RESEARCH ARTICLE

Incomplete recovery of ecosystem processes after two decades of riparian forest restoration

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Restoration of ecosystem processes such as carbon storage and nutrient cycling may lag behind the restoration of structural attributes of ecosystems, such as species richness and biomass. We used a replicated chronosequence of reforested sites on the Sacramento River floodplain to ask if ecosystem processes had reached functional equivalence with nearby remnant forest patches. We found that live and dead biomass pools had mostly recovered to remnant forest levels within two decades of replanting, but soil carbon and nitrogen stocks, rates of CO_2 efflux, N availability, and nutrient-use efficiency still differed significantly between restored and remnant forests. Reforested sites are thus still functionally distinct from remnants despite similarities of vegetation structure.

Key words: biomass, carbon, chronosequence, ecosystem services, nitrogen, nutrient availability, nutrient-use efficiency

Implications for Practice

- Restoration that recreates the vegetation structure of a reference site may not restore ecosystem processes on the same time scale.
- Enhancing biodiversity has typically been the primary goal of restoration. As managers are increasingly called on to provide multibenefit projects that include provision of ecosystem services, their monitoring responsibilities may need to expand from the recovery of flora and fauna to the recovery of ecosystem processes.
- In restored forests, measurements of carbon and nutrient stocks and turnover are among the metrics of recovery of ecosystem functioning that would be most feasible for managers to monitor, but the choice of metrics will necessarily depend on the manager's goals.

Introduction

In addition to providing habitats that shelter a diverse suite of flora and fauna, ecological restoration is increasingly called on to provide multiple benefits to people, including flood protection, carbon sequestration, pollination, and amelioration of lost soil fertility, among others (Clewell & Aronson 2006; Aronson et al. 2007; Wu et al. 2011). Unfortunately, data on aspects of ecosystem functioning that pertain to these ecosystem services are much less frequently collected at ecological restoration sites than the more readily observed facets of ecosystem structure that are relevant to biodiversity (Ruiz-Jaen & Aide 2005; Hossler et al. 2011; Golet et al. 2013). This contention is borne out by large datasets subjected to meta-analysis. For example, in a global meta-analysis of restored and reference wetland sites, comparisons of biological structure and diversity (e.g. species richness, plant biomass, macroinvertebrate density) were eight times more frequent than comparisons of nutrient cycling, and 25 times more frequent than any measures of hydrological function (Moreno-Mateos et al. 2012). Similarly, a meta-analysis of restoration success metrics worldwide (Benayas et al. 2009) found that measures of species richness and biomass (biodiversity and "provisioning" services) were far more common than measures of ecosystem processes (classed as "supporting" and "regulating" services).

A lack of data with which to compare restored and reference sites on ecosystem function not only slows the advance of ecology, but also can be a hindrance to land management, with implications for policy. Consider that in the United States, wetland impacts are permitted if their lost function can be mitigated by wetland creation or enhancement elsewhere (Dennison & Berry 1993). If restorations are evaluated only for their similarity in community composition with an intact reference site, but aspects of ecological functioning are slower to recover or unable to recover, restorations might be prematurely or incorrectly judged to be successful (Zedler & Callaway 1999; NRC 2001; Hossler et al. 2011). Many studies have found evidence for long lag times or nonlinearities (Knops & Tilman 2000; Wigginton et al. 2000; Maloney et al. 2008; Ballantine & Schneider 2009) in the recovery of ecosystem processes after disturbance or degradation. Meanwhile,

meta-analyses have shown that restoration may be only partly successful at restoring ecological function and ecosystem services in natural ecosystems (Benayas et al. 2009; Moreno-Mateos et al. 2012), though agroecosystems fare somewhat better (Barral et al. 2015). As interest grows in restoration providing humans with an increased suite of ecosystem services (Aronson et al. 2007; Chazdon 2008; Bullock et al. 2011; Funk et al. 2014), many of them linked to fluxes of energy, water, and nutrients, ecosystem processes must become critical metrics of the success of restoration efforts.

In this study, we examine key indicators of ecosystem function in floodplain forests restored along the Sacramento River in northern California, United States. Globally, dams, channelization, and floodplain development have resulted in the collapse of many riparian ecosystems (Nilsson & Berggren 2000). In California, virtually all major rivers are so altered, with a consequence that more than 95% of the state's former riparian forest area has been lost (Katibah 1984). In a recent reversal of this trend, more than 2,500 ha of floodplain along the Middle Sacramento have passed into conservation ownership and have been replanted, at a cost of more than U.S. \$30 million (Golet et al. 2013). These restoration sites have already been well characterized for the abundance and diversity of species in the plant canopy and understory (Alpert et al. 1999; Griggs & Golet 2002; Holl & Crone 2004; McClain et al. 2011) as well as in animal communities (summarized in Golet et al. 2008). However, the only peer-reviewed publication we know of that treats ecosystem function in these forests is a comparison of litter decomposition rates between young plantations and remnant forests (Borders et al. 2006).

Chronosequence approaches, or substitutions of space for time, are particularly useful for understanding those processes that recover from degradation over decadal or longer timescales (Walker et al. 2010). In order to generalize beyond a single site about the trajectory of change in ecosystem processes, chronosequences should be replicated—that is, they should have multiple, independently restored sites that are of the same or similar age. Because of the relative youth and small scale of many restoration efforts, it can be difficult to find several comparable landscape positions where similar restoration activities have been simultaneously performed over time. Consequently, although there are many restoration-age chronosequences in the literature (Rodgers et al. 2004; Meyer et al. 2008; Osland et al. 2012), including a well-studied North American tallgrass prairie chronosequence (Allison et al. 2005; Lane & BassiriRad 2005; Matamala et al. 2008; O'Brien & Jastrow 2013), the vast majority have only within-site replication.

Our sites along the Sacramento River are well-suited for a chronosequence approach because the restoration effort involved planting mixed riparian forest species on sites with similar soils, climate variables, and flood frequency, but was phased in along 161 km of river reach over a period of more than two decades. As a result, sites restored in the same year are separated by as much as 40 km, and sites that are physically adjacent differ by as much as 9 years in age, and are interspersed in the landscape with much older remnant forests. We used this replicated chronosequence to ask at what point, if at all, restored riparian forests recover key indicators of ecosystem function at levels comparable to those of remnant forests. We measured forest biomass pools, soil carbon and nitrogen content, rates of C and N mineralization, litterfall and fine-root productivity, litter decomposition, and nutrient-use efficiency. We chose these measures because belowground carbon and nutrient stocks are typically degraded by agricultural use, and because nutrient turnover is an important control on the dynamics of plant growth and community composition.

Methods

Study Sites

Site locations ranged from 40°N 05′02″, 122°W 05′45″ near Red Bluff, California to 39°N 11′38″, 122°W 0′40″ near Colusa, California. Sandy loams of the Columbia series (Oxyaquic Xerofluvents) underlie all plantations and remnant forests and sites are similar with respect to flooding frequency and soil depth. The sites experience a Mediterranean climate with a mean annual precipitation (MAP) of 676 mm and mean annual temperature (MAT) of 16.2°C. Mixed riparian forest plantings were performed on abandoned former agricultural land and are composed of Fremont cottonwood (*Populus fremontii*), box elder (*Acer negundo*), Oregon ash (*Fraxinus latifolia*), California sycamore (*Platanus racemosa*), valley oak (*Quercus lobata*), and the willows *Salix lasiolepis*, *S. exigua*, and *S. gooddingii* in the overstory, plus two shrubs, elderberry (*Sambucus mexicana*) and coyotebrush (*Baccharis pilularis*), in the understory. Remnant forests have a similar species composition that also includes *Juglans californica* as an overstory component. We chose remnant forest sites that were immediately adjacent to plantation sites and occupied similar landscape positions to provide the best possible comparison between plantations and native floodplain forests in the region. Details on the design and implementation of the restoration plantings can be found in Alpert et al. (1999).

In June and July 2012, we established study plots in sites belonging to each of the following age categories: young plantation (≤6 year, five sites), middle plantation (9–14 year, six sites), older plantation (≥15 year, four sites), and remnant forests of unknown age, estimated to be approximately 50–75 years old (five sites). Plots measured 750 m^2 and were randomly located within the site (three in each plantation site, one in each remnant due to the smaller size of the remnants). Within each plot, all trees and shrubs were measured, an estimate of coarse woody debris (CWD) was taken along two 15-m transects, and herbaceous and forest-floor biomass were measured in three subplots, which also served as locations for litter traps (see below). From each plot, we also took four soil cores for fine-root analysis, of which three were additionally used for soil nutrient assays and the fourth was additionally used to estimate soil bulk density. Regardless of the number of subsamples, the replicate in this study is the site, and subsamples at the plot or subplot level are always combined to avoid pseudoreplication (Hurlbert 1984).

Soil and Biomass Collection

We estimated aboveground and belowground biomass for trees of diameter greater than 5 cm at breast height, and all woody shrubs, using allometric equations (Matzek et al. 2015). CWD measurements were converted to biomass based on the diameter and decay class of the debris (Brown et al. 2004). We harvested herbaceous and forest-floor biomass down to the mineral soil in three subplots of 0.5625 m^2 randomly located within each plot. Herbaceous biomass included live and dead plants from the harvest year; weathered plant material from previous years was included with forest-floor biomass. Litterfall was collected in 0.5625 m^2 traps placed at the same three subplot locations, from June/July 2012 (before deciduous trees began to lose leaves) until January 2013 (when all canopy trees were bare). Litterfall included all plant material (leaves, reproductive tissues, and fine woody debris smaller than 5 cm diameter). Twelve of the 140 litterfall subplots had to be excluded from the analysis due to destruction of the litter traps by animals or flooding. Dry weight is used for all biomass comparisons.

Fine roots were sampled using an ingrowth core method (Vogt et al. 1998). At four randomly located positions within each plot, we extracted a 30-cm deep, 6.25-cm diameter soil core. The soil from each core was passed through a 2-mm sieve to remove litter and fine roots, and the soil repacked into a plastic mesh tube (0.05-cm^2 openings) of the same size as the extracted core. Additional sieved soil of the same type was used to compensate for the loss of soil to other soil measurements (see below). These root-ingrowth cores were then used to refill holes left by extracted cores. After 11 months, the ingrowth cores were re-excavated intact and immediately frozen. After thawing for 24 hours, cores were cut open, and soil and roots were rinsed over a nested set of sieves ranging in mesh size from 2 mm to 500 μm. The captured material was then washed into a set of white trays illuminated by a lighted magnifying lens and fine roots were removed by hand by a single observer in two periods of 15 minutes. We tested this method on randomly selected trial cores and found that doubling the time periods to 30 minutes each resulted in only small increases in root biomass (<10%, data not shown), suggesting that the vast majority of fine roots were found in the first 30 minutes of sorting. Roots were oven-dried before weighing.

Of the four 30-cm soil cores collected in each plot, one was used for calculating bulk density, and the other three were subsampled for C and N assays. To mitigate the confounding effect of soil bulk density on the carbon and nitrogen stock estimates, we calculated these stocks on an equal-mass rather than equal-volume basis (Ellert & Bettany 1995). Soil, fine root, and litterfall C and N were measured on pulverized, oven dry samples by flash combustion on an elemental analyzer (Jimenez & Ladha 1993).

Rates of Decomposition and Soil Nutrient Mineralization

To measure the rate of potential C mineralization in soils, we modified a Mason-jar incubation method (Sherrod et al. 2012). We placed 25 g air-dried soil samples, one from each collected soil core, into glass jars with lids fitted with rubber

septa. The sample was wetted to 60% water-filled pore space, calculated using a particle density of 2.56 g/cm^3 (Danielson & Sutherland 1986) and incubated at 30°C for 60 days, with venting every 2–3 days to avoid the anaerobic suppression of microbial respiration. On days 1, 2, 4, 8, 15, 30, and 60, we flushed the jars with lab air and resealed them for 24 hours, and then collected a headspace sample and injected it into a single-cell infrared gas analyzer (Li-COR, Lincoln, NE, U.S.A.) for measurement of CO_2 concentration. Additionally, an aliquot of incubated soil was extracted on day 0 and on day 60 in 2M KCl, agitated on an orbital shaker for 15 minutes, and then filtered on No. 1 Whatman paper. The soil extract was measured on an autoanalyzer for NH_4 (salicylate method) and NO_3 (cadmium reduction method). The change in total available nitrogen ($NH_4 + NO_3$) over 60 days gave us our measure of daily potential N mineralization (Parfitt et al. 2005). Potential C and N mineralization rates are expressed per mass of soil C or N, rather than per mass of soil, in order to avoid confounding the results with differences in soil C or N content across the age gradient.

Litter decomposition was measured in a common garden experiment in Santa Clara, California (37°N 21′06″, 121°W 56′32″, MAT = 15.4°C, MAP = 498 mm). Leaf material was separated from the total litterfall collected in each subplot and sealed into five fiberglass mesh bags (Bocock & Gilbert 1957), excepting two sites from which we had insufficient leaf material to conduct the experiment. Litterbags were placed in direct contact with the soil in outdoor raised beds filled with a mix of potting soil and compost, and then covered with a layer of coarse straw. We laid out the bags in June 2014 and harvested them at 2-month intervals in the following August, October, December, February, and April.

Statistical Analyses

For biomass and nutrient measures, we used one-way analysis of variance (ANOVA) with age class as a random effect to analyze differences in ecosystem functions along the chronosequence, followed by a post hoc Dunnett's test to determine differences between each plantation age class and the remnant at $\alpha = 0.05$. Data were log-transformed where necessary to correct heteroskedasticity. For CO_2 efflux and decomposition, we used mixed ANOVA with time as a within-subjects factor and age class as a between-subjects factor to test for an interaction between age class and the time of measurement. Interactions were nonsignificant after correction for nonsphericity, so post hoc tests were performed on main effects. For age class, we used Dunnett's test (plantation age classes vs. remnant), and for the main effect of time, we analyzed all pairwise comparisons of measurement timepoints with a Bonferroni correction for multiple contrasts. All statistical analyses were performed with the statistical software SPSS version 23 (IBM, released 2015).

Results

Total live biomass (Table 1) was typically higher in remnant forests than in reforested sites, but the oldest age class (15+

year) was indistinguishable from the remnants with respect to herbaceous and understory biomass. Tree biomass was more than 10-fold greater in the remnants than in the youngest restoration sites (≤ 6 year), and more than twice as high as the oldest restoration sites. With respect to detrital pools of biomass, the younger two age classes had virtually no CWD, while remnant forests had roughly 5-fold the amount of CWD than even the oldest age class (Table 1). Forest-floor biomass was significantly lower in the two youngest age classes, but not in the oldest age class, compared to the remnants (Table 1). Annual productivity in litterfall mirrored the forest-floor results, with significant differences only between the remnants and the two youngest age classes. Fine-root productivity exhibited a different pattern, with no significant differences except that the oldest age class had significantly more annual fine-root production than the remnants (Table 1). Additional measures of forest biomass and vegetation structure, including stem density, mean dbh, basal area, and total aboveground biomass, are shown in Table S1.

Soil carbon and nitrogen tended to increase with reforestation age, and remnant forests were significantly higher in soil %N, %C, N stocks, and C stocks than all reforestation age classes (Fig. 1A–D). Potential N mineralization rates were highly variable and did not differ significantly between remnant forests and any reforested age class (Fig. 1E). Soil bulk density declined as reforestation progressed, and was significantly lower in remnant soils than in the two youngest age classes (Fig. 1F).

C mineralization rates, as evidenced by the rate of efflux of CO_2 per unit soil carbon (Fig. 2), were significantly higher in remnant forest soils than in reforested areas throughout the 60-day incubation. Generally, the distinction between the remnant and reforested soils increased over time, so that by the end of the incubation, CO_2 efflux rates in the remnant soils were more than double those in the reforested areas (Table S2). Efflux decreased over the course of the 60 days, with each timepoint having significantly lower CO_2 emission than the ones preceding it, with the exception of the 1-day efflux rates, which were not different from the second or fourth day.

There were no significant differences between remnant and reforestation sites in the rate of decomposition of leaf (Fig. 3). Decomposition was slow, with about 70% of the initial leaf material remaining at the end of the 10-month experiment in all forest age classes (Table S3). Significant decreases in the mass of litter remaining were observed among timepoints only in the first 6 months; thereafter, the rate of decomposition slowed further and differences among the 6-, 8-, and 10-month timepoints were statistically indistinguishable.

Considering the ratio of fine-root productivity to fine-root N concentration as an index of nitrogen-use efficiency, remnant forests were significantly less N-use efficient than all reforested age classes (Fig. 4).

Discussion

Biomass accumulation over the restoration age gradient was rapid, and trends were generally consistent with expectations about canopy closure over the course of secondary succession:

as the tree canopy increased in size, the biomass of understory herbs and shrubs decreased, while pools of senesced biomass (forest floor and CWD) accumulated. By the end of two decades, most of these forest components were indistinguishable in reforested and remnant forests, except for tree biomass and CWD. Remnant forests generally had fewer, larger trees than the oldest reforested sites, suggesting that both of these trends are due to trees in the restoration sites not yet reaching the age of senescence. Cottonwoods and willows are relatively fast-growing and short-lived trees, and other studies have found even higher rates of biomass accumulation in the first few decades of forest regeneration. For example, early seral stages of cottonwood-dominated riparian forests in Oregon accumulated biomass in all aboveground pools at a rate of 9.6–14.1 Mg ha^{-1} yr^{-1}, larger than our finding of 128 Mg/ha after approximately 20 years of development (Fierke & Kauffman 2005). Along the lower Yellowstone River in Montana, aboveground biomass peaked at 193 Mg/ha in mature cottonwood forests with an average age of 92 years (Boggs & Weaver 1994), while Giese et al. (2003) found 197 Mg/ha in undisturbed riparian forests of approximately 60 years in age, both figures that are comparable to our remnant forest biomass results.

Litterfall productivity also increased over the age gradient in concert with the growth in canopy biomass, but, curiously, fine-root productivity stayed relatively constant with age. Fine-root productivity may appear to be insensitive to the large change in biomass in this system between young and remnant forests, because the younger, open-canopied restored forests have an understory chiefly composed of grasses. Fine-root production is higher in temperate grasslands than in any other biome, and the distribution of fine roots is more concentrated in the shallow surface soil in grasslands than in forests (Jackson et al. 1997), so the higher incidence of grasses in the biomass at younger sites may balance fine-root productivity across the age gradient. We considered the possibility that the similarity among sites is an artifact of our fine-root method, in which we standardized and limited the amount of time for root sorting. If the time for sorting was much lower than necessary to collect all the roots, then fine-root production numbers would simply reflect the amount of roots that could be sorted in 30 minutes, and no variation among sites would be evident. However, our tests of this method on sample cores suggested that virtually all the root material was removed from the core before the sampling period ended; therefore, we do not think this is a reasonable explanation.

Belowground carbon and nitrogen accumulation was slow, and virtually no soil properties had reached equivalence with remnant forests by the end of two decades. The soil organic matter (SOM) data are consistent with an explanation that during agricultural cultivation, floodplain soils had become compacted and deficient in organic matter (Young-Mathews et al. 2010). Generally, bulk density decreased, and soil carbon and nitrogen increased, as reforestation progressed, but 20 years was not enough time to rebuild stocks to remnant forest levels. The literature on belowground C and N in comparable temperate forest

Table 1. Biomass components for reforested and remnant sites. Pools are expressed in Mg/ha and annual fluxes in Mg ha^{-1} yr^{-1}. *F*-statistics and *p* values shown are for one-way ANOVA with age class as a main effect; degrees of freedom are 3,16 except for annual litterfall, which has degrees of freedom of 3,15. Statistical analyses were performed on log-transformed data for understory and coarse woody debris. Boldface values are significant for Dunnett's post hoc test comparing each reforested age class against the remnant, with asterisks indicating significance level. ***$p < 0.001$; **$p < 0.01$, and *$p < 0.05$.

|	*Young*	*Middle*	*Old*	*Remnant*	F$_{[3,16]}$	p
Herbaceous	**4.38 ± 0.68***	1.72 ± 0.62	1.98 ± 0.76	1.33 ± 0.68	4.2	0.023
Understory	**80.86 ± 23.30****	**59.23 ± 21.27***	29.34 ± 26.05	0.24 ± 23.30	6.1	0.006
Canopy	**11.35 ± 13.77*****	**60.17 ± 12.57*****	**97.01 ± 15.40*****	192.80 ± 13.77	31.4	<0.001
Coarse woody debris	**0.37 ± 3.97*****	**0.90 ± 3.63*****	**4.14 ± 4.44***	21.14 ± 3.97	10.1	0.001
Forest floor	**4.85 ± 1.03****	**5.52 ± 0.94****	8.10 ± 1.15	11.31 ± 1.03	8.3	0.002
Annual fineroot	0.062 ± .002	0.065 ± .001	**0.071 ± .002***	0.060 ± .002	7.0	0.003
Annual litterfall	**1.65 ± 0.46****	**2.73 ± 0.42****	4.08 ± 0.51	5.21 ± 0.51	10.3	0.001
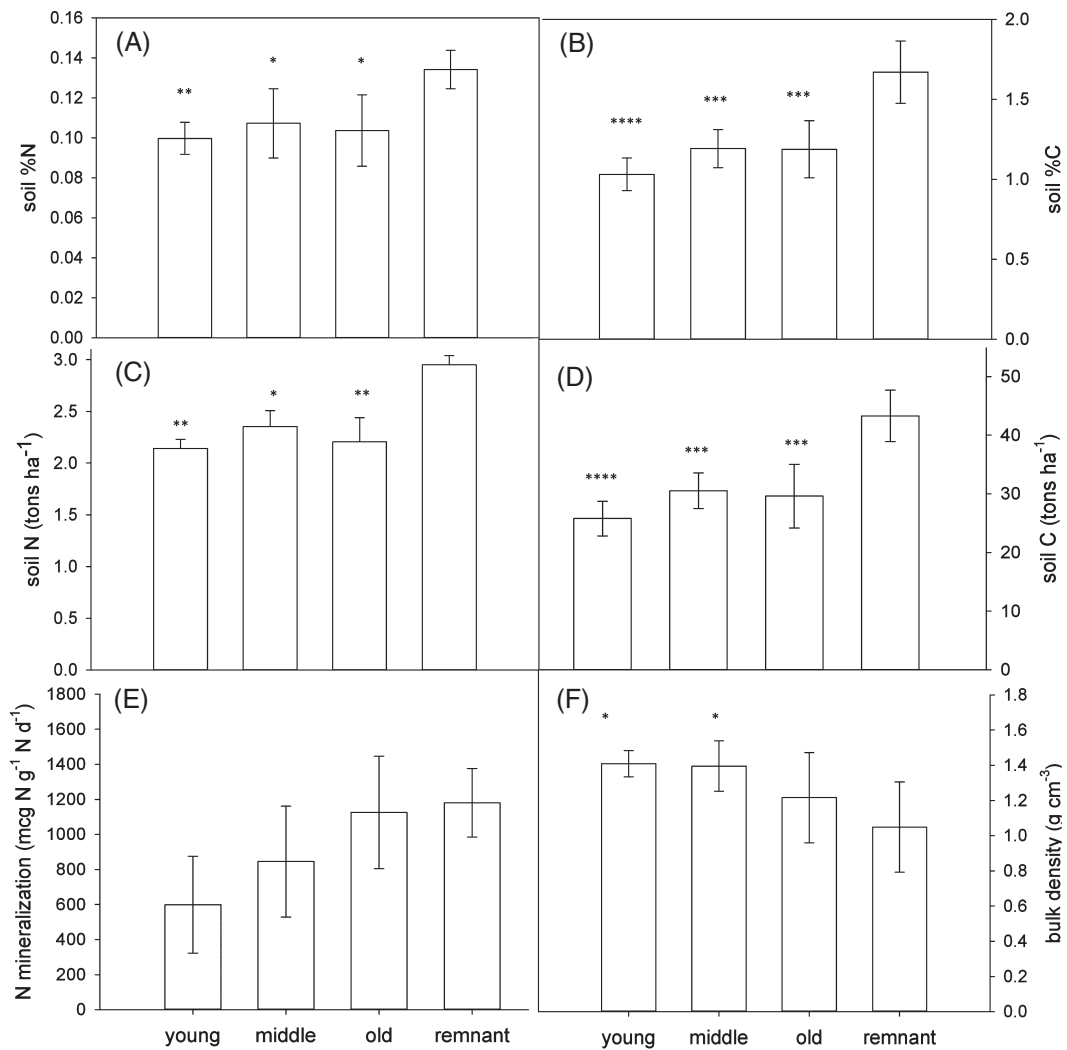
Figure 1. Nitrogen and carbon in soils as a percent (A, B), and as total stocks in Mg/ha (C, D). Soil bulk density (D) is expressed in g/cm and potential nitrogen mineralization (E) is expressed as the rate of production of available N (NH$_4$ and NO$_3$) per unit soil N over 60 days. Asterisks indicate levels of statistical significance by Dunnett's test of differences between reforestation age classes and the remnant forests, where *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, and ****$p < 0.0001$. Error bars represent ± SE.
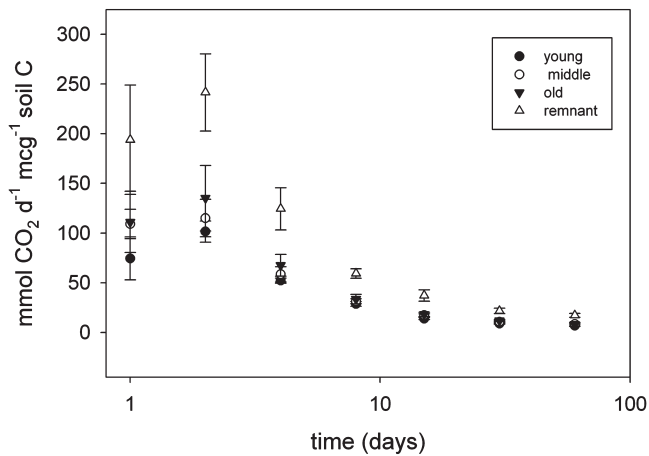
Figure 2. Exponential decay in CO_2 efflux rates over 60-day incubation of reforested and remnant forest soils. Soils were incubated at 30°C and 60% water-filled pore space over the course of a 60-day incubation period, with rates expressed in mmol CO_2 per 24 hours per mcg soil carbon. Age class had a significant effect on efflux ($F_{[3,16]} = 7.3$, $p < 0.01$), with remnant soils exhibiting significantly higher rates of CO_2 efflux per unit soil carbon than other age classes. Decreases in efflux over the course of the incubation were also significant ($F_{[6,96]} = 54.6$, $p < 0.001$); all time points differed significantly from each other except for the first day's rates, which were not significantly different from the next two time points. The *x*-axis is on a log scale; error bars represent ± SE.
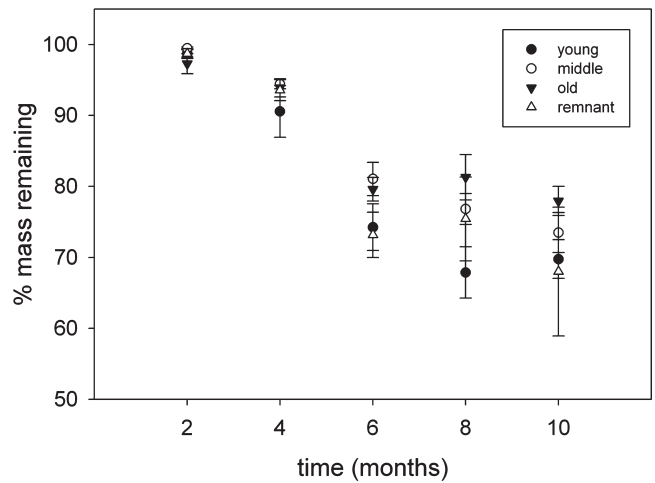

Figure 3. Decomposition of leaf litter in a 10-month common garden experiment. Data are expressed as percentage of initial mass remaining at each timepoint. No significant differences were found between remnant and reforested sites ($F_{[3,14]} = 1.8$, $p > 0.05$), but mass remaining did decrease significantly over time ($F_{[4,56]} = 78.2$, $p < 0.001$), at least for the first 6 months. The first three decomposition stages were significantly different from all other timepoints, but the last three timepoints were not significantly different from each other. Error bars represent ± SE.

soils is sparse, but a chronosequence of floodplain forest development in Texas found that the biggest increases in soil C and N stocks came early in forest succession, and that the relationship of soil C and N with age was quadratic, peaking at approximately 80 years and then declining in the most mature (approximately 150 year) forests (Bush & Van Auken 1986; Bush 2008). In those forests, nitrogen fixers are a large component of the early successional vegetation, whereas at our sites, N-fixing alders (*Alnus rhombifolia*) are present, but make up only 0.3% of stems over 5 cm diameter (Matzek unpublished). In addition to biological N fixation, nitrogen enters riparian floodplain forests through atmospheric deposition, silt deposited by floodwaters, and uptake of inorganic N from surface runoff and subsurface stream flow. Atmospheric deposition is unlikely to be systematically different between remnants and reforested areas because of the interspersion of our sites in the landscape, but inputs from silt and runoff would be lower if the reforested sites flooded less frequently than remnants. This is a distinct possibility, as some observers have suggested that the remnant forests in this landscape have avoided cultivation because they flood more frequently (Little 2007).

Although total N was lower in our reforested, postagricultural soils than in remnant forests, it was approximately twice as high as that found in the surface soils of newly established cottonwood forest (0.94–1.38 Mg/ha) along the Green and Yampa Rivers in Colorado (Adair et al. 2004), whereas remnant forests were comparable in N accumulation to mature cottonwood forests (3.1–3.86 Mg/ha). So, our plantation forests are not exceptionally low in nitrogen when compared to similar forests elsewhere in the West. Looking more broadly at changes
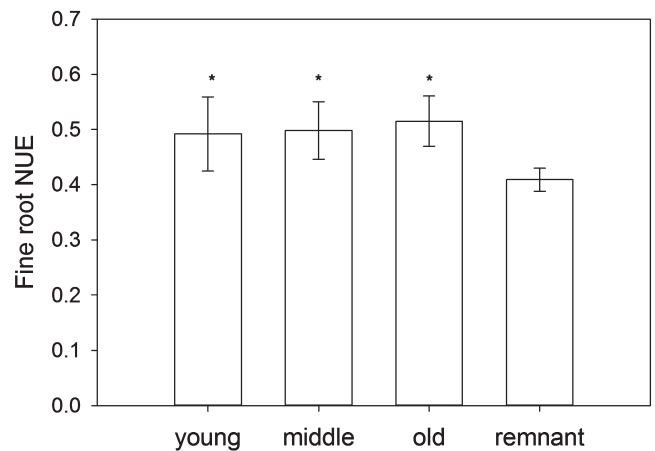

Figure 4. Fine-root nitrogen-use efficiency (NUE) is the annual productivity of fine roots divided by their nitrogen content. Asterisk indicates statistical significance at $\alpha = 0.05$ for Dunnett's post hoc test of differences between remnant and reforested sites, after one-way ANOVA with age class as a main effect. Error bars represent ± SE.

in soil C and N with forest succession, there is considerable evidence from global meta-analyses that recovery of these stocks is slow enough after agricultural use that significant increases are difficult to detect on decadal timescales (Berthrong et al. 2009; Marín-Spiotta & Sharma 2013).

Remnant forest soils had much higher rates of CO_2 efflux per mass of soil carbon than did reforested soils. One possible reason for this is that remnant-site soil C is more labile than that of reforested sites (Ågren & Bosatta 1996; Knorr et al. 2005), which could occur if litter inputs were of higher quality

in the older forests (e.g. lower C:N). Remnant forests did have slightly higher N concentrations in fine roots and lower C:N in leaves (data not shown). However, there was no difference in the rate of decomposition of litterfall from different sites when decomposed in a common garden; as this result should reflect litter quality, rather than site characteristics, we do not see strong indications that SOM inputs ought to be more labile. Another possibility is that the lower bulk density of the remnant soils means that SOM is less physically protected from breakdown by soil aggregates (Pulleman & Marinissen 2004), but this seems unlikely given the sandy texture of the Entisols at all sites, and given that soils had been sieved to remove gravel and roots prior to analysis. Instead, we speculate that remnant soils may differ in microbial biomass or in the makeup of the microbial community (Fontaine & Barot 2005).

Nitrogen mineralization rates showed a slight positive trend across the age gradient, but the results were highly variable and not statistically significant. Soil nutrient availability is notoriously heterogeneous (Robertson et al. 1999) and our soil sampling regime (12–15 cores per age class) may not have been sufficient to capture any trends with age. Data collected at Sacramento River reforestation sites that had been replanted 2 and 8 years prior to analysis also showed no difference in mineralization rates between remnants and young forests, but this work may also have been plagued by low replication, with only five cores per site (Brown & Wood unpublished). Whether due to insufficient replication or not, other workers have also found equivocal results or results suggesting little or no change over long periods of succession in riparian forest N mineralization rate (Adair et al. 2004; Merritt & Shafroth 2012).

It is important to note that we expressed N mineralization rate on a soil N basis, rather than on a soil mass or area basis, to avoid confounding the rate with the general uptick in soil N stocks over the age gradient. However, expressing mineralization on a per area basis may better reflect actual instantaneous availability of N to plants; when expressed this way, the remnants have higher N availability than all but the oldest reforestation age class. This suggests that replenishment of inorganic N from the SOM pool is sufficiently fast to support plant growth at levels seen in the remnant forest after only two decades of restoration. The high level of N availability in remnant soils may also explain why remnant forests can afford to be less nutrient-use efficient.

Overall, planting of riparian tree and shrub species on the Sacramento River floodplain resulted in forests that strongly resembled remnant forests with respect to biomass after only two decades. Soil properties and components of nutrient cycling were much slower to change with time, and did not appear to be on a clear trajectory toward parity with remnant forests. Remnant forests exhibited higher carbon efflux, bigger stocks of N and C in SOM, higher nitrogen availability, and lower nutrient-use efficiency, suggesting that restoration sites are still functionally distinct from remnant forests. We should point out that finding comparable reference sites or restoration targets is always a challenge in highly degraded landscapes. Although remnant forests are used here as an endpoint on the chronosequence because they are older, conditions in these forests are not necessarily the ideal reference for restoration—for instance, like all forests in the region, their understory has been invaded by nonnative grass and forb species (Holl & Crone 2004; McClain et al. 2011). Also, it is important to note that these measures of carbon and nitrogen accumulation and turnover are not the only possible measures of ecosystem function. Depending on the goals of a particular restoration, appropriate metrics might include pollination, seed dispersal, soil pH, or hydroperiod. Nonetheless, this study provides evidence that equivalence between restored and reference sites in biomass and vegetation structure does not necessarily equate to equivalence in functioning.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Site characteristics and additional attributes of forest structure.
Table S2. CO_2 efflux rates from soils.
Table S3. Decomposition of leaf litter at a common garden site.