



Restoration plantations accelerate dead wood accumulation in tropical premontane forests

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ABSTRACT

Dead wood stores 10–20% of global forest carbon stocks, but its recovery and restoration in secondary tropical forests are poorly documented. In this study, we evaluated (1) the recovery pattern of dead wood volumes across a chronosequence of secondary tropical forests that used to be former coffee plantations, and (2) the efficiency of two common restoration strategies to recover dead wood volumes similar to those found in old-growth forests, all in a tropical premontane landscape in southern Costa Rica. Restoration strategies consisted of plantations and natural regeneration. Plantations consist of plots where two endemic (*Terminalia amazonia* and *Vochysia guatemalensis*) and two naturalized (*Inga edulis* and *Erythrina poeppigiana*) species were planted in rows. Natural regeneration consists of plots where no trees were planted, but where agriculture or cattle are excluded through fencing and vegetation is allowed to regenerate naturally. We hypothesized that (1) dead wood volumes increase with forest age following a logistic shape, and that (2) restoration plantations recover dead wood volumes more quickly compared to naturally regenerated forests. We measured dead wood volumes in a total of 35 forest fragments that were former coffee plantations or are currently old-growth forests and 10 restoration plots containing either natural regeneration or restoration plantations that were former fallow or pasture using strip transects. Dead wood volumes significantly increased with forest age following a logistic shape, starting with very low values in early ages (3–5 years), increasing rapidly (6–50 years), and ending with high and relatively stable values after 50 years of age. In addition, plantations (16 to 17 years old) recovered 41% of dead wood volumes found in old-growth forests > 100 years old, whereas naturally regenerated forests of the same age only recovered 1.7% of dead wood volumes found in old-growth forests. Our study shows that restoration plantations not only accelerate the recovery of above ground biomass, but also accelerate the recovery of dead wood in premontane Neotropical ecosystems. This indicates that tree planting positively affects carbon storage, and potentially the preservation of dead wood-associated biodiversity.

1. Introduction

Dead wood represents 10–20% of carbon stocks in the world but it is one of the least understood carbon pools (Cornwell et al., 2009; Pan et al., 2011). While carbon budget studies seldom take dead biomass into account, anthropogenic activities such as timber harvesting significantly reduce carbon storage in dead wood (Harmon et al., 1990). Improving the accuracy of carbon budgets and climate change models requires the inclusion of all carbon sinks and sources into the calculations, yet dead wood is understudied in many parts of the globe. Through 2011, most dead wood data came from European and North American forests, with

one study from each of Africa, and Central and South America (Pan et al., 2011).

The amount of dead wood that accumulates on the forest floor will be a balance between input of dying trees and tree parts, and output as a result of woody decay. Deforestation and anthropogenic disturbances can decrease the amount of dead wood in forests by up to 50% (Harmon et al., 1990), and by up to 98% in boreal forests (Siitonen, 2001), and it is likely that the reduction in this portion of the carbon pool is increasing in the Neotropics, where deforestation rates are accelerating (Zepetello et al., 2020). Importantly, much time may be required for the dead wood pool to be re-established. The one study to our knowledge that assessed

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dead wood accumulation over time in tropical ecosystems found that 70 years are needed for dead wood volumes to reach those found in old-growth forests (DeWalt et al., 2003; Poorter et al., 2021). Forest restoration could be a good strategy to accelerate the recovery of dead wood after anthropogenic disturbance.

Forest restoration seeks to facilitate the recovery of ecosystems that have been damaged or destroyed (Gann et al., 2019). Two main strategies, active and passive restoration, are used across the world to restore forests. Natural regeneration is a viable and low cost option in many places because it involves minimum to no human intervention (Chazdon, 2017; Gann et al., 2019). However active revegetation is often preferable when sites have been heavily disturbed or when the goal is to speed up the regeneration process and the accumulation of biomass (Holl and Aide, 2011; Holl and Zahawi, 2014). While these two strategies are often compared and contrasted, they represent a spectrum of intervention intensity, with the specific strategy dependent on site history, landscape context, restoration goals, and resources available for active intervention (Chazdon et al., 2021). Knowing accurately whether active or passive restoration is more efficient at recovering dead wood carbon pools requires the evaluation of dead wood dynamics within paired plots on the same site (Reid et al., 2018).

In this study we (1) documented the accumulation patterns of dead wood through time following anthropogenic disturbance in a Neotropical forest setting, and (2) experimentally assessed the relative effectiveness of two common restoration strategies to re-establish dead wood amounts as they are found in old-growth forests. In meeting these objectives, we first tested the hypothesis that dead wood amounts increase through time following a logistic shape at our study site in Southern Costa Rica: soon after anthropogenic disturbance there is little to no dead wood due to primary or secondary forest logging and subsequent harvesting. As pioneer trees start colonizing the site they contribute to the dead wood pool with branchfall and eventually with their own deaths. As the forest reaches an old-growth state, there is a mix of short-lived pioneer trees and long-lived trees that continuously contribute large amounts of dead wood on the forest floor due to their larger size (Guariguata and Ostertag, 2001). This should result in a dead wood accumulation pattern with a logistic shape. Second, we hypothesized that active restoration recovers dead wood faster than passive restoration. This is because one study from our study system with paired active and passive restoration has shown that above ground biomass is higher in restoration plantations than in natural regeneration (Holl and Zahawi, 2014). To test our hypotheses, we evaluated dead wood volumes along a chronosequence of secondary forest fragments that were former coffee plantations and old-growth forests and inside replicated pairs of active and passive restoration that were fallow or pasture at the outset or restoration site establishment.

2. Methods

2.1. Study area

Restoration sites and chronosequence fragments were located in a tropical premontane rainforest zone as defined by Holdridge (1967). Restoration sites were located near the town of Agua Buena (8° 44' 36"N, 82° 58' 04"W) and the Las Cruces Biological Station (8° 47' 7"N, 82° 57' 32"W) in the Costa Rican county of Coto Brus. Elevation of our study sites ranges from 906 to 1363 m.a.s.l. Mean annual rainfall is 3500 mm with a dry season from December to March and mean annual temperature is 21 °C (Holl et al. 2011). Soils are volcanic, mildly acidic, low in phosphorus, and high in organic matter (Holl and Zahawi 2014). The landscape consists of a mosaic of forest fragments, agricultural land and pastureland (Zahawi et al. 2015).

2.2. Chronosequence fragments

To build a chronosequence of dead wood volumes across time, we

evaluated dead wood volumes inside 35 forest fragments across the study area. The fragments ranged in age from three to over 100 years (Table A.1; Fig. 1). Fragment age was estimated through oral communication with the owners. Prior land use on all chronosequence sites was former coffee plantation. The five old-growth forests near our restoration sites were added to this dataset to increase the number of old-growth forest fragments in the chronosequence from six to 11 old-growth forests (Table A.1). We considered as old-growth any forest for which the age of the forest estimated by the land owner was ≥ 100 years. Given that European settlement in this region began in the late 1940 s, forests classified as older than 100 years are likely to have never been cleared by Europeans and some could be several hundred or more years old (Zahawi et al., 2015).

2.3. Restoration sites

We evaluated dead wood volumes in five restoration sites. Each restoration site contains two treatments. Each restoration treatment consists of a 50 m $\times$ 50 m plot containing either a plantation or natural regeneration (Holl et al., 2011). At the time of the study, all restoration treatments were 16–17 years old. Each restoration site is located near to 50 m $\times$ 50 m plots that were established inside old-growth forests that are over 100 years old (Fig. 2a). These old-growth forests represent the reference ecosystem. The maximum distance between restoration treatments and old-growth forests was 0.3 km.

Plantations (Fig. 2b) consisted of four species of trees planted uniformly: *Erythrina poeppigiana* (Fabaceae), *Terminalia amazonia* (Combretaceae), *Vochysia guatemalensis* (Vochysiaceae), and *Inga edulis* (Fabaceae) (Holl et al., 2011). These species were chosen for planting because they are known for having high survival, good canopy development in the first few years after planting, were readily available in nurseries in the area, and are widely used in agroforestry in Central America (Holl et al., 2011). Both natural regeneration and plantations were hand cleared with machetes several times per year for the first two years of the study to control ruderal vegetation and both had fences established around them in order to remove cattle (Holl et al., 2011). Restoration sites were not harvested nor trimmed or weeded after this. The last land use before the establishment of both restoration treatments was either fallow or pasture (Holl et al., 2020). Planting density in plantations was 1252 trees hectare⁻¹ (Holl and Zahawi, 2014). Distance between trees was 4.0 m. In natural regeneration (Fig. 2c), no trees were planted. Before site establishment, all leftover live and dead trees as well as leftover dead wood were removed from both plantation and natural regeneration plots. At the time of dead wood assessment, plantation trees were on average 15 m tall and 18 cm in DBH with a canopy cover of 88%. Trees in natural regeneration were approximately 7 m tall and had an average DBH of 16 cm. Canopy cover was 20% (Holl, Zahawi, and Werden, unpublished data). We used a total of five plantations, five natural regeneration plots, and five old-growth forests (total = 15 plots).

2.4. Coarse woody debris volume survey

To quantify dead wood volumes in each of the chronosequence fragments and in each restoration plot we first established four parallel 1 m $\times$ 40 m strip transects separated by 10 m in each location. The transects were always at least 5 m inside the edge of the fragment. We chose the location of the transects haphazardly. Two old-growth forest fragments had extremely steep slopes, and in those fragments we used a section of the fragment where it was easier to transit. We then measured the diameter and length of all dead wood pieces ≥ 10 cm in diameter occurring within each transect. These dead wood pieces are hereafter referred to as coarse woody debris, abbreviated as CWD (Harmon et al., 1986; Spies et al., 1988). These measurements allowed us to calculate the volume of each piece of CWD using the formula of a cylinder [$\pi \times (\text{diameter}/2)^2 \times \text{length}$]. We measured CWD diameter as the length between two thin aluminum poles planted on both sides of each log and

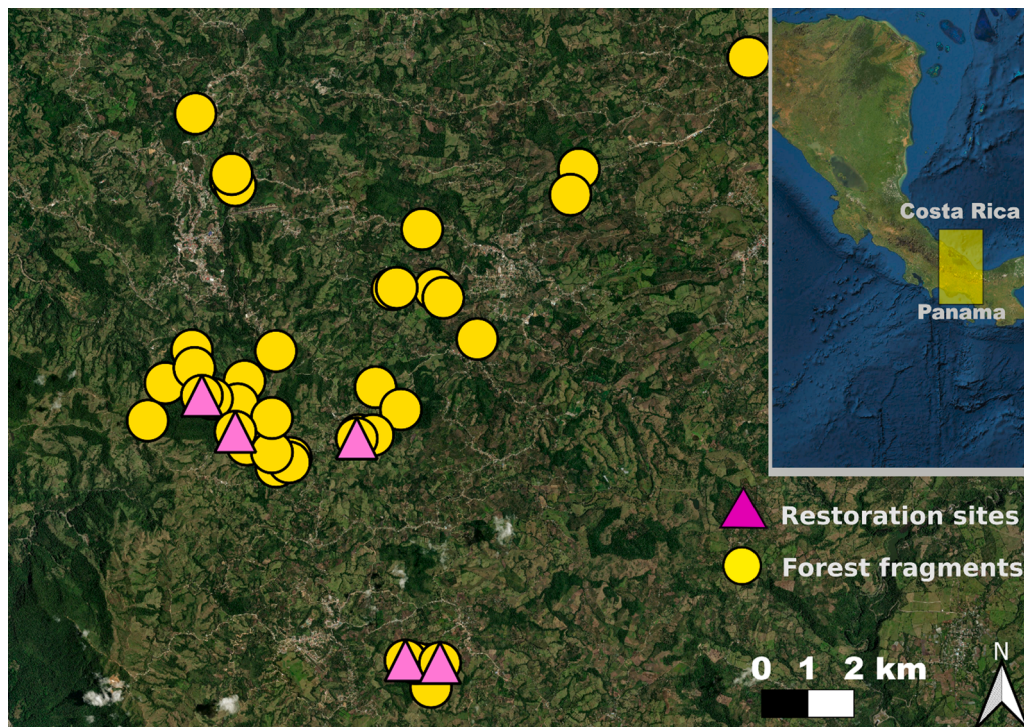


Fig. 1. Forest fragments used for building a chronosequence of coarse woody debris volumes. Coarse woody debris volumes in forest fragments (yellow dots) were compared to volumes found in restoration sites (pink triangles). QGIS Development Team, 2009. QGIS Geographic Information System. Open Source Geospatial Foundation. URL <http://qgis.org>.



Fig. 2. Restoration sites in Southern Costa Rica. Coarse woody debris volumes were measured in: (A) old-growth forests, the reference ecosystem, and two restoration treatments, (B) plantations and (C) natural regeneration. Old-growth forests are ≥ 100 years old. Plantations and natural regeneration were 16–17 years old at the time of the study. Photo credit: Juan Abel Rosales and Estefania Fernandez.

perpendicular to the forest floor. If logs had a conical shape, we measured the diameters at each end of the log and then calculated a mean diameter. For log length, we measured only the portion of the log that was contained within the transect.

2.5. Statistical analyses

2.5.1. Coarse woody debris over the chronosequence

To elucidate the pattern of coarse woody debris volumes through time we used a normal linear mixed model (function “lmer”, package “lme4”). We modelled total CWD volume per transect as a function of age using fragment ownership as a random blocking factor (CWD

volume = continuous dependent variable; age = continuous independent variable; fragment identity = categorical random blocking factor). The residual distribution of coarse woody debris volume per transect was not normal and slightly heteroscedastic, so we transformed these data as $\ln(x + 0.003)$. Diagnostic plots from the generalized linear model and a Breusch-Pagan test ($BP = 0.12, p \geq 0.05$) showed that the residual distribution of CWD volumes was homoscedastic and normal after transformation. To test for possible spatial autocorrelation among fragments from the same owner we performed a Moran's I and a Mantel test. Both of these tests showed that there was no significant spatial autocorrelation (Moran's I = 0.05, $p = 0.2$; Mantel's $r = 0.07, p = 0.15$). To assess the effect of age on CWD volumes in fragments from the chronosequence, we compared our full model to a null model that did not contain "age" as an independent variable using the "anova" function in R. All analyses were performed on the R software (R Core Team, 2021) and the packages "lme4" (Bates et al., 2015), "lmerTest" (Zeileis and Hothorn, 2002), "vegan" (Oksanen et al., 2020), and "multcomp" (Hothorn et al., 2008).

To learn how CWD volumes in plantations and natural regeneration compared to CWD volumes from fragments of different ages in the chronosequence, we calculated the 95% confidence intervals of CWD volumes from plantations, natural regeneration, and nearby old-growth forests ($n = 5$) and compared these confidence intervals to the 95% confidence intervals of CWD volumes from forest fragments from the chronosequence. Confidence intervals from the restoration sites were calculated using the function "CI" and the package "Rmisc" in R (Hope, 2013).

2.5.2. Coarse woody debris among restoration treatments

To assess how coarse woody debris volumes differ among plantations, natural regeneration, and old-growth forests, we compared CWD volumes from the restoration treatments to CWD volumes from the five nearby old-growth forests. We used Analysis of Variance to evaluate CWD volume as a function of restoration treatment. Our data were highly heteroscedastic and not normal even after transformation when using CWD volumes per transect. This was due to an overabundance of zeroes in the natural regeneration treatment where CWD was seldom found. However, the data were homoscedastic and normal after calculating the average CWD volumes per transect in each plot and transforming these values as $\ln(x + 0.003)$; (Breusch-Pagan test, $BP = 0.46, p \geq 0.05$; Shapiro-Wilk test; $W = 0.95, p \geq 0.05$). Therefore, we decided to use mean CWD volume per transect per plot even though this reduced our sample size from $n = 20$ to $n = 5$ per treatment. The variable "site" did not have a significant effect on CWD volumes ($F = 0.53, p > 0.05$), therefore we ran our analysis of variance without using "site" as a random blocking factor. Mean CWD volume per transect per plot was our dependent variable and restoration treatment (plantation, natural regeneration, or old-growth forest) was our independent variable. To compare volumes of CWD among restoration treatments and nearby old-growth forests we performed a multiple comparison test using Tukey tests.

3. Results

3.1. Coarse woody debris over the chronosequence

Coarse woody debris volumes were low to nonexistent in very young forests (5–10 years old), intermediate in middle-aged forest fragments (10–45 years old), and high in fragments 50 years or older (Fig. 3). CWD increased over time following a logistic shape. CWD volumes increased significantly with increasing forest age ($\chi^2 = 20.13; p < 0.001$). CWD accumulation rate between zero and 50 years old was $0.53 \text{ m}^3 \text{ hectare}^{-1} \text{ year}^{-1}$. CWD accumulation rate between 50 to 100 years old was $0.14 \text{ m}^3 \text{ hectare}^{-1} \text{ year}^{-1}$. While CWD volumes were on average highest in old-growth forests, there was a large range of CWD volumes in old-growth forests: some transects had no CWD whereas some transects

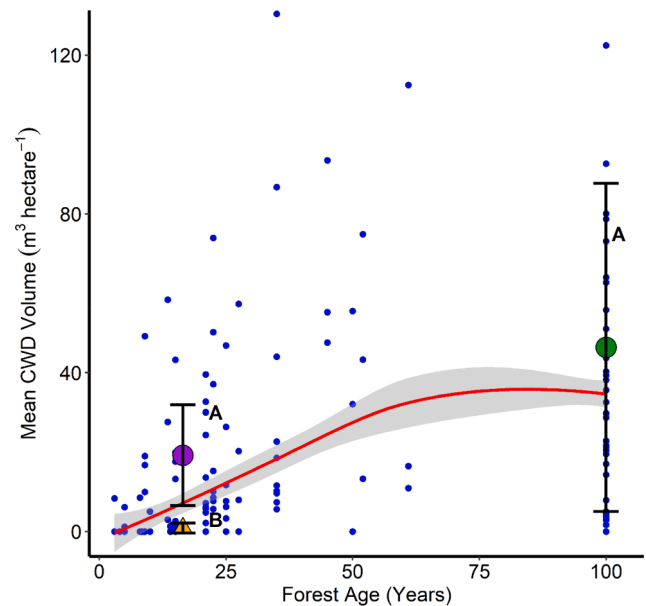


Fig. 3. Coarse woody debris volumes (m^3) as function of forest age in a chronosequence of secondary forests in southern Costa Rica. Blue dots represent the raw data (i.e. CWD volumes per hectare). The red line represents the predicted values from the generalized linear model plotted using a LOWESS smoothing function. Eight outliers that were included for the analysis where CWD volume per transect was $\geq 125 \text{ m}^3 \text{ ha}^{-1}$ were removed for better visualization. CWD volumes in plantations (purple dot), natural regeneration (yellow triangle) and five nearby old-growth forests (green dot) are also represented. Mean CWD volumes per hectare for each restoration plot ($n = 5$) and corresponding 95% confidence intervals are shown.

had up to $758 \text{ m}^3 \text{ hectare}^{-1}$ of CWD (Fig. 3).

3.2. Coarse woody debris among restoration treatments

Restoration plantations recovered $41.4\% (\pm 9.9\% \text{ SE})$ of the CWD volumes found in nearby old-growth forests, whereas natural regeneration recovered $1.7\% (\pm 0.9\% \text{ SE})$ of the CWD volumes found in their paired nearby old-growth forests (Fig. 3). This supports our second hypothesis that active restoration recovers dead wood faster compared to passive restoration. CWD volumes significantly differed among restoration treatments [$(F_{(2,12)} = 33.08, p \leq 0.01)$] (Fig. 3). Multiple comparisons showed that CWD volumes in old-growth forests were 63 times higher than CWD volumes found in natural regeneration ($p \leq 0.001$). In contrast, CWD volumes found in old-growth forests were not significantly different than volumes found in plantations ($p = 0.16$). Coarse woody debris volumes in plantations were significantly higher than CWD volumes found in natural regeneration ($p \leq 0.001$).

In terms of coarse woody debris volumes, plantations, which are chronologically 16–17 years old, are 36 years old (95% CI [11.6, 91.6]) on average in terms of CWD accumulation, whereas natural regeneration are four years old (95% CI [3.3, 9]) in terms of CWD accumulation. (Fig. 3).

4. Discussion

Our goals were to unveil the pattern of coarse woody debris accumulation through time in a premontane tropical forest landscape and to understand the efficiency of restoration treatments at recovering coarse woody debris amounts as found in reference old-growth forests. To our knowledge, our study is the first empirical example of CWD evaluation within paired passive and active restoration. Together, our results demonstrate that CWD recovers following a logistic shape through time and that restoration plantations recovered CWD more quickly than did

natural regeneration in premontane tropical forest ecosystems dominated by cattle ranching.

4.1. Coarse woody debris over the chronosequence

Coarse woody debris accumulation in the tropical rain forests of San Vito de Coto Brus increased linearly through time until 50 years of age, after which CWD volumes reached a high and relatively stable level. This confirms our first hypothesis that CWD increases through time following a logistic shape, that is, volumes are low initially, increase rapidly, and then plateau. While [Spies et al. \(1988\)](#) and [Sturtevant et al. \(1997\)](#) found that CWD accumulation followed a U-shaped pattern through time in temperate ecosystems, [DeWalt et al. \(2003\)](#) who evaluated CWD volumes across a chronosequence in Barro Colorado National Monument in Panama, found results similar to ours: CWD volumes increased linearly through time in forests 20 through 70 years old and they were relatively high and stable in forests 70 to ≥ 100 years old ([DeWalt et al., 2003](#)). The reason for the relative absence of dead wood at the beginning of succession might be that much of the branch fall and wood remains are typically harvested by local inhabitants and used as firewood after lands are abandoned in the Neotropics and in our study area.

While we were unable to find abandoned coffee plantations between the ages of 61 to 99 years, we believe that it is likely that if they were present in our area, they would contain high and stable volumes of CWD given the results obtained by [DeWalt et al. \(2003\)](#). The reason why we were unable to find any abandoned coffee plantations 61–99 years old could be that the majority of the forest clearing in our study area started in the late 1940's, with the arrival of refugees from WWII who became coffee farmers ([Zahawi et al., 2015](#)).

Coarse woody debris volumes were highly variable in the old-growth forests of our chronosequence (Fig. A.1). This variability might be due to two factors. First, while we know our forests are over 100 years old, we do not know exactly how much older they are. In fact, studies have shown that some old-growth forest fragments in our study area might be > 400 years old ([Clement and Horn, 2001](#)). Therefore, the heterogeneity in volumes of CWD might have been caused by our use of old-growth forests of potentially different ages. Second, old-growth forests are more heterogeneous in terms of tree sizes and species, and we might have missed picking up large dead trees in some of our strip transects. Overall, these results suggest that in some resilient post-agricultural, premontane tropical landscapes, CWD carbon stocks can attain the levels of old-growth forests in approximately 50 years.

4.2. Coarse woody debris among restoration treatments

Coarse woody debris volumes were highest in old-growth forests, intermediate in plantations, and lowest in natural regeneration. Natural regeneration from cattle pasture had virtually no CWD. This supports our second hypothesis that restoration plantations recover CWD faster compared to natural regeneration. When comparing CWD from the two restoration treatments to CWD from chronosequence fragments of the same age, we found that plantations accelerated CWD accumulation by 19 years compared to natural regeneration from former coffee plantations. In contrast, natural regeneration from the restoration sites had similar (though not significantly different) CWD volumes than natural regeneration from former coffee plantations of the same age.

There might be several reasons for the difference in CWD volumes between these two restoration treatments. First, most of the restoration sites were used for agriculture and the last land use prior to the establishment of restoration treatments was fallow or pasture ([Holl et al., 2020](#)). This previous land use included planting highly competitive pasture grasses for livestock. Second, all plots were cleared of vegetation for two years at the outset of restoration plot establishment ([Holl et al., 2011](#)). The combination of these two factors (pasture at the outset of restoration treatments plus clearing) might have (1) dramatically

reduced the amount of CWD on the forest floor in restoration sites, and (2) facilitated the persistence of exotic grasses which might have slowed regeneration by hampering tree regrowth, and in turn reduced the amount of CWD in this restoration treatment. This is in contrast to the amounts of CWD found in chronosequence fragments of the same age as the natural regeneration treatment: our chronosequence sites had abandoned coffee and shade trees, as well as colonizing shrubs at the outset of regeneration which might have led to higher amounts of CWD at the start of regeneration.

Our results suggest that plantations recover dead wood carbon stocks faster than natural regeneration and therefore might contribute to climate change mitigation more efficiently than passive restoration. The tree species planted in our restoration sites support the establishment of native trees in their understory (*Terminalia amazonia* and *Vochysia guatemalensis*; [Cusack and Montagnini, 2004](#); [Holl et al., 2011](#)) and provide fruits that attract birds (*Inga edulis*; [Holl et al., 2011](#)). In addition, plantations might be better at recovering CWD-associated biodiversity given that CWD is an important source of food and refuge for a diverse array of forest organisms ([Lohr et al., 2002](#); [Horn and Hanula, 2008](#); [Kluber et al., 2009](#); [Ulyshen and Sobotnik, 2018](#)).

It is important to note however, that the high amounts of CWD in our restoration plantations might have arisen from the fact that (1) plantations were neither thinned nor logged after site establishment, and (2) one of the planted fast-growing species, *Inga edulis*, was dying at the time of CWD survey ([Holl et al., 2020](#)). This might not be the case for many restoration plantations around the world where negotiations with landowners typically involve the harvesting of some trees at some point after site establishment ([Brancalion et al., 2020](#)).

5. Conclusions

Dead wood is an important carbon sink but it is rarely taken into account in carbon budget and climate change studies ([Pan et al., 2011](#)). Our research improves our understanding of forest processes by showing that dead wood carbon pools recover following a dynamic, logistic pattern through time in resilient post-agricultural sites. Knowing that carbon represents roughly 50% of the volume of a log, our study contributes to solving this problem by creating data that can be useful to predict carbon stocks more accurately. From a practical perspective, our study shows that tree planting not only accelerates aboveground biomass recovery, but it accelerates the recovery of CWD which is important for carbon sequestration and the conservation of dead-wood associated species.

CRedit authorship contribution statement

Estefania P. Fernandez Barrancos: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – review & editing. **Robert J. Marquis:** Conceptualization, Data curation, Methodology, Supervision, Validation, Writing – review & editing. **J. Leighton Reid:** Conceptualization, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120015>.

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