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USE OF NATIVE AND NONNATIVE NEST PLANTS BY RIPARIAN-NESTING BIRDS ALONG TWO STREAMS IN NEW MEXICO

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ABSTRACT

Nonnative plant invasions are a management concern, particularly in riparian forests, but little is known about mechanisms through which they influence vertebrate communities. In the American Southwest, native trees such as cottonwood (*Populus* spp.) are thought to provide better habitat for breeding birds than nonnative plants, which are more tolerant of human-altered conditions. To evaluate effects of riparian forest composition on riparian-nesting birds, we examined nest plant use along two rivers in New Mexico that differed in abundance of nonnative vegetation. Of the nests we observed, 49% along the Middle Rio Grande were constructed in nonnative plants, compared with 4% along the Gila River. Birds in the canopy and cavity-nesting guilds constructed less than 5% of their nests in nonnative plants along either river. At the Middle Rio Grande, birds in the subcanopy/shrub guild constructed 67% of their nests in nonnative plants. Despite the relatively low availability of cottonwoods, they were used by greater numbers of species than any other woody plant at either river. Riparian obligates and species of conservation concern in the canopy and cavity guilds were especially dependent on cottonwood and Arizona sycamore (*Platanus wrightii*). Our results show that, although nonnative trees and shrubs support large numbers of nests for certain birds, cottonwoods and other large native trees are disproportionately important to riparian bird communities. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS: biological diversity; breeding birds; cottonwood; nonnative vegetation; Gila River; Middle Rio Grande; riparian forest; saltcedar

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INTRODUCTION

Nonnative plant invasions threaten biological diversity through a variety of mechanisms. Nonnative plants alter riparian communities by directly competing with native species, transforming disturbance regimes and soil conditions and hindering restoration of degraded areas (Vitousek *et al*., 1996; Wilcove *et al*., 1998; Brooks *et al*., 2004). Invasions have been shown to affect terrestrial animal communities by altering habitat structure (Knick *et al*., 2003), replacing forage species (Trammell and Butler, 1995; DiTomaso, 2000) and reducing insect prey availability (Herrera and Dudley, 2003; Tallamy, 2004). There are several cases, however, of nonnative plants providing beneficial services to animal communities (Schlaepfer *et al*., 2011). Costs and benefits of nonnative plants, in comparison with native plants, must therefore be understood to properly manage invaded ecosystems.

Arid land riparian forests are important components of regional biological diversity. Because of increased water availability and disturbance frequency, structural and species diversity of plants is generally greater in riparian corridors than in adjacent uplands (Naiman *et al*., 1993). In turn, riparian forests support unique, diverse and abundant animal communities, most notably assemblages of birds (Knopf *et al*., 1988; Sabo *et al*., 2005; Brand *et al*., 2008). The biotic integrity of many riparian forests is imperilled, however, because conditions that encourage native plant diversity promote nonnative plant invasion as well (Stohlgren *et al*., 1998; Hood and Naiman, 2000). Moreover, human-induced changes in geomorphology and plant composition have increased invasion vulnerability along many rivers (Everitt, 1998; Stromberg *et al*., 2009).

Riparian forests of the American Southwest, even those invaded by nonnative vegetation, are essential to maintaining breeding bird populations because they offer a greater variety of nest sites than adjacent plant communities (Carothers *et al*., 1974; Hunter *et al*., 1987). In several cases, the presence of specific native plants, such as cottonwoods (*Populus* spp.) and sycamores (*Platanus* spp.), determines whether or not certain birds nest at a riparian forest site (Bock and Bock, 1984; Strong and Bock, 1990; Stoleson *et al*., 2000; Powell and Steidl, 2002). If nonnative plants provide nest sites for fewer bird species and nesting guilds than native plants, replacement of native plants by nonnatives could reduce species richness of riparian-nesting bird communities (Merritt and Bateman, 2012). Alternately, increased density of woody vegetation, a result of nonnative

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invasion, could increase abundance or diversity of certain nesting guilds along a river (Sogge *et al*., 2008). A detailed understanding of southwestern breeding birds' riparian nest plant associations is needed to better understand effects of nonnative plants on the region's biological diversity. To address this need, we analysed large, multi-year datasets from breeding bird studies along two rivers with different levels of nonnative invasion. We evaluated use of native and nonnative nest plants by their breeding bird communities to (i) describe differences in composition and use of nest plants between study areas; (ii) contrast consequences of nonnative invasion on three avian nesting guilds; and (iii) evaluate the importance of native and nonnative nest plant species to riparian obligate birds and species of conservation concern.

METHODS

Study areas

Between 1997 and 2008, forest service crews searched for nests in riparian forests as part of multi-year breeding bird studies in New Mexico (Brodhead *et al*., 2007; Smith *et al*., 2009b). Our Gila River study area (hereafter 'Gila') was composed of 34 riparian forest patches distributed through the floodplains of the Cliff-Gila Valley and the Gila Bird Area over approximately 17 river km in Grant County (Figure 1). In the Cliff-Gila Valley, 34 patches were located on private land, and one was managed by the Gila National Forest. The Gila Bird Area was managed by the forest service as well. Riparian patches varied from 0.01 to 7.8 ha in size and were separated by a matrix of river channels, irrigation ditches, pastures and hayfields (Brodhead *et al*., 2007). The riparian forest canopy was largely composed of large Fremont cottonwoods (scientific names of plants in Table I) and smaller-stature boxelders, which were also a component of the understory vegetation (Stoleson and Finch, 2003; Brodhead *et al*., 2007). Land cover bordering the riparian zone included grazed pastures, hay fields and upland desert scrub.

Our Middle Rio Grande (hereafter 'MRG') plots were located in the Rio Grande Rift Basin, which drains north to south through Sandoval, Bernalillo, Valencia and Socorro Counties (Whitney, 1996). We established 15 MRG study plots, which were sections of a continuous riparian forest that was distributed over approximately 230 river km. Plots ranged from 13.2 to 35.0 ha in size

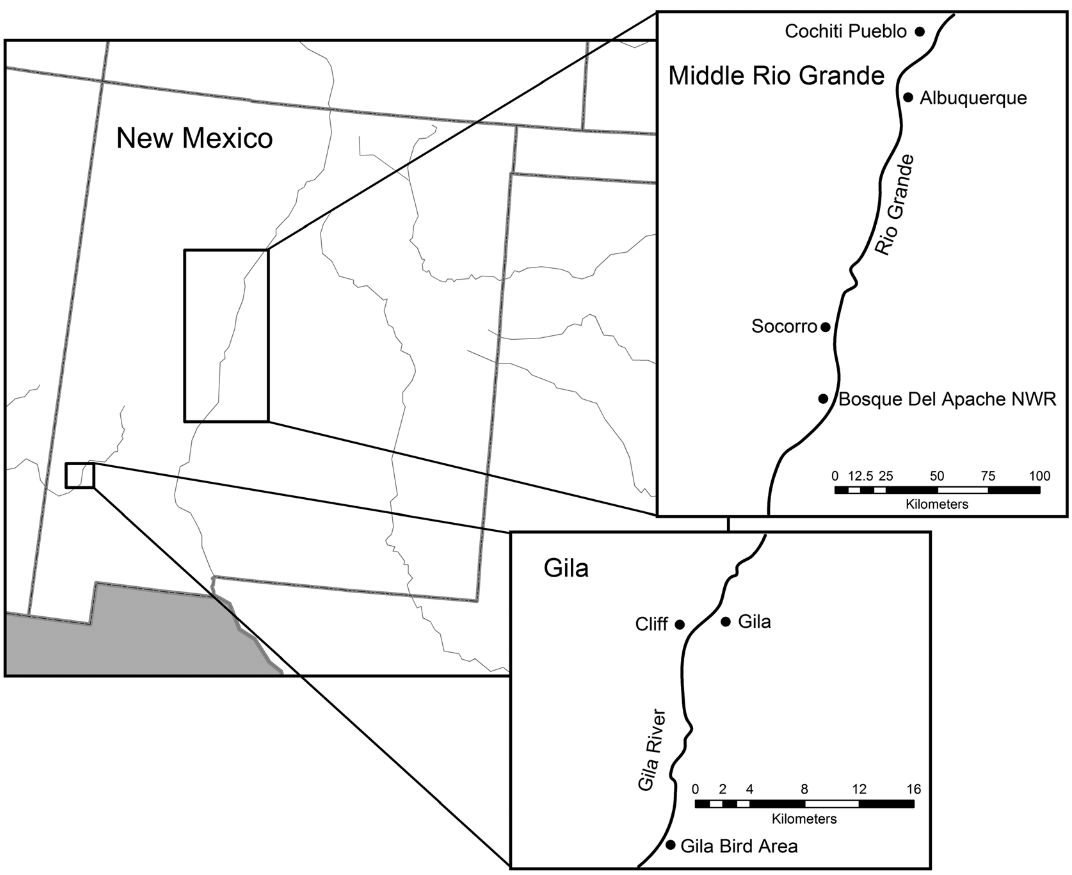

Figure 1. Location of Gila River and Middle Rio Grande study areas

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Table I. Status, mean nest height and number of species in each guild that nested in woody plant species at Gila River and Middle Rio Grande study areas

Study area	Species	Status	Nest height and range (m)	Number of canopy species	Number of cavity species	Number of subcanopy/shrub species
Gila	Fremont cottonwood *(Populus fremontii)*	Native	12.8 (0.90–38.0)	9	9	19
	Goodding's willow *(Salix gooddingii)*	Native	4.0 (0.2–17.8)	3	5	19
	Boxelder *(Acer negundo)*	Native	7.6 (0–22.9)	2	6	18
	Arizona sycamore *(Platanus wrightii)*	Native	10.8 (1.8–28.0)	3	4	10
	Russian olive *(Elaeagnus angustifolia)*	Nonnative	2.9 (0.1–8.0)	0	0	12
	Netleaf hackberry *(Celtis reticulata)*	Native	2.4 (1.0–5.4)	0	1	8
	Arizona alder *(Alnus oblongifolia)*	Native	5.1 (0.5–12.0)	0	0	7
	New Mexico locust *(Robinia neomexicana)*	Native	1.9 (0.7–2.6)	0	0	7
	Saltcedar *(Tamarix* spp.*)*	Nonnative	2.3 (1.1–3.6)	0	1	5
	Canyon grape *(Vitis arizonica)*	Native	1.7 (0.6–2.9)	0	0	6
	Seep willow *(Baccharis* spp.*)*	Native	1.5 (0.2–4.0)	0	0	5
	Arizona ash *(Fraxinus velutina)*	Native	5.6 (0.8–17.2)	1	0	4
	Coyote willow *(Salix exigua)*	Native	2.1 (0.4–4.2)	0	0	5
Middle Rio Grande	Rio Grande cottonwood *(Populus deltoides* ssp. *wislizenii)*	Native	8.7 (0.9–21.6)	8	12	10
	Saltcedar	Nonnative	2.8 (0.8-11.0)	0	1	12
	Russian olive	Nonnative	2.7 (0.6-10.0)	3	2	10
	Goodding's willow	Native	4.4 (0.5-13.4)	1	3	2
	Tree of heaven *(Ailanthus altissima)*	Nonnative	3.7(1.8-7.5)	0	0	1
	White mulberry *(Morus alba)*	Nonnative	3.7 (1.5-8.6)	0	0	1

Woody plant species in which ≥10 nests were found at a study area are included.

and were located between the Cochiti Lake and Bosque Del Apache National Wildlife Refuge (Figure 1). Three plots were managed by Cochiti Pueblo, 10 were managed by the MRG Conservancy District and two managed by the US Fish Wildlife Service. The MRG riparian forest was largely composed of a Rio Grande Cottonwood canopy that exceeded 100 m in width in some locations (Howe and Knopf, 1991). Nonnative woody species were present throughout the study area and formed much of the woody understory (Whitney, 1996; Smith *et al.*, 2009*b*). Land cover types bordering the riparian forests included agricultural fields, urban areas, grasslands and desert scrub.

Field methods

Crews visited Gila patches and MRG plots daily to systematically search for nests of all species encountered. Nest searches were conducted from late April to August each year from 1997 to 2001 along the Gila and from 2000 to 2008 along the MRG. At least once per week, crew members walked throughout each patch or plot to locate nests by following adults carrying material or food, incidentally flushing adults from nests or listening for begging sounds of nestlings. We recorded nest locations with a global positioning system receiver and revisited each nest when it was no longer active to record nest plant species and measure nest height, using a clinometer where necessary.

To record composition of woody vegetation at each study area, crews measured plants in vegetation sampling plots. At the Gila, we selected locations for vegetation sampling plots by establishing a grid of points 33.5 m apart on six of the largest Cliff-Gila nest-search patches. We randomly selected 235 of these points for 8-m-radius circular vegetation sampling plots. At the MRG, we systematically established sampling plots by establishing a transect north to south through the centre of each nest-search plot. At points every 50 m along the transect, we established two vegetation sampling plots in random directions 25 m from the point. This resulted in 10- to 16 4-m-radius vegetation sampling plots within each nest-search plot. At each study area, crews identified and counted all trees and shrubs tall enough to measure diameter at breast height within each sampling plot.

Data analyses

We estimated relative abundance of native and nonnative nest plant species using vegetation sampling plot data. We referred to Cox (2001) to determine if woody plant species were native or nonnative. Because sampling plot sizes differed between study areas, we report relative abundance for each species at each river, which we calculated by dividing the number of individuals of species *i* by the total number of plants recorded across all species.

We compared percent native and nonnative nest plant use among birds grouped into three nesting guilds. We first assigned species that typically nest in excavated or natural tree cavities to the cavity guild. We then separated open-nesting species into two guilds on the basis of their nest placement within riparian forest strata. If a species' mean nest height was <10 m and minimum nest height was <3 m, we assigned that species to the subcanopy/shrub guild. We assigned species to the canopy guild if their mean nest height was >10 m and minimum nest height was >3 m. In cases where sample size was too small to assign open-cup nesters to guilds on the basis of our data, we referred to nest height ranges reported by Ehrlich *et al*. (1988). To evaluate differences in the composition of nesting guilds, we tallied the number of bird species in each guild and identified conservation and habitat status of each species. We assigned conservation status on the basis of the classifications in the New Mexico Department of Game and Fish Comprehensive Wildlife Conservation Strategy (NMDGF, 2006). The state-listed levels of conservation priority were (in order of greatest to least) endangered species, threatened species, sensitive species and species of greatest conservation need (hereafter, SGCN). We considered nonlisted species to be widespread and abundant. We also classified each species as a riparian obligate, riparian dependant or ecological generalist using the list compiled by Rich (2002). For the purpose of this analysis, we only focus on the riparian obligates.

We compared percent use of nonnative vegetation between study areas for all species pooled and for each guild by calculating means, standard deviation and effect size. We calculated effect sizes using Cohen's *d* and interpreted values 0 to 0.2 as no effect of study area, 0.2 to 0.5 as a small effect, 0.5 to 0.8 as moderate and >0.8 as large (Cohen, 1988). We also evaluated the use of individual nest plant species by the three nesting guilds. At each river, we limited this analysis to nest plant species in which a total of 10 or more nests were observed during the study period.

RESULTS

Overall patterns of nest plant use

We located 2169 nests of 45 landbird species along the Gila River from 1997 to 2001 and 1167 nests of 38 species along the Middle Rio Grande from 2000 to 2008 (APPENDIX). Russian olive, which was relatively uncommon, was the nonnative species most frequently used as a nest plant at the Gila River (Figure. 2). The four other nonnative species in which nests were constructed along the Gila River were saltcedar, Siberian elm and black locust. Russian olive and saltcedar were the nonnative species most frequently used at the MRG and were the most relatively abundant (Figure. 2). Four other nonnative species, tree of heaven, honey locust, white mulberry and Siberian elm, comprised 4% of MRG nests plants and were used only by black-chinned hummingbirds (*Archilochus alexandri*). Nearly half the nests at the Gila were constructed in native boxelder, the most abundant woody plant (Figure. 2) with smaller percentages in Goodding's willow and Fremont cottonwood. Rio Grande cottonwood was the most abundant and frequently used native species along the MRG, supporting half of the nests we observed (Figure. 2).

Among the woody plant species in which at least 10 nests were constructed, cottonwoods were used as nest plants by the greatest number of bird species at the Gila and MRG (Table I). More than 25 species constructed nests in both boxelder and Goodding's willow at the Gila, but only seven species used these plants at the MRG. Despite its high relative abundance among native plant species, coyote willow was used by ≤5 bird species along either river. Greater numbers of bird species nested in Russian olive and saltcedar at the MRG than at the Gila (Table I). At each study area, the greatest ranges of nest height were found in cottonwoods, but the range of nest heights in Arizona sycamore and boxelder along the Gila was greater than in MRG cottonwoods (Table I).

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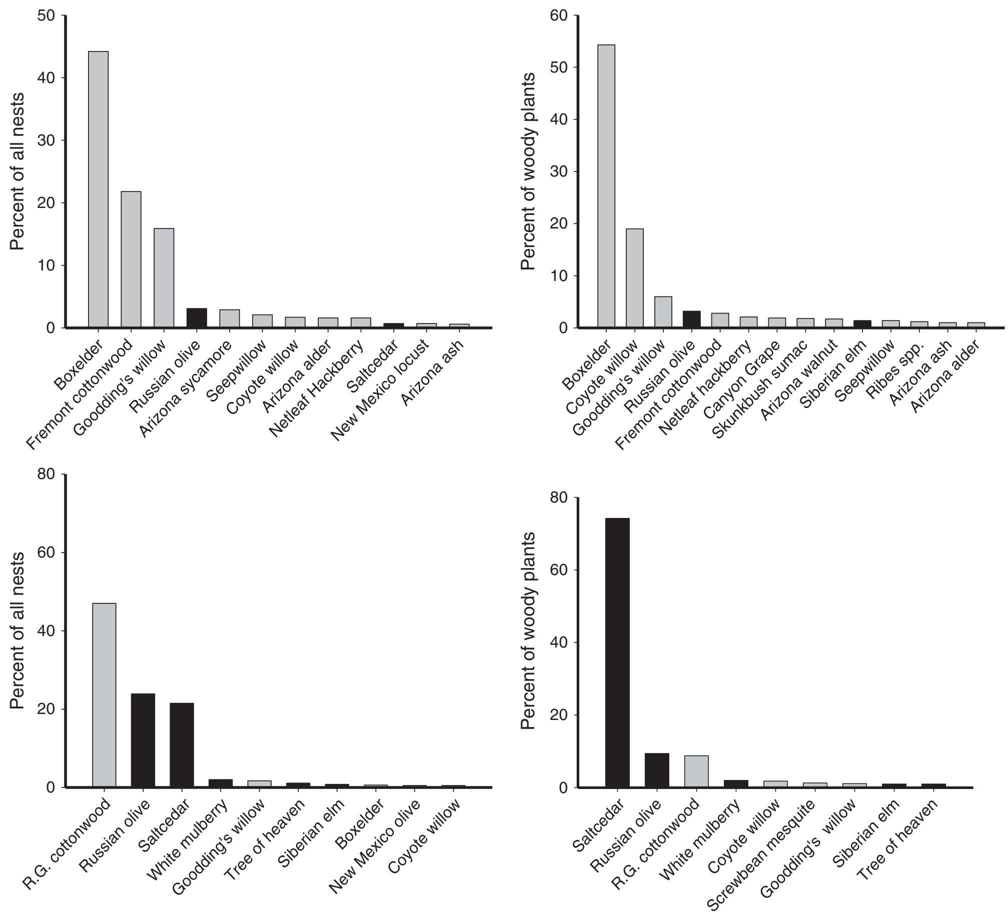

Figure 2. Percent of nests constructed in and percent availability of the most abundant woody plant species along the Gila River (top row) and Middle Rio Grande (bottom row) in New Mexico. Native species are represented by grey bars and nonnative species are represented by black bars

Breeding bird community composition

At each river, there were more avian species present in the subcanopy/shrub guild than in the canopy or cavity guilds (Table II). Ten species at the Gila were listed as endangered, threatened, sensitive or SGCN (APPENDIX). The MRG had one sensitive species (yellow-billed cuckoo, *Coccyzus americanus*) and two SGCN (mourning dove, *Zenaida macroura*, and Lucy's warbler, *Oreothlypis luciae*). A greater number of riparian obligates were present at the Gila than at the MRG (Table I). The Gila canopy nesting guild included one threatened riparian obligate (common black-hawk, *Buteogallus anthracinus*) and one SGCN (hooded oriole, *Icterus cucullatus*). The Gila cavity guild contained the threatened Gila woodpecker (*Melanerpes uropygialis*) and the SGCN Lucy's warbler. There were nine riparian obligate, shrub/subcanopy species present at the Gila, including the state and federally endangered southwestern willow flycatcher (*Empidonax traillii extimus*), the threatened Abert's towhee (*Pipilo aberti*) and the sensitive yellow-billed cuckoo. The Gila subcanopy/shrub guild also contained the threatened Bell's vireo (*Vireo bellii*), the SGCN mourning dove and the SGCN yellow warbler (*Setophaga petechia*). At the MRG, there was one riparian obligate canopy species, summer tanager (*Piranga rubra*),

Table II. Number of species in each nesting guild, number of species in each conservation status, and number of riparian obligate species at Gila River and Middle Rio Grande study areas in New Mexico

	Canopy		Cavity		Subcanopy/shrub	
	Gila	MRG	Gila	MRG	Gila	MRG
Total species	10	8	14	12	23	20
Endangered species	0	0	0	0	1	0
Threatened species	1	0	1	0	2	0
Sensitive species	0	0	0	0	1	1
Species of greatest conservation need	1	0	1	1	2	1
Riparian obligate species	2	1	0	0	8	4

MRG = Middle Rio Grande.

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but no state-listed species in this guild. The MRG cavity guild included the SGCN Lucy's warbler, but no riparian obligates. The MRG subcanopy/shrub guild contained four riparian obligates, including the sensitive yellow-billed cuckoo.

Nest plant use by guilds

At both rivers, subcanopy/shrub species used a greater number of woody plants (29 species along the Gila; 14 along the MRG) than did cavity (eight species along the Gila; four along the MRG) or canopy (eight species along the Gila; three along the MRG) nesters. Overall, nonnative nest plant use was greater at the MRG than at the Gila ($d = 2.4$; Figure. 3). Nonnative nest plant use was similar between Gila and MRG canopy species ($d = 0.1$), which constructed $<3\%$ of their nests in nonnative plants. Nonnative use by cavity species was low at both rivers but was greater along the MRG ($d = 0.5$). Nonnative use was greatest for shrub/subcanopy species along the MRG ($d = 3.6$), where $>50\%$ of nests were in nonnative plants (Figure. 3).

At the Gila and MRG, cottonwoods were used by greater numbers of cavity and canopy nesting species than any of the other trees present (Table I). Cottonwood, Goodding's willow and boxelder were used by a greater number of Gila subcanopy/shrub species than was Russian olive. At the MRG, saltcedar was used by a greater number of MRG subcanopy/shrub species than was Cottonwood or Russian olive (Table I).

Nest plant use by riparian obligates and listed species

At the Gila, cottonwoods were used by all riparian obligates except for common yellowthroat (*Geothlypis trichas*), boxelders were used by all riparian obligates except for common black-hawk and Goodding's willow was used by all riparian obligates except for common black-hawk and common yellowthroat. Russian olive was used by all riparian obligates except for common black-hawk and summer tanager. Arizona sycamore was used by four riparian obligates: common black-hawk, willow flycatcher, yellow warbler and blue grosbeak. At the MRG, cottonwood was used by two riparian obligates: summer tanager and blue grosbeak. Saltcedar was used by yellow-breasted chat and blue grosbeak, and Russian olive was used by all five riparian obligates present. Summer tanager was the only MRG riparian obligate to use Goodding's willow.

The threatened canopy and cavity species (common black-hawk and Gila woodpecker) present at the Gila nested only in cottonwood or Arizona sycamore. The threatened and endangered subcanopy/shrub species (willow flycatcher, Bell's vireo and Abert's towhee), however, nested in numerous woody plant species at the Gila. The sensitive yellow-billed cuckoo nested in several plants at the Gila but nested only in Russian olive at the MRG. Among the SGCN, hooded oriole nested in Arizona walnut and black locust at the Gila, and Lucy's warbler nested in cottonwood, Goodding's Willow and netleaf hackberry at the Gila, but only in cottonwoods at the MRG. Mourning dove nested in a variety of woody plants at each river, as did yellow warbler at the Gila.

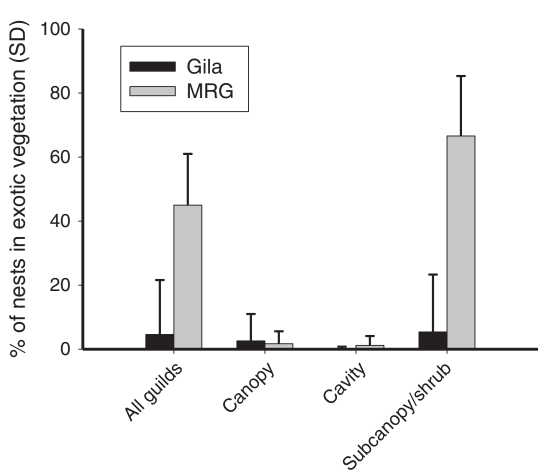

Figure 3. Percent of nests constructed in nonnative and native vegetation by all species of birds and by species separated into nesting guilds along the Gila River and Middle Rio Grande, New Mexico

DISCUSSION

Two patterns emerged from our comparison of nest plant use at our Gila study area, where riparian forest patches were dominated by native woody plants and our MRG study area, with riparian forest plots characterized by cottonwood canopy and nonnative understory. The first, unsurprising pattern was that nonnative plants were used for a greater percentage of nests by a greater number of species along the MRG than the Gila. The second pattern, with great implications for riparian bird conservation, was that, at each river, cottonwood was the nest plant used by the greatest number of species, particularly those in cavity and canopy guilds. Although cottonwoods were three times greater a component of the MRG plant community than the Gila's, their importance to each area's bird community was nearly equal.

Fremont and Rio Grande cottonwood, present and the Gila and MRG, respectively, are structurally similar and considered the same species by some authorities (Benson and Darrow, 1981). Cottonwoods have been shown to support large bird communities along several rivers in the American Southwest (Carothers *et al*., 1974; Strong and Bock, 1990) and Great Plains (Sedgwick and Knopf, 1990; Rumble and Gobeille, 2004). The importance of cottonwoods to riparian-nesting birds results largely from their architecture, which provides a large range of nest heights and

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opportunities for cavity excavation. At our study areas, cottonwoods provided nest sites for a variety of open-nesting species, from Cassin's kingbird (*Tyrannus vociferans*), which nests high in the upper portions of large trees, to spotted towhee (*Pipilo maculatus)*, which nests in woody vegetation near the ground (Greenlaw, 1996; Tweit and Tweit, 2000). Cottonwoods were also home to >70% of the cavity nests we observed. Arizona sycamore offered a range of nest heights and cavity nests, similar to cottonwood, along the Gila, but was used by fewer bird species, most likely because of its lower abundance. The only large trees, other than cottonwood, that were present along the MRG were Siberian elm and white mulberry, both nonnative species. These trees were confined to the northern portion of our study area and were used only by black-chinned hummingbird, the most abundant breeding bird at the MRG (Smith *et al*., 2009b). These observations indicate that, in the absence of cottonwoods, fewer species, especially those in the MRG canopy and cavity guilds, would have nested at our study areas. Cottonwoods were positively associated with estimates of riparian bird diversity in several count-based studies (Carothers *et al*., 1974; Hunter *et al*., 1987; Strong and Bock, 1990), but ours is the first to use data from a large number of nests to support these findings.

Although boxelder, Goodding's willow, Russian olive and saltcedar did not provide nest sites for as many species as cottonwood, they were frequently used by subcanopy/shrub birds. Boxelder and Goodding's willow were the two most abundant tree species along the Gila and, after cottonwood, were used by the greatest number of bird species. The endangered southwestern willow flycatcher (*E. traillii extimus*) and the threatened yellow-billed Cuckoo (*C. americanus)*, which has been petitioned for federal protection (Hughes, 1999), constructed 85% and 88% of their nests in these two trees, respectively. Although these tree species may not provide nest sites for as many species as cottonwoods, they clearly have high conservation importance along the Gila. The presence of boxelder, in fact, may explain the notably large population of southwestern willow flycatchers in the Gila study area (Stoleson and Finch, 2003). Russian olive and saltcedar, two nonnative species, were the most abundant trees along the MRG and were also used by the greatest number of bird species after cottonwood. Along the MRG, Russian olive and saltcedar contained more nests than other understory plant species but were used by fewer bird species than cottonwood. Although they were used by few birds in the canopy and cavity guilds, these nonnative species supported large numbers of nests for subcanopy/shrub species such as mourning dove and black-chinned hummingbird (Smith *et al*., 2009b, 2012). Russian olive and saltcedar may therefore play a larger role in promoting breeding bird abundance than breeding bird diversity at the MRG.

Birds in the canopy and cavity guilds were more specialized in nest plant use than subcanopy/shrub birds at our study area because of their dependence on large trees for canopy and cavity nest sites. The large branches of cottonwoods and sycamores are needed to support the heavy stick nests of raptors, including the state-threatened common black-hawk (*B. anthracinus*, Sadoti, 2008). Nonnative trees rarely grow large enough to support the nests of these large birds or tall enough to provide sites desirable to birds that nest at great heights (Hunter *et al*., 1987). Primary excavators, such as woodpeckers, rely on large trees with dead branches, live trees with rotting boles and snags for excavation sites (Sedgwick and Knopf, 1990; Li and Martin, 1991). Mature cottonwoods, which have relatively soft wood, frequent heart rot and large dead branches, meet these requirements (Sedgwick and Knopf, 1986; Remm and Lohmus, 2011). Nearly all of the cavity nests we observed were constructed in native trees because nonnative trees rarely grow large enough to be excavated by woodpeckers (Stoleson and Finch, 2001). Cottonwoods were used for 95% of the cavity nests along the MRG, but only 50% of the cavity nests along the Gila. These results suggest that cottonwood was more important to cavity nesters along the MRG because a greater number of native tree species were present at the Gila.

Subcanopy/shrub species used greater numbers of woody nest plants than cavity or canopy nesters, making this guild the most generalist. Birds in this guild also constructed a greater percentage of their nests in nonnative plants, particularly along the MRG. Frequent use of nonnative plants by generalist birds has been documented by several studies (Sogge *et al*., 2008), and our MRG results show that a forest understory dominated by nonnative species can support high densities of breeding birds (Smith *et al*., 2009b). Russian olive and saltcedar can therefore function in a manner similar to boxelder, Goodding's willow and other native plants by providing nest sites in the lower strata of riparian forests. Replacement of native by nonnative woody vegetation would likely have a greater effect on canopy and cavity nesters than on subcanopy/shrub nesters. Additional studies conducted across additional sites are needed, however, to build support for this conclusion.

Two riparian obligate canopy species were present at our sites and were largely dependent on native trees for nest sites. At the Gila, common black-hawks constructed 90% of their nests in cottonwood and 10% in Arizona sycamore. These percentages were similar to 97% of common black-hawk nests in cottonwood and 3% in sycamore at the Cliff-Gila Valley, reported by Sadoti (2008) and 79% in cottonwood and 11% in sycamore throughout Arizona and New Mexico, summarized by Millsap (1981). Sadoti (2008) found that common black-hawks preferred nest trees with larger crown diameters than random trees. Mature cottonwoods and

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sycamores had the largest canopies at our Gila study area and are therefore critical components of common black-hawk nesting habitat. As this species is entirely restricted to riparian forests of the American Southwest (Schnell, 1994), maintenance of large cottonwoods and sycamores is essential to its persistence in the US. Summer tanager, the other riparian obligate canopy species, has a larger range and is more generalist than common black-hawk (Robinson, 2012). At our study areas, tanagers nested in various tree species, including Russian olives. Replacement of native trees by nonnatives would likely have less of a negative impact on summer tanagers than on common black-hawks if nonnative trees such as Russian olives grow large enough to be used as nest sites.

There were greater numbers of riparian obligates in the subcanopy/shrub guild than in the canopy or cavity guilds at both rivers. Although southwestern populations of these birds are restricted to riparian zones, each riparian obligate species was generalist in terms of nest plants used. Each of the nine riparian obligate subcanopy/shrub species nested in Russian olive, and five of the nine species nested in saltcedar. These species are therefore less likely to be negatively affected by loss of native woody vegetation than riparian obligate canopy species, as long as some woody plants remain present.

The Gila forest patches supported more state-listed species than the MRG forest plots. Of the listed species at the Gila, common black-hawk and Gila woodpecker were the most specialized, and the other listed species nested in a variety of trees and shrubs. Of MRG listed species, yellow-billed cuckoo and Lucy's warbler were most specialized, nesting only in Russian olive and cottonwood, respectively. Mourning dove, the third species, nested in a variety of trees and shrubs (Smith *et al*., 2012). Although these species are capable of nesting in a variety of woody plants, nesting success may vary among tree and shrub species. For example, southwestern willow flycatchers nesting boxelder had lower rates of brown-headed cowbird parasitism than those nesting in other species at the Gila (Brodhead *et al*., 2007). Such information is needed for the other listed species to determine how their populations will respond to increases in nonnative vegetation.

Implications for conservation

Our results show that conversion from native to nonnative vegetation could decrease diversity of riparian-nesting birds. In addition, loss of certain groups of birds could alter ecosystem functions. Birds in four ecologically important orders (hawks, falcons, owls and woodpeckers) used only native trees for nest sites. Loss of native trees could therefore affect food web and nest web dynamics. A decrease in nest densities of diurnal raptors and owls would disrupt top–down control of vertebrate prey within and adjacent to the riparian forest. Because primary cavity nesters, including the state-threatened Gila woodpecker (*M. uropygialis)*, excavated only in native trees, few, if any, of these birds would likely nest in a nonnative-dominated forest. As a result, nesting opportunities for secondary cavity-nesting birds and mammals would be lost (Sedgwick, 1997; Martin *et al*., 2004).

Factors that determine balance of native and nonnative vegetation differed between our study areas. In southwestern riparian forests, nonnative invasions have resulted from changes in streamflow and geomorphology (Stromberg, 1998; Stromberg *et al*., 2009). By restricting surface flow and decreasing groundwater availability, dams and irrigation diversions limit reproduction of cottonwoods and willows along the MRG (Howe and Knopf, 1991; Molles *et al*., 1998). Increased fire frequency along this and other rivers has further encouraged the spread of nonnative species, such as saltcedar, which are better adapted to this disturbance than native species (Busch, 1995; Smith *et al*., 2009a). Without management intervention, MRG cottonwoods will continue to senesce, and nonnative species such as Russian olive and saltcedar will increase in dominance (Howe and Knopf, 1991). Under this scenario, the MRG forests would provide nest sites for many shrub and subcanopy-nesting birds, but the number of canopy and cavity nests would decline. In contrast, the stretch of Gila River we examined is less flow-restricted (Soles, 2008) and experiences fewer wildfires than the MRG. Occasional floods, shallow depth to groundwater and willow flycatcher habitat management have resulted in establishment and reproduction of native plants at our Gila study area (Boucher *et al*., 2003). Along flow-restricted western streams, human intervention in the form of pulsed dam releases, bar construction and nonnative plant removal is needed to create conditions suitable for cottonwood/willow reproduction (Cooper *et al*., 1999; Sprenger *et al*., 2002; Merritt and Poff, 2010). Such practices will maintain and restore breeding bird communities along the MRG (Farley *et al*., 1994). Several studies have shown that stands of nonnative vegetation can support large populations of birds, including threatened and endangered species (Sogge *et al*., 2008; Smith *et al*., 2009b; Paxson *et al*., 2011; Smith *et al*., 2012). These findings should not, however, overshadow the disproportionately large contributions of cottonwoods and other large trees to riparian ecosystem function.

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APPENDIX

CHARACTERISTICS OF BIRD SPECIES IN EACH NESTING GUILD ALONG THE GILA RIVER AND MIDDLE RIO GRANDE (MRG) IN NEW MEXICO.

Guild	Species	Population status[a]	Habitat status[b]	No. of nests Gila	No. of nests MRG	Nonnative use Gila (%)	Nonnative use MRG (%)
Canopy	Western wood-pewee *Contopus sordidulus*	WA	RD	94	14	1.1	0
Canopy	Cassin's kingbird *Tyrannus vociferans*	WA	GEN	47	0	2.1	—
Canopy	Summer tanager *Piranga rubra*	WA	RO	27	20	0	5.0
Canopy	Cooper's hawk *Accipiter cooperii*	WA	RD	2	34	0	0
Canopy	Western kingbird *Tyrannus verticalis*	WA	GEN	11	7	0	14.3
Canopy	Common black-hawk *Buteogallus anthracinus*	T	RO	10	0	0	—
Canopy	Swainson's hawk *Buteo swainsoni*	WA	RD	0	10	—	0
Canopy	Great-horned owl *Bubo virginianus*	WA	GEN	0	6	—	0
Canopy	American crow *Corvus brachyrhynchos*	WA	GEN	1	6	0	50.0
Canopy	Common raven *Corvus corax*	WA	GEN	1	2	0	0
Canopy	Hooded oriole *Icterus cucullatus*	SGCN	RD	2	0	50.0	—
Canopy	Red-tailed hawk *Buteo jamaicensis*	WA	GEN	1	0	0	—
Cavity	Bewick's wren *Thryomanes bewickii*	WA	RD	42	38	2.4	11.8
Cavity	European starling *Sturnus vulgaris*	WA	GEN	47	20	0	0
Cavity	Ash-throated flycatcher *Myiarchus cinerascens*	WA	GEN	15	46	0	2.2
Cavity	Northern flicker *Colaptes auratus*	WA	GEN	19	33	0	0
Cavity	Lucy's warbler *Oreothlypis luciae*	SGCN	RD	38	1	0	0
Cavity	Downy woodpecker *Picoides pubescens*	WA	GEN	0	46	—	0
Cavity	White-breasted nuthatch *Sitta carolinensis*	WA	GEN	7	11	0	0
Cavity	American kestrel *Falco sparverius*	WA	GEN	13	5	0	0
Cavity	Hairy woodpecker *Picoides villosus*	WA	GEN	0	13	—	0
Cavity	Black-capped chickadee *Poecile atricapillus*	WA	RD	0	10	—	0
Cavity	Violet-green swallow *Tachycineta thalassina*	WA	GEN	6	0	0	—
Cavity	Ladder-backed woodpecker *Picoides scalaris*	SW	GEN	3	3	0	0
Cavity	Brown-crested flycatcher *Myiarchus tyrannulus*	SW	RD	4	0	0	—
Cavity	Gila woodpecker *Melanerpes uropygialis*	T	RD	3	0	0	—
Cavity	Western screech-owl *Megascops kennicottii*	WA	GEN	1	0	0	—
Cavity	Eastern bluebird *Sialia sialis*	WA	GEN	0	1	—	0
Subcanopy/shrub	Black-chinned hummingbird *Archilochus alexandri*	WA	RD	191	527	2.1	67.8
Subcanopy/shrub	Southwestern willow flycatcher *Empidonax traillii extimus*	E	RO	619	0	4.4	—
Subcanopy/shrub	Mourning dove *Zenaida macroura*	SGCN	GEN	201	152	7.5	68.9
Subcanopy/shrub	Yellow-breasted chat *Icteria virens*	WA	RO	157	10	15.9	87.5
Subcanopy/shrub	Blue grosbeak *Passerina caerulea*	WA	RO	94	38	3.2	94.6
Subcanopy/shrub	Lesser goldfinch *Spinus psaltria*	WA	RD	111	12	0.9	60.0
Subcanopy/shrub	House finch *Carpodacus mexicanus*	WA	GEN	75	5	0	0
Subcanopy/shrub	Black-headed grosbeak *Pheucticus melanocephalus*	WA	RD	31	42	12.9	0.55
Subcanopy/shrub	Yellow warbler *Setophaga petechia*	SGCN	RO	53	0	3.8	—
Subcanopy/shrub	Yellow-billed cuckoo *Coccyzus americanus*	T	RO	48	4	4.2	—
Subcanopy/shrub	Vermilion flycatcher *Pyrocephalus rubinus*	SW	RO	46	0	4.3	—

Subcanopy/shrub	Bullock's oriole *Icterus bullockii*	WA	RD	40	1	2.5	0
Subcanopy/shrub	Spotted towhee *Pipilo maculatus*	WA	GEN	31	2	3.2	100
Subcanopy/shrub	Phainopepla *Phainopepla nitens*	SW	RD	2	27	0	22.2
Subcanopy/shrub	Abert's towhee *Melazone aberti*	T	RO	26	0	15.4	—
Subcanopy/shrub	Northern cardinal *Cardinalis cardinalis*	WA	GEN	15	0	6.7	—
Subcanopy/shrub	American robin *Turdus migratorius*	WA	GEN	12	1	0	0
Subcanopy/shrub	Plumbeous vireo *Vireo plumbeus*	WA	GEN	8	0	0	—
Subcanopy/shrub	Bell's vireo *Vireo bellii*	T	RD	6	0	0	—
Subcanopy/shrub	Lazuli bunting *Passerina amoena*	WA	RD	5	1	0	100
Subcanopy/shrub	Northern mockingbird *Mimus polyglottos*	WA	GEN	0	6	—	66.7
Subcanopy/shrub	Indigo bunting *Passerina cyanea*	WA	RD	3	3	0	66.7
Subcanopy/shrub	Bushtit *Psaltriparus minimus*	WA	GEN	0	3	—	0
Subcanopy/shrub	Greater roadrunner *Geococcyx californianus*	WA	GEN	0	3	—	100
Subcanopy/shrub	Common yellowthroat *Geothlypis trichas*	WA	GEN	2	0	50.0	—
Subcanopy/shrub	Chipping sparrow *Spizella passerine*	WA	GEN	0	2	—	50
Subcanopy/shrub	Black-billed magpie *Pica pica*	WA	GEN	0	1	—	100
Subcanopy/shrub	Western scrub-jay *Aphelocoma californica*	WA	GEN	1	0	0	—
Subcanopy/shrub	Grey catbird *Dumetella carolinensis*	WA	RO	0	1	—	100

[a]Population status designations, as listed by New Mexico Game and Fish, are endangered (E), threatened (T), sensitive (S), species of greatest conservation need (SGCN) and widespread and abundant (WA).[b]Habitat status designations, from Rich (2002), are riparian obligate (RO), riparian dependent (RD) and generalist (GEN).