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INFLUENCE OF ANNUAL FLOODING ON TERRESTRIAL ARTHROPOD ASSEMBLAGES OF A RIO GRANDE RIPARIAN FOREST

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ABSTRACT

Terrestrial arthropod communities remain poorly described for riparian ecosystems of the arid southwestern United States, and the effects of extensive river regulation and habitat alteration on these potentially important invertebrates are largely unknown. Beginning in 1991, surface-active arthropods were trapped at two riparian sites along the Rio Grande, in central New Mexico, for 2 years. One site was then experimentally flooded from mid-May to mid-June for each of the next 3 years to simulate historic, low intensity flooding, after which arthropod collections were continued. These primary sites, located outside the riverside levee, and isolated from flooding for about 50 years prior to the experiment, were compared with a naturally flooded site and a second non-flooded reference. Experimental flooding and observations of the naturally flooded site indicated that flooding did not affect total taxonomic richness, nor richness of spiders, beetles or ants. However, flooding may have slightly increased the number of carabid beetle taxa present. Flooding altered the overall composition for all taxa, insects, beetles and carabid beetles. Spider taxa composition may be insensitive to flooding, while ant responses were not clear. Abundance of terrestrial isopods and spiders decreased after flooding, while overall beetle abundance did not change. Abundance of crickets and carabid beetles increased, but the response was delayed until after the second flood. Changes in taxa composition and abundance after experimental flooding were generally consistent with arthropod community structure observed at a nearby naturally flooded site. This similarity suggests that reorganization of the terrestrial arthropod community may follow restoration of flooding to this riparian ecosystem. Copyright © 2001 John Wiley & Sons, Ltd.

KEY WORDS: arid; arthropod; biodiversity; disturbance; flood pulse; riparian; river regulation

INTRODUCTION

Periodic flooding controls a variety of functional and structural aspects of large river floodplain ecosystems (Junk *et al.*, 1989; Szaro, 1991; Bayley, 1995). For example, flooding creates habitat for seedling establishment of many riparian plants (Stromberg *et al.*, 1991; Malanson, 1993; Scott *et al.*, 1993), and regulates rates of nutrient cycling and productivity (Junk *et al.*, 1989; Sparks *et al.*, 1990; Gregory *et al.*, 1991; Bayley, 1995). However, along many floodplain rivers throughout the world, this hydrologic connection has been disrupted through modifications of river flow and channel morphology (Benke, 1990; National Resource Council, 1992; Dynesius and Nilsson, 1994; Poff *et al.*, 1997), which has resulted in extensive changes in riparian ecosystems (Fenner *et al.*, 1985; Rood and Mahoney, 1990; Howe and Knopf, 1991; Stromberg and Patton, 1991; Poff *et al.*, 1997). One component of riparian ecosystems often overlooked when assessing the effects of river regulation is the assemblage of terrestrial arthropods. While well studied in some systems, such as the floodplain forests of the Central Amazon, where terrestrial arthropods exhibit a variety of adaptations to cope with periods of inundation lasting up to 6 or 7 months (Adis, 1997), the effects of both natural flooding and river regulation on terrestrial arthropods in most riparian systems is unknown.

Arthropods dominate terrestrial ecosystems, both in terms of the number of species and the number of individuals (Erwin, 1982, 1988; Wilson, 1988; Gaston, 1991; Kremen *et al.*, 1993; Samways, 1994).

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Terrestrial arthropods play essential ecological roles, acting as detritivores, pollinators, herbivores, predators and parasites, influencing nutrient cycling, plant productivity, the abundance of other invertebrates, and serving as prey for many vertebrates (Price, 1984; Brown, 1991; Kellert, 1993; Kim, 1993; Williams, 1993). These arthropod assemblages remain poorly described for many ecosystems, however, especially relative to the more visible vertebrate fauna (Oliver and Beattie, 1996), even though inventories of terrestrial invertebrates may provide as useful information for environmental monitoring and conservation practices as similar inventories of vertebrates or flowering plants (Brown, 1991; Kremen *et al.*, 1993; Samways, 1994; Oliver and Beattie, 1996). Riparian areas of the arid southwestern United States are known to support a disproportionately high diversity and density of vertebrates compared with drier uplands (Ohmart and Anderson, 1982; Knopf *et al.*, 1988; Szaro, 1991), but little information is available on the composition of arthropod communities in these ecosystems. Further, while vegetational changes and decreased habitat availability in these riparian ecosystems have negatively affected vertebrate species, such as neotropical migrant birds (e.g. Kreuper, 1992; Hubbard, 1996; Yong and Finch, 1996), effects on local arthropod communities are largely unstudied. With little baseline information available to determine whether existing arthropod communities in riparian ecosystems represent those of pre-alteration conditions, it is difficult to know how the disruption of flooding has impacted these populations.

Efforts are now underway to restore flooding to a number of river–floodplain ecosystems (Poff *et al.*, 1997; Molles *et al.*, 1998; Schmidt *et al.*, 1998; Toth *et al.*, 1998). As part of a study examining effects of periodic flooding on the Rio Grande riparian forest in central New Mexico (Molles *et al.*, 1998), we monitored surface-active (epigeal) arthropods, typically dominated in richness by beetles, spiders and ants. This community is described by Crawford (1991) as the 'temporary dwellers' of the soil and litter, which are generally less restricted to the soil than the nematodes and microarthropods, such as collembolans and mites. These arthropods exhibit a range of trophic roles, including detritivores, predators and herbivores. Because they inhabit the forest floor, we expect this group to be immediately impacted by flooding. They are also relatively easy to capture and identify. We monitored surface-active arthropods at riparian sites isolated from flooding, following experimental flooding at one of these previously dry sites, and at a naturally flooded site.

We address three main questions with respect to the assemblage of surface-active arthropods: (1) Does flooding affect the number of taxa present?; (2) Does flooding affect the composition of taxa?; and (3) Does flooding affect the relative abundance of key populations?

METHODS

Study sites and experimental flooding

Two study sites were established during the summer of 1991, in a mixed cottonwood forest at the Bosque del Apache National Wildlife Refuge, elevation approximately 1400 m, Socorro County, New Mexico (Figure 1). The refuge contains approximately 14.5 km of the Rio Grande and its associated riparian vegetation. The 3.1 ha study sites were located 3.7 km apart in a strip of continuous forest, 200–300 m wide. The canopy was dominated by *Populus deltoides* subsp. *wislizenii* (Rio Grande cottonwood) ranging from 8 m to 15 m in height, with a subcanopy of *Salix gooddingii* (Goodding willow) and *Tamarix ramosissima* (saltcedar). Understory shrubs included *Baccharis glutinosa* (seepwillow) and *Forestiera neomexicana* (New Mexico olive) in varied proportions, as well as scattered *Elaeagnus angustifolia* (Russian olive), *Prosopis pubescens* (screwbean mesquite), *Lycium torreyi* (wolfberry) and *Amorpha fruticosa* (desert indigobush). The composition and density of the herbaceous understory varied among years, but generally included *Conyza canadensis*, *Chamaesyce serpyllifolia*, *Ratibida tagetes*, *Solanum elaeagnifolium*, and *Sphaeralcea angustifolia*. Patchy, but often deep, litter layers were present (Ellis *et al.*, 1999). Soils also varied considerably on a small spatial scale (often within meters), ranging from largely sandy to highly clayey (C.S. Crawford, unpublished data).

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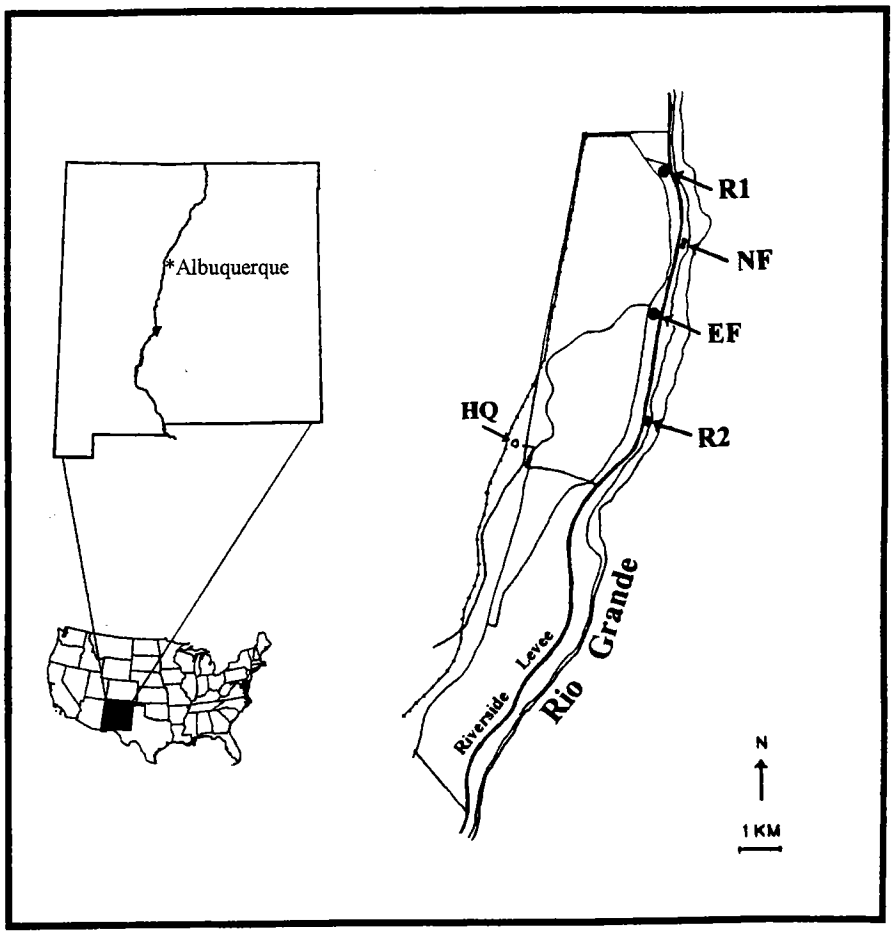

Figure 1. Location of study sites within Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico. The four study sites are Experimental Flood (EF), Natural Flood (NF), Reference-1 (R1), and Reference-2 (R2); refuge headquarters is indicated (HQ). The location of the refuge (▼) is indicated on the inset map of New Mexico

The sites were approximately 0.5 km west of the Rio Grande, and separated from it by the low-flow conveyance channel and riverside levee that parallel the river (Figure 1). After collecting baseline data at both sites for 2 years, one site, designated the 'Experimental Flood' site, was inundated for approximately 1 month during each of the following 3 years: 17 May–12 June 1993, 19 May–19 June 1994, and 17 May–17 June 1995. Floods were timed to match the historical peak flow for the upper Rio Grande, based on the mean annual hydrograph for 1889–1990 at the US Geological Survey gauging station at Embudo (Slack *et al.*, 1993), located upstream from major flow regulation. Water was taken from a riverside canal via a water diversion structure, and included a combination of water diverted directly from the Rio Grande, irrigation return flows from agricultural fields, and ground water recharge accumulated in the nearby low-flow channel (J. Taylor, personal communication). Experimental floods inundated approximately 10 ha of riparian forest floor at Experimental Flood during 1993, 1994 and 1995. Water depth varied from nearly 20 cm to 200 cm across the site as a result of topographic variation; average depth was about 50 cm. Throughout the study, the second site, 'Reference-1', remained unflooded.

In 1994, a section of forest within the refuge that was still flooded directly from the river was found, permitting comparison with the experimentally flooded site. This riparian forest was approximately 200 m east of the primary sites and bounded on the east side by the Rio Grande, and on the west by the levee (Figure 1). In August 1994, the 'Natural Flood' site was established, as well as an additional dry reference

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site ('Reference-2'), located south of Natural Flood in an area largely protected from flooding by a groin. These riverside sites each covered approximately 1.1 ha, and supported a primarily cottonwood forest, with understory vegetation including saltcedar, seepwillow, New Mexico olive and Russian olive. Herbaceous understory vegetation was sparse, particularly at Natural Flood, where the cottonwood canopy was more dense. Forest floor litter was also sparse at Natural Flood (Ellis *et al.*, 1999), while the soil had a well developed crumb structure and high silt content (C.S. Crawford, unpublished data). In contrast, forest floor litter was quite deep at Reference-2, and its soil had slightly higher proportions of sand and clay. In 1995, flooding at Natural Flood lasted for approximately 2.5 months from mid-May to late July, and surface water height measured at one typical location averaged about 20 cm.

Trapping procedures

Pitfall traps are commonly used for cursorial arthropods active on the soil surface, such as spiders, beetles and ants (Southwood, 1978). Although there are complications associated with any sampling method, pitfall traps can provide useful information for population and community studies (Southwood, 1978; Adis, 1979). In particular, such data can provide information on the species composition of communities, including comparisons between different sites within the same sampling period (Adis, 1979). To avoid sampling biases, we focused these analyses on relative differences between the flooded and reference sites during the study period, and, in particular, on changes at Experimental Flood, relative to Reference-1 after flooding.

Surface-active arthropods were sampled using 30 pitfall traps distributed throughout each site. At Experimental Flood and Reference-1, traps were oriented around a mammal trapping web, with 12 transects of 100 m radiating out from a center point. Beginning 65–75 m from the center of each transect, two or three pitfall traps (alternating lines) were located 10 m apart along the transect. Because the riparian forest was narrower at Natural Flood and Reference-2, parallel trapping lines were used instead of webs. Six pitfall traps were spaced at 10 m intervals along each of five transects at each site; transects were separated by 40 m. Each trap consisted of two plastic cups, 9 cm diameter and 12 cm deep, one inside the other and set into the ground, so the open tops were flush with the surface; the inner cup could be removed to collect specimens, while the outer cup maintained the trap location. Each trap was sheltered with a 15 × 15 cm wooden cover raised approximately 3 cm above the surface when open. Traps were left dry (no preservatives) at all times, but were kept closed between trapping sessions.

Traps were opened for 48 h during each trapping session, usually the third week of the given month. Collections at Experimental Flood and Reference-1 were made in July, August, October, and December 1991, and in February, April, June, August, October, and December during each of 1992, 1993, 1994, and 1995, with additional samples collected during May of 1993, 1994, and 1995, immediately prior to flooding. No collections were made in December 1992 because of heavy snowfall. Natural Flood and Reference-2 were sampled in August, October, and December 1994, and as at the other sites in 1995, except for June, which was excluded because Natural Flood was under water. Captured arthropods were collected into plastic bags and frozen, then later identified and counted. Identifications were made to the lowest taxonomic level practical, depending on the group and, thus, ranged from species to family (see Appendix A). Identifications were made by Fred Heinzelmann of the Museum of Southwestern Biology, Division of Arthropods, with some species determined by additional specialists. Vouchers are housed in the Museum of Southwestern Biology, Division of Arthropods.

Analyses

Taxonomic richness. We used random intervention analyses to detect changes in the number of taxa present after the introduction of annual flooding at Experimental Flood, relative to Reference-1. Random intervention analysis (RIA) is used to detect changes in a manipulated ecosystem, relative to an undisturbed reference system, based on paired time series of data from both systems before and after manipulation (Carpenter *et al.*, 1989). This analysis indicates whether a change has occurred in the manipulated system, relative to the reference system, but cannot determine causality (Carpenter *et al.*,

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1989). We, therefore, compared these results qualitatively with differences in the number of taxa between Natural Flood and Reference-2, to determine whether patterns after experimental flooding were similar to those at the naturally flooded site.

The analysis was repeated for the total taxonomic richness, and the total number of taxa in the following groups: spiders (Araneae), beetles (Coleoptera), ground beetles (Coleoptera: Carabidae), and ants (Hymenoptera: Formicidae). For each of these groups, we first summed the number of taxa present at each site during each trapping period throughout the study. We then calculated a time series of 'intersite differences' between paired totals for each taxonomic group during each trapping period, where the intersite difference equals the number present at the Experimental Flood site minus the number of taxa present at Reference-1. The test statistic was calculated as the absolute value of the difference between the mean pre-flood (July 1991–May 1993) intersite difference and the mean post-flood (June 1993–December 1995) intersite difference. Each p-value was estimated by determining where the actual test statistic fell in a distribution of test statistics calculated from 10000 random permutations of the intersite differences (Carpenter *et al.*, 1989), using a custom program written in MATLAB software. We also tested each series of intersite differences for autocorrelations (Carpenter *et al.*, 1989). We calculated intersite differences for the same taxonomic groups at Natural Flood and Reference-2 during the final nine trapping periods, to provide qualitative comparisons with the experimental sites. December and February trapping periods were excluded from this analysis for ants, as ants were rarely active above ground during those months; other taxonomic groups were analyzed across all trapping periods.

Taxonomic composition. We assessed the similarity in taxonomic composition among sample units using cluster analyses based on dissimilarity indexes. We treated Experimental Flood and Reference-1 before and after flooding as separate sample units, giving an overall comparison among six sample units (Experimental Flood before flooding, Reference-1 before flooding, Experimental Flood after flooding, Reference-1 after flooding, Natural Flood and Reference-2). We analyzed six taxonomic groups: all taxa combined, insects, spiders, all beetles, carabid beetles, and ants. Data were corrected for unequal sample effort among sample units by dividing the total number of individuals for each taxon captured by the number of collections for that sample unit (12 for each of Experimental Flood and Reference-1 before flooding, 18 for each of Experimental Flood and Reference-1 after flooding, and 11 for each of Natural Flood and Reference-2). These corrected abundance totals were then used to calculate distance matrices with all pair-wise comparisons among the six sample units, using three different combinations of dissimilarity indexes and transformations. Because the uneven sample effort might result in the inclusion of rare taxa at more heavily sampled sites, even after the preliminary abundance correction, we removed taxa represented by only one individual at each of Experimental Flood and Reference-1 before flooding, Natural Flood and Reference-2, or by two individuals at each of Experimental Flood and Reference-1 after flooding. To look for robust patterns in the data, results produced by the three methods were compared visually, and similarities and differences reported. Similarity analyses were based on Ludwig and Reynolds (1988) and J.A. Ludwig (personal communication). The three methods used were:

1) *Presence/Absence.* We calculated dissimilarities based on taxa presence or absence using the Q-mode Jaccard index (JI) between sites j and k, where

$$JI_{jk} = \frac{a}{a+b+c}$$

and a is the number of taxa present at both sample units, b is the number of taxa present only at sample unit j, and c is the number of taxa present only at sample unit k. This is converted to a dissimilarity index, JDI, where $JDI = 1 - JI$.

2) *Abundance.* We used the corrected abundance data to calculate dissimilarities using the Bray–Curtis percent dissimilarity (PD) index, computed as

$$PD = 1 - [2W/(A+B)]$$

where

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$$A = \sum_{i=1}^{S} X_{ij} \qquad B = \sum_{i=1}^{S} X_{ik} \qquad W = \sum_{i=1}^{S} [\min(X_{ij}, X_{ik})]$$

and X_{ij} is the corrected abundance of taxon i at sample unit j, X_{ik} is the corrected abundance of taxon i at sample unit k, and $\min(X_{ij}, X_{ik})$ is the smaller value of X_{ij} and X_{ik}, or the 'shared' abundance of taxon i at sites j and k. Therefore, W is the sum over all taxa of the shared abundances.

3) *Adjusted Abundance*. We applied an additional transformation on the abundance data to adjust for very abundant taxa, such as isopods, then re-calculated *PD* values as in 'Abundance', above. In this 'row transformation', all site abundances for a given taxon were divided by the maximum site abundance, yielding new values scaled from 0 to 1.

Each method resulted in a dissimilarity matrix for each taxonomic group. We used these to perform cluster analyses with the flexible strategy to create dendrograms indicating taxonomic similarity (Ludwig and Reynolds, 1988). Dendrograms for the three methods were then compared to determine robust patterns.

Abundance of key populations. A total of 192 taxa was collected, but we used random intervention analyses to compare only the abundance of exotic isopods (Isopoda: Armadillidiidae, *Armadillidium vulgare*), all spiders (Araneae), spiders of the family Lycosidae, native crickets (Orthoptera: Gryllidae, *Gryllus alogus*), all beetles (Coleoptera), beetles of the family Carabidae, and ants (Hymenoptera: Formicidae), at Experimental Flood and Reference-1, before and after flooding. As for taxa richness, the test statistics were based on comparisons of the average intersite differences for each group across pre- and post-flood trapping periods (abundance at Experimental Flood minus abundance at Reference-1; see section on 'Taxonomic richness' and Carpenter *et al.*, 1989). Series of intersite differences were tested for autocorrelations. Again, December and February trapping periods were excluded from this analysis for ants. p-values were adjusted for multiple comparisons within taxonomic groups (Araneae and Lycosidae; Coleoptera and Carabidae).

RESULTS

Taxonomic richness

Flooding did not affect the number of taxa of surface-active arthropods. Richness varied over time at both sites, but there was no significant change within any taxonomic group at Experimental Flood, relative to Reference-1 after the introduction of flooding (Table I, Figure 2). Numbers of taxa and the relative differences between sites at Natural Flood and Reference-2 were generally within the range of those for Experimental Flood and Reference-1 (Figure 2). Total richness was 56 taxa at Experimental Flood and 67 taxa at Reference-1 during the 12 periods prior to flooding, compared with 85 taxa and 88 taxa at these sites during 18 collections after flooding, and 49 and 53 taxa at Natural Flood and Reference-2, respectively, across nine trapping periods. Richness estimates were conservative, as identifications were not possible to species for all groups. Although not statistically significant, there was a

Table I. Probability values from random intervention analyses indicating possible changes in taxonomic richness after experimental flooding

Taxonomic group	p-value
Total taxa	0.57
Aranae	0.29
Coleoptera	0.88
Carabidae	0.11
Formicidae	0.77

p-values indicate the significance of the change in average pre- and post-flood intersite differences in richness, relative to a distribution of 10 000 random permutations of the intersite differences. No changes in richness were significant.

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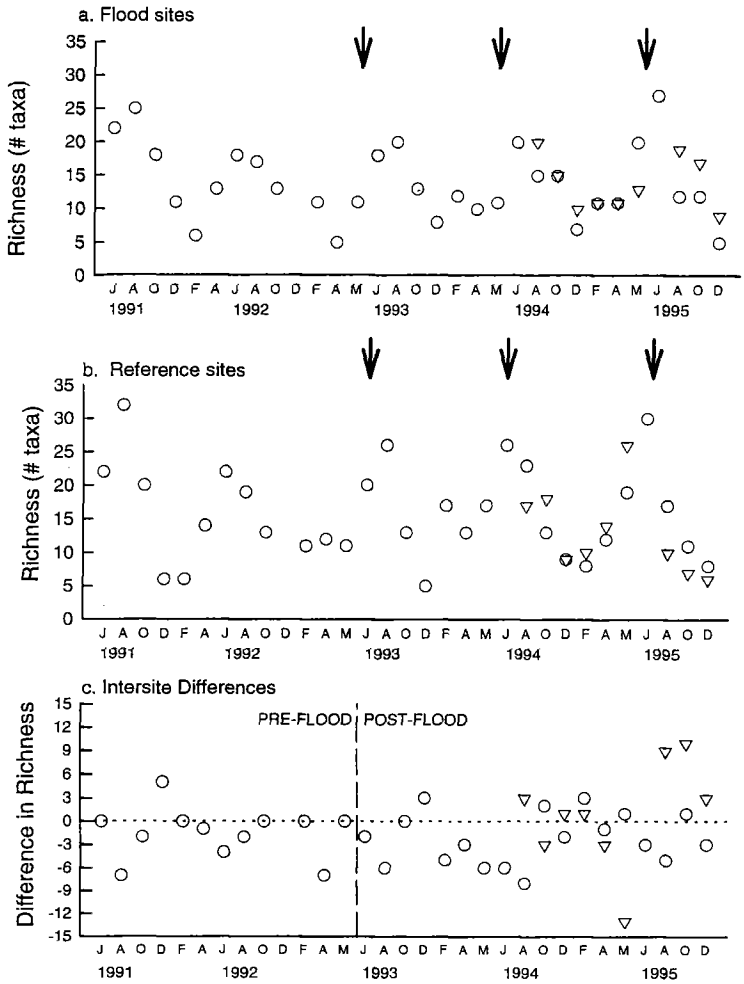

Figure 2. RIA for total taxonomic richness: (a) total richness at Experimental Flood (circles) and Natural Flood (triangles) across the sample period; (b) total richness at Reference-1 (circles) and Reference-2 (triangles); (c) difference between Experimental Flood and Reference-1 (circles), and between Natural Flood and Reference-2 (triangles). Arrows indicate timing of floods

tendency towards increased carabid beetle taxa richness after flooding, which is consistent with higher richness of carabids at Natural Flood, relative to Reference-2 (Figure 3). None of the time series of intersite differences had detectable autocorrelations. The full list of taxa present at all sites is presented in Appendix A.

Taxonomic composition

The taxonomic composition changed after flooding for four groups: all taxa, insects, all beetles and carabid beetles. While pre-flood assemblages for each of these groups at Experimental Flood were most similar to those at Reference-1 or Reference-2, post-flood assemblages were most similar to those at Natural Flood. The presence/absence and adjusted abundance methods yielded similar results for analyses of all taxa, with similarity among sites reflecting flooding (Figure 4(a)). However, when the raw abundance method was used for the analysis of all taxa, sites were clustered based entirely on isopod abundance, which greatly exceeded that of other taxa, and swamped out effects of flooding. This confirms the need to add the adjustment for very dominant taxa when abundance data are highly skewed.

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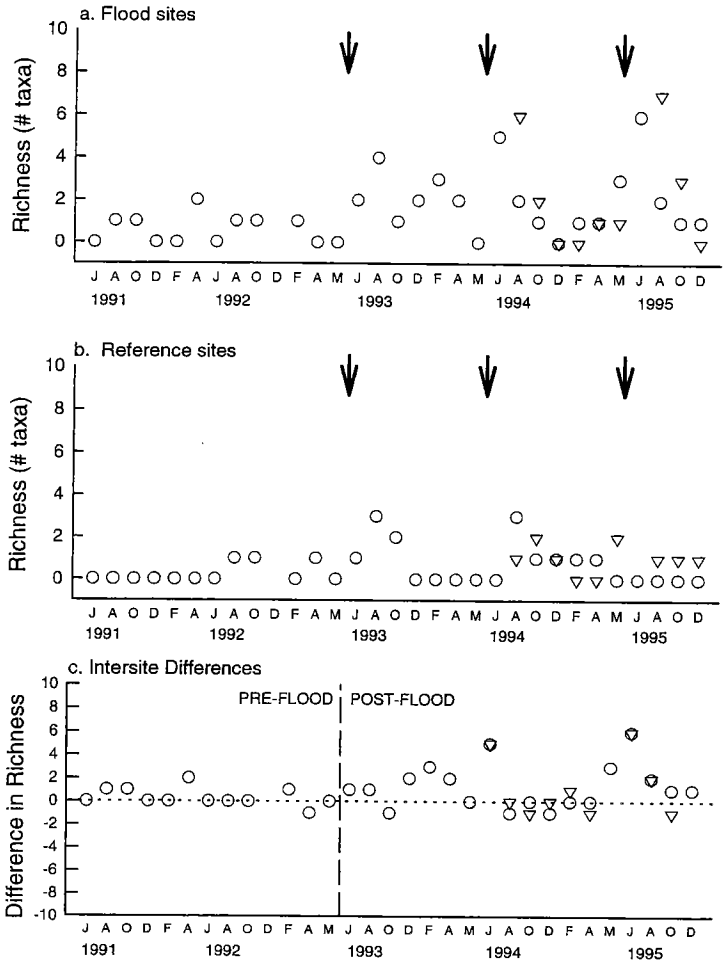

Figure 3. RIA for taxonomic richness of carabid beetles: (a) carabid richness at Experimental Flood (circles) and Natural Flood (triangles) across the sample period; (b) carabid richness at Reference-1 (circles) and Reference-2 (triangles); (c) difference between Experimental Flood and Reference-1 (circles) and between Natural Flood and Reference-2 (triangles). Arrows indicate timing of floods

When analyses were run for insects, all three methods clustered flooded sites together, while Experimental Flood prior to flooding was grouped with Reference-1. Similar patterns were observed for analyses of beetles, with consistent pairing of the two flood sites and of Experimental Flood and Reference-1 prior to flooding (Figure 4(b)). For carabid beetles, flood sites were again paired in two of three analyses (presence/absence and abundance; Figure 4(c)).

Beetles represented between 33 and 44% of the taxa richness for each sample unit, thus, beetle communities may drive the patterns observed. When beetles were excluded from analyses for all taxa, the similarity between flooded sites occurred when taxa presence/absence was considered (Figure 5(a)), but not when abundance was included (Figure 5(b)). Thus, the relative abundance of beetles among sites did influence the structuring of the community. Interestingly, the similarity between flooded sites for insects remained when beetles were excluded from the analysis, in spite of the fact that beetles comprised 45–62% of all insect taxa (Figure 5(c)). This clustering was largely driven by cricket abundance at flooded sites, and the pattern was lost when only taxa presence/absence was considered.

Carabids made up 4–19% of the beetle taxa at dry sites, but 32.4% of the beetles at Experimental Flood after flooding and 50% of the beetles at Natural Flood. Thus, carabids appeared to be particularly important at flooded sites. However, when carabids were excluded from the analyses, all three methods

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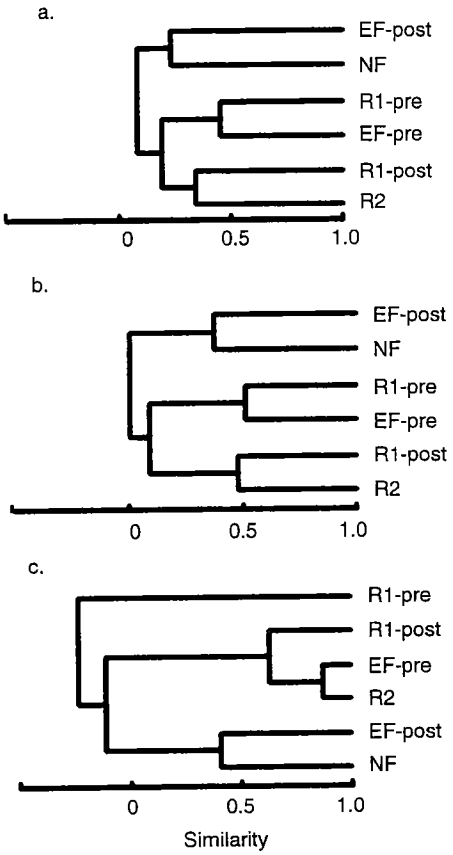

Figure 4. Similarity among sample units for (a) all taxa, (b) Coleoptera, and (c) Carabidae. Clustering along x-axis indicates degree of similarity. Dendrograms are based on abundance for Coleoptera and Carabidae, and adjusted abundance for all taxa; see text for comparisons of results for different methods. Sample units: Experimental Flood before flooding (EF-pre), Experimental Flood after flooding (EF-post), Reference-1 before flooding (R1-pre), Reference-1 after flooding (R1-post), Natural Flood (NF), and Reference-2 (R2)

still revealed a similarity between flooded sites (Figure 6). The primary non-carabid beetle taxa shared between flood sites were two members of the Staphylinidae. Also important may be the absence of taxa present at dry sites, including several staphylinids and tenebrionids.

There was little congruence among analyses for spiders, which showed no consistent pattern of similarity between flooded sites. In two of the three analyses, spider communities within each of Experimental Flood and Reference-1, before and after flooding, were grouped together, suggesting that spider communities did not change greatly over time. These results imply that spider composition was affected by factors other than flooding.

The composition of ant communities was also not clearly tied to flooding. The abundance method clustered the two flooded sites together and Experimental Flood with Reference-1 prior to flooding, but the other two methods each yielded different clustering patterns. The lack of congruence among methods made conclusions about ant community similarity impossible.

Abundance of key populations

The isopod *Armadillidium vulgare* was the most common taxon at all sites. Abundance of this non-native macrodetritivore decreased significantly after experimental flooding, relative to Reference-1 ($p = 0.003$; Figure 7). Although an increase in abundance of the native macrodetritivore cricket *Gryllus alogus* appeared significant ($p = 0.023$), an autocorrelation in this time series required that the probability

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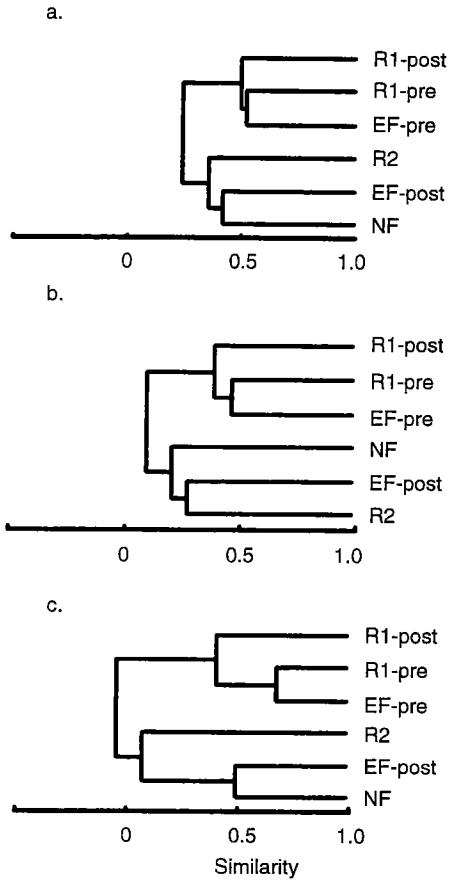

Figure 5. Similarity among sample units for (a) all taxa, excluding Coleoptera, based on presence/absence, (b) all taxa, excluding Coleoptera, based on adjusted abundance, and (c) insects, excluding Coleoptera, based on abundance. Clustering along X-axis indicates degree of similarity. See Figure 4 for definition of sample units

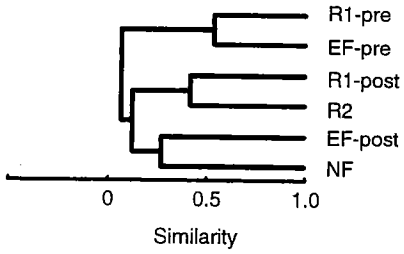

Figure 6. Similarity among sample units for Coleoptera, excluding Carabidae, based on abundance. Clustering along X-axis indicates degree of similarity. See Figure 4 for definition of sample units

level for significance be set at 0.01 (Carpenter *et al.*, 1989), thus, eliminating the effect. However, visual inspection of the time series revealed a lag effect, with the increase in cricket abundance occurring after the second flood (Figure 8). We, therefore, re-ran the RIA with the pre-flood period set for July 1991–May 1994, and the post-flood period set for June 1994–December 1995, thus, measuring the effects beginning after the second flood. This analysis indicated a significant increase in cricket abundance ($p = 0.0003$), even with the probability level for acceptance set at 0.01. Similar patterns in abundance were seen at Natural Flood, relative to Reference-2: isopod abundance tended to be lower at Natural Flood than at Reference-2, while the abundance of cricket tended to be higher.

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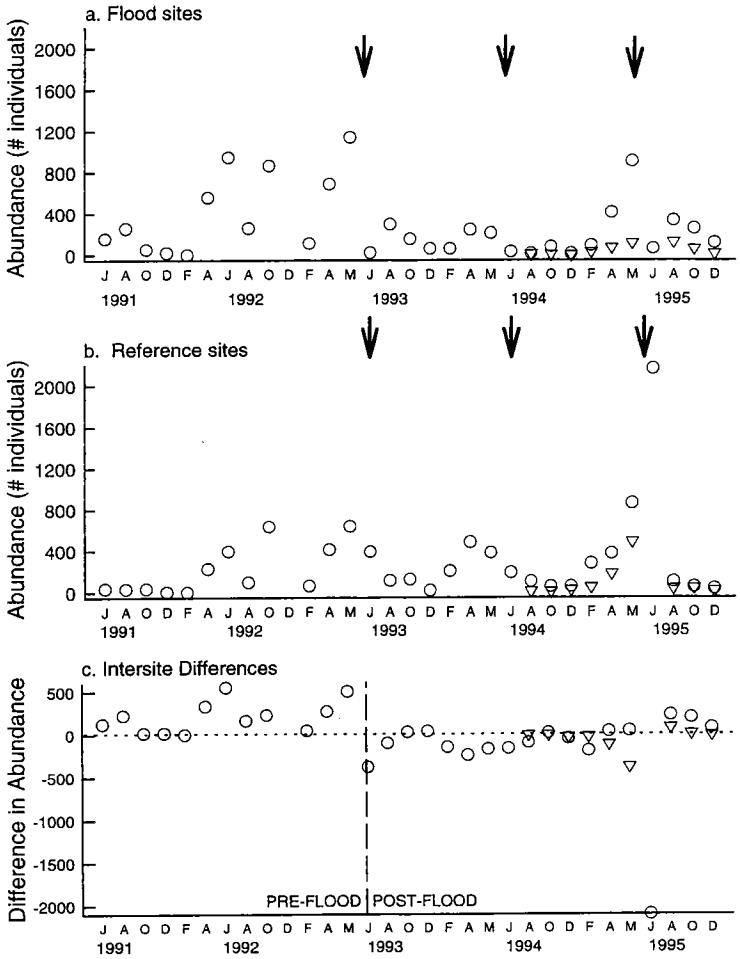

Figure 7. RIA for abundance of *Armadillidium vulgare*: (a) abundance at Experimental Flood (circles) and Natural Flood (triangles) across the sample period; (b) abundance at Reference-1 (circles) and Reference-2 (triangles); (c) difference between Experimental Flood and Reference-1 (circles), and between Natural Flood and Reference-2 (triangles). Arrows indicate timing of floods

The overall abundance of beetles did not change with flooding ($p = 0.70$). However, abundance of carabid beetles showed a pattern similar to that of crickets: although there was no change detected in the initial analysis ($p = 0.26$), when the RIA was re-run to determine possible effects beginning only after the second flood, there was an increase in carabid abundance ($p = 0.009$; Figure 9). This was significant, even with an adjusted probability level of 0.01 to compensate for an autocorrelation in the time series. Thus, both cricket and carabid abundances increased after flooding, but for both, there was a delay in the response until after the second flood. None of the abundance results, other than crickets and carabids, were affected by autocorrelations.

There was a significant decrease in the abundance of spiders at Experimental Flood, relative to Reference-1, when all spider taxa were considered together ($p = 0.009$; adjusted probability level set at 0.025 for multiple comparisons within spiders). However, this pattern was not present for members of the most common spider family, Lycosidae ($p = 0.82$).

Ant activity tended to be quite variable among sample dates. Although there was a trend toward decreasing captures of ants after flooding, this was not significant as a result of the high variation among collections ($p = 0.22$). Much of the relative difference between the two sites actually reflected increases at Reference-1. When abundance data was replaced with capture frequency, there was no change after flooding ($p = 0.88$).

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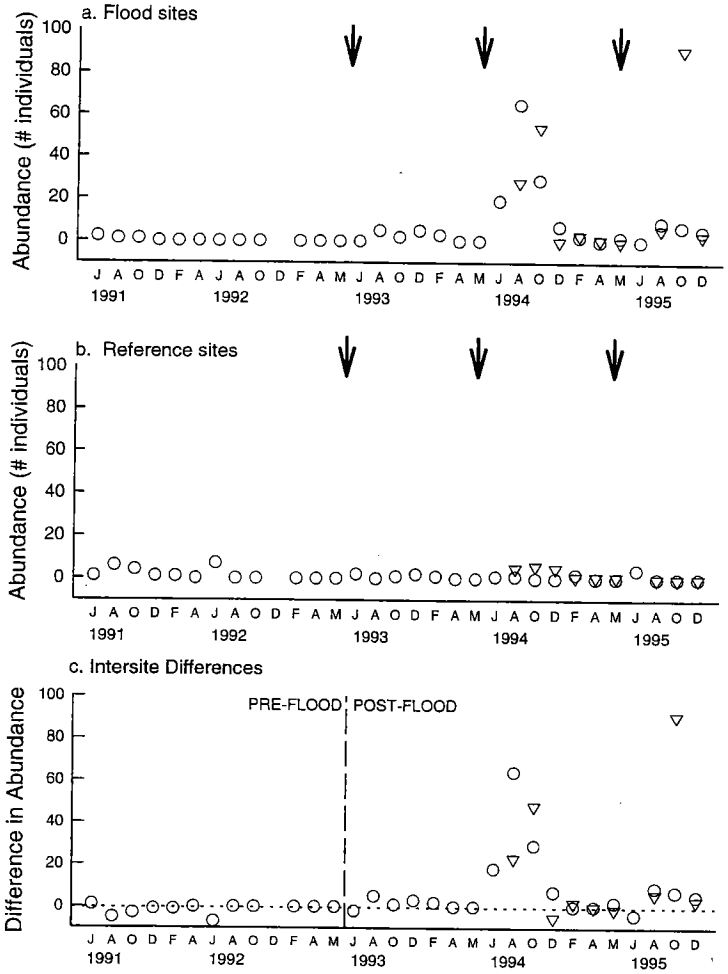

Figure 8. RIA for abundance of *Gryllus alogus*: (a) abundance at Experimental Flood (circles) and Natural Flood (triangles) across the sample period; (b) abundance at Reference-1 (circles) and Reference-2 (triangles); (c) difference between Experimental Flood and Reference-1 (circles) and between Natural Flood and Reference-2 (triangles). Arrows indicate timing of floods

DISCUSSION

Flooding did not affect the number of surface-active arthropod taxa present on the forest floor, but it did alter the composition of the community. The similarity in arthropod communities at the two flooded sites may be largely driven by the beetles, as well as crickets. Members of the beetle family Carabidae seem particularly important at flooded sites. The trend toward more carabid taxa, and the increase in individuals present at Experimental Flood following flooding, was consistent with richness and abundance patterns observed at Natural Flood, relative to Reference-2. After flooding, the composition of carabid beetles at Experimental Flood was most similar to that at Natural Flood, reflecting the addition of several hygrophilic species. *Agonum decorum* occurs at the border of standing water, while *Poecilus chalcites* (formerly *Pterostichus chalcites*) is typically found on damp soil, usually near water (Lindroth, 1966). These two species were particularly abundant at Natural Flood, and at Experimental Flood after flooding, with only one individual of *P. chalcites* captured at Reference-2. Several other carabids were captured only at one or both of the flooded sites, including three species of *Chlaenius*, which are described as occurring at the border of waters (Lindroth, 1969). In contrast, the most abundant carabid species at the dry sites, which was also fairly common at the flooded sites, was *Calathus opaculus*, a xerophilous species reported to be confined to sandy areas (Lindroth, 1966).

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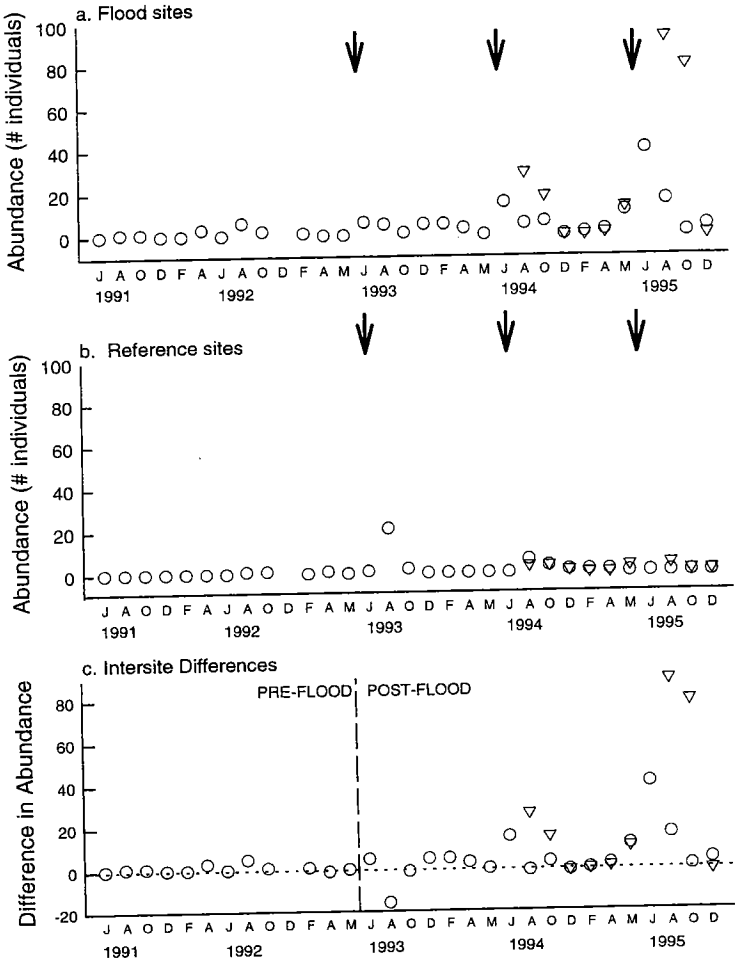

Figure 9. RIA for abundance of carabid beetles: (a) abundance at Experimental Flood (circles) and Natural Flood (triangles) across the sample period; (b) abundance at Reference-1 (circles) and Reference-2 (triangles); (c) difference between Experimental Flood and Reference-1 (circles), and between Natural Flood and Reference-2 (triangles). Arrows indicate timing of floods

Carabid species living in isolated or unstable habitats, such as the banks of temporary pools, rivers, or lakes, tend to have high dispersal powers (den Boer, 1990), and, thus, can rapidly colonize newly created habitats. Although the specific adaptations of local carabids to flood conditions are unknown, several strategies are used by carabids living in inundated Amazonian forests (Adis and Messner, 1991; Adis, 1997), and the family as a whole is known to be well adapted to floodplain conditions (Siepe, 1994). In floodplain forests of Central Europe, carabid communities differ not only between flooded and unflooded sites, but also among flooded sites that vary in the timing and intensity of inundation (Šustek, 1994). The delayed increase in carabid abundance observed in this study suggests that either two floods were needed to substantially change the habitat to benefit carabids, or that there was simply a delay in recruitment. Overall, these results suggest that careful documentation of carabid beetle species may be useful to understand current and historical flooding regimes.

Other changes in taxa presence or absence are easily explained by flooding. For example, water striders (*Gerris* sp.) were captured at Experimental Flood only after flooding. Mites decreased dramatically after experimental flooding, and were never captured at Natural Flood. Lepidopteran larvae were numerous at Reference-1 during the post-flood period, but only a few were caught at either flooded site, suggesting a low tolerance to inundation. *Eleodes suturalis*, a large and common tenebrionid beetle, also decreased

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after experimental flooding, while captures increased at Reference-1. Tenebrionids, which are major detritivores in the arid southwest (references in Crawford, 1991), were entirely absent from samples at Natural Flood, although several taxa were present at each of the other sites, as well as in drier saltcedar vegetation in the refuge (Ellis *et al.*, in press). One possible interpretation of the increase in carabids is that a decrease in understory vegetation following flooding may allow certain taxa to be captured more easily than others (Greenslade, 1964). However, although forb cover decreased at Experimental Flood, it remained slightly greater than at Reference-1, and there was an increase in grass cover (L.M. Ellis, unpublished data). The fact that *E. suturalis* was absent from Natural Flood, which had the least understory and leaf litter, and decreased at Experimental Flood after flooding, suggests that mobility did not influence its occurrence at these sites, and so other factors may have affected carabid beetles as well.

Native crickets increased, while non-native isopods decreased after flooding. Crickets were most abundant at Natural Flood, which had the fewest isopods of all sites. Crickets may have been the primary macrodetritivore prior to human alteration of the riparian ecosystems by flood control and the introduction of isopods. While isopods can consume relatively dry, intact leaf litter, crickets appear to prefer the partially decayed leaves available after annual inundation (C.S. Crawford, personal observation). Thus, changes in abundances of isopods and crickets after restoring flooding may reflect this resource availability. The lag in the response for crickets may indicate that two floods were needed to sufficiently change litter quality. Changes also may reflect a difference in direct tolerance to standing water. We observed large numbers of crickets fleeing in advance of the rising waters at the initiation of the 1994 flood. High post-flood numbers may, thus, reflect rapid recolonization after the water receded. Large numbers of early instars among the post-flood crickets also suggests that flooding promoted recruitment, but there was a delay before numbers increased substantially. In contrast to the behavior of crickets, isopods were regularly observed clinging to floating wood or tree trunks during the flood. Similar strategies have been reported for isopods (family Philosciidae) in floodplain forests along the Amazon River, which survive forest inundation of 6–7 months duration under loose bark, or in crevices on the lower trunks of trees, on termite mounds or on floating logs (Adis, 1997). The decrease in *A. vulgare* observed in this study thus may have been a temporary effect, reflecting the impact of long-absent flooding on this population. The decrease was greatest after the first flood, and numbers appeared to be increasing by 1995. Observations following additional floods might indicate whether these changes remain consistent with annual flooding. Unfortunately, this is impossible at these sites, because a fire in the summer of 1996 destroyed both the experimental and natural flood sites. Current sampling in other local riparian sites has revealed high isopod numbers in at least one site that receives some flooding.

Crematogaster cerasi was the most abundant ant taxa captured at Natural Flood, with six other taxa captured there in low numbers. *C. cerasi* was present at all sites and captures increased at both Experimental Flood and Reference-1 during the post-flood period. Although nests of *C. cerasi* in New Mexico have been reported to be under rocks (MacKay *et al.*, 1988), we observed a nest being moved from a log on the ground to a tree during the first experimental flood, and individuals were regularly observed moving about on vegetation during floods. Many species of the genus are arboreal nesters (Hölldobler and Wilson, 1990), so *C. cerasi* may be able to tolerate extended periods of inundation by moving its nests into trees. Hölldobler and Wilson (1990) suggest that, when present, species of the genus *Crematogaster* tend to dominate other ant species; such dominance typically forms the core of the local ant community, and may affect the composition and abundance of not only other ant species but other arthropods and plants as well. Thus, the tolerance of *C. cerasi* to flooding may influence the composition of surface-active arthropod communities in regularly flooded riparian sites. In contrast, *Monomorium minimum*, a ground nesting species adapted to forest clearings (Wheeler, 1926; Hölldobler and Wilson, 1990), may be particularly vulnerable to inundation. Captures of this species decreased at Experimental Flood after flooding, while remaining high at Reference-1, and it was never captured at either riverside site. Several other ant taxa were captured only at dry sites, including two species of *Pogonomyrmex*, large ground-dwelling harvester ants. At sites along the Rio Grande, north of our study area, Milford (1996) found that *Lasius pallitarsis* and *Formica pallidefulva* were most common in unflooded bosque, while *Crematogaster mormonum* and *Tapinoma sessile* were the dominant species at flooded sites. Milford (1996)

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also found higher overall densities of ants at unflooded riparian sites compared with flooded sites, and concluded that nesting habits, along with disturbance from flooding, affected riparian ant communities. Differences between ant communities in flooded and non-flooded forests also have been shown for Amazonian systems (Adis *et al.*, 1984; Majer and Delabie, 1994).

It is important to note that the floods discussed in this study were low intensity, prolonged inundations, simulating those typical of large, lowland rivers in average years, and in contrast to the high intensity, short duration floods characteristic of low order streams in mountain landscapes, of rivers in constrained channels, or of more extreme and infrequent floodplain floods (Junk *et al.*, 1989; Michener and Haeuber, 1998; Schmidt *et al.*, 1998; Swanson *et al.*, 1998). Flow rates at Natural Flood during peak inundation in 1996 averaged only 9.6 cm/s (Ellis *et al.*, 1999). This type of inundation may favor a different assemblage than would higher intensity floods.

Other changes in taxonomic composition between the pre- and post-flood periods were similar at Experimental Flood and Reference-1, and may reflect external factors, such as climatic variability. For example, spiders of the family Linyphiidae, subfamily Erigoninae were frequently captured at both Experimental Flood and Reference-1 prior to flooding, but after flooding, only one individual was captured at either site. The most common spider was a *Trochosa* sp., which remained common at both sites following flooding, and was also present at both riverside sites. The significant decrease in spider abundance may reflect small changes in a number of taxa, rather than a general pattern of decreased abundance. Analyses suggest that, as a group, spiders may be fairly insensitive to habitat changes associated with flooding.

Current efforts to restore natural hydrologic regimes to a number of large river-floodplain systems will have a broad range of ecological consequences. The primary emphasis of many recent studies has been on restoring native riparian vegetation and/or habitat for native fish species (Poff *et al.*, 1997), with little attention paid to terrestrial invertebrate communities, in spite of their importance in regulating many ecosystem processes. Results from this study indicate that some changes in the surface-active arthropod community were rapid after the restoration of flooding, and suggest that arthropod assemblages along regulated rivers may not represent those present prior to flow alteration. Such changes, ultimately, may affect vertebrate populations that depend upon riparian habitats. More extensive studies of terrestrial invertebrates along both regulated and unregulated rivers are needed.

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APPENDIX A. ARTHROPOD TAXALIST FOR ALL SITES

Arachnida
- **Pseudoscorpionida***
- **Araneae**
  - Agelenidae*
  - Araneidae*
  - Dictynidae†
    - *Mallos* sp.
  - Dysderidae
    - *Dysdera crocata* C.L. Koch
  - Gnaphosidae

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Drassyllus sp.
Haplodrassus sp.
Herpyllus ecclesiasticus Hentz
Herpyllus sp.
Zelotes anglo Gertsch and Reichert
Zelotes sp.
Hahniidae
Neoantistea sp.
Linyphiidae
Erigoninae*
Linyphiinae*
Lycosidae†
Alopecosa sp.
Trochosa sp. 1
Trochosa sp. 2
Pardosa sp.
Pirata sp.
Pholcidae
Psilochorus sp.
Salticidae
Habrocestum sp.
Habronattus sp.
Phidippus audax (Hentz)
Sitticus sp.
Family Tetragnathidae
Pachygnatha sp.
Tetragnatha sp.
Family Theridiidae†
Crustulina sp.
Euryopis sp.
Steatoda borealis (Hentz)
Steatoda sp.
Family Thomisidae†
Misumenops sp.
Xysticus sp.
Acari*
Malacostraca
Isopoda
Armadillidiidae
Armadillidium vulgare (Latreille)
Porcellionidae
Porcellio laevis Latreille
Chilopoda
Scolopendromorpha
Scolopendridae*
Lithobiomorpha†
Henicopidae*
Lithobiidae*
Insecta
Thysanura
Lepismatidae*
Nicoletiidae*
Orthoptera
Gryllidae
Gryllus alogus Rehn
Raphidophoridae
Ceuthophilus sp.
Blattaria*
Isoptera
Rhinotermitidae
Reticulitermes sp.
Termitidae*
Psocoptera*
Heteroptera†
Gerridae
Gerris sp.
Lygaeidae†
Cymodema breviceps (Stål)
Ochrimnus lineoloides (Slater)
Ozophora picturata Uhler
Peritrechus fraternus Uhler
Miridae
Oncerometopus sp.
Reduviidae†
Empicoris orthoneuron McAtee and Malloch
Gardena elkinsi Wygodzinsky
Homoptera†
Cicadellidae
Cicadidae
Delphacidae
Coleoptera†
Anobiidae*
Anthicidae
Baulius tenuis (LeConte)
Ischyropalpus sp.
Carabidae
Agonum decorum (Say)
Agonum sp.
Amara sp.
Badister sp.
Bemidion timidus (LeConte)
Bradycellus sp.
Calathus opaculus LeConte
Chlaenius sericeus (Forster)
Chlaenius tricolor Dejean
Chlaenius sp.
Evarthrus sp.
Harpalus pennsylvanicus (DeGeer)
Poecilus chalcites (Say)
Pterostichus sp.
Scarites lissopterus Chaudoir

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Tachys sp.
Perigonini*
Cerambycidae
Prionus sp.
Chrysomelidae
Chrysomela scripta (Fabricius)
Graphops sp.
Eumolpinae*
Coccinellidae*
Cryptophagidae
Cryptophagus sp.
Curculionidae
Anametis subfusca Fall
Hypera postica (Gyllenhal)
Cercopeus sp.
Otiorhynchus ovatus (Linneaus)
Rhypodillus brevicollis (Horn)
Sphenophorus sp.
Dermestidae*
Dytiscidae
Laccophilus sp.
Elateridae
Aeolus livens (LeConte)
Athos sp.
Heteteroderes sordidus (LeConte)
Eucnemidae*
Histeridae†
Euspilotus assimilis (Paykull)
Geomysaprinus pectoralis (LeConte)
Hypocaccus patruelis (LeConte)
Lathridiidae†
Corticaria sp.
Ochodaeidae
Ochodaeus sp.
Scarabaeidae
Ataenius sp.
Hoplia sp.
Onthophagus sp.
Pseudataenius sp.
Serica alternata LeConte
Serica sp.
Scraptiidae
Anaspis sp.
Staphylinidae†
Astenus longiusculus (Mannerheim)
Creophilus maxillosus (Linneaus)
Platydracus sp. 1
Platydracus sp. 2
Platydracus sp. 3
Reichenbachia sp.
Staphylinus ater (Gravenhorst)
Staphylinus sp.
Tachyporus sp.
Paederini*
Aleocharinae*
Paederinae*
Tenebrionidae†
Agroporis rufipes Champion
Araeoschizus decipiens Horn
Asidopsis opaca (Say)
Blapstinus fortis LeConte
Blapstinus pimalis Casey
Blapstinus sp.
Eleodes extricatus (Say)
Eleodes fusiformis LeConte
Eleodes longicollis LeConte
Eleodes obsoletus (Say)
Eleodes sponsus LeConte
Eleodes suturalis (Say)
Embaphion contusum LeConte
Embaphion sp.
Metoponium sp.
Family Trogidae
Trox punctatus Germar
Trox tuberculatus (DeGeer)
Neuroptera
Myrmeleontidae*
Lepidoptera†
Noctuidae*
Diptera†
Cecidomyiidae*
Chironomidae*
Sciaridae*
Sphaeroceridae*
Siphonaptera
Pulicidae*
Hymenoptera
Andrenidae*
Chalcidoidea*
Diapriidae*
Formicidae
Camponotus sansabeanus (Buckley)
Camponotus vicinus Mayr
Crematogaster cerasi (Fitch)
Dorymyrmex insana (Buckley)
Formica hewitti Wheeler
Formica neogagates Vierick
Hypoponera opaciceps (Mayr)
Hypoponera sp.
Lasius fallax Wilson
Lasius niger (Linneaus)
Leptothorax andrei Emery

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Leptothorax nitens Emery
Leptothorax obliquicanthus Cole
Leptothorax pergandei Emery
Leptothorax texanus Wheeler
Leptothorax sp.
Monomorium minimum (Buckley)
Myrmicinae*
Neivamyrmex nigrescens (Cresson)
Neivamyrmex sp.
Pheidole pilifera (Roger)
Pheidole sp.
Pogonomyrmex barbatus (Smith)
Pogonomyrmex occidentalis (Cresson)
Solenopsis molesta (Say)
Solenopsis sp.
Tapinoma sessile (Say)
Mutillidae
Dasymutilla sp.
Scelionidae*

* Indicates that taxa below this level were observed, but their identities were not determined.

† Indicates an order or family for which there are lower taxonomic levels determined, but which have at least one additional undetermined family (for orders) or species (for families).

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