

Flood pulsing and metacommunity dynamics in a desert riparian ecosystem

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Abstract

Questions: 1. Does flood pulsing drive metacommunity dynamics and provide insurance against catastrophic flooding in desert southwestern riparian ecosystems? 2. Do upland and wetland species in the floodplain differ in their dynamics?

Location: Southwestern USA.

Methods: We sampled vegetation and propagule banks in four communities along a floodplain hydrogradient. Plant species were classified as wetland or upland and community wetland indicator scores were calculated. ANOVA tested for differences between data categories amongst communities (extant vegetation and propagule banks) and soil depths. Sørensen's similarity coefficient was calculated to determine compositional similarity between vegetation and propagule banks.

Results: Community propagule banks had high similarity indicating broad dispersal by flood waters. Wetland propagules were present in soils from channel bars to floodplain edges, despite declines in wetland vegetation with distance from channel. Wetland communities in propagule banks were dissimilar from those in vegetation except on channel bars. Upland species (vegetation and propagule banks) increased with distance from channel. Propagules of upland species were most abundant in the litter, and were compositionally similar to upland species in most communities.

Conclusions: Flood pulsing is one mechanism that drives spatiotemporal metacommunity dynamics in dynamic desert riparian ecosystems. The homogenized regional propagule bank created by flood pulsing provides wetland species with a mechanism to escape local extinction by allowing for recolonization after flooding creates suitable establishment conditions. Upland species are able to germinate from *in-situ* sources after small-scale flooding or rainfall moistens soil. In fluctuating environments, these dynamics sustain biodiversity in the face of ongoing environmental change.

Keywords: Community dynamics; Disturbance dynamics; Population dynamics; Seed bank; Seed dispersal.

Nomenclature: Kearney & Peebles (1960).

Abbreviations: PAR = Photosynthetically active radiation; WIS = wetland indicator score.

Introduction

A metacommunity is a network of communities linked by dispersal of potentially interacting species (Hanski & Gilpin 1991; Wilson 1992; Holyoak et al. 2005). Metacommunity dynamics describe species dispersal between constituent communities and the consequent interactions between species within these communities (Holyoak et al. 2005). The theory that describes metacommunity dynamics gives ecologists a framework with which to understand and predict how landscape fragmentation impacts biodiversity and ultimately ecosystem functioning (Holyoak et al. 2005). Much of the work on metacommunity theory has focused on modeling (Loreau & Mouquet 1999; Klausmeier 2001; Mouquet & Loreau 2002, 2003) and small field experiments (Kolasa & Romanuk 2005; Miller & Kneitel 2005). Few attempts have been made to link metacommunity theory to empirical knowledge by examining dispersal patterns at the landscape scale (Condit et al. 2002; Tuomisto 2003; Chase et al. 2005).

Southwestern riparian ecosystems in the USA provide an excellent model in which to study metacommunity dynamics. The constituent communities of these spatially structured ecosystems are arrayed along a moisture and disturbance gradient and are connected by flood pulsing (Patten 1998). In this arid environment, the steep gradients in depth to groundwater and declines in flood intensity and frequency that occur with distance from the channel produce strong vegetation patterns (Stromberg et al. 1996).

The extreme flood regime of rivers in arid regions changes abiotic and biotic conditions within the floodplain and drives rapid hierarchical patch dynamics (*sensu* Pickett & White 1985; Stromberg et al. 1993, 1997). Communities may not re-establish in the same location after flood scour and may be replaced by a different community type altogether. In this fluctuating environment, annuals and short-lived perennials comprise the majority of plant species (Wolden et al. 1994; Makings

2003; Bagstad et al. 2005). These species probably escape local extinction in this unpredictable environment by producing persistent seeds and/or vegetative remnants capable of resprouting (Kalisz & McPeck 1993; Bazzaz 1996; Thompson 2000; Grime 2001).

The flood pulsing that structures riparian plant communities also connects the communities via flood dispersal (Schneider & Sharitz 1988; Naiman et al. 1993; Johansson et al. 1996; Cellot et al. 1998; Middleton 2000) and may drive riparian metacommunity dynamics. Flood pulsing may disrupt community propagule banks by dispersing propagules across the riparian landscape. As flood velocities decline, the entrained propagules and sediment settle contributing to a floodplain propagule bank. This common pool of species may represent a regional propagule bank that contains species with varying life history traits and strategies. In an ecosystem with fluctuating environmental conditions and rapid patch dynamics, floodplain propagule banks provide species with a mechanism that facilitates recruitment and helps prevent local extinction (Capon & Brock 2006).

Floodplains of arid regions are vegetated by a mixture of upland and wetland dominated communities and these two groups probably respond to spatiotemporal metacommunity dynamics differently. Metacommunities can exist as spatially structured communities along environmental gradients whose constituent species are linked by dispersal processes; however, the spatial location of the communities and their constituent species can change through time (Liebold et al. 2004). Wetland species require moist soils during the majority of the growing season (Penfound 1952), occupy frequently disturbed portions of the floodplain (Menges & Waller 1983), and show strong spatiotemporal dynamics (Leck & Brock 2000). Large-scale flood pulsing can restructure floodplain topography, alter depth to groundwater via soil aggradation or degradation processes, and increase stream and groundwater levels (Stromberg et al. 1991, 1993, 1997). Because flood pulsing disperses propagules of wetland species into a variety of communities, many with inappropriate moisture conditions, wetland species may escape local extinction by persisting in the propagule bank until flood pulsing creates moisture conditions that are more suitable (Leck & Brock 2000). Small-scale flood pulsing can change resource availability in the floodplain by temporarily moistening soils. Upland species, particularly annuals, may germinate relatively quickly after propagules are dispersed into new communities as they are drought evaders that germinate in response to increased moisture availability (Went 1949; Monson & Smith 1982; Freas & Kemp 1983). This response would enable upland species to rapidly exploit newly available resources, successfully establish in the new community, and make *in situ* contributions to the propagule bank.

The fluvial dynamism of free-flowing rivers in southwestern USA and the dominance of annuals and short-lived perennials in the associated riparian corridors led us to make the following predictions: 1. If flood pulsing drives metacommunity dynamics in these ecosystems and provide insurance for wetland species against catastrophic flooding then: A. The propagule bank composition of the constituent communities will be similar, indicating that flood pulsing disperses propagules across the entire floodplain and creates a regional species pool. B. Wetland species will be restricted to localized wet sites but their propagules will be found in deep and shallow propagule banks located throughout the floodplain. 2. If upland and wetland species show different spatiotemporal metacommunity dynamics then across the floodplain, the spatial patterns of abundance and compositional similarity between propagules in the soil and extant vegetation will differ between upland and wetland species.

The metacommunity dynamics that create avenues of persistence, both spatially and temporally, probably sustain biodiversity in the face of ongoing environmental change in southwestern riparian ecosystems. Understanding the processes that sustain the network of constituent communities in southwestern riparian metacommunities contributes to our understanding of how biodiversity would be impacted by fragmentation or loss of connectivity between communities in highly dynamic floodplains.

Methods

Study site

A 1-km free-flowing perennial reach of the Hassayampa River, located in the Sonoran Desert in central Arizona USA, was selected for study. The reach is within the Hassayampa River Preserve and is located near Wickenburg, Arizona (33°56'24" N, 112° 37'30" W) at an elevation of ca. 610 m. In the Sonoran Desert precipitation falls in a bimodal pattern. Pacific frontal storms occur during the winter months and monsoon storms occur from July through to mid-September (Dimmitt 2000). Mean annual rainfall in Wickenburg is 280 mm. During 1998, the study period, total precipitation was 39 cm and mean streamflow was 0.50 m³.s⁻¹. Peak flow was 17 m³.s⁻¹, which was equivalent to a flood with a recurrence interval of less than two years.

Four dominant plant communities (Wolden et al. 1994), active channel bar, *Populus-Salix* forest, *Hymenoclea* shrubland, and *Prosopis* forest were selected for study, as they reflect the range of fluvial surfaces, moisture conditions (surface wet to surface dry), and

disturbance regimes (high to low frequency) that exist on the Preserve (Table 1). These communities are distributed across a hydrogradient that occurs with increasing distance from and above the channel.

Vegetation surveys

Herbaceous vegetation was surveyed 15.05 - 29.06.1998 and 13.09 - 02.10.1998. The May - June survey captured cool season species that persisted late in the year due to a prolonged winter rainy season. Sampling in September to early October captured warm season species, including those that established after the monsoon season. Three 100-m² study sites were selected within each of the four communities. Five 1-m² plots were randomly selected for study within each site. Percent cover of species was visually estimated within each plot. Voucher specimens were deposited in the Arizona State University Herbarium (App. 1).

Propagule bank soil core collection, seed germination, and plant identification

Propagule bank samples were collected from 16.10-02.11.1998 within the same plots in which herbaceous vegetation was surveyed. Three soil samples were collected within each of five plots within each of the three sites for a total of 45 soil cores per community. Litter was collected from each core location before samples were taken. A 5 cm diameter split-core soil sampler was used to collect the soil cores to a maximum depth of 8 cm. Each soil core was divided into depths of 0 - 2, 2 - 5, and 5 - 8 cm. The three samples collected within plots were combined by depth.

We designed a seedling emergence method that would allow seeds to germinate under locally-mimicked abiotic conditions. To maximize the number of species and individuals that germinated from soil samples, samples were placed into a growth chamber using a random block design for two years under conditions that approximated local weather conditions. Mean maximum and minimum monthly temperatures were used to establish temperature ranges for each month

in the growth chamber. Temperature changes were ramped approximately ten times a day to mimic the gradual changes in diurnal temperature patterns. Mean day length data was used to program the growth chamber light timers. PAR (Photosynthetically Active Radiation) in the growth chamber could not mimic field site levels, but ranged from 118 to 221 μmol.m⁻².s⁻¹. Plants were bottom-watered frequently to minimize stress. To reduce competition, plants were counted and removed from trays when they could be identified (Thompson & Grime 1979; Thompson et al. 1997). At the end of two years, any remaining mature plants that had not flowered were placed in a greenhouse. Voucher specimens were deposited in the Arizona State University Herbarium (App. 1).

Data reduction and analyses

We used wetland indicator classes to differentiate wetland species (1 = obligate wetland, 2 = facultative wetland, 3 = facultative, and 4 = facultative upland) from upland species (class 5) (Table 2) (Reed 1997). This classification system, based on the probability of a species being found in a wetland, also allows calculation of the relative importance of wetland species at a site. We calculated wetland indicator scores for the extant vegetation and propagule banks by weighting the relative cover or density of plants in each of the five indicator classes using the following equation (Wentworth et al. 1988):

$$w_j = \frac{\sum_{i=1}^p I_{ij}E_j}{\sum_{i=1}^p I_{ij}} \tag{1}$$

Where:

- w_j = weighed mean score for site j ;
- I_{ij} = cover or density for species i in site j ;
- E_i = wetland indicator score for species i ; and
- p = the number of species occurring in the site.

To determine if propagules of upland and wetland species were equally distributed across the floodplain, differences in mean number of wetland and upland seedlings per m² between the communities were determined using one-way ANOVA or Kruskal Wallis ($\alpha = 0.05$).

Table 1. Soil moisture, depth to groundwater, and flow velocity of a 5-year recurrence flood at the study sites.

	Soil moisture	Depth to groundwater (m)	Flow velocity (m s ⁻¹)
Active channel bar	Wet	0.4 ± 0.1	6.0 ± 2.7
<i>Populus-Salix</i>	Dry	1.3 -2.2 ± 0.7	3.4 ± 1.3
<i>Hymenoclea</i>	Very Dry	2.0 ± 0.5	2.6 ± 0.3
<i>Prosopis</i>	Dry	2.7 ± 0.6	0.0 ± 0.0

Table 2. Indicator classes, wetland frequencies, and wetland index values for species occurrence in wetlands (Reed 1997).

Indicator Classes	Wetland Frequency	Wetland Index
Obligate wetland	> 99%	1
Facultative wetland	67-99%	2
Facultative	34-66%	3
Facultative upland	1-33%	4
Obligate upland	0%	5

The same analyses were used to test for significant differences in the mean cover of upland and wetland species between extant communities. One-way ANOVA was used to determine if propagule patterns varied in the soil profile ($\alpha = 0.05$), and the strength of the relationship between depth and wetland indicator score was determined using Pearson's correlation analysis ($\alpha = 0.05$).

Sørensen's similarity coefficient (Krebs 1999) was used to determine the degree of similarity in community composition between propagule banks and extant vegetation; this was done for all species and for wetland and upland species independently. Sørensen's similarity coefficient was also used to determine the degree of similarity in the composition among the various community propagule banks and among the various extant communities.

Scatter and probability plots were used to test the assumptions of homoscedasticity and normality (Sokal & Rohlf 1995). Square root or log transformations were used to correct heteroscedastic or non-normal data. Transformed data were not analysed if heteroscedasticity could not be corrected. *A posteriori* comparisons were completed using Tukey's or Nemenyi's method (Sokal & Rohlf 1995; Zar 1999).

Results

Compositional similarities in propagule banks and extant vegetation within and between communities

Sørensen's similarity scores reveal that while the compositional overlap between the various extant communities is relatively low (lowest score = 0.22 and highest score = 0.43), that between propagule banks of the various communities is relatively high (lowest score = 0.45 and highest score = 0.68) (Table 3).

Sørensen's similarity scores between propagule banks and extant vegetation are relatively low ranging among communities from 0.25 to 0.36 (Table 4). However, when considering upland and wetland groups independently, similarity between propagule banks and extant vegetation is higher (Table 4). Upland

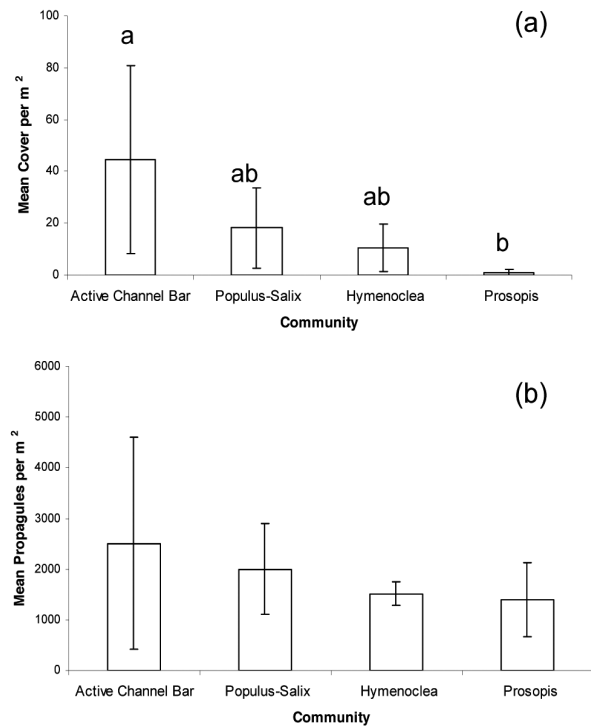


Fig. 1. (a) Mean cover of wetland species per m², ± 1 SD, by community. Dissimilar letters indicate a significant difference between communities. (b) Mean number of wetland propagules per m², ± 1 SD, in the propagule bank by community.

species in propagule banks had a moderately high degree of similarity with extant upland species in the three drier communities, while wetland propagules had moderately high similarity only with the active channel bar wetland community.

Spatial patterns of wetland and upland species in propagule banks and extant vegetation

The cover of wetland species decreased with distance from the channel ($F_{(3,8)} = 3.94$, $P < 0.05$) (Fig. 1a). Cover of wetland species was significantly higher in active channel than in *Prosopis* communities (Tukey HSD: $P < 0.05$) (Fig. 1a). Wetland propagules, however, were evenly distributed across floodplain

Table 3. Sørensen's similarity scores between extant vegetation and propagule banks of active channel bar, *Populus-Salix*, *Hymenoclea*, and *Prosopis* communities.

	Similarity between extant vegetation			Similarity between propagule banks		
	<i>Populus-Salix</i>	<i>Hymenoclea</i>	<i>Prosopis</i>	<i>Populus-Salix</i>	<i>Hymenoclea</i>	<i>Prosopis</i>
Active channel bar	0.43	0.30	0.22	0.45	0.52	0.47
<i>Populus-Salix</i>		0.43	0.42		0.68	0.68
<i>Hymenoclea</i>			0.25			0.63

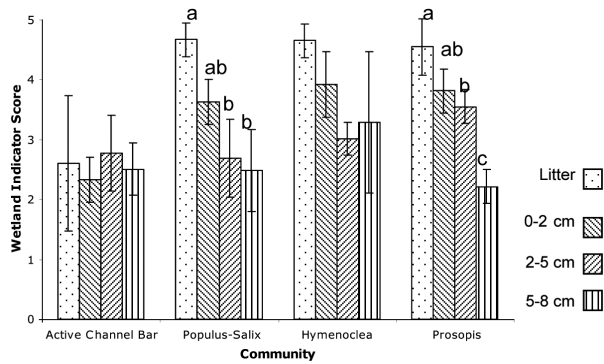


Fig. 2. Mean wetland indicator score per m² of propagule banks, ± 1 SD, by community and depth. Low WIS values indicate a higher probability of wetland species occurrence. Dissimilar letters indicate a significant difference between WIS values within a community.

communities ($F_{(3,8)} = 0.50, P > 0.05$) (Fig. 1b). Wetland propagules were present in all soil layers and in the drier communities had greatest relative abundance in deeper soil layers (Fig. 2). The pattern of decreasing wetland indicator score (i.e. increasing wetland dominance) with increasing depth was both significant and highly correlated in *Populus-Salix* ($F_{(3,8)} = 10.46, P < 0.05; r = -0.85, P < 0.05$) and *Prosopis* ($F_{(3,8)} = 44.41, P < 0.05; r = -0.91, P < 0.05$) communities (Fig. 2).

Upland species varied sharply in abundance along the hydrogradient both for extant vegetation and propagule banks. The mean cover ($F_{(3,8)} = 17.58, P < 0.05$) and propagule density ($F_{(3,8)} = 25.61, P < 0.05$) of upland species increased with distance from the channel (Fig. 3a,b). Upland cover in *Hymenoclea* and *Prosopis* communities was significantly higher than in active channel bar and *Populus-Salix* communities (Tukey HSD: $P < 0.05$) (Fig. 3a). Similarly, the mean number of upland propagules per m² was significantly higher in *Prosopis* communities than in active channel bar and *Populus-Salix* communities (Tukey HSD: $P < 0.05$) (Fig. 3b). Upland propagules were most abundant in litter in *Populus-Salix* and *Prosopis* communities (Tukey HSD: $P < 0.05$) (Fig. 2).

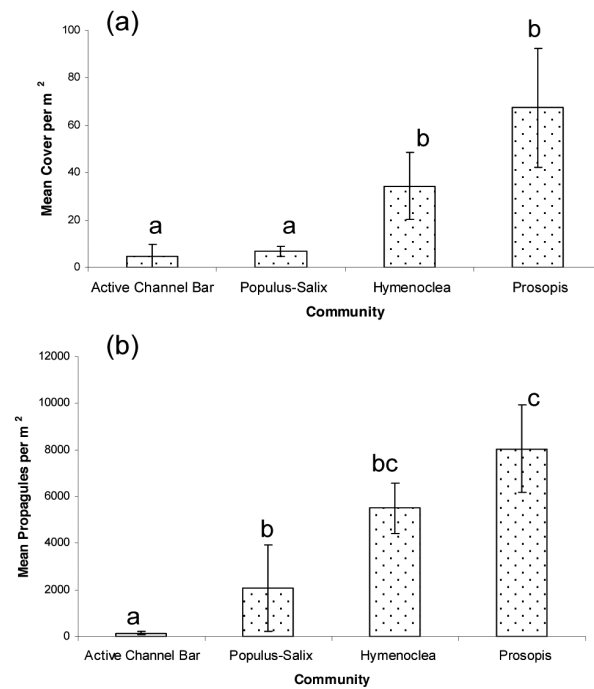


Fig. 3. (a) Mean cover of upland species per m², ± 1 SD, by community. (b) Mean number of upland propagules per m², ± 1 SD, in the propagule bank by community. Dissimilar letters indicate significant differences between communities.

Discussion

Flood pulse driven metacommunity dynamics

Flood pulsing disrupts community propagule banks, mixes the propagules together, and deposits them across the floodplain thereby linking together constituent communities through a regional propagule bank. The presence of wetland species in ‘deeper’ soils of communities located at the outer extent of the floodplain cannot be due to *in situ* seed production as wetland species are unable to establish where soil moisture is not maintained for the majority of the growing season (Penfound 1952). Although not all species are dispersed via flood pulsing alone (Drezner et al. 2001; Mouw & Alaback 2003), it is unlikely that the consistent distribution of high numbers of wetland propagules across the floodplain

Table 4. Sørensen’s Similarity scores between the composition of extant vegetation and propagule banks of all vegetation and of upland and wetland species.

	All propagules vs. all vegetation	Upland propagules vs. upland vegetation	Wetland propagules vs. wetland vegetation
Active channel bar	0.36	0.21	0.43
<i>Populus-Salix</i>	0.29	0.40	0.19
<i>Hymenoclea</i>	0.29	0.50	0.14
<i>Prosopis</i>	0.25	0.50	0.23

and the homogenization of floodplain propagule banks is primarily due to dispersal mechanisms other than large-scale flood pulsing.

Suggestions of flood pulse driven metacommunity dynamics have been found in propagule bank investigations of other wetland ecosystems. Studies of temperate riparian ecosystems in the USA found similarities in species composition between community propagule banks in the floodplain (Schneider & Sharitz 1986, 1988; Hanlon & Williams 1998; Middleton 2000). Keddy & Reznicek (1982) discussed the possibility of seed dispersal of common species from swampy bays and inlets to the shorelines of Matchedash Lake in Ontario, Canada. Seeds of species typical of wet meadows were found in other communities along riparian corridors in southeastern central Sweden (Skoglund 1990). An investigation of an arid region riparian ecosystem in Australia found many species in common in all community propagule banks of the floodplain (Capon & Brock 2006). The results of these studies, combined with our own, indicate that flood pulse driven metacommunity dynamics disperses propagules of a variety of species across artificial community boundaries resulting in the exposure of propagules to a range of environmental conditions.

Metacommunity dynamics of upland and wetland species

Species whose propagules are transported across the floodplain into a variety of communities with varying environmental conditions respond to flood pulse driven metacommunity dynamics according to their life-history traits and strategies. Upland species, with their ability to either tolerate or evade drought, show spatial metacommunity dynamics. The spatial pattern of upland propagule abundance mirrored that of extant vegetation in the Hassayampa River floodplain, with both increasing as aridity increased and disturbance decreased. Furthermore, the majority of viable upland propagules were found in litter and there was a higher degree of similarity between extant vegetation and propagule banks. Collectively, these patterns indicate that upland species are establishing from and contributing to *in situ* seed sources. Hydrochory may provide a colonization source for some upland species and this is augmented by zoochory (Drezner et al. 2001) and *in situ* production. Upland species are able to establish, persist, and reproduce in all floodplain communities due to the moist soil conditions either created by rainfall or small flood pulses (Went 1949; Monson & Smith 1982; Freas & Kemp 1983; Bagstad et al. 2005).

Wetland species respond to spatial metacommunity dynamics if propagules are dispersed into communities within their ecological range, but also respond strongly to temporal metacommunity dynamics within the floodplain.

The flood dispersed regional propagule pool allows wetland communities to rapidly re-establish after catastrophic flooding changes the spatial location of wetland sites. Indeed, following a large flood on the San Pedro River of Arizona, USA Bagstad et al. (2005) found many seedlings of species typical of wetland communities up to 300 m from the active channel. As in other temporally variable environments (Kalisz & McPeck 1993; Bazzaz 1996; Thompson 2000; Grime 2001), propagule banks provide wetland species in highly dynamic riparian ecosystems a mechanism to escape local extinction (Capon & Brock 2006).

Because riparian ecosystems are comprised of a variety of community types populated by species with varying life history traits and strategies (Naiman et al. 2005), a synthetic approach is needed when matching metacommunity models to observed dispersal patterns in the field. Of the four metacommunity dynamics models outlined by Chase et al. (2005), two (the species-sorting and mass effects models) apply to riparian ecosystems. According to the species-sorting model, environmental factors exert a strong influence on community composition along with, to a lesser degree, dispersal dynamics. Communities are arrayed along some environmental gradient (hydrogradients in riparian ecosystems: Hupp & Osterkamp 1996; Naiman et al. 2005) with species populating the communities in which their life history trade-offs and strategies allow them to be successful. The species-sorting model probably describes metacommunity dynamics of wetland species; although dispersal via hydrochory is of key importance in driving temporal dynamics, such species respond strongly to environmental conditions and occupy limited wet sites in the arid region riparian zone. Temporal dynamics within metacommunities then provide windows of opportunity for establishment of wetland species as extant conditions change due to flood pulse driven patch dynamics (*sensu* Pickett & White 1985).

The mass effects model incorporates a stronger role of dispersal, and can describe floodplain dynamics wherein a type of source-sink dynamic at the metacommunity scale operates to structure the various communities (Chase et al. 2005). Environmental gradients exist, and species are more successful in some communities than others; however, dispersal exerts a strong influence on the ability of species to exist in particular communities. Source-sink dynamics may help sustain populations of upland species at the outer edge of their ecological range in spatially structured metacommunities. For example, in the Hassayampa River ecosystem, sink populations of upland species, such as *Bromus diandrus* may be sustained in marginal sites such as active channel bars because individuals are dispersed from source populations located in *Populus-Salix* forests and other communities in which they have a high reproductive output.

Conclusion

Metacommunity dynamics in southwestern US riparian ecosystems are driven by several mechanisms including flood pulsing and other dispersal pathways. Metacommunity dynamics occur both spatially and temporally with wetland and upland species responding to each differently. Propagule banks enable many species to respond to the multidimensional dynamics by acting as a storage mechanism that can buffer populations in the face of ongoing environmental change. These multidimensional metacommunity dynamics, and the mechanisms that sustain them, help support biodiversity in ecosystems with rapid patch dynamics and can provide insurance for ecosystem functioning (Yachi & Loreau 1999; Loreau et al. 2003). Understanding riparian metacommunity dynamics can only improve management of these ecosystems by revealing that constituent communities are linked via dispersal pathways. Focused management or restoration of dominant constituent communities instead of management or restoration of the entire metacommunity, could jeopardize all riparian plant communities by disconnecting constituent communities from the propagule network.

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For App. 1, see below (online version)
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App. 1. Species found in Active channel bar, *Populus-Salix*, *Hymenoclea*, and *Prosopis* communities. Vegetation types in which the species were found: A = Active channel bar, P = *Populus-Salix*, H = *Hymenoclea*, PR = *Prosopis*, NP = not present

Species	Community Extant Vegetation	Community Propagule Bank	Species	Community Extant Vegetation	Community Propagule Bank
MAGNOLIOPSIDA			CRASSULACEAE		
AIZOACEAE			<i>Crassula connata</i>		
<i>Sesuvium verrucosum</i>	NP	P		NP	P,PR
AMARANTHACEAE			EUPHORBIACEAE		
<i>Amaranthus albus</i>	NP	A	<i>Chamaesyce hyssopifolia</i>		
<i>Amaranthus palmeri</i>	NP	P		H	NP
			<i>Chamaesyce micromera</i>		
				A	NP
			<i>Chamaesyce setiloba</i>		
				A	NP
APIACEAE			FABACEAE		
<i>Bowlesia incana</i>	NP	P,PR	<i>Melilotus</i> spp.		
<i>Daucus pusillus</i>	A,P	P		P,H	NP
			<i>Melilotus albus</i>		
				A	A,H
			<i>Melilotus indicus</i>		
				NP	A
			<i>Prosopis velutina</i>		
				PR	PR
ASTERACEAE			GENTIANACEAE		
<i>Baccharis salicifolia</i>	A,P	A,P,H	<i>Centaurium calycosum</i>		
<i>Baccharis sarothroides</i>	H	NP		NP	P,H,PR
<i>Conyza canadensis</i>	A	A,P,H,PR	GERANIACEAE		
<i>Eclipta prostrata</i>	A	A	<i>Erodium cicutarium</i>		
<i>Gnaphalium chilense</i>	H	NP		P,H	P
<i>Gnaphalium exilifolium</i>	NP	P,H,PR	LAMIACEAE		
<i>Gnaphalium luteo-album</i>	NP	A,P,H,PR	<i>Marrubium vulgare</i>		
<i>Gnaphalium palustre</i>	NP	A,P,H,PR		PR	P,PR
<i>Heterotheca psammophila</i>	P,H	P,H,PR	LYTHRACEAE		
<i>Hymenoclea</i> spp.	H	PR	<i>Lythrum californicum</i>		
<i>Pectis papposa</i>	A,H	NP		NP	H
<i>Sonchus oleraceus</i>	NP	PR	MALVACEAE		
<i>Xanthium strumarium</i>	H	NP	<i>Malva parviflora</i>		
				H	NP
BORAGINACEAE			NYCTAGINACEAE		
<i>Amsinckia intermedia</i>	A,H	A,H,PR	<i>Boerhaavia coccinea</i>		
<i>Cryptantha barbiger</i>	NP	P,H		A,H	NP
<i>Cryptantha circumscissa</i>	NP	P,H	<i>Boerhaavia coulteri</i>		
<i>Cryptantha crassisejala</i>	NP	A		H	NP
<i>Cryptantha micrantha</i>	NP	A,H	ONAGRACEAE		
<i>Heliotropium curassavicum</i>	NP	P	<i>Epilobium californicum</i>		
<i>Pectocarya recurvata</i>	NP	H		NP	H
<i>Tiquilia plicata</i>	H	NP	PLANTAGINACEAE		
			<i>Plantago insularis</i>		
BRASSICACEAE				P	P
<i>Draba cunifolia</i> var. <i>typica</i>	NP	PR	<i>Plantago patagonica</i>		
<i>Draba reptans</i>	NP	PR		NP	P,H
<i>Nasturtium officinale</i>	NP	P	<i>Plantago purshii</i>		
<i>Sisymbrium irio</i>	NP	P,H,PR		P	NP
<i>Sisymbrium linifolium</i>	NP	PR	POLEMONIACEAE		
<i>Thelypodium lasiophyllum</i>	NP	A,P,PR	<i>Eriastrum diffusum</i>		
				P	NP
			<i>Portulaca retusa</i>		
				A	NP
CAMPANULACEAE			POLYGONACEAE		
<i>Nemacladus glanduliferus</i>	NP	A	<i>Eriogonum polycladon</i>		
<i>Triodanis biflora</i>	NP	PR		H	H
CARYOPHYLLACEAE			PRIMULACEAE		
<i>Herniaria cinerea</i>	NP	A,P,H,PR	<i>Androsace occidentalis</i>		
<i>Silene antirrhina</i>	NP	P,PR		NP	P
<i>Stellaria nidens</i>	NP	PR	SALICACEAE		
			<i>Populus fremontii</i>		
				A,P	NP
			<i>Salix gooddingii</i>		
				A,P	NP
CHENOPODIACEAE					
<i>Atriplex elegans</i>	NP	P			
<i>Chenopodium fremontii</i> var. <i>incanum</i>	NP	P,PR			
<i>Chenopodium leptophyllum</i>	NP	P,H,PR			

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II

<i>App.1, cont.</i>	Community Extant vegetation	Community Propagule bank
<i>SCROPHULARIACEAE</i>		
<i>Maurandya antirrhiniflora</i>	NP	P,PR
<i>Mimulus guttatus</i>	NP	A,P,H,PR
<i>Mimulus pilosa</i>	NP	A,P
<i>Orthocarpus purpurascens</i>	NP	A,P
<i>Verbascum thapsus</i>	NP	P,H
<i>Veronica anagallis-aquatica</i>	A	A,P,H,PR
<i>Veronica peregrina</i>	NP	P,H,PR
<i>SOLANACEAE</i>		
<i>Calibrachoa parviflora</i>	A	A,P,H,PR
<i>Nicotiana glauca</i>	NP	P,H,PR
<i>Nicotiana trigonophylla</i>	H	A,P,PR
<i>UTRICACEAE</i>		
<i>Parietaria hespera</i>	NP	P
<i>VERBENACEAE</i>		
<i>Verbena bracteata</i>	NP	PR
<i>ZYGOPHYLLACEAE</i>		
<i>Kallstroemia grandiflora</i>	H	NP
<i>MAGNOLIOPHYTA - LILIOPSIDA</i>		
<i>CYPERACEAE</i>		
<i>Eleocharis montevidensis</i>	NP	PR
<i>Eleocharis parishii</i>	A	NP
<i>Juncus articulatus</i>	NP	A,P,H,PR
<i>Juncus bufonius</i>	NP	A,P,H,PR
<i>Juncus xiphioides</i>	A	P,PR
<i>POACEAE</i>		
<i>Bouteloua barbata</i>	H	NP
<i>Bromus carinatus</i>	NP	PR
<i>Bromus diandrus</i>	A,P,H,PR	P,H,PR
<i>Bromus rubens</i>	A,P,H,PR	P,H,PR
<i>Cynodon dactylon</i>	A,PH	NP
<i>Echinochloa colona</i>	NP	A
<i>Echinochloa crus-galli</i>	A	A
<i>Eragrostis cilianensis</i>	H	NP
<i>Eragrostis pectinacea</i>	H	P
<i>Erioneuron</i> spp.	NP	A,P,H
<i>Hordeum murinum</i>	P,H,PR	P,H,PR
<i>Leptochloa uninervia</i>	A	NP
<i>Panicum capillare</i>	A	NP
<i>Polypogon monspeliensis</i>	A,P,PR	A,P,H,PR
<i>Schismus</i> spp.	P	NP
<i>Schismus barbatus</i>	A,H,PR	A,P,H,PR
<i>Sporobolus contractus</i>	NP	A,P,H,PR
<i>Vulpia octoflora</i>	NP	P,H
<i>TYPHACEAE</i>		
<i>Typha domingensis</i>	A	NP