



RESEARCH ARTICLE

Optimizing carbon storage and biodiversity co-benefits in reforested riparian zones

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Abstract

1. Climate change and biodiversity loss are two global challenges that can be addressed simultaneously through reforestation of previously cleared land. However, carbon markets can encourage reforestations that focus on maximizing carbon storage, potentially at the expense of biodiversity conservation.
2. To identify opportunities to optimize reforestation design and management to meet both goals, we examined the forest stand features associated with carbon stocks in biomass and soil, as well as bird abundance and diversity, in remnant and restored riparian forest stands in central California, U.S.A.
3. Within three decades of reforestation, both planted and naturally regenerating riparian forest stands provided significantly greater carbon storage and avian biodiversity benefits compared to baseline conditions. They were also similar to a remnant riparian forest stand.
4. We identified a synergy between carbon storage and biodiversity benefits in their positive associations with understorey cover, but we also identified a trade-off in their relationships to forest stand density. Biomass carbon stocks were strongly positively related to stand density, while bird density and diversity suffered at the highest stand densities.
5. The variability in understorey cover across forest stands indicates an opportunity for further enhancement of carbon and biodiversity benefits in areas where understorey cover is low, while the variability in stand density suggests an opportunity to re-examine reforestation goals and consider thinning to achieve those goals.
6. *Synthesis and applications.* We identified synergies and trade-offs between carbon storage and biodiversity in their relationships to forest stand features, indicating opportunities to optimize reforestation design and management to achieve multiple goals. Our approach can be adapted to other reforestation efforts intended to simultaneously address the global challenges of climate change and biodiversity loss.

KEYWORDS

biodiversity conservation, bird community, carbon sequestration, habitat restoration, reforestation, riparian forest, stand density, understorey cover

1 | INTRODUCTION

Protecting, enhancing, and restoring forests is an internationally recognized strategy that has the potential to simultaneously tackle two global challenges: climate change and biodiversity loss (Intergovernmental Panel on Climate Change [IPCC], 2014; International Union for the Conservation of Nature [IUCN], 2016; United Nations, 2016). Forests absorb billions of tons of carbon dioxide (CO₂) annually (Canadell & Raupach, 2008), and reforestation efforts alone have the potential to alter the trajectory of climate change (Sonntag, Pongratz, Reick, & Schmidt, 2016). Reforestation is also expected to improve ecological integrity, providing additional benefits to biodiversity and human well-being (IUCN, 2016). Forest restoration and protection efforts around the world have successfully slowed deforestation rates and increased planting rates in recent decades (Keenan et al., 2015), but because of the broad definition of forests in these global assessments, these trends do not necessarily reflect increasing carbon storage or biodiversity benefits (Chazdon, 2008). In addition, weak carbon markets can encourage reforestations that focus on maximizing carbon storage, potentially at the expense of biodiversity conservation (Gilroy et al., 2014; Lindenmayer et al., 2012). For reforestations to effectively mitigate both climate change and biodiversity losses, trade-offs and synergies between these goals must be identified.

Many carbon storage and biodiversity studies have focused on tropical forests due to the alarming rates of deforestation and loss of biodiversity (Meyfroidt & Lambin, 2011), but there are also opportunities for reforestation to benefit carbon storage and biodiversity in temperate-zone forests. For example, riparian forests in temperate zones are well-known hotspots of biodiversity (Naiman, Decamps, & Pollock, 1993) that store substantial amounts of carbon in the soil and biomass (Naiman, Decamps, & McClain, 2010) and provide many valuable ecosystem services (Daigneault, Eppink, & Lee, 2017; Naiman et al., 2010; Seavy, Gardali, et al., 2009). However, the ability of riparian ecosystems to provide these services has been severely compromised world-wide by human activities, including the construction of dams and levees for water storage and flood control and the conversion of floodplains to agricultural fields and urban development (Nilsson & Berggren, 2000; Perry, Andersen, Reynolds, Nelson, & Shafroth, 2012). Riparian forest restoration projects can successfully enhance carbon storage (Bullinger-Weber, Le Bayon, Thébault, Schlaepfer, & Guenat, 2014; D'Elia, Liles, Viers, & Smart, 2017; Gageler et al., 2014; Matzek, Puleston, & Gunn, 2015) and biodiversity (Gardali et al., 2006; Ortega-Álvarez & Lindig-Cisneros, 2012), but the alignment between carbon storage and biodiversity, and the specific forest stand features associated with each benefit, remain unknown.

The prospective overlap of carbon storage in the soil and biomass with biodiversity benefits has been examined broadly with remote sensing data to identify regions where reforestation is likely to have a large impact on both goals (e.g., Strassburg et al., 2010; Thomas et al., 2013). Yet, local empirical studies are needed to

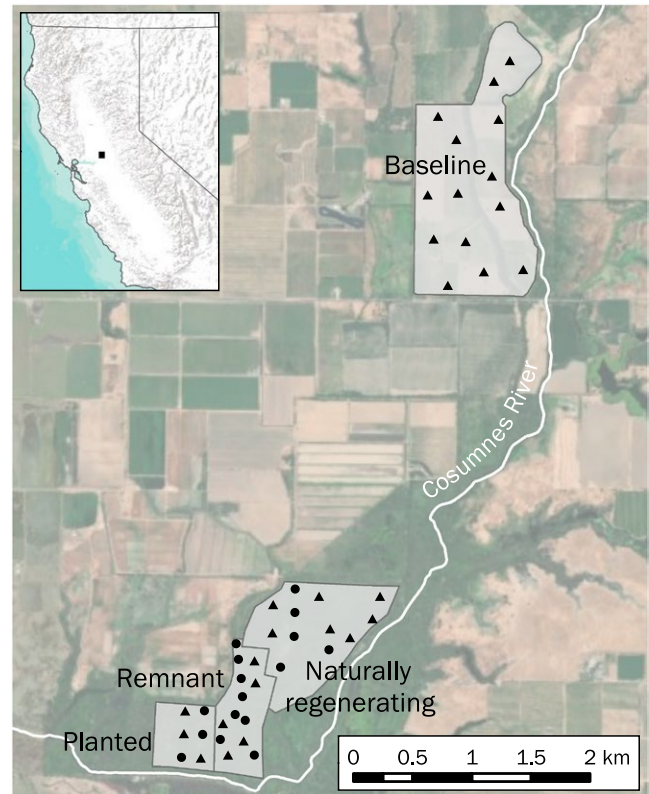


FIGURE 1 Map of sampling points within four study areas along the Cosumnes River in central California, USA. Data collected at sampling points marked with a circle included biodiversity metrics, soil samples, and vegetation cover, while those marked with a triangle also included vegetation transects for estimating stand density and biomass carbon stock

identify spatial variation in the realized carbon storage and biodiversity benefits and the factors that influence them. For example, both carbon storage and biodiversity are affected by forest stand features that can be influenced by reforestation design and subsequent management, such as stand size, isolation, age, density, and species composition (Cunningham et al., 2015; Gardali & Holmes, 2011; Hulvey et al., 2013; Magnago et al., 2015; Paul et al., 2016). However, carbon storage and biodiversity are often not fully aligned in their responses to fine-scale forest stand features (Beaudrot et al., 2016; Hatanaka, Wright, Loyn, & Mac Nally, 2011; Martin, Hurteau, Hungate, Koch, & North, 2015; Paul et al., 2016). By identifying the relationships between forest stand characteristics and their carbon storage and biodiversity benefits, reforestations can be optimized to achieve multiple goals (Larsen, Londoño-Murcia, & Turner, 2011; Paul et al., 2016).

We investigated whether reforestation of riparian areas is an effective strategy for mitigating both climate change and biodiversity losses by examining the alignment of carbon and biodiversity metrics in remnant and reforested riparian forest stands in central California, U.S.A. Specifically, we identified local stand features associated with biomass and soil carbon stocks, and bird abundance and bird species diversity, to reveal synergies and trade-offs between these metrics and inform reforestation design and management decisions.

TABLE 1 Summary of study areas and sampling effort. Data collected from sampling points included bird density, bird diversity, soil carbon stock, and estimates of vegetation cover. Vegetation transects provided estimates of stand density and biomass carbon stock

Study area	Description	Age	Area (ha)	Sampling points	Vegetation transects
Remnant	Remnant riparian forest	80+	41	13	5
Planted	Planted with acorns to reforest farm field	30	28	6	3
Naturally regenerating	Levee breach to promote forest regeneration on farm field	32 (22)	82	12	7
Baseline	Combination of levee breach and planting to reforest farm field	<3	150	14	14

2 | MATERIALS AND METHODS

2.1 | Study areas

Our analysis included four study areas within the Cosumnes River Preserve, which is a partnership of public agencies and non-governmental conservation organizations established in 1987 along the Cosumnes River in California's Central Valley (Figure 1). The four study areas are similar in that they are all located in the Cosumnes River floodplain and the soils are all primarily classified as Cosumnes silt loams (Natural Resources Conservation Service [NRCS], 2013), but each study area has a different history (Table 1). The first study area is a remnant riparian forest (hereafter, "remnant"), visible in aerial photographs from 1937 to 1939, and estimated to have been at least 80 years old in 2017 (Sommer, Whipple, & McGee, 2017; Tu, 2000). We considered this study area to be a reference forest for the other three study areas, which were all formerly cultivated and are now undergoing reforestation. One of these is a 30-yr-old planted forest ("planted"), where an extensive volunteer effort planted *Quercus lobata* acorns in 1987. Another reforestation was initiated when an unintentional levee breach and flood event in 1985 resulted in the recruitment and establishment of riparian vegetation, including a grove of cottonwood trees (*Populus fremontii*). This observation inspired a second, intentional levee breach 10 years later to improve floodplain connectivity and promote natural forest regeneration in the area (Swenson, Whitener, & Eaton, 2003). Thus, much of this study area ("naturally regenerating") was 22 years old in 2017, but the original cottonwood grove was 32 years old. The final study area ("baseline") is farther upstream and is the site of a newly established reforestation experiment. An intentional levee breach in 2014 enhanced floodplain connectivity, while experimental plots were established within the floodplain to test the effectiveness of three reforestation treatments: natural regeneration only, a limited planting of trees only, and an extensive planting of trees and shrubs with irrigation (Dybala, Dettling, et al., 2017). Planting was completed in 2016, resulting in little difference among treatments at the time of this study, so we did not distinguish between sampling points from different treatment plots. We considered this study area as

likely to resemble the baseline, pre-reforestation conditions at the naturally regenerating and planted study areas.

2.2 | Biodiversity

In May–June 2017, we sampled the bird community at 45 sampling points distributed across the four study areas. We focused on the bird community because they respond quickly to riparian reforestation (Gardali et al., 2006), and, because bird populations have been substantially impacted by riparian forest loss and degradation, they are often included in the goals of riparian reforestation efforts in California (Dybala, Clipperton, et al., 2017). We used sampling points that had been previously established for point count surveys of birds, systematically distributed at least 100 m apart and 50 m from study area edges (Figure 1). The total number of sampling points per study area varied due to the varying sizes of the study areas (Table 1). Once each during May and June, the peak of the bird breeding season, RGW conducted standardized 5-min point count surveys at each sampling point, between 15 min after local sunrise and 10:00 a.m., recording all bird species seen and heard and the estimated distance to each individual (Ralph, Droege, & Sauer, 1995). To minimize bias due to variation in detection probability with distance and by species, in this analysis we included only birds detected within 50 m. We also included only landbird species for which the point count survey protocol is appropriate. We calculated the maximum number of individuals of each species detected over the two surveys at each point, and used this information to calculate indices of total bird density (individuals/ha) and diversity (inverse Simpson) within 50 m of each sampling point. During the June point count survey, RGW also surveyed the vegetation within 50 m of each point, recording % cover of the canopy layer (>2 m height), understory layer (0.5–2 m height), and ground cover (<0.5 m height).

2.3 | Carbon stocks

In June and July, we revisited point count stations to collect data on the carbon stored in the soil and vegetation. We collected a

total of 90 soil samples, including samples at two depths (0–6 cm and 6–12 cm) from each of 45 sampling points. For each depth, we gently pushed a steel ring (6.0 cm height × 4.1 cm diameter) into the soil, excavated soil around the ring, and then transferred the contents of the ring to a tin box. After transport to the laboratory, the soil samples were dried at 105°C for 48 hr and then weighed to determine the bulk density (g/cm^3) of each sample. The dried soils were then ground with a mortar and pestle, sieved through a 60-mesh (250 μm) sieve, and 45–85 mg of the soils were weighed into tin capsules (5 × 9 mm for solids; Costech). The 90 samples were then analysed for total carbon (%) using an Elementar Vario Micro Cube elemental analyser (Elementar). We used the bulk density and total carbon to estimate the soil carbon stock ($\text{Mg C}/\text{ha}$) at each point on an equal mass (rather than equal volume) basis (Wendt & Hauser, 2013). We accomplished this by finding the 0–6 cm depth soil sample with the highest mass (i.e., most densely compacted soil), and estimating the proportion of the 6–12 cm depth soil sample at all other points (in addition to the entire mass of the 0–6 cm depth soil sample) that would be required to reach an equivalent mass of soil.

To estimate the carbon stored in woody vegetation in each study area, we randomly selected a subset of the sampling points in each study area at which we established 15 × 50 m vegetation transects (Table 1; Figure 1). Transects were centred on the sampling point and oriented perpendicular to the average slope in the local vicinity, to capture any elevational and hydrological gradients. Within each transect, we surveyed all standing live and dead trees ≥ 5 cm diameter at breast height (dbh, 1.37 m), recording species, dbh (cm), and height (m), estimated by using a clinometer to measure the slope to the top of a tree from a distance estimated with a range finder. For each transect, we calculated the forest stand density (stems/ha) and we used the protocol adopted by the California Air Resources Board (California Air Resources Board [CARB], 2015) to estimate the total above-ground and below-ground biomass (Mg/ha). Above-ground biomass (AB) was estimated by summing the individual above-ground tree biomasses, each estimated from species-specific allometric equations. Below-ground root biomass (RB) in each transect was estimated as a function AB using an allometric equation for temperate-zone forests (Cairns, Brown, Helmer, & Baumgardner, 1997):

$$RB = e^{-0.7747 + 0.8436 \ln(AB)}$$

We then corrected for broken top and decaying trees by estimating the decay condition and proportion of above-ground biomass missing for each tree (Harmon, Woodall, Fasth, Sexton, & Yatkov, 2011; USDA Forest Service, 2010). We estimated the biomass carbon stock (Mg/ha) as 50% of the total biomass stock in each transect (CARB, 2015). We were unable to account for the biomass carbon stored in California wild grape lianas (*Vitis californica*), which were particularly abundant at some of the remnant study area's sampling points. Thus, we consider the biomass carbon stock estimates to be minimum estimates.

2.4 | Synergies and trade-offs

To evaluate synergies and trade-offs between reforestation outcomes, we focused on four metrics: bird density, bird diversity, soil carbon stock, and biomass carbon stock. For each metric, we first examined differences among the four study areas by fitting linear models with the log-transformed metric as the response variable and study area as the independent variable, and correcting for multiple comparisons using Tukey's HSD. We also estimated the average annual growth of each metric in the planted and naturally regenerating study areas, by assuming the baseline study area represented baseline conditions for each of these metrics. To avoid overestimating the average annual growth of these metrics, we assumed the maximum age difference between study areas, such that we treated the entire naturally regenerating study area as though it were the maximum age of 32 years old, and we treated the entire baseline study area as though it were the minimum age of 0 years old.

We then examined sources of point-scale variation in each of the four primary metrics at each sampling point in the relatively mature forest of the remnant, planted, and naturally regenerating study areas. For each metric, we fit a global linear mixed-effects model with the log-transformed metric as the response variable and a random intercept for each study area. As candidate predictor variables, we considered forest stand characteristics that could be influenced by reforestation design or management and which had been previously shown to be related to carbon stocks or biodiversity, including stand density (Cunningham et al., 2015; Horner et al., 2010; Paul et al., 2016) and stand structural complexity, represented by % cover in each of the canopy, understorey, and ground cover layers (Nur, Ballard, & Geupel, 2008). However, canopy and ground cover were strongly negatively correlated ($r_s = -0.71$), and we chose to exclude ground cover from our analyses. None of the other predictor variables were strongly correlated (all $|r_s| < 0.50$). We centred and standardized each predictor to a mean of 0 and standard deviation of 1.

We anticipated nonlinear relationships between the predictor variables and metrics, reflecting optimum values at which each metric is maximized, so we fit a global model for each metric (m_i):

$$m_i \sim D + D^2 + C_c + C_c^2 + C_u + C_u^2 + A + (1|S)$$

where D is stand density, C_c is canopy cover, C_u is understorey cover, A is age, $(1|S)$ is a term reflecting a random intercept for each study area. We then fit subsets of the candidate predictor variables in the global model, including either no effect, linear, or linear and quadratic terms for each predictor variable, as well as an intercept-only null model. As a metric of the likelihood of each predictor variable being in the "best" model, we calculated the relative importance (RI) of each variable by summing the Akaike weights of all models containing each variable (Burnham & Anderson, 2004; Giam & Olden, 2016). To further visualize these relationships and potential trade-offs and synergies, we reduced each metric's model set to those with $\Delta\text{AIC}_c \leq 4$, and used a bootstrapping approach to estimate the

TABLE 2 Mean and standard error of carbon stock, biodiversity, and forest stand metrics by study area. Means in a row with different superscript letters indicate significantly different groups ($p < 0.05$)

	Remnant	Planted	Naturally regenerating	Baseline
Primary metrics				
Biomass carbon stock (Mg/ha)	80.4 ± 33.0 ^a	68.6 ± 4.1 ^a	114.8 ± 23.5 ^a	0.0 ± NA ^b
Soil carbon stock (Mg/ha)	38.7 ± 5.8 ^a	32.0 ± 1.0 ^a	25.0 ± 1.2 ^a	12.5 ± 1.0 ^b
Bird density index (birds/ha)	31.5 ± 2.0 ^a	22.9 ± 2.7 ^a	25.0 ± 2.6 ^a	6.6 ± 1.1 ^b
Bird species diversity index	12.1 ± 0.8 ^a	7.5 ± 0.9 ^a	8.4 ± 0.9 ^a	2.7 ± 0.3 ^b
Candidate predictor variables				
Stand density (stems/ha)	421.3 ± 114.0 ^b	400.0 ± 13.3 ^{ab}	880.0 ± 202.1 ^a	0.0 ± NA ^c
Canopy cover (%)	73.1 ± 2.7 ^a	81.2 ± 4.4 ^a	58.2 ± 7.0 ^a	0.1 ± 0.1 ^b
Understorey cover (%)	72.7 ± 4.2 ^a	15.8 ± 5.1 ^b	47.9 ± 6.8 ^a	1.3 ± 0.4 ^c

model-averaged predicted values and 95% bootstrap confidence intervals for each metric across a range of each candidate variable. For each of 1,000 iterations, we resampled the parameter estimates of each model, calculated predicted values from each model, and then model-averaged predicted values using Akaike weights.

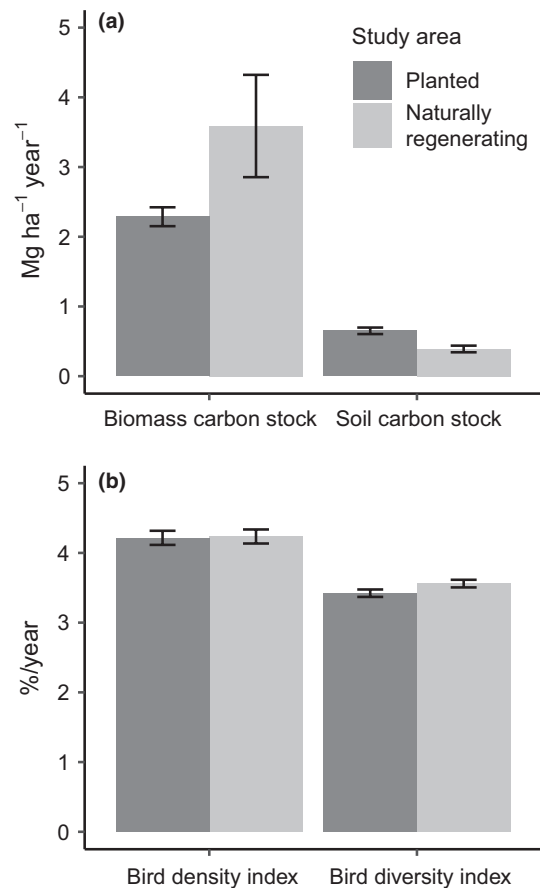
We also conducted a canonical correspondence analysis (CCA) to relate the predictor variables to the bird species composition at each point, because it is important to understand not only which predictors are associated with maximizing the bird diversity index at each sampling point but also how the total bird diversity across points can be maximized. We used species presence/absence data, treating the detection of each species within 50 m on either of the two surveys at each point as presence, and we used step-wise selection of variables using the “ordistep” function in the R package vegan to identify the subset of predictor variables associated with gradients in the species community composition.

All data management, data processing, analyses, and data visualizations were conducted in R (R Core Team, 2018), primarily using the tidyverse packages (Wickham, 2017), lme4 (Bates, Maechler, Bolker, & Walker, 2015), and vegan (Oksanen et al., 2018).

3 | RESULTS

3.1 | Carbon stocks

The remnant riparian forest along the Cosumnes River contained an average of 80.4 ± 33.0 Mg C/ha stored in the woody biomass and 38.7 ± 5.8 Mg C/ha stored in soil up to 12 cm deep (Table 2). Biomass and soil carbon stocks in the planted and naturally regenerating study areas were not significantly different from the remnant study area, whereas in the baseline study area there was no woody vegetation in any of the transects that met the minimum dbh of 5 cm, and soil carbon stocks were less than half that of the remnant study area (Table 2). Compared to the current biomass carbon stock of the baseline study area, we estimated the annual rate of biomass carbon accumulation as averaging 2.29 ± 0.14 Mg C ha⁻¹ year⁻¹ in the planted study area over the past 30 years, and a faster rate of at least 3.59 ± 0.73 Mg C ha⁻¹ year⁻¹ in the naturally

**FIGURE 2** Estimated average rate of change and standard error for each of the four primary metrics at the planted and naturally regenerating study areas over the last 30 and 32 years respectively. (a) Average annual increases in biomass and soil carbon stocks (Mg/ha/year). (b) Average annual growth rate of bird density and diversity indices (%/year)

regenerating study area over the past 32 years (Figure 2a). Similarly, we estimated that the soil carbon stocks of the planted and naturally regenerating study areas have doubled over the past 30 years, with average annual rates of 0.65 ± 0.05 Mg C ha⁻¹ year⁻¹ and 0.39 ± 0.05 Mg C ha⁻¹ year⁻¹ respectively (Figure 2a). However,

because the naturally regenerating study area was largely younger than 32 years old, and parts of the baseline study area were up to 3 years old, we considered these rates to be minimum estimates of biomass and soil carbon accumulation.

3.2 | Biodiversity

The remnant riparian forest supported an average bird density index of 31.5 ± 2.0 birds/ha, with an average species diversity index of 12.1 ± 0.8 (Table 2). As with the carbon stocks, we were unable to detect a difference in bird density or diversity indices between the remnant, planted, and naturally regenerating study areas (Table 2). However, the bird density and diversity indices in the baseline study

area were less than 25% of these indices in remnant study area. Assuming the baseline bird community of the planted and naturally regenerating study areas resembled the current bird community of the baseline study area, we estimated the rate of increase in bird density as averaging a very similar 0.54 ± 0.10 birds ha^{-1} year $^{-1}$ in the planted study area and 0.58 ± 0.09 birds ha^{-1} year $^{-1}$ in the naturally regenerating study area, equivalent to 4.22% and 4.24% annual growth rates respectively (Figure 2b). The rate of increase in bird diversity index was also similar across these two sites, averaging 0.16 ± 0.03 ha^{-1} year $^{-1}$ in the planted study area and 0.18 ± 0.03 ha^{-1} year $^{-1}$ in the naturally regenerating study area, equivalent to 3.42% and 3.56% annual growth rates respectively (Figure 2b).

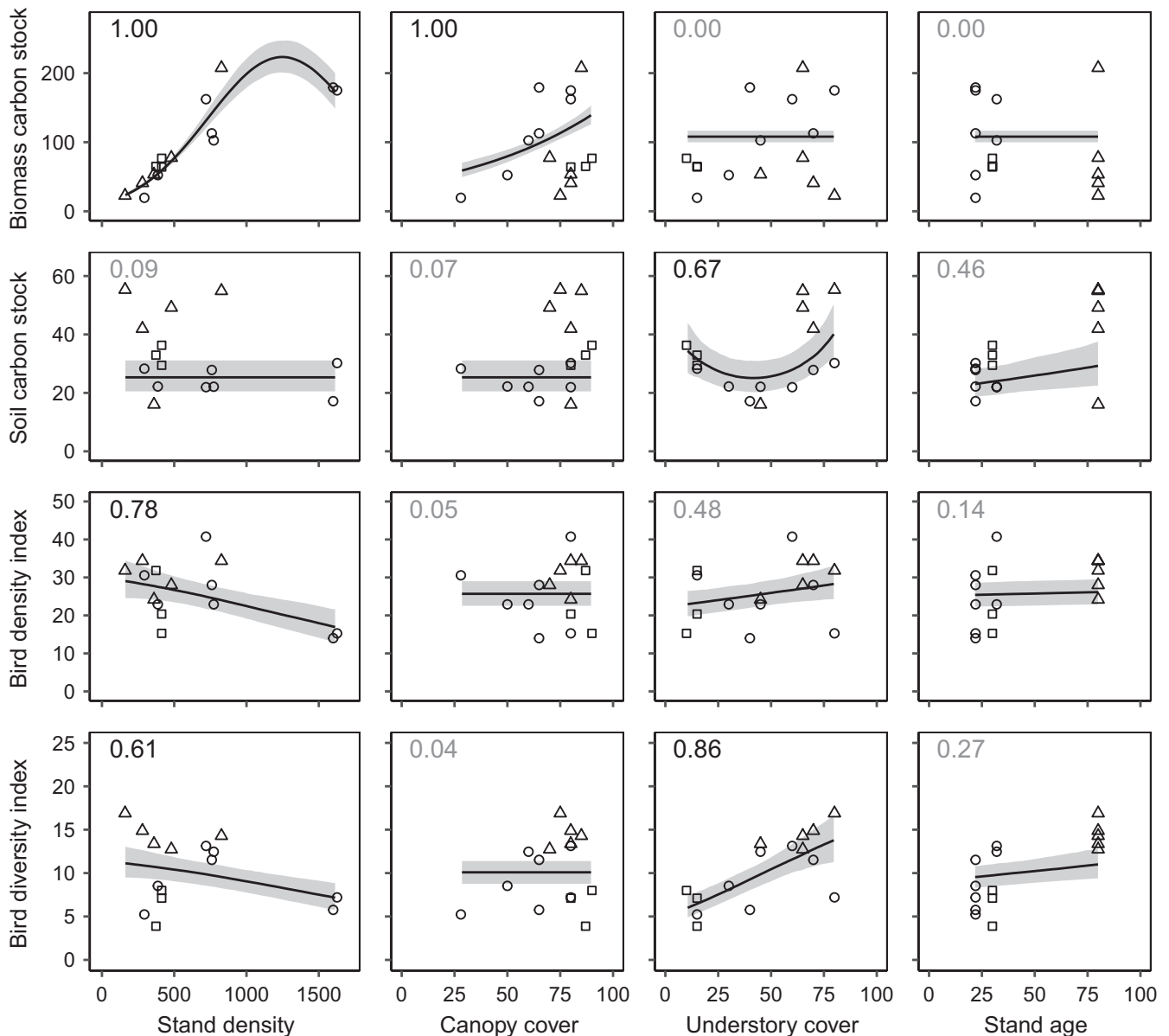


FIGURE 3 Model-averaged predicted values and 95% bootstrap confidence intervals for each of the four primary metrics (rows) over a range of values for each predictor variable (columns). Also shown are the observed values for sampling points in the remnant (triangles), planted (boxes), and naturally regenerating (circles) study areas. The relative importance (RI) values for each variable as a predictor for each metric are shown in a darker colour for RI > 0.50

3.3 | Synergies and trade-offs

Stand age was a relatively poor predictor of any of the carbon storage and biodiversity metrics among these relatively mature forest stands (Figure 3), although we would expect it to be more important in younger forest stands of less than 20 years. Stand density, canopy cover, and understorey cover were all relatively important predictors of one or more of the carbon storage and biodiversity metrics ($RI > 0.50$), meaning they were likely to be included in the best model, but none of these were important predictors of all four metrics (Figure 3). Stand density was strongly positively associated with biomass carbon stock, but negatively associated with both bird density and diversity, such that an increase in stand density would likely enhance biomass carbon stock while negatively affecting bird density and diversity (Figure 4). In contrast, canopy cover was positively associated with biomass carbon stock, and neutral with respect to all of the other metrics. Similarly, understorey cover was positively associated with both bird diversity and soil carbon stocks, and neutral with respect to the other metrics. Therefore, increases in canopy and understorey cover would be expected to provide enhanced carbon storage and biodiversity benefits without incurring any trade-offs. However, in the canonical correspondence analysis, canopy and understorey cover (but not stand density or age) were selected as important variables accounting for 22% of the variation in bird species composition between sampling points (Figure 5). Thus, while increases in canopy and understorey cover would not be expected to incur a trade-off among the four metrics we examined, there may be trade-offs in the presence of individual species of interest, such as riparian focal species for which regional conservation objectives have been defined (Dybala, Clipperton, et al., 2017). Maintaining some diversity in canopy and understorey cover within the study areas would likely enhance the total bird diversity.

4 | DISCUSSION

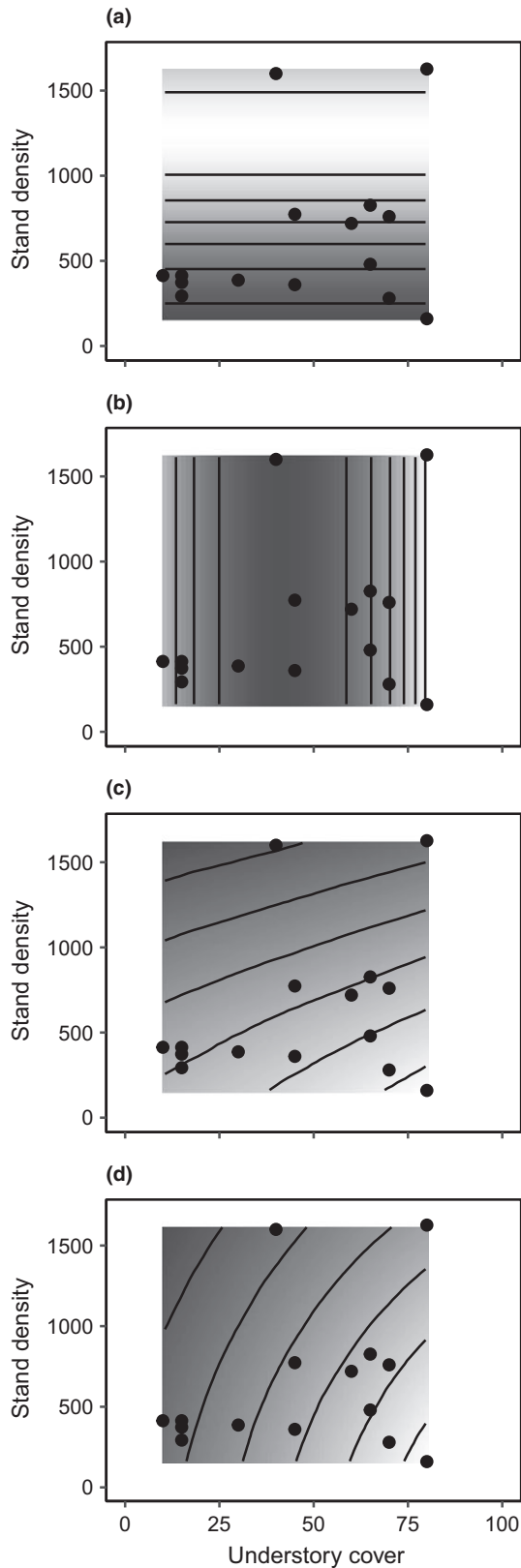
Reforestation efforts around the world have the potential to provide a multitude of benefits for nature and people, including contributing to the mitigation of climate change and biodiversity losses. Yet, empirical estimates of the realized carbon and biodiversity benefits of reforestation projects, and the trade-offs and synergies between them, are few. To our knowledge, our study is the first to examine riparian forest stand characteristics associated with both carbon storage and bird community benefits and to reveal trade-offs and synergies that can help maximize the success of riparian reforestation in achieving multiple goals simultaneously.

Within three decades of initiating reforestation, the carbon and biodiversity benefits provided by the planted and naturally regenerating study areas were largely similar to the remnant riparian forest, and were significantly greater than the more recently cultivated baseline study area (Table 2). Further, among these relatively mature forest stands, stand age was not an important predictor of carbon and biodiversity metrics (Figure 3), reflecting the overall similarity

among the three study areas in these metrics (Table 2). Studies of similar riparian reforestations in California found that after 10 years, bird populations were still increasing and new bird species were still arriving (Gardali et al., 2006), and after 20 years, biomass and soil carbon stocks had not yet matched that of remnant forest stands (Matzek, Warren, & Fisher, 2016). Thus, our results suggest that it will take at least 20–30 years to be able to quantify the full carbon storage and biodiversity benefits of riparian reforestation efforts in California, but provide further support for riparian forest restoration as an effective strategy for simultaneously mitigating both climate change and biodiversity losses. Simultaneously, we also identified substantial variation among the sampling points in the carbon and biodiversity metrics that suggested there was further room for improvement (Supporting Information Figure S1). Because the variation in these metrics was associated with variation in point-scale forest stand characteristics (Figure 3), changes in the current management of these study areas or in the design of future reforestation areas, may be able to maximize the carbon and biodiversity benefits.

Synergies represent no-regrets opportunities to further enhance the carbon and biodiversity benefits of riparian forests. We found that soil carbon stocks and biodiversity metrics were positively associated with understorey cover (0.5–2 m; Figure 3), and that understorey cover varied substantially across sampling points (Figure 4), indicating further room for enhancement of these reforestations. Understorey cover has also been associated with the abundance of many individual riparian bird species (Nur et al., 2008), and foliage height diversity is expected to benefit bird community diversity (MacArthur & MacArthur, 1961). More generally, stand structural complexity has been recommended for biodiversity conservation in forests (Lindenmayer, Franklin, & Fischer, 2006; Seavy, Viers, & Wood, 2009). Here, biomass carbon stock was unaffected by understorey cover, in alignment with a previous finding that shrub cover does not inhibit wood production of mature trees (Vilà et al., 2007). Soil carbon stock increased at sampling points with high understorey cover (Figure 3), possibly by contributing additional inputs of organic matter to the soil. Thus, efforts to design or manage riparian reforestation projects for further increases in understorey cover and structural complexity would be likely to enhance both carbon and biodiversity benefits.

Our results also indicated an important trade-off in the effects of forest stand density on achieving both carbon and biodiversity goals. While biomass carbon stocks are strongly positively related to stand density, we found that bird density and diversity suffer at the highest stand densities (Figure 3). Our results are in alignment with other studies that have demonstrated a positive relationship between stand densities and biomass carbon stocks (Cunningham et al., 2015; Paul et al., 2016), and reduced habitat quality at high stand densities (Horner et al., 2010; Vesk, Nolan, Thomson, Dorrough, & Nally, 2008). Here, we have evidence of a direct trade-off, and the optimal stand densities for each metric vary. For example, a riparian reforestation project aimed at maximizing bird density within 30 years would seek to manage stand density (through initial planting design or subsequent thinning) to less than 500 stems/ha,



while a project aimed at maximizing biomass carbon storage within 30 years might manage stand densities between 1,000 and 1,500 stems/ha (Figure 4).

FIGURE 4 Contour plots showing the model-averaged predicted relationships for each of the four primary metrics over the observed range of values for understory cover (%) and stand density (stems/ha): (a) biomass carbon stock (Mg/ha), (b) soil carbon stock (Mg/ha), (c) bird density index (birds/ha), and (d) bird diversity index (inverse Simpson). Lighter areas of the contour reflect higher predicted values for each metric. Also shown are the observed understory cover and stand density values from the remnant, planted, and naturally regenerating study areas

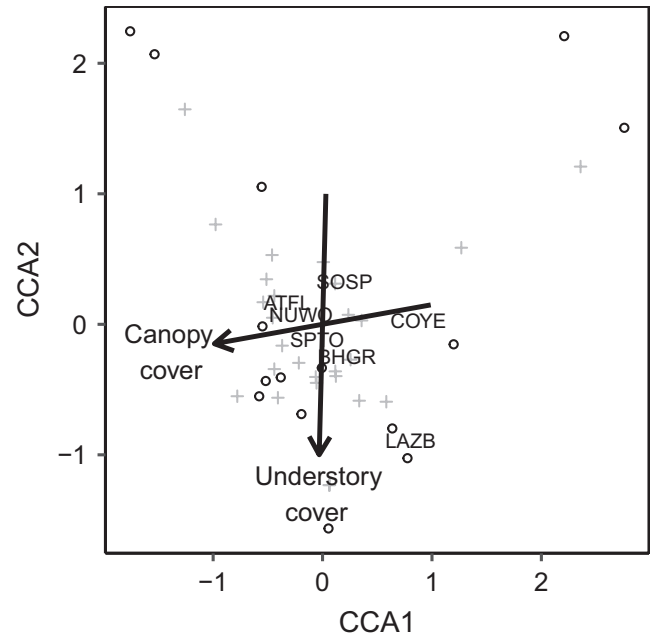


FIGURE 5 Biplot showing the results of the CCA with respect to canopy and understory cover gradients. Also shown are sampling points (circles), bird species (crosses), and the four-letter codes for seven riparian focal species (Dybala, Clipperton, et al., 2017): ATFL (Ash-throated Flycatcher, *Myiarchus cinerascens*), SOSP (Song Sparrow, *Melospiza melodia*), NUWO (Nuttall's Woodpecker, *Picoides nuttallii*), COYE (Common Yellowthroat, *Geothlypis trichas*), SPTO (Spotted Towhee, *Pipilo maculatus*), BHGR (Black-headed Grosbeak, *Pheucticus melanocephalus*), and LAZB (Lazuli Bunting, *Passerina amoena*)

Optimizing reforestation design and management over multiple goals requires recognizing these synergies and trade-offs, and clearly defining the objectives of the reforestation, including the metrics of interest and the minimum values of each metric required for the project to be considered a success (e.g., Poff et al., 2016; Underwood et al., 2017). Then, knowledge of the forest stand characteristics associated with each metric would help with planning the design and management of the reforestation project to achieve these objectives. Here, for example, if the goals of these reforestations include maximizing bird density and diversity at each sampling point, future management efforts might focus on increasing understory cover in areas where it is low and reducing stand densities in areas where it is very high (Figure 4). Alternatively, if the goals of these reforestations include enhancing the total bird diversity in

the region (rather than at each sampling point), management efforts may include maintaining or creating additional diversity in habitat structure and composition, such as more open, scrubby, early successional vegetation that is required by some riparian bird species (Dybala, Clipperton, et al., 2017).

Our study joins a growing body of work demonstrating the potential for riparian reforestation projects to provide numerous important benefits for nature and people, including improvements to water quality, protecting soil from erosion, reducing flood risk downstream, recharging groundwater basins, providing habitat for fish and wildlife, and other economic benefits (Capon et al., 2013; Carver, 2013; Naiman et al., 2010), in addition to the carbon storage and bird community benefits discussed here. In some cases, the value of the carbon benefit alone may be sufficient to pay for the projects (Matzek et al., 2015), but attempts to monetize just a few of these benefits have shown that they can be significantly greater than implementation costs (Daigneault et al., 2017; Holmes, Bergstrom, Huszar, Kask, & Orr, 2004). To our knowledge, we are the first to provide empirical estimates of both the realized carbon storage and bird community benefits of riparian reforestation, and identify trade-offs between them, but this is only the tip of a much larger benefit iceberg. Quantifying additional realized benefits, tracking the change from baseline, pre-reforestation conditions, and crucially, identifying the synergies and trade-offs among these benefits will improve the efficiency of reforestation design and management in achieving multiple goals. In turn, these efforts will help document and improve the cost-benefit ratio of these projects, accelerating the funding and implementation of these projects, and helping to address the global challenges of climate change and biodiversity loss.

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AUTHORS' CONTRIBUTIONS

K.E.D. conceived the idea, analysed the data, and led the writing of the manuscript; K.E.D., K.S., and N.E.S. designed methodology; R.G.W., K.E.D., and K.S. collected the data; K.S. and D.R.S. conducted laboratory analyses; K.E.D., K.S., N.E.S., and T.G. designed the scope and content of the manuscript. All authors contributed to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.2h63d10> (Dybala et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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