VEGETATION COMMUNITY RESPONSE TO HYDROLOGIC AND GEOMORPHIC CHANGES FOLLOWING DAM REMOVAL

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ABSTRACT

Dam removal can restore fish passage, natural flow regimes, sediment transport in streams, dispersal of organic matter, and drift of aquatic insects. However, dam removal also impacts the riparian vegetation, with both immediate and delayed responses. In this study, we measure vegetation change at the Merrimack Village Dam site on the Souhegan River in Merrimack, NH, USA. The August 2008 removal caused a ~3 meter drop in water level and rapid erosion of impounded sediment, with ~50% removed in the first three months. Terrace, floodplain, and wetland communities were surveyed in summer 2007, 2009, 2014 and 2015. Temporal change was quantified using Analysis of Similarity on the Bray-Curtis dissimilarity matrix. Only herbaceous vegetation closest to the river channel and in the off-channel wetland changed significantly. The herbaceous plots directly adjacent to the impoundment eroded to bare sand in 2009, but by 2014 the original riparian fringe community had re-established in the newly developed floodplain. Between 2007 and 2014, the off-channel wetland area changed from aquatic species to a stable terrestrial community that persisted without significant change in 2015. The vegetation response was greatest in areas with the largest geomorphic and hydrologic change. These included the channel margin where erosion and bank slumping created an unstable scarp. The mid-channel island and off-channel wetland were strongly effected by the lowered water table. However, large unvegetated areas never persisted nor did the areal coverage of invasive species expand, which are two frequent concerns of dam removal stakeholders.

INTRODUCTION

Dam removal is becoming more common throughout the world, driven by changing environmental policies, costs to maintain aging structures, public safety, and other considerations. Removal can restore ecosystem functions, but also has many potential repercussions for sediment transport, hydrology, aquatic macroinvertebrates, fish, and vegetation in and surrounding the impoundment. Much of the monitoring associated with dam removals has focused on changes in sediment transport and other geomorphic responses (Bellmore et al., 2017). Monitoring biological responses requires detailed surveys that are typically not included in the required pre-removal project assessments, such as anticipating erosion and deposition within and downstream of the impoundment. Moreover, vegetation response is long term and most dam removal monitoring studies conclude within a year or two of removal (Elzinga, 1998, Bellmore et al., 2017). To capture the response trajectory of different vegetation communities, repeated surveys over multiple years are often necessary.

Vegetation is crucial to riparian zone effectiveness as a buffer between the terrestrial and aquatic environments. The riparian zone is a key mediator in the exchange of material between the stream and banks or upland area. The vegetative characteristics of the interface affect the movement of sediments eroded or deposited by the river, and the flow of leaf litter and wood on the floodplain fringe (Naiman & Decamps, 1997). The riparian zone also plays a role in nutrient cycling between ecosystems, especially important for aquatic organisms and the underpinnings of the food chain. The vital role that riparian vegetation plays in the functioning of both aquatic and terrestrial ecosystems indicates the importance of this zone for recovery following anthropogenic changes.

Shafroth (2002) found that the riparian vegetation area upstream of small dams is often restricted to a narrow transitional space as a result of little flow variation or stage change in the reservoir. With a larger post-removal range of water levels, newly exposed sediment is quickly colonized in the expanded riparian zone and is expected to follow a classical succession trajectory (Shafroth, 2002). This vegetation development can be tempered by erosion of impounded sediment (Doyle & Stanley, 2005).

Orr & Stanley (2006) conducted a retrospective survey of 30 small dam removals (3-16 m high) in the south central and unglaciated region of Wisconsin. Of the 13 sites that were not actively managed post-removal, all riparian areas demonstrated persistent vegetation, without large expanses of unvegetated sediment. Sites with longer times since removal had higher total numbers of species, lower frequencies of aquatic species, and higher frequencies of trees (Orr & Stanley, 2006). Introduced species were found at every dam removal site, in an average of 75% of plots. A 50-60% frequency of a single introduced species negatively correlated with frequencies of natives, suggesting arrested development of the community. Tullos et al. (2016) evaluated non-native plant colonization of former reservoir areas across the United States and concluded that the non-native contribution to species richness (~30%) is similar to values reported for riparian area species richness around the world. They also found no relationship between the proportion of non-natives with time since dam removal or dam height.

Purpose and Scope

We investigated short- and long-term vegetation change of the riparian plant community upstream of the Merrimack Village Dam (MVD) on the Souhegan River in southern New Hampshire (Figure 1), which was removed in August 2008. We used previous surveys of tree, shrub and herbaceous plant species and abundance from 2007 and 2009, and replicated the assessments in 2014 and 2015, based on the methods of Collins et al. (2007). We surveyed the vegetation on terrace, floodplain, and wetland areas adjacent to the channel, and statistically analyzed them for changes. We expected that the most pronounced pre- to post-removal vegetation change would be seen in the most hydrologically and geomorphically impacted areas of the site and that the control vegetation community structure, upstream of the apparent dam influence, would not change. In particular, we tested two hypotheses:

1. The tree, shrub, and herbaceous vegetation categories on the terrace adjacent to the former impoundment would not change in the seven-year period following removal as this vegetation was spatially separate from the majority of dynamic post-removal effects. Detection of any post-removal changes would likely require a longer study period.
2. The floodplain and wetland communities, composed of only herbaceous vegetation, would change significantly following the post-removal transformation of the environmental conditions. Floodplain community species were expected to change from upland or facultative indicators to facultative wetland species. In the wetland

community, obligate wetland indicator species were expected to decrease, replaced by facultative and facultative wetland species.

Study Area

The hydrology of the MVD site has been recorded for over a century at USGS stream gauge number 01094000, located approximately one kilometer upstream. No major tributaries enter the river between the gauge and study reach. The geomorphic effects of the dam removal were documented by Pearson et al. (2011) and Collins et al. (2017).

The earliest documented dam at the site was 1734 associated with a grist and saw mill. A 3.9-meter-high run-of-river dam, with no ability to regulate flow, was built in 1907, remaining in place until removal (Pearson et al., 2011). The impoundment was drained in a single day on August 6, 2008. Deconstruction of the remaining dam structure continued over the following weeks. No sediment was dredged prior to the project and no attempts were made to influence or stabilize the rapidly eroding impoundment sediment. According to pre-removal estimates, the impoundment had accumulated 66,900 m^3 ± 9900 of mainly sand-sized sediment (Santaniello et al. 2011). In the first three months following removal, ~50% of the impoundment sediment eroded (Pearson et al., 2011). Figure 1 shows geomorphic and hydrologic changes between 2008 and 2014 associated with erosion of the bed, floodplain, and mid-channel island, and the decrease in water level in both the channel and adjacent, hydrologically connected wetland to the north.

The site vegetation is characterized by hemlock, oak, and maple forest with variable understory vegetation, and limited invasive species on sandy terraces on both sides of the former impoundment. Bordering land use is primarily suburban development. The vegetation control transects (V1 and V2) are in a reach upstream of the influence of the dam, characterized by a bedrock channel and steep surrounding banks and valley sides (Figure 1). The treatment area, assessed with transects V3 to V6, surrounds the former impoundment area and extends into adjacent forested terrace areas. V5R includes a well-vegetated mid-channel island (MCI) deposited within the former impoundment. V7 surveys the wetland area, an off-channel water body fed by a small tributary that was impounded by the dam.

METHODS

Experimental Design

We used the vegetation monitoring methods described by Collins et al. (2007). The study was designed and the first survey conducted in August 2007. Seven transects were installed perpendicular to the channel or wetland area, monumented with rebar pins at the upland end on either side (Figure 1). Survey plots were positioned at consistent distances along the transects. The second survey, completed in August 2009, did not include the V7 transect across the wetland area. We replicated the 2007 survey in July 2014 and July 2015, extending the impoundment transects toward the thalweg of the new channel and adding herbaceous plots to floodplain areas created after the dam removal lowered the water surface.

The sampling methodology varied by vegetation category (herbaceous, shrub, and tree). The herbaceous plots were sampled using a square-meter quadrat placed along the transect tape, downslope and downstream of the specified distance. At these plots, we recorded all herbaceous-stemmed plants as well as any woody-stemmed plants less than 1-m in height. Shrub plots encompassed a 5-m radius circle, centered on the distance marker on the tape, and included all woody-stemmed plants 1-6 meters tall with a diameter-breast-height (DBH) 1-13 cm. Tree plots encompassed a 9-m radius and recorded woody-stemmed vegetation taller than 6 m, with a DBH greater than 13 cm. Herbaceous, shrub, and tree plots were repeated every 5, 15 and 30 m along each transect, respectively, with plots added to capture transition areas after the dam removal.

Within these categories, plots were also distinguished by the geomorphic surface occupied (control: hillside; treatment: terrace, floodplain, wetland, and mid-channel island). Different geomorphic surfaces have vegetation communities (e.g., floodplain herbaceous or terrace trees) with distinct plant species composition and different responses to dam removal. Trees and shrubs were only present on the hillside and terrace geomorphic surfaces; herbaceous plants were found in all areas. More importantly, each surface had different responses to the geomorphic and hydrologic changes brought by the dam removal in 2008 (Figure 1), established by our geomorphic surveys that necessarily occurred at a different frequency and duration (Pearson et al., 2011; Collins et al., 2017). Thus, stratifying our sample plots by geomorphic surface was a proxy for direct, contemporaneous measurements of hydrologic and geomorphic change at each vegetation transect. For example, the pre-removal floodplain surface eroded away and then re-formed at a level ~3 m lower (Pearson et al., 2011; Collins et al., 2017). Both floodplain surfaces experienced a similar frequency of inundation because the run-of-the-river dam did not influence stage. In contrast, areas adjacent to the impoundment >1 m above the 2007 pre-removal water surface were never submerged by high flows, and thus were defined as terrace (Figure 1B). The terraces only eroded along the bank adjacent to the former impoundment. The off-channel wetland experienced dramatic hydrologic change with minimal erosion. The off-channel wetland and terraces were more effected by the post-removal water table change, rather than inundation changes.

Given that the geomorphology of the upstream control reach was different from that of the impoundment (bedrock channel with steep hillsides and no floodplain), the control transects were never directly compared to impoundment transects. Rather, they were used to evaluate vegetation change unrelated to dam removal over the study period and assess sampling consistency among different survey crews. We acknowledge that this is not a reference reach because we cannot use it to evaluate rigorously potential changes in vegetation communities in the study area that are unrelated to dam removal. However, no site exists nearby with similar hydrogeomorphology to that of the former impoundment.

In our analyses, the transects (Figure 1) organized the plots for survey purposes only. Vegetation community analyses were primarily accomplished by pooling plots across all treatment or control transects. For example, all terrace herbaceous plots were evaluated together. However, we also tracked individual plots through time, described as “pairwise temporal analyses” below, but these too were not reported by transect.

In the vegetation community assessments, both presence and relative abundance of species were considered. The percent areal coverage of plant foliage was assessed for each species. For herbaceous and shrub categories, this was achieved by visual estimation. Tree plots were assessed using basal area determined by DBH, with each species presented as a percentage of the total. Vegetation was identified to a reasonable specificity: species for most plants, but highly diverse groups such as grasses and sedges were identified to the genus and family level. Morphologically distinct grass species that were abundant in the pre-removal community, such as reed canary grass (*Phalaris arundinacea*) or deer-tongued grass (*Dichanthelium clandestinum*) were noted separately. In the analysis, we combined the percent cover for plants of similar morphology (family, genus) to focus on the overall vegetation trends within the community and attempt to minimize variability in identifications among researchers (Lisius, 2016).

Repeat photographs from ground stations at fixed locations described by Pearson et al. (2011) provided qualitative documentation of vegetative change at the site over the study years (Figure 1).

Data Analysis

Percent cover data from each plot were classified using Braun-Blanquet class scores to minimize variation between researchers. We analyzed changes in vegetation communities over time by employing Bray-Curtis dissimilarity matrices and Analysis of Similarity (ANOSIM) as described below. These techniques are commonly applied to longitudinal studies of vegetation change such as salt marsh restoration monitoring (Roman et al., 2002; Thom et al., 2002; Smith et al., 2009).

The Bray-Curtis dissimilarity calculation (*BC*) determines the degree of dissimilarity between two plots:

$$BC = 1 - \frac{2a}{(2a+b+c)}\,.$$

We used this equation two ways: considering binary presence/absence of species to generate an *unweighted BC* value and considering Braun-Blanquet cover classes for species to generate a *weighted BC* value. Respectively, *a* is the number of species common between both plots (or Braun-Blanquet cover class scores for the species found in both plots) and *b* and *c* are the number of species only found in one plot (or the cover class scores of species found only in one plot; Borcard, 2011). Both methods yield an output measure of dissimilarity that ranges between complete similarity (0) and complete dissimilarity (1). A *BC* dissimilarity value of 0.25 indicates that there is 25% difference between the two plots being compared or 75% similarity. The motivation for computing both the unweighted and weighted comparisons was to detect differences between community species that were present and evaluate whether any species changes impacted the overall vegetation community in a substantial way. While a weighted comparison largely considers the dominant species in a vegetation plot, the unweighted comparison can provide insight into changes in minor species, because a species with 56% coverage and a species with 1% coverage are both counted as present with a value of 1.

The *BC* analyses were primarily employed to compare temporal changes in identified plant communities. In these analyses, all of the plots in a community (e.g., terrace shrubs) for a given year were compared to each other via *BC* to determine the intra-survey variation for that year. Then, each plot for the community for that survey year was compared to every plot of the same community in the other survey years to determine inter-survey variability. ANOSIM, a rank-based test, was then employed to determine if the community changed significantly over time. It generates a test statistic, R, that describes the relationship of the intra-survey dissimilarity to the inter-survey dissimilarity (Oksanen, 2013). R ranges between -1 and +1, with a value near 0 indicating similar intra-survey and inter-survey variability. Positive R-values indicate greater inter-survey variability than intra-survey variability and suggest plant community change over time (Kent, 2011). Negative R values indicate intra-survey variability dominates, confounding a temporal signal. We assessed statistical significance using an alpha of 0.05 (two-sided test). Our ANOSIM analyses were completed using the R package ‘vegan’.

Although the temporal comparisons were our main interest, we also employed the *BC* and ANOSIM approach described above to confirm that our subdivision of the herbaceous category into subcategories defined by geomorphic surface were valid (trees and shrubs were only found on the terrace surface in the treatment area). To do this, for each survey year each community plot (e.g. terrace herbaceous) was compared via *BC* to every other terrace herbaceous plot for that survey to establish the intra-community variability. Each terrace herbaceous plot was then compared via *BC* to every floodplain herbaceous plot and every wetland herbaceous plot for the same survey year to establish the inter-community variability. ANOSIM was then used as described above to evaluate the strength of the relationship between the intra-community and inter-community variability for that survey year. We repeated this analysis for every survey year to confirm that the geomorphically defined subcategories of herbaceous plants were indeed distinct each year of the study. The mid-channel island (MCI) herbaceous community, although on a distinct geomorphic surface, only included three plots so it was not included in these comparisons.

We also conducted pairwise temporal analyses for the herbaceous vegetation categories only, in which *BC* was employed to compare the composition of a specific plot at the beginning of the study (2007) with a plot at the same location at the end of the study (2015). The herbaceous plots added during the study were counted as 100% dissimilarity because in 2007 the open water of the impoundment was not sampled for terrestrial vegetation.

To generate community composition figures the percent cover of unvegetated area, woody-stemmed and herbaceous-stemmed vegetation were summed across all plots for a given community in one survey. Data presented in mean percent cover figures was computed by summing the percent cover of each species across all plots in the community and dividing by the number of plots in the community, with the data of key vegetation species presented.

RESULTS AND DISCUSSION

Control plots of herbaceous, shrub, and tree vegetation categories in the upstream unimpounded area did not exhibit significant change over the study period (ANOSIM $p > 0.7$ in almost all cases; Supplementary Data Table 1), confirming that additional environmental factors are not affecting the vegetation at our study site, nor were results biased by different survey teams. Furthermore, the *BC* and ANOSIM analyses we did to evaluate the validity of subdividing the herbaceous category into floodplain, wetland, and terrace sub-communities in the treatment area (transects V4-V7, Figure 1) showed they were indeed distinct (Table 1A).

Overall, the total number of species in all herbaceous plots remained the same from pre-removal (2007) to the end of our study (2015), though all herbaceous communities experienced changes in species representation over the study period (Figure 2). Herbaceous communities most affected by the dam showed significant change over time (Table 1B). In the pairwise comparisons of plots, the mid-channel island (MCI), floodplain and wetland herbaceous communities all showed high dissimilarity from 2007 to 2015 (Figure 3), reflecting the dramatic and different geomorphic and hydrologic changes that occurred in these areas (Pearson et al., 2011; Collins et al., 2017). In contrast, the terrace community changed mostly at the eroding edges, and not in the areas farther removed from the impoundment (Figure 3). Here we present the results from the treatment plots for each of the vegetation communities, and relate these to the geomorphic and hydrologic changes experienced at each surface.

Terrace

Tree and shrub vegetation on the terraces flanking the former impoundment exhibited a <10% change in the community composition over the study period (Figure 4; ANOSIM $p > 0.1$; Supplementary Data Table 1), supporting our second hypothesis. These plots were only impacted at the edge of the pre-removal bank scarp with trees falling into the floodplain as a result of erosion (Figure 1C; Pearson et al., 2011). The similarity of tree and shrub community composition may indicate that the ~3-meter water level drop did not significantly affect these communities. Pre-removal, the root systems of this vegetation were adjusted to the fast-draining sandy soil. Post-removal changes may depend on the ability to extend roots to the lower water table. If the trees and shrubs did not have the root systems to accommodate the water table drop, the community appeared to compensate throughout the seven-year study period but longer-term compositional changes may yet be observed.

The terrace herbaceous vegetation showed modest post-removal change by 2015 (Table 1B). We interpret this to reflect gradual changes, associated with an increase in overall vegetation cover seen by 2014 (Figure 4A) and changes in species representation that began in 2014 and continued into 2015 (Figure 4B). Species variation and increase in vegetated area may have been due to changing light availability due to toppling of trees rooted in the eroding terrace and post-removal hydrologic changes. Consistent with this, bank top plots exhibited the highest change from 2007 to 2015 (Figure A). The pre-removal terrace community present near the bank top was composed of oak (Figure 4; *Quercus alba, Quercus bicolor, Quercus coccinea, Quercus rubra*, *Quercus velutina*), red maple (*Acer rubrum*), and poison ivy (*Toxicodendron radicans*). These species decreased throughout the study period as the terrace community was destabilized following removal. Instead, species such as sedges (*Carex sp. Sparganium americanum*) and goldenrods (*Solidago rugosa*, *Solidago graminifolia*, *Solidago speciosa*) were found at greater abundance in the post-removal community.

Floodplain

The perimeter of the impoundment underwent dramatic geomorphic change immediately following dam removal with the erosion of unconsolidated sand and 60% of the established vegetation cover (Pearson et al., 2011; Figures 1, 3 and 5A). This erosion and ~3 m water level drop resulted in a short-term increase in exposed sediment on the floodplain, from 34% pre-removal to 73% in 2009 (Figure 5B). Revegetation of the floodplain was evident qualitatively by 2011, and was quantified by the 2014 surveys, showing 37% unvegetated area (Figure 5). The newly expanded floodplain herbaceous community continued to develop in 2015, increasing in unvegetated area to 47%. The difference in pre- and post-removal floodplain vegetation communities was not statistically significant, indicating a reestablishment of the pre-removal community. When only the pre-removal floodplain plots were directly compared to their 2015 correlates, 31% dissimilarity was noted over the seven-year study period (Figure 3A). Within the entire spatially expanded post-removal floodplain community, some minor, but statistically significant changes in species composition were found among the highly vegetated floodplain surveys (2007, 2014, and 2015), shown by the unweighted analysis (Table 1B; Supplementary Data Table 1). These minor vegetation changes coincided with new deposition on the floodplain, particularly where the surface was raised and stabilized by large trees eroded from the terrace (Pearson et al., 2011; Collins et al., 2017; Figure 5A). Both the pre- and post-removal floodplain herbaceous communities were characterized by facultative wetland species such as cinnamon fern (*Osmunda cinnamomea*), deer-tongued grass (*Dichanthelium clandestinum*), and grass (*Agrostis sp. Digitaria sp. Poaceae* unidentified grass; Figure 5C). Species with facultative or upland wetland indicator status decreased in abundance following removal, such as groundnut (*Apias americana*) and wood aster (*Aster divaricatus*). The expansion of the pre-removal floodplain herbaceous community onto the newly exposed sediment was likely facilitated by stored seeds in the surrounding sand from the pre-removal community. It is not surprising that these species would be successful in the post-removal condition since they were already adapted to natural, frequent stage fluctuations that characterize a free-flowing river because the former dam was run-of-river and thus did not influence stage fluctuations.

Wetland

The wetland progressively drained from open water soon after the dam removal, to heavily vegetated pond-like area, to nearly bare soil with early vegetation colonization, to a heavily vegetated wet meadow by 2011 (Figures 1C and 6A). The herbaceous vegetation in this area showed a delayed response, evident in the low R value for the 2007-2009 comparison, but great overall change between 2007 and the 2014-2015 surveys (Table 1B). Comparing 2014 and 2015 suggests that the community may be stabilizing ($p = 0.06$) but minor species are still adjusting as indicated by our unweighted analyses (Supplementary Data Table 1). In a direct comparison of the wetland community plots, the average dissimilarity was 86% between 2007 and 2015 (Figure 3), representing the greatest transition in vegetation.

The submerged and floating obligate wetland species present in 2007 were replaced almost completely in subsequent surveys (Figure 6B). Terrestrial and woody vegetation increased within the herbaceous plots on post-removal exposed soil area. Facultative wetland species such as jewelweed (*Impatiens capensis*) and false nettle (*Boehmeria cylindrical*) increased in abundance six years after removal (Figure 6C). Facultative species such as goldenrod, found as often in wetlands as not, also increased in 2014, reflecting the slow draining of the wetland. Native vegetation established rapidly during the drainage period such that invasive species or unvegetated area did not dominate the new community.

We speculate that some species of aquatic plants were able to survive for several seasons following removal, and delay the vegetation transition in the wetland, because of three circumstances. First, the pre-removal vegetation in this off-channel wetland was protected from the erosion that occurred along the channel and bank edge. Second, the finer, organic-rich wetland sediment retained moisture and delayed the impact of the post-removal water-level drop. Third, beavers maintained a somewhat higher water table in the area for at least a year after removal.

Mid-Channel Island

The MCI is composed of sand deposited in the impoundment. Before dam removal, it had a vegetated surface, higher than the main floodplains, that was inundated infrequently (Figure 1). Vegetation response to dam removal here was controlled by fast initial erosion of a large part of the MCI. This was followed by slower species changes on the remaining island surface, associated with the drainage of the impoundment that caused drier conditions via water table lowering. The MCI herbaceous vegetation was initially dominated by invasive reed canary grass. The vegetation was most similar between 2007 and 2009, despite the substantial post-removal erosion producing large unvegetated sand areas in the 2009 survey (Figure 7). By 2014, the MCI vegetation had transformed to a near monoculture of invasive black swallowwort (*Cynanchum louiseae*), a species possibly better suited to the drier post-removal conditions. However, by 2015 a more balanced vegetation community structure appeared to be emerging with greater native species including goldenrod, asters, and six additional minor species. Over the course of the study, invasive reed canary grass decreased from 44% coverage to 8%, but the invasive black swallowwort increased to 32%, although it decreased from 2014 to 2015.

SUMMARY AND CONCLUSIONS

This study describes several vegetation response trajectories, in different parts of the riparian landscape, associated with the MVD removal. Our findings can help dam removal planners anticipate vegetation response to these projects and, importantly, suggest that allowing natural revegetation following a dam removal can result in the establishment of a diverse, dynamic vegetation community.

As we hypothesized, the treatment-area tree and shrub vegetation communities on the terrace adjacent to the former impoundment did not show significant change in the seven years following removal (Table 1B). These communities were able to accommodate changes in water level and water availability. The terrace herbaceous vegetation gradually changed and was significantly different from the pre-removal community only after seven years had elapsed since dam removal, likely driven by differences in post-removal sunlight and water availability rather than direct dam removal impacts.

The floodplain, wetland, and MCI herbaceous vegetation communities displayed the most prominent post-removal changes and the highest localized rates of dissimilarity (Table 1B; Figures 3, 5-7). As we expected, these areas also corresponded to the areas where geomorphic and hydrologic changes were greatest. On the floodplain, the pre-removal vegetation communities were adapted to hydrologic and geomorphologic variability in the run-of-the-river impoundment and thus were able to re-establish in the new riparian area with similar disturbance regime at an elevation ~3 m lower than prior to the removal (Figure 1). In the wetland, changes in water level were observed over the duration of the study, resulting in a substantial change in the vegetation community from one dominated by aquatic, obligate wetland vegetation to one with terrestrial, facultative species. In both the sandy floodplain and off-channel wetland, large expanses of unvegetated sediment did not persist for more than two years following removal, replicating a finding shown across Wisconsin dam removal sites (Orr & Stanley, 2006). On sediments exposed by the removal, a balanced vegetation community developed in all instances.

Shafroth (2002) and Orr & Stanley (2006) were concerned about invasive species dominating dam removal sites, with unvegetated sediments being particularly vulnerable to aggressive colonization. Wisconsin surveys suggested an average 75% frequency of introduced species post-removal across 13 dam removal sites, with more severe instances resulting in arrested vegetation development (Orr & Stanley, 2006). Across the MVD vegetation communities, invasive species were present intermittently throughout the study but did not establish stable monocultures. The only area with substantial, persistent invasive species colonization was the mid-channel island (MCI), but here there was merely a switch between a pre-removal community dominated by the invasive reed canary grass to a post-removal one dominated by the invasive black swallowwort. Further, by the end of our study there was evidence that a more balanced community was developing with increased occurrence of native herbaceous plants. Our findings support work by Doyle & Stanley (2005) that showed a great variety of species numbers between sites in the first 10 years post-removal. Our results are also in line with a recent review by Tullos et al. (2016) that found rates of non-native contributions to vegetation communities at dam removal sites were comparable to those in riparian areas in general worldwide. In our repeat surveys spanning eight years, there was little evidence for post-removal dominance of invasive species.

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TABLE

Table 1. Treatment area ANOSIM results

A. Validation of geomorphic surface distinctions (floodplain, terrace, wetland communities) made for the herbaceous class in each survey

Comparison Years	R-value	p-value
2007	0.625	**0.001**
2009	0.311	**0.006**
2014	0.291	**0.001**
2015	0.437	**0.001**

B. Temporal comparisons of geomorphically distinct herbaceous communities

	Floodplain		Terrace		Wetland	
Comparison Years	R-value	p-value	R-value	p-value	R-value	p-value
2007, 2009, 2014, 2015	0.080	**0.026**	0.027	**0.018**	0.184	**0.001**
2007, 2009	0.209	**0.005**	-0.002	0.438	0.019	0.345
2007, 2014	-0.007	0.464	0.011	0.185	0.299	**0.001**
2007, 2015	0.069	0.162	0.052	**0.014**	0.273	**0.001**
2007, 2014, 2015	0.038	0.163*	0.024	**0.033**	0.204	**0.010**
2014, 2015	0.044	0.206	0.009	0.203	0.055	0.062*

Values in bold are significant ($p < 0.05$). *Denotes results that are significant in the unweighted ANOSIM analysis.

FIGURE CAPTIONS

Figure 1. (A) Aerial photograph (taken 14 April 2011) of the former Merrimack Village Dam site, with vegetation monuments, transects (yellow lines), and endpoints marked. River flow is to the northeast, and transects are named L or R with respect to the downstream direction. Ground-level photograph stations and their orientations, and two geomorphic cross sections are noted. Inset shows location of the study area (star), Souhegan River watershed (green), drainage network of the Merrimack River (blue lines) in New Hampshire. (B and C) Geomorphic cross section surveys from before (June 2008) and after (July 2014) dam removal (Pearson et al., 2011; Collins et al., 2017).

Figure 2. Herbaceous species observed in each vegetation community by year.

Figure 3. (A) Aerial photograph (taken 14 April 2011) of the study area, with transects noted (Figure 1). Herbaceous plots are marked along transects at appropriate distances and color-coded based on the calculated Bray-Curtis dissimilarity for species composition between 2007 and 2015. The shape of the symbols denotes the geomorphic surface of the plot. (B) Graph showing the pairwise Bray-Curtis dissimilarity of the herbaceous vegetation communities between 2007 and 2015. The plots were sorted by dissimilarity, the percent dissimilarities were grouped, and the number of plots in each dissimilarity category were described as a percent of the total plots in the community.

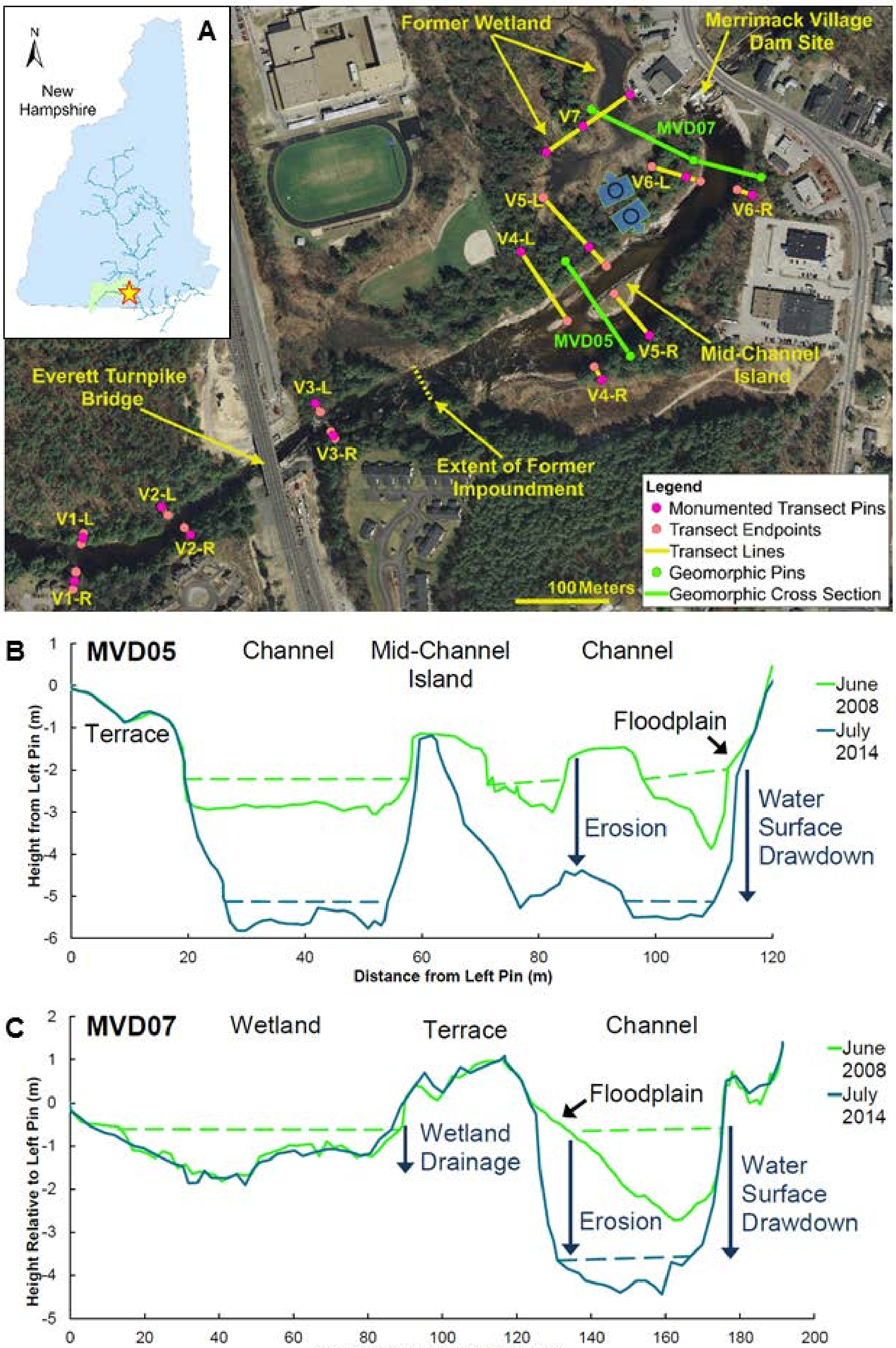
Figure 4. (A) The average areal coverage contributions fraction of each stem classification vegetation class observed during each survey in the terrace plots. (B) Percent cover of selected species observed in terrace plots during each survey. Unvegetated class is omitted.

Figure 5. (A) Ground-level photographs taken from the left (north) bank of geomorphic cross section MVD06 overlooking the downstream end of the mid-channel island (Figure 1). The time series details the pre-removal conditions, erosion of the bank and former floodplain zone, recruitment of large wood, and re-establishment of vegetation. Flow is from right to left. (B) Average areal coverage contributions of each stem classification observed during each survey in the floodplain plots. (C) Percent cover of selected species observed in floodplain plots during each survey. Unvegetated class is omitted.

Figure 6. (A) Ground-level photographs taken at the left (northeast) end of geomorphic cross section MVD07 (Figure 1A), looking across the wetland, detailing the pre-removal conditions, slow draining, and colonization of bare surfaces by vegetation over multiple years. Flow is from left to right. (B) Average areal coverage contributions of each stem classification observed during each survey in the wetland plots. “Aquatic” vegetation includes both submerged and floating-leaf vegetation. (C) Percent cover of selected species observed in wetland plots during each survey. Unvegetated class is omitted.

Figure 7. Species contributions observed during surveys of the mid-channel island (MCI).

Lisius et al., Figure 1 (top of page)



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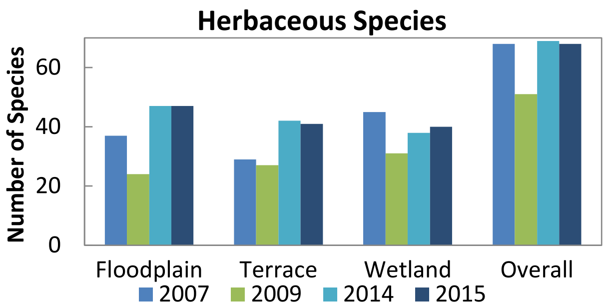

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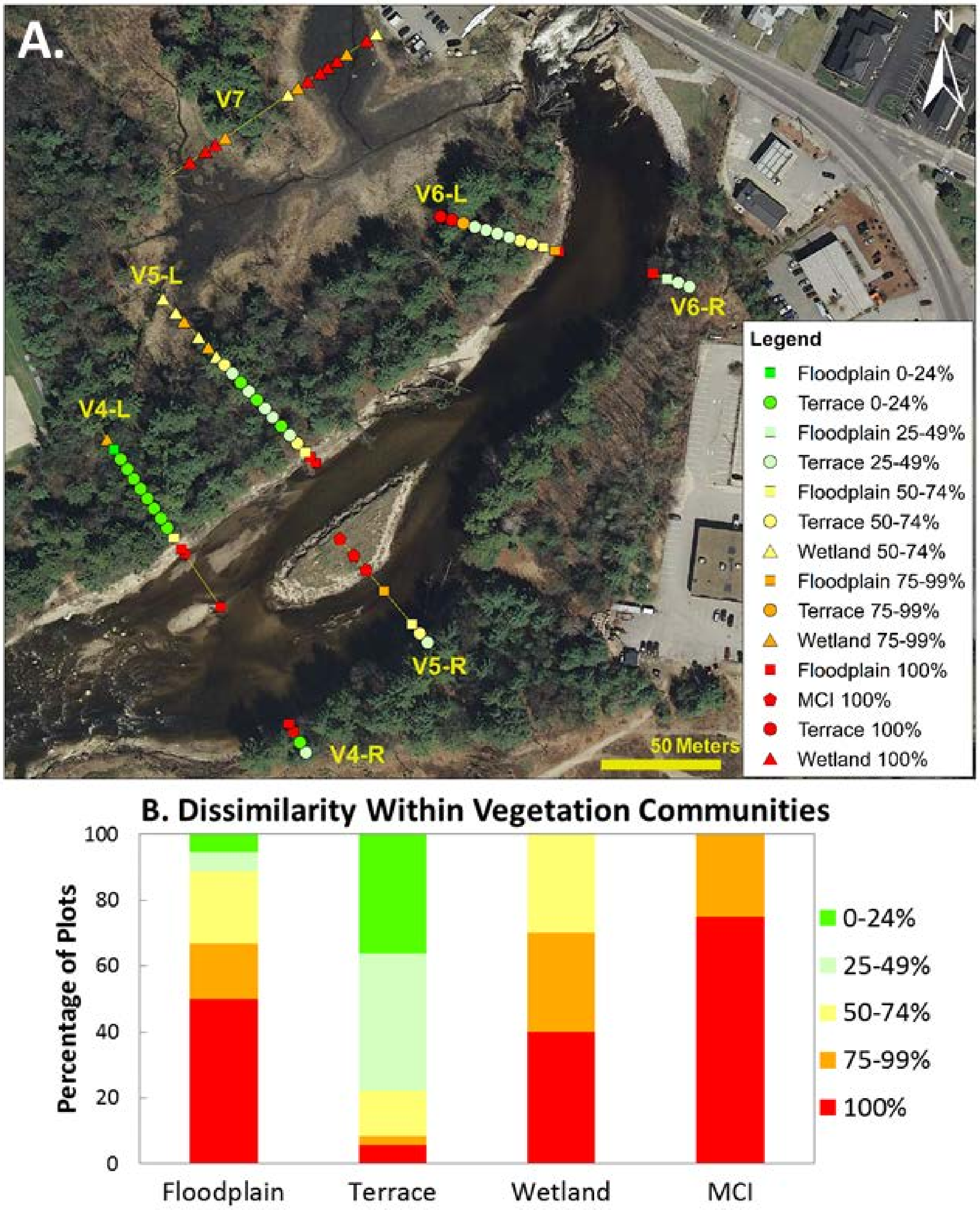

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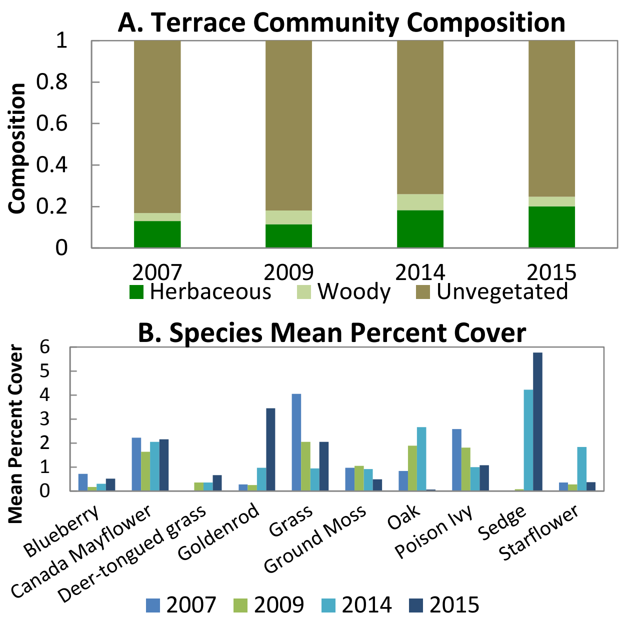

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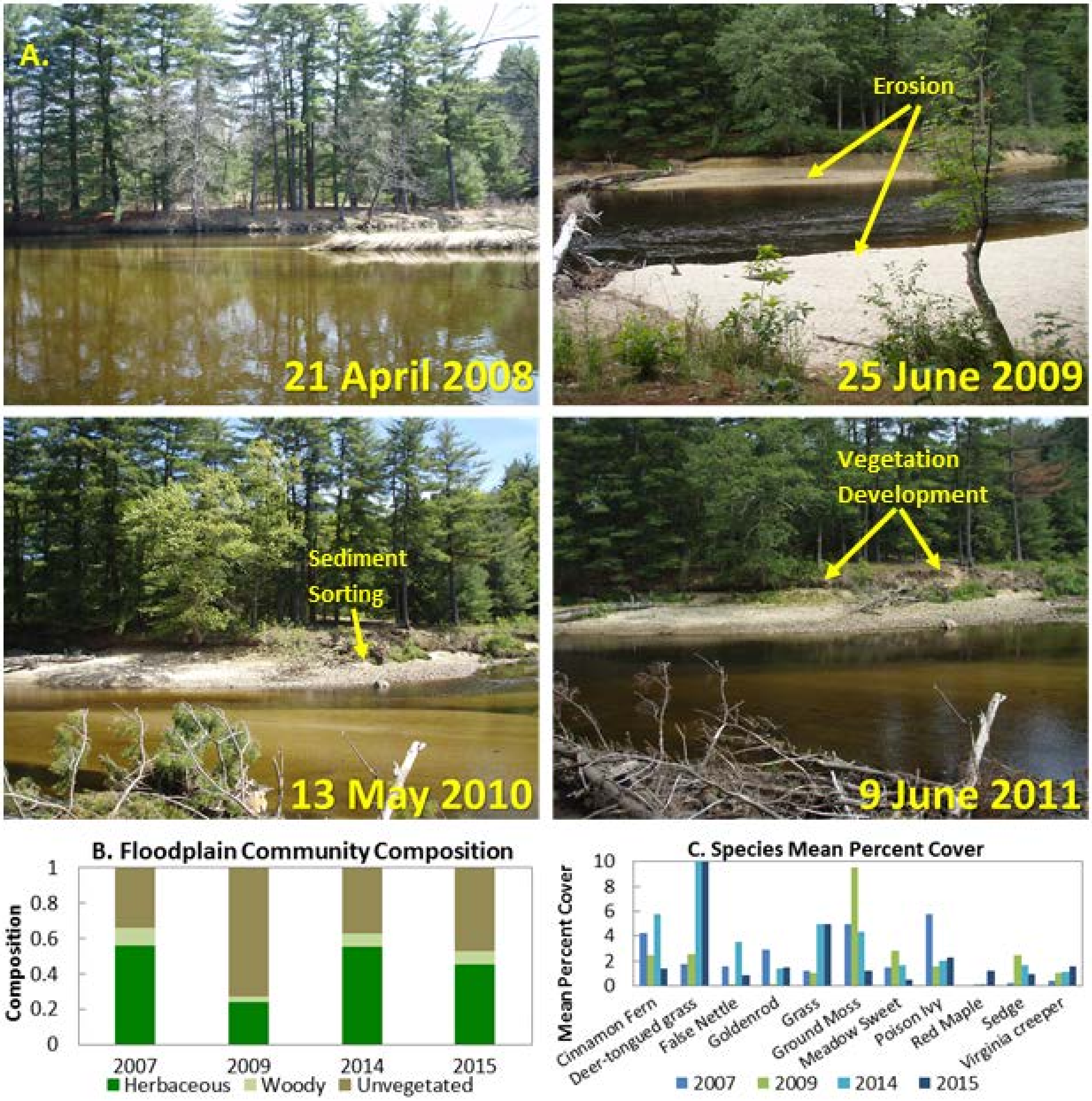

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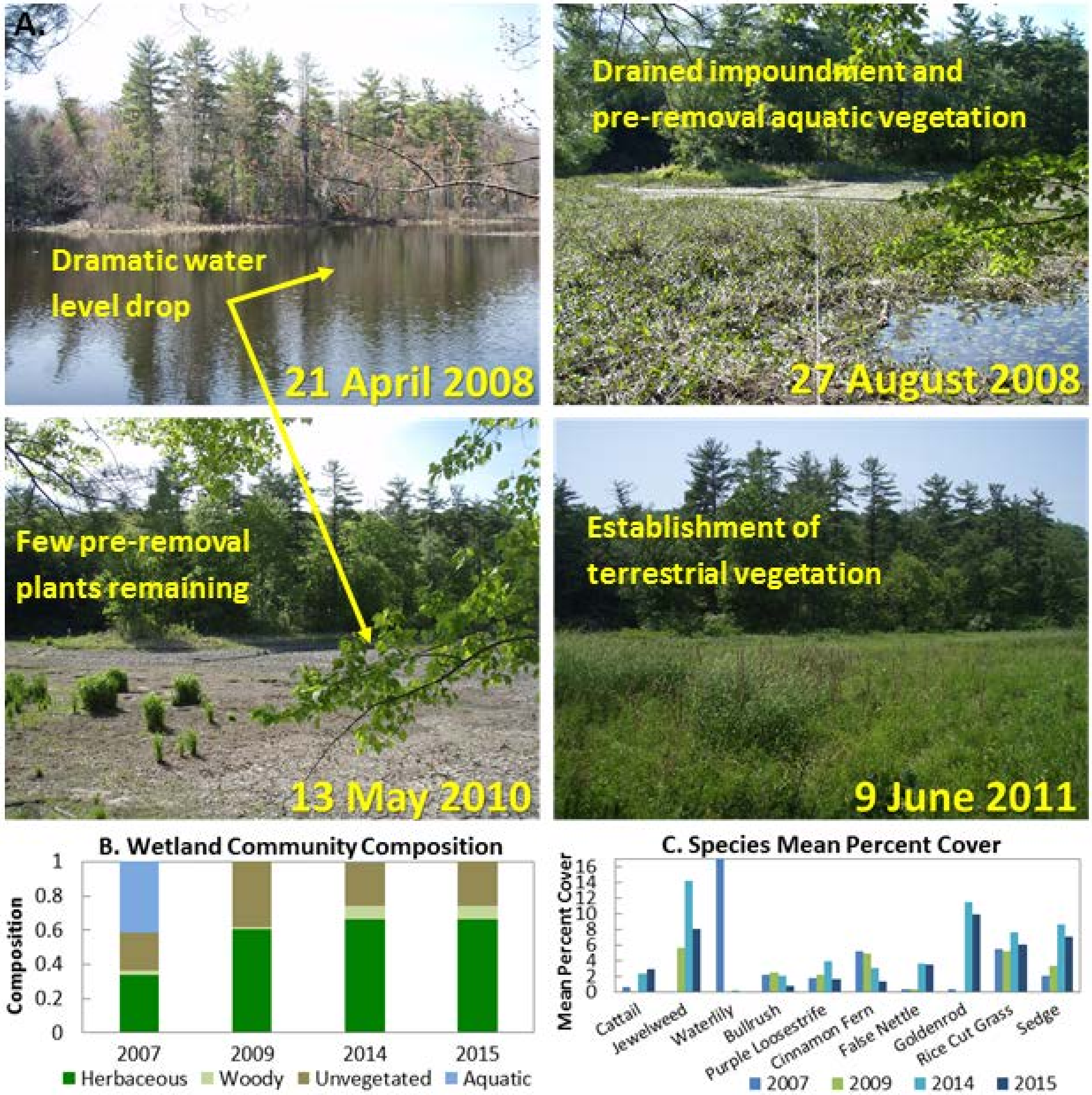
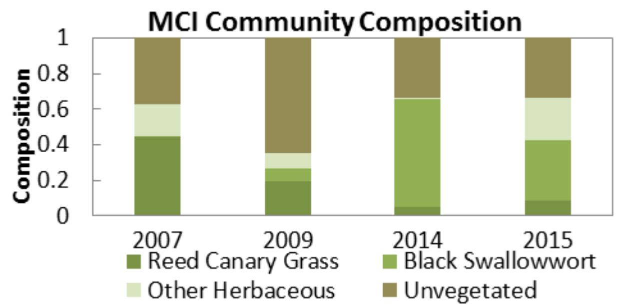


Lisius et al., Figure 7 (top of page)



Additional Supporting Information
Lisius et al., Vegetation community response to hydrologic and geomorphic changes following dam removal

Table S1. ANOSIM results for all comparisons

MVD Vegetation ANOSIM Results

Tree Control Plots (hillside)	**Weighted**		**Unweighted**	
Comparison Years	**R-value**	**p-value**	**R-value**	**p-value**
2007, 2009, 2014, 2015	-0.162	0.996	-0.152	0.994
2007, 2009	-0.141	0.939	-0.156	0.999
2007, 2014	-0.156	0.744	-0.188	0.999
2007, 2015	-0.177	0.748	-0.141	0.817
2007, 2014, 2015	-0.189	0.944	-0.170	0.966
2014, 2015	-0.198	0.919	-0.162	0.775
Tree Treatment Plots (terrace)	**Weighted**		**Unweighted**	
Comparison Years	**R-value**	**p-value**	**R-value**	**p-value**
2007, 2009, 2014, 2015	-0.022	0.813	-0.029	0.919
2007, 2009	0.030	0.233	-0.024	0.626
2007, 2014	0.033	0.172	0.003	0.393
2007, 2015	0.009	0.317	-0.015	0.714
2007, 2014, 2015	0.006	0.509	-0.015	0.696
2014, 2015	0.000	0.422	-0.035	0.879
Shrub Control Plots (hillside)	**Weighted**		**Unweighted**	
Comparison Years	**R-value**	**p-value**	**R-value**	**p-value**
2007, 2009, 2014, 2015	-0.175	0.952	-0.194	0.985
2007, 2009	-0.389	0.999	-0.324	0.935
2007, 2014	-0.083	0.693	-0.167	0.901
2007, 2015	-0.125	0.853	-0.125	0.841
2007, 2014, 2015	-0.097	0.823	-0.137	0.910
2014, 2015	0.062	0.551	-0.130	0.833
Shrub Treatment Plots (terrace)	**Weighted**		**Unweighted**	
Comparison Years	**R-value**	**p-value**	**R-value**	**p-value**
2007, 2009, 2014, 2015	0.011	0.208	0.033	0.055
2007, 2009	0.039	0.115	0.046	0.089
2007, 2014	0.025	0.169	0.023	0.198
2007, 2015	0.020	0.196	0.027	0.159
2007, 2014, 2015	0.014	0.222	0.014	0.221
2014, 2015	0.001	0.451	-0.006	0.519
Herbaceous Control Plots (hillside)	**Weighted**		**Unweighted**	
Comparison Years	**R-value**	**p-value**	**R-value**	**p-value**
2007, 2009, 2014, 2015	0.090	0.904	-0.091	0.904
2007, 2009	0.175	0.916	-0.174	0.907
2007, 2014	0.164	0.863	-0.164	0.862
2007, 2015	0.064	0.730	-0.064	0.773
2007, 2014, 2015	0.097	0.882	-0.097	0.859
2014, 2015	0.088	0.779	-0.088	0.756

Terrace, Floodplain, Wetland Herbaceous Community Comparison (all in the treatment area)

	Weighted		Unweighted	
Comparison Years	**R-value**	**p-value**	**R-value**	**p-value**
2007	0.625	**0.001**	0.619	**0.001**
2009	0.311	**0.006**	0.267	**0.004**
2014	0.2912	**0.001**	0.3037	**0.001**
2015	0.4368	**0.001**	0.4519	**0.001**

Herbaceous Terrace Plots

	Weighted		Unweighted	
Comparison Years	**R-value**	**p-value**	**R-value**	**p-value**
2007, 2009, 2014, 2015	0.027	**0.018**	0.044	**0.001**
2007, 2009	-0.002	0.438	0.001	0.369
2007, 2014	0.011	0.185	-0.002	0.444
2007, 2015	0.052	**0.014**	0.094	**0.004**
2007, 2014, 2015	0.024	**0.033**	0.044	**0.010**
2014, 2015	0.009	0.203	0.037	0.054

Herbaceous Floodplain Plots

	Weighted		Unweighted	
Comparison Years	**R-value**	**p-value**	**R-value**	**p-value**
2007, 2009, 2014, 2015	0.080	**0.026**	0.124	**0.004**
2007, 2009	0.209	**0.005**	0.212	**0.019**
2007, 2014	-0.007	0.464	0.086	0.135
2007, 2015	0.069	0.162	0.104	0.065
2007, 2014, 2015	0.038	0.163	0.083	**0.037**
2014, 2015	0.044	0.206	0.032	0.247

Herbaceous Wetland Plots

	Weighted		Unweighted	
Comparison Years	**R-value**	**p-value**	**R-value**	**p-value**
2007, 2009, 2014, 2015	0.184	**0.001**	0.173	**0.001**
2007, 2009*	0.019	0.345	0.008	0.432
2007, 2014	0.299	**0.001**	0.273	**0.001**
2007, 2015	0.273	**0.001**	0.230	**0.001**
2007, 2014, 2015	0.204	**0.010**	0.182	**0.001**
2014, 2015	0.055	0.062	0.065	**0.034**

Midchannel Island Plots

	Weighted		Unweighted	
Comparison Years	**R-value**	**p-value**	**R-value**	**p-value**
2007, 2009, 2014, 2015	0.005	0.403	-0.030	0.561
2007, 2009	0.111	0.300	0.074	0.400
2007, 2014	0.352	0.300	0.204	0.200
2007, 2015	0.056	0.349	0.046	0.424
2007, 2014, 2015	-0.018	0.474	0.013	0.438
2014, 2015	-0.250	0.837	-0.250	0.820