Hindawi Publishing Corporation
Journal of Insects
Volume 2013, Article ID 561617, 10 pages
http://dx.doi.org/10.1155/2013/561617

Research Article

Butterfly Assemblages Associated with Invasive Tamarisk (*Tamarix* spp.) Sites: Comparisons with Tamarisk Control and Native Vegetation Reference Sites

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Received 11 March 2013; Revised 13 June 2013; Accepted 14 July 2013

Academic Editor: Benjamin Hoffmann

We studied butterfly assemblages at six types of riparian landscapes in five different watersheds in the southwestern United States ($n = 34$ sites). Sites included exotic-invasive *Tamarix ramosissima* (tamarisk) dominated sites; sites where tamarisk was controlled, but not actively revegetated; sites revegetated with upland plants; sites where control was followed with riparian plant revegetation; native riparian vegetation sites; and sites that were a mixture of native and tamarisk vegetations. Local butterfly species were linked regionally by identifying species consisting of more sensitive butterflies that are less resilient to vegetation changes and environmental perturbations and then identifying a subgroup that was reported from all watersheds. This allowed for a regional assessment relevant to all watersheds. Significant differences were found between the abundance of these in-common disturbance sensitive species at different landscapes. Sites where tamarisk was removed without restoration had butterfly metrics similar to the low values at tamarisk sites. The assumption that tamarisk removal is sufficient to recover sensitive species was not true in cases we examined. Soil moisture and riparian condition were identified as important variables associated with abundance of more sensitive butterfly species. Results support the importance of reinstating stream-flow regimes and suggest active restoration of sites if sensitive riparian wildlife species are desired.

1. Introduction

Exotic plants can impact ecosystems through changes in fire regimes and hydrological cycles, hybridization with native species [1], displacement of native plants [2], and reductions in energy availability for native food webs [3]. Riparian ecosystems may be especially vulnerable to negative changes caused by invasives because of the ability of water to spread alien plant materials [4].

Tamarisks (*Tamarix*: Tamaricaceae), native to southern Eurasia, are invasive in the western United States and have replaced native plant communities in 470,000 to 650,000 ha of primarily riparian floodplain habitat in the western USA [5]. Tamarisk eradication and control projects are regularly undertaken for a variety of reasons (e.g., [6]), often with the goal of improving wildlife habitat [7].

Recognized data gaps for effects of tamarisk on wildlife include comparisons of tamarisk-invaded habitats and tamarisk removal sites with native riparian vegetation sites [8]. Studies examining effects of tamarisk and tamarisk control on wildlife have generally focused on single watersheds [9] and data is lacking for more widespread understanding of wildlife responses to affected landscapes. In the absence of these data, considerable debate exists around impacts to wildlife that occur with tamarisk control (e.g., [10–12]). Specifically, controversy exists with efforts to control tamarisk that may have negative effects on the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*), a bird which nests in riparian vegetation, including tamarisk [13]. Assessments of exotic plant impacts on biota are needed at regional and national scales to allow for broad interpretations of patterns and for evaluation of landscape restoration effectiveness. Many management issues are believed to become clearer at large spatial scales [14]. However, large scale assessments are often impeded by methodological problems, and it is recognized that spatial and physiographic variation impacts the ability to compare biological data at larger scales (e.g., [15]). But, despite these concerns, syntheses of biological data from across different watersheds have been successful in the past when in-common biota are used in a regional context (e.g., [16]).

Butterflies are a wildlife group that may be useful in the study of tamarisk environments. Butterflies are important to terrestrial ecosystem processes such as pollination and also are phytophagous insects that play a role in transfer of plant energy to higher trophic levels [17]. Butterflies have been used as indicators for landscape conservation [18], logging impacts [19], and wetland types [20], and butterflies appear to be effective indicators of riparian habitat quality [21], in part because some butterflies are host-plant specific. Some butterflies may also be widespread enough to allow for comparisons of sites from different watersheds.

We used native vegetation reference sites to evaluate the effectiveness of management activities on butterfly assemblages at five different watersheds in the southwestern United States. Our research focused on how native riparian vegetation butterfly assemblages compared with those associated with tamarisk, tamarisk control, and restoration sites. Local butterfly species were linked regionally by identifying species sensitive to anthropogenic disturbance and then identifying a subgroup of these that were reported from all watersheds. This allowed for comparison of all sites and made regional comparisons using the same assessment endpoint possible. We also examined environmental variables and their relationship with butterfly metrics.

We hypothesized that native vegetation sites would have highest butterfly metric values and have similarities with mixed vegetation and revegetation sites. We expected tamarisk sites and sites where tamarisk was controlled, but without revegetation, to have relatively low butterfly metric values.

2. Study Sites

We selected sites in 5 different lowland watersheds including the Arkansas River in Colorado, Canadian River in Texas, Las Vegas Wash in Nevada, and Pecos and Rio Grande Rivers in New Mexico. Sites and landscape categories (Table 1) were, in most cases, identified by land managers or other investigators with experience in the locations. Importantly, for comparison purposes, most systems contained a variety of landscape categories so as to allow for watershed contrasts within the region. Sites were associated, except for some portions of the Canadian River, with perennial flowing water. In many areas tamarisk has likely invaded because of altered hydrology associated with damming or diverting of rivers (e.g., [13]).

Landscape categories included native woody vegetation (native vegetation) ($n = 7$), a mixture of native and exotic woody vegetation (mixed) ($n = 5$), sites revegetated with riparian plants (revegetated-riparian) ($n = 4$), those revegetated with upland plants (revegetated-upland) ($n = 3$), tamarisk sites ($n = 6$), and sites where tamarisk was removed (treatment) ($n = 9$) but not actively revegetated with native plants. Treatments included burning, plowing, both burning and plowing, release of biocontrol agents, and a single site where the tamarisk understory below a native vegetation canopy was mechanically removed. Native vegetation sites typically contained cottonwood (*Populus* spp.) and willows (*Salix* spp.) with other woody understory plants often common (e.g., *Baccharis*). Tamarisk made up ≤10% of cover at native vegetation sites. Mixed sites contained native vegetation but also contained, on average, 34 ± 4% (SE) tamarisk cover. Revegetated-riparian sites also contained small amounts of tamarisk, and visual estimates of tamarisk averaged 20 ± 5% (SE). Revegetated-upland sites (39 ± 9% (SE)) had levels of tamarisk cover similar to that found at mixed sites (34 ± 4% (SE)). Both tamarisk (57 ± 6% (SE) tamarisk cover) and treatment (48 ± 7% (SE) tamarisk cover) sites had relatively similar levels of tamarisk cover. This was likely the result of regrowth at sites where tamarisk had been removed.

3. Methods

3.1. Butterflies. Species richness and abundance data were totaled from three surveys within a given year and summarized for each site. Three subsamples corresponding to different species flight periods (March/May, June/July, and August/September) were collected and used to describe the annual butterfly community. Data was collected from sites in either 2005 or 2006. Two different days were spent sampling butterflies and other variables at each site for 1.5 hours per day per person during each flight period. The three flight periods totaled to a sampling period of 9 hours per site. We counted individual butterflies during timed searches to provide data on both species presence and an index of abundance, with species richness and abundance summed across the year. Most butterflies were identified immediately by sight. Sweep nets were used for verification or identification of suspect species. We confined sampling to 2-ha sites that were resampled during each successive visit. Integrating data required similar sampling effort at sites because differences in effort affect many biological metrics [15].

Similar to the "checklist" methodology of Royer and others [22], we searched the entire 2-ha site for butterflies and were not confined to set transects. Two years of sampling were needed to increase sample size of the various landscapes, with individual sites sampled in only one of the two years. All landscape categories were sampled in both years.

3.2. Nectar Resources and Plant Richness. During butterfly surveys, we estimated the number of open flowers or inflorescences used as nectar sources by butterflies. Scott [23] indicated that there is little specificity in selection of flowers for nectaring; however, there are limits related to proboscis length. Therefore, flowers with large corolla depths, such as *Datura,* were not included in counts.

Although not a direct measure of nectar, Holl [24] reported a linear relationship between amount of nectar and number of inflorescences and suggests little gain in information from sugar quantification from nectar collection. Sampling took place within a 4-meter diameter circle at disjunct locations every 15–20 minutes during a survey

Table 1: Information associated with butterfly sampling sites. Most scientific names for plant taxa are identified in the text. Others are in footnotes below the table. Sites in CO and NM were sampled in 2005 while those in NV and TX were sampled in 2006.

River and counties where sites were located	Site code (initial letters correspond to the type of site)[a]	State	Easting/northing	Site characteristics	Flooding regime
Arkansas Pueblo County	NV-ARK-1	CO	13N0509892 4240492	Native woody vegetation.	Evidence of riparian processes and overbank flow.
	NV-ARK-2	CO	13N0511502 4238803	Native woody vegetation. Understory of reed canary grass[b] with thistles[c] coming in.	Evidence of riparian processes and overbank flow.
	NV-ARK-3	CO	13N0535655 4334008	Native woody vegetation.	Evidence of riparian processes and overbank flow.
	MIX-ARK-1	CO	13N0506741 4242669	Tamarisk very common, native woody vegetation mostly along rivers edge.	Fluctuations in hydroperiod, overbank flow during moderate flow events.
	MIX-ARK-2	CO	13N0525439 4235066	Mostly tamarisk with a few large senescent cottonwood. Some willow and small cottonwood in site. Knapweed common.	Fluctuations in hydroperiod, overbank flow during moderate flow events. Most of the flood-prone area confined by barriers.
	TAM-ARK-1	CO	13N0522352 4231526	A relatively narrow strip of tamarisk. A few small stature cottonwoods are present.	Evidence of riparian processes and overbank flow.
	TRT-ARK-1	CO	13N0507833 4241961	Root plowed to remove tamarisk. Weedy herbaceous plants common and tamarisk beginning to cover site again	Site sustained by natural water source, flood-prone area confined by barriers.
	TRT-ARK-2	CO	13N0525188 4235609	Tamarisk biocontrol agent *Diorhabda* release in 2001. Initial evidence of defoliation in 2003.	No evidence of overbank flows, flood-prone area confined by barriers.
Blue (Canadian watershed)	NV-CAN-1	TX	14S0258651 3956428	Native woody vegetation.	Evidence of riparian processes and overbank flow.
Canadian Carson, Hutchinson, Moore, and Potter Counties	NV-CAN-2	TX	14S0249539 3933708	Native woody vegetation. Park like.	Evidence of riparian processes and overbank flow.
	MIX-CAN-1	TX	14S0244314 3934875	Mostly tamarisk of small stature. *Baccharis* and Common reed are common at site.	Site sustained by natural water source, flood-prone area confined by barriers.
	TAM-CAN-1	TX	14S0253823 3941401	Dense mature tamarisk, understory is mostly kochia.	Site subject to fluctuations in flow, flood-prone area is confined.
	TRT-CAN-1	TX	14S0249678 3935561	Burned. Tamarisk is coming back vigorously. Undergrowth dominated by common reed and coyote willow[d].	Site subject to fluctuations in flow and overbank flow.
	TRT-CAN-2	TX	14S0255947 3941807	Burned and root pulled in 2003.	No evidence of riparian processes, no opportunity for overbank flows except in extreme events.
Las Vegas Wash Clark County	MIX-LVW-1	NV	11S0677388 3998831	Tamarisk and some weedy vegetation, few cottonwoods and mesquite. Tamarisk seedlings are common.	Site contains evidence of riparian processes, overbank flow during moderate flow events.
	RER-LVW-1	NV	11S0681529 3995320	Native woody revegetation. Alkali heliotrope is common but spotty. Control structure is present.	Evidence of riparian processes and overbank flow.
	RER-LVW-2	NV	11S0682033 3995392	Native woody revegetation. Common reed in site. Alkali heliotrope is common. Control structure is present.	Evidence of riparian processes and overbank flow.
	RER-LVW-3	NV	11S0682452 3795488	Control structure is present, native woody vegetation (willows) moving into site. Common reed abundant.	Evidence of riparian processes and overbank flow.

Table 1: Continued.

River and counties where sites were located	Site code (initial letters correspond to the type of site)[a]	State	Easting/northing	Site characteristics	Flooding regime
	REU-LVW-1	NV	11S0677707 3997928	Upland revegetation (quailbrush[e] interspersed with mesquite and *Acacia* sp.) with narrow band of tamarisk next to Wash.	No evidence of riparian processes, cut banks prevent overbank flow.
	REU-LVW-2	NV	11S0683368 3995895	Upland revegetation (mesquite and saltbush) with narrow band of riparian obligates next to Wash.	No evidence of riparian processes, cut banks prevent overbank flow except during moderate flow events.
	TAM-LVW-1	NV	11S0678114 3997545	Tamarisk mostly along Wash.	No evidence of riparian processes, channel incised so little opportunity of overbank flows.
Pecos Eddy County	TAM-PEC-1	NM	13S0564386 3610016	Tamarisk with understory of kochia.	No evident source of water supply, no opportunity for overbank flows.
	TRT-PEC-1	NM	13S0564086 3621134	Tamarisk sprayed with herbicide (Arsenal) in 2003. Kochia sparse.	No evidence of riparian processes, no opportunity for overbank flooding.
	TRT-PEC-1	NM	13S0561714 3607693	Mowed tamarisk. Near monoculture of kochia.	No evidence of riparian processes because of cut bank, overbank flow only in extreme events.
Rio Grande Socorro and Valencia Counties	NV-RIO-1	NM	13S035471 3728472	Native woody vegetation. Mostly small diameter Goodings willow[f] with understory of tamarisk and *Baccharis*. A few small cottonwoods are present.	Evidence of riparian processes and overbank flow.
	NV-RIO-2	NM	13S0307597 3715170	Native woody vegetation.	Site subject to fluctuations in flow, overbank flooding in moderate flow events.
	MIX-RIO-1	NM	13S1341506 3849356	Native woody vegetation, understory of tamarisk	Evidence of riparian processes and overbank flow.
	RER-RIO-1	NM	13S0341184 3841183	Revegetation site with some natural vegetation, topography altered for silvery minnow habitat.	Site subject to fluctuations in flow, overbank flow in moderate events.
	REU-RIO-1	NM	13S0313962 3727712	Upland revegetation site. Planted with saltbush[g] and quailbrush. Kochia common.	No evidence of riparian processes, no opportunity for overbank flooding.
	TAM-RIO-1	NM	13S0330010 3794426	Tamarisk with *Baccharis* understory.	No evidence of riparian processes, moderate opportunity for overbank flows.
	TAM-RIO-2	NM	13S0314012 3727308	Upland tamarisk, decadent cottonwood.	No evidence of riparian processes, no opportunity for overbank flows except in extreme events.
	TRT-RIO-1	NM	13S0342054 3850635	Tamarisk understory cleared below native woody vegetation.	Evidence of riparian processes and overbank flow.
	TRT-RIO-2	NM	13S0330246 3796452	Tamarisk cleared. Kochia is common but then replowed later in season	Natural water source but no evidence of riparian processes, potential for overbank flooding during moderate flow events.
	TRT-RIO-3	NM	13S0321945 374270	Tamarisk cleared.	No evidence of riparian processes, no opportunity for overbank flooding.

[a]NV: native vegetation, MIX: mixed, RER: revegetated with riparian vegetation, REU: revegetated with upland vegetation, TAM: tamarisk dominated, and TRT: treated to remove tamarisk. Plant species: [b]*Phalaris arundinacea*, [c]*Cirsium* spp., [d]*Salix exigua*, [e]*Atriplex lentiformis*, [f]*Salix gooddingii*, and [g]*Atriplex* spp.

($n = 10$ samples during each session). The use of a stopping time allowed for selection of a random point that was dependent only on the path that was taken immediately prior to the stopping time. To estimate herbaceous richness at each site, we conducted a running count of sight identified forb and graminoid richness, which resulted in a mean total number of taxa (pseudospecies in some cases) found in all circles for each session.

3.3. Other Environmental Variables. We used a riparian systems model (modified from [25]) to rank riparian condition. This qualitative model (riparian condition scores) includes spatial and structural diversity of native woody plants, contiguity of habitats, invasive vegetation, hydrology, topographic complexity, characteristics of flood-prone areas (evidence of flooding), and biogeochemical processing. These criteria consider the interaction between geology, hydrology, and organic and inorganic inputs to the system. Each criterion is ranked between 0 and 1, and scores are added so that the "best" score is an 8.

We measured soil moisture (% saturation relative to field capacity; Kelway soil moisture tester Model HB-2) at three locations through the middle portion of the site. Moist soils and seeps have been recognized as being important to butterflies [26] for puddling. We also measured wind speed (km/hr) and air temperature (°C) at the start of each sampling occasion because of their effects on butterfly detectability. Wikstroem and others [27] found butterfly detection unaffected by wind speeds up to five (29–38 km/hr) on the Beaufort scale, and Pollard [28] suggested 17°C as a minimum temperature for butterfly counts. Inclement weather was avoided.

3.4. Data Analysis. Because species pools differ across watershed boundaries (e.g., [29]) there could be difficulties in detection of treatment differences from across this wide geographical area. We used riparian butterfly disturbance susceptibility scores (DSS) [30] and species that were listed as being in common with all five watersheds (from [29]) to allow for community comparisons between types of landscapes collected from geographically disparate sites. Theoretically, species with high DSS should be present at undisturbed reference sites, while anthropogenically disturbed sites should be dominated by species with low scores.

We assigned each species a value from 1 to 4 in each of three categories contributing to disturbance susceptibility (e.g., [21]) using documented life history information [23, 31, 32]. Categories included adult mobility, larval host-plant specificity, and riparian dependence. We summed the scores for each category to create a DSS for each species (Online Resource 1 available at http://dx.doi.org/10.1155/2013/561617). Four different levels of DSS butterflies were created by determining 25, 50, and 75th percentiles for the range of DSS values. Percentiles were calculated from a database of 117 butterflies documented in riparian areas in the western USA. Categories containing DSS > 75th percentile were considered high (H-DSS, most sensitive); 50–75, moderately high (MH-DSS); 25–50, moderately low (ML-DSS); and <25th percentile were considered to have low DSS (L-DSS, least sensitive).

We used ANOVA to compare the abundance of H-DSS butterflies that were in common with all watersheds (hereafter known as the regional butterfly metric (RBM)); and environmental variables and riparian condition scores among landscape categories. Butterfly species richness in the various watershed counties (from the website [29]) ranged from 70 to 158 species. The counties associated with Las Vegas Wash, Pecos River, and Rio Grande River had similar species richness and ranged from 129 to 132 species. Highest species richness was found in Pueblo County, which contained the Arkansas River sites, with 158 species. The four counties associated with the Canadian River sample sites contained 70 butterfly species.

Dunnett's comparison was used to compare variables from all other sites to the native vegetation sites if the ANOVA indicated a significant difference ($P \leq 0.05$) between groups. Dunnett's test compares group means and is designed for situations where all groups are assessed against one "reference" group. The one-tailed version of Dunnett's test was used for comparison of groups. The Pearson correlation was used to examine relationships between variables. Data were transformed, if needed to normalize distributions, using $\ln(x + 1)$ or arcsine, squareroot.

Because butterfly observations were collected in two years, data might be from different statistical distributions, perhaps because of interannual weather differences. We used a data set from the Arkansas River that contained two each of native vegetation, mixed, and treatment sites from 2002 to 2006 to test the robustness of RBM to annual variability. Variation in weather occurred in this watershed, with soil moisture differing significantly between years (e.g., [21]). A 2-factor ANOVA was used to test for differences in mean RBM ($\ln(x + 1)$ transformed) between the three landscape categories and the five years. We hypothesized that RBM would differ between *landscape category*, but would not differ due to *year* or the *landscape category* ∗ *year interaction*. The absence of an interannual effect at Arkansas River sites would provide justification for regional treatment comparisons with the RBM using the different data years of 2005 and 2006.

Although there were several sites in each of the categories (see Table 1), this was not a manipulative study (e.g., [33]), and therefore replicates were not assigned to treatments, and landscape categories were not evenly represented across all watersheds. As an example, while tamarisk sites were found in all watersheds, revegetated-riparian and revegetated-upland sites were only found at Las Vegas wash and Rio Grande River sites (see Table 1). Because of the scale of landscape treatments, all variables cannot be held constant and butterflies could respond to something other than the presence/absence of tamarisk. There is some evidence [34] that dominance of woody taxa (e.g., *Tamarix* versus *Populus*) in southwestern rivers may be related to stream flow permanence and this characteristic, in and of itself, may influence insect communities. In addition, we lumped tamarisk sites treated with a variety of control methods together as treatment sites; however, this is justified by the findings of Harms and Hiebert [35] who found no differences in vegetation communities following tamarisk control using a variety of techniques. Perhaps the best description here is the "quasiexperiment" of Hargrove

Table 2: Environmental variables and butterfly species richness associated with landscape categories.

Landscape category	Environmental variables and species richness (mean of annual values, range in parentheses)				
	Soil moisture (%)	Riparian condition	Forb and graminoid richness (number/site)	Nectar (# florets/m^2)	Butterfly species richness
NV (n = 7)	61^a (14–98)	6.8^a (5.6–7.4)	9^a (1–14)	43.7^a (7.5–97.6)	19^a (13–26)
MIX (n = 5)	49^a (16–97)	5.1^b (4.6–6.5)	10^a (7–13)	46.8^a (28.1–77.3)	18^a (14–22)
RER (n = 4)	49^a (15–94)	5.9^a (5.3–6.6)	7^a (3–10)	37.5^a (21.0–57.3)	15^a (10–21)
REU (n = 3)	37^a (1–88)	3.7^b (3.0–4.4)	2^b (0–3)	2.8^b (1.0–3.8)	13^a (4–17)
TAM (n = 6)	53^a (1–99)	3.8^b (2.0–5.2)	5^a (2–14)	33.4^a (1.3–69.1)	14^a (4–24)
TRT (n = 9)	51^a (16–97)	3.6^b (2.0–5.9)	6^a (2–10)	22.7^a (0.0–42.9)	15^a (7–23)

Column values with dissimilar letters indicate significant ($P < 0.05$) differences (Dunnett's post hoc test) between landscape types and the reference sites NV. Variables as presented are not transformed; however, soil moisture and nectar were transformed for statistical purposes related to normality. NV: native vegetation, MIX: mixed, RER: revegetated with riparian vegetation, REU: revegetated with upland vegetation, TAM: tamarisk dominated, and TRT: treated to remove tamarisk.

and Pickering [36] where pseudoreplication is considered acceptable in exchange for realism. Achieving replication at the scale of hectares, despite concerns about replication and treatment interspersion, is important because it is characteristic of many tamarisk control/restoration projects. Osenberg and others [37] emphasized the importance of large-scale studies because small-scale experiments (e.g., 10 m^2) are poor at predicting actual restoration effects.

4. Results

Butterfly surveys occurred at wind speeds that were less than or equal to a light breeze (≤11.3 km/hr) on the Beaufort wind force scale, except for a single wind speed reading of 12.4 km/hr (at a Canadian River treatment site in May) (n = 63 total measurements). The lowest air temperature recorded was 19°C, thus all samples were collected at temperatures greater than the 17°C suggested as a minimum temperature for butterfly counts [28] and at wind speeds that do not affect butterfly detectability [27].

Testing of multiyear data from sites along the Arkansas River suggested that RBM was robust to annual variability (*year*; $F = 2.09$, $P = 0.1327$) (*year* × *landscape category*; $F = 1.00$, $P = 0.4718$) and provides evidence that the difference in collection year at other study sites plays no role in differences in RBM. Arkansas River RBMs, however, differed significantly ($F = 11.8$, $P = 0.008$) among landscape categories with native vegetation sites significantly different from treatment sites, while mixed sites were intermediate between native vegetation and treatment sites and not significantly different from either group.

4.1. Environmental Variables/Species Richness. No significant differences in soil moisture were detected between landscape categories and the native vegetation reference sites (Table 2). In the case of forb and graminoid richness and nectar amount, only revegetated-upland sites, which tended to be laterally separated from riverine environments, differed significantly from native vegetation sites (Table 2). Riparian condition scores indicated that restored riparian sites (revegetated-riparian) (mean riparian condition scores score = 5.9) did not differ significantly from native vegetation sites (mean riparian condition scores score = 6.8), while other sites were significantly different from native vegetation (Table 2). Treatment, tamarisk, and revegetated-upland sites all had relatively low riparian condition scores with mean values ranging from 3.6 to 3.8. No significant differences in butterfly species richness were detected between landscape categories (Table 2).

4.2. Riparian Condition Scores. Because riparian condition scores differed significantly with landscape categories, we examined separate components of the model in more detail. Characteristics that measured native woody plant coverage and spatial diversity, structural diversity, and biogeochemical processes differed between native vegetation reference sites and all other site types (Table 3). Contiguity of habitats and flood-prone area characteristics did not differ statistically between native vegetation, mixed, and revegetated-riparian sites. Revegetated-riparian sites also did not differ significantly from native vegetation sites in the categories: % invasive vegetation, hydrology, and micro- and macrotopographic complexities. Component values contained within riparian condition scores were often lowest at tamarisk, treatment, and revegetated-upland sites. Of the other variables, only forb and graminoid richness ($r = 0.5502$, $P = 0.0007$) and nectar abundance (($r = 0.6512$, $P < 0.0001$) ($\ln(x + 1)$) transformed) was significantly correlated with riparian condition scores.

Butterfly susceptibility to anthropogenic disturbance also appeared to be differentially related to riparian condition scores, with abundance of higher scoring butterflies significantly correlated with riparian condition while abundance of butterflies with the lowest scores were not correlated with riparian condition (Figure 1).

4.3. Butterfly Response to Landscape Category. H-DSS species that were reported from all five watersheds [29] included *Phyciodes tharos*, *Limenitis archippus*, *Asterocampa celtis*, and *Hesperopsis alpheus*; these in-common H-DSS species were used in analysis. While these four species are considered to be sensitive to anthropogenic disturbance, they differed in their

Table 3: Riparian condition scores associated with landscape categories.

Landscape category	Riparian condition scores for each component: Coverage and spatial diversity	Structural diversity	Contiguity of habitats	% of invasive vegetation	Hydrology	Micro- and macrotopographic complexity	Flood-prone area characteristics	Biogeochemical processes
NV	$.89^{a}$	$.77^{a}$	$.94^{a}$	$.67^{a}$	$.95^{a}$	$.81^{a}$	$.86^{a}$	$.93^{a}$
MIX	$.62^{b}$	$.57^{b}$	**$.85^{a}$**	$.44^{b}$	$.72^{b}$	$.51^{b}$	**$.72^{a}$**	$.71^{b}$
RER	$.68^{b}$	$.60^{b}$	**$.80^{a}$**	**$.56^{a}$**	**$.90^{a}$**	**$.85^{a}$**	**$.82^{a}$**	$.72^{b}$
REU	$.40^{b}$	$.47^{b}$	$.73^{b}$	$.44^{b}$	$.53^{b}$	$.28^{b}$	$.37^{b}$	$.44^{b}$
TAM	$.39^{b}$	$.40^{b}$	$.77^{b}$	$.28^{b}$	$.54^{b}$	$.32^{b}$	$.50^{b}$	$.59^{b}$
TRT	$.37^{b}$	$.34^{b}$	$.82^{b}$	$.35^{b}$	$.55^{b}$	$.30^{b}$	$.44^{b}$	$.46^{b}$

Column values with dissimilar letters indicate significant ($P < 0.05$) differences (Dunnett's post hoc test) when compared to the native vegetation reference sites. Bolded indicates condition scores statistically similar to those from reference sites (NV). NV: native vegetation, MIX: mixed, RER: revegetated with riparian vegetation, REU: revegetated with upland vegetation, TAM: tamarisk dominated, and TRT: treated to remove tamarisk.

natural history. For example, *L. archippus* is riparian dependent and feeds as larvae on cottonwood/willows, while *H. alpheus* has low dependence on riparian areas but is limited in mobility and feeds on only a single plant genus (*Atriplex*). *A. celtis* is limited to feeding on *Celtis* which is often associated with riparian areas in the western US. Unlike the other three butterflies which feed on woody vegetation as larvae, *P. tharos* feeds on herbaceous plants in the family Compositae and is typically found in moist meadows and fields [23]. We assumed that these RBM species would respond to landscape categories in a similar manner across geographic areas. The revegetated-riparian site from the Rio Grande watershed was omitted from the analysis because only a portion of the site had been restored, with a large section containing naturally occurring native vegetation. ANOVA comparing RBM among landscape categories indicated that there were significant differences between groups ($F = 3.38$, $P = 0.0170$) with native vegetation sites having highest RBM values and being significantly different from all other sites, with the exception of revegetated upland (one-sided Dunnett's multiple comparison) (Figure 2). The similarity in RBM between native vegetation and revegetated-upland sites was surprising since revegetated-upland sites were in areas away from water while native vegetation sites were typically immediately adjacent to waterways. Revegetated upland had the lowest mean values for forb and graminoid richness and nectar. Low forb and graminoid richness may be linked to relatively low soil moisture or the lack of flooding at these sites. The only RBM butterfly detected at revegetated-upland sites was *Hesperopsis alpheus* which feeds on *Atriplex* as larvae. *Atriplex* is often found in more upland areas but is also associated with riparian environments with higher salinity soils such as alkali sinks and playas [38]. This butterfly had a high DSS value because of its low mobility and high host plant specificity. However, its relatively low riparian dependency suggests that revegetated-upland sites differ in essential ways from native vegetation sites.

RBM was significantly correlated with riparian condition score ($r = 0.5034$, $P = 0.0024$) and soil moisture ($r = 0.4796$, $P = 0.0041$).

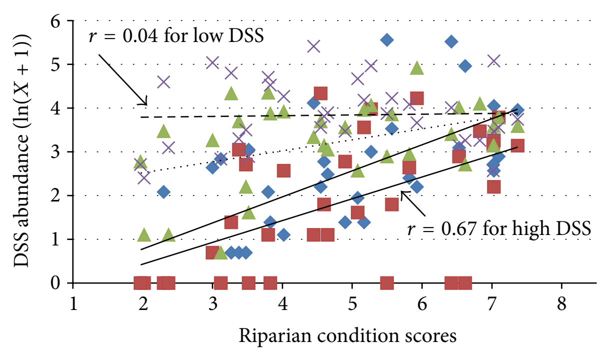

Figure 1: Comparison of the relationship of riparian condition scores with the abundance of butterflies in four different categories (high (H), moderately high (MH), moderately low (ML), and low (L)) of sensitivity to disturbance (disturbance susceptibility Scores (DSS)). Categories of butterflies varied in their correlation with riparian scores with more sensitive butterflies more highly correlated ((H-DSS; $r = 0.67$, $P < 0.0000$, ✦), (MH-DSS; $r = 0.54$, $P = 0.0009$, ■), (ML-DSS; $r = 0.42$, $P = 0.0123$, ▲), and (L-DSS; $r = 0.04$, $P = 0.8396$, ×)). Trend lines are shown as thick and solid for H-DSS, thin and solid for MH-DSS, small and dotted for ML-DSS, and thick and dashed for L-DSS.

5. Discussion

5.1. Tamarisk Management Effectiveness and Impact on Butterfly Communities. At the regional scale, butterfly communities (RBM) differed significantly between landscape categories. Mean RBM values differed between native vegetation sites and other sites, with the exception of revegetated-upland sites. Similarity between native vegetation and revegetated-upland sites was due to the presence of a sensitive butterfly species found in the upland environment.

Diversity and extent of riparian vegetation along with presence of cottonwood trees, saplings, and seedlings were higher at native vegetation sites and differentiated these sites from all others. Only mixed and revegetated-riparian sites had some aspects of riparian condition scores that were statistically indistinguishable from native vegetation values. This

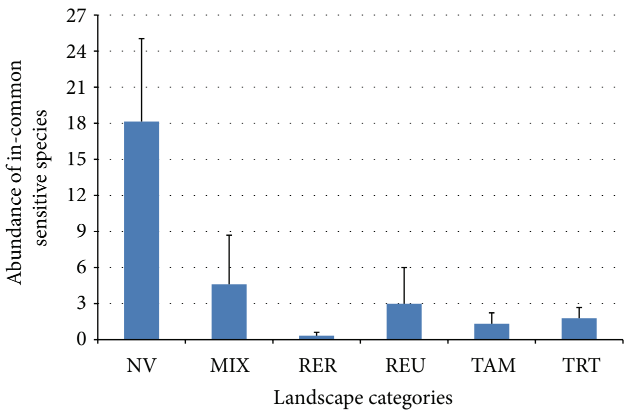

Figure 2: Comparison (means and standard error) of regionally in-common sensitive butterfly species abundance by landscape category. Values differed significantly between NV sites and other sites, with the exception of REU sites. NV: native vegetation, MIX: mixed, RER: revegetated with riparian vegetation, REU: revegetated with upland vegetation, TAM: tamarisk dominated, and TRT: treated to remove tamarisk.

level of riparian similarity did not lead to correspondence in RBM scores between mixed, revegetated-riparian, and native vegetation sites. The absence of a source of riparian obligate butterflies may explain this result at Las Vegas Wash revegetated-riparian sites. Restoration of landscapes after removal of tamarisk resulted in high-quality butterfly habitat along the Las Vegas Wash where erosion control structures have decreased the depth to groundwater and resulted in intermittent flooding of the landscape (e.g., [39]). Before the turn of the 20th century, the Las Vegas Wash was ephemeral for most of its length, except for a small wetland area and several springs, and may not have historically supported a diverse riparian butterfly community. There may not be a nearby source for other riparian obligates, such as *L. archippus*, despite the creation of high-value riparian areas. *L. archippus* and other riparian butterflies such as *Calephelis nemesis* are contained in the species list for Clark County [29], and habitat requirements for these species appear to be met by tamarisk control and revegetation projects along Las Vegas Wash. It may be necessary to introduce butterfly species to maximize their diversity in the Wash.

Sites with a mixture of native and exotic vegetation did not perform well as habitat for sensitive butterfly species. This occurred despite similarities in nectar and forb and graminoid richness with native vegetation sites. Native riparian vegetation diversity and coverage were lower at mixed sites compared to native vegetation sites and may have played a role in lower RBM scores at mixed sites.

Sites where tamarisk was treated, but without restoration, resulted in RBM scores similar to those found at untreated tamarisk sites. The assumption that invasive plant species removal is sufficient to recover sensitive butterfly species was not true in the cases that we examined. Without restoration these sites may take a long time to recover. Nelson and Wydoski [9] showed, after monitoring butterflies along the Arkansas River for five years, that treatment sites without revegetation did not trend towards native vegetation sites. In some cases regrowth of tamarisk occurred at sites where it had earlier been removed leading to similarities between treated and untreated tamarisk sites.

5.2. Response Consistency between Local and Regional Scales of Measurement. Our regional analysis results support findings of studies from single watersheds. Local level studies also found no recovery of butterfly communities at treated tamarisk sites [9] and also found significant differences in butterfly community metrics between riparian landscape categories [9, 39]. Riparian condition scores were significantly correlated with RBM butterflies at the regional scale; similar to results from single watershed studies (e.g., [9, 39]). We also found riparian condition scores to be highly correlated with abundance of sensitive butterflies and uncorrelated with butterflies that scored low on our sensitivity scale. Similar to our study, Clark and others [40] found that specialized butterflies disappeared faster than generalist butterflies did when exposed to increased urbanization. Our regional level study indicated that riparian condition score, which was correlated with both forb and graminoid richness and nectar abundance, was important in determining butterfly assemblages. Nectar production may respond to levels of landscape floodplain interaction because production is affected by plant-available soil moisture [41, 42]. A reduction in flower production may be a common consequence of water stress [43, 44] that may differ with landscape category and differentially affect butterfly communities. Local studies along the Oconee River in the eastern USA [45], the Muddy River (NV, USA) [46], Arkansas River (CO, USA) [9], and Las Vegas Wash (NV, USA) [39] also indicate the importance of plant species richness and nectar availability to butterfly communities. These studies, along with this one, suggest commonalities in response of butterflies to riparian alterations at both local and regional scales.

5.3. Riparian Restoration. Conceptual approaches to riparian restoration projects often differ. Many tamarisk control efforts are based on the belief that tamarisk removal will allow for recovery of native vegetation and that revegetation or modification of river processes is not needed (e.g., [35]). Others, however, suggest that hydrology is key and that biotic recovery will follow hydrologic and geomorphologic restoration [47, 48]. Evidence from our study suggests that tamarisk removal, interventions that increase floodplain interaction with the river, revegetation, and proximal sources of riparian butterflies are all required for system restoration. These results support suggestions of Nelson and Andersen [49] that restoration of hydrological processes and control of exotics are both needed for successful restoration of butterfly assemblages, especially for sensitive butterfly species. This rational is also promulgated by York and others [13] for development of Southwestern Willow Flycatcher habitat, indicating that very different taxonomic groups may need similar restoration efforts. Elucidation of mechanisms is provided by our regional study, with riparian condition scores pointing to the importance of native woody vegetation characteristics, annual flooding, and nectar resources in driving the makeup of riparian butterfly communities. In turn, enhanced butterfly biodiversity could lead to positive effects in the context of stability in ecosystem functions. Fire resistance from decreased plant biomass because of herbivory by insects (including butterfly larvae) and increased effectiveness of pollinator systems (often associated with highly biodiverse habitats) are two ways in which ecosystem function stability could be increased [50] through butterfly diversity enhancement.

Miller and Hobbs [51] indicate that identifying a target species or group of species is a necessary first step in habitat restoration in order to have a clearer and more systematic restoration approach. Our study suggests that butterflies are an appropriate focal group for monitoring lowland riparian restoration projects in the southwestern USA.

Acknowledgments

The authors thank Susan Broderick for having the foresight to implement this project and Curt Brown for much needed support. Two anonymous reviewers and the associate editor provided valuable direction in the improvement of the paper. This project was funded through the Bureau of Reclamation S&T program.

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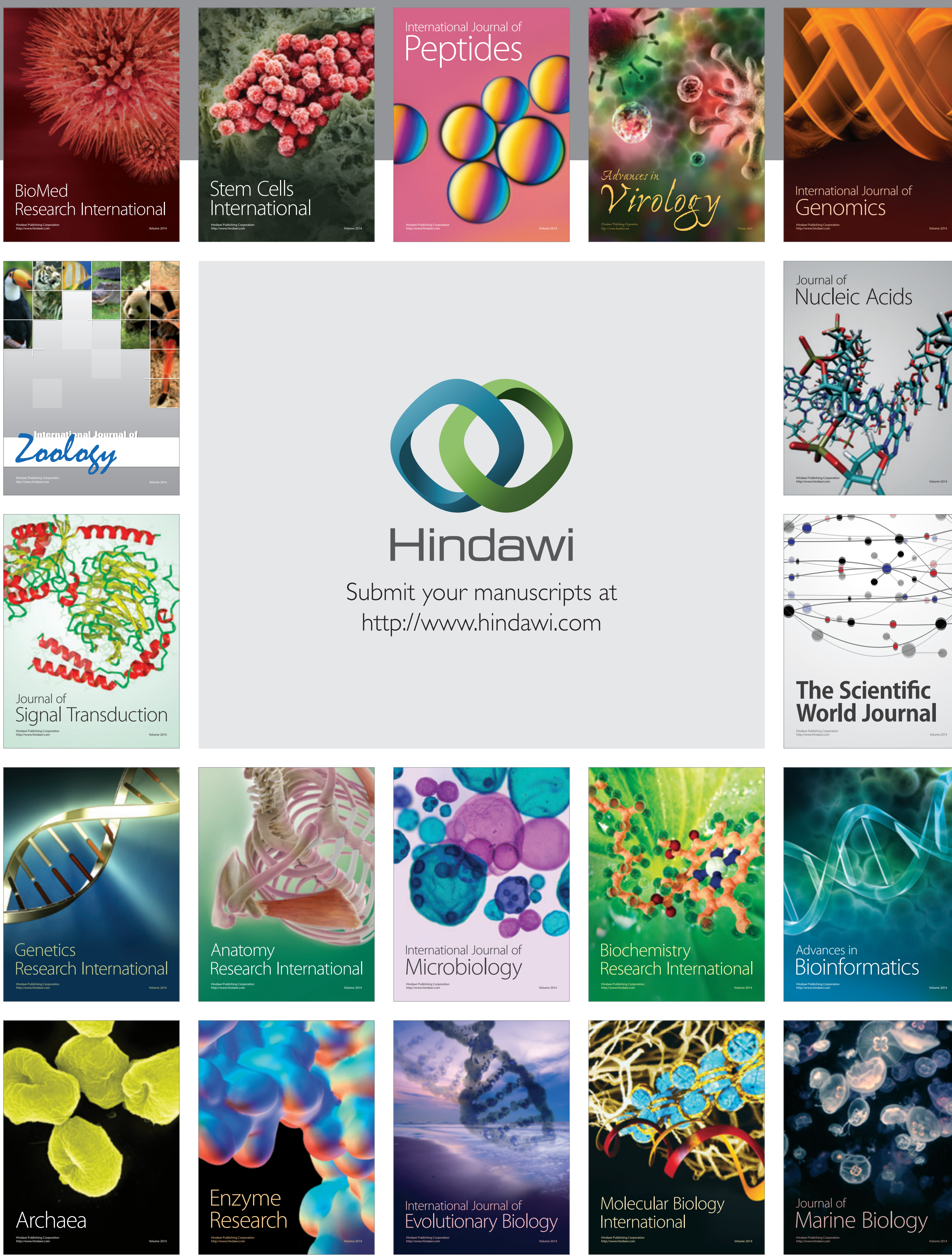
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