



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

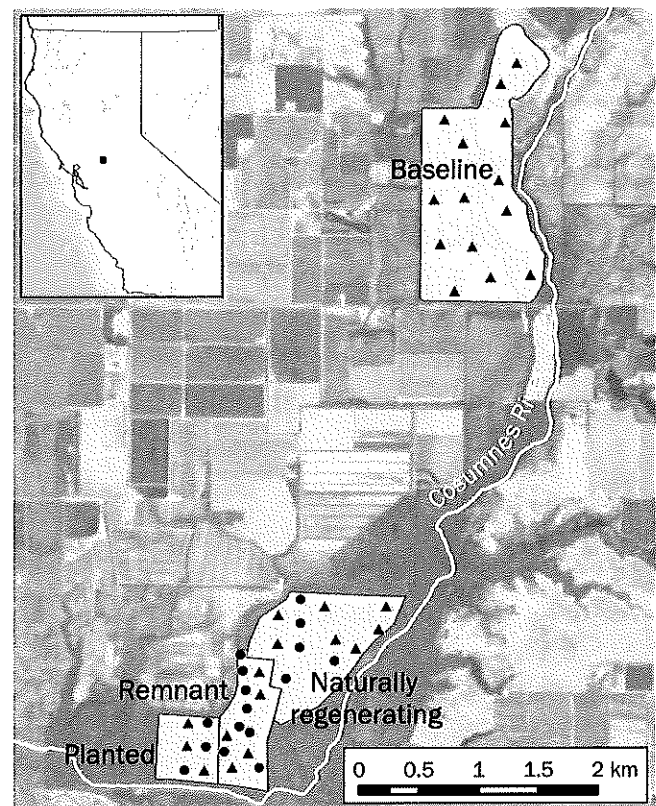


FIGURE 1 Map of sampling points within four study areas along the Cosumnes River in central California, USA. Data collected at sampling points marked with a circle included biodiversity metrics, soil samples, and vegetation cover, while those marked with a triangle also included vegetation transects 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 (Mg C/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

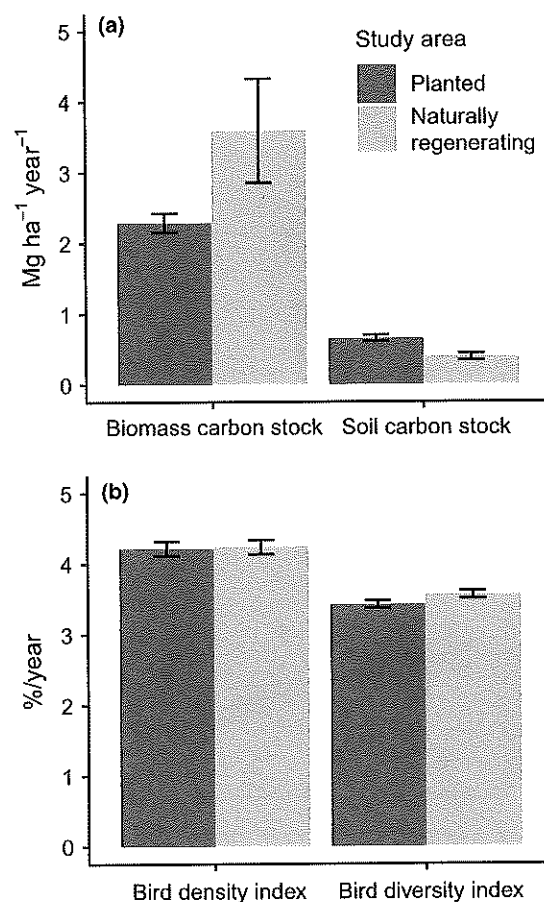


FIGURE 2 Estimated average rate of change and standard error for each of the four primary metrics at the planted and naturally regenerating study areas over the last 30 and 32 years respectively. (a) Average annual increases in biomass and soil carbon stocks (Mg/ha/year). (b) Average annual growth rate 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 $\text{ha}^{-1} \text{year}^{-1}$ in the planted study area and 0.58 ± 0.09 birds $\text{ha}^{-1} \text{year}^{-1}$ 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 $\text{ha}^{-1} \text{year}^{-1}$ in the planted study area and 0.18 ± 0.03 $\text{ha}^{-1} \text{year}^{-1}$ in the naturally regenerating study area, equivalent to 3.42% and 3.56% annual growth rates respectively (Figure 2b).

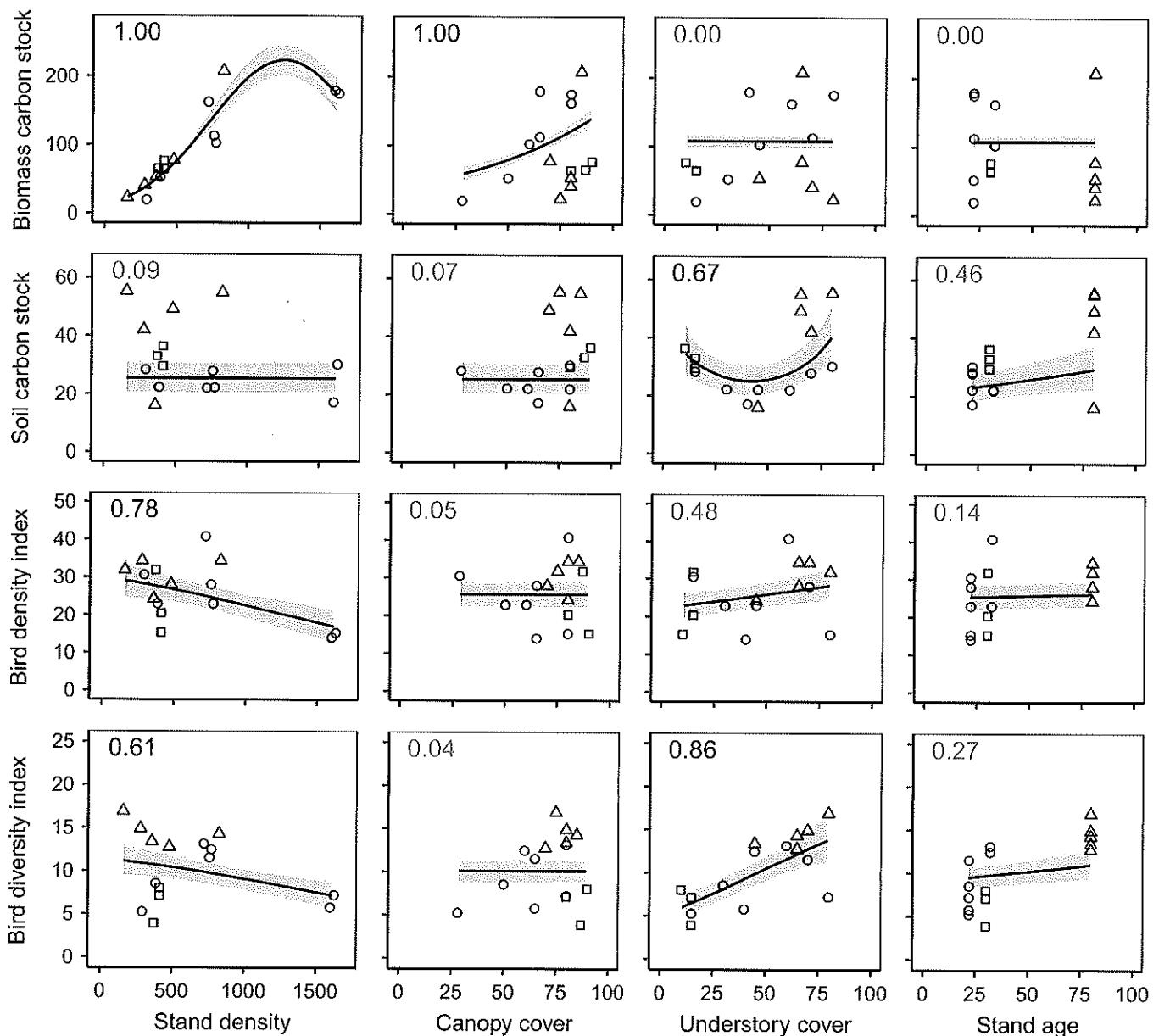


FIGURE 3 Model-averaged predicted values and 95% bootstrap confidence intervals for each of the four primary metrics (rows) over a range of values for each predictor variable (columns). Also shown are the observed values for sampling points in the remnant (triangles), planted (boxes), and naturally regenerating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

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

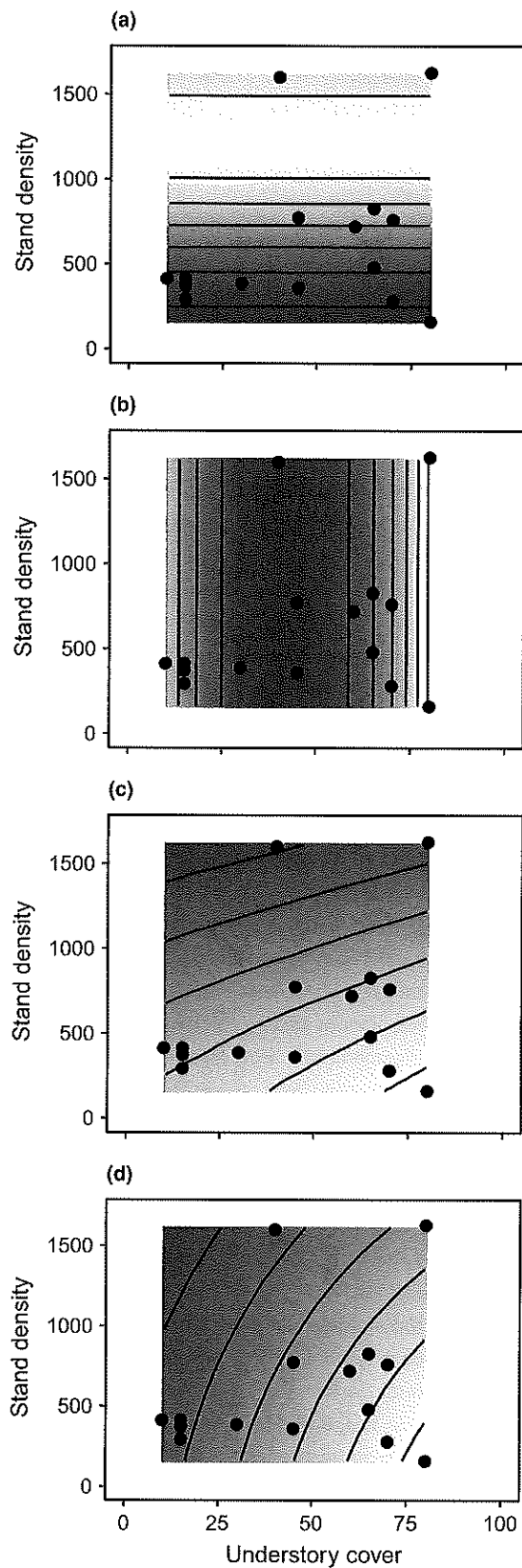
Reforestation efforts around the world have the potential to provide a multitude of benefits for nature and people, including contributing to the mitigation of climate change and biodiversity losses. Yet, empirical estimates of the realized carbon and biodiversity benefits of reforestation projects, 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; Vesik, Nolan, Thomson, Dorrrough, & 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

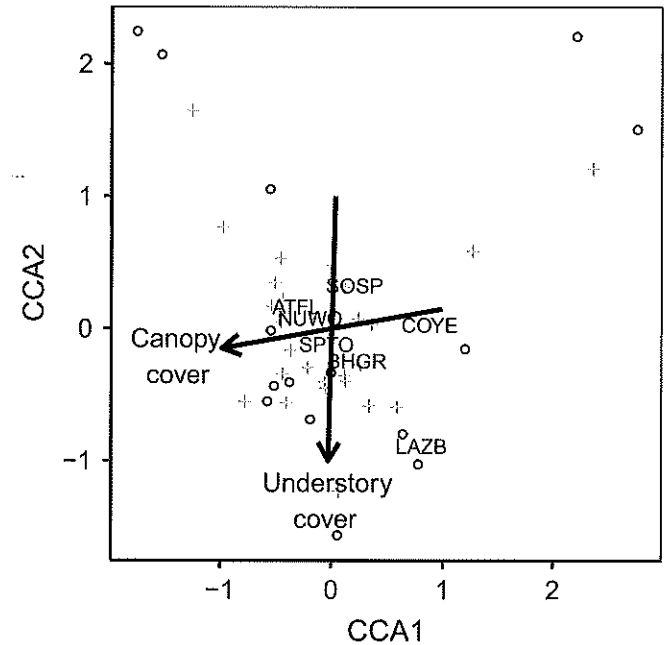


FIGURE 5 Biplot showing the results of the CCA with respect to canopy and understory cover gradients. Also shown are sampling points (circles), bird species (crosses), and the four-letter codes for seven riparian focal species (Dybala, Clipperton, et al., 2017): ATFL (Ash-throated Flycatcher, *Myiarchus 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-forestation 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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Natural climate solutions

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Better stewardship of land is needed to achieve the Paris Climate Agreement goal of holding warming to below 2 °C; however, confusion persists about the specific set of land stewardship options available and their mitigation potential. To address this, we identify and quantify “natural climate solutions” (NCS): 20 conservation, restoration, and improved land management actions that increase carbon storage and/or avoid greenhouse gas emissions across global forests, wetlands, grasslands, and agricultural lands. We find that the maximum potential of NCS—when constrained by food security, fiber security, and biodiversity conservation—is 23.8 petagrams of CO₂ equivalent (PgCO₂e) y⁻¹ (95% CI 20.3–37.4). This is ≥30% higher than prior estimates, which did not include the full range of options and safeguards considered here. About half of this maximum (11.3 PgCO₂e y⁻¹) represents cost-effective climate mitigation, assuming the social cost of CO₂ pollution is ≥100 USD MgCO₂e⁻¹ by 2030. Natural climate solutions can provide 37% of cost-effective CO₂ mitigation needed through 2030 for a >66% chance of holding warming to below 2 °C. One-third of this cost-effective NCS mitigation can be delivered at or below 10 USD MgCO₂e⁻¹. Most NCS actions—if effectively implemented—also offer water filtration, flood buffering, soil health, biodiversity habitat, and enhanced climate resilience. Work remains to better constrain uncertainty of NCS mitigation estimates. Nevertheless, existing knowledge reported here provides a robust basis for immediate global action to improve ecosystem stewardship as a major solution to climate change.

climate mitigation | forests | agriculture | wetlands | ecosystems

The Paris Climate Agreement declared a commitment to hold “the increase in the global average temperature to well below 2 °C above preindustrial levels” (1). Most Intergovernmental Panel on Climate Change (IPCC) scenarios consistent with limiting warming to below 2 °C assume large-scale use of carbon dioxide removal methods, in addition to reductions in greenhouse gas emissions from human activities such as burning fossil fuels and land use activities (2). The most mature carbon dioxide removal method is improved land stewardship, yet confusion persists about the specific set of actions that should be taken to both increase sinks with improved land stewardship and reduce emissions from land use activities (3).

The net emission from the land use sector is only 1.5 petagrams of CO₂ equivalent (PgCO₂e) y⁻¹, but this belies much larger gross emissions and sequestration. Plants and soils in terrestrial ecosystems currently absorb the equivalent of ~20% of anthropogenic greenhouse gas emissions measured in CO₂ equivalents (9.5 PgCO₂e y⁻¹) (4). This sink is offset by emissions from land

use change, including forestry (4.9 PgCO₂e y⁻¹) and agricultural activities (6.1 PgCO₂e y⁻¹), which generate methane (CH₄) and nitrous oxide (N₂O) in addition to CO₂ (4, 5). Thus, ecosystems have the potential for large additional climate mitigation by combining enhanced land sinks with reduced emissions.

Here we provide a comprehensive analysis of options to mitigate climate change by increasing carbon sequestration and reducing emissions of carbon and other greenhouse gases through conservation, restoration, and improved management practices in forest, wetland, and grassland biomes. This work updates and builds from work synthesized by IPCC Working Group III (WGIII) (6) for the greenhouse gas inventory sector referred to as agriculture, forestry, and other land use (AFOLU). We describe and quantify 20 discrete

Significance

Most nations recently agreed to hold global average temperature rise to well below 2 °C. We examine how much climate mitigation nature can contribute to this goal with a comprehensive analysis of “natural climate solutions” (NCS): 20 conservation, restoration, and/or improved land management actions that increase carbon storage and/or avoid greenhouse gas emissions across global forests, wetlands, grasslands, and agricultural lands. We show that NCS can provide over one-third of the cost-effective climate mitigation needed between now and 2030 to stabilize warming to below 2 °C. Alongside aggressive fossil fuel emissions reductions, NCS offer a powerful set of options for nations to deliver on the Paris Climate Agreement while improving soil productivity, cleaning our air and water, and maintaining biodiversity.

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Data deposition: A global spatial dataset of reforestation opportunities has been deposited on Zenodo (<https://zenodo.org/record/883444>).

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mitigation options (referred to hereafter as “pathways”) within the AFOLU sector. The pathways we report disaggregate eight options reported by the IPCC WGIII and fill gaps by including activities such as coastal wetland restoration and protection and avoided emissions from savanna fires. We also apply constraints to safeguard the production of food and fiber and habitat for biological diversity. We refer to these terrestrial conservation, restoration, and improved practices pathways, which include safeguards for food, fiber, and habitat, as “natural climate solutions” (NCS).

For each pathway, we estimate the maximum additional mitigation potential as a starting point for estimating mitigation potential at or below two price thresholds: 100 and 10 USD MgCO₂e⁻¹. The 100 USD level represents the maximum cost of emissions reductions to limit warming to below 2 °C (7), while 10 USD MgCO₂e⁻¹ approximates existing carbon prices (8). We aggregate mitigation opportunities at the 100 USD threshold to estimate the overall cost-effective contribution of NCS to limiting global warming to below 2 °C. For 10 of the most promising pathways, we provide global maps of mitigation potential. Most notably, we provide a global spatial dataset of reforestation opportunities (<https://zenodo.org/record/883444>) constrained by food security and biodiversity safeguards. We also review noncarbon ecosystem services associated with each pathway.

These findings are intended to help translate climate commitments into specific NCS actions that can be taken by government, private sector, and local stakeholders. We also conduct a comprehensive assessment of overall and pathway-specific uncertainty for our maximum estimates to expose the implications of variable data quality and to help prioritize research needs.

Results and Discussion

Maximum Mitigation Potential of NCS with Safeguards. We find that the maximum additional mitigation potential of all natural pathways is 23.8 PgCO₂e y⁻¹ (95% CI 20.3–37.4) at a 2030 reference year (Fig. 1 and *SI Appendix*, Table S1). This amount is not

constrained by costs, but it is constrained by a global land cover scenario with safeguards for meeting increasing human needs for food and fiber. We allow no reduction in existing cropland area, but we assume grazing lands in forested ecoregions can be reforested, consistent with agricultural intensification and diet change scenarios (9, 10). This maximum value is also constrained by excluding activities that would either negatively impact biodiversity (e.g., replacing native nonforest ecosystems with forests) (11) or have carbon benefits that are offset by net biophysical warming (e.g., albedo effects from expansion of boreal forests) (12). We avoid double-counting among pathways (*SI Appendix*, Table S2). We report uncertainty estimated empirically where possible (12 pathways) or from results of an expert elicitation (8 pathways). See Fig. 1 for synthesis of pathway results.

Our estimate of maximum potential NCS mitigation with safeguards is ≥30% higher than prior constrained and unconstrained maximum estimates (5, 9, 13–16). Our estimate is higher, despite our food, fiber, and biodiversity safeguards, because we include a larger number of natural pathways. Other estimates do not include all wetland pathways (5, 9, 13–16), agricultural pathways (13–16), or temperate and boreal ecosystems (13, 14). The next highest estimate (14) (18.3 PgCO₂ y⁻¹) was confined to tropical forests, but did not include a food production safeguard and was higher than our estimate for tropical forest elements of our pathways (12.6, 6.6–18.6 PgCO₂ y⁻¹). Similarly, our estimates for specific pathways are lower than other studies for biochar (17), conservation agriculture (15), and avoided coastal wetland impacts (18). We account for new research questioning the magnitude of potential for soil carbon sequestration through no-till agriculture (19) and grazing land management (20), among other refinements to pathways discussed below. Our estimate for avoided forest conversion falls between prior studies on deforestation emissions (21–24). Our spatially explicit estimate for reforestation was slightly higher compared with a prior nonspatially explicit estimate

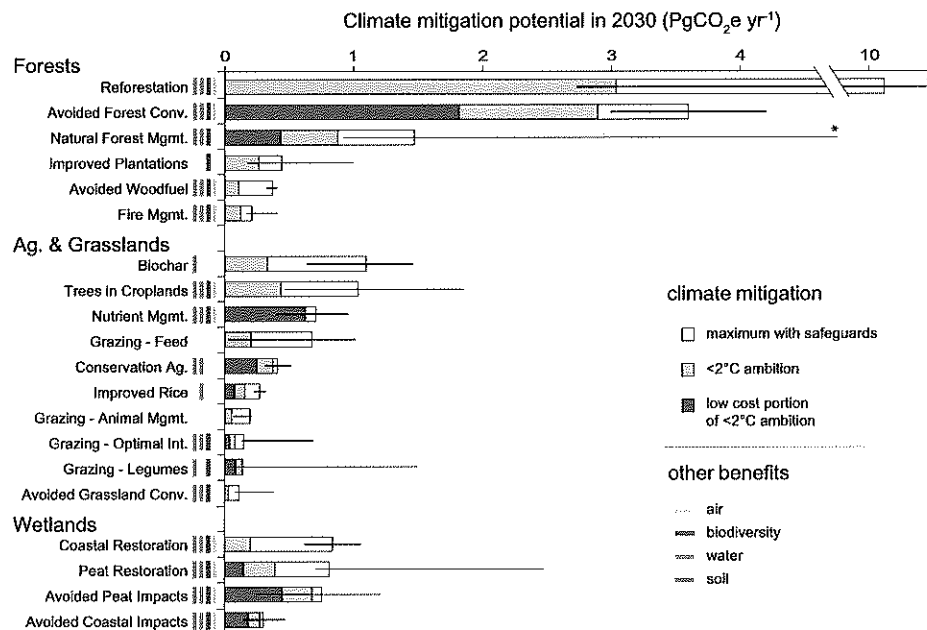


Fig. 1. Climate mitigation potential of 20 natural pathways. We estimate maximum climate mitigation potential with safeguards for reference year 2030. Light gray portions of bars represent cost-effective mitigation levels assuming a global ambition to hold warming to <2 °C (<100 USD MgCO₂e⁻¹ y⁻¹). Dark gray portions of bars indicate low cost (<10 USD MgCO₂e⁻¹ y⁻¹) portions of <2 °C levels. Wider error bars indicate empirical estimates of 95% confidence intervals, while narrower error bars indicate estimates derived from expert elicitation. Ecosystem service benefits linked with each pathway are indicated by colored bars for biodiversity, water (filtration and flood control), soil (enrichment), and air (filtration). Asterisks indicate truncated error bars. See *SI Appendix*, Tables S1, S2, S4, and S5 for detailed findings and sources.

(9). Natural pathway opportunities differ considerably among countries and regions (*SI Appendix*, Figs S1–S3 and Table S3).

Cost-Effective and Low-Cost NCS. We explore the proportion of maximum NCS mitigation potential that offers a cost-effective contribution to meeting the Paris Climate Agreement goal of limiting warming to below 2 °C. We define a <2 °C “cost-effective” level of mitigation as a marginal abatement cost not greater than ~100 USD MgCO₂⁻¹ as of 2030. This value is consistent with estimates for the avoided cost to society from holding warming to below 2 °C (7, 25). We find that about half (11.3 PgCO₂e y⁻¹) of the maximum NCS potential meets this cost-effective threshold. To estimate the portion of NCS that are cost effective for holding warming to below 2 °C, we estimated the fraction of the maximum potential of each natural pathway (high = 90%, medium = 60%, or low = 30%) that could be achieved without exceeding costs of ~100 USD MgCO₂⁻¹, informed by published marginal abatement cost curves. Our assignment of these indicative high, medium, and low cost-effective mitigation levels reflects the coarse resolution of knowledge on global marginal abatement costs for NCS. These default levels structured our collective judgment where cost curve data were incomplete (*SI Appendix*, Table S4). Using parallel methods, we find that more than one-third of the “<2 °C cost effective” levels for natural pathways are low cost (<10 USD MgCO₂⁻¹; 4.1 PgCO₂e y⁻¹; Fig. 1 and *SI Appendix*, Table S4).

The “low-cost” and cost-effective NCS carbon sequestration opportunities compare favorably with cost estimates for emerging technologies, most notably bioenergy with carbon capture and storage (BECCS)—which range from ~40 USD MgCO₂⁻¹ to over 1,000 USD MgCO₂⁻¹. Furthermore, large-scale BECCS is untested and likely to have significant impacts on water use, biodiversity, and other ecosystem services (2, 26).

Our 100 USD constrained estimate (11.3 PgCO₂e y⁻¹) is considerably higher than prior central estimates (6, 14, 27, 28), and it is somewhat higher than the upper-end estimate from the IPCC Fifth Assessment Report (AR5) (10.6 PgCO₂e y⁻¹). Aside from our inclusion of previously ignored pathways as discussed above, this aggregate difference belies larger individual pathway differences between our estimates and those reported in the IPCC AR5. We find a greater share of cost-constrained potential through reforestation, forestry, wetland protection, and trees in croplands than the IPCC AR5, despite our stronger constraints on land availability, biodiversity conservation, and biophysical suitability for forests (14, 29).

NCS Contribution to a <2 °C Pathway. To what extent can NCS contribute to carbon neutrality by helping achieve net emission targets during our transition to a decarbonized energy sector? Warming will likely be held to below 2 °C if natural pathways are implemented at cost-effective levels indicated in Fig. 1, and if we avoid increases in fossil fuel emissions for 10 y and then drive them down to 7% of current levels by 2050 and then to zero by 2095 (Fig. 2). This scenario (14) assumes a 10-y linear increase of NCS to the cost-effective mitigation levels, and a >66% likelihood of holding warming to below 2 °C following a model by Meinshausen et al. (30). Under this scenario, NCS provide 37% of the necessary CO₂e mitigation between now and 2030 and 20% between now and 2050. Thereafter, the proportion of total mitigation provided by NCS further declines as the proportion of necessary avoided fossil fuel emissions increases and as some NCS pathways saturate. Natural climate solutions are thus particularly important in the near term for our transition to a carbon neutral economy by the middle of this century. Given the magnitude of fossil fuel emissions reductions required under any <2 °C scenario, and the risk of relying heavily on negative emissions technologies (NETs) that remain decades from maturity (3), immediate action on NCS should not delay action on fossil fuel emissions reductions or investments in NETs.

Half of this cost-effective NCS mitigation is due to additional carbon sequestration of 5.6 PgCO₂e y⁻¹ by nine of the pathways,

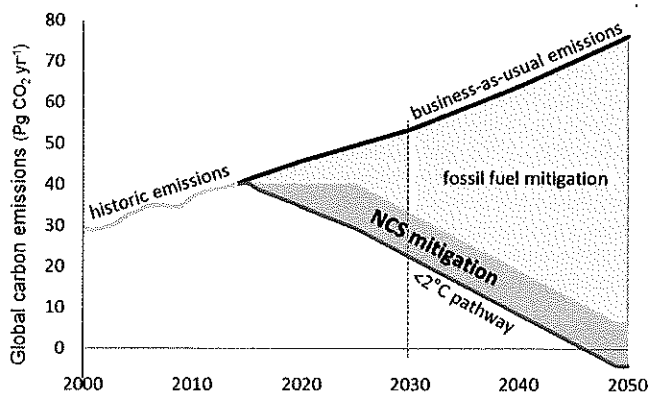


Fig. 2. Contribution of natural climate solutions (NCS) to stabilizing warming to below 2 °C. Historical anthropogenic CO₂ emissions before 2016 (gray line) prelude either business-as-usual (representative concentration pathway, scenario 8.5, black line) or a net emissions trajectory needed for >66% likelihood of holding global warming to below 2 °C (green line). The green area shows cost-effective NCS (aggregate of 20 pathways), offering 37% of needed mitigation through 2030, 29% at year 2030, 20% through 2050, and 9% through 2100. This scenario assumes that NCS are ramped up linearly over the next decade to <2 °C levels indicated in Fig. 1 and held at that level (=10.4 PgCO₂ y⁻¹, not including other greenhouse gases). It is assumed that fossil fuel emissions are held level over the next decade then decline linearly to reach 7% of current levels by 2050.

while the remainder is from pathways that avoid further emissions of CO₂, CH₄, and N₂O (*SI Appendix*, Fig. S4 and Table S1). Aggregate sequestration levels begin to taper off around 2060, although most pathways can maintain the 2030 mitigation levels we report for more than 50 years (Fig. 2 and pathway-specific saturation periods in *SI Appendix*, Table S1). The NCS scenario illustrated in Fig. 2 will require substantial near-term ratcheting up of both fossil fuel and NCS mitigation targets by countries to achieve the Paris Climate Agreement goal to hold warming to below 2 °C. Countries provided nationally determined contributions (NDCs) with 2025 or 2030 emissions targets as a part of the Paris Climate Agreement. While most NDCs indicate inclusion of land sector mitigation, only 38 specify land sector mitigation contributions, of 160 NDCs assessed (31). Despite these limitations, analyses indicate that if NDCs were fully implemented, NCS would contribute about 20% of climate mitigation (31) and about 2 PgCO₂e y⁻¹ mitigation by 2030 (31, 32). As such, a small portion of the 11.3 PgCO₂e y⁻¹ NCS opportunity we report here has been included in existing NDCs. Across all sectors, the NDCs fall short by 11–14 PgCO₂e y⁻¹ of mitigation needed to keep 2030 emissions in line with cost-optimal 2 °C scenarios (33). Hence, NCS could contribute a large portion—about 9 PgCO₂e y⁻¹—of the increased ambition needed by NDCs to achieve the Paris Climate Agreement.

Our assessment of the potential contribution of NCS to meeting the Paris Agreement is conservative in three ways. First, payments for ecosystem services other than carbon sequestration are not considered here and could spur cost-effective implementation of NCS beyond the levels we identified. Natural climate solutions enhance biodiversity habitat, water filtration, flood control, air filtration, and soil quality (Fig. 1) among other services, some of which have high monetary values (34–36) (see *SI Appendix*, Table S5 for details). Improved human health from dietary shifts toward plant-based foods reduce healthcare expenses and further offset NCS costs (37).

Second, our findings are conservative because we only include activities and greenhouse gas fluxes where data were sufficiently robust for global extrapolation. For example, we exclude no-till agriculture (Conservation Agriculture pathway), we exclude improved manure management in concentrated animal feed operations (Nutrient Management pathway), we exclude adaptive multipaddock grazing (Grazing pathways), and we exclude soil

carbon emissions that may occur with conversion of forests to pasture (Avoided Forest Conversion pathway). Future research may reveal a robust empirical basis for including such activities and fluxes within these pathways.

Third, the Paris Agreement states goals of limiting warming to “well below 2 °C” and pursuing “efforts to limit the temperature increase to 1.5 °C.” Our analysis specifies a >66% chance of holding warming to just below 2 °C (30). Additional investment in all mitigation efforts (i.e., beyond ~100 USD MgCO₂⁻¹), including NCS, would be warranted to keep warming to well below 2 °C, or to 1.5 °C, particularly if a very likely (90%) chance of success is desired.

Specific Pathway Contributions. Forest pathways offer over two-thirds of cost-effective NCS mitigation needed to hold warming to below 2 °C and about half of low-cost mitigation opportunities (*SI Appendix*, Table S4). Reforestation is the largest natural pathway and deserves more attention to identify low-cost mitigation opportunities. Reforestation may involve trade-offs with alternative land uses, can incur high costs of establishment, and is more expensive than Avoided Forest Conversion (38). However, this conclusion from available marginal abatement cost curves ignores opportunities to reduce costs, such as involving the private sector in reforestation activities by establishing plantations for an initial commercial harvest to facilitate natural and assisted forest regeneration (39). The high uncertainty of maximum reforestation mitigation potential with safeguards (95% CI 2.7–17.9 PgCO₂e y⁻¹) is due to the large range in existing constrained estimates of potential reforestation extent (345–1,779 Mha) (14, 16, 40–42). As with most forest pathways, reforestation has well-demonstrated cobenefits, including biodiversity habitat, air filtration, water filtration, flood control, and enhanced soil fertility (34). See *SI Appendix*, Table S5 for detailed review of ecosystem services across all pathways.

Our maximum reforestation mitigation potential estimate is somewhat sensitive to our assumption that all grazing land in forested ecoregions is reforested. If we assume that 25%, 50%, or 75% of forest ecoregion grazing lands were not reforested, it would result in 10%, 21%, and 31% reductions, respectively, in our estimate of reforestation maximum mitigation potential. While 42% of reforestation opportunities we identify are located on lands now used for grazing within forest ecoregions, at our <2 °C ambition mitigation level this would displace only ~4% of global grazing lands, many of which do not occur in forested ecoregions (20). Grazing lands can be released by shifting diets and/or implementing Grazing-Feed and Grazing-Animal Management pathways, which reduce the demand for grazing lands without reducing meat and milk supply (43).

Avoided Forest Conversion offers the second largest maximum and cost-effective mitigation potential. However, implementation costs may be secondary to public policy challenges in frontier landscapes lacking clear land tenure. The relative success of Brazil’s efforts to slow deforestation through a strong regulatory framework, accurate and transparent federal monitoring, and supply chain interventions provides a promising model (44), despite recent setbacks (45). We find relatively low uncertainty for Avoided Forest Conversion (±17%), reflecting considerable global forest monitoring research in the last decade stimulated by interest in reducing emissions from deforestation and forest degradation (REDD) (46).

Improved forest management (i.e., Natural Forest Management and Improved Plantations pathways) offers large and cost-effective mitigation opportunities, many of which could be implemented rapidly without changes in land use or tenure. While some activities can be implemented without reducing wood yield (e.g., reduced-impact logging), other activities (e.g., extended harvest cycles) would result in reduced near-term yields. This shortfall can be met by implementing the Reforestation pathway, which includes new commercial plantations. The Improved Plantations pathway

ultimately increases wood yields by extending rotation lengths from the optimum for economic profits to the optimum for wood yield.

Grassland and agriculture pathways offer one-fifth of the total NCS mitigation needed to hold warming below 2 °C, while maintaining or increasing food production and soil fertility. Collectively, the grassland and agriculture pathways offer one-quarter of low-cost NCS mitigation opportunities. Cropland Nutrient Management is the largest cost-effective agricultural pathway, followed by Trees in Croplands and Conservation Agriculture. Nutrient Management and Trees in Croplands also improve air quality, water quality, and provide habitat for biodiversity (*SI Appendix*, Table S5). Our analysis of nutrient management improves upon that presented by the IPCC AR5 in that we use more recent data for fertilizer use and we project future use of fertilizers under both a “business as usual” and a “best management practice” scenario. Future remote sensing analyses to improve detection of low-density trees in croplands (47) will constrain our uncertainty about the extent of this climate mitigation opportunity. The addition of biochar to soil offers the largest maximum mitigation potential among agricultural pathways, but unlike most other NCS options, it has not been well demonstrated beyond research settings. Hence trade-offs, cost, and feasibility of large scale implementation of biochar are poorly understood. From the livestock sector, two improved grazing pathways (Optimal Intensity and Legumes) increase soil carbon, while two others (Improved Feed and Animal Management) reduce methane emission.

Wetland pathways offer 14% of NCS mitigation opportunities needed to hold warming to <2 °C, and 19% of low-cost NCS mitigation. Wetlands are less extensive than forests and grasslands, yet per unit area they hold the highest carbon stocks and the highest delivery of hydrologic ecosystem services, including climate resilience (47). Avoiding the loss of wetlands—an urgent concern in developing countries—tends to be less expensive than wetland restoration (49). Improved mapping of global wetlands—particularly peatlands—is a priority for both reducing our reported uncertainty and for their conservation and restoration.

Challenges. Despite the large potential of NCS, land-based sequestration efforts receive only about 2.5% of climate mitigation dollars (50). Reasons may include not only uncertainties about the potential and cost of NCS that we discuss above, but also concerns about the permanence of natural carbon storage and social and political barriers to implementation. A major concern is the potential for Reforestation, Avoided Forest Conversion, and Wetland/Peatland pathways to compete with the need to increase food production. Reforestation and Avoided Forest Conversion remain the largest mitigation opportunities despite avoiding reforestation of mapped croplands and constraints we placed on avoiding forest conversion driven by subsistence agriculture (*SI Appendix*, Table S1). A large portion (42%) of our maximum reforestation mitigation potential depends on reduced need for pasture accomplished via increased efficiency of beef production and/or dietary shifts to reduce beef consumption. On the other hand, only a ~4% reduction in global grazing lands is needed to achieve <2 °C ambition reforestation mitigation levels, and reduced beef consumption can have large health benefits (51). A portion of wetland pathways would involve limited displacement of food production; however, the extremely high carbon density of wetlands and the valuable ecosystem services they provide suggest that protecting them offers a net societal benefit (52).

Feedbacks from climate change on terrestrial carbon stocks are uncertain. Increases in temperature, drought, fire, and pest outbreaks could negatively impact photosynthesis and carbon storage, while CO₂ fertilization has positive effects (53). Unchecked climate change could reverse terrestrial carbon sinks by midcentury and erode the long-term climate benefits of NCS (54). Thus, climate change puts terrestrial carbon stocks (2.3 exagrams) (55) at risk. Cost-effective implementation of NCS, by increasing terrestrial carbon stocks, would slightly increase (by 4%) the stocks at risk by

2050. However, the risk of net emissions from terrestrial carbon stocks is less likely under a <2 °C scenario. As such, NCS slightly increase the total risk exposure, yet will be a large component of any successful effort to mitigate climate change and thus help mitigate this risk. Further, most natural pathways can increase resilience to climate impacts. Rewetting wetlands reduces risk of peat fires (56). Reforestation that connects fragmented forests reduces exposure to forest edge disturbances (57). Fire management increases resilience to catastrophic fire (58). On the other hand, some of our pathways assume intensification of food and wood yields—and some conventional forms of intensification can reduce resilience to climate change (59). All of these challenges underscore the urgency of aggressive, simultaneous implementation of mitigation from both NCS and fossil fuel emissions reductions, as well as the importance of implementing NCS and land use intensification in locally appropriate ways with best practices that maximize resilience.

While the extent of changes needed in global land stewardship is large (*SI Appendix*, Tables S1 and S4), we find that the environmental ambition reflected in eight recent multilateral announcements is well aligned with our <2 °C NCS mitigation levels. However, only four of these announcements are specific enough for quantitative comparison: The New York Declaration on Forests, the Bonn Challenge, the World Business Council on Sustainable Development Vision 2050, and the “4 pour 1000” initiative (*SI Appendix*, Table S6). The first three of these have quantitative targets that are somewhat more ambitious than our <2 °C mitigation levels for some pathways, while the 4 pour 1000 initiative is considerably more ambitious for soil carbon storage. More explicit and comprehensive policy targets for all biomes and natural pathways are needed to clarify the role of NCS in holding warming to below 2 °C.

Next Steps. Considerable scientific work remains to refine and reduce the uncertainty of NCS mitigation estimates. Work also remains to refine methods for implementing pathways in socially and culturally responsible ways while enhancing resilience and improving food security for a growing human population (60). Nevertheless, our existing knowledge reported here provides a solid basis for immediately prioritizing NCS as a cost-effective way to provide $11 \text{ PgCO}_2\text{e y}^{-1}$ of climate mitigation within the next decade—a terrestrial ecosystem opportunity not fully recognized by prior roadmaps for decarbonization (15, 61). Delaying implementation of the 20 natural pathways presented here would increase the costs to society for both mitigation and adaptation, while degrading the capacity of natural systems to mitigate climate change and provide other ecosystem services (62). Regreening the planet through conservation, restoration, and improved land management is a necessary step for our transition to a carbon neutral global economy and a stable climate.

Methods

Estimating Maximum Mitigation Potential with Safeguards. We estimate the maximum additional annual mitigation potential above a business-as-usual baseline at a 2030 reference year, with constraints for food, fiber, and biodiversity safeguards (*SI Appendix*, Tables S1 and S2). For food, we allow no reduction in existing cropland area, but do allow the potential to reforest all grazing lands in forested ecoregions, consistent with agricultural intensification scenarios (9) and potential for dietary changes in meat consumption (10). For fiber, we assume that any reduced timber production associated with implementing our Natural Forest Management pathway is made up by additional wood production associated with Improved Plantations and/or Reforestation pathways. We also avoid activities within pathways that would negatively impact biodiversity, such as establishing forests where they are not the native cover type (11).

For most pathways, we generated estimates of the maximum mitigation potential (M_x) informed by a review of publications on the potential extent (A_x) and intensity of flux (F_x), where $M_x = A_x \times F_x$. Our estimates for the reforestation pathway involved geospatial analyses. For most pathways the applicable extent was measured in terms of area (hectares); however, for five of the pathways (Biochar, Cropland Nutrient Management, Grazing—Improved Feed, Grazing—Animal Management, and Avoided Woodfuel Harvest) other units of extent were used (*SI Appendix*, Table S1). For five pathways (Avoided Woodfuel

Harvest; Grazing—Optimal Intensity, Legumes, and Feed; and Conservation Agriculture) estimates were derived directly from an existing published estimate. An overview of pathway definitions, pathway-specific methods, and adjustments made to avoid double counting are provided in *SI Appendix*, Table S2. See *SI Appendix*, pp 36–79 for methods details.

Uncertainty Estimates. We estimated uncertainty for maximum mitigation estimates of each pathway using methods consistent with IPCC good practice guidance (63) for the 12 pathways where empirical uncertainty estimation was possible. For the remaining eight pathways (indicated in Fig. 1), we used the Delphi method of expert elicitation (64) following best practices outline by Mach et al. (65) where applicable and feasible. The Delphi method involved two rounds of explicit questions about expert opinion on the potential extent (A_x) and intensity of flux (F_x) posed to 20 pathway experts, half of whom were not coauthors (see *SI Appendix*, pp 38–39 for names). We combined A_x and F_x uncertainties using IPCC Approach 2 (Monte Carlo simulation),

Assigning Cost-Constrained Mitigation Levels. We assumed that a maximum marginal cost of ~ 100 US dollars $\text{MgCO}_2\text{e}^{-1} \text{y}^{-1}$ in 2030 would be required across all mitigation options (including fossil fuel emissions reductions and NCS) to hold warming to below 2 °C (7). This assumption is consistent with the values used in other modeling studies (16, 66) and was informed by a social cost of carbon in 2030 estimated to be 82–260 USD $\text{MgCO}_2\text{e}^{-1}$ to meet the 1.5–2 °C climate target (7).

To calibrate individual NCS pathways with a goal of holding warming to below 2 °C, we assessed which of three default mitigation levels—30%, 60%, or 90% of maximum—captures mitigation costs up to but not more than ~ 100 USD $\text{MgCO}_2\text{e}^{-1}$, informed by marginal abatement cost (MAC) curve literature. Our assignment of these default levels reflects that the MAC literature does not yet enable a precise understanding of the complex and geographically variable range of costs and benefits associated with our 20 natural pathways. We also assessed the proportion of NCS mitigation that could be achieved at low cost. For this we used a marginal cost threshold of ~ 10 USD $\text{MgCO}_2\text{e}^{-1}$, which is consistent with the current cost of emission reduction efforts underway and current prices on existing carbon markets. For references and details see *SI Appendix*.

Projecting NCS Contribution to Climate Mitigation. We projected the potential contributions of NCS to overall CO_2e mitigation action needed for a “likely” (greater than 66%) chance of holding warming to below 2 °C between 2016 and 2100. We compared this NCS scenario to a baseline scenario in which NCS are not implemented. In our NCS scenario, we assumed a linear ramp-up period between 2016 and 2025 to our <2 °C ambition mitigation levels reported in *SI Appendix*, Table S4. During this period, we assumed fossil fuel emissions were also held constant, after which they would decline. We assumed a maintenance of <2 °C ambition NCS mitigation levels through 2060, allowing for gradual pathway saturation represented as a linear decline of natural pathway mitigation from 2060 to 2090. We consider this a conservative assumption about overall NCS saturation, given the time periods we estimate before saturation reported in *SI Appendix*, Table S1. This scenario and the associated action on fossil fuel emissions reductions needed are represented in Fig. 2 through 2050. Scenario construction builds from ref. 14, with model parameters from Meinshausen et al. (30). The proportion of CO_2 mitigation provided by NCS according to the scenario described above is adjusted to a proportion of CO_2e with the assumption that non- CO_2 greenhouse gases are reduced at the same rate as CO_2 for NCS and other sectors.

Characterizing Activities and Cobenefits. We identified mitigation activities and noncarbon ecosystem services associated with each of the 20 natural pathways (*SI Appendix*, Tables S5 and S7). We used a taxonomy of conservation actions developed by the International Union for Conservation of Nature (IUCN) and the Conservation Measures Partnership (67) to link pathways with a known set of conservation activities. The IUCN taxonomy does not identify activities that are specific to many of our pathways, so we list examples of more specific activities associated with each pathway (*SI Appendix*, Table S7). We identify four generalized types of ecosystem services (biodiversity, water, soil, and air) that may be enhanced by implementation of activities within each natural pathway—but only where one or more peer-reviewed publication confirms the link (Fig. 1 and *SI Appendix*, Table S5).

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