RESEARCH ARTICLE

Successional Models as Guides for Restoration of Riparian Forest Understory

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Abstract

We compare two successional models as guides for restoring native riparian understory species along a 160-km stretch of the Sacramento River in California. In 2001 and 2007, we surveyed cover, frequency, and richness of native and exotic understory species in 15 sites planted (1989–1996) with overstory species to determine whether native understory species colonized naturally (passive relay floristics model). In 2007, we surveyed 20 additional sites (planted 1997–2003) in 14 of which understory species were planted (initial floristics model) to evaluate whether planting accelerated community recovery. We surveyed 10 remnant forests as references for successional trajectories. Mean cover and frequency of natives changed little over time in sites where they were not planted initially; increases in native cover in a few sites were primarily due to a single common species (*Galium aparine*). Species composition shifted from light-demanding to shade-adapted species, both exotic and native, in response to a doubling of overstory cover. Sites with high intensity understory plantings had greater cover and frequency of native understory species than unplanted sites, but were still low relative to reference forests. Light-demanding natives (e.g., *Artemisia douglasiana*, *Rubus ursinus*, and grasses) established in sites where they were planted; however, a shade-adapted species (*Carex barbarae*) did not survive well. Our research indicates that the passive relay floristics and the initial floristic composition approaches serve to restore a few common native understory species, but that planting species as site conditions become appropriate (active relay floristics model) will be needed to restore entire native understory communities.

Key words: competition, initial floristic composition, relay floristics, Sacramento River, succession, understory.

Introduction

Ecological succession provides insights into how plant communities are assembled and how best to restore them (Ashton et al. 2001; Young et al. 2005; del Moral et al. 2007; Hobbs et al. 2007; Walker et al. 2007; Cramer et al. 2008). The relay floristics (RF) model describes successive appearances of groups of species in which one group creates conditions favorable for the next colonizing group (Cowles 1911; Clements 1916; Connell & Slatyer 1977). The initial floristic composition (IFC) model predicts that some of the species present early on will persist and thus the composition of the mature community will reflect early establishment (Gleason 1926; Egler 1954). Understanding which of these models most closely applies to particular ecosystems can help to guide restoration. For example, if the RF model applies, planting early successional species at the outset of restoration to create appropriate conditions for later successional species may be advisable,

whereas introducing all desired species at the outset of restoration makes the most sense if the system follows an IFC model.

Many forest restoration projects take a "passive relay" floristics approach (Clewell 1999; McLachlan & Bazely 2003; de Souza & Batista 2004) in which restorationists plant several species, commonly trees and shrubs that are well adapted to disturbed, early successional conditions, in the first year of restoration assuming they will facilitate (sensu Connell & Slatyer 1977) the establishment of other woody and understory species, as well as a host of fauna, over time. This passive RF approach has been called the "Field of Dreams" (i.e., if you build it, they will come: Palmer et al. 1997; Hilderbrand et al. 2005), but the long-term efficacy of this approach has rarely been tested. If propagule limitation is a concern, which is common in restoration, then taking an "active" RF approach, in which species are introduced over time as conditions become appropriate, would be advisable (Parrotta & Knowles 1999; Cabin et al. 2002; Bonilla-Moheno & Holl, in press). Because of logistical and cost constraints, however, this approach is rarely used.

Few restoration projects use the IFC approach of introducing a large number of species at the outset and not intervening later, probably due to the costs and propagation knowledge required. One of the few IFC examples, efforts to restore Jarrah

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Forest on bauxite mines in Australia, suggests that intensive seeding and planting of overstory and understory species at the outset succeeds in restoring the majority of forest species within 1 year after restoration (Koch & Ward 1994; Norman et al. 2006; Koch 2007). An IFC restoration approach ensures that all species of interest are introduced to the site; but, they may not survive due to inappropriate abiotic and biotic conditions early in succession (Johnston 2009). Moreover, if natural recruitment is high, then colonizing species may overwhelm any effects of planting on the longer-term floristic composition.

Much of forest restoration has focused on planting trees and shrubs with less attention toward establishing understory vegetation. However, understory plants contribute more than 80% of the overall species richness in some forests and play critical roles in nutrient cycling (Gilliam 2007). They provide food and shelter for birds, mammals, and insects (Golet et al. 2008), and help control the flow of water during flooding events that threaten developed areas further down-regulated rivers (Tabacchi et al. 2000). Restorationists are increasingly recognizing the importance of the understory layer and have begun to include understory species into forest restoration designs.

Large-scale restoration efforts along the Sacramento River, California, U.S.A. provide an excellent system to compare successional models in restoration, given the extensive replication of different restoration approaches. Over the last 150 years, more than 98% of the riparian forests along the river were converted primarily to agricultural and to a lesser degree developed land (Griggs 1993). Since 1989, restorationists have planted more than 3,000 ha of forest in an effort to provide critical habitat for endangered and threatened wildlife (Golet et al. 2008). Initial efforts were geared toward establishing trees and shrubs, assuming that later successional understory species would colonize over time (passive RF). In 2001, Holl and Crone (2004) surveyed the understory vegetation in 15 of these sites and found they were dominated by early successional, exotic plant species. Native understory species comprised a much lower cover and species richness than in remnant forests in the region, suggesting RF was not occurring; it is possible, however, that insufficient time had elapsed for later successional species to colonize.

Recent restoration efforts along the Sacramento River have taken an IFC approach by introducing a variety of early and late-successional understory species at the outset (Efseaff et al. 2008). Many of these restoration sites have met or exceeded survival of 75–80% of planted woody and herbaceous species 3 years after planting (R. Luster 2007, The Nature Conservancy and H. Swagerty, River Partners, personal communication), after which management and monitoring cease; survival of planted species and changes in overall vegetation community composition are not measured by managers beyond the 3-year initial restoration period.

The broad goals of our study were to determine how initial planting approach and time since restoration affect the successional trajectory of riparian understory communities and to compare successional models as a guide for improving efforts to restore riparian forest along the Sacramento River. First, we asked whether native understory plants have colonized and spread in sites where they were not planted in the 6 years since the previous survey (passive RF model), and whether they have reached values comparable to reference forests (nearby forests that have not been cleared or logged). We further explored whether the species composition of the understory in these restored sites is becoming more similar to reference forest understory communities over time, following the RF model. To answer these questions, we took advantage of a prior data set provided by Holl and Crone (2004) to compare changes in native understory species and overall species composition in sites surveyed in 2001 and 2007. If natives (which are the focus of restoration efforts) are colonizing, then a significant increase in cover, frequency, and richness would be expected, and overall species composition would be approaching that of reference forests.

Second, we measured whether native understory species that are planted at the beginning of restoration efforts survive and spread, thereby influencing the successional trajectory (IFC model). For the IFC model, we surveyed a separate set of restored sites (not used to address our first set of questions) and compared understory cover, frequency, and richness in sites not planted with understory species to sites where they were planted and to reference forests. We also compared three understory species that were commonly planted in this system and native grass cover.

Methods

We conducted this research at restoration sites along a 160-km stretch of the Sacramento River between Red Bluff and Colusa, California, U.S.A. Red Bluff, at 106 m above sea level, receives an average 611 mm of precipitation annually with average monthly temperatures ranging from 8°C in December to 28°C in July (California Department of Water Resources). Colusa, at 15 m above sea level, receives an average 429 mm of precipitation annually with average monthly temperatures ranging from 8°C in December to 25°C in July (California Department of Water Resources). All study sites were within the 10-year floodplain and flood partly or entirely in high rainfall years with extensive flooding in 1997 and 2006. Water flow on the river is regulated by Shasta Dam.

We surveyed the understory vegetation at 15 sites restored between 1989 and 1996 (by planting woody species only) that had been previously surveyed in 2001 by Holl and Crone (2004) and 20 sites restored between 1997 and 2003 (some with and some without understory species planted) in late May through June 2007; this included one to five sites restored in every year between 1989 and 2003 (Appendix S1).

Holl and Crone (2004) surveyed five reference forests in 2001 and we surveyed five additional reference forests in 2008. Preliminary tests showed there were no substantial differences between 2001 and 2008 reference forest data, so they were combined for analyses. Reference forests consisted of 15–20 ha remnant forest fragments located throughout the study area. The natural vegetation in these sites has been altered from historic conditions due to changes in hydrology brought about

by dams and levees; however, the floodplains along this stretch of the river are wide enough to allow channel meandering, sediment deposition, and hydrochory. Remnant fragments do contain a full suite of native species targeted for restoration and the majority of the understory cover is native making them useful references. It is important to note, however, that like all forests in this region, they have been invaded by several exotic species, including *Bromus diandrus, Rubus discolor, Anthriscus caucalis,* and *Torilis arvensis*, which comprise approximately 20% understory cover on average (Holl & Crone 2004). Sites of different ages and with and without understory plantings were interspersed with reference forests throughout the study region.

All restoration sites surveyed ranged from 5 to 60 ha in area (Appendix S1) and were previously used for row crops and/or orchards for 30 years or more. Restoration at each site occurred over a 3-year period. Site preparation and management included disking, planting, mowing, irrigation, weed control, and monitoring to ensure at least 75% survival over the first 3 years, although survival was lower in some of the sites restored between 1989 and 1993 (Alpert et al. 1999). Planting densities ranged from 520 to 1300 plants/ha. Plants were placed 3–4 m apart along rows which were separated by 5–7 m. Sites restored between 1989 and 1996 (all sites used to answer questions about the RF model) included five native tree species: *Acer negundo* (box elder), *Fraxinus latifolia* (Oregon ash), *Platanus racemosa* (western sycamore), *Populus fremontii* (Fremont cottonwood), and *Quercus lobata* (valley oak), and six native shrub species: *Rosa californica* (California rose), *Baccharis pilularis* (coyote brush), *Salix exigua* (narrow leaf willow), *S. gooddingii* (Goodding's black willow), *S. lasiolepis* (arroyo willow), and *Sambucus mexicana* (blue elderberry). Of the 20 sites restored between 1997 and 2003 (sites used to test the IF model), all included the above tree and shrub species (considered overstory species from now on) and 14 sites also were planted with different subsets of 17 understory species, that are a mix of herbs, vines, grasses and low shrubs common in reference forests and grasslands in the area (Table 1, Appendix S2). Overstory plants were 12- to 18-month-old and 10- to 50-cm tall when outplanted; understory species were 6- to 12-month-old and 5- to 30-cm tall at outplanting.

As is typical of restoration projects, the exact restoration procedures have changed to a certain degree over time and the earlier restoration procedures were not well documented. The large-scale nature of this study helps to overcome this limitation and to allow for generalizations across the range of restoration approaches used.

Our vegetation sampling methods were identical to those of Holl and Crone (2004) in order to facilitate comparisons. Total cover of both native and exotic species in restored sites was higher in 2007 than in 2001, which certainly in part was due to the timing of our 2007 survey being a month later in the growing season than the earlier survey; therefore, we used the ratio of native/total cover (hereafter referred to as relative native cover) and frequency data, both of which are less affected by phenological differences.

We took 20–80 vegetation measurements per site in 1 × 1–m quadrats on a systematic grid of points separated by 40–80 m. The distances between sampling locations at restoration sites were determined by their sizes: 40 m (4–8 ha); 50 m (8–16 ha); 60 m (16–24 ha); 70 m (24–36 ha); 80 m ($\geq$36 ha). In order to avoid sampling at the same location relative to rows of planted trees and shrubs, we walked a random distance ranging from 0 to 5 m to the left or right of the perpendicular to the transect line to locate the sampling quadrat. We averaged quadrat values to obtain a site mean for all analysis, except for comparisons of changes within individual sites between 2001 and 2007.

For each quadrat, we estimated total live cover, total litter cover, and bare ground to the nearest 5%, and estimated the cover of individual species using a modified Braun Banquet ranking scale: 0–1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–100% (Mueller-Dombois & Ellenberg 1974). The midpoints of these ranges were used for statistical analyses. Understory plants were defined as any species not included in the 1989–1996 restoration design and any vegetation less than or equal to 1.5 m tall. As our focus was on naturally colonizing understory species, we did not consider woody seedlings of planted species as understory (primarily *A. negundo* and *Q. lobata* which comprised <2% of the native cover). We lumped together two species in each of four genera (*Geranium, Medicago, Epilobium,* and *Lotus*), and two species of Apiaceae (*Anthriscus caucalis* and *Torilis arvensis*) because of an inability to distinguish them consistently in the field. As Holl and Crone (2004) found that overstory cover was an important explanatory variable for understory cover, we measured overstory cover in four directions at each point using a spherical densiometer and averaged the values for analysis. Nomenclature follows *The Jepson Manual* (Hickman 1993).

To answer questions related to the RF model, we used one-way analysis of variance (ANOVA) with native and exotic vegetation cover, frequency, and richness as the dependent variable and site type (data from 2001 and 2007 in 15 sites that had not been planted with understory species and data from reference forests) as a fixed independent variable. We tested for changes over time in relative native cover within each of the 15 restored sites using unpaired *t* tests. One widespread native species (*Galium aparine*) comprised approximately 50% of relative native cover on average and thus dominated the results; therefore, we ran the tests with and without it.

We used non-metric multidimensional scaling (NMS) in PC-ORD version 5.0 (McCune & Mefford 1999) to determine whether the understory composition of restored sites was following a successional trajectory toward that of reference forests. Ordination procedures, such as NMS, aim to extract overall trends in community composition; because native species in restoration sites comprised a low percentage of overall cover and were dominated by one species, running the analysis with both natives and exotics together provided more insight into overall successional trajectories. One site (Princeton East valley oak riparian forest) was removed from the analysis because it fell greater than three standard deviations from the mean of all sites, so it had undue influence on

Table 1. Understory species included in restoration plans.

Scientific Name	Common Name	Growth	N_p	P_{pf}	P_f	P_{rf}
Agrostis exarata	Bent grass	Grass	1	0.0	0.0	0.0
Aristolochia californica	California pipevine	Vine	5	0.4	0.1	0.9
Artemisia douglasiana	Mugwort	Forb	5	0.8	0.7	1.0
Carex barbarae	Santa Barbara sedge	Forb	7	0.6	0.4	0.9
Clematis ligusticifolia	Virgin's bower	Vine	5	0.2	0.1	0.4
Elymus glaucus	Blue wildrye	Grass	7	0.9	0.3	0.5
Elymus trachycaulus	Slender wheatgrass	Grass	1	0.0	0.0	0.0
Euthamia occidentalis	Western goldenrod	Forb	3	1.0	0.5	0.0
Hordeum brachyantherum	Barley	Grass	3	0.0	0.0	0.0
Leymus triticoides	Creeping wildrye	Grass	6	0.3	0.2	0.5
Melica californica	California melic	Grass	1	0.0	0.0	0.0
Muhlenbergia rigens	Deergrass	Grass	4	0.0	0.0	0.0
Nassella pulchra	Purple needlegrass	Grass	6	0.0	0.0	0.0
Rubus ursinus	California blackberry	Shrub	10	0.7	0.4	0.9
Toxicodendron diversilobum	Poison oak	Shrub	2	0.0	0.2	0.7
Urtica dioica	Stinging nettle	Forb	2	0.5	0.3	0.3
Vitis californica	California wild grape	Vine	3	0.3	0.3	1.0

N_p: number of restored sites (14 sites with some understory species planted) in which the species was planted; P_{pf}: proportion of sites where the species was planted in which the species was recorded in surveys; P_f: proportion of restored sites (35 total) in which the species was recorded in surveys; P_{rf}: proportion of reference sites (10 total) in which the species was recorded in surveys.

the ordination; it was an outlier due to the dominance of three exotic species (*Convolvulus arvensis*, *Lolium multiflorum*, and *Medicago* spp.) with almost no native species colonization. We arcsine square-root transformed relative cover values for both native and exotic understory species and used the general procedure described by McCune and Grace (2002) to run ordinations. We then used multi-response permutation procedures (MRPP) analysis (McCune & Grace 2002) to test for differences among the 2001, 2007, and reference surveys.

To answer our question about the IFC model, we compared restoration sites where native understory species (Table 1, Appendix S2) were planted to sites (restored between 1997 and 2003) where they were not planted and reference forest sites. We determined native understory species planting densities and composition from restoration plans and reports; we also consulted with the staff at the restoration agencies when reports were incomplete. Based on the available data (Appendix S2), we grouped sites that had understory species planted at "low intensity" (1–3 understory species planted at a total density of ≤88 seedlings/ha and no species seeded) or "high intensity" (5–11 understory species planted); all high intensity sites except two were seeded with native species, primarily grasses, at 9.2–14.9 kg/ha and were planted at densities ranging from 20 to 1005 seedlings/ha. Understory planting has become increasingly common over time, so although we only compared the more recently restored (≤10 years old) unplanted sites to minimize confounding site age with understory planting, the unplanted sites (8.5 ± 0.4 years since restoration) were slightly older than low (6.5 ± 0.5 years) or high (5.4 ± 0.5 years) intensity sites. We used one-way ANOVA with overstory cover, native cover and frequency (with and without *G. aparine*), and native species richness as the dependent variables and site type (restored no understory planted $n = 6$, restored low intensity understory planting

$n = 7$, restored high intensity understory planting $n = 7$, reference $n = 10$) as a fixed independent variable.

Finally, we compared the cover and frequency of the three native understory species that were planted in a sufficient number of sites and native grass cover in sites where they were not planted to sites where they were planted and to reference sites using a similar one-way ANOVA to those described previously. All analyses except NMS were done using SAS version 9.13. Cover and frequency data were arcsine square-root transformed when necessary to meet assumptions of normality. We used ranked data when transforming did not meet normality. Standard error of the mean is reported throughout.

Results

Understory Vegetation Changes Over Time

Mean overstory cover in the sites restored between 1989 and 1996 (without native understory species planted) was twice as high in 2007 compared to 2001 (Table 2). Relative native and exotic understory cover and frequency did not differ significantly between the two surveys. There was a trend toward higher total relative native cover in restored sites in 2007, but this was largely drive by *Galium aparine*, the most abundant native understory species, which increased in cover from 6% in 2001 to 15% in 2007. Cover of native species excluding *G. aparine* was similar in the two surveys (Table 2). On average, we found nearly two more native species per site in 2007 than in 2001, whereas exotic species richness did not change over time. Cover, frequency, and species richness of native species were higher in reference sites compared to both surveys of restored sites, whereas the reverse was true for exotic species (Table 2).

Table 2. Vegetation cover (with and without *Galium aparine–Ga*), frequency and richness in 2001 and 2007 in 15 restoration sites not planted with understory species compared to 10 reference forests.

	2001	*2007*	*Reference*	*F*	*p*
Overstory cover	29.2 ± 4.4^a	59.6 ± 5.7^b	78.8 ± 2.5^c	25.5	<0.0001
Relative exotic cover	78.6 ± 4.4^a	66.7 ± 6.5^a	34.2 ± 5.4^b	15.0	<0.0001
Relative native cover	20.7 ± 4.0^a	32.3 ± 6.4^a	65.2 ± 5.5^b	15.3	<0.0001
Relative native cover (no *Ga*)	14.7 ± 3.3^a	17.0 ± 4.0^a	45.4 ± 6.2^b	11.9	<0.0001
Exotic frequency	91.0 ± 2.1^a	83.6 ± 3.9^a	56.5 ± 7.4^b	15.4	<0.0001
Native frequency	48.1 ± 5.2^a	56.0 ± 6.3^a	87.2 ± 3.7^b	11.9	0.0001
Exotic richness per site	15.5 ± 1.3^a	14.9 ± 1.3^a	9.3 ± 1.6^b	5.4	0.0091
Native richness per site	4.7 ± 0.5^a	6.5 ± 0.5^b	10.1 ± 0.6^c	26.6	<0.0001

Values are means $\pm$ SE compared using one-way ANOVA. Means with the same letter are not significantly different ($\alpha = 0.05$) based on Tukey–Kramer comparisons. Note that relative exotic and native cover add up to slightly less than 100 as a few young plants could not be identified to species.

Changes in mean relative native understory cover varied substantially across individual sites, ranging from −16 to +62%; cover increased significantly in five sites and did not change in 10 (Appendix S3). These changes were positively correlated with changes in mean overstory cover ($r^2 = 0.3$, $F_{[1,13]} = 4.9$, $p = 0.0459$). The increase in cover of native understory plants in five sites ($37.3 \pm 7.3\%$ across those sites) was largely due to one species (*G. aparine* increased $30.3 \pm 9.4\%$). Several native species including *Rubus ursinus*, *Toxicodendron diversilobum*, and *Vitis californica* made up less than 5% of the total cover within each of the five sites during both surveys but were widespread in reference forest sites.

The best NMS solution for vegetation composition was obtained in three dimensions (final stress = 13.6; Monte Carlo *p*-value = 0.0040) with the most variation explained along the first (33.8%) and third (28.7%) axes. The MRPP showed understory composition in terms of relative cover was significantly different between the 2001 and 2007 surveys of the same restoration sites, and that in both years restoration sites were different from reference forests (T = −11.8, *p* < 0.0001). The vegetation composition in most of the restoration sites shifted toward the reference forests along axis 1 (see Table 3 for the correlations of the 25 most abundant species with NMS axes; Fig. 1). *Brassica nigra* was strongly

Table 3. Kendall's non-parametric (tau) correlations between understory species abundance and ordination scores in NMS.

Scientific Name	*Common Name*	*Status*	*Axis 1*	*Axis 3*
Anthriscus caucalis/Torilis arvensis	Bur-chervil	E	−0.4	−0.3
Brassica nigra	Black mustard	E	0.7	−0.1
Bromus diandrus	Ripgut grass	E	−0.3	−0.4
Bromus hordeaceus	Brome	E	0.1	−0.6
Centaurea solstitialis	Yellow star-thistle	E	0.3	−0.4
Convolvulus arvensis	Bindweed	E	0.5	−0.1
Cynodon dactylon	Bermuda grass	E	0.2	0.0
Kickxia elatine	Fluellin	E	0.2	−0.2
Lepidium latifolium	Perennial pepperweed	E	0.0	0.0
Lolium multiflorum	Italian ryegrass	E	0.3	0.1
Rubus discolor	Himalayan blackberry	E	−0.4	0.2
Rumex crispus	Curly dock	E	0.4	0.1
Sorghum halapense	Johnsongrass	E	0.6	−0.4
Vulpia spp.	Vulpia	E	0.2	−0.5
Artemisia douglasiana	Mugwort	N	0.0	0.4
Carex barbarae	Santa Barbara sedge	N	−0.5	0.2
Clematis ligusticifolia	Virgin's bower	N	−0.1	0.4
Conyza canadensis	Horseweed	N	0.3	0.0
Elymus glaucus	Blue wildrye	N	−0.4	0.2
Epilobium spp.	Fireweed	N	0.4	−0.1
Galium aparine	Goose grass	N	−0.4	0.3
Leymus triticoides	Creeping wildrye	N	−0.5	0.0
Rubus ursinus	California blackberry	N	−0.3	0.2
Toxicodendron diversilobum	Poison oak	N	−0.4	0.1
Vitis californica	California wild grape	N	−0.5	0.3

The 25 species with the highest overall cover are shown. Kendall's tau rank correlation coefficient measures the degree of correspondence between rankings. Values closer to 1.0 imply positive correlations in cover with axis locations, and values closer to −1.0 show negative correlations with axis locations. Zero indicates the rankings are independent. E: exotic; N: native.
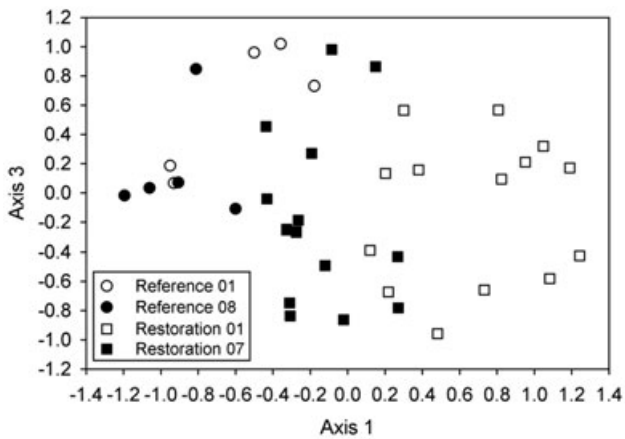
Figure 1. Results of NMS ordination based on relative native and exotic cover for 14 sites surveyed in 2001 and again in 2007 with reference data from five remnant forest sites in 2001 and five sites in 2008 for comparison. Final stress for three-dimensional solution = 13.6; Monte Carlo *p*-value = 0.0040.

correlated along this axis, as relative cover of *B. nigra* was highest in 2001 (10.1 ± 1.8%), but dropped to 3.5 ± 1.8% in 2007 which was not statistically different from the 0.5 ± 2.2% cover measured in reference sites ($F_{[2,35]} = 11.2$, $p = 0.0002$). Likewise, five other exotics (*Centaurea solstitialis, Convolvulus arvensis, Lolium multiflorum, Rumex crispus*, and *Sorghum halapense*) and two light-demanding natives (*Conyza canadensis* and *Epilobium* spp.) were positively correlated (tau ≥0.3) along the first axis (i.e., decreased in cover between 2001 and 2007 to a level similar to reference sites).

In contrast, the relative covers of the exotic species *Rubus discolor* and *Anthriscus caucalis/Torilis arvensis* were generally higher in restored sites in 2007 and in reference forests (tau = −0.4 for first axis, Table 3). For example, *R. discolor* increased from 0.9 ± 0.5% in 2001 to 8.1 ± 2.4% cover in 2007 which was similar to the 6.9 ± 2.0% found in reference forests (F$_{[2,35]}$ = 8.4, $p = 0.0011$). Seven natives (Table 3) were more common in the second survey, although their cover and frequency was still much lower than in the remnant forests (tau ≤−0.3 for first axis). A few understory species such as *Aristolochia californica* and *Vitis californica* were found in most remnant sites, but rarely in restoration sites.

Along axis three, four natives (*Artemisia douglasiana, Clematis ligusticifolia, G. aparine*, and *V. californica*) were positively correlated, and six early successional exotics (*A. caucalis/T. arvensis, Bromus diandrus, Bromus hordeaceus, Centaurea solstitialis, S. halapense*, and *Vulpia* spp.) were negative correlated.

Comparison of Planted and Unplanted Younger Restoration Sites

We measured higher cover and frequency of native species (with and without *G. aparine*) and higher native species richness in sites with high intensity understory plantings compared to unplanted sites, although values were still generally

below those found in reference sites (Table 4). Planted species comprised the vast majority of the native cover (excluding *G. aparine*) at high intensity planting sites (91.5 ± 5.6%). Only about half (54.5 ± 8.7%) of the native species richness in these sites was due to planted species, as a some native, widespread, wind-dispersed species, including *A. douglasiana, C. canadensis, E. occidentalis,* and *Epilobium* spp., recruited occasionally in sites where they were not planted. Low intensity planting did not increase any native understory variable compared to no planting. Overstory cover was higher in unplanted sites (8.5 ± 0.4 years since restoration) compared to high (5.4 ± 0.5 years) or low (6.5 ± 0.5 years) intensity sites, as was expected due to their age differences. The cover and frequency of *R. ursinus* and native grasses was higher in sites in which they were planted, and values were similar to those recorded in reference sites (Table 5). *A. douglasiana* and *C. barbarae* showed no difference in cover or frequency in planted versus unplanted sites; however, the cover and frequency of *A. douglasiana* was similar to those values found in reference sites. Although several native grass species, such as *Muhlenbergia rigens* and *Nassella pulchra* were commonly planted (Table 1) and seeded, only two (*E. glaucus* and *L. triticoides*) were recorded in restoration sites; moreover, the overall cover in planted sites (6.4%) was relatively low given that native grasses were drill seeded throughout most high intensity sites.

Discussion

The results of our and other previous studies (Shear et al. 1996; Parrotta & Knowles 1999; Holl 2002) suggest that forest restoration based on a passive RF approach may be sufficient for restoring some widespread native understory species (e.g., *Artemisia douglasiana, Galium aparine*, and *Epilobium* spp.), but that this approach does not serve to restore entire native understory communities over the time period studied (11–18 years following planting). Native understory species common to remnant forests colonized several of the older restoration sites where they were not planted, however less common species recruited infrequently, and the rate of recovery was variable across sites. We primarily recorded increases in *G. aparine*, a native species that is widely distributed globally in post-agricultural lands (Defelice 2002), as well as increases in shade-tolerant exotic species common in remnant forests. The increase in site level native species richness and small increases in some other native species suggest that with more time native species richness and cover may approach that of the reference forest, but whether this will actually happen remains to be seen.

Dispersal limitation, an altered flood regime, and competition with exotics may explain why less common native species colonized infrequently (Christensen & Gilliam 2003). Understory species colonization may be limited by seed size and output (Mabry 2004), proximity to remnant forests (Jacquemyn et al. 2003; McLachlan & Bazely 2003) and mode of dispersal (Matlack 1994; McLachlan & Bazely 2001). Species may fail to colonize due to human-induced changes in the hydrologic

Table 4. Comparison of overstory cover, relative native cover, and frequency with and without *G. aparine* (*Ga*), and native species richness in restoration sites with no understory planted (*n* = 6), restoration sites with low intensity understory plantings (*n* = 7), restoration sites with high intensity plantings (*n* = 7), and reference sites (*n* = 10).

	No Understory	Low	High	Reference	F	p
Overstory cover	64.2 ± 7.0^{ab}	31.0 ± 5.7^{c}	39.3 ± 10.0^{bc}	78.8 ± 2.5^{a}	15.1	<0.0001
Relative native cover	18.5 ± 5.2^{a}	16.3 ± 5.3^{a}	29.4 ± 7.4^{ab}	65.2 ± 5.5^{b}	14.9	<0.0001
Relative native cover (no *Ga*)	2.9 ± 1.9^{a}	10.0 ± 3.9^{ab}	20.6 ± 4.5^{b}	45.4 ± 6.3^{c}	13.3	<0.0001
Native frequency	41.8 ± 7.6^{a}	41.2 ± 9.3^{a}	65.2 ± 2.8^{ab}	87.2 ± 3.7^{b}	13.1	<0.0001
Native frequency (no *Ga*)	12.1 ± 5.8^{a}	30.1 ± 8.7^{ab}	54.8 ± 5.2^{bc}	75.4 ± 4.1^{c}	13.5	<0.0001
Native species richness	3.5 ± 0.9^{a}	4.9 ± 1.1^{ab}	6.0 ± 0.6	10.1 ± 5.7^{c}	12.1	<0.0001

Values are means ± SE compared using one-way ANOVA. Means with the same letter are not significantly different (α = 0.05) based on Tukey–Kramer comparisons.

Table 5. Comparisons of cover and frequency of a native forb, graminoid, shrub, and grasses in unplanted, planted and reference sites using one-way ANOVA.

		n	Not Planted	n	Planted	n	Reference	F	p
Artemisia douglasiana	Cover	12	3.9 ± 2.0^{a}	5	6.0 ± 3.6^{ab}	10	13.6 ± 4.8^{b}	4.3	0.0256
	Frequency	12	10.0 ± 4.6^{a}	5	20.6 ± 9.9^{ab}	10	24.9 ± 5.8^{b}	3.8	0.0357
Carex barbarae	Cover	10	0.1 ± 0.1^{a}	7	1.3 ± 0.7^{a}	10	7.8 ± 1.8^{b}	17.7	<0.0001
	Frequency	10	0.3 ± 0.3^{a}	7	4.0 ± 1.8^{a}	10	18.8 ± 3.3^{b}	20.4	<0.0001
Rubus ursinus	Cover	7	0.0 ± 0.0^{a}	8	6.4 ± 3.4^{b}	10	10.3 ± 2.5^{b}	10.5	0.0006
	Frequency	7	0.0 ± 0.0^{a}	8	11.3 ± 5.7^{b}	10	17.4 ± 3.7^{b}	11.2	0.0004
Native grasses	Cover	9	0.2 ± 0.2^{a}	8	6.4 ± 3.2^{b}	10	3.0 ± 1.0^{b}	5.1	0.0141
	Frequency	9	0.5 ± 0.5^{a}	8	20.5 ± 7.1^{b}	10	18.5 ± 4.1^{ab}	6.0	0.0079

Values are means ± SE. Means with the same letter are not significantly different (α = 0.05) based on Tukey–Kramer comparisons.

process that influence riparian vegetation patterns (Bendix & Hupp 2000; Singer 2007). Exotic species can further inhibit native understory recruitment by establishing persistent communities (Kulmatiski 2006), altering habitat quality (Gilliam 2006), and outcompeting natives (Vila & Weiner 2004; Garcia-Serrana et al. 2007). Separating out the relative importance of these factors requires manipulative studies that include introducing plants as seeds, because recruitment is often limited at the seed germination or early seedling development stage.

Our NMS results show that the entire understory community (natives and exotics) in unplanted restored sites is changing and becoming increasingly similar to the reference forests over time, which is consistent with an RF model. The problem, however, is that this trend is driven in large part by exotic species, some of which are invasives of concern (e.g., *Rubus discolor, Torilis arvensis* – California Invasive Plant Council 2006). The case of successional trajectories dominated by exotic species is becoming increasingly common in areas where exotics are prevalent throughout the landscape (Chazdon 2008; Hartman & McCarthy 2008; Ostertag et al. 2008; several chapters in Hobbs & Suding 2009), and brings into question how often a passive RF approach will be suitable in restoration. In such systems, a passive RF model often leads to a trajectory toward an alternative stable state dominated by exotics (many examples in Hobbs & Suding 2009).

The changes in understory composition from light- demanding to shade-adapted species as the canopy closes are consistent with other studies that found increases in similarity of understory plant composition between restored and reference

forests over time (Reay & Norton 1999; Holl 2002; McLachlan & Bazely 2003). Many studies have shown how canopy closure can alter understory species composition through shading (Menges 1986; Canham et al. 1994; Cole & Weltzin 2005; Copenheaver 2008; Jules et al. 2008) and facilitate the establishment of late-successional species (Gomez-Aparicio et al. 2004).

Our results suggest that the initial floristics composition approach had mixed success. Intensive planting efforts helped increase native understory richness and cover in this and another system (Norman et al. 2006; Koch 2007) and may help to resist invasion by exotic species (Fargione & Tilman 2005; Maron & Marler 2007). In our study, however, the increases in cover and species richness were relatively small and highly variable across sites, in part due to differences in planting practices. Not surprisingly, species' ability to survive and grow when planted at the beginning of succession depended on their ability to tolerate conditions with little or no overstory. In our study, restorationists had the most success planting *R. ursinus*, marginal success planting *A. douglasiana*, and poor establishment of some native grass species, all of which are adapted to growing in open conditions found in young restoration sites. The failure of some grasses to survive is likely a combination of exotic competition and altered site conditions (discussed previously; Stromberg et al. 2007). The results of this and a related study (Johnston 2009) show that survival is much lower for other native understory species (e.g., *A. californica, C. barbarae,* and *C. ligustifolia*) that are less tolerant of site conditions at the onset of restoration.

Shade-adapted species that do not readily colonize naturally should be planted later in succession after the forest canopy has developed (Mottl et al. 2006; Johnston 2009; Bonilla-Moheno & Holl in press).

The strong, ongoing human impacts on this system, including regulation of river flows, transboundary impacts of agriculture, and abundant sources of exotic plant species, are typical of many large river systems and raise the question of what is a feasible target for restoration. Although reference forests provide one way to evaluate the success of restoration, they can be problematic as restoration end-points (Hughes et al. 2005). The remnant forests along the Sacramento River have high levels of exotic species and are generally lower on the floodplain than restored sites (Little 2007) reflecting historic forest clearing patterns. Successional trajectories within restoration sites will likely differ from naturally regenerating forests lower on the floodplain (Villarin et al. 2009). Nonetheless, there are no easy alternatives. Another approach to evaluating success of restoration in this system is to set specific targets for cover of native understory species and richness based on expert opinion (Mitsch & Wilson 1996), but deciding on realistic targets in this highly anthropogenically impacted system is difficult. What is clear, however, is that restoring the full complement of native species within the first two decades will require introduction of species over time (an active RF approach) that is resource intensive.

Implications for Practice

- Planting a subset of species early in forest restoration to facilitate the colonization of later successional species may be sufficient for restoring some common native understory species, but is not likely to restore entire native understory communities within a couple of decades.
- Planting the full suite of species at the outset serves to increase cover of species that are adapted to disturbed conditions, but not shade-adapted species.
- To reintroduce the full complement of native understory species, it is necessary to introduce species over time as conditions become appropriate for later successional species.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Description of restored sites.

Table S2. Density of plants (seedlings/ha) and seeds (kg/ha) planted in high (H) and low (L) intensity understory planting sites. Plants (P) are in regular font and seeds (S) are in italics. TotSpPl = Total number of species planted and/or seeded. TotPlDe = Total plant density. TotSeDe = Total seed density. NDD = no density data available.

Table S3. Mean relative native understory cover (with *G. aparine* included) in 15 sites surveyed in 2001 and again in 2007. Overstory species were not included. Values are means per quadrat $\pm$ SE compared using unpaired two-tailed *t*tests. F: Flynn; K: Kopta Slough; L: Lohman; P2: Phelan Island 2; PEM: Princeton East mixed riparian; PEV: Princeton East valley oak; RU: River Unit; RV: Rio Vista; SS: Sam Slough; SM: Shaw mixed riparian; SP: Shaw cottonwood/willow. Δ = cover 2007−cover 2001.

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