Aerial dispersal of aquatic invertebrates along and away from arid-land streams

Michael T. Bogan[1] AND Kate S. Boersma[2]

Zoology Department, 3029 Cordley Hall, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. Dispersal is an essential process in metapopulation and metacommunity dynamics. Most studies of aquatic invertebrate dispersal in streams have focused on in-stream drift of larvae. However, understanding aerial dispersal is important for predicting community assembly in isolated habitats after disturbance or stream restoration. We used artificial pools placed at 3 distances (5, 75, and 250 m) from 1 perennial and 1 ephemeral arid-land stream to examine aerial-dispersal dynamics of aquatic invertebrates over a 6-wk period in summer 2009. We also conducted a 2-wk experiment to examine the relationship between daily rainfall and disperser abundance at the perennial site. Sixty-six aquatic invertebrate taxa (including many Coleoptera and Diptera and fewer Hemiptera, Ephemeroptera, Trichoptera, and noninsect taxa) colonized the artificial pools. They represented ⅓ of taxa documented from neighboring perennial streams. Abundance and species richness declined with distance away from both streams. This result suggests that ephemeral stream channels may serve as important aerial dispersal corridors for aquatic invertebrates even when no surface water is present. Mean species richness tripled after 58 mm of rain during the 4th wk of the experiment. Data from the 2-wk experiment highlighted the role of rainfall as a dispersal cue in this system. Amount of daily rainfall explained 48 to 77% of the variation in disperser abundance at 5, 75, and 250 m from the perennial site. We used spatiotemporal dispersal patterns observed in our study to identify 5 modes of aerial dispersal among 56 taxa: 1) widespread common, 2) widespread haphazard, 3) range-restricted, 4) cue-limited, and 5) infrequent. Classification of specific aerial-dispersal modes provides a conceptual framework for modeling spatially explicit community responses to disturbance, stream restoration, and climate-change-induced habitat contraction or expansion.

Key words: dispersal, colonization, community assembly, perennial, ephemeral, aquatic invertebrates.

Dispersal, the movement of individuals from one site to another, is an important process in the maintenance of local populations (Hanksi 1998), and is essential to local community composition (Palmer et al. 1996, Leibold et al. 2004). Dispersal allows inbreeding avoidance and escape from predation, competition, or deteriorating environmental conditions in local habitat patches. These benefits come with risks, though, because individual dispersers may not find suitable mates in new habitats or may not find any appropriate habitat to colonize (Bilton et al. 2001). Freshwater invertebrates were long thought to be frequent or widespread dispersers (Bohonak and Jenkins 2003). However, recent genetic and stable-isotope studies have indicated that although some species disperse frequently or over long distances, dispersal abilities vary greatly among freshwater invertebrate taxa (Macneale et al. 2005, Hughes et al. 2009).

In streams, drift dispersal often is portrayed as the most important mechanism for invertebrate colonization of new or disturbed habitat patches (Williams and Hynes 1976, Gore 1982, Mackay 1992). This apparent primacy of drift (and instream movement) over aerial dispersal may reflect the bias of published studies toward low-order, perennial, temperate streams. In contrast, aerial dispersal was identified as the primary colonization pathway in arid-land (Gray and Fisher 1981) and equatorial (Hynes 1975) streams. In addition, aerial dispersal probably is important in colonization of large temperate-river floodplains (Tronstad et al. 2007). Aerial distance from colonist source streams can be an important predictor of local invertebrate diversity in streams recovering from anthropogenic disturbance, especially during the early years of recovery (Patrick and Swan 2011). Thus, understanding the role aerial dispersal in establishing or maintaining invertebrate populations in streams is essential for predicting community assembly in changing climatic conditions and for

[1] E-mail addresses: boganmi@science.oregonstate.edu

[2] boersmak@science.oregonstate.edu

implementing biodiversity restoration and monitoring projects (Parkyn and Smith 2011).

To advance our understanding of aerial dispersal of stream invertebrates, 2 key topics require attention: 1) the extent of dispersal along vs away from stream corridors and 2) the environmental conditions that trigger or facilitate aerial dispersal. Most studies indicate that the vast majority of adult aquatic invertebrates disperse <50 m away from stream corridors (Jackson and Resh 1989, Petersen et al. 2004, Winterbourn et al. 2007). In a few studies, however, adult aquatic invertebrates have been found several hundred meters (Macneale et al. 2005) to several kilometers (Kovats et al. 1996, Briers et al. 2004) away from their natal streams. These occasional long-distance dispersal events are difficult to observe but may be extremely important for maintaining local populations (Bilton et al. 2001). Genetic analyses indicate that reach-scale genetic structure in some streams may be the result of only a few matings of adult aquatic invertebrates (Bunn and Hughes 1997).

Numerous environmental factors may trigger or facilitate aerial dispersal of aquatic invertebrates along and away from stream channels. Deteriorating local habitat conditions during seasonal drought, including reduced water levels and increased water temperatures, are often cited as cues to overland dispersal (Kingsley 1985, Velasco and Millán 1998). Some invertebrates (e.g., Belostomatidae) use intense rainfall as a cue to migrate from perennial stream habitats to seasonally flooded habitats (Lytle and Smith 2004), but rainfall may be negatively correlated with aerial dispersal of macroinvertebrates in other systems (Miguelez and Valladares 2008). Increased aerial dispersal and colonization of aquatic habitats by microinvertebrates also has been associated with heavy rain (Caceres and Soluk 2002, Williams et al. 2007). Additional environmental factors that facilitate aerial dispersal include increased air temperature (Pajunen and Jansson 1969, Ryker 1975, Briers et al. 2003, Miguelez and Valladares 2008) and decreased humidity and wind (Briers et al. 2003, Boix et al. 2011). Additionally, aerial dispersers may be more likely to fly at times of day with maximum reflectivity of light off water, which enhances the detectability of potential colonization sites (Csabai et al. 2006). Thus, to understand aerial dispersal processes fully, both spatial (i.e., where dispersers travel across the landscape) and temporal (i.e., when dispersers leave their habitat) aspects of dispersal must be quantified.

We examined spatial and temporal patterns of aerial dispersal and community assembly along and away from 2 arid-land streams in Arizona. Most streams in the region naturally contract to a series of small pools during the dry season. These pools can be connected by tiny trickles of flow or be completely isolated from one another (Bogan and Lytle 2007). One study stream was perennial, whereas the other was ephemeral and contained no surface water during the experiment. Tracking multiple species of aerial dispersers from one habitat to another is difficult to impossible, so we used plastic tanks to mimic isolated stream pools and quantified invertebrate arrival at these novel aquatic habitats. We placed artificial pools at 3 distances away from the 2 study streams and allowed them to be colonized over a 6-wk period. We also examined the potential role of rainfall in triggering or facilitating dispersal by quantifying colonist arrivals at 12-h intervals in a separate set of artificial pools over 2 wk and correlating colonist abundance with rainfall. These experiments allowed us to quantify the arrival of dispersing adults (who may or may not have remained in pools >12 h [2-wk experiment]) and general community development arising from aerial dispersal (adult arrival and oviposition and subsequent larval recruitment [6-wk experiment]). We predicted that species richness and abundance would decrease and community composition would change significantly with increasing distance from the stream at the perennial but not at the ephemeral site because the dry stream channel would be the source of few, if any, dispersers. We also predicted that colonist abundances would be highest after rain events if rainfall serves as a cue to disperse in search of newly wetted habitats. We used the observed spatiotemporal dispersal patterns of individual species, including their responses to rainfall, to classify species into aerial dispersal modes.

Methods

Study location

We conducted our study along 2 arid-land streams in the Chiricahua Mountains of southeast Arizona. Cave Creek (lat 31.8824°N, long 109.2050°W) is perennial. Graveyard Canyon (lat 31.9327°N, long 109.2067°W) is ephemeral and flows only briefly during very intense precipitation events. No flow occurred in this stream for at least 10 mo before the start of our study. The 2 sites have similar elevations (1675 m asl) but are separated from one another by 4.5 km and a mountain ridge that rises to 2440 m asl (Fig. 1). No ponds occur in the Chiricahua Mountains, so streams provide the only aquatic habitat in the range. Upland areas of both study sites are oak (*Quercus*), pine (*Pinus*), and juniper (*Juniperus*) woodlands. Cave Creek has a riparian forest of sycamore (*Platanus*), cottonwood (*Populus*), and willow (*Salix*), whereas only oak, pine, and juniper occur in the
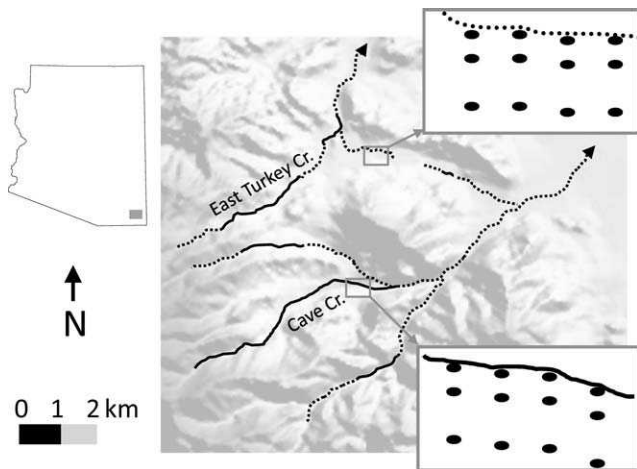
FIG. 1. Study location and topography near the sites at Cave Creek (perennial) and Graveyard Canyon (ephemeral; tributary to East Turkey Creek) in the Chiricahua Mountains of southeastern Arizona. Inset boxes show the experimental design, with 4 replicate artificial pools placed at each of 3 distances (5, 75, 250 m) from the stream channels at Cave Creek and Graveyard Canyon.

riparian area of Graveyard Canyon. The Cave Creek study site was on the grounds of the American Museum of Natural History's Southwestern Research Station. Mean annual precipitation at the Southwestern Research Station is ~450 mm and bimodal, with roughly half the precipitation occurring during brief, violent summer monsoon (July–September) storms and half during more prolonged winter storms (November–April). Daily rainfall over the study period was measured at the Southwestern Research Station.

Six-week colonization experiment

We measured colonization trends in artificial pools along and away from our 2 study streams for 6 wk (30 May–10 Jul 2009). This period was selected to encompass the peak of the spring (April–June) dry period and the beginning of the summer monsoon rains. We used 24 replicate 60-L black plastic tanks as artificial pools. We drilled holes at the top of each tank and screened them with 500-μm mesh to allow overflow. We filled each tank with well water and then added 10 g of dried oak (*Quercus*) and sycamore (*Platanus*) leaves to provide a food source and cover for colonists. We placed 12 artificial pools along Cave Creek and 12 artificial pools along Graveyard Canyon. At each stream, we placed 4 replicate artificial pools, spaced 100 m apart, at each of 3 distances (5, 75, and 250 m) from the stream channel (Fig. 1). We filled the artificial pools on 30 May and monitored them twice a week to remove large debris and check water levels. We conducted weekly visual

surveys of species presence/absence in each tank, without removing observed individuals, starting in week 2 of the experiment. Several genera of Chironomidae and most noninsect invertebrates (e.g., mites, springtails) were too small to be identified visually and were not included in analyses of visual survey data. Tank water was replenished by both rainfall and supplemental well water until 10 July, when we filtered the contents of each tank through a 250-μm-mesh net and preserved the contents of the net in 95% ethanol. We sorted, identified to the finest taxonomic level practical (species for Coleoptera and Hemiptera, genus for all other insects, family or order for noninsects), and enumerated aquatic invertebrates at Oregon State University.

We used 2-way analysis of variance (ANOVA) to test for differences in species richness and abundance with distance from channel (5, 75, 250 m) and stream (Cave Creek, Graveyard Canyon) as factors. We used 2-way nonparametric, permutation-based multivariate ANOVA (PERMANOVA) (PC-ORD, version 5.0, MjM Software, Gleneden Beach, Oregon; Anderson 2001) to analyze differences in final community composition with distance and stream as factors.

To ensure that our visual surveys were reliable, we quantified similarity between community matrices arising from final visual surveys and destructive sampling of each replicate pool using Sørensen's distances (a community dissimilarity measure). We used nonmetric multidimensional scaling (NMDS) ordination of a Sørensen distance matrix based on presence–absence data from the visual surveys to examine community assembly in the artificial pools over the 6-wk study period (PC-ORD).

Two-week colonization rate experiment

We conducted a 2-wk experiment (22 June–5 July 2009) to examine the relationship between aerial colonization rate and rainfall. We used 4 replicate artificial pools at each of 3 distances from the stream channel (5, 75, 250 m), but deployed artificial pools only along Cave Creek. We did not add leaf litter to the artificial pools, and we removed all aquatic invertebrate colonists every 12 h. The lack of leaf litter as a food source and the frequent removal of all aquatic invertebrates prevented community development, but preliminary observations indicated that the mere presence of water would be enough to induce many taxa to colonize otherwise empty artificial pools. We chose a 12-h sampling interval as compromise between logistical difficulties of more frequent sampling and capturing colonists before they left the resource-poor artificial pools.
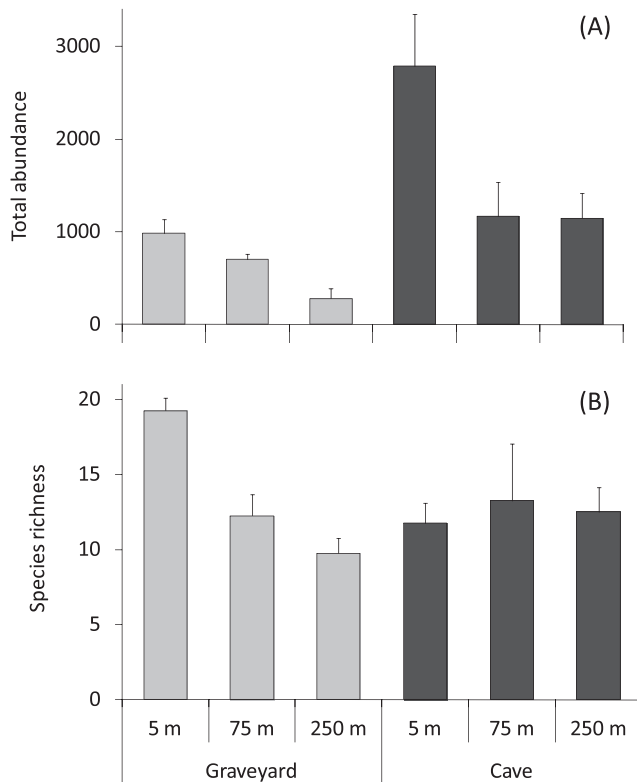
FIG. 2.   Mean (±1 SE) total abundance (A) and species richness (B) in replicate artificial pools at 3 distances (5 m, 75 m, 250 m) away from Cave Creek (perennial) and Graveyard Canyon (ephemeral) from destructive sampling of the artificial pools at the end of the 6-wk experiment.

We used linear regression to analyze the relationship between 24-h rainfall totals and abundance of colonists during the same 24-h period. We analyzed rainfall–colonist relationships for each treatment distance separately (5, 75, 250 m) and for the mean of all distances.

Results

Rainfall

Total rainfall was 105.4 mm over the 6-wk study period, and most (79.8 mm) occurred during a series of storms from 25–29 June. Weekly rainfall totals (mm) during the 6-wk colonization experiment were 0, 1.8, 0.5, 58.2, 30.7, and 14.2 mm for weeks 1 to 6, respectively. The 2-wk experiment ran during weeks 3 and 4 of the 6-wk experiment and included the late-June storms that marked the onset of the summer monsoon season. Daily rainfall totals during the 2-wk experiment (22 June–5 July) varied from 0 to 21.8 mm.

Six-week colonization experiment

Sixty-six taxa colonized the 24 artificial pools during the 6-wk colonization experiment (Appendix 1). These taxa included 38 Coleoptera, 13 Diptera, 2 Ephemeroptera, 7 Hemiptera, 1 Odonata, 1 Trichoptera, and 4 noninsect taxa. Nearly all individuals were insects (99.8%). Of the 66 taxa, 45 were in the adult stage and 21 taxa were larvae (Appendix 1).

The 12 artificial pools along Cave Creek contained 20,379 invertebrates and 47 taxa. These taxa represented 35% of summer-season taxa known from Cave Creek (based on June 2009 surveys; MTB, unpublished data). The 12 artificial pools along Graveyard Canyon contained 7861 invertebrates and 33 taxa. These taxa represented 30% of summer-season taxa known from the nearest perennial habitat, East Turkey Creek (based on June surveys from 2004–2009; Bogan and Lytle 2007, MTB, unpublished data). All taxa collected from artificial pools along Cave Creek also were found in Cave Creek, and all but 4 taxa from artificial pools along Graveyard Canyon were collected from nearby East Turkey Creek. These 4 taxa (*Copelatus chevrolati renovatus*, *Laccophilus sonorensis*, *Berosus infuscatus/fraternus*, and *Berosus stylifer*) are known from seasonal ponds 14 km east of Graveyard Canyon (Bogan et al., in press). Many of the taxa from Cave and East Turkey Creeks that did not colonize the artificial pools were Ephemeroptera, Plecoptera, and Trichoptera that prefer cool or running water (e.g., *Ecdyonurus* [Heptageniidae], *Siphlonurus* [Siphlonuridae], *Amphinemura* [Nemouridae] *Atopsyche* [Hydrobiosidae], and *Lepidostoma* [Lepidostomatidae]).

Mean invertebrate abundances were significantly higher (2–3×) in artificial pools 5 m away from both streams than in artificial pools at 75 and 250 m (Fig. 2, Table 1). Mean invertebrate abundances in artificial pools at all 3 distances were 2 to 3× higher along Cave Creek than along Graveyard Canyon. Mean invertebrate richness in artificial pools did not differ between streams, and when averaged across both streams, was marginally higher in artificial pools closest to the channel. The significant distance × stream interaction indicated that richness declined significantly with distance from the channel at Graveyard Canyon but not at Cave Creek (Fig. 2, Table 1).

Community structure in artificial pools differed significantly among distances from the stream channel and between Cave Creek and Graveyard Canyon, and the effect of distance differed between streams (Table 1). The most abundant taxa in artificial pools along both streams were *Callibaetis* (Baetidae) and *Apedilum* (Chironomidae). *Culiseta* (Culicidae), *Liodessus* (Dytiscidae), and early-instar Libellulidae also were common colonists at both sites. *Fallceon* (Baetidae), *Stempellinella*, *Paramerina*, and *Phaenopsectra* (Chironomidae) were common in Cave Creek artificial pools, but were rare or absent in Graveyard Canyon artificial pools.

TABLE 1. Results of analysis of variance (abundance and richness) and nonparametric permutation-based multivariate analysis of variance (community structure) for the effect of distance (5 m, 75 m, 250 m) and stream (perennial Cave Creek vs ephemeral Graveyard Canyon) on the abundance, richness, and community structure in replicate artificial pools at the end of the 6-wk experiment.

Source	df	Abundance		Richness		Community composition	
		F	p	F	p	F	p
Distance	2	8.275	0.003	3.448	0.053	3.5651	0.0004
Stream	1	17.455	0.001	0.221	0.644	4.7283	0.0004
Interaction	2	2.511	0.109	4.823	0.021	2.8073	0.002
Residuals	18						

Invertebrate richness in artificial pools increased slowly during the first 3 wk of our visual surveys, especially in the 75- and 250-m artificial pools (Fig. 3). Adult Coleoptera and Hemiptera arrived quickly in many artificial pools, often within minutes of filling. Culicidae and Chironomidae larvae and Ephemeroptera nymphs appeared in week 2, Hydroporinae beetle larvae appeared in week 3, and Odonata nymphs appeared in week 5. Mean species richness more than tripled in week 4 (mean increase in number of taxa =

FIG. 3. Mean (±1 SE) species richness from weekly visual surveys (beginning week 2) of replicate artificial pools at 3 distances (5, 75, 250 m) from Cave Creek (perennial) (A) and Graveyard Canyon (ephemeral) (B). Little rain fell during the first 3 wk of the experiment, but heavy monsoon rains began between weeks 3 and 4.

6.8 ± 1.5 [SD] after the 58.2 mm of rain that fell during week 3). This tripling of species richness was mainly the result of the arrival of new beetle taxa (see cue-limited taxa in Appendix 1). Species richness then leveled off or declined slightly in the last 2 wk of the experiment. Results from the NMDS ordination (stress: 0.21, $p = 0.02$) of the weekly visual survey presence/absence distance matrix mirrored the species richness results. Communities shifted weekly along the dominant NMDS axis 2 ($R^2 = 0.42$) until the 4th wk of the experiment (Fig. 4). In weeks 4 through 6, community types differed little along NMDS axis 2 (Fig. 4), a result suggesting that the community composition described by that axis had at least temporarily stabilized. Mean Sørensen's distance between the composition of final visual surveys and the destructive sampling of each artificial pool was 0.11 ± 0.2 (SE), indicating nearly 90% overlap in taxa identified visually and with a microscope.

Spatial and temporal presence/absence data from the visual surveys suggested 5 aerial dispersal modes among the colonist taxa documented during our study: 1) *widespread common* (found in most surveys, no spatiotemporal pattern), 2) *widespread haphazard* (found in 5–50% of surveys, no spatiotemporal pattern), 3) *cue-limited* (found >2.5× more frequently after rainfall), 4) *range-restricted* (found >2.5× more frequently in 5-m artificial pools), and 5) *infrequent* (found in <5% of surveys) (Table 2, Fig. 5). We placed 56 of the 66 taxa identified during the 6-wk colonization experiment into one of these 5 modes (Appendix 1). The remaining 10 taxa were not detected during weekly visual surveys, so we could not assign them to an aerial dispersal mode. Over 43% of these 56 taxa were infrequent dispersers, 34% were cue-limited, 11% were widespread haphazard, 7% were range-restricted, and 5% were widespread common. Infrequent dispersers included Coleoptera, Hemiptera, Ephemeroptera, Trichoptera, Odonata, and noninsects. Cue-limited dispersers were predominantly Coleoptera, whereas widespread haphazard
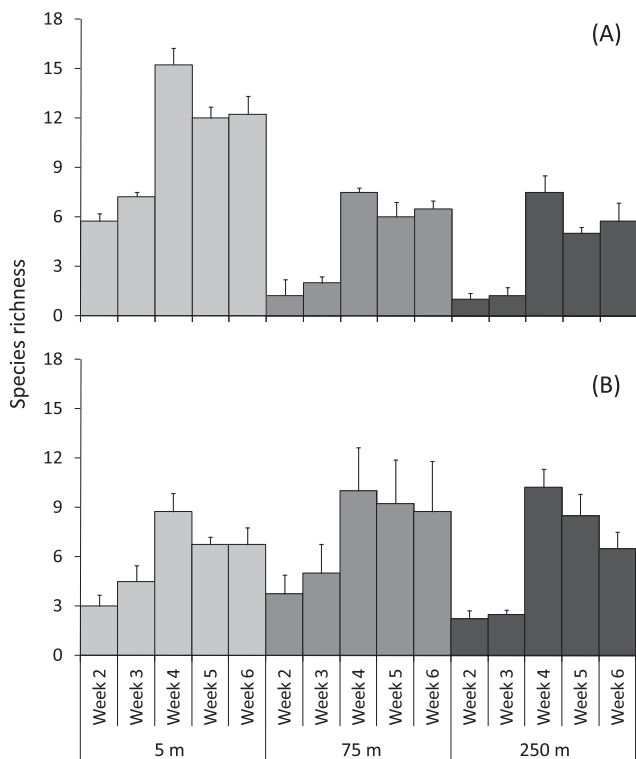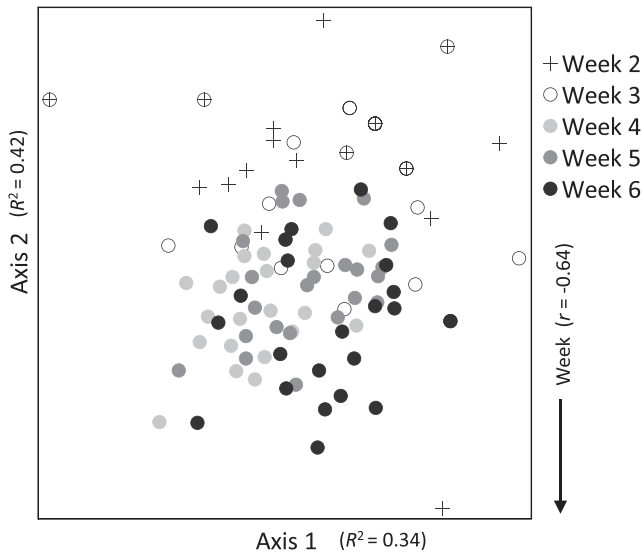
FIG. 4. Nonmetric multidimensional scaling ordination plot of community development in all 24 artificial pools based on a presence/absence community matrix derived from weekly visual surveys during the 6-wk experiment. Artificial pool communities changed progressively along axis 2 through week 3, but were fairly similar to one another in weeks 4 through 6.

dispersers included Coleoptera and Diptera. Range-restricted dispersers were exclusively Diptera, and widespread common dispersers included one taxon each of Coleoptera, Hemiptera, and Diptera.

Two-week colonization rate experiment

We identified 21 colonist taxa (20 Coleoptera and 1 Hemiptera) during the 2-wk colonization experiment. Despite the short time period of the experiment and the lack of leaf-litter and potential prey base, 2593 Coleoptera and Hemiptera colonized the 12 artificial pools. Using the modes suggested by the 6-wk

experiment, nearly 48% of the taxa from the 2-wk experiment were cue-limited dispersers, 33% were infrequent, 9% were widespread common, and 9% were widespread haphazard. Total abundance of colonists summed across all 12 artificial pools was strongly associated with amount of daily rainfall amount (Fig. 6). Rainfall amount explained 75% of the variation in colonization rate when averaged across the 3 distances ($\beta = 0.83$, $p < 0.001$; Fig. 7). When considered individually, regression coefficients were highest and the most variance in colonization rate was explained by rainfall in the 250 m artificial pools ($R^2 = 0.77$, $\beta = 1.73$, $p < 0.001$), with decreasing but still significant regression coefficients at 75 m ($R^2 = 0.48$, $\beta = 0.41$, $p = 0.006$) and 5 m ($R^2 = 0.70$, $\beta = 0.34$, $p < 0.001$).

Differences between the experiments

All 21 taxa collected during the 2-wk experiment also were collected during the 6-wk colonization experiment. Relative abundances of the 5 aerial dispersal modes for those 21 taxa largely followed the patterns found in the 6-wk experiment, except for the lack of range-restricted taxa, a higher percentage of cue-limited taxa, and a lower percentage of infrequent taxa. Taxa from the 6-wk experiment that were not found in the 2-wk experiment (Appendix 2) included larvae of all Chironomidae and Culicidae, Ephemeroptera and Odonata nymphs, larval Coleoptera, numerous adult Coleoptera and Hemiptera, and noninsect invertebrates.

Discussion

Aerial dispersal of aquatic invertebrates along and among drainages is important for maintaining local populations, but spatial and temporal variation in aerial dispersal is rarely measured. The spatial and temporal patterns of aerial dispersal varied significantly among species at relatively small spatial scales

TABLE 2. Five aerial dispersal modes suggested by visual surveys over the 6-wk colonization experiment. Visual surveys were conducted in weeks 2 through 6 in all 24 artificial pools along and away from Cave Creek and Graveyard Canyon, resulting in 120 possible pool × week occurrences for any given taxon. For cue-limited taxa, >2.5× as many occurrences were documented in weeks 4 through 6 after heavy rainfall than in prior weeks. For range-restricted taxa, >2.5× as many occurrences were documented in artificial pools 5 m from stream than in artificial pools 75 and 250 m from the stream combined. See Fig. 5 for a diagrammatic representation of the 5 dispersal modes.

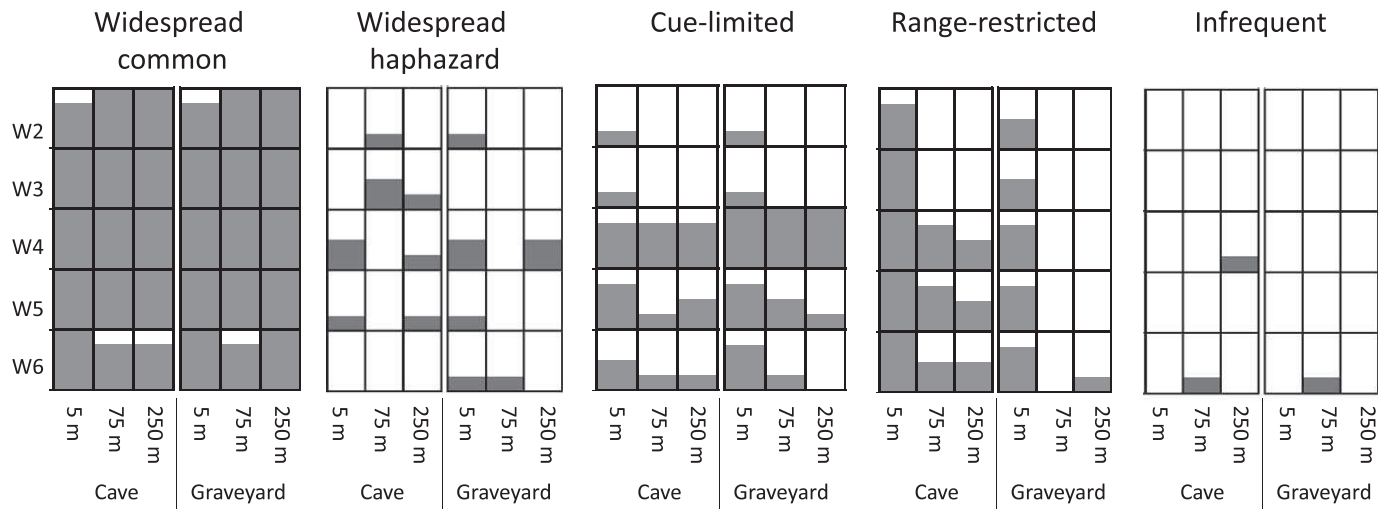| Aerial dispersal mode	% occurrence in surveys			Occurrences after rainfall		Occurrences next to stream	
	>50%	5–50%	<5%	>2.5× higher	No pattern	>2.5× higher	No pattern
Widespread common	X				X		X
Widespread haphazard		X			X		X
Cue-limited		X		X			X
Range-restricted		X			X	X	
Infrequent			X		X		X

FIG. 5. Diagrammatic representation of the 5 aerial dispersal modes identified in weekly visual surveys during weeks 2 through 6 (W2–W6) of the 6-wk experiment. A box completely shaded with dark grey indicates that a given species was found in all 4 replicate artificial pools at that distance for that site and week, whereas a box with no grey indicates that the species was not detected in any artificial pools at that site and week. Species used to illustrate the dispersal modes here are *Liodessus* (widespread common), *Sanfilippodytes* (widespread haphazard), *Rhantus gutticollis* (cue-limited), *Culex* (range-restricted), and *Berosus moerens* (infrequent).

(<250 m). This species-specific variation in aerial dispersal mode resulted in discernible patterns in the abundance and composition of colonists in artificial pools at different distances from our arid-land study streams.

Spatial dispersal patterns

Abundance of aquatic invertebrates decreased with increasing distance from the stream channel at the perennial site, Cave Creek, as we predicted. Decreasing abundance of dispersing aquatic invertebrates
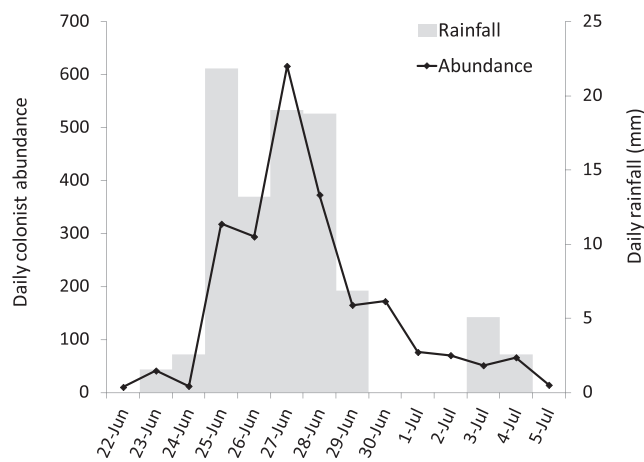
with increasing distance from potential source populations has been observed in Odonata (McCauley 2006), Chironomidae (Delettre and Morvan 2000), Dytiscidae (Wilcox 2001), Ephemeroptera, Plecoptera, and Trichoptera (e.g., Petersen et al. 2004), and adult aquatic insects as a group (Jackson and Resh 1989). Contrary to our predictions, the effect of distance on abundance of dispersers also was significant at the

FIG. 6. Synchronicity of daily rainfall (mm) and the sum of colonist abundances across the 12 artificial pools during the 2-wk experiment.
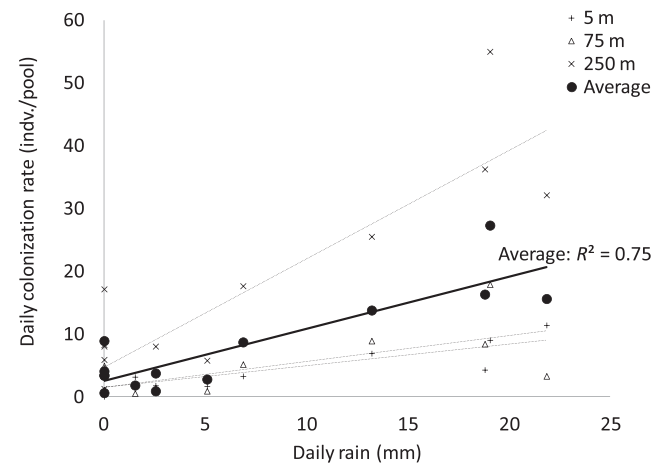

FIG. 7. Regression for colonization rate as a function of daily rainfall during the 2-wk experiment. The regressions were significant for each of the 3 treatment distances (5, 75, 250 m), but the slope became steeper at greater distances from the stream. Rainfall explained 75% of the variation in the mean colonization rate of all 3 treatment distances combined.

ephemeral site. We had expected that because no local source of dispersers was apparent in the dry channel of Graveyard Canyon, invertebrates dispersing overland from other sources would be equally likely to encounter artificial pools along and away from the dry channel. Instead, artificial pools 5 m from the dry channel contained significantly more invertebrates than artificial pools 75 and 250 m away from the channel. This result suggests that aquatic invertebrates dispersing from nearby perennial sources (e.g., East Turkey Creek; Fig. 1) may preferentially follow dry stream courses in search of new habitat. In New Zealand, Winterbourn et al. (2007) also found that dry streams may be important dispersal corridors for adult aquatic insects. Light-colored fine substrata in some dry channels (e.g., quartz-dominated sands) may reflect more light than the surrounding vegetated landscape, perhaps providing an attractive pathway for taxa that use reflected light to find colonization sites (Csabai et al. 2006). Moreover, stream channels are the lowest areas of the surrounding landscape, so aerial dispersers might simply avoid ridges and follow the lowest pathways through the landscape. We studied only one ephemeral stream, and therefore, are limited in our ability to generalize, but our findings provide support for the idea that ephemeral stream channels could be important dispersal corridors for adult aquatic invertebrates.

Communities in more isolated habitats tend to have fewer species because they experience lower rates of dispersal from source habitats (Cadotte 2006). However, we found no relationship between distance and richness at the perennial Cave Creek and a strong decline in richness with distance at the ephemeral Graveyard Canyon. To explore what may be driving this surprising result, we examined the occurrences of common species in artificial pools at both sites. At Graveyard Canyon, all abundant taxa were more likely to be found in artificial pools adjacent to rather than away from the stream channel. However, at Cave Creek, several abundant taxa, including Libellulidae dragonfly nymphs, the midge *Pseudochironomus*, and the beetles *Anacaena*, *Hydraena*, and *Liodessus,* were rarely or never encountered in artificial pools adjacent to the stream, but were common in the more distant 75- and 250-m artificial pools. A post hoc assessment of the contrasting effects of distance on the presence and abundance of these 5 taxa between the 2 streams was sufficient to explain the lack of distance effect on species richness at Cave Creek (Fig. 2B). When these 5 taxa were removed from analyses, invertebrate richness and abundance both decreased with distance from Cave Creek and Graveyard Canyon.

Rather than being a violation of the long-standing idea that disperser or colonist abundance and richness decrease with increasing isolation (MacArthur and Wilson 1967), the pattern that these 5 taxa exhibited in Cave Creek artificial pools may be an example of a hump-shaped relationship between isolation and disperser abundance. McCauley et al. (2009) noted such a hump-shaped isolation–abundance relationship for the backswimmer *Notonecta irrorata* in artificial pools placed 0 to 1200 m from potential source populations. Dispersing individuals of some species may not colonize sites closest to their natal habitat, and instead colonize sites at moderate distances, presumably a mechanism to avoid inbreeding or deteriorating environmental conditions associated with the natal habitat (McCauley et al. 2009). If taxa were dispersing away from Cave Creek, they may have flown past the closest artificial pools and preferentially colonized more distant pools. In contrast, taxa dispersing along or away from the ephemeral channel of Graveyard Canyon already would have traveled a minimum of 900 m from the nearest perennial pools in East Turkey Creek and may not have been able to risk further travel in search of aquatic habitat. The spatial scale of our study does not allow us to quantify the exact hump-shaped isolation–abundance relationship for these 5 taxa, but they appear to increase in abundance between 0 and 250 m and then decrease in abundance by 900 m, if not closer. Further studies on species-specific aerial dispersal patterns over moderate spatial scales (≥ 1 km) are needed to determine whether hump-shaped isolation–abundance patterns are common or rare for aquatic invertebrate taxa.

Temporal dispersal patterns

During the warm dry weather in the first half of our 6-wk experiment, several Coleoptera and Hemiptera species and a few species of Chironomidae and Culicidae arrived and oviposited and their larvae began to develop in the artificial pools. Warm dry weather conditions have previously been associated with increased dispersal of multiple species of aquatic Coleoptera (Ryker 1975, Miguelez and Valladares 2008) and Hemiptera (Pajunen and Jansson 1969). Additionally, arid-land streams often have large swarms of midges on warm summer evenings (Jackson 1988). Chironomidae colonization of artificial pools in the floodplain of a large Alabama river also peaked in warm summer months (Tronstad et al. 2007). Up to 14 chironomid taxa, including 4 of the same genera that colonized our artificial pools (*Apedilum*, *Larsia*, *Labrundinia*, and *Tanytarsus*) colonized artificial pools in the

Alabama floodplain in <3 wk. In other studies examining the colonization of artificial pools, chironomids (e.g., *Chironomus*) and culicids (e.g., *Culiseta*) often were among the first colonists to arrive, regardless of season (Velasco et al. 1993). One third of the taxa detected during our 2-wk experiment colonized artificial pools in low numbers on dry days, indicating a small, but measureable background rate of dispersal for several aquatic species.

The slow arrival of a limited number of species during dry weather was interrupted by the onset of monsoon rainfall when nearly 60 mm of rain fell between our visual surveys in weeks 3 and 4 of the 6-wk experiment. Heavy rainfall and high humidity have been associated with reduced dispersal of aquatic macroinvertebrates (Miguelez and Valladares 2008, Boix et al. 2011), but species richness in our artificial pools more than doubled during that rainy week (Fig. 3A, B). The results from our 2-wk experiment provide support for the importance of rainfall in triggering or facilitating aquatic invertebrate dispersal in our study system. Daily rainfall amount explained up to 77% of the variation in daily abundance of tank colonists (Figs 6, 7). Furthermore, the slope of the relationship between rainfall and number of colonists increased with distance from the stream, a result indicating that rainfall was important for facilitating dispersal to more isolated habitats. The contrast between our findings and those in past studies may be a result of our study's arid location. Rainfall in arid regions may be a signal that new, seasonal habitats are available and could trigger dispersal to these new habitats, as it does for some Belostomatidae (Lytle and Smith 2004) and Scaphiopodidae anurans (Stebbins 2003). Moreover, in a hot arid landscape, the increased humidity associated with rainfall may facilitate successful dispersal by reducing the risk of desiccation while traveling through the terrestrial environment.

Rainfall explained up to 77% of the variation in aerial disperser abundance in our study, but other environmental factors are also likely to be important triggers or facilitators of aerial dispersal. Drying habitat and rising stream temperatures can trigger aerial dispersal from isolated arid-land stream pools (Velasco and Millan 1998). The process of pool habitat contraction was occurring in our perennial study streams before monsoon rains began (MTB and KSB, personal observation). These decreasing pool levels probably provided a cue that local habitat conditions were deteriorating and may have provided additional impetus to leave the pool as soon as rainfall signaled that newly wetted habitats might be available. We did not measure wind direction or intensity, but it is likely that calmer conditions immediately after monsoon rains would make it easier for many species to fly because lighter winds have been correlated with higher rates of aerial dispersal in other studies (Briers et al. 2003, Boix et al. 2011). However, aerial dispersal of the smallest stream invertebrate species may increase during windy conditions because these smaller taxa are carried farther by wind than they would be able to disperse on their own (e.g., flightless microcrustaceans: Caceres and Soluk 2002, microcaddisflies: Jackson and Resh 1989). Small, flightless invertebrates were too rare in our study to assess the effects of environmental factors on their aerial dispersal. Future studies should incorporate measurements of wind direction and speed to separate the effects of wind and precipitation on aerial dispersal patterns.

Aerial dispersal modes

We classified taxa from our study into 1 of 5 spatiotemporal aerial dispersal modes based on the timing and extent of their colonization of artificial pools (Table 2, Fig. 5). These 5 modes provide substantially more information about the tendency of a given species to disperse through time and the distance or direction that it might disperse than do previously published aerial dispersal modes (Poff et al. 2006, Bonada et al. 2007). Our modes also take into account the potential importance of precipitation as a dispersal cue. Time-consuming work is required to quantify the aerial dispersal ability of individual species, but we argue that the utility of this information makes the effort worthwhile. Understanding species-specific variation in aerial dispersal ability will allow researchers and managers to develop spatially explicit predictive models of community responses to anthropogenic disturbance (Patrick and Swan 2011), stream restoration (Parkyn and Smith 2011), and climate change (Bonada et al. 2007).

In streams that experience large seasonal or interannual expansion and contraction of wetted habitat, such as arid-land streams (Stanley et al. 1997, Bogan and Lytle 2007) and large temperate rivers (Tronstad et al. 2007), aerial dispersal can be the primary means of recolonizing rewetted habitats. In our study region, long-term drought is causing isolated formerly perennial streams to experience unprecedented drying. After total stream drying and subsequent rewetting at one Arizona stream, French Joe Canyon, the hemipteran *Microvelia* and the coleopteran *Liodessus* were both early colonizers and dominant post-drying community members (Bogan and Lytle 2011), as would be predicted given the widespread common dispersal mode we assigned these taxa. Several taxa incapable of aerial dispersal were extirpated by the

drying event at French Joe and had not recolonized the stream 4 y after the initial drying and rewetting event. Taxa classified as infrequent or range-restricted aerial dispersers would be unlikely to recolonize isolated habitats, such as French Joe, after drought-induced stream drying or other disturbances.

We used artificial pools to measure aerial dispersal of aquatic invertebrates, but the dispersal of some taxa may not be detected by this method. Local perennial stream habitat is dominated by isolated pools during the dry season, but small lotic patches do remain and most of the rheophilic Ephemeroptera, Plecoptera, and Trichoptera taxa found in these patches (e.g., Heptageniidae, Nemouridae, and Hydrobiosidae) did not colonize our artificial pools. Other methods, such as sticky or Malaise traps (Jackson and Resh 1989, Petersen et al. 2004) or pan traps (Delettre and Morvan 2000), may be necessary to identify aerial dispersal modes for these taxa. In addition, researchers could use recirculating pumps and coarse mineral substrate in artificial pools to encourage colonization by dispersing rheophilic taxa. That relatively few range-restricted taxa were identified in our study probably was the result of our failure to detect rheophilic dispersers. Many rheophilic Ephemeroptera, Plecoptera, and Trichoptera preferentially disperse along rather than away from streams (Petersen et al. 2004, Macneale et al. 2005, Winterbourn et al. 2007).

In addition to quantifying aerial dispersal modes of rheophilic taxa, future investigations should address the seasonality of aerial dispersal and precise arrival times of influential taxa (e.g., predators). Many investigators have found that aerial dispersal of aquatic invertebrates tends to peak during summer months (e.g., Tronstad et al. 2007), but many Odonata, Coleoptera, and Hemiptera taxa undergo spring and autumn migration flights (Corbet 1999, Stevens et al. 2007). In Spain, numerous species colonized artificial pools throughout the year, including during the cold winter months of January and February (Velasco et al. 1993). In our study region, large mixed-species dispersal swarms of thousands of aquatic Coleoptera and Hemiptera occur in both spring and autumn (Stevens et al. 2007). These large swarms also are likely to have strong ecological effects on the pools they colonize. The arrival of large predatory taxa, like Dytiscidae, could negatively affect the presence or abundance of other early colonists in new habitats. Additional studies are needed that quantify or manipulate the precise arrival patterns of such predatory taxa to determine the effect of their arrival on other early colonists.

The results of our 2 complementary experiments suggest that any future studies must acknowledge the different information content provided by various measures of dispersal. We destructively sampled artificial pools in the 2-wk experiment every 12 h, thereby preventing community development (Appendix 2). We included a leaf-litter food source and destructively sampled only once in the 6-wk experiment, thereby allowing communities to develop through time. Our 2-wk experiment was more likely to measure arrival at new habitats than colonization per se. Both arrival and colonization are important measures of dispersal, but they provide different types of information about the capacity to find new habitats vs the decision to stay and reproduce in the new habitat. In studies of community development, these 2 mechanisms are often impossible to differentiate (Vonesh et al. 2009), but our paired experiments provided a means to tease apart these different yet complementary processes and may provide a model for future studies.

Acknowledgements

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APPENDIX 1. All taxa collected from or observed in artificial pools during the 6-wk experiment listed in order of their aerial dispersal modes. Taxa not identified during visual surveys (i.e., only from destructive sampling) could not be associated with a dispersal mode and are listed as unknown. All taxa listed represent adult invertebrate colonists unless indicated by an (L) for larvae.

Aerial dispersal mode	Order	Family	Genus/species
Widespread common	Coleoptera	Dytiscidae	*Liodessus*
	Diptera	Chironomidae	*Apedilum* (L)
	Hemiptera	Veliidae	*Microvelia*
Widespread haphazard	Coleoptera	Dytiscidae	*Sanfilippodytes*
		Dytiscidae	*Stictotarsus aequinoctialis*
		Hydrophilidae	*Tropisternus ellipticus*
	Diptera	Chironomidae	*Chironomus* (L)
			Paratanytarsus (L)
			Psuedochironomus (L)
Cue-limited	Coleoptera	Dryopidae	*Helichus suturalis*
			Helichus triangularis
			Postelichus immsi
		Dytiscidae	*Copelatus chevrolati renovatus*
			Desmopachria portmanni
			Hydroporinae (L)
			Laccophilus fasciatus
			Neoclypeodytes
			Rhantus atricolor
			Rhantus gutticollis gutticollis
			Rhantus gutticollis mexicanus
			Rhantus (L)
		Hydraenidae	*Hydraena*
		Hydrophilidae	*Berosus salvini*
			Berosus (L)
			Cymbiodyta
			Helophorus
	Ephemeroptera	Baetidae	*Callibaetis* (L)
	Hemiptera	Corixidae	*Graptocorixa serrulata*
Range-restricted	Diptera	Culicidae	*Anopheles* (L)
			Culex (L)
			Culiseta (L)
		Chironomidae	*Paramerina* (L)
Infrequent	Coleoptera	Dytiscidae	*Laccophilus maculosus*
			Laccophilus pictus
			Laccophilus sonorensis
			Stictotarsus corvinus
			Stictotarsus striatellus
		Gyrinidae	*Dineutus sublineatus*
			Gyrinus plicifer
		Haliplidae	*Peltodytes dispersus*
		Hydrophilidae	*Anacaena*
			Berosus infuscatus/fraternus
			Berosus moerens
			Berosus stylifer
			Enochrus carinatus
			Helochares normatus
			Laccobius cf. *hardyi*
	Ephemeroptera	Baetidae	*Fallceon* (L)
	Hemiptera	Gerridae	*Aquarius remigis*
		Naucoridae	*Ambrysus woodburyi*
		Nepidae	*Ranatra quadridentata*
		Notonectidae	*Notonecta lobata*
		Veliidae	*Rhagovelia varipes*
	Odonata	Libellulidae	Indeterminate (L)
	Trichoptera	Helicopsychidae	*Helicopsyche* (L)
	Noninsect	Hydracarina	Indeterminate (L)

Appendix 1. Continued.

Aerial dispersal mode	Order	Family	Genus/species
Unknown	Coleoptera	Hydraenidae	*Octhebius* cf. *lineatus*
			Octhebius cf. *puncticollis*
	Diptera	Chironomidae	*Labrundinia* (L)
			Larsia (L)
			Phaenopsectra (L)
			Stempellinella (L)
			Tanytarsus (L)
	Noninsect	Copepoda	Copepoda
	Noninsect	Hydracarina	*Mucronothrus*
	Noninsect	Collembola	Sminthuridae

Appendix 2. Taxa recorded from the 6-wk experiment (artificial pools with leaf litter that were not sampled destructively until the end of week 6) that were not recorded from the 2-wk experiment (artificial pools with no leaf litter that were sampled destructively every 12 h), listed in columns by aerial dispersal mode.

Widespread common	Widespread haphazard	Cue-limited	Range-restricted	Infrequent	Unknown
Apedilum	*Stictotarsus aequinoctialis*	*Berosus* (larvae)	*Anopheles*	*Ambrysus woodburyi*	Copepoda
	Chironomus	*Callibaetis*	*Culex*	*Aquarius remigis*	*Labrundinia*
	Paratanytarsus	*Graptocorixa serrulata*	*Culiseta*	*Dineutus sublineatus*	*Larsia*
	Pseudochironomus	*Helichus triangularis*	*Paramerina*	*Fallceon quilleri*	*Mucronothrus*
		Hydroporinae (larvae)		*Gyrinus plicifer*	*Phaenopsectra*
		Neoclypeodytes		*Helicopsyche*	Sminthuridae
		Postelichus immsi		*Helochares normatus*	*Stempellinella*
		Rhantus gutticollis mexicanus		Hydracarina	*Tanytarsus*
		Rhantus (larvae)			
				Laccobius cf. *hardyi*	
				Laccophilus maculosus	
				Laccophilus sonorensis	
				Libellulidae	
				Notonecta lobata	
				Peltodytes dispersus	
				Ranatra quadridentata	
				Rhagovelia varipes	
				Stictotarsus corvinus	
				Stictotarsus striatellus	