

INFLUENCE OF VEGETATION ON MONTANE RIPARIAN BIRD COMMUNITIES IN THE SKY ISLANDS OF ARIZONA, USA

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ABSTRACT—Montane riparian areas across the Sky Island region of the southwestern United States and northwestern Mexico contribute disproportionately to biodiversity at local and regional scales. We explored how composition and structure of vegetation influenced species richness and community composition of songbirds breeding in riparian areas of southern Arizona. We surveyed birds and vegetation during two breeding seasons at 45 stations established across three riparian canyons in two mountain ranges. Species richness of songbirds increased as volume of understory vegetation, density of Arizona sycamore (*Platanus wrightii*), and density of alligator juniper (*Juniperus deppeana*) increased; species richness decreased as density of *Acacia* and *Mimosa* species increased and oak (*Quercus*) trees increased. Composition of breeding bird communities was structured along an elevation and vegetation gradient, from open-canopy desert scrub to closed-canopy oak woodlands. Richness and composition of breeding bird communities in these biologically diverse montane riparian canyons were governed by both floristic composition and physical structure of dominant riparian vegetation.

RESUMEN—Las zonas riparias de montaña ubicadas en la región de las Islas Serranas en el suroeste de los Estados Unidos y el noroeste de México contribuyen desproporcionadamente a la biodiversidad local y regional. Exploramos la manera en que la composición y estructura de la vegetación influyen en la riqueza de especies y la estructura de las comunidades de aves canoras que se reproducen en las zonas riparias del sur de Arizona. Muestreamos aves y vegetación durante dos temporadas reproductivas en 45 estaciones establecidas a lo largo de tres cañones de ribera en dos cadenas montañosas. La riqueza de especies de aves canoras aumentó cuando el volumen de la vegetación del sotobosque, densidad de sicómoro de Arizona (*Platanus wrightii*) y densidad de enebro cocodrilo (*Juniperus deppeana*) aumentaron; la riqueza de especies disminuyó a medida que aumentó la densidad de *Acacia* y *Mimosa*, y del roble (*Quercus*). La composición de las comunidades de aves reproductivas se estructuró en torno a un gradiente de elevación y de vegetación que incluyó desde matorral desértico del dosel abierto hasta bosques de robles de dosel cerrado. La riqueza y estructura de las comunidades reproductivas de aves en estos cañones riparios de montaña biológicamente diversos se rigen por la composición vegetal y la estructura de la vegetación riparia dominante.

Although many biotic and abiotic factors can influence the structure of bird communities, vegetation characteristics, including vertical structure (MacArthur and MacArthur, 1961; Fleishman et al., 2003), horizontal patchiness (Roth, 1976; Kotliar and Wiens, 1990), and floristics (Rice et al., 1984; Strong and Bock, 1990) have been recognized consistently as key structural determinants of terrestrial bird communities (James, 1971; Wiens, 1989). Vegetation is an important resource for birds and other animals because it provides food resources, cover from predators and harsh environmental conditions, and nesting sites.

Plants respond to a host of site-specific factors, but in arid environments water is the key limiting resource (Noy-Meir, 1973). Given that water is limited across much of the southwestern United States, broad-leaved deciduous

plant communities are rare and restricted primarily to mesic riparian zones (Johnson and Jones, 1977). In this region, there is a stark contrast between upland and riparian vegetation communities, with upland zones characterized predominantly by species that are drought tolerant and riparian zones characterized by species with large leaves, tall canopies, and high vegetation volume. These vegetation features are important to habitat for many animals and consequently they govern the structure of many animal communities (Soykan et al., 2012).

Riparian woodlands in arid regions of North America support disproportionately high species richness of birds (Szaro, 1980; Knopf and Samson, 1994; Krueper et al., 2003; Flesch, 2008). In the Sky Island region of southern Arizona and northern Sonora, Mexico, mesic riparian areas comprise <0.5% of the landscape, but support the

majority of the region's vertebrate diversity, especially birds (Johnson and Jones, 1977; Soykan et al., 2012). Research on birds in these riparian areas has focused on plant communities dominated by cottonwood (*Populus fremontia*), willow (*Salix* species), and exotic saltcedar (*Tamarix* species) along the Colorado, San Pedro, and other major rivers of the region (e.g., Carothers et al., 1974; Rice et al., 1984; Rosenberg et al., 1991; Brand et al., 2010). Less research, however, has focused on narrower, montane riparian areas that are more common, such as those that occur where Sonoran desert scrub grades into Madrean evergreen woodland (Strong and Bock, 1990). Hence, there is little information on associations between bird diversity and vegetation in these biologically diverse zones.

We sought to understand the influence of vegetation features on species richness and community composition of breeding birds in riparian canyons of southern Arizona, especially to identify those vegetation features that are associated most strongly with variation in composition of these bird communities. Understanding how bird communities change in response to vegetation can help to identify key structural and floristic features of these landscapes that will be essential to maintaining biodiversity in these biologically diverse areas.

MATERIALS AND METHODS—Study Area—We studied bird communities in three riparian canyons in two mountain ranges in southern Arizona that we selected because of their similarities in elevation (1,200–1,550 m), aspect (east-facing), and topography. Brown Canyon (1,200–1,550 m), part of the Buenos Aires National Wildlife Refuge, is in the Baboquivari Mountains and encompasses two distinct life zones. Lower-elevation areas of the canyon are characterized as Arizona uplands subdivision of Sonoran desert scrub (Brown, 1982) and are dominated by velvet mesquite trees (*Prosopis velutina*) and other spinecent shrubs (Powell and Steidl, 2000); upper-elevation areas of the canyon are characterized as Madrean evergreen woodland (Brown, 1982) and dominated by oaks (Arizona white [*Quercus arizonica*], Mexican blue [*Quercus oblongifolia*], and Emory [*Quercus emoryi*]), Arizona walnut (*Juglans major*), and Arizona sycamore (*Platanus wrightii*). The riparian zone is classified as interior riparian deciduous forest (Brown, 1982) and is dominated by sycamore and netleaf hackberry (*Celtis reticulata*), which occur in lower-elevation areas of the canyon. Flow of surface water is intermittent in most years. The other two canyons, Lost Dog (1,350–1,490 m) and Ramanote (1,300–1,525 m), are in the Atascosa Mountains, approximately 50 km east of Brown Canyon. Vegetation in both canyons is similar to upper Brown Canyon and is dominated by Madrean evergreen woodland that is composed mostly of oaks and alligator juniper (*Juniperus deppeana*). These canyons have few mesic riparian shrubs or trees in their riparian zones, and vegetation in uplands is similar to south-facing uplands in Brown Canyon. Flow of surface water in these two canyons is ephemeral.

Bird Surveys—In 1997 and 1998, we surveyed birds at stations spaced ≥ 250 m apart along canyon bottoms: 27 in Brown Canyon, 9 in Ramanote, and 9 in Lost Dog. We counted all birds heard or seen at each station four times each year between 15

April and 15 July, which is peak breeding season for most birds in these areas (Corman and Wise-Gervais, 2005). Surveys were 10 min in duration, with those on a given day initiated 20 min before sunrise and terminated no later than 3 h after sunrise. During surveys, we classified species and sex of each bird detected within 125 m of each point and measured the distance between each bird and the surveyor. We excluded birds in flight unless the birds landed or flights originated within a 125-m radius of the station center.

Vegetation Surveys—We characterized physical structure and floristic composition of vegetation at 10 subplots established at random within 100 m of each station center. At each subplot, we estimated percent canopy cover using a spherical densitometer, estimated visually percent cover of all herbaceous vegetation (in 5% increments) within a 1-m radius of subplot center, and counted the number of shrubs (plants ≤ 8 cm diameter at breast height) within a 5-m radius of station center. We estimated density of trees (plants > 8 cm diameter at breast height) by species using the point-quarter method (Cottam and Curtis, 1956) by recording distance to and diameter at breast height of the nearest tree in each of four quadrants. We combined densities of all *Quercus* into one group and *Acacia* and *Mimosa* into another group because these species have similar growth forms; we combined uncommon species (mean = 3.6% of overall tree density) into an “other” group. We estimated percent vegetation volume within a 5-m radius circle centered on each subplot within three height strata: 0–1.5 m (understory), 1.5–4.0 m (midstory), and > 4 m (overstory); specifically, we estimated volume of leaves and branches that filled an imaginary cylinder that extended from the bottom to the top of each stratum (Powell and Steidl, 2000).

Data Analysis—We estimated species richness and characterized community composition of breeding birds at each survey station. To estimate species richness, we used the first-order jackknife estimator, which allows detection probabilities to vary among species (Burnham and Overton, 1978). To identify vegetation features associated with richness of birds, we used multiple linear regression to model richness as a function of all vegetation characteristics and used stepwise-variable selection to retain variables with explanatory power ($P < 0.15$ to enter, < 0.05 to stay). To characterize composition of the bird and vegetation communities at each survey station, we used principal components analysis on correlation matrices from bird and vegetation surveys, respectively. For the bird community, we used the total number of detections at each survey station for each of the 41 bird species that we detected ≥ 15 times across all canyons and both years. For the vegetation community, we used means of vegetation features at each survey station and log transformed variables where necessary. To determine bird species and vegetation characteristics that influenced composition of the bird and vegetation communities most, we correlated principal components for each ordination with the original survey data. To determine vegetation features associated most closely with bird community structure, we correlated the first principal component for the bird community with the original vegetation data from each survey station.

Finally, to determine the relative contributions of vegetation structure versus floristic composition in explaining composition of the bird community, we first used principal components analysis to characterize vegetation structure on the basis only of structural variables (canopy cover, herbaceous cover, number of

shrubs, density of all tree species combined, and vegetation volume in all strata), and floristic composition on the basis only of species-specific densities of tree species and species groups. For both structural and floristic ordinations, we retained three principal components, which explained 80% of the variation in the original data for both sets of variables. We then used multiple regression to model bird community composition (first principal component based on bird-survey data, described above) solely as a function of vegetation structure, then as a function of both vegetation structure and floristic composition components to contrast the amount of variation (r^2) explained by structure individually and structure and floristics combined.

RESULTS—We detected 3,674 birds of 73 species across all stations that we surveyed in 1997–1998. The most common species were white-winged doves (*Zenaidura asiatica*, $n = 294$ detections), Mexican jays (*Aphelocoma wollweberi*, 288), and Bewick's wrens (*Thryomanes bewickii*, 274) (Table 1). We observed an average of 22.3 ($SE = 0.9$) species per station in Lost Dog Canyon, 23.4 (0.7) in Ramanote Canyon, and 26.2 (0.6) in Brown Canyon, and estimated species richness per station to be 31.7 (1.3) for Lost Dog Canyon, 31.8 (1.3) for Ramanote Canyon, and 37.9 (1.7) for Brown Canyon.

Estimated species richness of breeding songbirds was associated with five vegetation features ($F_{6,38} = 9.5$, $P < 0.001$, adjusted $r^2 = 0.54$). Richness increased as vegetation volume in the understory (regression coefficient = 0.44% \pm 0.22% [SE], $t = 2.2$, $P = 0.03$), density of Arizona sycamore (2.0 log[stems/ha] \pm 0.58, $t = 3.55$, $P = 0.001$), and density of alligator juniper (1.53 log[stems/ha] \pm 0.61, $t = 2.50$, $P = 0.02$) all increased. Richness decreased as density of *Acacia* and *Mimosa* trees combined increased (-2.59 log[stems/ha] \pm 0.94, $t = -2.75$, $P = 0.009$) and density of all *Quercus* trees increased (-1.83 log[stems/ha] \pm 0.67, $t = -2.70$, $P = 0.01$).

Composition of the bird community, as described by the first principal component that explained 28% of the original bird-survey data, reflected a gradient in composition from species common to oak woodlands that loaded negatively on this axis (e.g., dusky-capped flycatcher [*Myiarchus tuberculifer*], black-headed grosbeak [*Pheucticus melanocephalus*], and bridled titmouse [*Baeolophus wollweberi*]) to species common to desert scrub and riparian vegetation that loaded positively on this axis (e.g., Bell's vireo [*Vireo bellii*], verdin [*Auriparus flaviceps*], and northern cardinal [*Cardinalis cardinalis*]).

Vegetation characteristics, as described by the first principal component that explained 43% of the original vegetation data, reflected a structural and compositional gradient from relatively open oak woodlands to mesic riparian woodlands with high vegetation density and diversity (Table 2). Vegetation along this axis transitioned from areas dominated by oaks, alligator juniper, and manzanita (*Arctostaphylos pungens*) that loaded negatively on this axis to areas dominated by netleaf hackberry, Arizona sycamore, *Acacia* and *Mimosa* species, and other

areas with high vegetation volume in the understory and midstory that loaded positively on this axis.

Community composition of breeding songbirds was correlated strongly with compositional and structural attributes of vegetation ($r = 0.93$, $P < 0.0001$). Specifically, composition of the bird community varied with density of netleaf hackberry ($r = 0.91$), oaks ($r = -0.87$), Arizona sycamore ($r = 0.77$), *Acacia* and *Mimosa* ($r = 0.75$), velvet mesquite ($r = 0.71$), and alligator juniper trees ($r = -0.71$), as well as vegetation volume in the understory ($r = 0.83$) and number of shrubs ($r = 0.56$; P for all correlations < 0.0001 , $n = 45$). Vegetation structure alone explained 62% of variation in composition of the bird community, whereas vegetation structure and floristic composition combined explained 92% of variation in composition of the bird community, suggesting that both vegetation structure and composition were important to composition of the bird community (Fig. 1).

DISCUSSION—Species richness and composition of the breeding bird community in the southwestern riparian canyons we studied were governed by both structural and floristic features of vegetation. In general, dense vegetation in the understory and overstory, which occurs more commonly in riparian areas than in adjacent uplands, was a key predictor of bird species richness. Vertical vegetation structure plays an important role in governing avian diversity because areas with high vegetation structure provide more sites for foraging, nesting, and protection from predators (MacArthur and MacArthur, 1961; Whitmore, 1981; Wiens, 1989). Consequently, vegetation structure is considered to be among the most important predictors of bird abundance and richness in the southwestern United States (Fleishman et al., 2003).

In addition to vegetation structure, bird communities are also influenced by the particular species composition of the plant community (Rice et al. 1984). We found that composition of the bird communities in these montane riparian areas changed as the dominant tree species changed. For example, species associated with deciduous riparian vegetation, such as Bell's vireos and yellow-breasted chats (*Icteria virens*), inhabited areas where vegetation composition differed markedly from species associated typically with oak woodlands, such as Mexican jays, dusky-capped flycatchers, and hepatic tanagers (*Piranga flava*).

Tree species that are structurally dominant in more mesic riparian areas, such as Arizona sycamore, netleaf hackberry, and cottonwood, are especially important habitat features for many bird species in arid and semiarid environments (Bock and Bock, 1984; Powell and Steidl, 2000; Brand et al., 2010). High species richness of birds in riparian areas relative to adjacent uplands has been attributed to structural complexity of the vegetation (Bull and Skovlin, 1982; Knopf and Samson, 1994), but may also be related to local

TABLE 1—Mean detection rate (no. detections/survey), correlation coefficient (r), and P -value for correlation with first principal component (PC1) for the most abundant bird species in three riparian canyons in southern Arizona, 1997–1998.

Common name	Scientific name	Canyon			PC1	
		Brown	Lost Dog	Ramanote	r	P
Montezuma quail	<i>Cyrtonyx montezumae</i>	—	0.08	0.18	−0.12	0.45
White-winged dove	<i>Zenaida asiatica</i>	0.75	1.01	0.82	0.30	0.05
Mourning dove	<i>Zenaida macroura</i>	0.08	0.17	0.26	−0.07	0.65
Broad-billed hummingbird	<i>Cynanthus latirostris</i>	0.22	0.35	0.49	−0.36	0.02
Costa's hummingbird	<i>Calypte costae</i>	0.18	—	—	0.50	<0.001
Acorn woodpecker	<i>Melanerpes formicivorus</i>	0.11	0.17	0.08	−0.21	0.17
Ladder-backed woodpecker	<i>Picooides scalaris</i>	0.26	0.06	0.13	0.49	<0.001
Northern beardless-tyrannulet	<i>Camptostoma imberbe</i>	0.07	—	—	0.49	<0.001
Dusky-capped flycatcher	<i>Myiarchus tuberculifer</i>	0.29	0.57	0.82	−0.87	<0.001
Ash-throated flycatcher	<i>Myiarchus cinerascens</i>	0.32	0.75	0.51	−0.19	0.22
Brown-crested flycatcher	<i>Myiarchus tyrannulus</i>	0.12	0.03	0.03	0.58	<0.001
Sulphur-bellied flycatcher	<i>Myiodynastes luteiventris</i>	0.08	—	0.01	−0.05	0.72
Cassin's kingbird	<i>Tyrannus vociferans</i>	0.22	0.01	0.04	0.62	<0.001
Bell's vireo	<i>Vireo bellii</i>	0.77	—	—	0.82	<0.001
Plumbeous vireo	<i>Vireo plumbeus</i>	0.08	—	—	−0.16	0.30
Mexican jay	<i>Aphelocoma wollweberi</i>	0.56	1.06	1.28	−0.69	<0.001
Bridled titmouse	<i>Baeolophus wollweberi</i>	0.17	0.67	0.76	−0.75	<0.001
Verdin	<i>Auriparus flaviceps</i>	0.34	0.01	0.01	0.78	<0.001
Bushtit	<i>Psaltriparus minimus</i>	0.03	0.19	—	−0.03	0.85
White-breasted nuthatch	<i>Sitta carolinensis</i>	—	0.11	0.17	−0.44	0.002
Cactus wren	<i>Campylorhynchus brunneicapillus</i>	0.44	—	0.06	0.44	0.003
Canyon wren	<i>Catherpes mexicanus</i>	0.19	0.32	0.47	−0.57	<0.001
Bewick's wren	<i>Thryomanes bewickii</i>	0.69	0.94	0.78	−0.35	0.02
Blue-gray gnatcatcher	<i>Poliotilta caerulea</i>	0.17	—	0.03	−0.29	0.05
Northern mockingbird	<i>Mimus polyglottos</i>	0.03	0.31	0.25	−0.18	0.24
Phainopepla	<i>Phainopepla nitens</i>	0.30	0.36	0.25	0.50	<0.001
Lucy's warbler	<i>Oreothlypis luciae</i>	0.21	0.31	0.07	0.42	0.004
Painted redstart	<i>Myioborus pictus</i>	0.05	0.03	0.19	−0.59	<0.001
Yellow-breasted chat	<i>Icteria virens</i>	0.13	—	—	0.62	<0.001
Hepatic tanager	<i>Piranga flava</i>	0.08	0.06	0.14	−0.51	<0.001
Summer tanager	<i>Piranga rubra</i>	0.39	0.10	0.19	0.63	<0.001
Canyon towhee	<i>Melospiza fusca</i>	0.13	0.14	0.03	−0.02	0.92
Rufous-crowned sparrow	<i>Aimophila ruficeps</i>	0.19	0.42	0.51	−0.60	<0.001
Northern cardinal	<i>Cardinalis cardinalis</i>	0.92	—	—	0.89	<0.001
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>	0.16	0.91	0.51	−0.78	<0.001
Blue grosbeak	<i>Passerina caerulea</i>	0.20	0.06	0.10	0.72	<0.001
Varied bunting	<i>Passerina versicolor</i>	0.15	0.18	0.04	0.35	0.02
Brown-headed cowbird	<i>Molothrus ater</i>	0.28	0.28	0.32	0.31	0.04
Hooded oriole	<i>Icterus cucullatus</i>	0.38	—	0.01	0.41	0.005
Scott's oriole	<i>Icterus parisorum</i>	0.26	0.25	0.56	−0.62	<0.001
House finch	<i>Haemorhous mexicanus</i>	0.26	0.13	0.13	0.29	0.05

abundance of available water and invertebrate prey (Kirkpatrick et al., 2007). Brown Canyon was the only canyon we studied that supported mesic riparian trees, which helped explain the higher species richness of breeding birds in that canyon. Riparian forests have consistently higher species richness and abundance of birds compared with adjacent upland areas for most, but not all, taxa (Sabo et al., 2005; Soykan et al., 2012). High heterogeneity in vegetation structure and floristics also promotes high species richness in riparian areas (Wiens, 1985; Sisk et al., 1997), which further explains higher

species richness of birds in Brown Canyon. Compared with the other canyons we surveyed, Brown Canyon included a broader mix of dominant plant species that changed quickly with elevation and topography. At lower elevations of Brown Canyon, vegetation was predominantly Sonoran Desert uplands; at higher elevations, vegetation was predominantly oak woodlands. The area of highest bird species richness was the ecotonal transition between these two vegetation communities, which occurred within a span of only a few hundred meters. Ecotones frequently have higher alpha diversity (Gates

TABLE 2—Mean and standard deviation (*SD*) of vegetation characteristics averaged across survey points and correlation coefficient (*r*) and *P*-value for correlation with first principal component (PC1) within three riparian canyons in southern Arizona, 1997.

Category	Measure	Brown		Lost Dog		Ramanote		PC1	
		Mean	<i>SD</i>	Mean	<i>SD</i>	Mean	<i>SD</i>	<i>r</i>	<i>P</i>
Vegetation volume (%)	Understory (0–1.5 m)	40.4	11.4	29.2	6.4	27.4	5.8	0.82	<0.001
	Midstory (1.5–4 m)	35.2	9.7	31.6	8.2	33.2	5.1	0.55	<0.001
	Overstory (>4 m)	19.2	7.8	15.4	8.3	17.7	4.8	0.30	0.045
Canopy cover (%)	Cover	52.6	14.0	52.0	15.6	50.2	13.3	0.14	0.36
Number of shrubs	Number	5.8	0.6	3.9	0.9	4.1	1.3	0.57	<0.001
Tree density (stems/ha)	Oaks	90.9	103.3	196.6	82.9	290.7	179.8	−0.86	<0.001
	Acacia and Mimosa	13.2	17.7	—	—	—	—	0.86	<0.001
	Alligator juniper	2.7	4.7	13.7	18.1	40.5	30.6	−0.76	<0.001
	Arizona walnut	14.1	19.3	—	—	—	—	0.02	0.92
	Manzanita	—	—	17.5	18.2	12.0	11.2	−0.58	<0.001
	Velvet mesquite	140.5	101.9	122.2	71.9	37.5	50.5	0.64	<0.001
	Netleaf hackberry	48.1	47.9	—	—	—	—	0.92	<0.001
	Arizona sycamore	38.2	30.6	—	—	—	—	0.83	<0.001

and Giffen, 1991), and these areas have received increased focus recently because of the anticipated changes in these areas in response to climate change (Allen and Breshears, 1998; Weltzin and McPherson, 2000).

In the southwestern United States, considerable scientific and conservation effort has been focused on valley-bottom riparian forests along major river courses (e.g., Stromberg and Tellman, 2009), which are well established as important migratory corridors for birds (e.g., Skagen et al., 1998). Most valley-bottom riparian areas are threatened by groundwater pumping that can adversely affect groundwater-dependent riparian trees directly (Stromberg et al., 1996; Lite and Stromberg,

2005), which in turn will affect birds and other wildlife that depend on them (Brand et al., 2011; Merritt and Bateman, 2012). Fewer conservation efforts have been focused on the riparian deciduous forests of the interior southwestern United States that we studied. Keystone plants in these forests, especially Arizona sycamore, are functionally essential to maintenance of biodiversity in these areas (Bock and Bock, 1984; Hall and Mannan, 1999; Powell and Steidl, 2000). In many canyons, rheocrene springs, shallow groundwater, and surface water flows support sycamore trees (Stromberg, 2002), which can be affected adversely by both local and regional threats, including groundwater pumping and short-term declines in rainfall (Katz et al., 2009). Because establish-

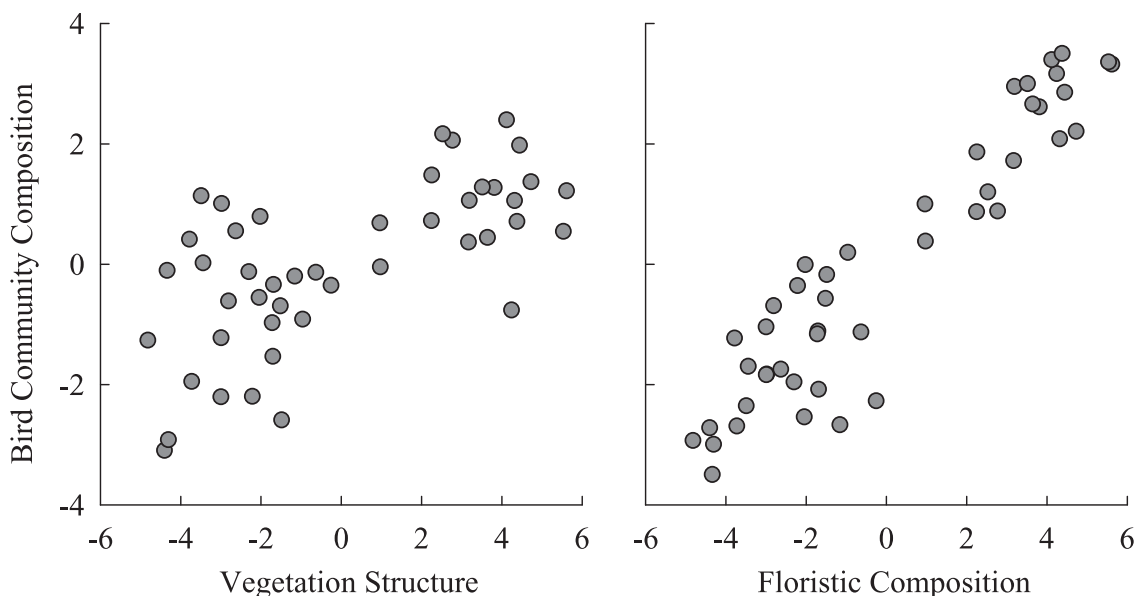


FIG. 1—Composition of the bird community (first principal component) varied with both vegetation structure (second principal component of variables measuring vegetation structure) and floristic composition (first principal component of species-specific tree densities) in riparian canyons of southern Arizona, 1997–1998.

ment and survival of Arizona sycamore seedlings require perennial or near-surface flows (Stromberg, 2001), especially during wet winters with abundant spring runoff, persistence of this species in smaller canyons will likely be threatened over the long term if projected impacts of climate change for the region are realized (Karl et al., 2009).

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