, subcanopy, and canopy layers (FHD_4); and (3) the coefficient of horizontal variation in percent canopy cover (HCV_{cc}). All data were collected within exotic *Tamarix ramosissima* and native vegetation along the middle Rio Grande, Socorro County, New Mexico, during the fall migrations of 1999–2002.

Avian variable	CVRD	FHD_4	HCV_{cc}
Avian species composition	0.304 (**0.001**)	0.110 (0.100)	0.120 (0.075)
Total avian abundance	−0.502 (0.012)	0.004 (0.986)	0.601 (**0.002**)
Total avian energy consumption	−0.534 (**0.007**)	−0.011 (0.960)	0.601 (**0.002**)
Evenness	0.712 (**0.000**)	0.478 (0.018)	0.486 (0.016)[a]
Avian species richness	0.205 (0.337)	0.385 (0.063)	0.513 (0.010)
Avian species diversity	0.704 (**0.000**)	0.573 (**0.003**)	0.098 (0.649)

[a] Spearman rank correlations.
Correlations significant at α = 0.0083 (*n* = 6) set by Bonferroni correction shown in bold.

basis of the square of the *r* values given in Table 4, the indices of plant community structure tended to explain a greater amount (9–51%, where associations were significant) of the variation in avian species composition and community structure than the direct floristic and physiognomic measures alone (which explained 3–18%, where associations were significant). Moreover, migrant species-composition and community-structure associations with the plant community-structure indices did not parallel those with the direct measures of floristics and physiognomy when using the more conservative alpha of 0.0083 (Bonferroni correction, α = 0.05/6). Although avian species composition (Mantel's *r* = 0.304, *P* = 0.001) and evenness (Mantel's *r* = 0.712, *P* = 0.000) were significantly correlated solely with the floristic index CVRD, which was highest in the native vegetation types, total avian abundance was significantly correlated (Pearson coefficient = 0.601, *P* = 0.002) solely with HCV_{cc} (a physiognomic index that was highest in the exotic vegetation types), and total avian energy consumption was significantly correlated with both CVRD (Pearson coefficient = −0.534, *P* = 0.007; partial correlation holding HCV_{cc} constant = −0.569, *P* = 0.005) and HCV_{cc} (Pearson coefficient = 0.601, *P* = 0.002; partial correlation holding CVRD constant = 0.629, *P* = 0.001) (Table 4). In addition, although avian species diversity was significantly correlated with both CVRD (Pearson coefficient = 0.704, *P* = 0.000) and FHD_4 (a physiognomic index that was highest in tall vegetation types; Pearson coefficient = 0.573, *P* = 0.003), it was significantly correlated only with CVRD (Partial correlation = 0.673, *P* = 0.001) when the confounding effects of covariation between CVRD and FHD4 were eliminated (Table 4). Furthermore, avian species richness was not significantly correlated with any of the plant community-structure indices (Table 4).

Discussion

My results from the migratory period support research from the breeding season that shows that avian community organization is influenced by vegetation structure (MacArthur and MacArthur 1961, MacArthur 1964, MacArthur et al. 1966, Recher 1969, Karr and Roth 1971, Willson 1974, Roth 1976). However, the present study is among the few (Rice et al. 1983, 1984; Fleishman et al. 2003) to document that avian community organization is also associated with floristics. Although *en route* migrant landbird community organization in exotic and native vegetation was associated with both floristics and physiognomy, the results of the present study indicate that direct measures of floristics (plant species coverages) are relatively more important in influencing which bird species are present and their abundances, whereas direct measures of physiognomy are relatively more important in influencing how many bird species are present. However, my data also reveal that birds respond to floristic and physiognomic complexity of exotic and native vegetation, and that avian associations with vegetational diversity do not parallel those with direct vegetation measures. Specifically, avian species diversity increased with increasing floristic diversity, and avian abundance was positively associated with horizontal structural diversity—the reverse of avian associations with direct vegetation measures. I also found that bird–vegetation associations were scale dependent, which is in agreement with studies by Hutto (1985), Wiens et al. (1987), and others that have shown that birds select and use habitats on the basis of a hierarchical spatial scaling process. Associations between migrant community parameters and floristics tended to be detected at both micro- and macrohabitat scales, whereas associations between migrant community measures and physiognomy tended to be evident at only the microhabitat scale. The finding that the power of floristics and physiognomy in predicting avian community parameters depended on the floristic and physiognomic measures used and the scale investigated demonstrates the necessity both for evaluation of which vegetation measures are biological meaningful and for incorporation of variability in spatial scale when formulating generalizations regarding broad habitat-occupancy patterns of birds.

Although the associations described here are correlative, I believe that they reflect true ecological relationships. During stopover, migrants select among available habitats and for components within a habitat to balance energy needs with conflicting demands, such as finding refuge from inclement weather and predation and avoiding competition with other migrants and resident birds for foraging opportunities (Moore and Simons 1992, Moore 2000). Patterns in the data reported here strongly suggest that migrants stopped at the study location primarily to replenish fat, nutrient, and water stores depleted by migratory flight and that bird–vegetation associations were a consequence of underlying respective relationships of floristics and physiognomy to forage quality.

I found that (1) avian species composition, total avian abundance, total avian energy consumption, and evenness were all more strongly associated with direct measures of floristics than with direct measures of physiognomy and (2) floristic diversity, compared to physiognomic diversity, was a better predictor of avian species composition, evenness, and avian diversity.

My results are consistent with assertions by others that the species of plants present determine the specific types and abundances of food resources (e.g., fruits, seeds, arthropods) available, and, thereby, which bird species and how many of each can be supported (Rotenberry 1985, Rodewald and Abrams 2002, Fleishman et al. 2003). Most of the migrants captured at the study area were insectivorous, and it is reasonable that availability of arthropod prey differed between Tamarisk and native vegetation, given that Tamarisk and native plant species differ in the composition (e.g., aerial, foliage), timing of availability (e.g., emergence), and quality (i.e., abundance and energy content) of their respective arthropod communities (Glinski and Ohmart 1984, Hunter et al. 1988, Andersen 1994, Mund-Meyerson 1998, Drost et al. 2003). In fact, the observation that total avian abundance and total avian energy consumption both were higher in the exotic vegetation types indicates that Tamarisk-dominated vegetation can provide higher-quality foraging habitat for some migrants (such as Wilson's Warbler and other common insectivorous foliage-gleaners) than native vegetation. Tamarisk-dominated vegetation might provide a high-quality arthropod prey base for insectivorous migrants during fall migration because, among other arthropods, the exotic leafhopper *Opsius stactogalus*, accidentally introduced along with Tamarisk, is a good source of arthropod prey (Drost et al. 2003, Yard et al. 2004).

The finding that total avian abundance and total avian energy consumption both increased with increasing horizontal patchiness in canopy cover provides another line of evidence supporting the supposition that relationships of floristics and physiognomy to forage quality were driving bird–vegetation associations. Horizontal patchiness in canopy cover corresponds to the number of gaps in canopy foliage, and the number of gaps within a vegetation patch can determine food-resource availability and the number of birds supported (Blake and Hoppes 1986). Insolation tends to be higher in gaps, and this increased energy input can promote groundcover and foliage density, which can increase the abundance and types of arthropod prey available to foliage- and ground-gleaner bird species (Blake and Hoppes 1986, Böhning-Gaese 1997, Bailey et al. 2004). Thus, more individuals and biomass of migrants were likely supported by the exotic vegetation types because the relatively higher horizontal patchiness in canopy cover in the Tamarisk-dominated vegetation tended to increase arthropod prey abundance.

Forage quality for birds is not determined only by the presence and abundance of food types, but also by the ability of birds to acquire them. The configuration of the vegetation affects bird motility and food visibility, as well as the number of patches or microhabitats (e.g., foraging microhabitats) that can be divided (i.e., niche-partitioning) by different bird species (MacArthur 1964, Cody 1985). My finding that avian species richness was significantly associated with physiognomy but not floristics indicates that the number of bird species that "pack" into exotic and native vegetation patches is related to how many foraging microhabitats are available, thus providing a third line of evidence supporting the supposition that relationships of floristics and physiognomy to forage quality were driving bird–vegetation associations.

Conservation implications.—The results and interpretations presented here contribute not only to understanding the respective roles of floristics and physiognomy in avian community organization, but also to understanding which mechanisms underlie habitat selection, preference, and use during stopover. An important caveat is that, because I cannot dismiss the possibility that the vegetation associations of migrant landbirds were attributable to other important factors not measured, additional research is needed to tease apart underlying mechanisms. Future research should evaluate the extent to which community organization, as well as physiological condition (e.g., fat loadings, corticosterone levels, plasma metabolite profiles), of migrants during both spring and fall are related to quantitative measures of resources, such as food, foraging substrates, and shelter from predators and physiological stress. Irrespective of this caveat, my approach of investigating bird–vegetation relationships in exotic-dominated vegetation provides information necessary for developing scientifically based conservation and management strategies aimed at stemming the environmental, social, and economic consequences of anthropogenic habitat destruction. I found that the effects of exotic Tamarisk on migrant communities depended on the extent to which Tamarisk-infested vegetation was a "functional replacement," both floristically and structurally, for native vegetation. Specifically, I found that Tamarisk-dominated vegetation that was floristically dissimilar to the native vegetation supported different avian species compositions. However, Tamarisk-dominated vegetation that was structurally similar to native vegetation supported similar species richness and diversity of migrants, and both low and tall-statured Tamarisk vegetation, particularly with horizontal patchiness in canopy cover, provided stopover habitat of equal or better quality for certain bird species as native vegetation. These results are germane to many federal, state, and tribal agencies undertaking aggressive campaigns to reduce or eradicate Tamarisk in the Southwest through mechanical, chemical, and biological control. Eradication of Tamarisk is considered a priority by most management agencies because this introduced species alters the abiotic environment of southwestern riparian ecosystems by changing soil salinity, groundwater availability, and fire frequency (DeLoach et al. 2000, Lovich and DeGouvenain 1998). However, eradication efforts are being undertaken on a site-specific basis without sufficient quantitative data on the habitat value of Tamarisk to wildlife, specifically avifauna (Fleishman et al. 2003), and on whether removal of Tamarisk will result in ecological gains. Because complete eradication of Tamarisk is often constrained by fiscal and economic concerns, such quantitative data are necessary in developing decision trees for prioritizing which types of Tamarisk-dominated vegetation should be removed and restored. For those management efforts seeking to control Tamarisk while protecting both *en route* migrant landbirds and their stopover habitats, results from this research indicate that structurally homogeneous monocultures of Tamarisk should be a priority for removal, whereas removal of horizontally and vertically complex stands of Tamarisk that contain some attendant native plant species should be deferred until some native vegetation has been restored.

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