

Comparison of Surface-active Beetle (Order: Coleoptera) Assemblages in Remnant and Restored Riparian Forests of Varying Ages on the Middle Sacramento River, California.

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Abstract. Composition of epigeal (surface-active) beetle assemblages (Order: Coleoptera) from monthly invertebrate sampling within younger riparian restoration sites (1-3 years old), older riparian restoration sites (6-10 years old), and remnant riparian forests (>25 years old) were compared in order to examine effects of forest age and riparian restoration efforts on beetles along the Sacramento River, California. Six restoration sites (1-10 years old) planted by The Nature Conservancy's Sacramento River Project were selected for sampling and separated categorically into young and old restoration sites. Restoration sites were compared to three adjacent remnant riparian forest sites. Pitfall sampling of epigeal beetles was carried out monthly between December 2000 and November 2001. All beetles were sorted into a temporary alphanumeric "morphospecies" reference collection and database for subsequent identification. Morphospecies were identified to the lowest taxonomic level practicable. We used nonmetric multidimensional scaling, cluster analysis, and multiple response permutation procedures to examine sample assemblage response to forest type at the order and family level. For individual morphospecies we used either analysis of variance or a Kruskal-Wallis nonparametric test of the mean monthly trap catches to determine whether forest type significantly affected morphospecies abundance. Indicator species analysis was performed on mean monthly trap catches to calculate individual morphospecies' values as "indicators" of different forest types.

Ordination and cluster analysis at the order level, and for at least three families, showed a strong response of sample assemblages to forest age. We also found that sample assemblages showed a significant effect of categorical forest type. Temporal analyses of sample assemblages at the order level also showed a significant difference

between forest type “trajectories” for the sample-year. Analysis of trap data for individual morphospecies indicated a significant response to forest type by a large number of species. Neither Shannon-Weiner diversity indices nor species richness were significantly different between forest types; however, these metrics did not reflect differences in sample assemblage composition between either sites or forest types (i.e. young restoration, old restoration, and remnant riparian forest sites). Monthly abundance was significantly higher in remnant riparian habitats, but was related to species-specific trap abundances. Because of these factors, diversity, species richness, and trap abundance were not considered reflective of differences in compositional characteristics of epigeal beetle communities in these forest types. Results indicate that: 1) samples from forests of different ages contain characteristic species; 2) epigeal beetle assemblages within remnant riparian sites were most similar to one another; 3) younger restoration sites showed greater differences in composition amongst themselves and through time than did old restoration and remnant riparian forest sites; 4) response of epigeal beetle assemblages to restoration efforts varied at the family level; 5) several species which showed significant effect of forest type also had restricted geographic and/or seasonal distributions within the study area; and 6) a general assemblage trajectory based on forest age appears to be demonstrated in the data. From these results it appears that riparian restoration efforts are providing habitat for many species of beetles characteristic of remnant riparian forests.

Introduction

Habitat restoration has become one of the most important tools in contemporary conservation. One of the biggest challenges in restoration ecology is the lack of information regarding historic conditions of habitats (including species presence/absence, distribution, and seasonality) prior to large-scale landscape disturbance. This information is fundamental to development of appropriate restoration goals and measures of restoration success. The destruction and alteration of habitat throughout the world has resulted in a rapid loss of both documented and undocumented biodiversity (Wilson 1992). Arthropods represent one of the most diverse components of biodiversity within any terrestrial ecosystem (Wilson 1992). Because of their overwhelming diversity and cryptic nature, as well as researcher bias toward more “charismatic” species, the effects of habitat destruction and alteration on these arthropod communities have been poorly documented, and historic composition of these communities is typically unknown. This is especially true in North America, where botany and (vertebrate) wildlife biology have been the primary disciplines employed in terrestrial biological monitoring. However, many studies have documented the usefulness of sampling invertebrate assemblages when management objectives involved overall community composition (Bess et al. 2002; French and Elliot 1997; Oliver and Beattie 1996b; Refseth 1980; Williams 2000). Terrestrial invertebrates have many attributes that make them well suited to studies of ecosystem change in restoration projects. These include their abundance, species richness, restricted home ranges, and short generation times. Current technology available in personal computers, in combination with multivariate analytical methods and appropriate study design, now makes it possible to approach very diverse taxa, quickly manipulate huge sets of data, and extract meaningful insight from these data (McCune et al. 2000). These factors have made historic limitations of these types of analyses, barring fundamental difficulties of taxonomy, largely moot.

Habitat restoration along the riparian corridor of northern California’s Sacramento River has now become one of the largest efforts of its kind in the country. These restoration efforts stem from loss of the historic Sacramento River riparian corridor, which some estimates place as high as 97% (Warner and Hendrix 1984). Over the last

decade and a half, efforts by organizations such as The Nature Conservancy's Sacramento River Project and Sacramento River Partners to restore riparian habitat along northern California's Sacramento River have resulted in thousands of acres being planted with native woody species using adaptations of standard orchard planting techniques. Replicated horticultural restoration sites along the Sacramento River provide a tremendous opportunity to examine the success of these restoration efforts at site-specific and river-wide (i.e. ecosystem) scales. To date several investigations have been carried out in the context of these restoration efforts ranging from detailed modeling analyses of historic and current hydrologic processes (Larsen et al. 2002) to response of plant and animal communities to restoration (Small et al. 1999; Whisson and Engilis unpub.; Hubbell 1997; Peterson 2002; Efsaaff 1997; Golet et al. in press). With the exception of surveys for the federally threatened valley longhorn elderberry beetle (*Desmocerus californicus dimorphicus*) we know of no studies focusing on the Sacramento River that examine the effects of restoration efforts on terrestrial arthropod communities. Riparian restoration efforts have been targeted at offsetting habitat loss and fragmentation implicated in the decline of the valley elderberry longhorn beetle (VELB) and migrant bird communities (including the state endangered yellow-billed cuckoo). Examination of riparian arthropod communities may provide important insights into the community ecology of these target species and their associated riparian system. Thus our study is the first attempt to monitor riparian arthropod assemblages in the context of riparian restoration efforts as called for by the CALFED Bay Delta Program Comprehensive Monitoring, Assessment and Research Program (CMARP; Anonymous, 1999).

Terrestrial arthropod communities along the Sacramento River have been subject not only to large-scale anthropogenic disturbance (forest clearing, introduced plant and animal species, altered river hydrology, etc.), but are also threatened with the introduction of at least two invasive invertebrate pests: the argentine ant (*Linepithema humili*) and the imported red fire ant (*Solenopsis invicta*) (Holway, 1995; Human and Gordon, 1997). Argentine ants have been recorded as far north as Humboldt County in California (Knight and Rust, 1990), but their distribution along the Sacramento River within the study area has not been adequately documented. These factors lend some urgency to an examination of current arthropod communities within this system.

In this study we utilized beetles (Order: Coleoptera) to assess potential effects of habitat restoration on arthropod communities along a 19-mile stretch (31 “river miles”) of the Sacramento River. Specifically, we sampled epigeal (species actively moving about the forest floor) beetles monthly over the course of one year within remnant riparian forests and riparian restoration sites utilizing pitfall traps (see Methods, below). A morphospecies collection was developed following adaptations of methods used by Oliver and Beattie (1996a and 1996b) for initial cataloguing of specimens, development of a specimen database, and as a reference collection for further taxonomic clarification. We examined, in an exploratory fashion, differences in sample assemblages through time for different forest types at different taxonomic levels--order, family, and species (where information allowed).

The goals of this study were two-fold: (1) to generally characterize composition of one component of the arthropod community in these different forest types and (2) to examine the utility and feasibility of employing this methodology. In addressing the first goal we hypothesized that sample assemblages (at the order, family, and species level) would be significantly affected by forest type overall, and that sample assemblage would differ by forest type through time (i.e. that patterns of change in community composition through the year would differ significantly between forest types). In addressing the second goal, we reasoned that using a morphospecies approach would maximize processing of our diverse samples while still providing useful information prior to confirmation of distinct ecological units (i.e. a “true” taxonomic classification). A number of difficulties in species level identification of terrestrial invertebrates exist, ranging from lack of accessible reference collections and/or taxonomic expertise for verification to lack of well-developed taxonomies for some groups. Because of these difficulties, a morphospecies (or similar) approach has often been used. The shortcoming of a morphospecies approach is the lack of explicit assignment of species designations, or distinct evolutionary units. There have been several published arguments regarding the relative importance of this shortcoming. Still, we consider that the morphospecies approach has two primary advantages that outweigh the lack of species level designations. These advantages are: 1) development of a geographically, rather than phylogenetically, explicit reference collection useful to non-experts, ecologists, and/or

land managers to whom assemblages of a given geographic area are most useful; and 2) rapid development of datasets for higher taxonomic levels useful in examining general differences in invertebrate community characteristics in the context of hypothetically important landscape features (e.g. “forest types”). Thus, a morphospecies approach allows exploration of community characteristics while providing the basis for development of more accurate taxonomies and finer scale questions in a geographically explicit context. Lastly, the development of phylogenetically broad, but geographically explicit reference collections and datasets are probably far more useful to questions of land management, community ecology, and general natural history than their availability would reflect. Currently, many collections house thousands of designated species from broad geographic regions. These invaluable collections are, however, difficult and expensive to maintain (because of their sheer magnitude), and may be somewhat “unapproachable” to the non-expert due to their broad scope. Geographically explicit collections, on the other hand, are much smaller (thus cheaper to maintain) and are referenced to plants, animals, and habitats familiar to non-experts.

Several hypotheses were proposed at the outset of this study: (1) that sample assemblages of epigeal beetles would differ significantly between forest “types”; (2) that phenology of these sample assemblages would differ significantly between forest types through time (specifically because younger, less developed forests should be less buffered against seasonal changes in environmental variables and thus they might fluctuate more in abundance or composition than would older, more developed forests); (3) that different forest types would contain morphospecies significantly associated with that forest type; and (4) that some morphospecies would show significant trends in seasonal abundance. These simple hypotheses also serve as a starting point for developing foundational knowledge of the terrestrial invertebrate community of this ecosystem.

Study Area

The Sacramento River riparian corridor lies within the alluvial floodplain of the Sacramento River. Floodplain topography is characterized by a gently undulating landscape with elevation changes rarely exceeding 15' (approx. 5m). Most of the soils in this region are classified as Columbian loam with varying degrees of clay, silt and sand. Historically, the higher, drier upland sites were dominated by valley oak (*Quercus lobata*) woodlands, most of which have been cleared. These woodlands may have graded, to varying degrees, with more dense and wetter forests on lower sites. Lower sites were probably dominated by Fremont cottonwood (*Populus fremontii*), various willow species (*Salix spp.*), box elder (*Acer negundo*), California wild grape (*Vitis californica*), and Oregon ash (*Fraxinus latifolia*). Western sycamore (*Platanus racemosa*) may have been distributed along a wide moisture gradient. There is some difficulty in determining the precise historic composition of this vegetation type because historic records are poor prior to widespread destruction of this habitat (Thompson, 1961).

Sampling sites for this study were selected in cottonwood riparian forest, the most available vegetation type across habitat restoration sites and remnant riparian habitats (Holland, 1986). Forests that fall within this classification are characterized by a dominance of Fremont cottonwood, box elder, and various willow species. Subdominant woody species may include Oregon ash, California wild rose (*Rosa californica*), western sycamore, and black walnut (*Juglans californica*). Though restoration sites selected approximated this forest type overall, some sites contained a species composition more similar to mixed riparian forest (Holland, 1986), with a greater percentage of species such as valley oak, western sycamore, coyote brush (*Baccharis pilularis*) and wild rose and a corresponding decrease in relative abundance of Fremont cottonwood and willows.

Restoration sites consist of former agricultural (primarily orchard) lands that have been replanted with native, woody riparian species. Remnant riparian habitats tend to occur in the lowest areas, which are less useful for agriculture because of a higher flood frequency. It is important to note that these remnant riparian "reference sites" are more mesic than restoration sites, most of which consist of restored orchard lands on higher, drier sites.

All sites within the study area contained varying mixes of exotic plant species. Restoration sites generally had few, if any, nonnative woody species, but maintained substantial populations of nonnative herbaceous species such as yellow-star thistle (*Centaurea solstitialis*), annual ryegrass (*Lolium multiflorum*), ripgut brome (*Bromus diandrus*), and wild oats (*Avena fatua*). Remnant riparian forests commonly maintained populations of nonnative woody species such as black walnut (*Juglans californica*), Himalayan blackberry (*Rubus discolor*), giant reed (*Arundo donax*), and edible fig (*Ficus carica*), along with patches of nonnative herbaceous species.

Seeds and cuttings for restoration planting stocks are typically acquired from remnant patches of native vegetation in the vicinity of the restoration sites. These sites are then replanted with rows of native woody riparian species using conventional orchard planting techniques. Through time the obvious row pattern of the plantings becomes difficult to discern due to the variable morphology of the individuals within the plantings and changes resulting from subsequent flood events.

Methods

Study sites

This study was carried out between December 2000 and November 2001 at nine sites along a 19 mile (30 river-miles) stretch of the Sacramento River between The Nature Conservancy's (TNC) Phelan Island restoration site (river mile 191) six miles south of Hamilton City in Glenn County and TNC's Kopta Slough restoration site (river mile 221) approximately six miles east of the town of Corning, Tehama County, CA (Figure 1).

Sampling design

We sampled nine sites at four geographic locations along the riparian corridor (Figure 1 and Table 1). Sample sites were selected and stratified by age:

- 1) Young Restoration – less than 4 years old
- 2) Old Restoration – greater than 6 years old
- 3) Remnant Riparian Forests– greater than 25 years old

Structural differences among sites included canopy height, percent canopy cover, shrub density, degree and composition of herbaceous cover, and degree and composition of litter cover. Because Fremont cottonwood and willows have relatively rapid growth rates, differences between height and volume of vegetation in young restoration sites compared with old restoration sites were pronounced. Choice of remnant riparian habitat to be sampled was based primarily on proximity of these sites to restoration sampling sites. An attempt was made to control for potential influence of plant community assemblage by selecting sites most similar to restoration sites in overall woody species composition (i.e. cottonwood dominated mixed riparian forest). General habitat characteristics were recorded at each transect (soil texture and canopy cover) and for each trap (ocular estimation of percent herbaceous cover, percent deciduous vs. herbaceous litter cover, and percent woody debris).

Sampling at all sites was carried out using doubly nested 450mL clear plastic beer cups buried such that the lip of the upper cup was flush with the soil surface (Fig. 2), following methods summarized by Scudder (2000). The lower (outer) cup remained

buried in the ground and served as a permanent “sleeve” cup throughout the study. The upper (inner) cup acted as the “trap” cup. A 2.5 cm deep reservoir of propylene glycol was placed in the trap cup to capture and preserve invertebrates falling into the trap. A 15 cm² cardboard pseudo-cover wrapped in brown, waterproof packaging tape was anchored with two nails 2-3 cm above the trap. This cover functioned to prevent debris (i.e. falling leaves and twigs) and rain from falling into the cups and allowed us to close the trap in between sampling periods, thus preventing them from acting as a local sink and affecting future sampling. One concern that has been raised is that cover-boards may preferentially select for nocturnal species (Spence and Niemala, 1994), however this bias appears to be slight, and the technique has been widely used (Scudder 2000). Because pitfall traps are considered behavioral traps, it is assumed that each species has a unique data pattern based on that species ecology and “response” to trapping (Baars 1979; Halsall and Wratten 1988). For these reasons, direct interspecific comparisons of abundance are considered invalid. It has been argued that substrate, general environmental conditions, and a myriad of other variables can have an important influence on intraspecific trap abundances between sites (Greenslade 1964; Mitchell 1963) and thus provide questionable results. However, in a study examining these arguments Baars (1979) showed (both experimentally and through examination of previously published data) that pitfall trapping over a substantial period of time (e.g. an entire year) yielded intraspecific abundances closely proportional to mean densities between habitat types. We attempted to control for these potential biases by employing the same sampling method simultaneously across sites over an entire year and limiting analyses to whole sample-assemblage data and intraspecific sample abundances. We agree with Dufrene and Legendre (1997) that multivariate statistical methods can be appropriately applied to whole assemblage data even though pair-wise comparisons of interspecific data sets would be inappropriate.

At each of the nine sites, traps were placed 15 meters apart in a 3 x 4 grid. Grids were oriented along the cardinal directions (Fig. 2). The nine easternmost traps were considered the primary sampling units (900 m²). The three westernmost traps served as extras in an attempt to offset data loss due to trap disturbance, loss, or other unexpected

problems. Traps were opened at all sites for 1 week per month between December 2001 and November 2002.

All beetles collected were sorted into an alphanumeric morphospecies reference collection. Species taxonomy was then determined using reference texts (Arnett and Thomas 2002; Arnett and Thomas 2000; Hatch 1953) and by examining collections housed at the Bohart Museum of Entomology, University of California, Davis and the collection at the California Department of Food and Agriculture's Integrated Pest Control Branch, Sacramento California. Voucher specimens are stored in the entomology collection at California State University, Chico.

All specimens were either mounted in a reference collection or preserved in ethanol. Information regarding collection date, site, and trap location for each specimen was recorded and entered into a relational database (Microsoft Access). This database also included a taxonomic reference table, which allowed datasets to be updated as true taxonomy of morphospecies was elucidated, as well as tables containing data on site and trap characteristics (site age, GPS coordinates, habitat characteristics of individual traps, etc.).

Statistical analyses

Order- and Family-level Analyses:

Methods described below for processing community data follow those put forth by McCune and Grace (2002) using the analysis program PcOrd (McCune and Mefford 1999). Prior to analysis, total site-year trap catches for morphospecies were relativized by the total collected at each site over the entire trap-year (e.g. individual species' abundances were converted to percent of total sample abundance), then arcsine-square root transformed. Relativization of species data by sample total reduced the weight of species whose abundances were several orders of magnitude greater than other species. Relativization also allowed for comparison of sample units when significant trap loss resulted in different samples being composed of unequal numbers of subsamples. Transformation of community data was performed in order to reduce the influence of extremely abundant or rare species (outliers) on analyses.

Ordination and cluster analyses were performed to examine sample assemblage responses to forest age (chronosequence). Ordination of sites based on overall site totals for all morphospecies was performed using nonmetric multidimensional scaling (NMS) with PcOrd. Stress values for ordinations were calculated to gauge the strength of ordination axes and reliability of ordination interpretation. Stress values can range from 0 to 100, with lower stress values indicating better reliability (and thus interpretability) of ordination results; a stress value < 10 indicates a highly reliable graphical representation of the data (Clark 1993). A Monte Carlo test (50 randomizations of data between sample units) of each ordination was performed to test the probability of acquiring the calculated stress value (and thus the strength of the ordination axes) against that generated by chance. Cluster analysis was performed for comparative graphical purposes using group-average linking of Bray-Curtis values on relativized-root transformed data with the program BioPro (McAleece et al. 1998). The test for effect of forest type (young restoration, old restoration, and remnant riparian sites) on community composition was performed using a ranked multi-response permutation procedure (MRPP) with PcOrd.

Ordination of mean monthly totals (transformed and relativized) for each forest type was performed in order to examine potential differences in sample assemblage phenology for the entire sampling area throughout the year. Ordination was performed using NMS (as above). Again, a Monte Carlo test of the ordination was performed to test the probability of acquiring the calculated stress value and an MRPP performed to test for effect of forest type on community composition phenology.

Species-level Analyses:

Analysis of individual morphospecies as indicators of forest type was performed using mean-monthly trap catch across sites from each forest type. Indicator species analysis was performed with PcOrd on all morphospecies. Indicator species analysis calculates indicator values (IV) from 0 to 100 based on the product of a species' relative abundance (percent) and frequency of occurrence (percent) within and between treatments (i.e. forest types; Dufrene and Legendre 1997). Species with higher IVs are interpreted as better indicators of a given treatment. A Monte Carlo test was performed to calculate the significance of morphospecies' IVs (e.g. the probability of a calculated

IV being assigned based on that species abundance and frequency of occurrence across forest types). For comparative purposes analysis of variance (ANOVA) or a one-way Kruskal-Wallis nonparametric test (depending on sample size for a given species) using the program JMP (SAS Institute 2002) were also performed on all morphospecies to test for effect of forest type.

Results

Sampling was conducted over the course of one calendar year. Due to logistical and personnel constraints, 2 sites were sampled for only 10 months and all other sites for 12 months (Table 2). Periodic trap disturbance (presumably coyote, raccoon, opossum, and/or other large vertebrates) resulted in a variable number of “usable” traps collected per month from each site (Table 2). During the course of the sampling year, approximately 25,000 individual beetles of 188 morphospecies were sorted. Of these 188, 87 morphospecies were trapped only once (Table 3). Two sites (PC YR and PC RR) were sampled for only ten months (not sampled during August and September). Means for diversity, richness, and abundance were derived from averages of monthly totals (including August and September) for each forest type. Mean monthly abundance (± 1 standard error) per site ranged from 127.8 ± 23.2 (RVVI) to 473.5 ± 125.0 (PCWCB) and mean monthly species richness per site ranging from 15.1 ± 1.4 (RVVI) to 19.3 ± 3.1 (RVWCB) (Table 3). Neither mean monthly species diversity ($n=12$) nor mean monthly species richness ($n=12$) was significantly different between treatment types, however these data did not reflect differences in overall assemblage characteristics between treatment types. Mean monthly abundance ($n=12$) was significantly higher in remnant riparian forests (ANOVA $p < 0.05$) than in restoration sites, however, abundances were directly related to species-specific trap abundances. That is to say, abundance was largely dependent upon the presence or absence of a given species and those species’ “trapabilities” rather than overall differences in assemblage abundances.

Order-level analyses

Year-end site totals:

Because two sites (PC YR and PC RR) were sampled for only ten months, ordinations of year-end site-totals included only those months for which data was collected at all sites simultaneously. NMS ordination of year-end totals for coleopteran sample assemblages (Fig. 3) depicted a strong effect of forest age with little potential for misinterpretation (final stress for 2-dimensional solution = 3.498; Monte Carlo $p = 0.03$). Young restoration sites were spread relatively far from one another and the other forest

types (Fig. 3), older restoration sites clustered more closely to remnant riparian forests than did young restoration sites, and remnant riparian forest sites clustered most closely together, apart from the others. MRPP also showed a significant effect of forest type on coleopteran sample assemblages ($A = 0.24$; $p = 0.002$). Cluster analysis of Bray-Curtis values showed a similar pattern of forest type groupings based on percent similarity (Fig. 4). Forest types grouped by age, with RV OR (the youngest and most open OR site) grouping with YR sites and RR sites lumping more closely to one another and OR sites than to YR sites. These results support the hypothesis of a general community trajectory from YR to OR to RR sites.

Monthly composition by forest type:

NMS ordination of monthly totals by forest type showed different degrees of variability in sample assemblages through the sample year (Fig. 5). Because the sample used in this ordination was mean abundance by forest type (i.e. species totals were divided by the number of sites within a given forest type sampled per month), all months ($n=12$) were included in the analysis. The ordination showed that the young restoration forest phenology followed a “longer path” through time than the remnant riparian forest phenology and the old restoration phenology fell somewhat in-between these two (final stress for 2-dimensional solution = 12; Monte Carlo $p = 0.01$). All forest types followed a generally circular path through the year (though the young restoration forest type was somewhat more circuitous). MRPP results ($p < 0.001$) showed a significant difference in these trajectories through the year based on forest type. The stress value of 12 indicates that caution should be used in interpreting too much detail in the ordination. However, some features of the ordination may be of interest. The overall circular geometry of each forest type trajectory through time indicates a potentially circular assemblage phenology through the year using this sampling method. Secondly, similar patterns for YR and OR sites during the months of December-February may indicate greater assemblage similarity between these sites during the winter months (possibly due to harsher winter conditions on the less “developed” forest floors of younger sites). Similar ordination patterns for OR and RR sites during the months of April-June may indicate some similar environmental variables at this time of year, possibly related to canopy structure,

condition of the forest floor, or assemblage behavior (adult emergence patterns). Again, the stress value indicates caution in interpreting details of the ordination, as interesting as they may appear to be.

Family-level analyses

Carabidae:

NMS ordination of year-end totals for carabid beetle sample assemblages (Fig. 6) also depicted a strong effect of forest age with little potential for misinterpretation (final stress for 2-dimensional solution = 5.6; Monte Carlo $p = 0.03$). Graphical results showed a pattern similar to Figure 4. MRPP also showed a significant effect of forest type on carabid sample assemblages ($A = 0.271$; $p = 0.003$). Cluster analysis of Bray-Curtis values resulted in a similar pattern of forest type groupings for Carabidae (Fig. 7). Again, sites were generally ordered by age, but the oldest YR site (RV YR) clumped more closely to the OR sites and the two youngest sites grouped separately.

Staphylinidae:

NMS ordinations of year-end totals for staphylinid beetle assemblages resulted in an ordination not significantly different from that generated by chance (stress >2 ; Monte Carlo $p > 0.10$). Though the stress value was low (indicating little chance of misinterpretation of the ordination), Monte Carlo results indicate the strength of the ordination axes (and thus the calculated stress value) were not significantly different than that generated by chance and no clustering pattern was observed. However, MRPP showed a significant effect of forest type on staphylinid assemblages ($A = 0.240$; $p = 0.01$) and cluster analysis of Bray-Curtis values resulted in a grouping pattern reflective of forest age (Fig. 8). Here, old restoration and remnant riparian forest sites formed a mixed cluster separate from young restoration sites.

Tenebrionidae:

NMS ordination of year-end totals for tenebrionid beetle assemblages (Fig. 9) resulted in strong ordination results (final stress for 2-dimensional solution = 0.001; Monte Carlo $p < 0.02$). However, graphical representation was poor due to similar forest

types having a tendency to “ordinate” immediately upon one another. All young restoration sites, two old restoration sites (RVII and PHRU), and three of the remaining sites (KS, PHRR, and PCWCB) ordinated immediately on top of one another with one remnant riparian forest site (RVWCB) ordinating separately from all other sites. Each of these clusters was approximately equidistant from one another. This “stacking” may be due to either the relatively low number of species found in this sample assemblage and/or the apparently strong affinities of species in this family to a given forest type. MRPP showed a significant effect of forest type on the sample assemblages ($A = 0.425$; $p = 0.01$). Cluster analysis of Bray-Curtis values for tenebrionid beetles (Fig. 10) resulted in an ordination, reflective of forest age, split into two groups with a relatively low percent similarity. RR sites (again) clustered closely together. However, YR sites clustered most closely together. OR sites were split between YR and RR clusters, with KS OR (the oldest OR site) clustering with RR sites.

Species-level analyses

Indicator species analysis resulted in statistically significant IVs greater than 25 for 31 morphospecies in 12 families (Tables 3 and 4). Subsequent ANOVA and Kruskal-Wallis tests showed a statistically significant effect of forest type ($p < 0.05$) on mean monthly trap catches of 43 morphospecies (25 and 18 species, respectively for the two tests) in 14 families. Tukey pair-wise comparisons of ANOVA results showed that 10 morphospecies were caught within older forest types significantly more than in younger ones, 11 morphospecies were caught within younger forest types significantly more than in older ones, and 3 morphospecies were caught within old restoration sites significantly more than in young restoration sites or remnant riparian forests. Pair-wise comparisons were not performed on morphospecies showing significant effect of forest type using Kruskal-Wallis (data forthcoming). Carabidae (10 species), Tenebrionidae (7 species), and Staphylinidae (6 species) were the three most abundant families represented in these results. Species-specific response at the family level is discussed below.

Carabidae:

Ten morphospecies of carabid beetles showed a significant effect of forest type on mean monthly trap samples. Pairwise comparisons showed that four morphospecies

(*Perigona* sp. 1, *Pterostichus (Hypherpes)* sp. 1, *Dichierus dilatatus*, and *Microlestes* sp.) were caught in significantly higher numbers on young restoration sites (Tukey pairwise comparison; $p < 0.05$) and two species (*Pterostichus lustrans*, *Poecilus occidentalis*) were caught in significantly higher numbers in remnant riparian forests ($p < 0.05$). Three other morphospecies showed a significant effect of forest type (Kruskal-Wallis), but pairwise comparisons were not made (data forthcoming). Of these three, one genus (*Amara*) and two morphospecies (*Calosoma cancellatum*, *Platynus* sp. 1) were trapped in higher mean numbers on young restoration sites and one morphospecies (*Pterostichus (Hypherpes)* sp. 2) was trapped in higher mean numbers within old restoration sites and remnant riparian forests.

Staphylinidae:

Eight species of staphylinid beetles showed a significant effect of forest type on mean monthly trap samples. Pairwise comparisons showed that one morphospecies (*Medon languidum*) was caught in significantly higher numbers on old restoration sites (Tukey pairwise comparison; $p < 0.05$) and two morphospecies (*Sepedophilus castaneus* and *Bisnius* sp.) were caught in significantly higher numbers in remnant riparian forests ($p < 0.05$). Five other morphospecies showed a significant effect of forest type (Kruskal-Wallis), but pairwise comparisons were not made (data forthcoming). Of these five, one species (*Tachyporus californicus*) was trapped in higher mean numbers on young restoration sites and four morphospecies (*Dinothenarus* sp., *Paederinae* sp. 1, *Staphylinidae* sp 1., and *Xantholinus longiventris*) were trapped in higher mean numbers within old restoration sites and remnant riparian forests.

Tenebrionidae:

Seven species of tenebrionid beetles showed a significant effect of forest type on mean monthly trap samples. Pairwise comparisons showed that one genus (*Blapstinus*) was caught in significantly higher numbers on young restoration sites (Tukey pairwise comparison; $p < 0.05$) and four species (*Nyctoporis sponosa*, *N. aequicollis*, *Eleodes cordatus*, and *Eulabis bicarinatus*) were caught in significantly higher numbers in remnant riparian forests ($p < 0.05$). Two other species showed a significant effect of forest

type (Kruskall-Wallis), but pairwise comparisons were not made (data forthcoming). Of these two, one species (*Eleodes dentipes*) was trapped in higher mean numbers on young restoration sites and one species (*E. littoralis*) was trapped in higher mean numbers within old restoration sites and remnant riparian forests.

Discussion

Order-level analyses

Ordination and cluster analysis of coleopterans at the order level indicated a strong response of these sample assemblages to forest site age (i.e. chronosequence). MRPP analysis also showed a significant effect of forest type (i.e. age class). Young restoration site sample assemblages appeared distinctly separate from old restoration and remnant riparian forest types and also exhibited the highest within-type variation. Both these effects may be largely attributed to the more pronounced seasonal variation in temperature, radiation and other related factors at young restoration sites. Though these effects were not directly measured, all young restoration sites were relatively open and lacking in canopy, therefore, young restoration sites were most subject to extreme changes in seasonal temperature/radiation, moisture, and related environmental variables characteristic of the Mediterranean climate. As a result, coleopteran species found in young restoration sites are most likely to exhibit behavioral and physiological adaptations to extreme changes in site conditions. These adaptations may include avoidance of extreme summer conditions through emigration to more suitable habitats, reduced activity during periods of extreme high or low temperatures, or, conversely, increased activity during periods of seasonal extreme when other species are less active. We hypothesize that differences among sites within the young restoration sites may also be partly due to a degree of randomness in “initial assemblage” composition. That is to say, the species composition immediately after the site disturbance resulting from restoration activities may reflect more assemblage “chaos” or randomness. Individuals of flying species that are highly mobile and/or dispersing (and not reflective of forest floor community composition) are also caught more readily in traps within young restoration sites because of the openness of these sites, adding to more “sample noise”.

As hypothesized, old restoration sites appear to fall in-between young restoration sites and remnant riparian forests, suggesting an underlying trajectory for community composition in relation to forest age.

Remnant riparian sites appeared most similar to one another as a group suggesting higher relative stability in community structure. We hypothesize that these similarities

may be due to several factors of remnant forests, such as their greater environmental “buoyancy” (the ability of closed forests to buffer extreme environmental conditions through the year; greater habitat complexity (i.e. presence of downed woody debris and fallen trees, more complex trophic structure related to decomposition of this organic debris, and greater structural complexity of surface soils and litter layer related to site age); and higher flood frequency (remnant forests, as stated above, generally occur lower on the flood plain).

Examination of overall species composition by forest type over the sample year indicates that young restoration site assemblages vary more widely than do old restoration and remnant riparian forest sites. This supports the hypothesis that older sites share certain characteristics that increase the stability of their assemblage compositions through time.

Family-level analyses

Analyses of three families of beetles indicates that response of coleopterans varied at different taxonomic levels, particularly as portrayed by NMS, though MRPP showed a statistically significant effect of forest type for all families analyzed. Carabid beetles showed a clear response to forest type. This family was the most speciose group sampled and is a typical target taxon utilizing this sampling method. Sampling of this somewhat omnivorous and large group showed a clear sample assemblage response to forest age and a significant effect of forest type. Staphylinid beetles showed the most ambiguous results of the three families analyzed. Though this family showed a significant response to forest type based on MRPP results and cluster analysis portrayed a general assemblage response to forest age, NMS ordination results were poor and ambiguous. Lastly, tenebrionid beetles showed the strongest response to forest age and type. Many members of this, the least speciose family appeared to have a strong affinity to particular forest types. In addition, all tenebrionid beetles sampled in this study were flightless and slow moving, which greatly reduces their dispersal potential between habitat types. Restricted dispersal may in turn be related to the strong habitat affinities that tenebrionids display (e.g. greater adaptation to a habitat type in which individuals and their offspring are likely to remain for their entire lives).

Individual species analyses

A thorough discussion of the life history attributes that make particular coleopteran species better indicators than others is beyond the scope of this report. However it is worth noting that many of the species sampled are characteristic of certain habitat types (“indicator species”), appear to have limited distributions, or show strong effects of season. For example, remnant riparian forest indicator species include *Pterostichus lustrans* (Carabidae), and *Eulabis bicarinatus* (Tenebrionidae). *Amara* spp. (Carabidae), *Blapstinus* spp. (Tenebrionidae), and *Aeolus livens* (Elateridae) are characteristic of young restoration sites. Species that were caught in significantly higher numbers at specific geographic locations while showing a strong effect of treatment type include *Pterostichus (Hypherpes)* sp.1, *Notoxus* sp. (Anthicidae) and two species of *Nyctoporis* (Tenebrionidae). Species with strong seasonal abundances included *Calosoma cancellatum* (Carabidae) and *Eleodes dentipes* (Tenebrionidae).

Conclusion

Data presented here indicate that restoration efforts along the Sacramento River are providing habitat for large numbers of invertebrate species associated with remnant riparian forests. Furthermore, these data show that sampling invertebrate assemblages utilizing simple methods can provide a rich source of information about community composition, structure, and function in these different habitats. These data also show that invertebrate assemblages can be useful in revealing general effects of restoration efforts on community structure. By choosing a relatively discrete habitat component (e.g. the forest floor), community level sampling revealed different patterns related to effects of geography, seasonality, and forest age at the order, family and morphospecies level. Furthermore, results show that habitat restoration efforts along the Sacramento River are having a significant effect on surface-active coleopteran assemblages and that many species associated with remnant riparian forests are utilizing older restoration sites. Given the general differences between forest types (e.g. lack of canopy in young restoration sites and closed forest conditions in remnant riparian sites), these differences in sample assemblages are not surprising. However, examination of these general

differences contributes to our understanding of these poorly documented communities and their response to habitat change at various taxonomic levels. Variability in response at different taxonomic levels may also reflect differences in overall community functioning. For example, many species of tenebrionid beetles are associated with woody debris and fallen trees, a resource most commonly found in remnant riparian forests and generally lacking in younger forest types. Features associated with an increase in forest age and probably related to epigeal beetle composition (as well as a myriad of other arthropods) are an overall increase in canopy closure and percent cover of deciduous leaf litter and woody debris. Though not directly measured here, development of a forest interior is known to provide a buffer against extreme fluctuations (characteristic of younger more open sites) in several interrelated environmental factors (e.g. wind, temperature/radiation, and moisture).

Future work should examine more closely those species that appear to be indicative of selected forest types and their relative importance within these communities (i.e. as predators, prey, detritivores, competitors, etc.), as well as microhabitat parameters important to these species, especially native species with limited distributions and those that are most dispersal limited. There is also a need to better understand how arthropod communities within these riparian forests will respond to likely (or presently occurring) invasions of exotic species (such as argentine ants). This research would provide important insight into these riparian communities as a whole, and useful information for appropriate natural area reserve design and planning along the Sacramento River. Lastly, an analysis of the importance of structural elements of the forest floor (e.g. woody debris) for these (and other) taxa may provide important information to restoration as a practical and applied science.

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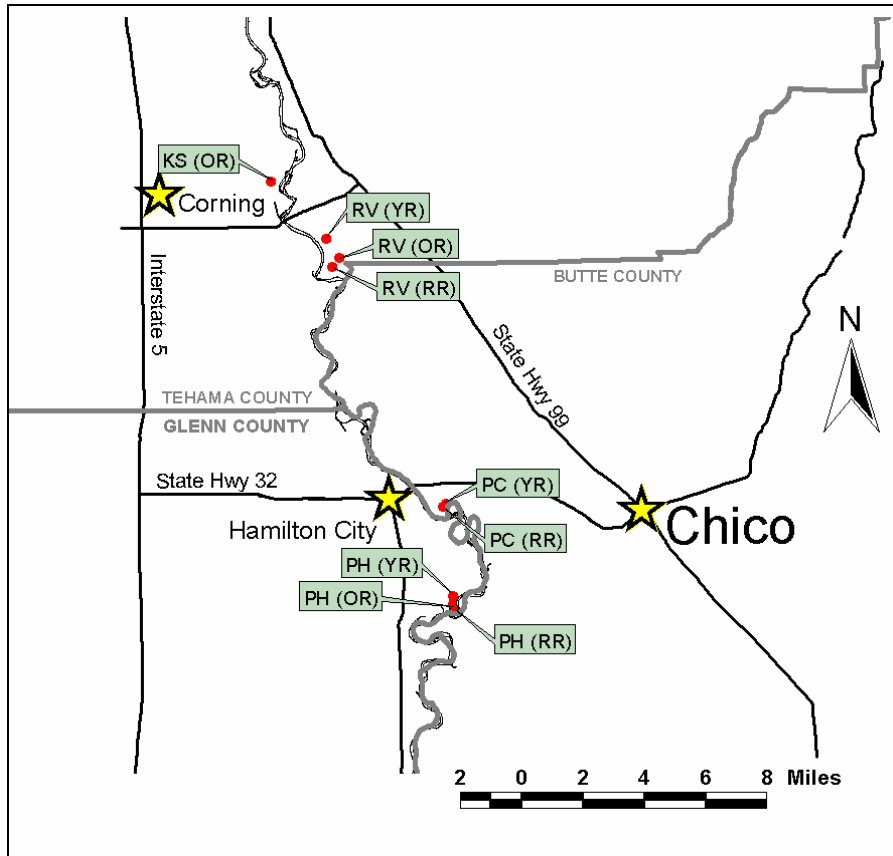
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**Figure. 1. Regional location map of pitfall trap transect locations along the middle Sacramento River between The Nature Conservancy’s Kopta Slough restoration site (Tehama County, California) and Phelan Island restoration site (Glenn County, California).
 Site location: KS=Kopta Slough; RV=River Vista; PC=Pine Creek; PH=Phelan Island
 Forest type: YR=Young restoration; OR=Old restoration; RR=Remnant riparian forest**

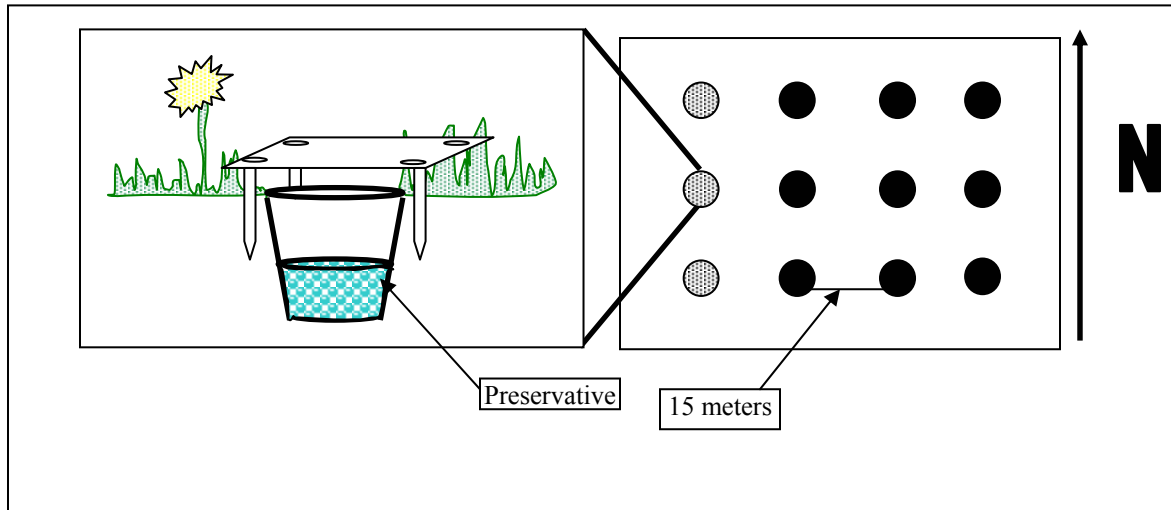
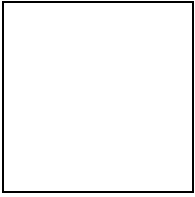


Figure 2. Diagram of individual pitfall trap (right) and pitfall transect layout (left). Primary trap locations represented by black circles (n=9) and secondary traps (traps used for data replacement in event of trap disturbance or loss) represented by shaded circles (n=3).



**Figure 3. NMS ordination of year-end totals for coleopteran sample assemblages (final stress for 2-dimensional solution= 3.5; Monte Carol p= 0.03).
Site location: KS=Kopta Slough; RV=River Vista; PC=Pine Creek; PH=Phelan Island.
Forest type: YR=Young restoration; OR=Old restoration; RR=Remnant riparian forest**

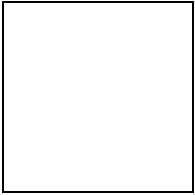


Figure. 4 Cluster analysis of Bray-Curtis values for year-end totals of coleopteran sample assemblages.
Site location: KS=Kopta Slough; RV=River Vista; PC=Pine Creek; PH=Phelan Island
Forest type: YR=Young restoration; OR=Old restoration; RR=Remnant riparian forest

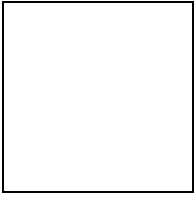
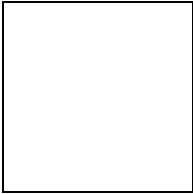
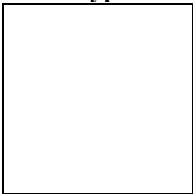


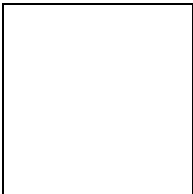
Figure 5. NMS ordination of monthly sample assemblages by forest type over entire study area. For all forest types n=3 per month except Aug-Sep n=2 for young restoration sites and remnant riparian forests (final stress for 2-dimensional solution= 12; Monte Carlo p= 0.01). MRPP for effect of forest type highly statistically significant (p< 0.0001)



**Figure 6. NMS ordination of year-end totals for carabid beetle sample assemblages. (final stress for 2-dimensional solution= 5.6; Monte Carol p= 0.03).
Site location: KS=Kopta Slough; RV=River Vista; PC=Pine Creek; PH=Phelan Island
Forest type: YR=Young restoration; OR=Old restoration; RR=Remnant riparian forest**



**Figure 7. Cluster analysis of Bray-Curtis values for year-end totals of carabid beetle sample assemblages.
Site location: KS=Kopta Slough; RV=River Vista; PC=Pine Creek; PH=Phelan Island
Forest type: YR=Young restoration; OR=Old restoration; RR=Remnant riparian forest**



**Figure 8. Cluster analysis of Bray-Curtis values for year-end totals of staphylinid beetle sample assemblages.
Site location: KS=Kopta Slough; RV=River Vista; PC=Pine Creek; PH=Phelan Island
Forest type: YR=Young restoration; OR=Old restoration; RR=Remnant riparian forest**

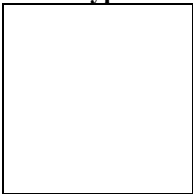


Figure 9. NMS ordination of year-end totals for tenebrionid beetle sample assemblages (final stress for 2-dimensional solution < 0.001; Monte Carol p= 0.02).

Site location: KS=Kopta Slough; RV=River Vista; PC=Pine Creek; PH=Phelan Island

Forest type: YR=Young restoration; OR=Old restoration; RR=Remnant riparian forest

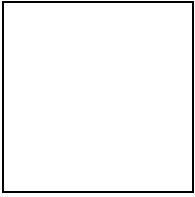


Figure 10. Cluster analysis of Bray-Curtis values for year-end totals of tenebrionid beetle sample assemblages.
Site location: KS=Kopta Slough; RV=River Vista; PC=Pine Creek; PH=Phelan Island
Forest type: YR=Young restoration; OR=Old restoration; RR=Remnant riparian forest

Table 1. Forest type, acronym, site name, age, and acreage of pitfall trap location study sites between Kopta Slough, Tehama County, California and Phelan Island, Glenn County, California.

Treatment	Site name	Acronym	Planted	Acres
"Young" Restoration Sites				
	Phelan Island '99	PH (YR)	1999	56.62
	Pine Creek '98	PC (YR)	1998	79.22
	River Vista Unit VI	RV (YR)	1998	131.57
"Old" restoration Sites				
	River Vista Unit II	RV (OR)	1994	109.81
	Phelan Island, River Unit	PH (OR)	1991	34.16
	Kopta Slough	KS (OR)	1990	59.4
Remnant riparian forest				
	River Vista, Wildlife Conservation Board	RV (RR)	NA	>500
	Pine Creek, Wildlife Conservation Board	PC (RR)	NA	>300
	Phelan Island Remnant Riparian	PH (RR)	NA	>50

Forest type:	Young Restoration Sites			Old Restoration Sites			Riparian Forest Sites			Total # Traps
Date	PH99	PC98	RVVI	RVII	PHRU	KS	RVWCB	PCWCB	PHRR	
12/15/2000	6	9	9	8	8	9	9	5	9	72
1/12/2001	9	8	9	8	7	8	9	8	9	75
2/9/2001	9	9	9	9	9	9	9	9	9	81
3/16/2001	9	9	9	9	9	9	9	9	9	81
4/12/2001	9	8	9	9	9	9	9	9	9	80
5/12/2001	9	9	9	9	9	9	9	9	9	81
6/11/2001	8	6	8	9	9	9	7	7	9	72
7/11/2001	9	9	9	9	9	9	9	9	9	81
8/8/2001	9	NS	9	9	9	9	9	NS	9	63
9/4/2001	9	NS	9	9	9	9	8	NS	9	62
10/4/2001	9	9	9	9	9	9	9	9	9	81
11/3/2001	9	9	8	9	9	9	9	9	9	80
Total	104	85	106	106	105	107	105	83	108	909

Table 2. Sampling calendar showing site, collection date, and number of traps collected over the course of 1-year during monthly week-long sampling periods along the middle Sacramento River between The Nature Conservancy’s Kopta Slough restoration site (Tehama County, California) and Phelan Island restoration site (Glenn County, California: NS = site not sampled that month).

Table 3. Monthly abundance and morphospecies richness data for nine study sites between Kopta Slough, Tehama County, California and Phelan Island, Glenn County, California (see Table 1 for site descriptions).

Site location: KS = Kopta Slough; RV = River Vista; PC = Pine Creek; PH = Phelan Island

	Site								
	Young restoration			Old restoration			Remnant riparian forest		
	PH	PC	RV	PH	RV	KS	PH	PC	RV
Monthly abundance data									
Mean # Individuals	182.9	158.1	127.8	163.1	181.7	268.7	212.0	473.5	387.6
Standard Error	51.3	39.5	23.2	35.9	46.4	75.9	49.5	125.0	79.7
Total # Individuals	2,238	1,585	1,525	1,957	2,177	3,225	2,538	4,732	4,649
Monthly morphospecies richness data									
Mean # morphospecies	18.6	14.9	15.1	16.3	17.7	16.6	18.3	19.1	19.3
Standard Error	2.5	0.6	1.4	2.7	2.2	2.7	2.8	2.6	3.1
Min	9	11	9	4	10	6	11	13	11
Max	38	29	25	34	30	38	40	37	47
Total # morphospecies	76	60	59	73	69	63	75	70	74
<hr/>									
Total # Individuals	24,626								
# Species with only 1 occurrence	87								
# Species with only 2 occurrences	25								
Total Tentative # species	188								

Table 4. ANOVA results and Indicator Values (IV) of species showing significant effect of forest type on mean monthly trap catch (Indicator Values range from 0 for non-indicators to 100 for perfect indicators). Forest type: YR=young restoration sites; OR=old restoration sites; RR=remnant riparian forest sites.

Species	YR		OR		RR		ANOVA P*	Indicator Spp. Analysis	
	x ± 1 SE	IV	x ± 1 SE	IV	x ± 1 SE	IV		IV _{max}	P**
Anobiidae									
<i>Ptinus</i> sp.			0.3 ± 0.2 ^a	1	7.5 ± 3.7 ^a	73	0.0218	72.6	0.002
Anthicidae									
<i>Formicilla munda</i>	4.53 ± 2.3	83					0.0211	83.3	0.001
Carabidae									
<i>Dichierus dilatatus</i>	0.32 ± 0.2	42					0.022	41.7	0.011
<i>Microlestes</i> sp.	3.8 ± 1.8 ^a	75	0.4 ± 0.2 ^a	5			0.0229	75.1	0.001
<i>Perigona</i> sp.	0.6 ± 0.2 ^a	48	0.3 ± 0.3 ^b				0.004	47.8	0.001
<i>Poecilus occidentalis</i>	3.4 ± 1.8 ^a	3	25.3 ± 9.7 ^{ab}	25	65.7 ± 19.1 ^b	70	0.0027	69.7	0.002
<i>Pterostichus (Hyperperes)</i> sp. 1	15.4 ± 5.9 ^a	59	8.4 ± 2.8 ^{ab}	35	0.4 ± 0.2 ^b		0.0085	58.8	0.008
<i>Pterostichus lustrans</i>	0.14 ± 0.7 ^a		5.1 ± 1.6 ^{ab}	5	96.00 ± 26.4 ^c	95	<0.0001	94.8	0.001
Curculionidae									
<i>Hypera posticta</i>	2.5 ± 1.7 ^a	56	0.3 ± 0.3 ^b		0.6 ± 0.4 ^b		0.0077	56.4	0.001
<i>Listroderes costirostris obliquus</i>	0.17 ± 0.8	33					0.0158	33.3	0.022
Curculionidea sp. 4			0.7 ± 0.4	58			0.0365	58.3	0.002
Elateridae									
<i>Aeolus livens</i>	5.9 ± 2.3 ^a	82	0.8 ± 0.9 ^b				0.0024	82.2	0.001
Latridiidae									
<i>Melanophthalma</i> sp.	5.8 ± 2.8 ^a	57	1.4 ± 0.5 ^{ab}	14	0.2 ± 0.1 ^b	1	0.0161	57.1	0.015
Melyridae									
<i>Acanthinus</i> sp.	0.5 ± 0.2	58					0.0016	58.3	0.001
Mycetophagidae									
<i>Mycetophagus californicus</i>			0.3 ± 0.3 ^a		0.5 ± 0.2 ^a	39	0.0327	39.4	0.011
Staphylinidae									
<i>Bisnius</i> sp.			1.6 ± 0.7 ^a	53	0.4 ± 0.1 ^a	14	0.0249	53	0.013
<i>Medon languidum</i>			0.8 ± 0.5	25			0.0365	25	0.098
<i>Sepedophilus castaneus</i>			0.8 ± 0.5 ^a	3	0.7 ± 0.3 ^b	59	0.0066	59.3	0.001
Tenebrionidae									
<i>Blapstinus histricus</i>	48.7 ± 24.3 ^a	78	6.8 ± 2.9 ^a	7	2.5 ± 1.2 ^a	3	0.0417	77.8	0.004
<i>Eleodes cordatus</i>			1.7 ± 0.8 ^a	5	14.4 ± 6.8 ^b	75	0.0222	74.7	0.001
<i>Eulabis bicarinatus</i>			0.3 ± 0.2 ^a	4	1.3 ± 0.6 ^a	48	0.0247	48.2	0.006
<i>Nyctoporis sponsa</i>					1.2 ± 0.5	50	0.0046	50	0.002
<i>Nyctoporis aequicollis</i>					1.6 ± 0.8	50	0.0184	50	0.003
Throscidae									
<i>Aulonothroscus</i> sp.			0.8 ± 0.5	25			0.0365	25	0.102

Notes: Entries with the same letter superscripts are not significantly different ($P < 0.05$) according to Tukey post hoc analysis

IV= Indicator value for indicator species analysis carried out in PC-ORD

P*=Significance value resulting from one-way ANOVA

P**=Significance of Monte Carlo test of maximum (IV_{max}) indicator value

Table 5. Kruskal-Wallis and Indicator Values (IV) of species showing significant effect of forest type on mean monthly trap catch (Indicator Values range from 0 for non-indicators to 100 for perfect indicators). Forest type: YR=young restoration sites; OR=old restoration sites; RR=remnant riparian forest sites.

Species	YR		OR		RR		K-W P*	Indicator Spp. Analysis	
	x ± 1 SE	IV	x ± 1 SE	IV	x ± 1 SE	IV		IV _{max}	P**
Anthicidae									
<i>Notoxus</i> sp.			0.5 ± 0.4	39	0.3 ± 0.3		0.0	40	0.0
Carabidae									
<i>Amara</i> spp.	18.3 ± 8.3	68	4.1 ± 1.9	14	2.7 ± 1.0	6	0.0	68	0.0
<i>Calosoma cancellatum</i>	2.0 ± 1.5	33	0.3 ± 0.3				0.0	33	0.0
<i>Platynus</i> sp.	0.3 ± 0.3	2	0.1 ± 0.5	27			0.1	27	0.1
<i>Pterostichus (Hypherpes)</i> sp. 2	0.6 ± 0.2	4	1.9 ± 0.6	15	7.2 ± 3.4	62	0.0	62	0.0
Curculionidae									
<i>Curculionidea</i> sp. 6	0.8 ± 0.5	25					0.0	25	0.1
Erotylidae									
<i>Dacne californica</i>	0.2 ± 0.1	1	9.9 ± 7.4	53	3.8 ± 2.2	14	0.0	53	0.1
Latridiidae									
<i>Corticaria</i> sp.	3.3 ± 1.6	54	2.4 ± 0.9	23	0.5 ± 0.4	3	0.0	54	0.0
Leptodiridae									
<i>Leptodiridae</i> sp.	0.5 ± 0.3	8	1.6 ± 0.9	38			0.0	38	0.0
Silphidae									
<i>Nicrophorus marginatus</i>	1.6 ± 2.0	24			0.6 ± 0.4	1	0.2	24	0.1
Staphylinidae									
<i>Dinothenarus</i> sp.	0.4 ± 0.2		31.3 ± 14.7	65	16.6 ± 6.8	34	<0.0001	65	0.0
<i>Tachyporus californicus</i>	0.5 ± 0.3	30	0.6 ± 0.4	2			0.1	30	0.1
<i>Xantholinus longiventris</i>			0.1 ± 0.7	6	0.4 ± 0.3	32	0.1	32	0.1
<i>Paederinae</i> sp. 1	2.9 ± 1.3	2	35.1 ± 16.7	55	26.4 ± 14.6	41	0.0	55	0.1
<i>Staphylinidae</i> sp. 1	0.5 ± 0.3	1	8.7 ± 3.7	56	6.3 ± 2.5	27	0.0	56	0.0
Tenebrionidae									
<i>Eleodes dentipes</i>	0.5 ± 0.3	33					0.0	33	0.0
<i>Eleodes littoralis</i>	0.6 ± 0.4		6.5 ± 2.9	19	22.1 ± 15.9	58	0.0	58	0.1

IV= Indicator value for indicator species analysis carried out in PC-ORD

P*=Significance value from Kruskal-Wallis nonparametric test effect of forest type by species

P**= Significance of Monte Carlo test of maximum (IV_{max}) indicator value

Appendix Table 1. List of all beetles caught during duration of study. Numbers are year total trap catch over all sites, and site year total trap catch for each species. YR1=PC98; YR2=PH99; YR3=RVVI; OR1=KS; OR2=PHRU; OR3=RVII; RR1=PCWCB; RR2=PHRR; RR3=RVWCB.

Species	Year Total	Young Restoration			Old Restoration			Remnant Riparian		
		YR1	YR2	YR3	OR1	OR2	OR3	RR1	RR2	RR3
Anobiidae										
Anobiidae sp. 1 ^T	1				1					
Anobiidae sp. 2	1						1			
<i>Ptinus</i> sp.	275				2	7		20	161	85
<i>Tricorynus</i> sp.	39			1		16	1		11	10
Anthicidae										
<i>Acanthinus</i> sp. ^T	17	5	9	3						
<i>Formicilla munda</i> LeConte 1851	130	3	127							
<i>Notoxus</i> sp.	19					18			1	
Bostrichidae										
<i>Trogoxylon</i> sp. ^T	4	1	1	1	1					
Cantharidae										
<i>Cantharus consors</i> LeConte 1851	9				2		6			1
<i>Podabrus</i> sp.	16	2			3		1	1	1	8
Carabidae										
<i>Agonum</i> sp. ^T	1	1								
<i>Amara californica</i> Dejean 1828 ^T	175	88	19	33	12	1	9	9	1	3
<i>Amara erraticus</i> Duftschmid 1812 ^T	695	458	18	32	6	105	16	45	12	3
<i>Amara</i> sp.	3									3
<i>Anisodactylis californicus</i> Dejean 1829 ^T	2	1						1		
<i>Axinopalpus biplagiatus</i> Dejean 1825	137	49	53	19	2	1	5		5	3
<i>Bembidion obliquulum</i> LeConte 1859	109					2		85	13	9
<i>Bembidion quadrimaculata</i> Linnaeus 1761	9	4			3	2				
<i>Bembidion satelles</i> Casey 1918 ^T	29	6	1		1	3	1	16	1	
<i>Bembidion</i> sp. 1	36	1	1		11	3		17	2	1
<i>Bembidion</i> sp. 2	2				1	1				
<i>Calathus ruficollis</i> Dejean 1828	1825	52	78	124	181	290	226	279	217	378
<i>Calosoma cancellatum</i> Eschscholtz 1833	71	13	57		1					
<i>Carabidae</i> sp. 1	1	1								
<i>Carabidae</i> sp. 2	1							1		
<i>Chlaenius tricolor</i> Dejean 1826	14				5	1	2	5		1
<i>Dicheirus dilatatus</i> Dejean 1829 ^T	10	2	6	2						
<i>Harpalus caliginosus</i> Fabricius 1775	1			1						
<i>Harpalus pensylvanicus</i> De Geer 1774	17	1	10		3		3			
<i>Harpalus</i> sp.	2		1							1
<i>Laemostenus terricola</i> Herbst 1784 ^T	5				5					
<i>Loricera foveata</i> LeConte 1863	20	1		4	5	1	2			7
<i>Microlestes</i> sp.	141	70	33	23	3		12			
<i>Notiobia</i> sp. ^T	1							1		
<i>Notiopholus</i> sp.	1			1						
<i>Perigona</i> sp. ^T	22	6	11	4	1					
<i>Platynus</i> sp. ^T	5			1	2	1	1			
<i>Poecilus occidentalis</i> Dejean 1828	3269	19	9	90	203	206	500	689	280	1273
<i>Pterostichus (Hypherpes)</i> sp. 1	864		8	546		2	297	6	2	3
<i>Pterostichus (Hypherpes)</i> sp. 2	356		3	20	6	4	63	4	37	219
<i>Pterostichus lustrans</i> LeConte 1851	3640	4	1		13	170	2	2136	608	706
<i>Tanystoma maculicolle</i> Dejean 1828 ^T	580	62	59	98	12	2	12	331		4
Chrysomelidae										
<i>Saxinis saucia</i> LeConte 1857	1		1							

Appendix Table 1. Continued.

Species	Year Total	Young Restoration			Old Restoration			Remnant Riparian		
		YR1	YR2	YR3	OR1	OR2	OR3	RR1	RR2	RR3
Coccinellidae										

Coccinellidae sp. 1	4			1			2	1		
Coccinellidae sp. 2	2						1		1	
Coccinellidae sp. 3	3			3						
Coccinellidae sp. 4	2							1		1
Coccinellidae sp. 5	1							1		
<i>Hippodamia</i> sp.	4			3				1		
Corylophidae										
Corylophidae sp.1 ^T	3		3							
<i>Sericoderus</i> sp.	439	1	57	33	71	32	172	4	45	24
Curculionidae										
Curculionidae sp. 1	2	1	1							
Curculionidae sp. 2	1					1				
Curculionidae sp. 3	55	48	5	1	1					
Curculionidae sp. 4	24				11		13			
Curculionidae sp. 5	4					1		2	1	
Curculionidae sp. 6	3	1		2						
Curculionidae sp. 7	2									2
Curculionidae sp. 8	2		2							
Curculionidae sp. 9	6		1		1				4	
<i>Dorytomus inaequalis</i> Casey 1892	12					6		3	1	2
<i>Hypera postica</i> Gyllenhal 1813	92	79	2	8		1		2		
<i>Listroderes costirostris obliquus</i> Klug 1829	6	3	3							
<i>Sphenophorus venatus ssp. glyceria</i> (Chitiarden 1919) ^T	5		2		1	1	1			
<i>Sphenophorus venatus ssp. vestitus</i> (Chitt.)	8					3			4	1
Dermestidae										
<i>Dermestes</i> sp.	3							1	2	
Elateridae										
<i>Aeolus livens</i> LeConte 1853	184	39	96	46			3			
<i>Agriotella</i> sp.	23		8	1	2	4		6		2
<i>Anchastus cinereipennis</i> Eschscholtz 1829 ^T	132	1	9	18	32	6	13	43	8	2
<i>Cardiophorus</i> sp.	1				1					
Elateridae sp. 1	1						1			
Elateridae sp. 2	14			8	5		1			
Elateridae sp. 3	4						2	1		1
Elateridae sp. 4	1							1		
Elateridae sp. 5	13	1	2		2	7			1	
Elateridae sp. 6	3							3		
Elateridae sp. 7	3				1	1				1
Elateridae sp. 8	1			1						
<i>Neotrichophorus</i> sp.	2									2
<i>Oistus</i> sp.	3								1	2
Erotylidae										
<i>Dacne californica</i> Horn 1870	497		7	1	50	247	58	38	57	39
Glaphyridae										
<i>Lichnanthe apina</i> Carlson 1980										
Histeridae										
<i>Hister furtivus</i> LeConte 1860 ^T	2							1		1
<i>Hister sellatus</i> LeConte 1857	1							1		
Histeridae sp. 1	2								1	1
Histeridae sp. 2	1							1		
Histeridae sp. 3	1							1		
<i>Stictostix californicus</i> Horn 1870	12	1		1		2	2	2	4	

Appendix Table 1. Continued.

Species	Year Total	Young Restoration			Old Restoration			Remnant Riparian		
		YR1	YR2	YR3	OR1	OR2	OR3	RR1	RR2	RR3
Laemophloidae										
Laemophloidae sp. ^T	1								1	
Latridiidae										
<i>Corticaria</i> sp. ^T	216	8	90	16	71	4	10	11	1	5
<i>Melanopthalma</i> sp.	213	1	135	20	5	3	43	2	3	1
Leioididae										

<i>Colon</i> sp.	7					6		1		
<i>Ptomophagus</i> sp. 1	43	1	6	10		1	9	2	12	2
<i>Ptomophagus</i> sp. 2	13		7	2		1				3
Leptodiridae										
Leptodiridae sp. ^T	75			17		16	42			
Meloidae										
<i>Epicauta puncticollis</i> Mannerheim 1843 ^T	1		1							
Melyridae										
<i>Collops</i> sp.	2	2								
Melyridae sp. 1	1		1							
<i>Pseudosydates</i> sp.	1									1
<i>Tanaops</i> sp. ^T	1							1		
Mordellidae										
<i>Mordella</i> sp.	21		1		2	1	1	1	6	9
<i>Mordellistena</i> sp.	3		1			1			1	
Mycetophagidae										
<i>Mycetophagus californicus</i> Horn 1878	18						1	1	7	9
Nitidulidae										
<i>Lobiopa</i> sp.	1			1						
Nitidulidae sp. 1 ^T	4		2		1	1				
Nitidulidae sp. 2	1									1
Phalacridae										
<i>Phalcrus</i> sp.	29		4	5			1	19		
Pyrochroidae										
<i>Pedilus</i> sp. 1	1									1
<i>Pedilus</i> sp. 2	1								1	
Scarabaeidae										
<i>Aphodius</i> sp.	1		1							
<i>Hoplia</i> sp.	40	3				2	1	5	6	23
<i>Onthophagus taurus</i> Schreber	4	1	2			1				
Scarabaeidae sp. 1	1		1							
Scarabaeidae sp. 2	2								2	
<i>Serica</i> sp.	16		3			2			5	6
Scraptiidae										
<i>Neoscraptia testacea</i> Fender 1946	1							1		
Siliphidae										
<i>Heterosilpha ramosa</i> Say 1823	263	29	52	19	78	1	68	12	2	2
<i>Nicrophorus marginatus</i> Fabricius 1801	60	1	57					1	1	
<i>Nicrophorus nigritus</i> Mannerheim 1843	12						4		8	
Staphylinidae										
<i>Aleochara</i> sp.	1		1							
Aleocharinae sp. 1	2		2							
Aleocharinae sp. 2	2		2							
<i>Athetalia</i> sp. ^T	179	7	20	29	51	7	10	15	11	29
<i>Bisnius</i> sp.	73				50	1	7	4	2	9
<i>Bledius</i> sp.	1				1					
<i>Dinothenarus</i> sp. ^T	1732		1	12	531	279	315	274	144	176

Appendix Table 1. Continued.

Species	Year Total	Young Restoration			Old Restoration			Remnant Riparian		
		YR1	YR2	YR3	OR1	OR2	OR3	RR1	RR2	RR3
<i>Eusphalerum</i> sp. 1	3									3
<i>Eusphalerum</i> sp. 2	1									1
<i>Lathrobium armatum</i> Say 1834 ^T	26					1		24	1	
<i>Medon languida</i> Casey 1886 ^T	3						3			
<i>Medon</i> sp.	15	1	3	4	6			1		
<i>Oxypoda</i> sp. ^T	118	8	5	17	3	2	4	2	66	11
Paederinae sp. 1	2312	26	38	42	1077	172	16	234	208	499
Paederinae sp. 2	1	1								
<i>Philonthus</i> sp. 1	4	3	1							
<i>Philonthus</i> sp. 2 ^T	1						1			
<i>Reichenbachia</i> sp.	2						2			

<i>Sepedophilus castaneus</i> Horn 1877	27				2	1			7	17
Staphylinidae sp. 1	558	2	5	10	213	37	63	32	47	149
Staphylinidae sp. 3	18	2				1		4	7	4
Staphylinidae sp. 4	55		6	3	34		8		4	
Staphylinidae sp. 5	15	5	1				3		1	5
Staphylinidae sp. 6	1								1	
Staphylinidae sp. 7	142			2	134			1		5
Staphylinidae sp. 8	1				1					
Staphylinidae sp. 9	1						1			
Staphylinidae sp. 10	1						1			
Staphylininae sp.	18			1		6		2	4	5
<i>Stenus</i> sp. 1	92			6	78	2	2	3	1	
<i>Stenus</i> sp. 2	1			1						
<i>Stictolinus grandiceps</i> LeConte 1863	6		1	1				3	1	
<i>Tachinus</i> sp. 1	1									1
<i>Tachinus</i> sp. 2	1								1	
<i>Tachyporus</i> sp. 1	71				6	22	1	8	21	13
<i>Tachyporus californicus</i> Horn 1877	19	5	12		1	1				
<i>Xantholinus longiventris</i> Heer 1839	17				1	3		1	3	9
Tenebrionidae										
<i>Blapstinus dilatatus</i> LeConte 1851	8			4		2	1			1
<i>Blapstinus histricus</i> Casey 1890	1912	430	1006	176		131	88	16	49	16
<i>Cibdelis blaschkii</i> Mannerheim 1843	2					1				1
<i>Coniontus viatica</i> spp. group	50	2				8	3		9	28
<i>Eleodes cordata</i> Eschscholtz 1833	539				15	41	4	24	28	427
<i>Eleodes dentipes</i> Eschscholtz 1833	17	7	5	5						
<i>Eleodes littoralis</i> Eschscholtz 1831	1030	1	1		188	24	22	178	321	295
<i>Eulabis bicarinata</i> Eschscholtz 1829	52				1	9		1	16	25
<i>Helops simulator</i> Blaisdell 1921	5		1			1	3			
<i>Nyctoporis aequicollis</i> Eschscholtz 1831	55									55
<i>Nyctoporis cristata</i> Eschscholtz 1831	2									2
<i>Nyctoporis sponsa</i> Casey 1907	37								37	
Tenebrionidae sp. 1	1	1								
Tenebrionidae sp. 2	1	1								
Tenebrionidae sp. 3	4	3					1			
Tenebrionidae sp. 4	1								1	
Throscidae										
<i>Aulonothroscus</i> sp.	3				1	1	1			
Coleoptera sp. 1	4					1			3	
Coleoptera sp. 2	15		2	1		7	3		2	
Coleoptera sp. 3	1						1			
Coleoptera sp. 4	30	1	4		10	2	7	1	4	1

Appendix Table 1. Continued.

Species	Year Total	Young Restoration			Old Restoration			Remnant Riparian		
		YR1	YR2	YR3	OR1	OR2	OR3	RR1	RR2	RR3
Coleoptera sp. 5	4		1						3	
Coleoptera sp. 6	1								1	
Coleoptera sp. 7	1							1		
Coleoptera sp. 8	1									1
Coleoptera sp. 9	1		1							
Coleoptera sp. 10	1								1	
Coleoptera sp. 11	1								1	
Coleoptera sp. 12	1									1
Coleoptera sp. 13	1		1							
Coleoptera sp. 14	2	2								
Coleoptera sp. 15	1	1								
Total: 188										

¹: Tentative taxonomic designation. All tenebrionid taxonomic names verified by Kirby Brown.