Received: 14 February 2024 | Revised: 30 May 2024 | Accepted: 25 June 2024
DOI: 10.1111/gcb.17432

Global Change Biology
WILEY

RESEARCH ARTICLE

Demographic but not competitive time lags can transiently amplify climate-induced changes in vegetation carbon storage

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Funding information
Princeton University Carbon Mitigation Initiative supported by bp; ETH Zurich

Abstract

How terrestrial ecosystems will accumulate carbon as the climate continues to change is a major source of uncertainty in projections of future climate. Under growth-stimulating environmental change, time lags inherent in population and community dynamic processes have been posed to dampen, or alternatively amplify, short-term carbon gain in terrestrial vegetation, but these outcomes can be difficult to predict. To theoretically frame this problem, we developed a simple model of vegetation dynamics that identifies the stage-structured demographic and competitive processes that could govern the timescales of carbon storage and loss. We show that demographic lags associated with growth-stimulating environmental change can allow a rapid increase in population-level carbon storage that is lost back to the atmosphere in later years. However, this transient carbon storage only emerges when environmental change increases the transition of adult individuals into a larger size class that suffers markedly higher mortality. Otherwise, demographic lags simply slow carbon accumulation. Counterintuitively, an analogous tradeoff between maximum adult size and survivorship in two-species models, coupled with environmental change-driven replacement, does not generate the transient carbon gain seen in the single-species models. Instead lags in competitive replacement slow the approach to the eventual carbon trajectory. Together, our results suggest that time lags inherent in demographic and compositional turnover tend to slow carbon accumulation in systems responding to growth-stimulating environmental change. Only under specific conditions will lagged demographic processes in such systems drive transient carbon accumulation, conditions that investigators can examine in nature to help project future carbon trajectories.

KEYWORDS
carbon storage, climate change, competition, demography, time lags, vegetation

1 | INTRODUCTION

Much of the uncertainty in the future climate projected by Earth System Models arises from the unknown future of the terrestrial carbon sink (Booth et al., 2015; Friedlingstein et al., 2014; Hubau et al., 2020). The amount of carbon stored in terrestrial vegetation has been increasing globally due to a combination of succession, and the effects of elevated CO_2 and warming (Hubau et al., 2020; Pan et al., 2011;

Pugh et al., 2019). There are, however, signs that the rate of carbon accumulation is beginning to decline (Brienen et al., 2015; Hubau et al., 2020), and whether terrestrial vegetation continues to act as a carbon sink (absorbing atmospheric carbon), or shifts to becoming a carbon source (releasing carbon) will determine whether these ecosystems dampen or enhance future climate change (Friedlingstein et al., 2014; Hubau et al., 2020). Yet, the extent to which population and community-level time lags impact these temporal dynamics in terrestrial carbon sequestration remains poorly resolved.

Temporal lags emerge in vegetation dynamics because the ecophysiological responses of individual plants to factors such as warming and elevated CO_2 do not translate simply into carbon storage at the ecosystem level (Jiang et al., 2019; Norby et al., 2005). Instead, these ecophysiological responses alter the growth and mortality of individuals, which in turn drive population and community dynamic processes, processes with embedded time lags (Block et al., 2022). For example, increasing the growth rates of individual plants drives demographic changes that can equilibrate slowly, with unexpected transient and long-term dynamics (Ezard et al., 2010; Haridas & Tuljapurkar, 2007; McGraw & Wulff, 1983; Townley et al., 2007). Indeed, Körner (2017) has argued that climate-induced increases in vegetation growth may only be temporary, because faster-growing individuals will complete their life cycle sooner, eventually leading to greater mortality and carbon release. The implied growth-survival tradeoff is commonly assumed among forest ecologists and can arise when faster-growing individuals enter size classes with greater mortality (Bigler & Veblen, 2009; Brienen et al., 2020; Friend et al., 2014; Needham et al., 2020). Such tradeoffs could play a central role in shaping transient vegetation carbon storage under environmental change (Brienen et al., 2020; Needham et al., 2020).

Other temporal lags emerge when environmental change differentially advantages one species over others, and competitive replacement rather than demographic turnover drives changes in carbon storage (Van Houtven et al., 2019). Consider, for example, two competitors differing in their potential to store carbon at the population level. Even with environmental change sufficient to allow one of the competitors to displace the other over the long term, the timescale for this competitive replacement, and the concomitant shift in ecosystem-level carbon storage, can be long (Block et al., 2022). This is especially so for perennial species in which existing adult individuals need to die before new individuals can take their place (Bond-Lamberty et al., 2014; Iida et al., 2014; van Mantgem et al., 2009). In sum, when environmental change increases plant growth rates, total carbon storage might lag behind, or alternatively get a transient boost, depending on the timescale at which the size structure and community structure of the plant system equilibrates.

Given the importance of the terrestrial carbon balance, a mechanistic framework is urgently needed to predict these short and long-term population- and community-level responses to global change. To build this framework, we can borrow from demographers, who have long understood that perturbing structured populations amplifies or attenuates population growth and other demographic measures relative to what would be observed in a population at its stable stage distribution (Caswell, 2007; Ezard et al., 2010; Haridas & Tuljapurkar, 2007; Koons et al., 2016; Townley et al., 2007). Much of this work focusses on the demographic response to perturbations, rather than temporally trending vital rates (but see Koons et al., 2016), and tends to apply to systems without density-dependent regulation (but see Caswell, 2007). Still, a consistent pattern emerging from this work is that the structure of a perturbed population can show transient dynamics that shape population features—including growth rate and size—that equilibrate long after the initial change. Similar results exist at the community level, where lagged effects of interactions generate transient dynamics very different than the long-term fate of the system (Tang & Allesina, 2014). Despite the potential of these demographic and competitive time lags to govern the ecosystem-level responses of vegetation to climate change (Friend et al., 2014; Körner, 2017; Needham et al., 2020; Pugh et al., 2019; Purves & Pacala, 2008), we lack a mathematical framework for testing and evaluating their role.

Here, we explore how temporal lags inherent in population and community dynamic processes may contribute to the trajectory of vegetation carbon storage in response to growth-stimulating environmental change. We adopt a demographic modeling approach to identify the conditions under which such lags can generate transient increases in carbon storage (as posed by Körner, 2017), versus simply slow its eventual rise. Although one can think of the model as applying to a population of woody plants stimulated by environmental change, our aim was to explore how demographic and competitive lags shape the response of a wide range of perennial vegetation. First, we present the carbon storage dynamics for a single-species model of vegetation responding to growth-enhancing environmental change. We show how demographic lags influence the trajectory of carbon storage by comparing the simulated trajectory of carbon to its trajectory in a system in which the structure of the population is in equilibrium with the changing environmental conditions. We then analyze a two-species vegetation model to evaluate how our single-species model conclusions about the contribution of demographic lags to carbon storage dynamics apply when interspecific competitive dynamics drive changes in size structure of the community.

2 | MATERIALS AND METHODS

2.1 | Single-species model of population and carbon dynamics

We explored the conditions under which simple single and multi-species models of vegetation are capable of generating transient carbon accumulation due to demographic and competitive lags. The simplicity of these models preserves our ability to derive deeper understanding through equilibrium solutions and analytical results, but also means that these models are not meant to represent a specific species or system. The equilibrium solutions possible with this approach prove particularly valuable for quantifying the effects of time lags on carbon storage because they allow us to project the counterfactual dynamics that would emerge if the system were always in demographic equilibrium with the changing environmental conditions. Meanwhile the analytical work allows us to draw conclusions irrespective of the specific parameterization. Our focus on demographic mechanisms also means that we did not model the many plant ecophysiological mechanisms that could underpin these demographic responses. Instead, the physiological effects of environmental change are implicit in changing vital rates through time.

For our single-species model (Figure 1), we analyzed a system of difference equations describing the dynamics on an annual time scale of a woody plant population composed of a number (or density) of seedlings/juveniles (U_t), small adults (B_t), and large adults (A_t) at time t. When individuals of these three classes die, they contribute to a pool of dead individuals (D_t).

$$U_{t+1} = r\left(m_B B_t + A_t\right) + s_U U_t\left(1 - \frac{g_U}{1 + \alpha\left(B_t + A_t\right)}\right), \tag{1}$$

$$B_{t+1} = \frac{s_U g_U U_t}{1 + \alpha\left(B_t + A_t\right)} + \left(1 - g_B\right)s_B B_t, \tag{2}$$

$$A_{t+1} = g_B s_B B_t + s_A A_t, \tag{3}$$

$$D_{t+1} = (1 - d)D_t + \left(1 - s_A\right)A_t + m_B\left(1 - s_B\right)B_t + m_U\left(1 - s_U\right)U_t. \tag{4}$$

The number of seedling/juvenile individuals (hereafter "juveniles") in the following year, U_{t+1}, is the sum of recruitment—the per adult recruitment rate r multiplied by the summed (and mass scaled) density of the two adult stages $\left(m_B B_t + A_t\right)$, and the surviving juveniles, $s_U U_t$, that fail to mature to adults (described by the density-dependent parenthetical term; explained in the next paragraph). The number of small adults B_{t+1} is the sum of the number of juveniles that survive and grow to the small adult stage (the first term of the summation), plus those small adults that survive and fail to grow to large adults: $\left(1 - g_B\right)s_B B_t$. The number of large adults, A_{t+1}, is the sum of the number of small adults that survive and grow to the larger class, $g_B s_B B_t$, plus the number of surviving large adults from the prior year, $s_A A_t$. Finally, the number of dead individuals, D_{t+1} (expressed in units of large adults) is the number of dead individuals the year prior multiplied by the non-decomposing proportion $(1 - d)$, and this is added to the number of newly dead juvenile, small, and large adults, each scaled by their mass relative to a large adult (m_U and m_B). All parameters are catalogued in Table 1, with simulation starting values explained in the next section.

Density dependence in the model only occurs in the rate at which adult individuals suppress juvenile growth. The proportion of surviving juveniles that grow to the adult stage is an innate growth rate g_U divided by the density of adults $\left(B_t + A_t\right)$ multiplied by an interaction strength α. Specifically, with increasing α, juveniles have increasing difficulty reaching the adult stage with a given number of adults. This would arise, for example, with increasing shading of the juveniles, which is known to have a strong negative impact on juvenile growth. Suppression of maturation for juveniles also reduces their survival by forcing individuals to spend greater time in this higher mortality life stage. While this form of density dependence follows from interactions in woody plant populations (Canham, 1988; Pacala et al., 1994), density-dependent regulations can emerge from interactions between other life stages (Yoda et al., 1963), and our model is flexible enough to include these other mechanisms as well. Without any density-dependent effects, the model could be expressed as a classic stage-structured matrix model of population growth (Supporting Information A).

By assuming that individuals in the population can be binned into one of several size classes—a major simplification of the size structure and growth increments of real populations—we enable analytical solutions to the system of equations (Supporting Information A). The system of three Equations (1–3) corresponding to the living stages can be solved for equilibrium values because the dynamics of

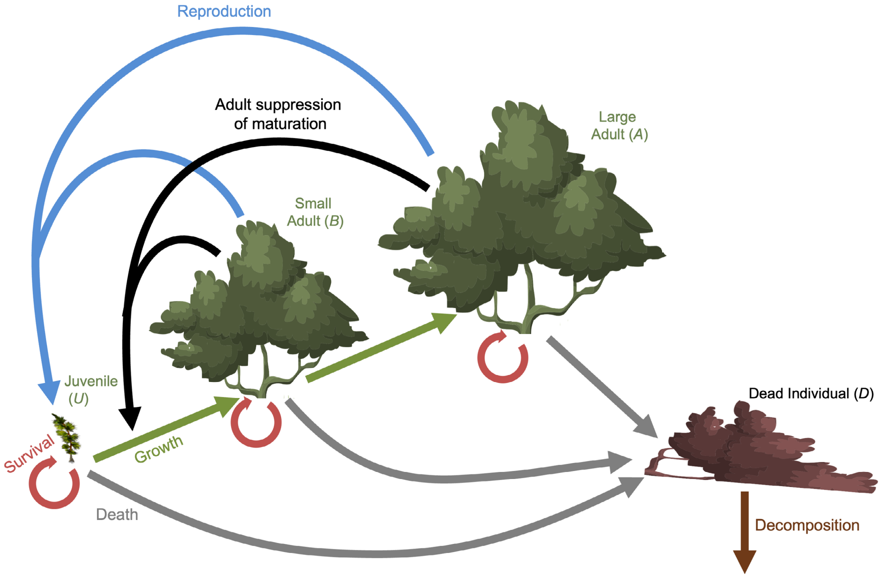

FIGURE 1 Single-species model (Equations 1–4). The model describes the dynamics of each of the four stages from left to right. All arrows show demographic transitions except the black arrows, which depict the effects of adults on juvenile growth to adults. OpenClipart-Vectors from Pixabay.

TABLE 1 Model parameters, starting values, and immediate and long-term effects of parameter increases on carbon storage (C) in a single-species population.

Parameter	Simulation starting value	Immediate carbon effect including lags (Supporting Information D)	Long-term carbon effect (Supporting Information E)
r juvenile recruitment per large adult	7	+	+
s_U juvenile survival	0.60	+	+
g_U[a] innate juvenile to small adult growth rate	0.05	+	+
α adult effect on juvenile growth	0.50	–	–
s_B small adult survival	0.98	+	+[b]
g_B[c] proportion of small adults growing to large adults	0.01	+	+/–[b]
s_A large adult survival	0.94	0	+
d decomposition rate of dead individuals	0.1	–	–
m_U mass ratio of juveniles to large adults	0.001	+	+
m_B mass ratio of small to large adults	0.70	+	+
b tons C per large adult	2.0	+	+

[a] Parameter rising under environmental change in Figures 3a,b and 4.

[b] Sign of the effect was determined through numerical rather than analytical methods.

[c] Parameter rising under environmental change in Figure 2.

the living stages depend only on one another. The number of dead individuals depends on the number of live individuals but has no feedback to their dynamics, and thus the equilibrium dead individual pool can simply be calculated from the equilibrium values of each live individual stage.

The model outlined thus far describes the dynamics of different individual stages in population dynamics units- density or numbers. However, model dynamics can also be expressed in carbon equivalent units, revealing how population dynamic processes affect the dynamics of carbon storage in the system (Supporting Information B). The total carbon in the system (C_{t+1}) at year $t+1$ is the sum of the carbon in the three living stages of the population plus that in the dead individual pool.

$$C_{t+1} = b\left(A_{t+1} + m_B B_{t+1} + m_U U_{t+1} + D_{t+1}\right), \tag{5}$$

b is the mass of carbon in a large adult, and as noted earlier, m_U and m_B are the proportional masses of a juvenile and a small adult relative to a large adult.

2.2 | Simulation approach and quantifying the effects of demographic lags

We used simulations in R version 4.4.0 (R Core Team, 2024) to evaluate the non-stationary dynamics of the system. We started each population at its equilibrium stage structure, then imposed an increasingly strong "press" perturbation by changing parameter values in each subsequent year, as arises in a global change scenario (as in Brienen et al., 2020). Although our analytical work on the model in Equations (1–4) will show that the central results presented here are, with few exceptions, independent of any reasonable parameterization, we demonstrate dynamics with parameters illustrative of a long-lived woody plant population.

Specifically, we began by assuming that larger adults have a lower survival rate (0.94) than smaller adults (0.98) (Table 1). These survival rates are the key parameters for many of the results emerging from our model and are consistent with values for a number of tree species in forests worldwide (Brienen et al., 2020; Hurst et al., 2011; Johnson et al., 2018). We also explored cases where adult survival rates are the same across the two size classes. We chose the remaining parameters to generate an equilibrium population that is numerically dominated by juvenile individuals (stage U) with one to two orders of magnitude fewer adults (stages B and A). Of the adults, the majority are of the smaller size (stage B), as growth of these individuals into larger adults (stage A) only becomes common under future environmental conditions. The number of dead individuals (stage D) approximately equals the number of large adults (stage A), which we achieve by setting the decomposition rate, d, equal to 0.1, a high value, but within the range noted by Chambers et al. (2000) for dead trees. To holistically assess how well the parameterization of our model aligns with stage-structured demographic models built for real populations of woody plants, we calculated the summed elasticities of the finite rate of increase to fecundity, growth, and survival (following Silvertown et al., 1993). We then compared our parameterized model to models for real tree and shrub populations in the COMPADRE Plant Matrix Database (2023). The results of this demographic analysis position our model system at the edge of natural woody plant systems in the three-dimensional life history space defined by the three elasticities (Supporting Information C).

We first simulated cases where environmental change increases adult growth rates through time, as expected with some effects of CO_2 fertilization (Norby et al., 2005) or longer temperate zone growing seasons (Jiang et al., 2019). To initiate a simulation, the number of individuals in each stage was set to their equilibrium values given the parameters in Table 1. We therefore assumed that the

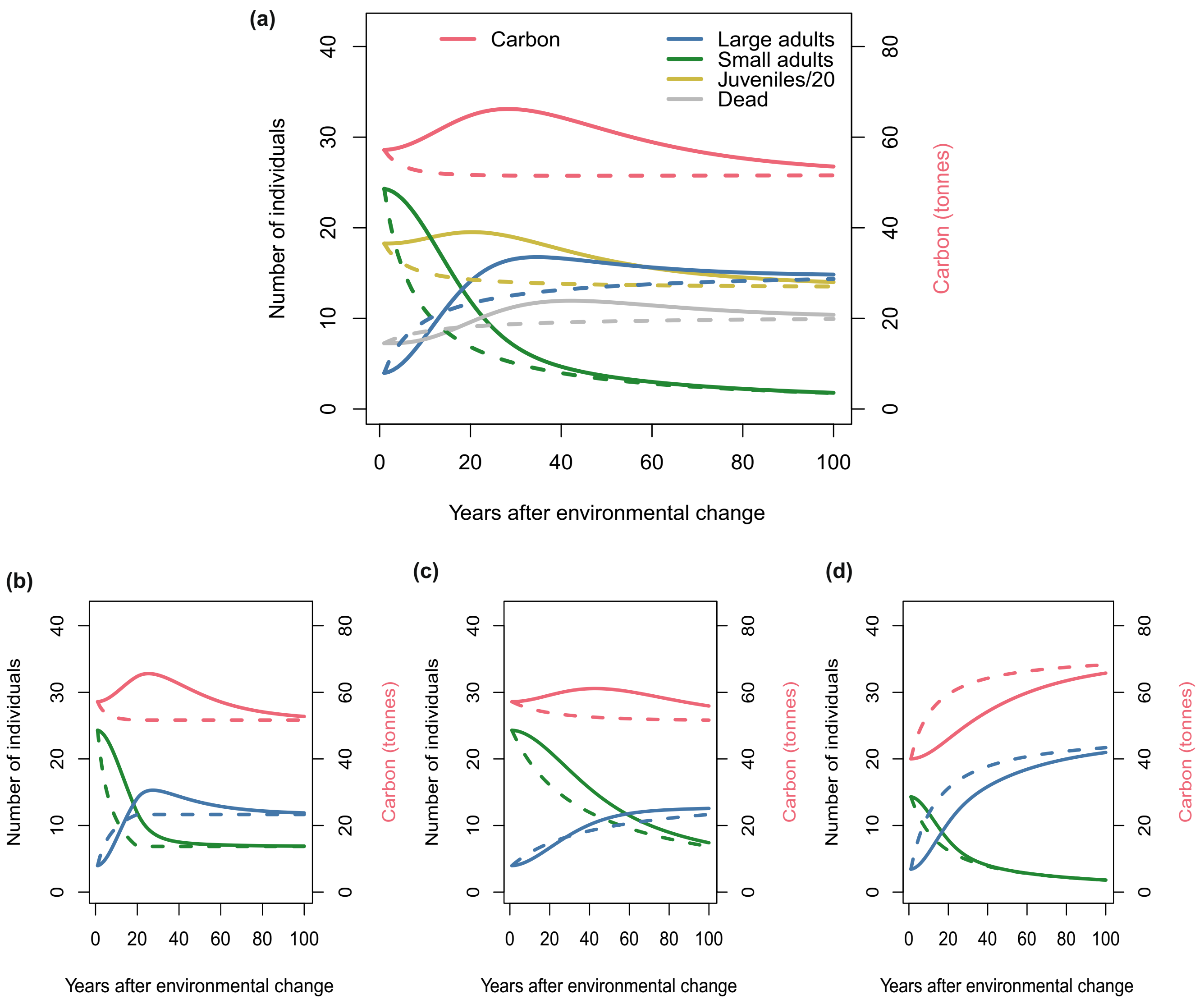

FIGURE 2 Trajectories of carbon storage under environmental change that increases the probability small adults grow to large adults (g_B). In (a), this growth rate linearly increases from 0.01 to 0.50 over 100 years of the simulation. In (b), the growth rate rises at the same rate as in A, but stops rising at Year 20, when the growth rate has reached 0.104. In (c), the growth rate takes 100 rather than 20 years to reach 0.104. In (d), the growth rate rises from 0.01 to 0.50 over 100 years, but the large and small adult survival rates are now equivalent at 0.96, rather than 0.98 and 0.94 for the small and large adults respectively, in panels (a–c). Solid lines show the dynamics allowing for demographic lags, while the dashed lines show trajectories assuming the population is in equilibrium with the environmental conditions of any given year. Note that the solid and dashed lines converge in panel (b) because the parameters stop changing after Year 20, and the system reaches equilibrium. All life stages of the population are shown in panel (a), but for clarity, the juvenile dynamics (which contribute little carbon storage) and dead individual dynamics are removed from panels (b–d).

initial environment shows no long-term trends prior to the initiation of growth-stimulating environmental change. We then linearly increased adult growth from the smaller to large size class over a 100-year period. This form of increase and lack of variance around the trend is not based on an empirically predicted trajectory, but was chosen to ensure that any complex dynamics that emerge over time are indeed driven by the internal population dynamics of the system, and not a complex forcing function. After demographic lag effects were quantified for these simpler scenarios, we also explored the effects of more realistic nonlinear changes, as well as the effects of simultaneously changing multiple vital rates. In particular, we explored the case where higher growth into the large adult class is associated with greater mortality in that class–one mechanism that can generate a growth- survival tradeoff (Brienen et al., 2020).

To quantify the contribution of the demographic lags to the trajectory of carbon storage, we compared the simulated trajectories to what would transpire were there no demographic lags in the system. If there were no demographic lags, the population would instantly reach its equilibrium size structure and carbon storage under the current environmental conditions and parameter values of each

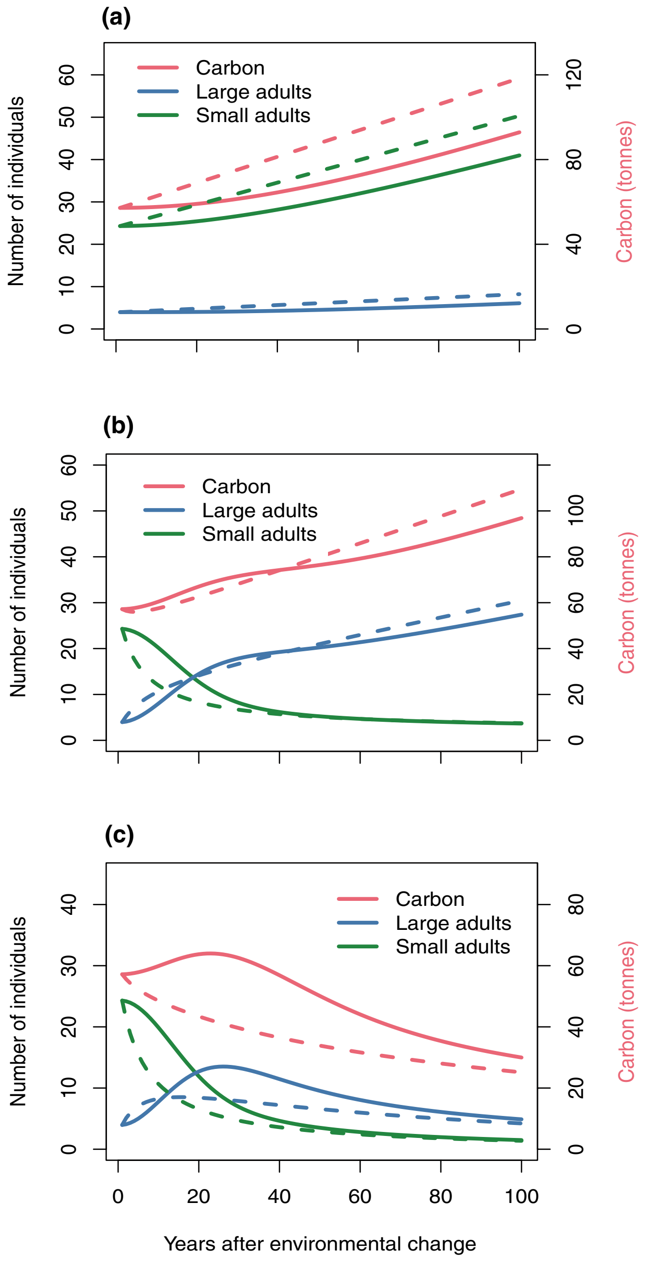

FIGURE 3 Trajectories of carbon storage under environmental change that (a). increases the probability that juveniles grow to small adults (g_U) from 0.05 to 0.10 over 100 years, and (b). simultaneously increases the probability small adults grow to large adults (g_B) from 0.01 to 0.50. In (c), environmental change increases the probability small adults grow to large adults from 0.01 to 0.50 over 100 years, while simultaneously decreasing large adult survival (s_A) from 0.94 to 0.84. Solid lines show the dynamics allowing for demographic lags, while the dashed lines show trajectories assuming the population is in equilibrium with the environmental conditions of any given year. For clarity, the juvenile and dead individual dynamics are not shown, but do contribute to the total carbon shown.

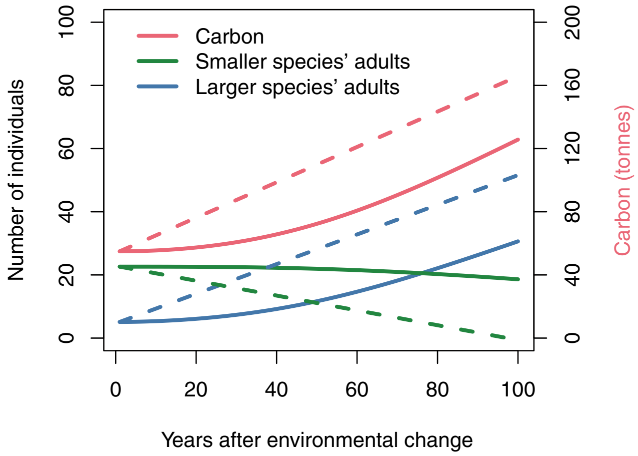

FIGURE 4 Trajectories of carbon storage in a two-species system under environmental change. Environmental change increases the probability that juveniles of the larger species grow to adults ($g_{U,i}$ for species i) from 0.05 to 0.15 over 100 years. Solid lines show the dynamics allowing for competitive lags, while the dashed lines show trajectories assuming the community is in equilibrium with the environmental conditions of any given year. For clarity, the juvenile and dead individual dynamics are not shown, but contribute to total carbon.

year. We obtained this "no lag" expectation by the calculating the equilibrium under the current parameter values at each year of the environmental change sequence. In other words, we explored the case where the demographic dynamics are very fast relative to the changing environmental conditions. The difference between the simulated trajectory of carbon storage and the "no lag" trajectory thereby quantifies the contribution of demographic lags to carbon storage at any given time point.

2.3 | Multispecies model of community and carbon dynamics

We next asked whether competitive displacement of a smaller *species* by a larger *species* has the same tendency to generate transient carbon storage as explored for growth from smaller to larger *individuals within species*. To be clear, we were not exploring whether our results based on shifts in size structure within species hold when multiple species simultaneously experience these same shifts, as we see little reason to think otherwise. Rather, we were testing whether competitive displacement between species can generate transient carbon storage in the same way as demographic transitions between stages within species.

To do so, we built a two-species version of our single-species model. Our two-species model allows a smaller adult species *j* to be competitively displaced by a larger adult species *i* under environmental change. Because this multispecies mechanism does not revolve around within-species size structure, which makes the model more complex to analyze, we modeled the two species, *i* and *j*, each with a single juvenile and single adult life stage, $U_{i,t}$ and $A_{i,t}$, respectively (a three-stage version is presented in Supporting Information G). The dynamics of species *i* competing with species *j* can be expressed as follows:

$$U_{i,t+1} = r_i A_{i,t} + s_{U,i} U_{i,t}\left(1 - \frac{g_{U,i}}{1 + \alpha_{ii} A_{i,t} + \alpha_{ij} A_{j,t}}\right), \tag{6}$$

$$A_{i,t+1} = \frac{s_{U,i}g_{U,i}U_{i,t}}{1+\alpha_{ii}A_{i,t}+\alpha_{ij}A_{j,t}} + s_{A,i}A_{i,t}. \tag{7}$$

All parameters have the same meaning as in Table 1, with the i and j additions to the subscripts indicating the species-specific rates and state variables. The three-stage single-species model in Equations (1–3), collapses to this two-stage model (minus the interspecific competition) by assuming zero growth from the smaller to larger adult stage ($g_B = 0$). This makes the smaller adult stage the terminal live stage (hence our renaming it A in Equation 7). The growth of juvenile individuals into adults is suppressed by both con and heterospecific adults with per capita effects α_{ii} and α_{ij}, respectively. Equations for the dynamics of species j are achieved by reversing the i and j subscripts in Equations (6 and 7).

The dynamics of dead individuals (D_t) and carbon (C_t) follow from the dynamics of species i and j, and were motivated by the same logic as the analogous single-species model in Equations (4 and 5).

$$\begin{aligned} D_{t+1} = {} & (1-d)D_t + (1-s_{A,i})A_{i,t} + m_{U,i}(1-s_{U,i}) \\ & U_{i,t} + m_{A,j}(1-s_{A,j})A_{j,t} + m_{U,j}(1-s_{U,j})U_{j,t}, \end{aligned} \tag{8}$$

$$C_{t+1} = b\left(D_{t+1} + A_{i,t} + m_{U,i}U_{i,t} + m_{A,j}A_{j,t} + m_{U,j}U_{j,t}\right). \tag{9}$$

The dead individual pool is the sum of the contributions of dead individuals from both stages of both species plus the undecomposed fraction of the prior year's dead individual pool. Dead individuals are expressed in units of species i adult equivalents, hence the new scaling factors which relate the mass of a species j adult to a species i adult ($m_{A,j}$), and a species j juvenile to a species i adult ($m_{U,j}$), and a species i juvenile to a species i adult ($m_{U,i}$). These scaling terms also enter into the dynamics for total carbon in the system (Equation 9), which is the sum of carbon in both living stages of both species plus the dead individual pool. The equilibrium abundances of the two live stages of both species, the dead individual pool, and carbon can be solved analytically, as shown in Supporting Information F.

We explored simulations where both species possessed the juvenile vital rates in Table 1. Following the survival rates of the small and large adults in the single-species model, the larger species i had a lower adult survival rate than species j ($s_{A,i}$=0.94 vs. $s_{A,j}$=0.98). The larger species had a higher per adult recruitment rate (r_i=14 vs. $r_j = 7$), and for both species, intraspecific was greater than interspecific juvenile suppression ($\alpha_{ii} = \alpha_{jj} = 1$ vs. $\alpha_{ij} = \alpha_{ji} = 0.5$). These recruitment and competition assumptions were necessary to allow species coexistence in the stationary period prior to environmental change, despite differences in their adult survival (but are not the driver of subsequent dynamics). Juvenile individuals of the two species are the same mass, and following the adult size differences in the single-species model, the adults of the smaller species were 0.7 times the mass of the larger species. These parameters combine to give a system dominated by the smaller species prior to parameter/environmental change, positioning us to ask how species turnover toward the larger species influences carbon storage in the short and long term. Note that in both the single and two-species model, a small adult is replaced by a larger adult with higher mortality. In the single-species model, its B being replaced by the larger A. In the two-species model, it is A_j being replaced by the larger A_i.

3 | RESULTS

3.1 | Requirements for transient carbon accumulation in single-species models

We found that under certain conditions, demographic lags induced by a linear increase in the rate at which smaller adults grow to larger adults (g_B) can increase carbon storage in the short term, but decrease carbon in the long term, what we refer to as transient carbon gain (solid red line in Figure 2a). For example, when the proportion of small adults growing to large adults with greater mortality linearly increases from 0.01 to 0.5 over 100 years (a steep trajectory, relaxed below), the population shifts from small to large adult dominance. Although population-level carbon storage has increased by over 16% in 30 years, this increase is only transient, because eventually, carbon storage drops to an even lower state than before the growth-stimulating environmental change. This occurs because of a population-level growth-survival tradeoff—the larger canopy individuals have a greater mortality rate in our model, which reverses the increase and eventually leads to less carbon storage in a population dominated by large adults.

We know that this transient carbon accumulation emerges because of a demographic time lag because the “no lag” carbon storage trajectory (dashed red line) shows that increasing adult growth rate reduces long-term carbon storage (due to the greater death rate of larger adults). The impact of non-equilibrium demographics can be visualized by comparing the solid lines in Figure 2a to the dashed “no lag” trajectories where the system is always in equilibrium with the small canopy individual growth rate. Transient carbon storage is maximized in year 29, a time when 22% of the carbon stored in the vegetation can be attributed to the demographic lag.

Increasing the proportion of small adults growing to large adults from 0.01 to 0.5 over 100 years, as in Figure 2a, represents a massive and rapid demographic shift. One could view this as a scenario where, in effect, environmental change induces a wholescale shift in the size of adults. Importantly, it is the rapid speed of this adult size transition, more than the eventual growth rate, that is critical to the magnitude of the spike in carbon in Figure 2a. Even if the growth rate of small adults increases by 0.00495 per year (as in Figure 2a), but only until year 20 (stopping at a stable 0.104 probability small adults mature to large adults), the dynamics of the system remain very similar (Figure 2b). If instead, that growth rate takes 100 years to reach a value of 0.104, transient carbon storage persists but the spike is smaller with only a 6.9% rise in carbon before its downward trajectory (Figure 2c). However, all of these results generating transient carbon storage depend critically on the greater mortality of the larger adults (0.94 survival probability vs. 0.98 for smaller adults). If we assume that the large adults have the same survival as the small adults, the entire mechanism behind the lagged loss in carbon disappears, and carbon storage monotonically rises through time (Figure 2d), lagging its eventual fate.

Although we have presented one scenario where non-equilibrium demographic dynamics generate transient carbon storage, this leads to the natural question of how general or parameter-dependent this outcome might be. In particular, the modeled scenario in Figure 2 depends specifically on increasing the growth rate of adults (g_B). We next assess whether changes in other demographic rates also generate transient carbon storage. To do so, we evaluated partial derivatives that quantify changes in carbon storage with respect to changes in individual demographic parameters. Two different sets of partial derivatives were quantified to capture either the short-term impacts of parameter changes (including demographic lags), or their long-term impacts on equilibrium carbon storage. The first set of partial derivatives (detailed in Supporting Information D) reveal how next year's carbon stock changes with respect to each parameter, assuming the system is initially at equilibrium. This partial derivative allows for demographic lags, and can be determined analytically. The second set of partial derivatives is with respect to the *equilibrium* carbon storage (Supporting Information E), and sometimes requires visual inspection of the equation or numerical evaluation. The signs of these two sets of partial derivatives (Table 1) reveal whether increasing each vital rate or interaction coefficient will increase or decrease carbon storage in the short term and long term. To make our calculations, we always assumed that the system that has equilibrated to the environment prior to parameter/environmental change, matching our simulations.

A comparison of the sign of the short versus long-term effect of increasing each vital rate or interaction strength showed that only changes in the growth rate of small canopy individuals (g_B) can cause short-term carbon gain and long-term carbon loss (Table 1). Indeed, the sign of the short-term effect of increasing small adult growth on carbon storage is always positive, while the long-term effect can be positive or negative in sign. Negative long-term effects depend on the larger adults having greater mortality rates than the smaller adults, as we assumed in the simulations generating Figure 2a–c, but not Figure 2d (see Supporting Information E). Changes to all other vital rates and the interaction coefficients have short- and long-term effects on carbon storage with the same sign (Table 1), indicating that demographic lags in our model cannot qualitatively reverse short-term carbon gains or losses. One vital rate, adult survival has zero short-term effect because death in our model does not immediately reduce its mass; this only happens in years after death during the decomposition of dead individuals. In sum, we found that short-term carbon storage followed by long-term carbon release requires two conditions (i) a life history wherein mortality is in later, larger life stages (senescence) and (ii) environmental change causes an increased rate of growth into these later, larger life stages. Together these conditions generate a growth-survival tradeoff for the population (Brienen et al., 2020). Linear changes in all other vital rates in our model could not generate both short-term carbon gain and equilibrium carbon loss.

3.2 | Demographic lags that slow carbon accumulation

Even when the short- and long-term effect of vital rate change share the same sign in our partial derivative analysis (Table 1), the magnitude of these effects may differ greatly, predicting an important quantitative rather than qualitative effect of demographic lags. In general, and as might be expected, carbon dynamics resulting from linear changes in these parameters through time are a lagged version of the long-term "no lag" response. For example, if environmental change increases the rate at which juveniles grow to small adults (g_U) from 0.05 to 0.10 over 100 years, carbon dynamics including lags (Figure 3a solid line) would increase at a slower rate than the "no lag" dynamics (shown by the dashed line). Of course, the trends depicted in Figure 3a follow from our assumption that environmental change linearly increases the vital rates over time. In reality, such demographic trends cannot go on indefinitely; internal physiological limits and density-dependent interactions among adult individuals would eventually limit vital rates.

3.3 | Effects of simultaneous changes in multiple vital rates

Our results thus far have shown how carbon storage responds to changes in a single demographic rate at a time, but in reality, environmental change will simultaneously affect multiple rates, and likely foster more complex dynamics. Without the partial derivative solutions to bound the possible dynamics, the outcomes of such simultaneous changes are difficult to exhaustively explore. Still we can use simulations to explore this complexity. For example, the transient carbon accumulation arising from increasing small adult growth (as shown in Figure 2a) can be overwhelmed over time by a simultaneous increase in the innate growth rate of juveniles to the adult class (Figure 3b). In this scenario, demographic lags initially cause the system to accumulate more carbon than would occur without such lags, but this effect reverses at Year 40, and demographic lags retard the system's ability to reach its carbon storage potential.

We also found that reductions in large adult survival alongside rising growth into that large adult stage—a second mechanisms behind a growth-survival tradeoff—causes the contribution of demographic lags to carbon storage to grow from the maximal value of 22% in Figure 2a to 37% (Figure 3c). Regardless of the operation of demographic lags, carbon storage in this scenario declines over the 100 years of environmental change, as the forest cannot sustain its carbon with increasing mortality rates. These declines follow from the fact that the rising growth rate forces more individuals into the larger size class, making the population as a whole more vulnerable to the declining survival.

3.4 | Multispecies results

Our intuition suggested that the same conditions that induced transient carbon storage in the single-species population should also apply in multispecies communities assuming environmental change causes a smaller, high survival species to be replaced by a larger, lower survival species. But this is not what we found. Although environmental change that favors the larger species does increase carbon storage, the carbon trajectory including lags never exceeds the "no lag" carbon storage in the system, nor does carbon storage ever decline. More specifically, linearly increasing the larger species' juvenile to adult growth rate (g_{Ui}) from 0.05 to 0.15 over 100 years, as might arise from a species-specific response to environmental change, increases the dominance of the larger species through time (Figure 4). But unlike the carbon trajectory in the analogous single-species model (Figure 2a), we saw no rapid short-term carbon accumulation associated with the increased dominance of the larger competitor species, nor a long-term decline in carbon storage once that species became dominant. Instead, the compositional shift in the population from the smaller to the larger species increased carbon storage in both the short and long term. The carbon storage trajectory including demographic and competitive lags is simply a slower version of the long-term trajectory; carbon stored at any time point (the solid line in Figure 4) is far less than the eventual storage after the demographic and community dynamics lags pass through the system (the dashed line in Figure 4).

Stimulating the demographic performance of the larger, higher mortality species always increases long-term carbon storage because the demographic changes required for its rise to dominance in our model effectively guarantee greater carbon storage. This can be understood by comparing expressions for equilibrium carbon storage and equilibrium relative abundance. As we show in Supporting Information F, the aggregate innate demographic potential of each species *i*, integrating growth, survival, and recruitment terms, can be expressed as η_i, a rate that increases with environmentally induced increases in any component vital rate. The equilibrium abundance of the larger species (A_i^*) rises linearly with its demographic potential η_i as shown by the following expression (Supporting Information F):

$$A_i^* = \frac{\alpha_{jj}}{\alpha_{ii}\alpha_{jj} - \alpha_{ij}\alpha_{ji}} \left(\eta_i - \frac{\alpha_{ij}}{\alpha_{jj}} \eta_j \right). \qquad (10)$$

Meanwhile, the carbon stored in the two-species community at equilibrium is the following (obtained by substituting Equation (10) into Equation (9), and assuming a negligible carbon contribution of juveniles):

$$C^* = b\left(D^* + \frac{\left(\alpha_{jj} - m_{A,j}\alpha_{ji}\right)\eta_i + \left(m_{A,j}\alpha_{ii} - \alpha_{ij}\right)\eta_j}{\alpha_{ii}\alpha_{jj} - \alpha_{ij}\alpha_{ji}} \right). \qquad (11)$$

Thus, increasing η_i, the demographic potential of species *i*, not only increases the equilibrium abundance of species *i* (Equation 10), but also increases total carbon storage in live biomass at equilibrium (Equation 11). In other words, it is difficult for growth-stimulating environmental change to favor the larger tree species without also increasing carbon storage in the stand.

The main requirement for this result is that $\alpha_{jj} / \alpha_{ji} > m_{A,j}$ a condition likely to hold given that the suppressive effects of competitors are often a saturating function of competitor mass (Harper, 1977). Also required, and something we already assumed in all our multispecies simulations, is some nonzero stabilizing niche difference between the competitors $\left(\alpha_{ii}\alpha_{jj} > \alpha_{ij}\alpha_{ji}\right)$. Taken together, this analysis indicates that in our model, when environmental change increases the competitive ability of a larger species with higher mortality rates, that species' abundance and stand-level carbon storage will both increase, preventing the possibility of transient carbon storage. Finally, we note that the contrasting transient carbon storage results in the single-species versus multispecies model are not an artefact of the additional life stage in the single-species model. The multispecies model with three life stages (equivalent to the number of stages in the single-species model) produces results (in Supporting Information G) very similar to the two-stage version in Figure 4.

4 | DISCUSSION

When considering how demographic and competitive lags influence the trajectory of carbon storage under growth-stimulating environmental change, a natural expectation is that these lags would simply slow the rate at which carbon stocks reach their eventual value. And indeed, our results support this default expectation for environmental effects on most demographic rates in our single and multispecies models. Nonetheless, the recent proposition that demographic lags could yield far more complex carbon trajectories (Brienen et al., 2020; Friend et al., 2014; Körner, 2017), including transient carbon gain, necessitates quantitatively exploring the conditions under which these alternative trajectories might emerge. We found that transient carbon storage can emerge in our single-species model. However, far from a universal phenomenon arising from demographic lags, transient carbon storage only emerged under rather specific assumptions about the life stages affected by global change and the existence of particular within-species tradeoffs in vital rates that amount to a growth-survival tradeoff.

4.1 | Demographic dynamics

In line with previous expectations, we found that carbon storage could increase in the short term when environmental change increases the rate at which adults grow to a larger size class, even when those larger adults have higher mortality. This carbon accumulation, however, is temporary and will be limited to the period after adults have begun to grow larger, but before their large size causes them to die in significant numbers. Eventually, the larger adults thin to a point that overall population carbon storage declines. Demographic life history theory has established that a disequilibrium between the vital rates and stage structure of a population can transiently amplify or attenuate the population growth rate (Caswell, 2007; Ezard et al., 2010; Haridas & Tuljapurkar, 2007; Koons et al., 2016; Townley et al., 2007). Our result extends this transient effect to carbon accumulation in a system with continuously changing vital rates as might be expected under environmental change.

Importantly, we found that this transient carbon storage dynamic only emerged under a very narrow set of conditions—specifically that environmental change stimulates growth and the species' life history exhibits senescence whereby the largest life stages experience markedly higher mortality; this generates a growth-survival tradeoff for the population (Brienen et al., 2020). If the large adults did not suffer greater mortality, or if environmental change stimulated a vital rate other than adult growth, we saw no transient carbon gain followed by long-term loss. This conclusion emerges from both simulations and analytical expressions for the effects of a small change in each vital rate on transient and long-term carbon storage (Supporting Information C and D).

Determining whether the conditions for transient carbon gain are general or common in nature eventually requires examining how multiple species demographically respond to environmental change. Still, because several prior data-driven modeling approaches have come to similar conclusions about the potential for demographic lags to derive transient carbon gain, our results could be quite general. First, forest stands have long been known to overshoot their carrying capacity (Jump et al., 2017), a process similar to the one generating transient carbon storage in our model. Second, size-dependent mortality is known to constrain the increased carbon storage resulting from rising growth rates (Needham et al., 2020). Third, and even more to the mechanism of our model, Brienen et al. (2020) simulated the stand dynamics of black spruce with a growth-survival tradeoff directly informed by tree ring data. Similar to our model result, their empirical projection shows that a 50 year "press" perturbation that increasingly stimulates growth initially causes spruce individuals to achieve larger stem diameters, which increases carbon storage. However, as in our model, these larger individuals have higher mortality rates, which subsequently reverses the carbon gain. Complementary to Brienen et al. (2020), our approach incorporates multigenerational dynamics and equilibrium solutions that allow quantitative attribution of the carbon storage to demographic lags. Regardless, the fact that two approaches coming at the problem from different perspectives—a population demographic approach and a tree ring data-driven approach—come to similar conclusions speaks to the possible generality of those conclusions.

Even if nature does not align with the strict requirements for transient carbon gain we have identified, lags still might play a subdominant role in carbon trajectories. For example, if larger adult individuals show only modestly greater mortality, we might expect demographic lags to help store carbon in the short term, before the larger individuals begin to die. Similarly, other changing factors might conceal demographic lag effects, including the simultaneous response of other life stages to environmental change. For example, in many populations, the younger individuals (equivalent to juveniles in our model) might be expected to experience the greatest growth response to environmental change. This would not prevent demographic lags arising from dynamics at the adult stage, but it could prevent them from reversing carbon gain, as shown in Figure 3b.

4.2 | Community dynamics

We hypothesized that the transient carbon storage produced by shifting demography at the population level could be replicated by shifting species composition at the community level. However, in contrast to this expectation, the changes in the larger species' demographic rates necessary to shift relative abundance in its favor, always made this species more capable of storing carbon at the community level. Thus, carbon storage monotonically increased over time as the composition of the community gradually shifted toward a species with higher carbon storage capacity, and competitive lags only delayed this increase.

The contrast between the transient carbon gain in the single-species model (Figure 2a) and slower but persistent carbon gain in the multispecies model (Figure 4) raises two questions. First, *why is there little immediate carbon gain when the vital rates of the larger competitor species increase?* (carbon storage is roughly flat over the first 30 years of the simulation). The answer is that increasing adult size and carbon storage via competitive replacement takes considerably longer than simply maturing into a larger individual from a smaller one, as occurs in the single-species model. In the multispecies system, in fact, replacement of the smaller species requires its death, which is slow given its 0.98 annual survival rate. As a consequence, species' abundance trajectories with and without demographic and competitive lags can differ considerably (the solid vs. dashed lines in Figure 4). Even though conditions by Year 100 in Figure 4 would cause the smaller species to be nearly eliminated from the community in the long term (the green dashed line is near zero abundance), this smaller species has only modestly declined over the 100-year period (the solid green line), and its intact canopy hinders the rise of the larger competitor.

The second question raised is *why is there no long-term loss in carbon storage when the larger species with a greater mortality rate gains dominance?* The answer follows from the fact that, in the single-species model, the transition from smaller to larger adults depends simply on the growth rate from small to large trees (an imposed parameter) and has nothing to do with either stage's ability to store carbon at the population level. By contrast, in the multispecies model, increasing competitive dominance arises from superior demographic potential, the same attribute that tends to make the competitive dominant better able to store carbon at the population level. In other words, it is difficult to increase the competitive ability of the larger species i through time without also increasing carbon storage at the community level.

Our results suggest that competitive (and most demographic) lags will slow the carbon accumulation associated with any rise in dominance of larger woody plant species.

For a real-world scenario, Van Houtven et al. (2019) project rising abundance of red maple, chestnut oak, and other trees in the northeastern United States under environmental change, alongside a rise in carbon storage. Competitive (and demographic) lags should slow this carbon accumulation. However, competitive lags can also have the reverse effect on carbon when the increasingly dominant species reduce carbon storage. Lianas, which are both competitors and parasites, are increasing in abundance in many tropical forests and are thought to decrease carbon storage at the stand level (Meunier et al., 2021). In this scenario, demographic and competitive lags should slow the carbon loss.

4.3 | Future extensions and conclusions

Our model, and its key assumptions noted in the methods suggest several interesting questions for future study. First, how continuous size variation, in contrast to the discrete size classes of our model influences the likelihood of demographic lags is an important question for subsequent work. To this end, integral projection model approaches (Easterling et al., 2000), in which size is a continuous variable predicting demographic transitions, could be modified to address the same questions raised in this paper (but see Doak et al., 2021). Similarly, our model assumes adults suppress the maturation of juveniles, but whether different forms of interspecific competition differ in their propensity to generate transient carbon storage is an interesting and open question. Finally, given that our model is not parameterized with information from a particular population or species, future work could tailor model parameters to specific life histories for individual populations, revealing the potential for transient carbon gain in different demographic contexts (as in Brienen et al., 2020).

Understanding the role of time lags in shaping trajectories of carbon storage is important for predicting the future of the land sink (Friend et al., 2014; Körner, 2017). Our work supports recent arguments that demographic lags can contribute to short-term carbon gains that gradually subside over time (Brienen et al., 2020; Körner, 2017). However, demographic lags remain challenging to incorporate into predictions of land carbon storage because they are overlayed on vegetation's more rapid ecophysiological adjustments to changing environmental conditions. In fact, the role of demographic time lags was highly apparent in our work because we forced the system with a simple linearly increasing growth response over time. The more complicated reality of nonlinear ecophysiological responses to multiple global change agents, which themselves are changing nonlinearly with time, makes the contribution of demographic and community dynamics lags particularly challenging to quantify. How might we meet this challenge?

We believe that the spirit of the modeling approach we have taken here, where transient responses to changing environmental conditions are compared to the dynamics of a system instantly equilibrating to environmental conditions (the "no lag" case) is broadly applicable to quantifying the contribution of lagged vegetation processes in more complex models tailored to specific ecosystems, including models of forest dynamics (see Block et al., 2022 for an application in alpine vegetation). Although the analytical equilibrium solutions to our models are convenient, simulation approaches can achieve the same end for complex population or community models, with the only limit being computation time. Regardless of the best path forward, our work supports the hypothesis that incorporating demographic lags into projections of carbon storage may be important for accurately characterizing future carbon dynamics.

AUTHOR CONTRIBUTIONS

Jonathan M. Levine: Conceptualization; formal analysis; funding acquisition; investigation; methodology; writing – original draft; writing – review and editing. **Janneke HilleRisLambers:** Investigation; methodology; writing – review and editing. **William K. Petry:** Formal analysis; investigation; methodology; writing – review and editing. **Jacob Usinowicz:** Investigation; methodology; writing – review and editing. **Thomas W. Crowther:** Conceptualization; investigation; methodology; writing – review and editing.

ACKNOWLEDGMENTS

JML acknowledges funding from the Carbon Mitigation Initiative at Princeton University supported by bp. All authors acknowledge funding from ETH Zurich.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The code that generates all of the simulation results in this study is openly available in figshare at https://doi.org/10.6084/m9.figshare.26198024. The simulated data in Figures 2–4 are openly available in figshare at https://doi.org/10.6084/m9.figshare.26224172.v1.

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SUPPORTING INFORMATION

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

How to cite this article: Levine, J. M., HilleRisLambers, J., Petry, W. K., Usinowicz, J., & Crowther, T. W. (2024). Demographic but not competitive time lags can transiently amplify climate-induced changes in vegetation carbon storage. *Global Change Biology*, *30*, e17432. https://doi.org/10.1111/gcb.17432