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RESEARCH ARTICLE

Efficacy of Low and High Complexity Vegetation Treatments for Reestablishing Terrestrial Arthropod Assemblages during Montane Wetland Restoration

Jeffrey G. Holmquist,^{1,2} Jutta Schmidt-Gengenbach,¹ and Athena Demetry³

Abstract

Assessments of faunal reassembly during wetland restorations have typically been derived from relatively benign, lower-elevation environments. We investigated recovery of terrestrial arthropod assemblages in conjunction with restoration of a montane wet meadow in Sequoia National Park (Sierra Nevada, California, U.S.A.). Our goal was to assess response of arthropod assemblages to wetland restoration in this winter-dominated environment, including comparison of faunal reassembly in (1) areas of sparse plugs (planted over several years) and (2) dual-density plantings with additional heterogeneity, complexity, and connectance to source habitats provided by high-density bands running through sparsely planted habitat (final study year only). Results across all restoration treatments indicated varying levels of faunal reassembly, but convergence of faunal assemblages with reference habitat had not occurred

after recovery periods as long as 5 years. Similarity indices and multivariate compositional results indicated a slower recovery than did univariate trends for assemblage metrics and abundances for some individual taxa, highlighting the utility of assessments using a range of taxa and analytical approaches. Faunal recovery did not appear to lag behind that of vegetation structure, despite the short growing season. The dual-density plantings indicated faster recovery after 1 year, across almost all metrics, than was observed after several years for the sparse plantings. Restoration configurations that increase habitat complexity, heterogeneity, and/or connectance may disproportionately increase rates of passive faunal reassembly and prove to be cost-effective approaches for promoting recovery of ecosystem function.

Key words: faunal reassembly, habitat complexity, habitat heterogeneity, habitat structure, insects, Sequoia National Park, Sierra Nevada, spiders.

Introduction

The ultimate goal of restoration is re-creation of ecological function versus achieving a targeted plant density or general appearance (Zedler 2000; Pik et al. 2002). Reassembly of invertebrate assemblages, although somewhat under-investigated, is important for successful restoration. Invertebrates have remarkably high diversity and trophic complexity, function as pollinators, integrate ecological processes, and are likely to affect the success of the vegetation restoration via powerful feedback loops (Pik et al. 2002; Dixon 2009; Pocock et al. 2012). Reassembly of fauna can, however, be slower than that of plants (Brady et al. 2002; Woodcock et al. 2012; Rácz et al. 2013; Watts et al. 2008), and direct extrapolation from plant reestablishment to faunal recolonization is not reliable (Woodcock et al. 2010). Recovery of invertebrate assemblages in restored montane wetlands may be particularly slow given

the short growing season and harsh conditions in the mountain environment (Nagy & Grabherr 2009), although other wetland environments can be stressed by annual drying (Williams 2006). Arthropod diversity and abundance are known to drop precipitously in wetlands as the 2- to 3-month montane growing season ends, minimum temperatures again fall below freezing, and snowfall returns (Holmquist et al. 2013a, 2013b).

Restoration inherently alters the meso-landscape, and the nature of these changes to landscape configuration may have important influences on faunal reassembly. Habitat heterogeneity (compositional differences among patches) and complexity (density of structural components) shape invertebrate assemblage structure (Stoner & Lewis 1985; Wiens 1995) and may be especially important during restoration (Palmer et al. 1997; Armitage et al. 2013). Increasing connectivity (Wiens 1995) with source habitat via reduced patch boundary contrast (Holmquist 1998; Collinge & Palmer 2002) or provision of corridors (Dixon 2009; Eggers et al. 2009) might be expected to promote recolonization of restored habitats (Knop et al. 2011).

Our study evaluated arthropod colonization of two restoration treatments, each with a different meso-landscape arrangement, as part of a montane wetland restoration: *Sparse*, a single habitat configuration of low heterogeneity and complexity, consisting of areas of small, sparsely distributed plug plantings, and *Dual*,

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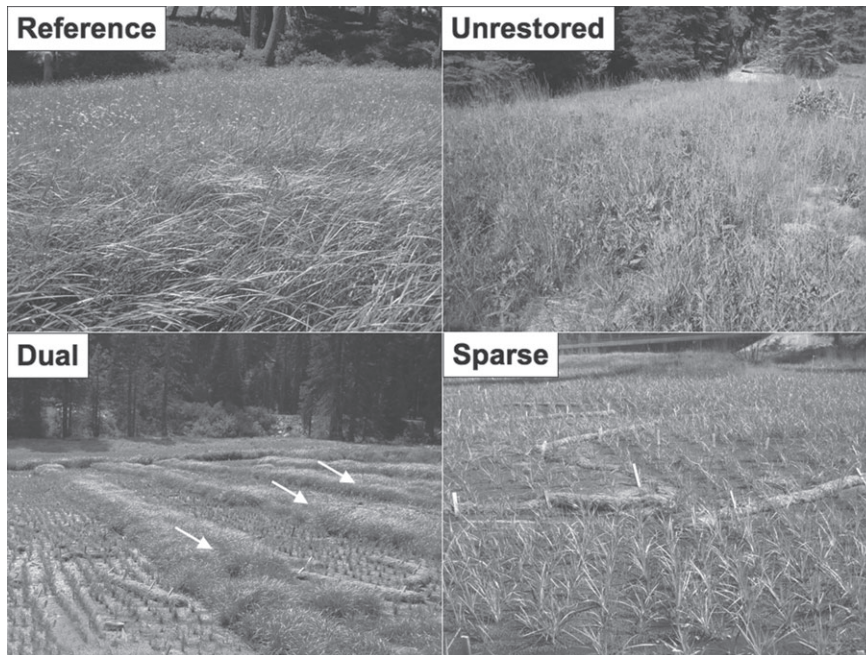


Figure 1. Investigated treatments; Sparse indicates dispersed plug plantings; Dual references a mix of Sparse habitat and bands of higher-density habitat (arrows).

with higher heterogeneity and overall complexity, including habitat as described for Sparse, alternating with bands of a second habitat configuration consisting of unbroken strips of taller, dense vegetation that spanned the width of the Dual treatment at equidistant intervals (Fig. 1). The bands of additional habitat had the potential to disproportionately benefit fauna by providing patches of high complexity habitat and by reducing boundary contrast with, and establishing corridors to, intact habitat. We assessed reassembly of faunal assemblages in these two restoration configurations via comparison with both Unrestored and Reference habitat (Fig. 1), as use of unrestored habitat alone is not ideal for comparisons of restoration efficacy (Downes et al. 2002). The Unrestored and Reference habitats both represent a third landscape arrangement (unbroken patches of tall, dense vegetation), but each with a different physical environment (degraded vs. intact wetland hydrology and substrate) and differing plant species composition.

Our investigation was developed in conjunction with restoration of a wet meadow in Sequoia National Park (Sierra Nevada, California, U.S.A.), which entailed planting of vegetation (Wolf & Cooper 2011) but no efforts to reintroduce fauna; such a passive restoration approach for fauna is common (Palmer et al. 1997; Scott et al. 2001). There were Sparse plantings during three different years over a 6-year period, which we assessed at two points in time, and faunal response to Sparse was compared with initial response to the Dual treatment, which managers added later in the study. Our objectives were to (1) assess response of the arthropod assemblage to wetland restoration in the montane environment and (2) assess the potential benefit to fauna of the additional heterogeneity, complexity, and connectance to source habitats provided by the Dual treatment.

Methods

Site, Restoration Overview, and Study Design

Halstead Meadow (Fig. 1), in montane habitat at 2,120 m elevation (36°37'02" N, 118°47'03" W), was in a severely degraded state in 2007 (Wolf & Cooper 2011). Geomorphology, hydrology, and vegetation had been altered by cattle grazing through the early 1900s, and construction of a road in 1934 that disrupted sheet flow and led to gully formation. The Halstead physical environment is dominated by winter snowfall, which occurs from October through May (mean seasonal precipitation = 109.8 cm; Western Regional Climate Center, station 045026, wrcc.dri.edu), and occasionally in June and September, versus infrequent summer thunderstorms ($x = 6.5$ cm). The short growing season is characterized by cool days (mean daily maximum = 22.1°C; station 045026) and cold nights (mean daily minimum = 5.1°C). The wetland is surrounded by upland forest, typified by *Abies concolor* (white fir), *A. magnifica* (red fir), and *Calocedrus decurrens* (incense cedar).

Intact wetland habitat and unrestored habitat were both present at Halstead throughout the project (Fig. 1). Intact habitat, used as the reference treatment, was characterized by shallow sheet flow (<2 cm deep) in most areas throughout the year and was dominated by *Scirpus microcarpus* (panicked bulrush); *Oxypolis occidentalis* (cowbane) and *Glyceria elata* (tall mannagrass) were of secondary importance. Unrestored habitat was never saturated and was in contrast dominated by *Elymus glaucus* (blue wildrye), *Solidago canadensis* (meadow goldenrod), and *Lupinus polyphyllus* (large-leaved lupine; Fig. 1).

Filling of gullies and restoration of sheet flow began in 2007, and portions of the meadow with newly restored

geomorphology and hydrology were planted incrementally beginning in 2008 (Wolf & Cooper 2011). Sparse plantings were made during, and/or in the non-growing seasons prior to the summers of 2008, 2010, and 2013. Vegetation plugs, from plants grown in containers with sterilized soil, were inserted through erosion control blanket at a density of approximately 5–10 plugs/m²; densities varied within and among treatments, but the 2013 plantings tended to be densest. Plugs were 2.5–4.0 cm in diameter, and there were up to five plants per plug, depending upon individual plant sizes (Fig. 1). Dual plantings were made in 2013, in order to speed vegetation recovery, and consisted of 3.7-m-wide bands of plugs as described above for Sparse, alternating with 1.8-m-wide bands of plants in much higher densities (~500/m²; Fig. 1) grown in coir matting. Plantings were primarily *Scirpus*, and percent cover by *Scirpus* was higher overall in restoration treatments than in Reference. Some plantings also contained smaller numbers of *Oxypolis* and *Glyceria* plugs; survivorship of the latter planted taxa was lower than that of *Scirpus*, but *Oxypolis* and *Glyceria* also quickly colonized restorations passively. All plants were grown from local seeds. Areas available for sampling were as follows: Reference 1.6 ha; Unrestored 1.4; '08 Sparse 0.40; '10 Sparse 0.24; '13 Sparse 0.53; '13 Dual 0.51. Assessment of the geomorphological, hydrological, and vegetation components of the restoration are beyond the scope of this paper, but are planned (Cooper, Wolf, and colleagues).

Management interventions such as the Halstead restoration can be used as powerful large-scale experiments, but study designs often must be built post hoc around existing management plans (Konrad et al. 2011). Plantings were established as contiguous units because of pressing management needs, rather than dispersed among a series of blocks, and Dual was only installed as a treatment in the final year of the study. Such limitations are common (Taillefer & Wheeler 2012). A strength of the study was similar proximity of arthropod source (Reference) habitat to all restoration treatments (<20 m). An additional strong element was the extensive nature of our sampling approach (sweep netting, see section *Sampling and Lab*) that incorporated an area of ~2,400 m² in each sampling series for each treatment, thus sampling a large proportion of the populations of interest in each treatment area. We therefore sampled about 16% of Restored and Unrestored area, about half of '08 Sparse, '13 Sparse, and Dual, and essentially all of the '10 Sparse habitat.

Sampling and Lab

We sampled at the apex of the growing season which coincides with highest arthropod diversity and abundance in these mountain wetlands (Holmquist et al. 2011, 2013a). Sampling at this time is important, because diversity and abundance of fauna decline sharply thereafter, and distinguishing treatment effects would become difficult. Sampled treatments included Reference, Unrestored, '08 Sparse, and '10 Sparse in 2010, and these four treatments plus '13 Sparse and '13 Dual in 2013. We collected six random samples from each treatment in each year over several days. Samples in Dual integrated both low- and

high-density elements. Each sample of fauna living in the vegetation canopy consisted of 50 standard sweeps with a conical sweep net (30.5 cm aperture, mesh size of 0.5 × 0.75 mm), and ~400 m² was covered by each collection (additional faunal sampling details in Holmquist et al. 2010). We identified specimens to family and morphospecies (genus and species when possible). Use of families and morphospecies as response variables is common in ecological assessments (Kremen et al. 1993; Oliver & Beattie 1996), including evaluation of restoration efforts (Pik et al. 2002; Davis & Utrup 2009).

We made vegetation and physical measurements after each faunal sample in order to minimize disturbance to arthropods. We used a centered and randomly oriented point-intercept transect to estimate percent vegetation cover. Canopy height, litter depth, and complexity were measured at two randomly selected points along the transect, the latter using the pole-touch method (2013 only; Bestelmeyer & Wiens 2001). In order to evaluate physical parameters that could not have been affected by the restoration, but could have covaried with treatment, we measured wind speed and air temperature with a Kestrel 3000 digital meter and tree cover with a convex densiometer. Wind speed ($x = 6.5$ km/h, SE = 0.41), temperature ($x = 17.3^\circ\text{C}$, SE = 0.71), and tree cover ($x = 5.2\%$, SE = 1.7) did not differ by treatment ($p = 0.16, 0.12, \text{ and } 0.35$, respectively; analysis of variances [ANOVAs], see below).

Analysis

Univariate analyses were 1×4 (2010; df treatment = 3, df residual error = 20) and 1×6 (2013; df 5, 30) ANOVAs followed by Tukey's tests (SYSTAT 12). Multiple comparisons were adjusted to per-family error rate with the sequential Bonferroni correction using MacBonferroni 1.6. Vegetation dependent variables included canopy height, litter depth, % bare ground, and complexity. Faunal dependent variables included total arthropod abundance, family and morphospecies richness (the latter on a per-sample basis), expected number of morphospecies via rarefaction (scaling to the number of individuals in the sample with the fewest individuals; Magurran 2004; calculated with Diversity 1.4), dominance (percent of total sample abundance represented by the most abundant taxon of each sample), percentage of less-motile taxa, and individual order and family abundances. We square-root transformed ($[y]^{0.5} + [y + 1]^{0.5}$) proportional variables and log-transformed ($\log [y + 1]$) other variables.

We examined differences by treatment across populations using several methods. We compared similarity of treatments to reference (Woodcock et al. 2010) using the Sørensen quantitative index; such use of abundances, versus simple presence-absence, is superior for evaluating similarity when sufficient data are available (Magurran 2004). Assemblage composition at the conclusion of the study was contrasted by treatment using PerMANOVA (df 5, 30) and nonmetric multidimensional scaling (NMS) in PC-ORD 6 (Peck 2010) and analyses of dispersion using PERMDISP2 (Anderson 2004). Response and explanatory matrices contained all treatments and samples. The response matrix included taxa that were collected

in at least three samples in order to reduce sparsity (Peck 2010) yet not discard too much information, as NMS is sensitive to such losses (Poos and Jackson 2012). The final matrix included 57 such families, and 69.6% of the cells contained zeros. The response matrix was log-transformed, and the coefficient of variation was 107%. The explanatory matrix included treatment type, as well as all vegetation and physical variables noted in the sampling protocol and cover estimates for the dominant plant taxa listed in the site description. We used the Sørensen distance measure for all analyses. The PerMANOVA and permutational analysis of dispersion were based on 9,999 permutations, and the latter was interpreted on the basis of deviation from spatial medians using ANOVA tables. Dimensionality for the NMS was assessed with stress tests and scree plots. We assessed up to four dimensions, but the best balance of stress and dimensionality was with two dimensions. Two dimensions were then used with 50 runs with real data; the final stress was 15.9, which was less than expected by chance ($p = 0.020$, Monte Carlo test, 50 runs). There were 78 final iterations. Stability was assessed with stress versus iteration plots; stress fell steeply and smoothly and stabilized at 46 iterations. We confirmed consistency of results with five additional NMS analyses.

Results

Habitat structure for fauna was less well-developed in all restoration treatments than in Reference, in both years, but absolute differences were reduced in 2013 relative to 2010 (Fig. 2). Five years after planting, the initial '08 Sparse treatment had

not yet produced habitat structure analogous to Reference, and still had nominally poorer habitat structure than Unrestored. The fastest improvement was apparent for bare ground, whereas litter accumulation was slow to develop. The Dual treatment provided better faunal habitat from the outset than did new Sparse treatments ('10 Sparse in 2010 and '13 Sparse in 2013), and Dual habitat quality appeared to be equal to or greater than that provided by the three year old '10 Sparse planting (Fig. 2).

Faunal assemblage metrics on restoration plots in 2010 indicated a more depauperate assemblage than was present in Reference and Unrestored, but these metrics were similar across treatments by 2013 (Fig. 3). In 2010, '10 Sparse had lower values than Reference, Unrestored, and '08 Sparse for all metrics, and '08 Sparse was lower than Reference and Unrestored in terms of abundance and richness, but had analogous expected number of species and dominance. There were no significant differences across treatments in 2013, and Dual had nominally higher abundance and richness than older Sparse treatments (Fig. 3).

Differences between Reference and restoration treatments were more persistent, and variable, for several individual faunal orders than for assemblage metrics, but the overall trend of increased abundances in the older restorations was similar (Fig. 4). Results for Hemiptera (true bugs), Hymenoptera (wasps, bees, ants), and Araneae (spiders) were analogous to those for assemblage metrics: lower abundances in restoration treatments than in Reference and/or Unrestored in 2010 but similar abundances in 2013. Dual in fact had the highest nominal abundance of Hemiptera in 2013 across all treatments, including Reference. Unrestored and Reference had higher abundances of

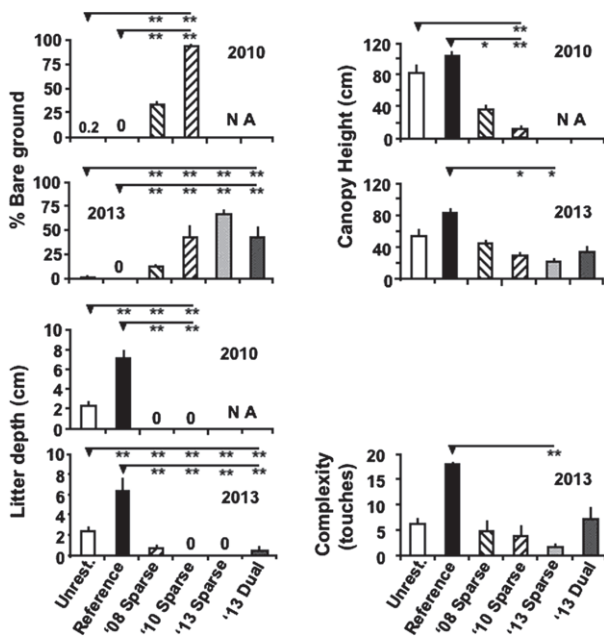


Figure 2. Habitat structural response to restoration treatments. Each horizontal bar indicates one or more significant differences (asterisks) relative to the treatment below the small vertical arrow (* and **: $p < 0.05$ before and after, respectively, sequential Bonferroni correction across all comparisons in a single year).

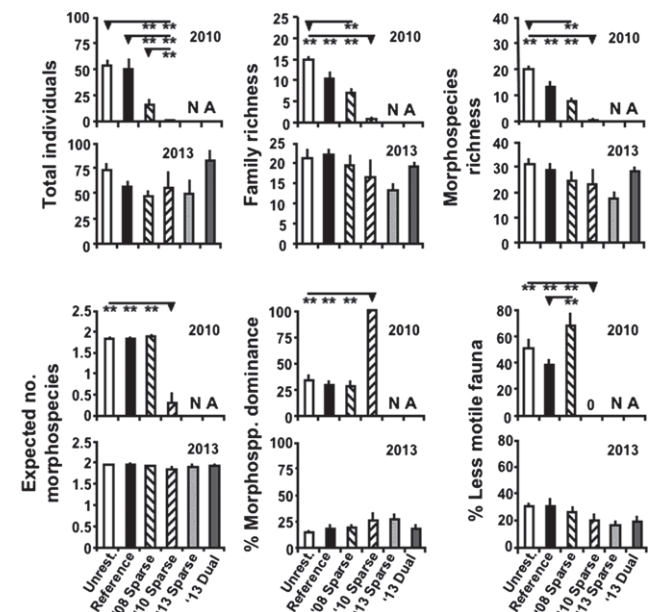


Figure 3. Response of faunal assemblage metrics, all based upon 50 sweeps, to restoration treatments. Expected number of morphospecies indicates results of rarefaction (scaling to the number of individuals in the sample with the fewest individuals). See Figure 2 for indications of statistical differences.

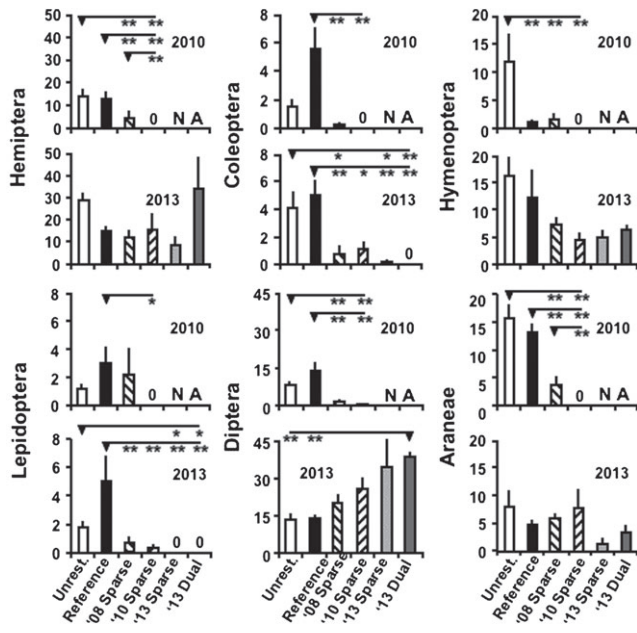


Figure 4. Response of common faunal order abundances (per 50 sweeps) to restoration treatments. See Figure 2 for indications of statistical differences.

Diptera (flies) than the restoration treatments in 2010, but in 2013 the restoration treatments, particularly Dual, had higher fly abundances than Unrestored and Reference (Fig. 4). In contrast, the higher 2010 abundances of Coleoptera (beetles) and Lepidoptera (moths, butterflies) in Reference and Unrestored were again present in 2013, and Dual was as depauperate as the other restoration treatments for these taxa.

Abundances for the most common families generally increased between 2010 and 2013 in the older restoration treatments, but there was again variability among taxa (Fig. 5). Mirid plant bugs and thomisid crab spiders had higher abundances on Reference and/or Unrestored than in either restoration treatment in 2010, but only had higher numbers than '13 Sparse in 2013. The highest abundance of Formicidae (ants) was on Unrestored in 2010 and again in 2013, but numbers increased in '08 and '10 Sparse by 2013, and only '13 Sparse and Dual differed from Unrestored (Fig. 5). Cicadellid leafhoppers were most abundant in Unrestored in both 2010 and 2013, although differences were less in 2013, and abundances in Dual were higher than in Reference and all restoration treatments, albeit not significantly so. Aphididae (aphids) did not differ across treatments in 2010, but Dual had the highest abundances of all treatments in 2013 (Fig. 5). Similarly, there were no treatment differences for muscid "house" flies in 2010, but 2013 abundances were highest in '08 and '10 Sparse and Dual.

Compositional differences between restoration treatments and Reference decreased between 2010 and 2013, as indicated by the Sørensen quantitative index that made use of abundances of all taxa (Fig. 6). In 2010, the '08 and '10 Sparse treatments were far less similar to Reference than was Unrestored, which had a similarity of only 42%. By 2013, these two restoration treatments were as similar to Reference as was Unrestored, that

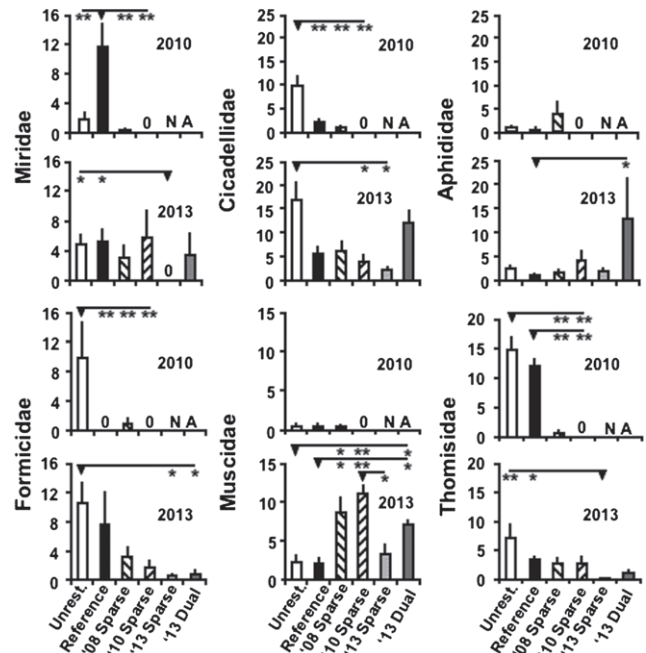


Figure 5. Response of dominant family abundances (per 50 sweeps) to restoration treatments. See Figure 2 for indications of statistical differences.

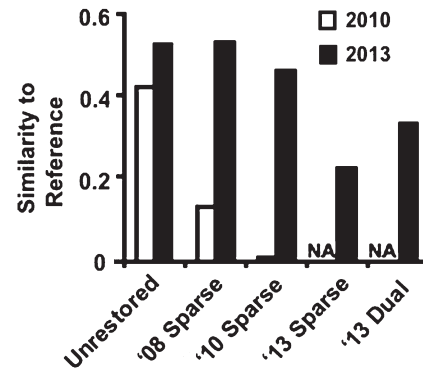


Figure 6. Sørensen quantitative index indicating similarity of other treatments to Reference.

is, still only 52% similarity (Fig. 6). Although '13 Sparse and Dual had lower similarity than the older restoration treatments had in 2013, both had greater similarity to Reference in their first year than the older treatments had in 2010. The 2013 treatments remained relatively divergent in multivariate composition as indicated by PerMANOVA ($p=0.00010$). All 15 pairwise comparisons among treatments were different (all $p < 0.05$ after sequential Bonferroni correction) with the exception of '08 versus '10 Sparse ($p=0.66$). There was only a single significant difference for the permutational analysis of dispersion ('08 vs. '13 Sparse, $p=0.012$, ns after sequential Bonferroni), indicating that the pairwise differences from the PerMANOVA were due to differing assemblage composition versus assemblage variability, with the possible exception of '08 versus '13 Sparse.

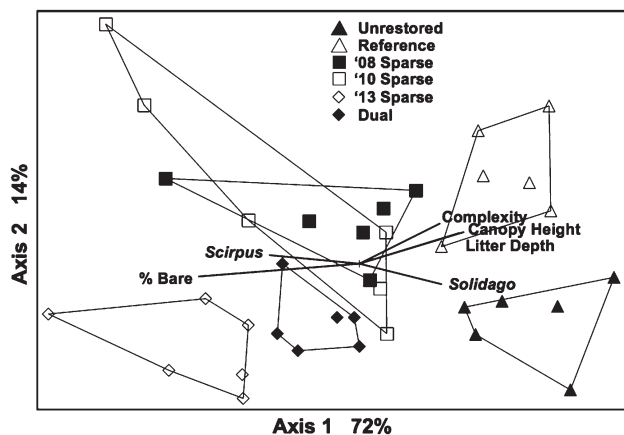


Figure 7. Ordination of 2013 assemblage composition across sites in two-dimensional space using nonmetric multidimensional scaling. Distance between sample icons approximates dissimilarity between samples; convex hulls surround samples from a given treatment. Orthogonality was 100%. Axis labels include R^2 values estimating post hoc percent of variation within the distance matrix that was explained by each axis. Cumulative R^2 was 0.86. Explanatory variables are labeled in joint plot. Minimum explanatory variable–axis correlation for inclusion in the joint plot was $R^2 = 0.25$. Note that vectors for canopy height and litter depth are superimposed and are approximately the same length.

NMS indicated that all treatments except '08 and '10 Sparse were distinct in ordinal space and that no restoration treatments were similar in multivariate composition to Reference (Fig. 7). Dual was however closer to Reference in ordinal space than '13 Sparse and was already as close to Reference as the older restorations. There were relatively high correlations with explanatory habitat variables, which were most strongly associated with axis 1: bare ground ($R^2 = 0.57$), litter depth (0.37), canopy height (0.35), % *Scirpus* cover (0.32), % *Solidago* cover (0.29), and complexity (0.28).

Discussion

Results across all restoration treatments indicated varying levels of reassembly, but convergence of faunal assemblages and vegetation structure with reference habitat was far from complete. Univariate trends for assemblage metrics and abundances for some individual taxa would indicate that reassembly proceeded relatively rapidly, yet similarity indices and multivariate compositional results indicated that restoration treatments were still divergent from reference habitat. In comparison, terrestrial arthropods in the Sierra Nevada have a higher similarity (0.63; Holmquist et al. 2011) between intact wet meadows and intact fens—different wetland types—than was observed between any restoration treatment and reference habitat (maximum of 0.52) in the current study. Interannual variability may have obscured some trends among treatments. The differing perspectives offered by various taxa and metrics underscore the value of using all epigeic arthropod groups and multiple analytical approaches. We might have observed stronger effects had we also examined aquatic and infauna/soil fauna, as these

organisms would have been expected to respond directly to restored sheet flow.

Recovery of terrestrial arthropods in conjunction with vegetation restoration can occur within 4–7 years (Gratton & Denno 2005; Watts et al. 2008) or require several decades (Davis & Utrup 2009; Woodcock et al. 2012). Faunal recovery time in our montane ecosystem would likely fall between these two extremes, although comparisons across habitats, study designs, and taxa are difficult (Scott et al. 2001). Complete reassembly after only 5 years would not have been expected for this study, and the short growing season and long, cold winter (Nagy & Grabherr 2009) may lead to a somewhat more protracted recovery than might be anticipated for an otherwise similar restoration in a more benign ecosystem. The challenging environment probably limits faunal recovery both directly, because most populations are only active for 2 to 3 months at the height of the summer (Holmquist et al. 2013a, 2013b), and indirectly, as a function of incompletely restored habitat (Palmer et al. 1997; Scott et al. 2001), also likely in part due to the short growing season. Significant reassembly nonetheless occurred during the course of the study, and faunal recovery did not appear to lag behind that of vegetation structure (Brady et al. 2002; Woodcock et al. 2012; Rácz et al. 2013), which may have been limiting.

Recovery of the arthropod assemblage was unlikely to have been significantly delayed by either faunal dispersal capabilities or proximity to source habitat. Terrestrial arthropods are dominated by aerial dispersers, which facilitates reassembly (Brady et al. 2002). Even some comparatively less-motile organisms were as abundant in restored as in Reference habitat in our study; nominally sedentary taxa such as spiders can disperse via mechanisms such as ballooning (Bell et al. 2001). Proximity to source habitat can be an important limiting factor (Watts et al. 2008; Knop et al. 2011), and both intra- and inter-wetland colonization may have contributed to reassembly (Gratton & Denno 2005) in our study. Our restoration treatments were within 20 m of source habitat, and there were also several similar wetlands within 0.5–1 km of the restoration. The directly adjoining habitat was probably a more important source of colonists, and faunal reassembly would likely have progressed more slowly had the entire meadow been initially degraded, that is, no adjacent source habitat.

The Dual treatment was added to enhance restoration of wetland vegetation but also appeared to significantly benefit arthropod reassembly, particularly abundances, relative to both the 2013 and earlier Sparse plantings (Rácz et al. 2013). These benefits were obtained by increasing vegetation density in only one-third of the planted area for this treatment, and the approach thus appears to be a cost-effective method for enhancing recovery of ecosystem function. The rapid colonization was likely a function of arthropod response to meso-landscape configuration, but artifacts and stochastic factors can influence restoration effects as well (Palmer et al. 1997; Zedler 2000; Woodcock et al. 2010). Although introductions could have contributed to the observed results, transported faunas are likely to suffer considerable mortality en route and during the planting process (Woodcock et al. 2011).

Further, we did not detect taxa on the restoration plots that were unlikely to be found locally; the most common species in the Dual treatment, *Macrosteles fascifrons* (aster leafhopper), *Rhopalosiphum padi* (bird cherry-oat aphid), *Sitobion avenae* (grain aphid), and *Atrichopogon fuscus* (biting midges, Ceratopogonidae) are distributed widely throughout the area and were abundant in Reference habitat.

Habitat heterogeneity and complexity (Stoner & Lewis 1985; Wiens 1995), reduced boundary contrast (Holmquist 1998; Collinge & Palmer 2002), and presence of corridors (Dixon 2009; Eggers et al. 2009) are likely to have contributed to the apparent success of the dual-density treatment in facilitating faunal reassembly. This initial study, however, investigated Dual as an integrated whole, and the proportional roles of these potential influences remain unknown. Results may have been driven by higher diversity and abundance in the high-complexity component of Dual alone. Landscape heterogeneity (presence of two distinct habitat elements) may have been important in increasing reassembly and overall diversity. The high-complexity component of Dual may have benefited leafhoppers and aphids, whereas the open, wet substrate between plugs in the low-complexity component may have provided good habitat for a variety of Diptera. Orientation of the high-complexity component of Dual may have made a secondary contribution to observed responses. These landscape elements were arranged such that the ends of the high-density bands adjoined reference habitat, not for corridor provision, but rather as a result of the shape of the restoration area and hydrological imperatives. If these components had been aligned differently, there would have been identical increases in Dual treatment heterogeneity and complexity but no corridor function or reduction in boundary contrast. The role of habitat configuration in restoration is thus fertile ground for additional testing of hypotheses (Palmer et al. 1997). Findings could at once suggest treatment configurations that might increase faunal reassembly at little or no additional cost as well as provide empirical tests of landscape theory that could prove difficult to arrange independently of the large-scale manipulations possible in a restoration context.

Implications for Practice

- Fauna will passively recolonize wetland restorations in a mountain environment, despite a short growing season bracketed by freezing nights and deep snow cover.
- Attention to landscape configuration should enhance the cost-effectiveness of restorations. Including higher-density plantings amid larger areas of lower-density plantings should improve cost:benefit ratio. Simply locating planned restoration areas, particularly higher-density plantings, adjacent to relatively undisturbed habitat should increase recovery rates at no additional cost.

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