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Russian olive habitat along an arid river supports fewer bird species, functional groups and a different species composition relative to mixed vegetation habitats

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ABSTRACT

The establishment and naturalization of non-native Russian olive (*Elaeagnus angustifolia*) in southwestern US riparian habitats is hypothesized to have negative implications for native flora and fauna. Despite the potential for Russian olive establishment in new riparian habitats, much of its ecology remains unclear. Arid river systems are important stopover sites and breeding grounds for birds, including some endangered species, and understanding how birds use Russian olive habitats has important implications for effective non-native species management. We compared native bird use of sites that varied in the amount of Russian olive and mixed native/non-native vegetation along the San Juan River, UT, USA. From presence/absence surveys conducted in 2016 during the breeding season, we found 1) fewer bird species and functional groups used Russian olive habitats and 2) the composition of species within Russian olive habitats was different from the composition of species in mixed native/non-native habitats. Our results suggest Russian olive may support different bird compositions during the breeding season and as Russian olive continues to naturalize, bird communities may change. Finally, we highlight the paucity of research surrounding Russian olive ecology and stress the need for rigorous studies to improve our understanding of Russian olive ecology.

1. Introduction

Invasive species can impact native species and biodiversity worldwide (Vilà et al., 2011) and predicting how native species utilize non-natives remains an important management challenge (Ortega et al., 2014). Arid ecosystems may be especially susceptible to non-native establishment due to anthropogenic changes to water availability (Stromberg, 1998), flood regimes (Stromberg et al., 2007) and nutrient levels (Davis et al., 2000). Increasing human populations (Ma et al., 2005) and climate change-induced drought (USGCRP, 2017) may further increase the establishment of non-native plants (Diez et al., 2012). Riparian areas in the arid environments of the Southwestern United States (hereafter Southwest) are particularly vulnerable, and have experienced dramatic shifts from native to non-native plant-dominated habitats (Gitlin et al., 2006).

Anthropogenic changes to river systems in the Southwestern USA, such as damming, have altered hydrologic regimes and have reduced the recruitment of native trees and shrubs, and this now facilitates non-native plant establishment (Stromberg, 1998; Cooper et al., 1999; Stromberg et al., 2007). As a result, non-native plants are common in riparian habitat along Southwest rivers (Friedman et al., 2005). Riparian habitats in arid ecosystems provide native fauna with important habitat by providing refugia from the relatively warmer and drier surrounding upland areas and opportunities for food (Naiman et al., 1993), therefore non-native plant establishment has important implications for the fauna that inhabit them.

Russian olive (*Elaeagnus angustifolia*) is a non-native tree that has become established in many Southwest riparian habitats after being introduced to the US from Europe and Asia in the late 1800s (Christiansen, 1963). Russian olive is a functionally distinct member of

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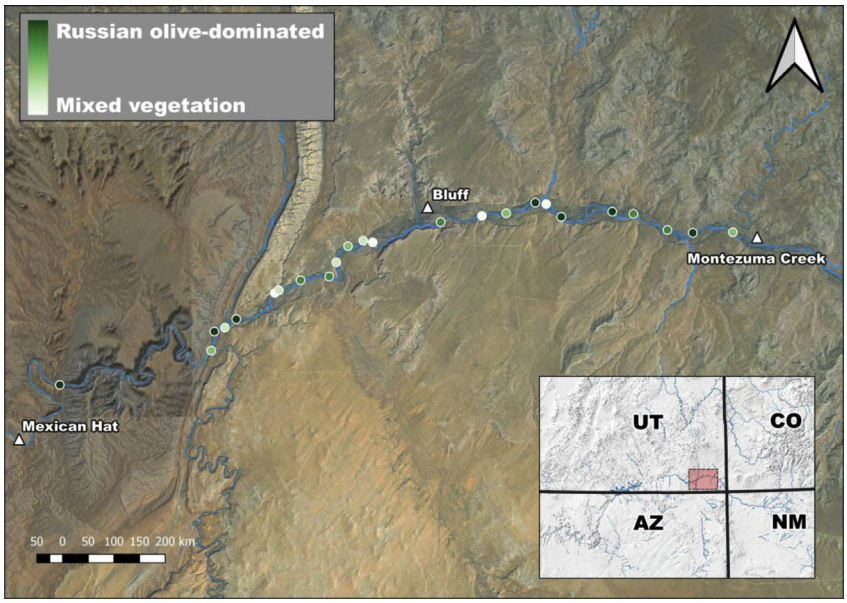

Fig. 1. Map indicating study sites along the San Juan River drainage in UT, USA (circles). Color gradient of points represents vegetation composition of each study site based on principle component (PC1) scores with darker green (black in gray-scale print) representing more Russian olive and lighter green (white in gray-scale print) representing a mix of native and non-native vegetation. For reference, Mexican Hat, Bluff and Montezuma Creek, UT are indicated by white triangles. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the Southwestern riparian plant community. Whereas most already established species (e.g. native cottonwood, *Populus fremontii*, willow, *Salix gooddinggii, Baccharis* spp. and non-native tamarisk, *Tamarix* spp.) are adapted for frequent and high intensity flood regimes by producing copious quantities of small wind-pollinated seeds and investing little in wood density (Stromberg and Merritt, 2015), Russian olive produces large seeded fruits from insect-pollinated flowers and has high wood density, suggesting adaptation to reduced or altered disturbance regimes (Katz and Shafroth, 2003). Russian olive may also be more drought tolerant than native species (see review by Katz and Shafroth, 2003) and can germinate under conditions unfavorable for native cottonwoods (*Populus deltoides*; Shafroth et al., 1995). These attributes will allow Russian olive to persist and further expand its range on regulated and unregulated rivers in the Southwest even under continued warming and drying, whereas native plant species will likely suffer. Because most wildlife in the arid Southwest rely on riparian habitat at some point in their annual cycle for food or shelter (Grinnell, 1914; Lowe, 1989; Rosenberg et al., 1991), Russian olive establishment is a legitimate concern for Southwest fauna.

Russian olive is estimated to be the fourth most dominant woody plant in western riparian areas (Friedman et al., 2005) and its extensive establishment is particularly concerning for native birds, because although only 1% of the western landscape is riparian, riparian habitats support disproportionately more breeding birds than all other western habitats combined (Anderson and Ohmart, 1984; Knopf et al., 1988). Southwest riparian habitats also support ~10x higher densities of overwintering and migratory birds than surrounding upland areas (Stevens et al., 1977). This includes two federally endangered birds, the Southwestern willow flycatcher (*Empidonax traillii extimus*) and the Yellow-billed cuckoo (*Coccyzus americanus*), whose critical habitat has been reduced and threatened by invasive plants like Russian olive (Bateman and Paxton, 2009).

Russian olive has been hypothesized to benefit wildlife generally and birds specifically because it produces fruits that may be eaten by frugivores (Borell, 1976; Knopf and Olson, 1984) and its flowers may attract insects that are consumed by insectivores. Early studies report up to 24 bird species occurring in Russian olive-cottonwood forests (Freehling, 1982). Knopf and Olson (1984) found intermediate bird richness and diversity, but higher evenness in Russian olive habitats than in native riparian or upland areas. Another study found bird richness, abundance and density was lower in Russian olive habitats relative to willow-dominated habitats (Brown, 1990). However, Fischer et al. (2012) concluded overall vegetation cover, not Russian olive cover, was the most important predictor variable of bird species richness, density and community composition in areas with extensive Russian olive cover. But birds may nest in Russian olive less than expected based on its relative availability, at least in some sites (Smith and Finch, 2014).

Bird response to Russian olive also appears to be species-specific. Black-chinned hummingbirds (*Archilochus alexandri*) commonly nest in understory Russian olive and removal forces hummingbirds to build nests in the overstory where they may experience higher nest predation risk (Smith et al., 2009). Mourning doves (*Zenaida macroura*) and yellow-breasted chats (*Icteria virens*) have been found to preferentially nest in Russian olive, while others, such as blue grosbeaks (*Guiraca caerulea*) do not (Stoleson and Finch, 2001). Willow flycatchers are more likely to experience nest predation in Russian olive (Stoleson and Finch, 2001). Primary and secondary cavity nesters have been found to be absent from Russian olive stands (Stoleson and Finch, 2001). Nest predation may be higher in Russian olive habitat due to relatively higher densities of black-billed magpies (*Pica hudsonia*; Knight and Fitzner, 1985) and American crows (*Corvus brachyrhynchos*; Gazada et al., 2002). Finally, during migration periods, Kelly et al. (2000) found marginally lower warbler richness in Russian olive-dominated sites compared to areas with more native vegetation.

To better understand the impact of Russian olive naturalization in the Southwest, we assessed bird use of habitats along a gradient of increasing Russian olive cover. The objectives of our study were to compare bird 1) species richness, 2) functional groups and 3) species composition in sites that varied in the amount of Russian olive. Insight into how birds utilize Russian olive is important for understanding how non-native plants in arid ecosystems, which may continue to proliferate, impact native fauna.

2. Methods

2.1. Study area

We conducted our study along the San Juan River, from Montezuma Creek, UT, USA to Mexican Hat, UT, USA where Russian olive is extensively naturalized (Fig. 1). Because of private and Navajo Nation land ownership along the San Juan River, our study sites were restricted to public lands managed by the Bureau of Land Management on the north bank of the river (Table 1). In 2015, we established 24 study sites

Table 1
Study sites, location data (UTM E and N zone 12N), site area (ha), transect length (km), first principle component score (PC1 score, 34% of variation) based on overstory and understory vegetation composition, bird species richness (richness), and number of functional groups present in each site based on presence/absence surveys along the San Juan River, UT, USA during the breeding season in June and July 2016.

Site Name	UTM E	UTM N	Area	Transect length	PC1 score[a]	Richness	Functional groups
3 Below	645939	4125655	19.6	1.5	−2.44	9	4
Big Stick	614067	4119092	14.4	2	−2.85	16	5
Butler Island	618367	4121828	1.61	0.4	1.79	6	3
Chinle Island	613862	4117818	2.21	0.4	0.06	5	3
Comb Wash	615528	4119909	8.75	1.6	−1.87	7	4
First Cliff	637172	4126722	8.9	0.7	−1.07	7	2
Foot Bridge	629137	4126374	19.5	1.4	0.19	12	4
Heron Island	633509	4126961	26.6	2.3	−1.41	13	4
Lime Creek	644248	4125851	5.89	1.8	−2.76	8	4
Lower Bluff	603770	4115532	2.6	0.4	3.34	5	1
Lower Butler Wash	624622	4125022	55.8	4.2	3.29	14	5
Lower Comb Wash	618094	4121652	8.66	1.2	2.08	6	3
Lower Gold Mine	614769	4119351	36.1	2.5	−1.04	14	3
Lower McCracken Wash	621717	4122744	52.2	4.5	−2.64	14	4
McCracken Wash	640572	4127070	34	3	−1.19	16	4
Cow Patch	641982	4126920	19	1.6	−1.83	9	3
Montezuma Creek	648608	4125695	9.6	0.9	−0.14	8	6
Recapture Creek	635447	4127668	13.3	1.2	−2.18	20	6
Sand Island	622971	4124763	16.1	1.3	−0.13	14	4
Upper Butler Wash	619808	4122497	48	4.1	−1.07	17	4
Upper Gold Mine	622186	4123696	12	1.4	2.08	8	3
Upper Nelson	631893	4126782	10.5	1.3	3.8	7	3
Upper Recapture	636171	4127576	16.6	2	3.8	7	3
Upper Sand Island	623989	4125132	9.3	1.4	1.62	14	4

[a] PC1 scores > 0 represent sites with more overstory and understory Russian olive.

in riparian areas that varied in amount of Russian olive cover (Table S1). Although some sites in our study area were predominately Russian olive, no site was purely native vegetation, and instead was mix of native (cottonwood and willow) and non-native vegetation (tamarisk and Russian olive). We quantified both the overstory and understory vegetation composition of our study sites. As in similar studies (i.e. Mahoney et al., 2017), two observers independently estimated the overall percentage of overstory plant cover to the nearest 5% from a high point overlooking each study site (Table S1). At all sites, overstory plants were cottonwood and/or Russian olive. One observer also estimated the overall percentage of understory cover to the nearest 5% while walking the presence/absence survey transects (Table S1). The understory generally comprised of some combination of seven plant species: Russian olive, cottonwood, coyote willow, tamarisk, Russian knapweed (*Rhaponticum repens*), rabbitbrush (*Ericameria nauseosa*) and sagebrush (*Artemisia tridentata*). We did not quantify herbaceous ground cover at our study sites. Prior to site categorization, observers received standardized US Fish and Wildlife Service training to ensure that cover estimates were consistent between observers. In rare cases, the observer's cover estimates did not agree, and the midpoint (to the closest 5%) of the estimates was used.

2.2. Bird presence/absence surveys

To compare bird use of habitats with varying amounts of Russian olive during breeding periods, we conducted presence/absence surveys during morning hours (0500–1100) on clear days with low wind from June to July 2016 simultaneously during routine willow flycatcher and yellow-billed cuckoo surveys. In each study site, we established non-linear, 100 m wide belt-transects that varied in length (Table 1) and were proportional to the area (ha) of the study site ($R^2 = 0.9$, $p < 0.0001$, Table 1). Each transect was arranged up-stream to down-stream and traversed through the habitat (Fig. S1) so that all areas of the study site were traveled through. We recorded any bird species that was seen or heard within our belt transect while traveling through the habitat or while conducting playback surveys for willow flycatcher and yellow-billed cuckoos. If an observer detected a bird species during at least one survey period we considered that bird species to be present at the site. We considered a species to be absent from a site if no observers detected that species during either survey period. To minimize observer bias, different observers surveyed each site every survey period. Due to the density of vegetation we did not record individual bird detections or make distance estimates, so densities and diversity indices could not be calculated. Birds not directly using the habitat, such as birds flying overhead, were not recorded.

We visited each site two times (one survey/month in June and July) for a total of 68 h (31 and 37 h in survey 1 and 2, respectively). Because survey effort was proportional to study site size (ha) of study site ($R^2 = 0.31$, $p = 0.005$) and transect length (km, $R^2 = 0.27$, $p = 0.009$) and effort was similar in each survey period (Welch's *t*-test: $t = -0.71$, $p = 0.48$), we used species richness (number of species in each site) in subsequent analyses.

2.3. Data analysis

We performed all analyses in program R (v. 3.4.0, R Development Core Team, 2015). We characterized our study sites using an unbiased and unsupervised approach by summarizing the understory and overstory vegetation composition with a Principle Components Analysis (PCA). For our analyses, we retained all PCs with eigenvalues > 1 and those required to explain cumulatively 50% or more of the variation.

To test for differences in bird species richness in sites with varying amounts of Russian olive, we calculated simple species richness by summing the number of species detected at each site. We then used a linear regression to assess the relationship between bird species richness and vegetation composition, represented by the principle component that explained the most amount of variation (PC1). To assess the relationship between bird functional groups and vegetation composition, each bird species was assigned a functional group based on the classification during the breeding season from the Birds of North America (bna.org, accessed 27 December 2018). We then summed the number of unique functional groups for each site and used a linear regression to test the relationship between functional groups and vegetation PC1. We evaluated these models under the null hypothesis that

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Table 2
Bird species detected, proportion of sites in each survey where the species was detected, each species' functional group and migratory status in sites along the San Juan River, UT, USA based on presence/absence surveys during June and July 2016 (survey 1–2 respectively).

Species	Survey 1	Survey 2	Functional group[a]	Migratory Status[b]
American Robin *Turdus migratorius*	0.04	0.13	Generalist	Short Distance Migrant
Ash-throated flycatcher *Myiarchus cinerascens*	0.33	0.50	Insectivore	Neotropical Migrant
Black-billed magpie *Pica hudsonia*	0.04	0.08	Generalist	Permanent Resident
Black chinned hummingbird *Archilochus alexandri*	0.25	0.33	Nectarivore	Partial Migrant
Bell's vireo *Vireo bellii*	0.00	0.04	Insectivore	Neotropical Migrant
Blue-gray gnatchatcher *Polioptila caerulea*	0.33	0.33	Insectivore	Neotropical Migrant
Brown-headed cowbird *Molothrus ater*	0.42	0.71	Generalist	Short Distance Migrant
Black-headed grosbeak *Pheucticus melanocephalus*	0.50	0.67	Generalist	Neotropical Migrant
Blue grosbeak *Passerina caerulea*	0.25	0.46	Generalist	Neotropical Migrant
Black phoebe *Sayornis nigricans*	0.08	0.08	Insectivore	Permanent Resident
Black-throated sparrow *Amphispiza bilineata*	0.00	0.04	Generalist	Permanent Resident
Bushtit *Psaltriparus minimus*	0.00	0.04	Insectivore	Permanent Resident
Canyon wren *Catherpes mexicanus*	0.04	0.04	Insectivore	Permanent Resident
Cedar Waxwing *Bombycilla cedrorum*	0.13	0.13	Frugivore	Neotropical Migrant
Common raven *Corvus corax*	0.08	0.21	Generalist	Permanent Resident
Common yellowthroat *Geothlypis trichas*	0.08	0.17	Insectivore	Neotropical Migrant
Cooper's hawk *Accipiter cooperii*	0.08	0.29	Carnivore	Partial Migrant
Gambel's quail *Callipepla gambelii*	0.00	0.08	Granivore	Permanent Resident
Great blue heron *Ardea herodias*	0.04	0.13	Carnivore	Permanent Resident
Great horned owl *Bubo virginianus*	0.00	0.04	Carnivore	Permanent Resident
House finch *Haemorhous mexicanus*	0.13	0.29	Granivore	Short Distance Migrant
Indigo bunting *Passerina cyanea*	0.04	0.04	Insectivore	Neotropical Migrant
Lazuli bunting *Passerina amoena*	0.08	0.08	Insectivore	Neotropical Migrant
Lesser goldfinch *Spinus psaltria*	0.17	0.33	Granivore	Short Distance Migrant
Lucy's warbler *Oreothlypis luciae*	0.33	0.50	Insectivore	Short Distance Migrant
Mountain chickadee *Poecile gambeli*	0.08	0.08	Insectivore	Permanent Resident
Mourning dove *Zenaida macroura*	0.38	0.54	Granivore	Short Distance Migrant
Northern flicker *Colaptes auratus*	0.04	0.25	Insectivore	Short Distance Migrant
Peregrine Falcon *Falco peregrinus*	0.04	0.04	Carnivore	Neotropical Migrant
Plumbeous vireo *Vireo plumbeus*	0.13	0.42	Insectivore	Neotropical Migrant
Redtail hawk *Buteo jamacensis*	0.04	0.13	Carnivore	Partial Migrant
Rock wren *Salpinctes obsoletus*	0.00	0.04	Insectivore	Permanent Resident
Spotted sandpiper *Actitis macularis*	0.04	0.04	Insectivore	Neotropical Migrant
Spotted towhee *Pipilo maculatus*	0.88	1.00	Generalist	Neotropical Migrant
Turkey vulture *Cathartes aura*	0.04	0.04	Scavenger	Neotropical Migrant
Violet green swallow *Tachycineta thalassina*	0.08	0.17	Insectivore	Neotropical Migrant
White-crowned sparrow	0.00	0.04	Generalist	Short Distance Migrant

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Table 2 (*continued*)

Species	Survey 1	Survey 2	Functional group[a]	Migratory Status[b]
Zonotrichia leucophrys				
Western wood-pewee	0.04	0.08	Insectivore	Neotropical Migrant
Contopus sordidulus				
Wild turkey	0.00	0.04	Generalist	Permanent Resident
Meleagris gallopavo				
Yellow-breasted chat	0.75	0.88	Insectivore	Neotropical Migrant
Icteria virens				
Yellow warbler	0.83	0.92	Insectivore	Neotropical Migrant
Setophaga petechia				
Yellow-headed blackbird	0.08	0.08	Insectivore	Neotropical Migrant
Xanthocephalus xanthocephalus				
Total species richness	42			

[a] Foraging guild assigned based on Birds of North America (bna.org): Insectivore (insect-eating), granivore (seed-eating), generalist (plant- and insect-eating), frugivore (fruit-eating), and carnivore (meat-eating).

[b] Migratory status assigned based on Birds of North America: Neotropical migrant (over-winters in Central and/or South America), short distance migrant (over-winters at lower North American latitudes), partial migrant (over-winters in lower North American latitudes and higher Central American latitudes), permanent resident (present year-round).

if vegetation composition had no effect on bird presence/absence, there would be no linear relationship (i.e. flat regression line).

We quantified the species composition of each site using a non-metric multidimensional scaling (NMDS) analysis of the bird presence/absence data using Euclidean distances in the vegan package for R (Oksanen et al., 2013). NMDS is similar to a PCA in that it reduces multivariate data to a few axes that explain the most variation in the dataset. We then plotted NMDS axis 1 and 2 and conducted a permutational analysis of variance (PERMANOVA) using Euclidean distances to test for differences in species composition. For this analysis, we grouped sites into two categories based on the vegetation PC1 scores (either mixed or Russian olive-dominated).

3. Results

3.1. Habitat characteristics

From our PCA of the vegetation composition of each site, the first four PCs had eigenvalues > 1 and explained ~80% of the variation (Table S2). PC1 explained ~34% of the variation in vegetation composition and our analyses are based on these scores. Negative PC1 scores are representative of sites with more understory tamarisk, understory cottonwood and overstory cottonwood (Table S2, i.e. mixed habitats). Positive PC1 scores are representative of sites with more Russian olive overstory and Russian knapweed ground cover (Table S2, i.e. Russian olive-dominated habitats). Therefore for our analyses of community composition, sites with negative PC1 scores were categorized as “mixed sites” and sites with positive PC1 scores were categorized as “Russian olive-dominated sites.”

3.2. Species richness, functional groups and species composition

Overall, we detected 42 bird species at least once during our surveys (Table 2). We found richness was negatively correlated with vegetation PC1 (Fig. 2. $R^2 = 0.18$, $p = 0.04$). The number of functional groups detected in each site also declined with increasing vegetation PC1 (Fig. 2. $R^2 = 0.2$, $p = 0.03$).

On average, species composition in mixed habitats significantly differed from the composition in Russian olive-dominated habitats as modeled by our NMDS analysis (Fig. 3, PERMANOVA: pseudo-$F_{1,22} = 1.7$, $p = 0.03$, NMDS stress = 0.09, $k = 3$). Positive NMDS axis 1 scores were associated with more detections of Black-chinned hummingbirds (*Archilochus alexandri*), White-crowned sparrows (*Zonotrichia leucophrys*), Canyon wrens (*Catherpes mexicanus*), Black phoebes (*Sayornis negricans*), Black-throated sparrows (*Amphispiza bilienata*), Peregrine falcons (*Falco peregrinus*), Lazuli buntings (*Passerina amoena*), and Common yellowthroats (*Geothlypis trichas*, Table S3). Negative NMDS axis 1 scores were associated with Turkey vultures (*Cathartes aura*), Mountain chickadees (*Poecile gambeli*), Cedar waxwings (*Bombycilla cedrorum*), Wild turkeys (*Meleagris gallopavo*), Lesser goldfinches (*Spinus psaltria*), Western wood-pewees (*Contopus sordidulus*), Violet-green swallows (*Tachycineta thalassina*), and American robins (*Turdus migratorus*, Table S3). Positive NMDS axis 2 scores were associated with more detections of Yellow-headed blackbirds (*Xanthocephalus xanthocephalus*), Black-throated sparrows, and Great-blue herons (*Ardea herodias*), while negative NMDS axis 2 scores were associated with more detections of Bushtits (*Psaltriparus minimus*), Northern flickers (*Colaptes auratus*), Common ravens *(Corvus corax*) and Blue-gray gnatcatchers (*Polioptila caerulea*, Table S3).

4. Discussion

4.1. Bird use of Russian olive

In our study, Russian olive habitat supported different bird assemblages compared to mixed habitats based on species richness, species composition, and functional group analyses during breeding periods. Riparian vegetation in the Southwest is important habitat for native birds (van Riper et al., 2008), and our results suggest that fewer bird species occupy riparian sites invaded by non-native Russian olive and that the species composition of birds within the habitat is different than that of mixed habitats. Given the Southwest is projected to become more arid (Seager et al., 2007; GRPCC, 2017) and Russian olive's ability to germinate under drought conditions (Shafroth et al., 1995), it is important to understand the value of Russian olive relative to other habitats in regards to native wildlife.

Structural complexity has been shown to increase bird diversity in the Southwest (Rice et al., 1984). We hypothesize that mixed sites support higher bird richness and functional groups for two reasons. First, mixed sites may be more structurally complex which may provide more nesting substrate. In our study area, mixed sites often had more understory vegetation, which would benefit species that nest in the sub-canopy, such as black-chinned hummingbirds and yellow-breasted chats (Smith et al., 2009). Our study sites that were dominated by Russian olive often had high percentages of Russian knapweed ground cover, which was typically < 0.25 m in height, so this may have limited nesting opportunities for sub-canopy and ground nesting species and may have forced species to nest in the Russian olive-dominated canopy where nest predation may be higher for at least some species (Stoleson and Finch, 2001).

Secondly, mixed vegetation habitats may provide more food resources than in Russian olive-dominated habitats. Insectivorous birds in

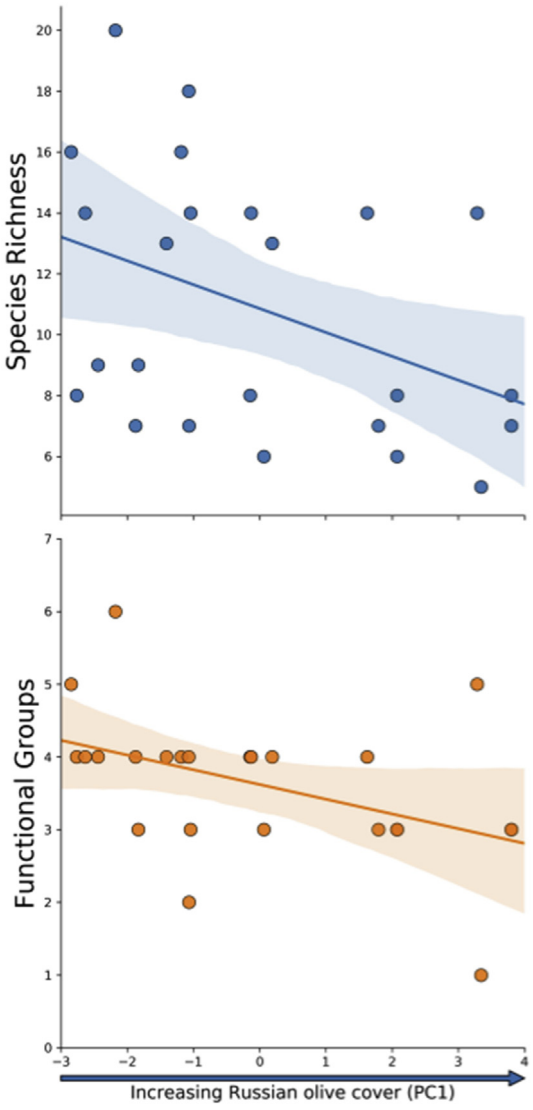

Fig. 2. Top panel: Scatter plot of vegetation PC1 (34% of variation) and bird species richness. Positive PC1 scores represent more Russian olive at the study site. Species richness declined with increasing Russian olive cover ($R^2 = 0.18$, $p = 0.04$). Bottom panel: Scatter plot of vegetation PC1 (34% of variation) and number of functional groups at each study site. The number of functional groups declined with increasing Russian olive cover ($R^2 = 0.2$, $p = 0.03$). Shaded area around regression lines represents 95% bootstrapped confidence level.

particular often respond positively to increased habitat structure (van Riper et al., 2008). Mixed vegetation sites may also support more diverse food resources, whereas in Russian olive-dominated habitats, arthropods may be restricted to those only associated with Russian olive. Although little is known regarding the arthropod communities associated with Russian olive, Katz and Shafroth (2003) present data from an unpublished study of the San Juan River that found similar arthropod species richness and intermediate densities on Russian olive relative to cottonwood, the dominant native tree at our sites. A more recent study found no difference in insect abundance between Russian olive and native Woods' rose (*Rosa woodsii*) and Saskatoon (*Amelanchier alnifolia*, Collette and Pither, 2015). Many gaps exist in our understanding of Russian olive ecology (Bateman and Paxton, 2009), and a better understanding of the arthropod communities associated with Russian olive is important to evaluate the overall value of Russian olive on the landscape.

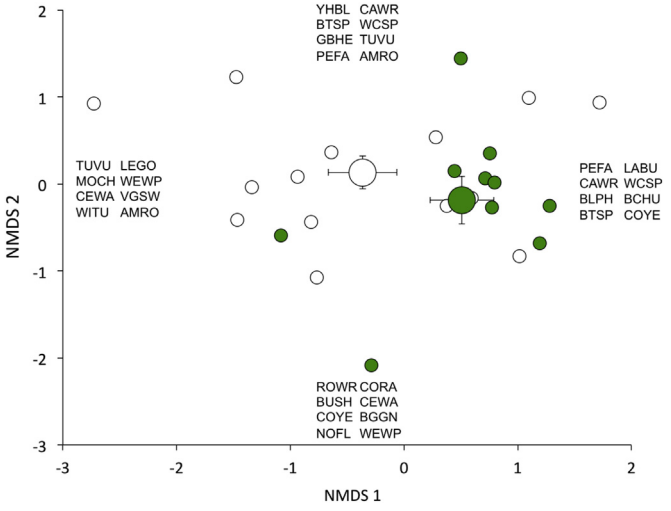

Fig. 3. Scatter plot representing bird species composition in mixed vegetation (white points) and Russian olive-dominated sites (green points, black in gray-scale print) as modeled using a non-metric multidimensional scaling (NMDS) analyses (stress = 0.09, k = 3). Larger dots represent mean (± SE) NMDS 1 and 2 scores. Bird species associated with each axis are indicated using alpha codes. Species composition between habitats was significantly different (PERMANOVA: pseudo-$F_{1,22} = 1.7$, $p = 0.03$). Sites were categorized based on a principle components analysis of overstory and understory vegetation composition. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.2. Parallels with non-native tamarisk

Another non-native in the Southwest, tamarisk, is widespread and may have both facilitative and suppressive ecological influences (reviewed in Stromberg et al., 2009) depending upon the ecological context within which it occurs. Early studies of avian use of tamarisk suggested it is unsuitable habitat for native birds. Anderson and Ohmart (1984) found lower bird densities in tamarisk-dominated habitat along the lower Colorado River. Ellis (1995) found fewer avian guilds in tamarisk-dominated habitat than in native-dominated habitat. However, a later study on the Pecos River found higher avian abundance in tamarisk-dominated habitat (Hunter et al., 1988). Tamarisk presence below Glen Canyon Dam in Arizona has increased bird populations, as compared to pre-tamarisk habitat (Brown and Trosset, 1989), although at these sites overall vegetation increased. During migration, birds may respond best to a mixture of native and tamarisk vegetation, suggesting a tamarisk threshold (van Riper et al., 2008). It is becoming increasing accepted that birds occupy tamarisk-dominated habitat (Hunter et al., 1988; Ellis, 1995; van Riper et al., 2008; Mahoney et al., 2017), but the relative value of tamarisk habitat continues to be debated (Dudley and Deloach, 2004; Sogge et al., 2008). Both tamarisk and Russian olive have been established in North America since the early 1800s, and co-occur in many areas, including the San Juan River, however tamarisk has received disproportionally more research attention.

4.3. Future research and implications for Russian olive management

We caution that occupancy is not necessarily an indication of habitat quality (van Horne, 1983), and we stress the need for studies to assess densities, abundances and nest success of bird communities between habitats. Although we found fewer species and functional groups in Russian olive habitats, it is important to note that these study sites were not depauperate of native birds. Therefore, in the absence of active restoration, complete removal of Russian olive may not be the best management practice to maintain habitat for native birds. Previous tamarisk research has made similar conclusions (van Riper et al., 2008). The cost of non-native species removal is often expensive, so complete

eradication of Russian olive may also be cost prohibitive. For example, tamarisk removal in the Southwest is estimated at $1,400 to $1,700/ha (McDaniel and Taylor, 2003) and will denude areas critical to native fauna of vegetation. Therefore, to maintain habitat for native fauna, prioritized removal, followed by smaller-scale restoration, may be a more effective management technique in the Southwest.

5. Conclusions

Climate change is expected to increase drought in the Southwest (Seager et al., 2007; USGCRP, 2017), which is likely to advantage more drought-tolerant species, including non-natives (Diez et al., 2012). Anthropogenic changes to flood regimes and ground water tables further exacerbate reductions in native recruitment rates by limiting the disturbance and seasonality of moist substrate necessary to germinate many native trees (Stromberg, 1998). Because riparian habitats offer native fauna with refugia from surrounding warmer and drier upland areas (Naiman et al., 1993), understanding how native fauna respond to vegetation shifts to non-native dominance has important implications for maintaining faunal communities in arid ecosystems.

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Appendix A. Supplementary data

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