



















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Memories of Trees Past: Coexistence Implications of Legacy Conspecific Density Dependence

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ABSTRACT

The Janzen-Connell Hypothesis posits that plant species diversity is maintained by a reduction in seedling survival near living conspecific trees relative to heterospecifics—known as negative conspecific density dependence (CDD). CDD facilitates coexistence if stronger than heterospecific density dependence (HDD). However, whether and how long CDD persists after trees die is unknown. In a three-year study across three forests, we monitored seedling survival near living and dead trees, both conspecific and heterospecific, across a seven-year chrono-sequence since tree death. CDD persisted for at least 5 years after tree death ('legacy CDD'), and most species showed stronger CDD relative to HDD through time. We used our empirical findings to parametrize a theoretical community dynamics model. Our model suggests that both stabilising niche differences and fitness differences persist after tree death. While legacy CDD can facilitate coexistence, fitness differences often overwhelmed niche differences, making competitive exclusion the most likely outcome.

Lukas J. Magee and Daniel J.B. Smith contributed equally to this manuscript.

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1 | Introduction

The Janzen–Connell Hypothesis has frequently been invoked to describe the maintenance of local forest diversity. The premise is simple: seed and seedling survival decrease near parent trees or other conspecifics due to the accumulation of species-specific enemies (e.g., phytopathogens; Connell 1971; Janzen 1970; Terborgh 2012). These dynamics—commonly referred to as negative conspecific density dependence (CDD)—can prevent competitive exclusion and promote species coexistence by conferring a per-capita advantage to rare species (Levi et al. 2019; Wright 2002). Numerous studies show that seedling or sapling survival decreases under conspecific trees relative to heterospecific trees (Comita et al. 2014; Song et al. 2021). Importantly, these studies almost exclusively measure survival under *living* trees. Therefore, our understanding of CDD is based upon the implicit assumption that negative intraspecific effects disappear after conspecific trees die.

However, CDD can persist after tree mortality. Recent experiments provided evidence of this ‘legacy CDD’ in the form of persistent plant–soil feedbacks (Bennett et al. 2022; Esch and Kobe 2021; Heinen et al. 2020; Wubs and Bezemer 2018). For example, lingering negative plant–soil feedbacks generated by canopy trees decreased conspecific seedling survival for several years after tree death (Bennett et al. 2022), and soil-borne, host-specific pathogens can persist around dead trees for up to 3.5 years (Esch et al. 2021). This experimental evidence generally suggests that legacies of dead individuals continue to negatively affect living conspecifics (Detto and Muller-Landau 2016; Magee et al. 2024). However, legacy CDD has not been studied systematically across species, nor do we understand its capacity to influence species coexistence.

If legacy CDD proves to be a general phenomenon after tree mortality, it could profoundly impact how plant ecologists perceive its potential to facilitate species coexistence. Under the traditional assumption that interactions among trees cease upon death, living conspecifics that remain in the vicinity of dead trees would be expected to disproportionately benefit because they would not be subject to the intraspecific processes that negatively affect their performance (i.e., negative CDD disappears upon tree death). Release from negative CDD should reduce species diversity by promoting self-replacement, all else being equal (Bagchi et al. 2010; Doolittle and LaManna 2025). However, if negative CDD persists on the landscape following tree death, then living conspecifics in the vicinity should still be adversely affected, favouring heterospecific replacement. This could enhance local biodiversity if conspecific self-limitation sufficiently exceeds heterospecific self-limitation (Smith 2022; Stump and Chesson 2015).

Recent work has emphasised that the ability of CDD to impact coexistence depends on the strength of conspecific effects relative to heterospecifics, sometimes referred to as *stabilising* CDD (Hülsmann et al. 2024; LaManna et al. 2024). Moreover, most simulations of Janzen–Connell dynamics assume dead trees cease to affect the biotic community. Given the accumulating empirical evidence for stabilising legacy CDD, this assumption should be revisited. Indeed, Miller and Allesina (2021)

demonstrated how the ‘memory’ of a previous patch occupant alters competitive outcomes. Similarly, simulations show that the timespan over which specialised pathogens and mutualists persist in the soil affects tree community coexistence (Ke and Levine 2021; Schroeder et al. 2020).

How CDD strengthens or diminishes following tree mortality is also important for understanding its role in shaping species diversity. Legacy CDD could facilitate diversity maintenance by promoting heterospecific recruitment over conspecific recruitment, increasing the strength of stabilising effects. However, if legacy CDD effects decay rapidly (relative to HDD) they could increase the probability of conspecific recruitment, eroding coexistence. Furthermore, coexistence theory identifies two components that regulate competitive outcomes: (stabilising) niche differences that quantify how much species limit themselves as compared to heterospecifics, and fitness differences, which quantify differences in species’ competitive abilities. Niche differences must exceed fitness differences for stable coexistence (Chesson 2000). In addition to influencing stabilising CDD, inter-specific variation in legacy conspecific and heterospecific effects on survival could also alter fitness differences (Yan et al. 2022). Legacy effects may function to increase interspecific fitness differences, inhibiting coexistence.

Here, we investigated the presence of legacy CDD following tree mortality in a multi-year field study across three North American forests. We determined time since mortality for canopy trees and monitored seedling survival near dead and living trees. We estimated the strength and probability of stabilising CDD at different times since the canopy trees died. Finally, we constructed a model of community dynamics that we parameterised with our empirical results to evaluate the coexistence implications of legacy CDD at the seedling life stage.

2 | Materials and Methods

2.1 | Study Sites

We collected data at three temperate forest research sites in the eastern United States: Harvard Forest (HF; 42°54′ N, −72°18′ W), the Smithsonian Environmental Research Center (SERC; 38°53′ N, 76°33′ W), and the Smithsonian Conservation Biology Institute (SCBI; 38°89′ N, 78°09′ W). Each site contains a long-term Forest Global Earth Observatory (ForestGEO) dynamics plot, where all stems ≥ 1 cm DBH are identified, tagged, mapped, and measured according to standardised protocols (Davies et al. 2021). Follow-up censuses occur at five-year intervals to document forest change. The HF plot is a 35-ha hemlock-hardwood forest in Massachusetts (Orwig et al. 2022); SERC is a 16-ha, low-elevation, deciduous broadleaf forest on the Chesapeake Bay of Maryland (McMahon et al. 2023); and SCBI is a 25.6-ha mature secondary forest located in the Blue Ridge Mountains of northern Virginia (Gonzalez-Akre et al. 2016). All three forest plots are co-located within National Ecological Observatory Network (NEON) sites, and aerial images at 1 m² resolution exist for these research sites through semi-annual campaigns of an aerial observatory platform (AOP).

2.2 | Study Design

2.2.1 | Canopy Tree Mortality Detection

To test how CDD changes after tree death, we monitored the survival of seedlings in plots near live and dead canopy trees. We used a combination of complete ForestGEO censuses, annual mortality surveys of trees > 10 cm DBH, and aerial orthophotos (NEON AOP) analysed with the *DeepForest* python package (Weinstein et al. 2019, 2020) to detect the year of mortality for canopy trees at each site. We randomly selected large trees (> 30 cm DBH) of species that had at least three dead individuals per year (or 6 for two-year observation windows) over the preceding 5 years (detailed methods in Supplementary Methods A). We refined candidate species by focusing on species that were likely present as seedlings in the areas surrounding at least 30% of the dead large trees (Jevon et al. 2022; Johnson et al. 2014; and *personal communication with local scientists*). Two species met these criteria at SERC (*Fraxinus pennsylvanica* Marsh. and *Quercus alba* L.), at SCBI (*Fraxinus americana* L. and *Quercus velutina* Lam.) and Harvard Forest (*Acer rubrum* L. and *Quercus rubra* L.).

2.2.2 | Time Since Tree Death Classification

We did not have an annual resolution for some site-by-year combinations due to gaps in field surveys and/or NEON AOP flights. For example, in 2020, the NEON AOP was not deployed, resulting in a two-year window between successive flights (2019–2021; Table A1). To account for these uncertainties in time since tree death, we used four discrete classes: living trees, < 2 years since death, 2–5 years since death and 5–7 years since death.

2.2.3 | Plot Establishment and Seedling Data Collection

In summer 2021, we established three transects radiating at 0°, 120°, and 240° from each dead canopy tree ($n = 140$). Along each transect, we established one 1 × 1 m seedling plot 2 m from the bole of the dead canopy tree (Figure A1). Within the 1 m² plot, we identified, measured for height, tagged, and mapped each seedling (woody trees < 1.5 m height). In the summer of year two (2022), we recorded seedling mortality and heights in both new seedling plots (set around newly dead trees, $n = 28$) and existing seedling plots. We also expanded the scope of sampling in 2022 by adding transects under large (> 30 cm DBH) living trees ($n = 22$). Not all study species had living trees > 30 cm DBH (e.g., *Fraxinus pennsylvanica*); therefore, we could not evaluate seedling survival around live trees of these species. In the final sampling year, June–August 2023, we recorded the survival of seedlings and measured the height of surviving individuals ($n = 190$ total trees; $n = 1130$ total seedling plots).

2.3 | Statistical Analysis

2.3.1 | Model Structure

To quantify the effects of CDD around living and dead canopy trees, we used a generalised linear mixed model (GLMM) fit in

a Bayesian framework. We examined seedling survival around living and dead canopy trees as a function of conspecific or heterospecific status of the nearby canopy tree (hereafter ‘gapsp,’ conspecific or heterospecific; ‘CON’ and ‘HET’, respectively), the status of the canopy tree –living or dead (hereafter ‘gapstatus’), and if dead, how long since the tree died. Other factors influence seedling survival; therefore, we accounted for individual seedling height (log-transformed) as a model covariate. The covariate content of the statistical models was logically derived from the use of a causally explicit analytical framework (see details on the causal diagram in Supporting Information, Figure A1).

To answer our research questions related to legacy CDD, we used two Bayesian multilevel models to analyse seedling survival, treating survival as a Bernoulli likelihood (Equation 1; 1 = survival, 0 = mortality), with a logit link-function for the linear combination of covariates (Equation 2). We built the models using an ‘index variable approach’ (McElreath 2018, 447), consisting of all combinations of the factorial variables having their own intercept. We built the multilevel structure of the models to allow survival probabilities for each of the six study species to have their own response (i.e., slope parameter) to *gapsp*, *gapstatus*, and *Height* while accounting for plot- and site-level variation through varying intercepts. The survival probability of seedling individual i of species s in plot k at forest site g follows:

$$\text{survival}_{\text{iskg}} \sim \text{Bernoulli}(p_{\text{iskg}}) \quad (1)$$

$$\text{logit}(p_{\text{iskg}}) = \alpha_{s[i],\text{gapsp}[\text{gapstatus}[i]]} + \beta_{s[i]} \text{Height}_i + \epsilon_{k[i]} + \tau_{g[i]} \quad (2)$$

$$\begin{bmatrix} \alpha_{j,\text{con,alive}} \\ \alpha_{j,\text{het,alive}} \\ \alpha_{j,\text{con,dead}} \\ \alpha_{j,\text{het,dead}} \\ \beta_j \end{bmatrix} \sim \text{MVNormal} \left(\begin{bmatrix} \gamma_{\text{con,alive}} \\ \gamma_{\text{het,alive}} \\ \gamma_{\text{con,dead}} \\ \gamma_{\text{het,dead}} \\ \beta \end{bmatrix}, S_{\text{species}} \right) \text{ for } j = \text{species } 1, 2, \dots, 6 \quad (3)$$

$$S_{\text{species}} = \begin{pmatrix} \sigma_{\alpha_{\text{con,alive}}} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{\alpha_{\text{het,alive}}} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{\alpha_{\text{con,dead}}} & 0 & 0 \\ 0 & 0 & 0 & \sigma_{\alpha_{\text{het,dead}}} & 0 \\ 0 & 0 & 0 & 0 & \sigma_{\beta} \end{pmatrix} \mathbf{R} \begin{pmatrix} \sigma_{\alpha_{\text{con,alive}}} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{\alpha_{\text{het,alive}}} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{\alpha_{\text{con,dead}}} & 0 & 0 \\ 0 & 0 & 0 & \sigma_{\alpha_{\text{het,dead}}} & 0 \\ 0 & 0 & 0 & 0 & \sigma_{\beta} \end{pmatrix} \quad (4)$$

where $\gamma_{\text{gapsp},\text{gapstatus}}$ is the average (i.e., across species s) log-odds of each combination of the levels of the factors *gapsp* and *gapstatus* (see further detail in Supplementary methods Equation A1–A15), $\alpha_{s,\text{gapsp},\text{gapstatus}}$ is the species-level deviation from the corresponding $\gamma_{\text{gapsp},\text{gapstatus}}$ (detailed in Supplementary Equation A1–A7; equivalent to an interaction term between *gapsp* and *gapstatus*), where β and β_s are the average height effect and species-level deviations from the grand average, respectively, and where the covariances among the

parameters in S are determined by the matrix R (Supplement Equation A4–A6), resulting in adaptively regularising priors and partial pooling and shrinkage, limiting the risks of overfitting (McElreath 2018). Varying intercept for plots and sites are ϵ_k and τ_g , respectively. The notation $s[i]$ indicates the value of species s on row i , with the bracket notation used to avoid subscript of subscript (e.g., α_{gapsp}). The first statistical model included *gapstatus* as a binary variable (live or dead), and the second statistical model allowed for variation in time since tree death (live, < 2, 2–5, 5–7 years), following the same index variable approach as used in model 1 (more details in Supplementary Equation A8–A14).

2.4 | Hypothesis Testing and Bayesian Inference

The Bayesian survival GLMMs produced community-level (all species) and species-level estimates for seedling survival adjacent to living and dead canopy trees. Based on each posterior draw, we calculated the CDD estimate as the predicted seedling survival near a conspecific canopy tree minus the predicted seedling survival near a heterospecific canopy tree (Hülsmann et al. 2024; LaManna et al. 2022). This subtraction—or contrast—allowed us to evaluate the posterior probability that the change in seedling survival (survival adjacent to Heterospecific versus Conspecific tree) was less than zero, corresponding to the probability of stabilising CDD (*sensu* LaManna et al. 2024), while propagating uncertainty from all parameter estimates. We generated this counterfactual change for an average-sized seedling (9.01 cm height) first at the community level and then for each species individually. We repeated this process for the second model, in which we considered how long the adjacent canopy tree had been dead. We did not have sufficient observations or seedling mortality events for some combinations of species and time since canopy tree death (Table A2).

2.5 | Community Dynamics Model

To examine how live and legacy CDD and HDD effects at the seedling life history stage influence tree species coexistence in each forest site, we parameterise a dynamic competition model with our seedling survival measurements.

2.5.1 | Model Overview

We consider a spatially implicit patch occupancy model, similar to Chisholm and Muller-Landau (2011) and Stump and Comita (2018), to evaluate how legacy CDD affects species coexistence. The model describes a community of discrete patches, each containing a single adult (Figure 1A). Seedlings disperse to patches. Seedling mortality is modified by the adult species occupying the patch (both before and after adult death; Figure 1B,C). After adult death and T years of legacy effects, seedlings enter a lottery competition for the gap (Figure 1D). We derived deterministic coexistence conditions for a two-species system (Figure 1D,E), which we apply to the species pairs at each site. See Table B1 for a summary of variables and parameters.

2.5.2 | Seedling Dynamics

Seedlings grow in cohorts defined at the patch level (each square patch in Figure 1A). Let $S_{ik}(y)$ represent the number of seedlings of species i on a patch occupied by a tree of species k in state y . y indexes the time since tree mortality on a patch, with $y = L$ signifying the patch is occupied by a living tree. Trees of species i produce seeds that germinate into seedlings at fecundity rate f_i . Trees disperse a proportion D of seeds uniformly throughout the community and retain the remaining $1 - D$ on the local patch. Seedling dynamics for species i beneath live trees are described by

$$\frac{dS_{ik}(L)}{dt} = f_i N_i D - m_{ik}(L) S_{ik}(L)$$

$$\frac{dS_{ii}(L)}{dt} = f_i (N_i D + 1 - D) - m_{ii}(L) S_{ii}(L)$$

for patches occupied by heterospecific and conspecific adults, respectively, $i, k = 1, 2, i \neq k$. N_i is the proportion of patches in the community occupied by adult of species i (see *Adult tree dynamics*). $f_i N_i D$ and $f_i (N_i D + 1 - D)$ are the rates at which species i disperses seedlings to heterospecific occupied patches and conspecific occupied patches, respectively. $m_{ik}(L)$ and $m_{ii}(L)$ are the *per capita* seedling mortality rates on heterospecific and conspecific patches occupied by live adults, respectively, which capture live HDD and CDD effects. The total number of seedlings on a patch is described by two ODEs. For example, for a patch occupied by an adult of species 1, seedling dynamics of species 2 and 1 dynamics are described by $dS_{21}(L)/dt$ and $dS_{11}(L)/dt$, respectively.

Because seedling dynamics are faster than adult dynamics for long-lived trees, we assume that $S_{ik}(L)$ and $S_{ii}(L)$ come to equilibrium (denoted $\hat{S}(L)$), with

$$\hat{S}_{ik}(L) = N_i D f_i E_{ik}(L)$$

$$\hat{S}_{ii}(L) = f_i (N_i D + 1 - D) E_{ii}(L)$$

$E_{ik}(L) = 1/m_{ik}(L)$ and $E_{ii}(L) = 1/m_{ii}(L)$ quantify how patch identity (conspecific vs. heterospecific) affects seedling survival under live L trees. For simplicity, we assume the seedling that wins that patch is from the initial cohort set by $\hat{S}_{ii}(L)$ and $\hat{S}_{ik}(L)$. Therefore, after adult death, we only model the survival of the seedlings with initial abundances $\hat{S}_{ii}(L)$ and $\hat{S}_{ik}(L)$. We relax this assumption in Supplement B.3.

Following adult death, a proportion of the initial seedling cohort dies annually, reflecting legacy CDD and HDD. Let $E_{ik}(y)$ and $E_{ii}(y)$ represent the probability a seedling of species i survives from year $y - 1$ to year y after the death of a heterospecific or conspecific adult, respectively for $y \neq L$. In terms of mortality rates $m_{ik}(y)$ and $m_{ii}(y)$, $E_{ik}(y) = e^{-m_{ik}(y)}$ and $E_{ii}(y) = e^{-m_{ii}(y)}$, $y \neq L$. $y = L$ represents the special case of live effects where $E_{ik}(L)$ and $E_{ii}(L)$ are reciprocals of mortality rate. Then, the expected seedling abundances of species i on conspecific and heterospecific occupied patches T years are:

$$S_{ik}(T) = f_i N_i D \underbrace{\prod_{y=L}^T E_{ik}(y)}_{Y_{ik}(T)} \quad (5)$$

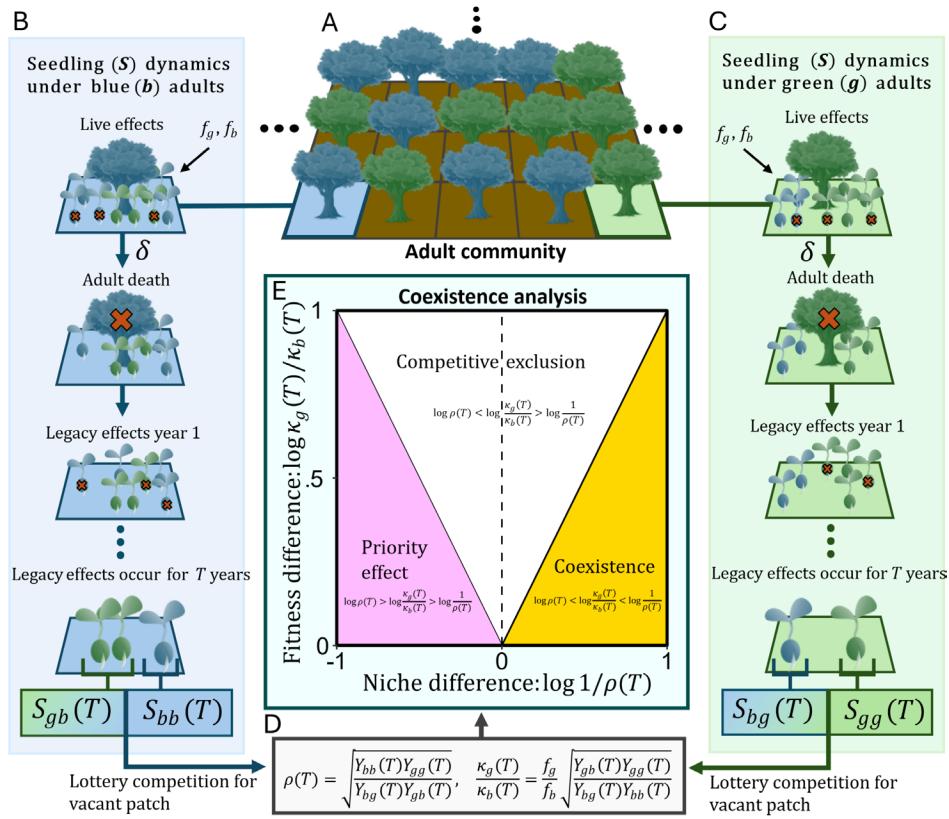


FIGURE 1 | Visualisation of legacy effects and competition model. We subdivide the community into discrete patches (A). Consider the focal patches coloured blue and green (B and C). Seedling S of each species (blue b and green g) are dispersed and accumulate on each patch at rates proportional to fecundity f_g and f_b . Each patch contains a cohort of seedlings. Under live trees (blue trees in B, green trees in C), seedlings die at a rate that depends on the species identity of the tree occupying the patch. After the tree on the patch dies, the initial cohort of living seedlings (seedlings without x 's under 'Live effects') experience an annual mortality probability that depends on the species identity of the dead occupant. Legacy effects persists for T years on every patch, leading to expected seedling abundances $S_{gb}(T)$, $S_{bb}(T)$, $S_{bg}(T)$, and $S_{gg}(T)$, wherein for example, $S_{gb}(T)$ is the expected number of seedlings of species g on patches previously occupied by trees of species b after T years of thinning from legacy effects. One of the remaining seedlings replaces the vacated patch via a lottery competition, which occurs after the seedling cohort experiences T years of thinning. From the expected outcomes of lottery competitions, we derive quantities for niche differences $\log 1 / \rho(T)$ and fitness differences $\log \kappa_g(T) / \kappa_b(T)$ which shape competitive outcomes (D and E). The terms that comprise $\rho(T)$ and $\kappa_g(T) / \kappa_b(T)$ ($Y_{bb}(T)$, $Y_{gg}(T)$, $Y_{bg}(T)$, and $Y_{gb}(T)$) quantify how CDD and HDD affect the survival of seedlings (see Equation 5).

$$S_{ii}(T) = f_i(N_i D + 1 - D) \underbrace{\prod_{y=L}^T E_{ii}(y)}_{Y_{ii}(T)}$$

$y = L, 1, 2, \dots, T$ (Figure 1B,C). $Y_{ik}(T)$ and $Y_{ii}(T)$, comprised of the E_{ik} and E_{ii} terms, summarise how heterospecific and conspecific patch occupancy regulate the survival of species i 's seedlings.

2.5.3 | Adult Tree Dynamics

All adult trees die at rate δ . After tree death, the patch is filled by one of the seedlings in the cohort beneath it via a lottery competition that accounts T years of legacy effects. All seedlings in each cohort of the forest experience the same number of years (T) of legacy CDD or HDD thinning before entering the lottery. T can be interpreted as the time-to-replacement after adult death. Like traditional lottery models, we assume seedling competition for the gap is short relative to tree turnover. This separation of timescales is an appropriate assumption because we consider

$T \leq 7$ years and examine long-lived canopy trees. Thus, over a timescale in which adult proportions N_i do not change, two processes occur. First, seedlings cohorts beneath dead trees are thinned by legacy for T years, reaching abundances $S_{ii}(T)$ and $S_{ik}(T)$. After T years of thinning, one of the seedling is selected to replace the death tree via lottery competition. From this, the dynamics of the expected proportion of patches occupied by species i are given by:

$$\frac{dN_i}{dt} = \delta \left(\underbrace{N_i \frac{S_{ii}(T)}{S_{ii}(T) + S_{ki}(T)}}_{\text{Conspecific patch colonization}} + \underbrace{N_k \frac{S_{ik}(T)}{S_{kk}(T) + S_{ik}(T)}}_{\text{Heterospecific patch colonization}} - \underbrace{N_i}_{\text{mortality}} \right) \quad (6)$$

$i, k = 1, 2, i \neq k$ (see Supplementary B.1).

2.5.4 | Coexistence Analysis

We derived a mutual invasion criterion for (Equation 6) (when both species deterministically invade the other when rare; Supplementary B.2). Using notation similar to Chesson (2000), coexistence requires: $\log \rho < \log \frac{\kappa_1}{\kappa_2} < \log 1/\rho$ where $\log 1/\rho$ and $\log \frac{\kappa_1}{\kappa_2}$ are defined as “(stabilizing) niche differences” and ‘fitness differences’ between species 1 and 2, respectively. Niche differences must exceed fitness differences for coexistence (Chesson 2018). Possible outcomes are: coexistence ($\log \rho < \log \frac{\kappa_1}{\kappa_2} < \log 1/\rho$), priority effect ($\log \rho > \log \frac{\kappa_1}{\kappa_2} > \log 1/\rho$), and competitive exclusion ($\log \rho > \log \frac{\kappa_1}{\kappa_2} < \log 1/\rho$ or $\log \rho < \log \frac{\kappa_1}{\kappa_2} > \log 1/\rho$).

In our analyses, we examine niche and fitness differences in two ways. First, we consider the overall effect CDD and HDD have on niche and fitness differences. To this end, assuming $D = 1$ (global dispersal) and $N_1 + N_2 = 1$:

$$\rho(T) = \sqrt{\frac{Y_{11}(T)Y_{22}(T)}{Y_{12}(T)Y_{21}(T)}} \text{ and } \frac{\kappa_1(T)}{\kappa_2(T)} = \frac{f_1}{f_2} \sqrt{\frac{Y_{12}(T)Y_{11}(T)}{Y_{21}(T)Y_{22}(T)}} \quad (7)$$

where $\rho(T)$ and $\kappa_1(T)/\kappa_2(T)$ define niche and fitness differences due to live effects and T years of legacy effects where, as noted above, T indicates the time-to-replacement after adult death. $Y_{ik}(T)$ and $Y_{ii}(T)$ resemble $1/a_{ik}$ and $1/a_{ii}$ from the Lotka-Volterra competition model. Similar expressions can be derived when $D < 1$ or $N_1 + N_2 \neq 1$ (Supporting Information B.2).

Second, we examine the contribution to niche and fitness differences produced by each discrete time interval y of live and legacy HDD and CDD:

$$\tilde{\rho}(y) = \sqrt{\frac{E_{11}(y)E_{22}(y)}{E_{12}(y)E_{21}(y)}} \text{ and } \frac{\tilde{\kappa}_1(y)}{\tilde{\kappa}_2(y)} = \sqrt{\frac{E_{12}(y)E_{11}(y)}{E_{21}(y)E_{22}(y)}} \quad (8)$$

$y = L, 1, 2, \dots$ recalling that $E_{ii}(y)$ and $E_{ik}(y)$ are the reciprocal of mortality rates for $y = L$ and the annual survival probabilities otherwise. For example, $\tilde{\rho}(2 < y \leq 5)$ quantifies the *interval-specific* niche differences generated by legacy CDD and HDD from a single year under adults that have been dead for 2–5 years. This contrasts e.g., $\rho(T = 5)$, which quantifies niche differences due to all live and legacy CDD and HDD effects up to T years.

2.6 | Model Parameterization

We parameterized niche and fitness differences in (Equations 7 and 8) for each species pair at Harvard Forest, SCBI and SERC using the posterior distributions of average-sized seedling survival for each species. We parameterized annual post-tree-mortality seedling survival on heterospecific and conspecific patches ($E_{ik}(y)$ and $E_{ii}(y)$) using the median of the seedling survival posterior distributions for each species near heterospecific and conspecific trees, respectively, at each time interval ($y \leq 2$, $2 < y \leq 5$, and $5 < y \leq 7$ years). We calculated live tree effects ($E_{ik}(L)$ and $E_{ii}(L)$) using annual survival data near live trees. Let P_{ik} be the median annual survival probability species

i 's seedlings near a live tree of species k . Then, $E_{ik}(L) = \log P_{ik}$. To parameterize (Equation 7), we calculated $Y_{ik}(T)$ and $Y_{ii}(T)$ for $L \leq T \leq 7$ using our estimates of $E_{ik}(y)$ and $E_{ii}(y)$ (Equation 5).

To generate error ranges, we sampled from model posterior distributions, yielding corresponding posteriors for $E_{ik}(y)$, $Y_{ik}(T)$, niche differences, and fitness differences. We additionally calculated the proportion of samples from the derived posterior niche and fitness difference distributions that corresponded to each competitive outcome (coexistence, priority effect, or competitive exclusion) at every time interval for each of (Equations 7 and 8).

At Harvard Forest, we parameterized interval-specific niche and fitness differences every time interval ($y = L$, $y \leq 2$, $2 < y \leq 5$, and $5 < y \leq 7$ years). Data at SERC and SCBI allowed interval-specific niche and fitness difference parameterizations at $y \leq 2$ and $2 < y \leq 5$ years; we lacked sufficient data for live trees and $5 < y \leq 7$ years. We assumed identical live CDD and HDD at SERC and SCBI ($E_{12}(L) = E_{21}(L) = E_{11}(L) = E_{22}(L)$) such that live effects did not impact fitness or niche differences. Fecundity f was assumed to be equivalent between species. Therefore, our analysis examines only niche and fitness differences generated by survival at the seedling stage. We approximated each site as a two-species system, assuming $N_1 + N_2 = 1$; relaxing this assumption did not qualitatively change results (Supplement B, Figures B9 and B10). Relaxing the assumption that seedlings recruit only before adult death also did not qualitatively change results (see Supplement B Figures B11–B13).

3 | Results

3.1 | Living CDD Versus Legacy CDD

Seedling survival was lower near living conspecifics than living heterospecifics when averaged across species and sites (Figure 2, top left) and for most individual species (Figure 2, bottom). Averaged across species, predicted seedling survival probability near living conspecifics was 0.67 [90%-HPDI: 0.46, 0.88], and median seedling survival near living heterospecific canopy trees was 0.85 [0.70, 0.96]. The probability that survival was lower near living conspecifics: $\Pr(\text{survival}_{\text{CON}_{\text{live}}-\text{HET}_{\text{live}}}) < 0$, which corresponds to stabilising living CDD, was 0.97 (i.e., 97% of the counterfactual contrasts were < 0). When adjacent canopy trees were dead, the difference in seedling survival adjacent to conspecific versus heterospecific trees became smaller. Median seedling survival under dead conspecifics was 0.79 [0.64, 0.92], while under dead heterospecifics, it was 0.85 [0.74, 0.96], and the probability of stabilising legacy CDD ($\Pr(\text{survival}_{\text{CON}_{\text{dead}}-\text{HET}_{\text{dead}}}) < 0$) was 0.90. There was high interspecific variation in both living and legacy CDD (Figure 2, Figure A4). All species evaluated showed clear evidence of living stabilising CDD, but not all species showed clear evidence of legacy stabilising CDD (e.g., *Quercus rubra*).

3.2 | Duration and Dynamics of Legacy CDD

Seedling survival of most species remained significantly lower when near dead conspecifics than near dead heterospecific

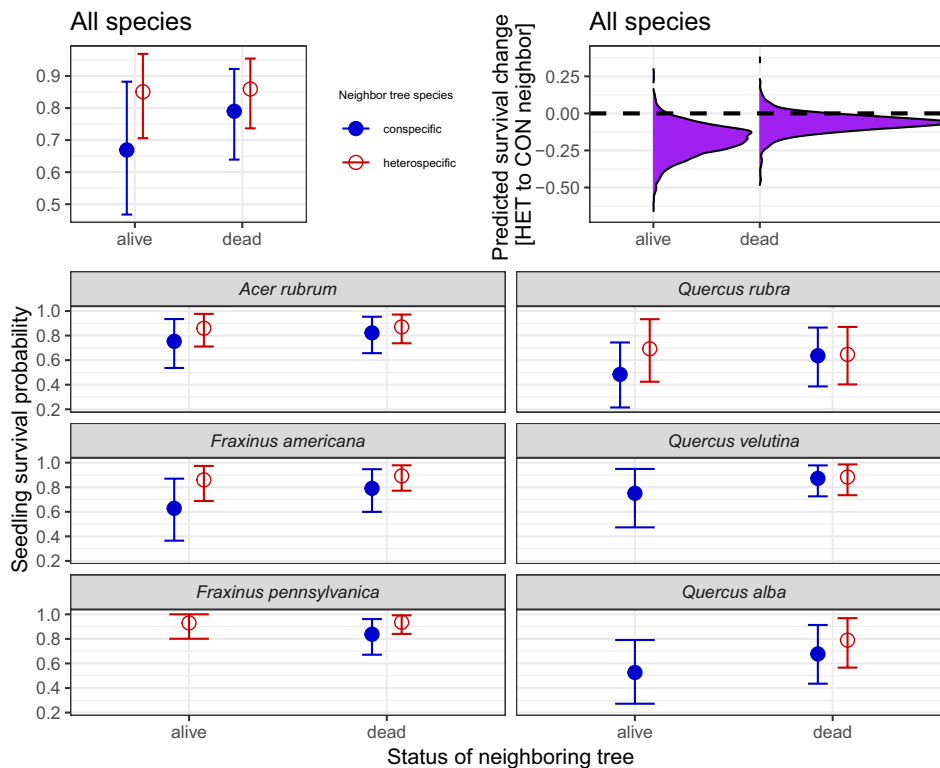


FIGURE 2 | Predicted annual survival probability for seedlings growing adjacent (2m) to living and dead conspecific (blue) and heterospecific (red) canopy trees averaged across sites and species (top left) and separated species by species and forest (lower panel). Points are median estimates for an average seedling height derived from the joint posterior distribution, and error bars show 90%-highest posterior density interval. The predicted survival change for a counterfactual switch from a heterospecific to a conspecific is shown for both living and dead neighbours, where dashed lines delineate no predicted change, while negative values indicate lower survival under conspecifics than heterospecifics (topright). Species pairs are organized by study location: Harvard Forest (top; *A. rubrum* and *Q. rubra*), SCBI (middle), SERC (bottom).

trees (Figures 3 and 4). This pattern of stabilising legacy CDD held with increasing time since canopy tree death. Across species, legacy stabilising CDD appeared to temporarily diminish initially after tree death (i.e., 0–2 years since tree mortality) but then re-establish as time progressed (Figure 4). This initial weakening of stabilising CDD at the 0–2 year window was heavily influenced by one species, *Quercus rubra*, that had a very low probability of stabilising CDD during this time window (0.09; Figure 4). Despite the substantial interspecific variation in CDD dynamics, the average probability of seedling survival near conspecific trees was nearly always lower than near heterospecific trees across the time windows—i.e., stabilising legacy CDD effects persisted for the full period of observation (5–7 years after canopy tree death).

3.3 | Coexistence Predictions

Legacy CDD generated stabilising niche differences ($\log 1/\tilde{\rho}(y) > 0$) at each discrete time interval since tree death (Figure 5a–c; also see Equation 7) except for the initial 2 years at Harvard Forest (Figure 5a, $y \leq 2$). The strength of *interval-specific* niche differences generated by legacy CDD increased with the length of time since tree mortality in all sites ($\log 1/\tilde{\rho}(y)$ increased with y at all sites, excluding live effects; Figure 5a–c). Cumulative niche differences generated by T years of legacy effects were always stabilising ($\log 1/\rho(T) > 0$ for all T at all

sites; see Equation 7). $\log 1/\rho(T)$ increased with T in all cases except for Harvard Forest over the first 2 years following adult-mortality (Figure 6a,c).

Although legacy CDD generated niche differences, fitness differences due to inter-specific variation in seedling survival were usually larger. We found fitness differences at each time interval ($\log \hat{\kappa}_1(y)/\hat{\kappa}_2(y) > 0$; Figure 5d–f), which, throughout the course of seedling thinning, result potentially large fitness differences ($\log \kappa_1(T)/\kappa_2(T) > 0$, Figure 6d–f). The median niche difference exceeded the median fitness difference only at SCBI, 2–5 years post-tree-mortality (Figure 5h, $2 < y \leq 5$) which can be largely attributed to a reduction in fitness differences during this interval (Figure 5e). Median fitness differences otherwise exceeded median niche differences (Figure 5g,i). Accordingly, median niche and fitness differences due to legacy effects predicted coexistence at SCBI and competitive exclusion at Harvard Forest and SERC (Figure 6g–i). At SCBI, legacy effects including $T = 5$ years predicted coexistence in ~64% of draws from the posterior distribution, competitive exclusion in ~32%, and a priority effect in ~3% (Figure 6h, $T = 5$). At Harvard Forest, legacy effects up to $T = 6$ years yielded coexistence in ~2% of draws and predicted competitive exclusion in the remaining ~98% (Figure 6g, $T = 6$). Legacy effects up to $T = 5$ years at SERC generated coexistence in ~25% of draws and competitive exclusion in ~75% of draws (Figure 6i).

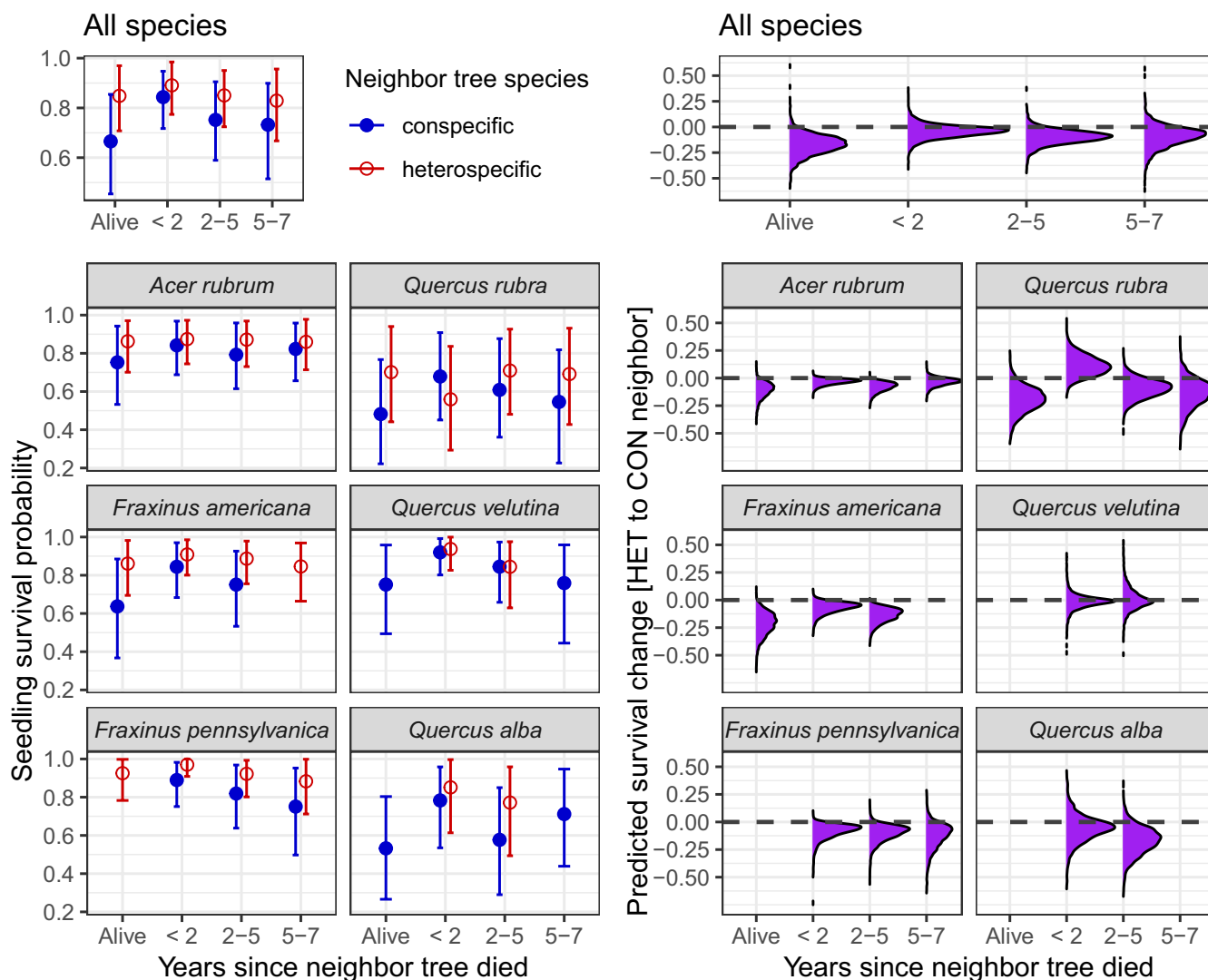


FIGURE 3 | Predicted survival probability for an average height (9.1 cm) seedling adjacent (2 m) to conspecific and heterospecific canopy trees (living trees and different times since canopy tree death) (left). Points are posterior medians and error bars show 90%-highest posterior density interval. The right panel shows distributions of predicted seedling survival for a counterfactual switch from a heterospecific to a conspecific neighbour. Dashed lines delineate no predicted change, while negative values indicate lower survival under conspecifics than heterospecifics. Species pairs are organized by study location: Harvard Forest (top; *A. rubrum* and *Q. rubra*), SCBI (middle), SERC (bottom).

Dispersal limitation decreased the probability of coexistence, primarily by decreasing niche differences (Supplement B, Figures B1–B8).

4 | Discussion

Here, we documented evidence of legacy negative CDD across multiple species and sites (Figures 2, 3). As predicted by the Janzen-Connell Hypothesis, seedling survival was lower near living conspecific canopy trees than living heterospecific trees (Figure 2). This stabilising negative CDD appeared to diminish slightly after canopy tree death; then temporarily strengthened again with increasing time since canopy tree death (Figures 3 and 4). A model of community dynamics, parameterised with our field data, suggested that although legacy CDD increased stabilising niche difference (and thus acted as a stabilising mechanism that promotes coexistence),

interspecific differences in mean fitness (due to variation in seedling survival) were large. At two of the three forest sites, fitness differences, from seedling survival, exceeded stabilising niche differences due to CDD. Below, we discuss the importance of legacy CDD, its probable mechanisms, and its implications for species coexistence.

4.1 | Stabilising Legacy CDD

An implicit assumption of the Janzen-Connell hypothesis has been that when trees die, their influence on the extant community disappears. We found evidence to reject this assumption, in agreement with recent experiments (Bennett et al. 2022; Esch and Kobe 2021) and community-wide observations (Detto and Muller-Landau 2016; Magee et al. 2024). We showed that stabilising CDD—whereby the negative effect of conspecific neighbours on vital rates exceeds that of heterospecific neighbours

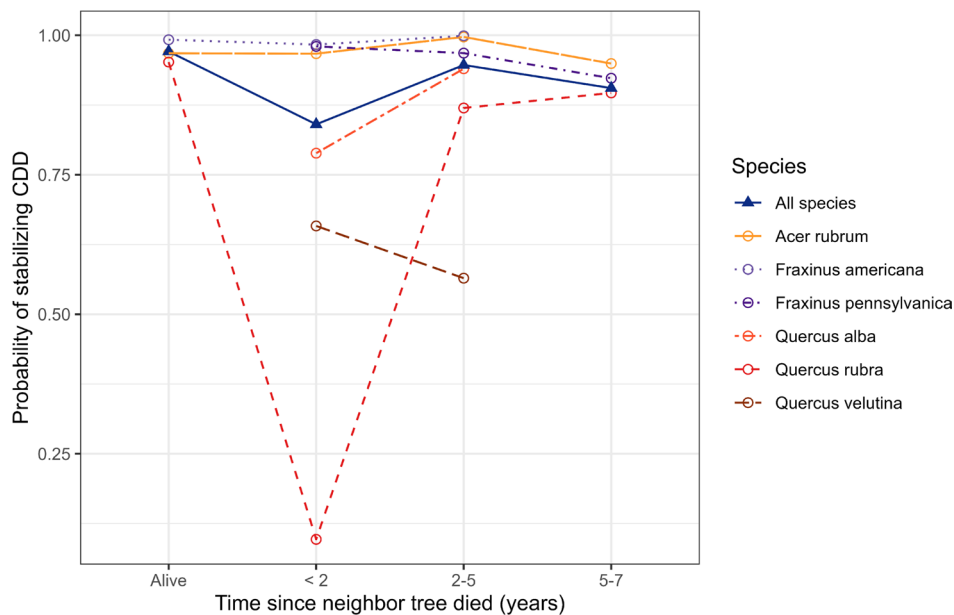


FIGURE 4 | Probability of *stabilising CDD* (i.e., seedling survival lower near conspecifics than heterospecifics) as a function of canopy tree status. Different line colours and points represent the six study species, including the estimates for all species combined. Posterior probabilities were calculated as the probability mass of the posterior distributions shown in Figure 3 that was below zero.

(LaManna et al. 2024)—operates both during and after the life of neighbour trees.

4.2 | Importance, Duration, and Dynamics of Legacy CDD

The rate at which negative CDD changes following tree death, in addition to the absolute time it persists, impacts species coexistence (Ke and Levine 2021; Ke et al. 2024). Dynamics of legacy CDD are important because there is no time more crucial for a humble seedling than when a neighbouring tree dies and produces a canopy gap (Brokaw and Busing 2000; Stone et al. 2025). Any disadvantage during gap dynamics, such as that caused by legacy negative CDD, could prevent a seedling from capitalising on a gap and reaching the sapling life stage (Canham 1989). Our results of increased survival surrounding dead trees, both conspecific and heterospecific trees, support the role of gaps in seedling recruitment. However, higher seedling survival near dead heterospecific trees relative to dead conspecifics also reflects a persistent conspecific disadvantage, or stabilising legacy CDD, that can persist more than 5 years after neighbour tree death.

Our results indicate legacy effects persist longer than previously recognised. For example, while negative legacy CDD has been found in *Prunus serotina*—a species with a well-documented oomycete pathogen (Packer and Clay 2000, 2003) – its seedlings exhibited a decrease in survival around dead conspecific trees relative to survival in soils distant from conspecific trees for ~1.5 years (Esch and Kobe 2021). We found the duration of legacy CDD extends more than 1.5 years, and for most species, the probability of stabilising legacy CDD was greater than 0.88, even more than 5 years after adjacent canopy tree death. The extended duration and strengthening of negative CDD agree with

the community-wide observations in other large forest plots that showed legacy CDD persisting for up to 10 years (Detto and Muller-Landau 2016; Magee et al. 2024).

4.3 | Biological Explanations of Legacy CDD

Our study was observational, and we do not know the exact agents or processes that caused legacy CDD (causal model in Figure A2). Legacy CDD could result from negative plant–soil feedback processes if canopy trees alter nearby soils against conspecific seeds and seedlings (Bever et al. 2015; Crawford et al. 2019; Mangan et al. 2010; Ke et al. 2024). Temporal reports of plant–soil feedback have indicated persistent feedbacks across host-plant generations (Chung 2023). Plant–soil feedbacks around dead trees could arise through intraspecific competition that persists via nutrient depletion adjacent to the canopy tree (Bigelow and Canham 2002). However, most studies of plant–soil feedback around living trees typically find evidence that microbial natural enemies (e.g., pathogenic fungi) drive negative CDD (Bagchi et al. 2014; Mangan et al. 2010). Soil-borne microbes could also persist around the necro-mass (Esch et al. 2021). An important future research direction is to identify the various mechanisms that decrease or increase legacy CDD strength.

Interspecific variation in the stabilising legacy CDD strength we observed may reflect the mycorrhizal associations of each species. Oak species (*Quercus* spp.), which form associations with ectomycorrhizal mutualists, exhibited overall weaker stabilising legacy CDD than the arbuscular mycorrhizal associated ash species (*Fraxinus* spp.) and *Acer rubrum* (Figure 4). Mycorrhizal associations have been attributed to differences in CDD that arise from living trees, and the temporal dynamics of mutualists in soil around dead trees might provide an explanation for legacy CDD patterns.

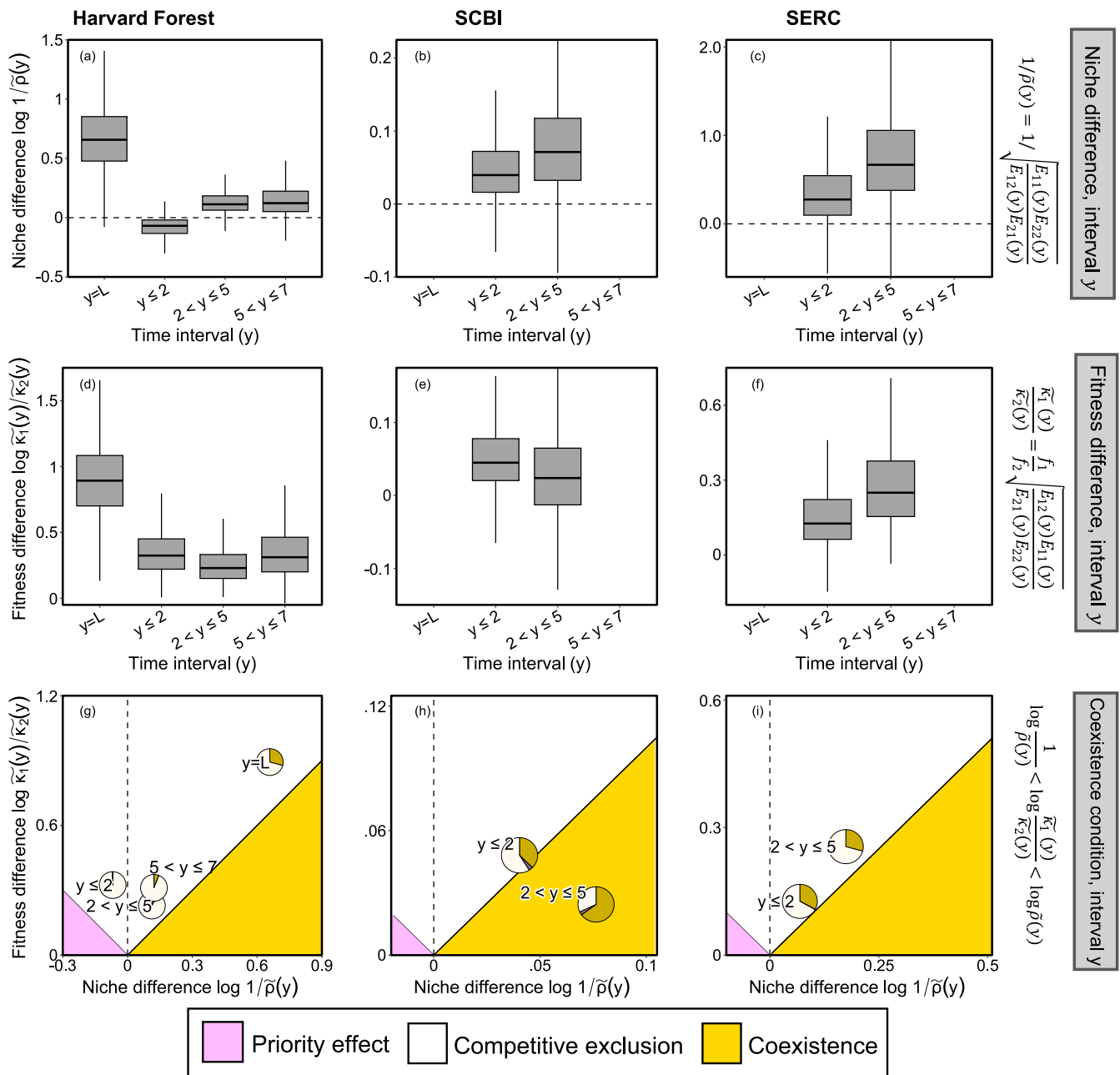


FIGURE 5 | Snapshots at each time interval of niche and fitness differences generated by legacy CDD and HDD. Each panel depicts niche and/or fitness differences due to CDD and HDD effects at the seedling life history stage, at each discrete time interval y in isolation, at each site (see Equation 8). Panels a-c depict the niche overlap $\log 1/\tilde{\rho}(y)$ where $\log 1/\tilde{\rho}(y) > 0$ indicates stabilisation (above the dashed line). Panels d-f show fitness differences $\log \tilde{\kappa}_1(y)/\tilde{\kappa}_2(y)$ at each site. Fitness differences are standardised such that median $\log \tilde{\kappa}_1(y)/\tilde{\kappa}_2(y) \geq 0$ (the species with higher fitness is assigned to be species 1). Panels g-i depict competitive outcomes (coexistence, gold; competitive exclusion, white; priority effects, pink) as defined by the niche overlap and fitness differences from legacy CDD and HDD effects at each individual time interval. Each pie chart is centred at the median and is labelled with the time since adult tree mortality ($y = L$ (Live), $y < 2$ years, etc.). The pie charts were generated from sampling niche difference and fitness difference values from the posterior distributions of each patch type (conspecific and heterospecific) for each species at each time interval y . The pie charts depict the proportion of posterior distribution samples that predicted coexistence (gold), competitive exclusion (white), and priority effects (pink) at that time interval y . Right of the dashed line depicts stabilisation. At Harvard Forest, species 1 is *Acer rubrum* and species 2 is *Quercus rubra*. At SCBI, species 1 is *Quercus velutina* and species 2 is *Fraxinus americana*. At SERC, species 1 is *Fraxinus americana* and species 2 is *Quercus alba*.

We observed a temporary decline in stabilising CDD the first few years after tree mortality (0–2 year gaps), which we attribute to an increase in resources. When accounting for overhead light, however, the same temporary decline was apparent (Appendix A, Figure A4), suggesting that the resource pulse

was due to belowground processes. The increasing strength in stabilising CDD at the 2–5 and 5–7 time since neighbour tree mortality intervals supports the hypothesis of a temporary resource pulse that was subsequently overwhelmed by other CDD mechanisms (i.e., natural enemies). Although we observed a

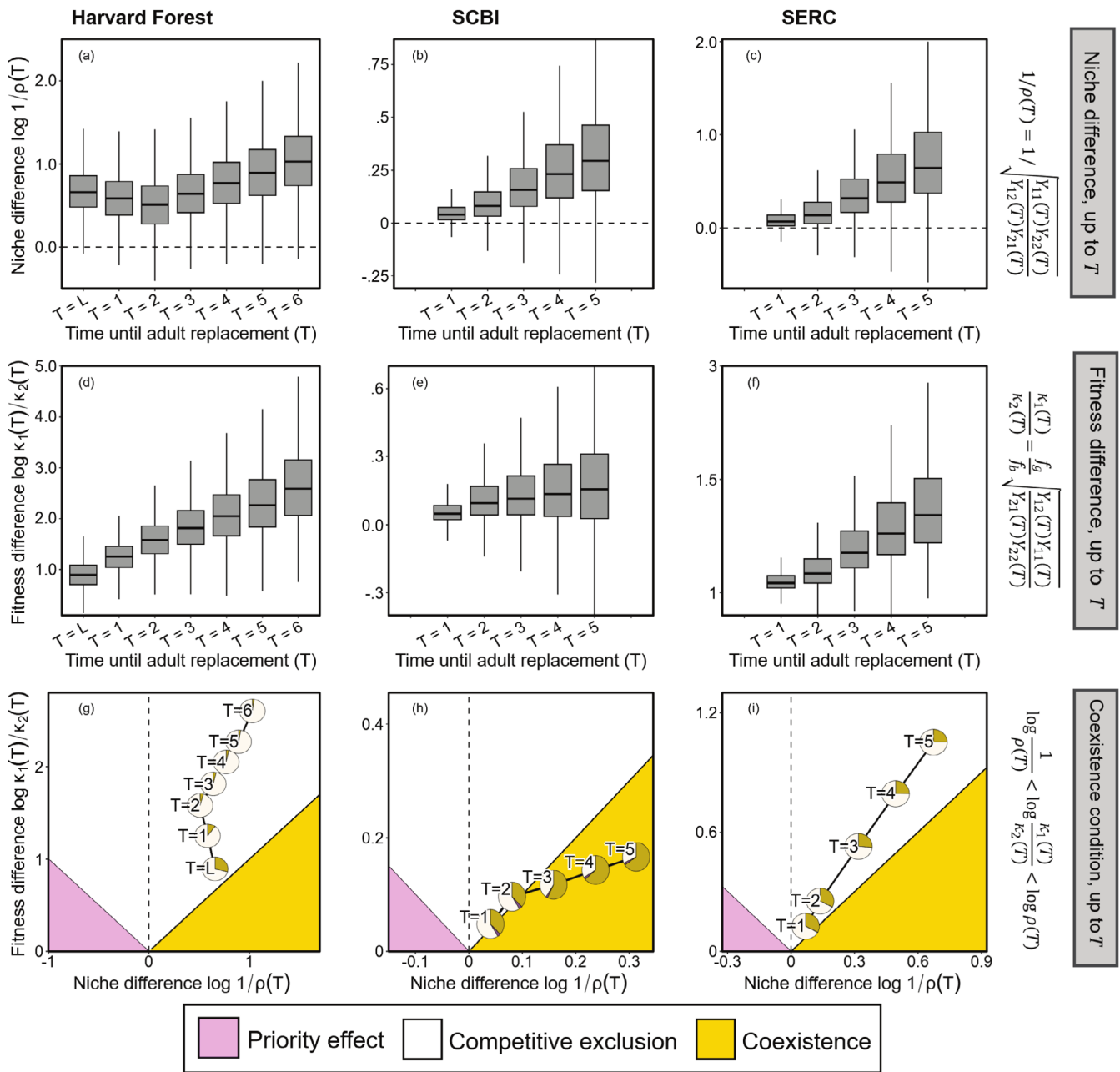


FIGURE 6 | Legacy effects increase niche differences, but fitness differences due to inter-specific variation in seedling survival often predict competitive exclusion. Each panel depicts niche differences (a–c), fitness differences due to inter-specific variation in seedling survival (d–f) or both (g–i) as a function of the time-to-replacement T , as defined in (Equation 7). Each panel can be interpreted in the same way as the matching panel in as Figure 5, except here the panels show niche and fitness differences for the combined effects of all time intervals up to T instead of those generated at each individual time interval separately. For example, $T = 5$ shows the niche (a–c) and fitness differences (d–f) stemming from live effects up until 5 years post-adult-mortality. Thus, juxtaposing $T = 1$ and $T = 5$ compares the niche and/or fitness differences from a single year of legacy effects (i.e., if the lottery took place a single year post-adult-mortality) to those generated over all years up to the 5th year of legacy effects. Species identities are the same as those in Figure 5.

strengthening of stabilising CDD after the initial 2 years since tree mortality, it is important to note that legacy CDD at 2–5 and 5–7 years was still weaker than stabilising CDD around living trees. Furthermore, we do not expect legacy CDD to continue to strengthen, nor last indefinitely, as this would eliminate any rare species advantage hypothesised by CDD, de-stabilising coexistence.

4.4 | Coexistence Implications

Some research indicates that CDD strongly promotes species coexistence (e.g., Terborgh 2012; Levi et al. 2019); other studies argue that CDD or Janzen-Connell dynamics are weak compared to differences in species' competitive abilities (Chisholm and Fung 2020). We found mixed results. We indeed found

legacy CDD almost always generated stabilising niche differences that increased with time (Figures 5–6). However, this stabilising force was often overwhelmed by interspecific fitness differences in seedling survival (Figure 6g,i), yielding competitive exclusion.

The fitness differences we measured reflect interspecific variation in a single stage-specific demographic parameter, seedling mortality. This approach is similar to Chisholm and Fung (2020), who found niche differences generated by CDD are weak relative to fitness differences parameterised with data on fecundity and low-density seedling recruitment. However, species experience trade-offs between life history stages (Muller-Landau 2010; Stearns 1989; Wright et al. 2010), which modulate key vital rates (fecundity, survival and growth). Life history trade-offs may equalise fitness differences that appear large when only a single life history stage or vital rate is measured (Chesson 2000). Thus, the stabilising niche differences we measured due to legacy CDD may still play an important role in maintaining coexistence at all sites if fitness is otherwise equalised.

4.5 | Caveats/Simplifying Assumptions

In our models, we assumed that the nearest canopy tree alone conditioned the seedling environment, excluding the effects of more distant, neighbouring trees. However, other, more distant, trees likely impacted seedling dynamics, as shown by spatially explicit neighbourhood analyses (Comita et al. 2010; Rinella and Reinhart 2018). This assumption likely underestimates the importance of CDD in determining outcomes, which increase in strength with spatial scale (Smith 2022). A next step is to consider how the spatial-temporal dynamics of legacy CDD affect forest diversity using spatially explicit analyses (Kalyuzhny et al. 2023). Our analysis included only a single species pair at each site. This complicates comparisons between sites, as it is difficult to distinguish between site-specific effects and species-pair effects. Future work that includes more than two species per forest site should help disentangle these effects.

4.6 | Further Considerations for Studying Legacy CDD

By showing that several species across multiple communities exhibit legacy CDD, this study raises several new questions. A plethora of studies have examined interspecific variation in negative conspecific density dependence (CDD) that arises from living neighbour trees. For example, species with faster growth rates (Zhu et al. 2018), smaller seed sizes (Lebrija-Trejos et al. 2016), intolerance to understory conditions (Kobe and Vriesendorp 2011), and species nearer to their range limits (Swenson et al. 2023) tend to be more sensitive to CDD. Considering the importance of tree mortality and gap creation to seedling recruitment (Canham 1989; Hubbell et al. 1999), variation in legacy CDD across functional traits and life-history strategies should disproportionately influence community assembly, especially considering that gaps are rare in many forests and most gaps close quickly (Marthens et al. 2008). Furthermore, with tree mortality increasing in some regions (McDowell et al.

2020), legacy effects during forest regeneration might become more pronounced.

More generally, our study adds to the growing literature on ecological memory (Ogle et al. 2015). We show that antecedent conditions continue to drive extant community dynamics for at least several years after a canopy tree has died. Future studies should examine the successional implications of legacy CDD. During successional changes, conspecifics tend not to replace following mortality but are more likely to replace other species (Pham et al. 2004). Additionally, the timescale of legacy CDD may interact with the generation time of species (e.g., the fast-slow continuum; Salguero-Gómez et al. 2016). Species that experience legacy effects that are short vs. long relative to their generation times likely experience CDD very differently (Piovesan and Biondi 2021). Legacy CDD, therefore, adds an additional spatial-temporal axis to successional dynamics. Legacy CDD may provide a mechanism for long-recognised and widely observed successional replacement patterns prevalent in ecological communities (Connell and Slatyer 1977).

Author Contributions

L.J.M., D.J.J., and D.J.B.S. conceived the study. L.J.M., D.J.J., S.B., J.L., and R.M.C. designed the sampling. L.J.M., S.B., B.W., and S.M. processed the remote sensing data. L.J.M. and D.J.J. collected field data. L.J.M., D.B., and S.M. conducted the statistical analysis. D.J.B.S. derived the mathematical models. L.J.M. and D.J.B.S. wrote the first draft with feedback from J.F.G., R.B., D.B., D.J.J., P.K., J.A.L., and J.L. All authors provided feedback and approved the final version.

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Data Availability Statement

All seedling data and code are publicly available on figshare: <https://figshare.com/s/b1bb900e97888589a863>.

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70197>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70197-sup-0001-DataS1.docx. **Data S2:** ele70197-sup-0002-DataS2.docx.