Maintenance of high diversity in mechanistic forest dynamics models of competition for light

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Running Head: light competition and forest diversity

Open Research Statement: No data were collected or used for this study. The code is available in the supplementary material

Abstract

Although early theoretical work suggests that competition for light erodes successional diversity in forests, verbal models and recent numerical work with complex mechanistic forest simulators suggest that disturbance in such systems can maintain successional diversity. Nonetheless, if and how allocation tradeoffs between competitors interact with disturbance to maintain high diversity in successional systems remains poorly understood. Here, using mechanistic and analytically tractable models, we show that a theoretically unlimited number of coexisting species can be maintained by allocational tradeoffs such as investing in light-harvesting organs vs. height growth, investing in reproduction vs. growth or survival vs. growth. The models describe the successional dynamics of a forest composed of many patches subjected to random or periodic disturbance, and are consistent with physiologically mechanistic terrestrial ecosystem models, including the terrestrial components of recent Earth System Models. We show that coexistence arises in our models because species specialize in the successional time they best exploit the light environment and convert resources into seeds or contribute to advance regeneration. We also show that our results are relevant to non-forested ecosystems by demonstrating the emergence of similar dynamics in a mechanistic model of competition for light among annual plant species. Finally, we show that coexistence in our models is relatively robust to the introduction of intraspecific variability that weakens the competitive hierarchy caused by asymmetric competition for light.

Key words/phrases: Coexistence; Forest succession; growth-mortality tradeoff; Light competition; Terrestrial ecosystem model

Introduction

One of the most accessible examples of rapid community dynamics in nature is the species turnover that occurs during secondary succession in a forest. After severe disturbance, dominance shifts from relatively short to relatively tall species with a series of repeated and rapid competitive exclusions, each taking place within a single generation (Horn 1974; Huston & Smith 1987). Competition for light is typically the dominant cause of species turnover when forest succession is rapid, although competition for water and nutrients is undoubtedly also important in many forests. Rapid competitive exclusion happens when all individuals of a species become overtopped by taller competitors, because of the 10-100 fold drop in light intensity and corresponding large decrease in carbon gain. Succession, however, raises a long-standing coexistence puzzle: if succession predictably leads to the exclusion of earlier taxa, how is the diversity of species observed over the successional sequence maintained?

Despite decades of competition theory targeting succession (Horn 1975; Tilman 1985; Kohyama 1993; Harte *et al.* 1999), we do not have an analytically tractable mechanistic theory for the maintenance of successional diversity in systems structured by light competition. There are several reasons for this gap. First, light is not an easily partitioned resource, and thus most models of light competition between trees predict little coexistence, leading to speculation that light competition is simply not conducive to high plant diversity (Barot & Gignoux 2004; Nevai & Vance 2008; Parvinen & Meszéna 2009; Gravel *et al.* 2010). Second, existing models that do predict high diversity through a successional process, such as those with a competition-colonization tradeoff (Levins & Culver 1971; Horn & MacArthur 1972; Tilman 1994; Kinzig *et al.* 1999; Arora & Boer 2006) or disturbance-maintained spatial and temporal environmental heterogeneity (Horn 1975; Connell 1978; Chesson 2000a), are highly abstract, and at least as presented in the original papers, not consistent with the mechanisms that drive forest succession (Pacala & Rees 1998). Verbal models such as those that underpin the Intermediate Disturbance Hypothesis are not intended to explain the high observed successional diversity, but rather the qualitative pattern of elevated diversity at intermediate levels of disturbance (Bongers *et al.* 2009). Third, an analytically tractable and mechanistic theory of the maintenance of successional diversity is mathematically challenging. Individual trees range in stature by five or six orders of magnitude during succession, which implies the need for a size-structured model (Kohyama 1992). Even more challenging, mechanistic modeling of succession requires that one solve nonlinear differential equations for the system's time-dependent solution to predict compositional turnover. Such solutions are analytically impractical for almost all nonlinear systems, including the seemingly simple Lotka-Volterra competition equations. Without a time-dependent analytical solution, it is impossible to rigorously connect the functional traits of trees and the tradeoffs between them to coexistence mechanisms in successional systems. Resolving these gaps in understanding with analytical theory is important for better resolving the influence of terrestrial vegetation on climate in Earth System Models (ESM's) because critical ecosystem functions in ESM's are affected by the amount of successional diversity they contain (Rüger *et al.* 2020).

One path forward involves building models simple enough to provide analytical solutions but complex enough to include the key elements of the successional process. Because competition for light is highly asymmetric (Weiner 2012), existing simple competition models for a single resource (MacArthur 1970; Tilman 1994) are not sufficient for this task. At the other end of the complexity spectrum, individual-based, size-structured forest models of asymmetrical competition for light are highly successful in reproducing successional dynamics (Shugart *et al.*

1992; Botkin 1993; Pacala *et al.* 1993; Huth *et al.* 1996). Nonetheless, their predictions are difficult to apply to the successional coexistence problem because the models are both analytically intractable and computationally expensive. These models often predict the co-occurrence of multiple plant species through the end of a numerical simulation, but it is not clear that this represents deterministic coexistence (Koven *et al.* 2019; Fisher & Koven 2020; Martínez Cano *et al.* 2020). In the simulations of Rüger *et al.* (2020) for example, fast-growing species were excluded, but this still took 400-500 years. In contrast, Falster *et al.* (2017) built a numerical simulation model fast enough to convincingly demonstrate species coexistence.

Empirical and theoretical studies of forest successional diversity have traditionally focused on the shade-tolerance axis when aiming to explain coexistence (Grubb 1977; Kohyama 1993; Pacala *et al.* 1993; Hubbell *et al.* 1999; Wright *et al.* 2010). Indeed, many plant ecologists describe forest succession as a shift from species that grow quickly in full sun, but have low understory survival, to species with low high-light growth and high low-light survival. The many reported examples of this growth-mortality tradeoff are reviewed in Russo et al. (2020). Falster et al., (2017) found that a growth-mortality tradeoff could, by itself, generates stable coexistence among a small number of trees species. However, interspecific variation in the size at which trees divert carbon from growth to reproduction enabled a much higher diversity of coexisting species in the same model, and when combined, the growth-mortality and reproduction-growth tradeoffs maintained high diversity of shade tolerant species, as is observed in tropical forests. These results are consistent with recent suggestions that the growth–mortality tradeoff is not a sufficiently general mechanism for coexistence in highly diverse forests (Russo *et al.* 2020), and that other life-history tradeoffs or a combination of them might drive the assembly of diverse communities (Salguero-Gómez *et al.* 2016; Rüger *et al.* 2018). Resolving how these and other tradeoffs maintain the diversity of competing species requires an analytical model of successional diversity for species competing for light.

In this paper, we produce analytically tractable mechanistic models of successional diversity where species compete only for light in a successional mosaic of patches that are periodically or randomly disturbed. To do so, we extend the single-species forest model of Farrior *et al.* (2016) to an arbitrary number of species, and also introduce a physiological sub-model that predicts the growth, mortality and reproduction of each individual plant from the plant's light-limited carbon economy. Farrior *et al*. (2016) developed arguably the simplest analytically tractable formulation using two approximations that successfully scale-up individual-based dynamics in forest and climate models - the ecosystem demography (ED) approximation (Moorcroft *et al.* 2001), which handles the successional mosaic created by gap formation and recovery, and the perfect plasticity approximation (PPA) (Strigul *et al.* 2008), which greatly simplifies the mathematics of trees overtopping one another.

Analysis of the models explains how any one of four different interspecific tradeoffs among plant vital rates can maintain successional diversity, by which we mean stable coexistence in a successional mosaic without external seeds input, with each species achieving its highest relative biomass at a different time following disturbance:

I) "Up vs. Out" is the tradeoff between carbon allocated to crown area expansion vs. stem height growth (Uyehara 2019). Crown growth in full sun yields a nonlinear increase in energy harvesting for reproduction, but height growth keeps a plant from being overtopped by neighbors, which would greatly slow energy harvesting.

II) “Growth vs. Survival” is the oft-reported shade tolerance tradeoff between growth in the canopy and survival in the understory.

III) “Growth vs. Reproduction” is a tradeoff between carbon allocated to seed production vs. biomass growth in reproductively mature plants.

IV) “Maturation vs. Growth” is a tradeoff between diverting carbon from growth to reproduction later in life, when larger plants can devote more carbon to reproduction per unit time, versus earlier in life, which allows plants to extend the total time for reproduction.

We show that each of these tradeoffs can maintain a large number of coexisting species in our models (theoretically up to an infinite number), and for the same population dynamic reason - these tradeoffs grant species time intervals over which they are the superior competitor. We also show that the same mechanism can maintain high diversity in a model of an annual plant community, demonstrating the broad applicability of these coexisting mechanisms, as well as the robustness of these mechanisms to intraspecific variation in model parameters.

Methods

To maintain broad accessibility, we verbally describe the models and analysis in the Methods section while providing the mathematical analyses in five sections of Appendix S1. However, in the Results section, we provide the formulae for the mathematical results derived in the Appendix S1, such as equilibrium abundances and coexistence criteria. We begin by describing a model where the fundamental difference between tree species relates to their carbon allocation to crown vs. stem (the out vs. up tradeoff), and then permute that model to examine the impact of the reproductive tradeoffs, growth-survival tradeoff, dynamics in an annual plant community and intraspecific variability in a parameter determining plant growth rates.

The successional forest model is defined in continuous time and envisions trees occurring in an infinite mosaic of patches. Trees interact only with neighbors within the same patch by overtopping and shading one another, and patches are dynamically coupled through seed dispersal. Reproduction is continuous and size-dependent, and dispersing seeds have equal probability of landing in any patch. Patches suffer random or periodic disturbances, which kill all the trees and reset succession. Seeds and juveniles who are still alive after a disturbance when the forest floor is in full sun, start growing and reproducing (Fig. 1). Appendix S1: section 1 describes how the equations and models can be derived from some physiologically mechanistic models of interacting individual plants. Although the analyses in the paper can be followed without assimilating Appendix S1: section 1, some of the assumptions may be difficult to fully understand without the mechanistic context.

Growth and Reproduction. Immediately after disturbance within a patch, all surviving juvenile plants of S different species are exposed to direct sunlight. Species differ only in their allocation to stem, and energy devoted to the stem cannot be spent on the crown and *vice versa*. This generates an out vs. up tradeoff (Appendix S1: section1). Specifically, for species i individuals growing in full sun starting at negligible initial size, crown area $C_i(t)$, height $H_i(t)$, and stem and branch mass $M_i(t)$ at time t are given by:

(1a) $$C_i(t) = k_i t^{\gamma}$$

(1b) $$H_i(t) = r_i t^{\delta}$$

(1c) $$M_i(t) = G_i k_i t^{\gamma+1}$$

where γ and δ are constants common to all species defining the power of time t over which growth in $C_i(t)$ and $H_i(t)$ is linear, k_i and r_i are *inversely related* species-specific parameters defining canopy and height growth rates, and G_i is a species-dependent parameter defining growth in branch and stem mass. The power-function growth in equations (1a-c) is a consequence of the carbon balance imposed by power-function allometries relating crown area, stem and branch mass, and leaf and fine root area (Appendix S1: section 1). If we rank individuals of the same age from largest to smallest value of r_i, then this would also be their ranking from: *i*) tallest to shortest, *ii*) smallest to largest k_i, and *iii*) smallest to largest crown area.

All individuals growing in full sun produce seeds at a constant rate per unit crown area, which are distributed randomly among the patches. Individuals in the understory are assumed to have negligible growth and reproduction, which is consistent both with the physiological consequences of a 10 to 100-fold drop in light intensity, and myriad observations in forests with the high leaf area indices that indicate strong light limitation and weak nutrient and water constraints (e.g., Ricard *et al.* 2003). However, this assumption does exclude shade tolerant understory shrubs and trees that reproduce in deep shade. A model where plants grow at reduced rates in the understory remains tractable, but analytical results are much more cumbersome (Appendix S1: section 3.6) and qualitatively similar to those from a version of the annual plant community model with non-zero understory growth, a case we also analyzed.

Mortality. Species in the model can have any level of shade tolerance. Species that are completely shade-intolerant die immediately in the understory and are thus assumed to delay germination until disturbance opens a patch, at which point they germinate immediately. Shade intolerant seeds survive under closed canopy with mortality rate m_s. Species with at least some degree of shade tolerance germinate immediately after seed dispersal and have mortality rate m_u in the understory, but do not grow or set seeds until the canopy opens following a disturbance. After a disturbance, plants in full sun grow at the rates given by Eq. (1) with negligible mortality until they become overtopped by taller competitors (**Error! Reference source not found.**). Once overtopped, they resume dying at rate m_u if they have some degree of shade tolerance, or die immediately if completely shade intolerant.

Canopy closure is governed by the perfect plasticity approximation (PPA). The PPA simply sums the crown areas of plants in a patch from tallest to shortest. This sum of crown area divided by patch area will be less than one when crowns are too small to fill the canopy, and must remain at one after the canopy closes, despite continued growth, which means that the shortest plants in the patch are continually being overtopped and sent to the understory (where they stop growing and reproducing). When the height threshold separating canopy and understory falls within a same-height cohort, then the cohort is split into two fractions to keep the total crown area density of the canopy equal to one. Although the PPA may sound extreme, it works well, both in individual-based models with realistic levels of plastic growth (Strigul *et al.* 2008), and for trees in the field (Purves *et al.* 2008).

More formally, the crown growth and the PPA imply a series of canopy closure thresholds ($t_1, t_2, \ldots, t_S$) for a patch that can be calculated from the densities of each species present and their high-light growth rates. The first threshold, t_S, represents the time after a disturbance at which the canopy first closes (the sum of all S species crown area densities first reaches 1). Overtopping thus begins at t_S. At first, all overtopped individuals will be members of species-S, because they are the shortest, though they will also have the largest crown areas by virtue of having allocated little to stem. After t_S, canopy growth continues until a second time, t_{S-1}, when the last of species-S is overtopped, and the combined crown areas of the remaining S-1 species first fill the canopy. After t_{S-1}, further growth of the canopy individuals continually leaves individuals of species-(S-1) behind in the understory, until a third time, t_{S-2}, when the last individual of species-(S-1) is overtopped, and so on. Note that species-1 is the tallest and so is never overtopped by another species.

The density of seeds that germinate in both natural forests and in the model (given realistic parameter values) is very large – of order hundreds per square meter (Leck *et al.* 1989). For this reason, the canopy closes almost immediately in the model ($t_S \approx 0$), which allows us to greatly simplify the mathematical results by ignoring seeds that disperse to the patch and germinate after the disturbance but before the first canopy closure. For some forests, high initial density may require that the model applies to the entirety of the successional sequence from herbs to canopy trees.

Disturbance. The above description applies to succession in an individual patch, but the model follows species dynamics in a system with an infinite number of patches. Doing so requires knowledge of the distribution of patch ages. Most of our analytical results are presented for the case in which disturbances are periodic, i.e. they occur once every t_0 years, so that at any one time the patch-age distribution is uniform. These results isolate a successional coexistence mechanism that depends on species specialization on the spatial heterogeneity created by asynchronous disturbance, and does not depend on variation in the interval between disturbances. We also provide results for some other patch age distributions, including the exponential distribution produced from purely random disturbance, which generate variable intervals among disturbances. These results show that a second coexistence mechanism is created by species specialization on different intervals between disturbances. For example, with random disturbance, some patches reach ages far older than the mean age of the mosaic. These patches allow the persistence of species that require a long interval to reach expected lifetime reproductive success greater than one, and thus cannot persist if disturbance have the same mean interval but are periodic. Together, the two successional coexistence mechanisms lead to higher diversity than either can on its own.

Disturbances in our model are assumed to kill all saplings and adults larger than seedling size, which is consistent with the Ecosystem Demography (ED) approximation of Moorecroft et al. (2004) (see next section). If the species are completely shade intolerant no seedlings are present when a disturbance takes place. But for shade tolerant species, this assumption is formally equivalent to assuming that disturbances only kill canopy trees, as long as understory recruits that become canopy trees after the next disturbance have a vanishingly low probability of returning to the canopy again after being overtopped. This assumption was also made in Falster et al. (2017) and prohibits the possibility of canopy capture by super-shade tolerant juveniles that survive for perhaps a century or more in the understory through repeated periods of growth suppression and release, even though examples of such situations have been reported (Canham 1985).

Once overtopped, individuals formerly in the canopy do not set seed, have negligible growth and die either before or at the time of the next disturbance, and thus it is unnecessary to track their number. In contrast, small individuals and seeds do survive the disturbance event (or at least survive with positive probability), forming the pool of recruits available to grow thereafter. Thus, their mortality rate in the understory determines the initial condition of succession in a patch. Our formulation for this initial condition is exact in the case of periodic disturbance. However, with random disturbance, we use an approximation that the understory juvenile or seed turnover is faster than patch turnover, so when the disturbance hits the patch, the seed or juvenile pool is at equilibrium.

A connection to stochastic individual-based spatial forest simulators. Our forest model is individual-based in the sense that all of the birth, growth and death rates in it, with the exception of patch-level disturbance rates, are vital rates of individual plants such as the growth rates predicted by Eqs (1). Indeed, Appendix S1: section 1 shows one way in which these vital rates may be derived from a physiological model of an individual plant. Moreover, the division of the landscape into patches, together with the assumption that all density-independent mortality is per-patch rather than per individual, is consistent with the Ecosystem Demography Approximation (ED, Moorcroft *et al.* 2001). This approximation and the PPA were originally developed to correctly scale-up spatially explicit stochastic models of interacting individual trees into models precisely like our forest model, which predicts the time evolution of $N_i(T, t)$, the population density of the *cohort* of species-i plants at time T in a patch t years since the last disturbance. The point here is that our forest model was specifically designed to be consistent with some physiologically-grounded models and with models of interacting individual plants, and so our results should be directly relevant to stochastic spatial forest simulators such as (Dietze & Latimer 2012) and to physiologically structured global vegetation models based on the ED and the PPA such as Koven *et al.* (2019) and Martínez Cano *et al.* (2020).

Model Permutation 1: Alternative tradeoffs. We examine the robustness of our results by analyzing three different permutations of the forest model with the up vs. out tradeoff. First, we replace the out vs. up tradeoff with each of the two tradeoffs between growth and reproduction and the tradeoff between high-light growth and understory survival in shade (**Error! Reference**

source not found.). Again, Appendix S1: section 1 shows one way in which each of these tradeoffs can be generated by interspecific variation in a single physiological parameter. The *up vs. out tradeoff* between k and r in equation (1) occurs if there is variation in a single allometric parameter that constrains allocation to stem. The *fecundity vs. growth tradeoff* occurs if species differ only in their partitioning of surplus energy between reproduction and biomass growth (surplus energy = energy left over from photosynthesis after paying respiration costs and replacing senescent leaves and fine roots, see **Error! Reference source not found.**B and Appendix S1: section 1). With this tradeoff, k and r now increase together as allocation to fecundity decreases and vice versa. Growth parameters k and r are no longer inversely related, because all species are now assumed to have the same allometries, which constrain allocation to stem growth. Finally, increased carbon allocation to reproduction, increases the rate of seed production per unit sun-exposed crown area. In the *maturation vs. growth tradeoff* species have the same allocation of surplus energy to reproduction when sexually mature, but they differ in the threshold size at which individuals in full sun stop growing and begin to devote all surplus energy to reproduction (Fig.1C). For the *growth-survival tradeoff*, a species' sun exposed growth rates, r and k, trade-off against its understory death rate m_u, which is now species specific. Appendix S1: section 1 shows how this tradeoff could result solely from interspecific variation in maximum photosynthetic capacity of leaves in full light. Because of the higher costs related to maintaining high-capacity photosynthetic machinery, the seedlings in the understory will have less available carbon for investments that enhance understory survival. These include investments in chemical or structural defenses against lethal pathogens and herbivores, or in carbon storage that help a plant to survive in the stochastic sun-flecked light environment in the understory (Kitajima 1994). Less investment in survival means a higher understory mortality rate. The observed interspecific tradeoff between survival in the understory and growth in high light (e.g., Kitajima 1994; Wright *et al.* 2010; Russo *et al.* 2020) can be used to infer the relationship between investment in understory survival and the mortality rate. Here we chose a simple form for the relationship between the species' mortality rate in shady understory $m_{u,i}$ and its growth rate determined by k_i (Appendix S1: section 1.5):

(2) $$m_{u,i} = m_0[1 - (k_i/k_+)^{1/\gamma}]^{-c}$$

where m_0 is background mortality, k_+ is a scaling factor and c is an exponent larger than one to ensure the curve is concaved up (Russo *et al.* 2020). The height growth parameter r_i will also be an increasing function of k_i, but we do not need its specific form to produce the results in the paper.

Model Permutation 2: An annual life history. We study whether or not our results might apply to biomes other than forests. On the one hand, competition for water and nutrients is likely to be more important than competition for light in many non-forested ecosystems. On the other, competition for light does occur in many of these systems, at least some of the time, and so we ask: Is there anything *structurally* special about forest dynamics that would restrict our results exclusively to forests? To address this question, we consider systems at the other end of the terrestrial plant size spectrum. High-diversity communities of annual plants in Mediterranean ecosystems undergo repeated succession each year when winter rains arrive, and succession is reset annually with the onset of the dry summer dormant period. Studies in California confirm that the plants compete for light, water and nitrogen (Going *et al.* 2009), and that succession proceeds from short to tall plants until the cessation of seasonal rain eventually ends the growing season (Godoy & Levine 2014), and each plant sets seed before dying.

The forest model can be modified rather simply to describe the between-year dynamics of an annual plant community at a single location based on the continuous-time dynamics of individuals over a growing season. In this model, seeds germinate at the beginning of the season and plants with an out vs. up tradeoff (allocation to leaf vs. stem) compete for light by overtopping one another as they grow through the year, and ultimately set seeds in proportion to size each individual reaches at the end of the season. Appendix S1: section 1.6 contains a physiological sub-model of an annual plant consistent with the growth functions (1). We derive a time-dependent solution for the within-season model that gives next year's germinating seeds as a function of this year's germinating seeds. This defines a system of finite-difference competition equations ($N_{i,T+1}$ as a function of $N_{1,T}, N_{2,T}, \dots, N_{S,T}$) that are much simpler than the nonlinear integral equations of the forest model that govern the continuous-time evolution of $N_1(T,t), N_2(T,t), \dots, N_S(T,t)$.

We examine two different responses to overtopping in the annual model. In the first, overtopped individuals immediately set seed and then die without further growth. In the second, individuals keep growing in the understory but at a reduced rate (reduced k_i and r_i in Eq. 1) below the canopy of their competitors. Seed set can be any allometric function of plant size, but we provide results for seed set proportional to either crown area or plant mass. End-of-season senescence is the only density-independent source of mortality, though similar results can be obtained if we allow within-season density-independent mortality. Results are far simpler without it, and within season density-independent mortality in these systems is likely to be much smaller than density-dependent mortality. Total seed set is multiplied by a germination probability to give the number of seedlings at the beginning of the next growing season. We assume no between-year seed dormancy, but the model remains tractable with it (see Appendix S1: section 2.3).

Model Permutation 3: Within Species Variation.

Model predictions resulting from a competitive tradeoff are often disrupted by introducing real-world complexity, such as intraspecific variation in each species' position along the tradeoff axis. This is particularly true if a small difference in position along a tradeoff radically changes a species' competitive ability (Hara 1993; Adler & Mosquera 2000), as occurs in both competition-colonization models and our model of competition for light. In our model, if two species have nearly the same allocation to growth, then a small decrease in either species' rate of carbon gain can reverse which of the two is capable of overtopping the other.

We, therefore, introduced random intraspecific variation among the growth rates of individuals, and study how this affects diversity. Specifically, let ω be a random variable with probability density $P(\omega)$. At birth, each plant is assigned a value of ω that it keeps for life, and that modifies its growth rate in full sun. An individual's value of ω phenomenologically combines all of the genetic and environmental factors, other than time and species identity, that affect an individual's growth rates. The addition of ω breaks the strict competitive hierarchy because a high-ω member of a low-r_i species can be taller than a low-ω member of a high-r_i species if the r's of the two species are sufficiently similar. The time-dependent forms of C, H, and M are identical to Eqs 1a-c, except that we multiply t by ω. Appendix S1: section 1.3 explains that this is the correct form if ω modifies a plant's rate of net carbon assimilation.

The random variable ω is governed by a parameter θ, such that intraspecific variability increases as $\theta \to 0$, and the system resembles the strict hierarchy as $\theta \to \infty$. Appendix S1: Fig. S9 shows the distribution of the height growth rates for ten hypothetical species and for different values of θ. Note that the height growth rate hierarchy becomes better defined as θ increases.

Mathematical Equations and Analysis. All dynamical equations and the mathematical analyses are presented in Appendix S1: section 2-5: Appendix S1: section 2 – derivation of the dynamical equations. Appendix S1: section 3 – analysis and results for the forest and annuals models with the out vs. up tradeoff, Appendix S1: section 4 – analysis of the model with intraspecific variability, Appendix S1: section 5 – analysis and results for the forest models with the reproduction vs. growth, maturation vs. growth tradeoffs and survival vs. growth. The Appendix S1: section 3 contain equilibrium abundances, coexistence criteria and continuous limits for an arbitrary number of species in all models, except the one with intraspecific variability. Note that our understanding of the forest model with the maturation vs. growth tradeoff model is less complete than for the others, because its dynamics are considerably more complicated, including multiple simultaneously stable states (Appendix S1: section 4).

Results

In what follows, species are labeled in order of their investment in height growth. For the out vs. up tradeoff, species-1 has the largest allocation to stem - the largest r and smallest k in Eq. (1) (Appendix S1: section 1), whereas species-S allocates the least to stem. For the reproduction vs. growth tradeoff, species-1 is the species with the largest r and k and the lowest rate of seed production per unit sunlit crown area, and species-S is the reverse. With the maturation vs. growth tradeoff, all species have the same values of r and k before they reach their species-specific reproductive size, z_i, after which growth ceases, and species are labeled so that $z_1 > z_2 > \cdots > z_S$. Finally, for the survival vs. growth tradeoffs, species-1 is the species with the largest r and k and the highest mortality in shade m_u. With either the out vs. up, reproduction vs. growth, or survival vs. growth tradeoff, all individuals of species-1 will always be taller than any individual of species-2, which will be taller than any individual of species-3, and so on. This is also true under the maturation vs. growth tradeoff *after* individuals have reached sexual maturity, but before they reach sexual maturity, any two living individuals will have identical heights, regardless of species

Equilibrium

The equilibrium population densities for the forest mosaic with asynchronous, fixed interval disturbance, t_0, and the out vs. up tradeoff for the tallest species (subscripted 1) and all shorter species i are:

$$(3) \qquad N_1 = F\frac{\gamma}{\gamma+1}\frac{t_0-t_1}{t_0} + F\frac{1}{\gamma+1} \text{ and } N_i = F\frac{\gamma}{\gamma+1}\frac{t_{i-1}-t_i}{t_0} \text{ for } i > 1,$$

where N_i is the equilibrium density of species-i seedlings that are present within each patch after disturbance, F is the product of the rate of seed production per unit sunlit crown area, and $\frac{1-e^{-mt_0}}{m}$, the average survivorship of seeds in the understory ($m = m_s$) if all species are completely shade intolerant, or the average survivorship of understory plants ($m = m_u$) if all species are at least partially shade tolerant. Again, t_i $(i > 0)$ is the time since the last disturbance within a patch, when the first individual of species-i is overtopped. Between t_i and t_{i-1}, the closed canopy contains only species-1 through i, and species-i is the fastest crown expanding species still in the canopy. The equilibrium densities of all species are proportional to the time interval over which they are the fastest growing competitor. The time thresholds for overtopping are defined by:

(4) $$t_i = \left(\sum_{j=1}^{i} k_j N_j\right)^{-1/\gamma}$$

By the time the next disturbance arrives at a patch in an equilibrium mosaic, all individuals have been overtopped, except some members of species-1. The last term in the equation for species-1 ($F/(\gamma+1)$) represents the seed production of those individuals.

Surprisingly, Eqs (3, 4) also give the equilibrium population densities (measured immediately after gap opening) for the annual plant system, if a plant's fecundity is proportional to end-of-life mass. However, the constant F is now the product of seed production per unit end-of-life mass, the probability of seed survival from the end of one growing season to the beginning of the next, the probability of germination, and t_0, which is now the length of the growing season. The equilibrium for the annual plant model with crown area-dependent fecundity is qualitatively very similar to that for mass-dependent fecundity (Appendix S1: section 2.3).

In Eqs (3), the abundance of each species-i on the LHS depends only on itself and all taller species on the RHS (all species-j, where $j \leq i$). This property reflects the asymmetry of competition for light, which causes amensalistic population dynamics both in the annuals model and near equilibrium in the forest model. Although Eqs (3) and (4) cannot be explicitly solved for the N_i (except for the special case $\gamma = 1$) because of the nonlinearity in t_i (Eq. 4) we can use their amensalistic structure to prove a number of things about the equilibria of the system. There are 2^S equilibria because each equation can be solved for exactly two values of equilibrium density on the LHS (one of these values is zero, and some may be unfeasible because they are negative). In Appendix S1: section 3.4, we show, using the annual plant dynamic system (unfortunately, the same stability analysis cannot be performed on the forest mosaic), that only the larger of these two equilibria is locally stable, and when the larger is positive, the species can successfully invade an equilibrium community of the remaining species and *vice versa*. Moreover, because of the system's amensalistic structure, we can solve for positive equilibria or invasion rates sequentially, beginning with species-1, either numerically or using explicit linearized forms (Appendix S1: section 3.7).

Invasibility conditions

We can also derive the conditions for species' invasion and highly accurate approximations of species richness and species abundance in communities with high diversity. In short, we show that successful invasion is independent of all species that allocate less to stem than the invader, but depends critically on the invader's stem allocation relative to taller species. Suppose that we select species from the range of possible values of the k's (determining allocation to canopy rather than stem), up to a theoretical maximum, k_{max}, which corresponds to the largest possible allocation to crown and the smallest to stem height (i.e. $\phi_i = 0$ in Appendix S1: section 1.1). Appendix S1: section 3.3 shows the k_i's of species that will coexist at equilibrium must satisfy:

(5) $$k_i \geq k_{i-1}^*$$

where k_{i-1}^* is the minimum canopy growth constant for the successful invasion of the i^{th} species into an equilibrium resident community of i-1 taller species (the lifetime reproductive success (LRS) of invading species i equals one if $k_i = k_{i-1}^*$, **Error! Reference source not found.**). This limit is:

(6) $$k_{i-1}^* = k_0(t_0/t_{i-1})^{\gamma+1}$$

where k_0 is the minimum feasible k. Any species with k less than k_0 would have too little crown growth to reach lifetime reproductive success (LRS) greater than one between disturbances even though it is never overtopped. From Eqs. (3) and (4), a species with k_0 would close the canopy at equilibrium at precisely the inter-patch disturbance interval, t_0 (i.e. $t_1 = t_0$), and that:

(7) $$k_0 = \frac{\gamma+1}{F t_0^{\gamma}}.$$

The invasibility condition (5) also ensures long-term coexistence in a sequence of invasions from tallest to shortest, because the i-1 species with higher rank (i.e. higher allocation to stem) are not affected by the presence of species with lower rank, so a successful invasion means species-i will reach a stable equilibrium without perturbing the resident community.

Species richness and continuous limit

If S k's are drawn entirely randomly from the interval between 0 and k_{max}, the interval $k_i - k_{i-1}^*$ is then an exponentially distributed random variable with expectation $\lambda = k_{max}/(S+1)$ (see Appendix S1: section 3.3). It follows that the expected number of coexisting species S_c is:

(8) $$S_c = 2(S+1)\frac{k_{max}-\bar{k}_1^*}{k_{max}} + 1$$

where $\bar{k}_1^*$is the expected value of k_1^* when $k_1 = k_0 + \lambda$. As S increases, the intervals between consecutive strategies, $\Delta k_i = k_i - k_{i-1}$ (Fig. 2), decrease, which suggests that we can pass to a continuous distribution by taking the limit $n(k) = \lim_{\Delta k \to 0} \frac{N(k)}{\Delta k}$. This limit is (Appendix S1: section 3.3):

(9) $$n(k) = \gamma(\gamma+1)^{-\frac{2\gamma+1}{\gamma+1}} \left(\frac{F}{t_0}\right)^{\frac{\gamma}{\gamma+1}} k^{-\frac{\gamma+2}{\gamma+1}}$$

The solution for a finite number of species in (3,4) collapses to the infinite-species limit (9), by dividing N_i by $k_i^* - k_{i-1}^*$ (Appendix S1: section 3.3). The bottom panels of **Error! Reference source not found.** show that the scaling is highly accurate and it can be extended to any model.

Error! Reference source not found.a shows equilibrium species densities for surviving species of the forest mosaic and the annual plant system after k's were drawn randomly from the interval between k_0 and k_{max}. When N_i is plotted against k_i, no particular patterns of species abundance relative to k emerge. When N_i are normalized by the corresponding interval Δk_i^* (**Error! Reference source not found.**), they collapse along the theoretical continuous distribution (9) (**Error! Reference source not found.**b). **Error! Reference source not found.**c,d show several analogous runs of the annual system in which plants continue to grow at a reduced rate after they are overtopped (analytical work in Appendix S1: section 3.6, including the continuous distribution analogous to Eq. (9)).

Although equilibrium abundance decreases monotonically as investment in stem decreases, the distribution is U-shaped if growth in the understory is sufficiently fast, indicating that growth in the understory can compensate for being overtopped early (amber curve in **Error! Reference source not found.**d).

The same coexistence mechanism that leads to the infinite diversity of the continuum solution (9) is also present in the forest model with the reproduction vs. growth and survival vs. growth tradeoffs (Appendix S1: section 5). In the reproduction vs. growth tradeoff model, species that allocate most surplus carbon to reproduction grow slowly in height and are overtopped early by species that allocate less to reproduction and more to growth. Similarly, in the understory survival vs. growth in light tradeoff model, species with lower photosynthetic capacity grow slower are overtopped early by species with higher photosynthetic capacity. The equilibrium abundances for these tradeoffs are also given by (3,4) if we make F a decreasing function of k_i (Appendix S1: section 1.5). The corresponding continuum distributions analogous to Eq. (9) are derived in Appendix S1: sections 3.6, 5.4 and 5.5, and also is highly accurate (**Error! Reference source not found.**f,h).

The number of species in the equilibrium community can be fairly well predicted by the expected number in Eq. (8), which shows three key factors determining species richness: the initial number of species in the pool, S, k_{max} and the k_0, which indirectly affects $\bar{k}_1^*$ (Fig. 4a).

Disturbance regime and habitat heterogeneity

When the disturbance is not periodic, we expected that the extra variability would increase diversity by allowing the coexistence of species that specialize in different disturbance intervals. We were correct that random intervals increased diversity, but not for the reasons we expected. Inter-disturbance intervals are exponentially distributed if disturbance is entirely at random, as is the equilibrium distribution of patch age. The coefficient of variation (CV) of an exponential distribution is one. As CV becomes larger than one, the habitat is increasingly divided into areas with extremely long or extremely short intervals between disturbances. Because dispersal is assumed to be infinite, these could be different habitats like ridge tops prone to windthrow and valley bottoms with comparatively low wind speeds. While equilibrium diversity does indeed increase with the CV of the disturbance intervals (**Error! Reference source not found.**), the effect appears to be entirely due to a decrease in k_0 (**Error! Reference source not found.**c). k_0, the minimum feasible crown expansion rate, is inversely proportional to fecundity and directly proportional to the disturbance rate. Longer disturbance intervals allow for even later successional strategies and thereby extend the range of coexisting k's, increasing richness. Habitats that include places with chronically low disturbance can support significantly more extreme late-successional strategies, but the earliest successional strategy in an equilibrium community is almost independent of patch age CV. This is because the late-successional extreme is set by exogenous disturbance, whereas the early-successional extreme is set endogenously by canopy closure early in succession.

Maturation vs. growth tradeoff

The maturation vs. growth tradeoff is also capable of producing stable coexistence of up to an infinite number of species, and by the same population dynamic mechanism responsible for coexistence with the out vs. up and reproduction vs. growth tradeoffs (Appendix S1: section 5.1). However, multispecies diversity maintained by the maturation vs. growth tradeoff is much more fragile than that maintained by the other two tradeoffs, because it requires ecologically unreasonable restrictions on the pool of available strategies.

The pairwise invasibility plot in **Error! Reference source not found.**a,b explains why. The resident's full-sun LRS is maximized at intermediate reproductive threshold (which is reached at 90 years of age in this example). Resident strategies between this optimum (dashed line in **Error! Reference source not found.**b) and the black and grey areas to its right, *cannot be invaded by any strategy.* Below this optimum, the resident can be invaded by later successional strategies (black and gray areas to the left of the dashed line), and sufficiently above the optimum, by sufficiently earlier successional strategies (black and gray areas to the right of the dashed line). However, only a very limited region allows reciprocal invasion, which implies coexistence (gray areas). The important point here is that coexistence *requires the absence of the* *optimal species* (Appendix S1: section 5.3). In contrast, the case with the reproduction vs. growth tradeoff is qualitatively very similar to the case with the out vs. up tradeoff. Although the full-sun LRS also has an optimum with the reproduction vs. growth tradeoff (**Error! Reference source not found.**c), all the strategies on the left can invade, and some coexist with the full-sun optimum (**Error! Reference source not found.**d).

In addition, population dynamics with the maturation vs. growth tradeoff are complicated by multiple stable states, such as the broad area of founder control in **Error! Reference source not found.**b (hatched area). Appendix S1: section 5.3 shows that this founder control is caused by the assumption that all trees have the same height growth rate before sexual maturation. In short, the condition for the successful invasion by a later reproductive species requires that the LRS of the members of the invader that remain in the canopy after reaching maturity is greater than the LRS of the members of the resident that remain in the canopy after reaching maturity. This precludes any invasion to the right of the optimal reproductive strategy (**Error! Reference source not found.**a). The condition for successful invasion by a species reproducing earlier than the resident requires the invader to reproduce in a limited interval between the time it reaches maturity and the time the resident closes the canopy, which precludes invasive strategies too similar to the resident. This leaves a broad range of strategies where neither of the above conditions for invasion is met.

Intraspecific variability and coexistence

If we allow some individuals of species with higher ranks (greater allocation to stem) to suffer competition from some individuals of species with lower rank, the system becomes considerably more complex (Appendix S1: section 4).

Two-species invasibility plots in **Error! Reference source not found.** show that in the case of a strict hierarchy ($\theta = \infty$), the invader is always successful if it has a smaller k than the resident and is thus taller than the resident, or if its k is larger than the sum of the resident's k plus a limit to similarity (shown by the white region) (see Eqs. 5-6). However, the limit to similarity vanishes as the resident's k approaches k_0 (note the grey wedge which touches down at the point (1,1) in **Error! Reference source not found.**a. Thus, the k of the shorter of two coexisting species can be almost identical to that of the taller species, if the taller species is itself close to the tallest feasible limit (k_0). A diverse species pool will tend to contain a k_1 close to k_0, which means a small limit to similarity, allowing $k_2$to be close to k_1, and so on for subsequent invasions. The important point is that infinite diversity can be maintained in the model because limits to similarity vanish as more and more species are added to a community.

In contrast, if $\theta < \infty$, then the limit to similarity between the k's of the resident and successful invader never vanishes because a classic ESS emerges (where the two black and two white regions all touch in **Error! Reference source not found.**b-c). The height of the black area above the ESS shows how similar the k of a successful invader can be to the ESS strategy. The fact that grey areas never touch the 1:1 line if $\theta < \infty$, means that no two strategies can coexist unless they are dissimilar by a finite amount. This obviously will decrease diversity relative to the case where $\theta = \infty$. If it extends to communities with more than two species, as we conjecture it does, it means that the infinite diversity possible in the model with a strict hierarchy is structurally unstable to the introduction of any θ less than infinity. On the other hand, because the allowed species packing decreases smoothly as θ decreases (**Error! Reference source not found.**), we conjecture that models with realistic values of intraspecific variability would still be capable of supporting large numbers of coexisting species.

In order to explore these conjectures, we performed a set of simulations of the annuals model with different initial number of species, different values of θ and different ranges of available strategies. The long-term equilibrium was obtained by iterating the annual plant dynamic system for 10,000 seasons starting from random species abundances with k's randomly drawn between k_0 and k_{max} (in the majority of the cases 100 iterations were sufficient to reach equilibrium). Results in **Error! Reference source not found.** support the conjecture that diversity increases smoothly with θ and k_{max}, though some of the patterns are non-monotonic.

All computations were performed in Matlab (R2019a). A commented code to compute the equilibrium density for each model is provided (Data S1: Equilibrium Density.m).

Discussion

In this paper, we introduce mechanistic models of coexistence among light-competing species that differ in the period of time during succession over which each is able to increase its LRS more rapidly than any other species. This model is built on realistic plant allometries, and applies most naturally to forest trees in a mosaic of differing patch ages, but may also apply to annual plant communities during periods of light competition. Differentiation along the successional niche axis is caused by one of three allocational tradeoffs: growth in height vs. crown area (out vs. up), growth vs. reproduction, or growth vs. understory survival. All three tradeoffs could generate coexistence via similar mechanisms and have the potential to maintain an unlimited number of coexisting species. And though intraspecific variation erodes this coexistence to some extent, all but the growth vs. maturation time tradeoff would still generate large amounts of coexistence under reasonable assumptions. Most generally, we have shown that the combination of unavoidable allocation tradeoffs in plants, asymmetric light competition, and disturbance-driven heterogeneity in forest systems or seasonal mortality in annual systems enables a high degree of coexistence.

The out vs. up tradeoff

To understand the mechanism of coexistence caused by competition for light with the out vs. up tradeoff, we focus first on the models of annual plants with no understory growth, where the story is simplest. Because the annual plant models are amensalistic (tall plants harm shorter plants but not the reverse), the coexistence problem reduces to a sequence of invasions when rare by successively shorter species. Our results show that all species will coexist at equilibrium if the tallest species (that allocating most to stem) can invade an empty habitat, the next tallest species can invade an equilibrium monoculture of the tallest species, the third tallest species can invade an equilibrium community of the two taller competitors, and so on.

Evaluating these invasion criteria requires determining the time needed to reach a plant mass sufficient for lifetime reproductive success (LRS) to be 1 (after mass is converted to next year's germinating individuals that survive to reproduce). Because seed set in our model is proportional to end-of-life size, all species have the same replacement size t_r- the minimum size an individual must attain to replace itself in the next season with at least one germinant. However, species that grow quickly in crown area and mass reach replacement size before species that grow quickly in height. Thus, the time required by plants of species i to reach replacement size, $t_{r,i}$ increases with the species' height growth rate r_i and decreases with its crown area growth rate k_i (Eqs. 1).

The tallest annual species, species-1 by our labeling convention, can invade when rare if the total season length, t_0, is greater than its replacement time $t_{r,1}$. Then its population density will grow until its canopy closes (before t_0), because shading is the only factor that controls population growth. Overtopped individuals of species-1 have a reduced LRS simply because they stop growing when they fall into shade and are thus forced to switch to reproduction at reduced size. Population growth shortens the time of first canopy closure, t_1, until the mean LRS of the species-1 monoculture is one. At equilibrium, and even without intraspecific variation in model parameters, the population includes both individuals larger than replacement size with LRS>1, and individuals smaller than replacement size with LRS<1, because the mean LRS must be one (blue curves in **Error! Reference source not found.**). As a consequence, for any given species, the timing of when it first closes the canopy - when LRS <1, is earlier than the replacement time - when LRS = 1.

Each subsequent invasion of a shorter species into an equilibrium community of taller ones (e.g. sp.2 invading sp.1, sp.3 invading sp.1 and 2, and so on) is directly analogous to the invasion of species-1, if we replace the end of the growing season for species-1, with the de facto end of the season for an invading species, which is t_{i-1}, the time at which the canopy of the equilibrium resident community closes. Each invader succeeds if and only if its replacement time is less than the canopy closure time of its taller competitor - $t_{r,i} < t_{i-1}$, which will be met if it has a sufficiently higher canopy area growth rate. Once a successful invader-i reaches equilibrium, its replacement time $t_{r,i}$ will be sandwiched between the two canopy closure times $t_i < t_{r,i} < t_{i-1}$ (**Error! Reference source not found.**). In this sense, taller species competitively suppress shorter species simply by shortening the time available to grow.

Because $t_{r,i}$ decreases as the crown area growth rate k_i increases, successful invasion requires that k_i exceeds a threshold, k^*_{i-1}, *which is a property of the resident community*. The threshold k^*_{i-1} is the value of k_i that would make $t_{r,i} = t_{i-1}$ (Eq. 6), and is always greater than the crown growth rate of the resident species ($k^*_{i-1} > k_{i-1}$). Given that $k_i > k^*_{i-1} > k_{i-1}$ is necessary for each successive invasion, and thus for coexistence, each successive invader faces a limiting similarity between its crown growth rate and that of the resident species just taller than it. Nonetheless, very high diversity can be maintained because the sizes of the limiting similarities are not fixed, but instead depend on species packing. The closer the shortest resident is to the limiting similarity that governed its invasion, then the less abundant it will be, and the smaller the limiting similarity between it and any shorter invader. Repeated invasions by species with randomly chosen k's will thus tend to find successful k_i's ever closer to the limiting similarities that govern their invasions, which will produce ever smaller limiting similarities for subsequent invaders. Repeated invasions thus create positive feedback that reduces barriers to species packing and leads in the limit to the infinite diversity of our continuum solution.

At first glance, the annuals and forest models appear to be drastically different. One is a non-spatial system defined by a set of simple amensalistic finite difference equations and the other is a spatially structured system composed of a set of complex non-amensalistic integral equations. The forest model is not amensalistic because all species have some understory mortality at the seed or seedling stage which affects population dynamics. Shade cast by every species in a closed-canopy patch thus causes increased understory mortality of the seeds or seedlings that dispersed to the patch since the last disturbance.

Despite their differences, *the coexistence equilibria of the annuals and forest models have mathematically identical structure* if annual plant fecundity is proportional to mass and if forest disturbance is periodic. This implies that the above explanation of coexistence in the annuals models applies equally to the forest model. It also implies that coexistence caused by competition for light and the allocation tradeoffs is surprisingly robust to changes in plant life history.

There are four reasons why the annuals and forest models with the out vs. up tradeoff predict structurally identical equilibrium communities. First, if seed production is proportional to crown area from birth until death, as it is in the forest model, then it is also proportional to end-of-life mass, as in the annuals model, because mass is a cumulative function of the photosynthetic rate, which is directly proportional to crown area (Appendix S1: section 1.1). Second, as justified by empirical and theoretical arguments, we have assumed that the forest canopy closes immediately after disturbance at the high total abundances found at equilibrium (i.e. dozens of seedlings m^{-2}). This removes the non-amensalistic effect of shade on seed survival from the equilibrium equations of the forest model. Third, the overtopping dynamics of annuals within a growing season of fixed length are quantitatively identical to those of trees within a patch during a fixed inter-disturbance interval, except for the temporal and spatial scales involved. Fourth, the forest mosaic is ergodic when at equilibrium, which means that spatial variation in seed production between patches at any one time is the same as the temporal variation within a patch. Suppose that, in an equilibrium forest mosaic with periodic disturbance, we select a disturbed patch at random and then collect all of the seeds produced inside the patch until the next disturbance event, and then divide by the inter-disturbance interval. This temporal average of the densities of seeds produced by each species will be the same as the yearly seed rain in the model at any given time point or, equivalently, the spatial average of seed production in all patches. According to this temporal average seed production, the annual system always assembles by saving all seeds produced throughout one growing season until the beginning of the next.

The surprising alignment of results from the forest and annual plant community models can be used to infer the modern coexistence theory mechanisms (Chesson 2000b) underlying our central findings. As noted in the prior paragraph, although the forest models with periodic disturbance are simulated over a mosaic of patches, the coexistence and relative abundance observed at any one time is the same as in any single isolated patch averaged over time. Thus, as with the annual plant community model, the coexistence in the forest models follows into temporal coexistence mechanisms, and the temporal storage effect (Chesson 2000b) in particular seems well-aligned with our results. Consider that each coexisting species has an interval of time after disturbance over which it is the fastest grower. In the period before its favored interval (when it is not the fastest grower), it suffers none from faster growing species due to their lower height (with the out-versus-up tradeoff). Meanwhile, in the period after its favored interval, it falls into the understory, and by virtue of converting biomass to competition-invulnerable seeds, or having a reduced growth rate independent of the dynamics of the taller species, it avoids interspecific competition. In fact, the true competitive effect of a later/taller species on an earlier species is to reduce the time it has the maximal growth (and conspecifics always have this effect). In fact, even the forest models with random disturbance rely on purely temporal coexistence mechanisms as they generate no more coexistence than would be observed in a single isolated patch periodically disturbed at a time interval long enough for the slowest species to be viable.

All of our forest models also have a spatial diversity-enhancing equalizing mechanism, which advantages reproductive output of early successional species relative to late. This equalizing mechanism generates from random dispersal and the spatial variability in the environment (i.e. the mosaic of patch ages). To understand that, imagine periodic disturbances perfectly synchronous that create a uniform mosaic of patches of even age at any moment in time. This scenario penalizes earlier reproductive species that must wait a long time before their seeds can germinate, and because seeds have a survival probability<1, this might also prevent very early successional species from persisting. This equalizing mechanism is equivalent to conversion into seeds in the annual plant model, as there is no penalty to convert seeds earlier in the season. Recent studies by (Ellner *et al.* 2016, 2019) provide the needed simulation tools for modern coexistence theory to test the conjectures we pose here.

Relationship to competition-colonization models

A second surprising convergence is the similarity between the mathematics of coexistence in our models and models of the competition-colonization tradeoff (Levins & Culver 1971). Wth the Up vs. Out tradeoff, allocation to crown growth increases a plant's ability to rapidly capture sunlit area currently unused, whereas allocation to stem growth increases a plant's ability to take sunlight that is already being used by a shorter species; meanwhile, shorter plants do not affect taller competitors. This is directly analogous to the tradeoff in competition colonization models between a species' per-capita rate of vacant space capture and its ability to take space from a poorer competitor. Similar arguments show that the other three tradeoffs we consider can also be recast as competition-colonization tradeoffs, as do others that we do not investigate but may work the same way, (e.g. the tradeoff between many small seeds and a few large ones Muller-Landau 2010). Like our models, competition-colonization models: i) have amensalistic dynamics (only near equilibrium for the forest model), ii) include inefficient space capture by good competitors, which allows the persistence of good colonizers, iii) are affected by limiting similarities as in our model, iv) can maintain theoretically infinite diversity, and v) predict high diversity that is fragile in the sense that removing a single species can cause a cascade of further extinctions (Kinzig *et al.* 1999; Adler & Mosquera 2000).

Random Disturbance

The system with random disturbances still produces the same dynamics among and within species, but it contains a new element. For a given mean patch age, disturbances that are more variable in time generate more variable patch age distributions across space. Thus, the probability of finding a very old patch is higher in a more variable landscape. The presence of these old patches simply stretches the range of late-successional strategies viable at equilibrium. For example, in a landscape that is randomly disturbed, some patches remain undisturbed for much longer than the mean inter-disturbance interval. These long-lived patches are eventually dominated by strategies that cannot get to replacement size by the mean inter-disturbance interval. Moreover, the tallest strategy that persists at equilibrium dominates the canopy in only a tiny fraction of the patches, because the patch-age distribution decreases exponentially.

Reproductive tradeoffs

The system with the reproduction vs. growth tradeoff has very similar dynamics to the system with the out vs. up tradeoff. Species with allocation to seeds at the optimal value for plants growing in full sun (**Error! Reference source not found.**c) are early successional specialists like species that invest heavily in crown growth. They reach replacement size early, but are soon overtopped by species that grow more quickly in height. Species with low allocation to fecundity are like species that allocate heavily to stem growth; they dominate late in succession because they grow quickly in height. Both tradeoffs can maintain infinite species richness for the same reason. The last species to reach replacement size grows faster in height than any other species present, but cannot close the canopy until relatively late in succession *because it is slow to reach replacement size*. The next tallest species persists because it reaches its replacement size before the tallest species closes the canopy, but it too leaves a sunlit period during which the subsequent species in the series can reach its replacement size, and so on.

Although the maturation vs. growth tradeoff can also maintain theoretically infinite diversity, as suggested by Falster (2017), this requires that we artificially restrict the species pool to exclude superior strategies and that we manage the order in which species are introduced when the community is assembled. The fundamental difference with the other tradeoffs, is that pre-reproductive individuals are the same size under maturation vs. growth and therefore capable of harming all other individuals for some period of time. This causes non-amensalistic dynamics and leads to founder control.

The survival-growth tradeoff

The survival-growth tradeoff is dynamically similar to the reproduction-growth tradeoff. In both cases, species that grow relatively slowly at high light – because of high allocation to reproduction with the reproduction-growth tradeoff and low A_{max} with the survival-growth tradeoff, produce a relatively high density of new juveniles that survive until the next disturbance in the patches where they land. These dynamics are determined by high reproductive investment with the reproduction-growth tradeoff and high survivorship of juveniles with the survival-growth tradeoff. However, the two tradeoffs produce different patterns of equilibrium abundance because of the strong nonlinear increase in understory survival that accompanies slow growth with the survival-growth tradeoff (Eq. 2). The fastest growing species has the highest abundance with the reproduction-growth tradeoff (Fig. 3e), but not with the survival-growth tradeoff (Fig. 3g). Collectively, the relatively shade tolerant species that can survive at least ten years on average in the understory are both much more abundant and much more diverse than less-tolerant species (Fig. 3g). This high shade tolerant diversity is consistent with patterns observed old-growth tropical forests (Hubbell *et al.* 1999) and the results of Falster (2017). Also, the cause of the coexistence produced by the survivorship-growth tradeoff may be similar to that in the early size-structured model of Kohyama (1993), but this is difficult to say with certainty because Koyama's results are numerical.

One complication is that there are at least two kinds of shade intolerant species (Canham 1985). Pioneers have rapid growth, short longevity, and high early investment in reproduction. They typically dominate after large and severe disturbances, especially disturbances such as fires that kill all advanced regeneration (saplings). So-called gap-phase species are also relatively shade intolerant and grow rapidly, but may live as long as shade tolerant species and are conspicuous elements of late successional forests. Yellow birch (*Betula alleganiensis*) is an example of a gap-phase species in the temperate zone, whereas pin cherry (*Prunus pensylvanica*) is a pure pioneer. In the tropics, most *Cecropia* species are pure pioneers, where as many of the largest and long-lived canopy giants are often shade intolerant, such as several species of the genus *Ceiba*. Thus, one class of shade intolerant species reaches its maximum stand-level biomass early in succession, while the other does so very late, with the shade tolerant species in the middle. The up vs. out and reproduction vs. growth tradeoffs with all species shade intolerant, predict succession from relatively short and short-lived species (short-lived because of overtopping), to taller and longer-lived species. The short-lived early-successional species thus may correspond to pioneers like *Cecropia* and pin cherry. In contrast, the survival vs. growth tradeoff predicts succession from shade tolerant species, which dominate immediately after disturbance because of advanced regeneration, to progressively faster-growing and less shade tolerant species. These relatively shade intolerant late-successional species thus may correspond to the shade intolerant giants in old growth tropical forests, and to gap phase species in temperate old growth forests. The coexistence of shade tolerant species with both classes of shade intolerants may require the simultaneous operation of several tradeoffs (e.g. Rüger et al., 2020, Falster et al., 2017) .

Intraspecific variability

The results confirm that breaking the PPA's strict interspecific overtopping hierarchy does reduce diversity. Nonetheless, these results also demonstrate that high diversity is still maintained, given sufficiently low levels of random intraspecific variation. Our results also suggest, but do not prove, that the infinite diversity, theoretically possible with a perfect height hierarchy, is structurally unstable to the introduction of any intraspecific variation in height growth whatsoever.

A random factor that generates different growth rates among conspecifics allows some individuals of lower-ranked species to overtop some individuals of higher-rank species. Fundamentally, this increases the interspecific effect of shorter on taller species, and therefore generating larger limits to similarity for stable coexistence. These results are consistent with earlier studies that have explored the asymmetry of resource competition, showing that smoothing the competitiveness function, which describes competitive success as a function of mortality rate, reduces coexistence (Geritz 1995; Adler & Mosquera 2000) and other studies showing that random individual variation in competitive ability promotes competitive exclusion (Barabás & D'Andrea 2016; Hart *et al.* 2016).

Intraspecific variability has long been recognized to have profound ecological implications (Macarthur & Levins 1967; Violle *et al.* 2012), and, in natural settings, it is generated by many factors (Bolnick *et al.* 2003). In our model, intraspecific variability is mostly intended as non-heritable phenotypic variation that affects the vital rates of an individual during its entire life. If caused by habitat variability, then it must be assumed to have very small spatial scale in our model, because each individual within a patch receives a separate random draw of the growth-rate modifier.

Limitations. To obtain analytical results, we made a series of simplifying assumptions beyond the PPA and ED. Here we discuss the implications of three of these.

First, although technically consistent with the ED approximation in Moorecroft et al. (2001), our specific implementation of ED prohibits plants from surviving two or more disturbances and also eliminates all density-independent mortality of individuals within a patch between disturbances. Collectively, these assumptions do not allow a slow-growing shade tolerant individual to be released from suppression more than once. Relaxing them should thus favor shade tolerant strategies.

Falster et al. (2017) assumed that patch-level disturbance kills all plants in the patch, but also included density-independent mortality which may have allowed the partial release of suppressed individuals before disturbance. Also, in Kohyama's (1993) model, a fraction of individuals survived as advanced regeneration in a newly-formed gap. However, as in our results, coexistence in these studies required patch-level disturbance, indicating that density-independent mortality between disturbances and survival across multiple disturbance events are not the crucial mechanisms for the maintenance of successional diversity.

A second potentially restrictive assumption is that all species' combined seedling densities in the forest models are high enough that the canopy closes almost immediately after disturbance. This assumption avoids continuous recruitment after gap formation and dealing with plants of different ages within the same patch. Relaxing it makes the mathematical treatment more complex, but typically has little impact on the competitive outcome. This is because the number of viable seeds that disperse and germinate into a patch after gap formation is typically small relative to the number of seeds and seedlings waiting the forest floor to grow when a gap forms. Also, because younger recruits tend to be smaller than the older ones, regardless of species, they tend to be overtopped disproportionately early, generating small LRS and limited impacts on population dynamics.

A third simplification is the absence of any reproductive threshold in models with the out vs. up survival vs .growth or reproduction vs. growth tradeoffs. Plants simply begin to reproduce as seedlings. A more realistic model would have a species-independent reproductive threshold, after which an individual allocates a fraction of its surplus energy to reproduction instead of growth (Wright *et al.* 2005; Visser *et al.* 2016). Although this change might improve quantitative predictions and is simple to handle, it is not likely to modify competitive outcomes much because seed production increases nonlinearly with age. So, species-level LRS is already dominated by the largest individuals in the models, as often the case in natural systems (Samson & Werk 1986). The maturation vs. growth tradeoff we modeled incorporates a size threshold but is unrealistic because it assumes that trees stop growing altogether once they begin reproducing. Another way to think about this is that the two growth-reproduction tradeoffs should represent two orthogonal axes: time to maturity and the fraction of carbon allocated to reproduction. We analyze them separately, but they probably should be considered in conjunction (e.g. like Falster et al., 2017).

Our models contain numerous other assumptions, including species that are identical except for their position along a single tradeoff axis, infinite dispersal, no water or nutrient limitation, and the omission of numerous other processes known to affect succession and community composition. However, the most general message of our paper is that the combination of unavoidable allocational tradeoffs in plants, amensalistic interactions characteristic of light competition, and disturbance can generate a high degree of coexistence in successional systems. So unless relaxing an assumption reduces the competitive asymmetry in the model, we expect this fundament result to hold.

Conclusions

We have shown that several different allocational tradeoffs, including the classic growth-mortality tradeoff, can maintain the successional diversity of a theoretically infinite number of species. The models' ability to generate coexistence requires two endogenous factors: species-specific allocation strategies and asymmetric light competition, and one exogenous factor: a disturbance regime. These results challenge the classic view that successional diversity depends exclusively on species tradeoffs along a shade-tolerant axis, or on a combination of shade-tolerance with other tradeoffs. Each of the tradeoffs we consider can by itself maintain high successional diversity, including the shade tolerance tradeoff. Each may thus contribute significantly and independently to the maintenance of successional diversity in nature. Further studies are required to better understand whether different tradeoff axes interact synergistically or antagonistically, and operate with other limiting factors, such as water and nutrients. Further empirical work is also required to document the carbon and reproductive allocation tradeoffs operating in natural forests, and their consistency with observed patterns of coexistence.

Acknowledgments. This work is supported by the Carbon Mitigation Initiative at Princeton University. We thank the two anonymous reviewers for their constructive criticisms and suggestions.

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Figure captions:

Figure 1. Illustration of the competitive dynamics within an individual patch under different tradeoffs. Seedlings accumulated in the patch due to *in situ* seed production and the arrival of seeds from other patches. Seedlings survive in the shade and start growing and reproducing according to species-specific allocation tradeoffs only after a disturbance kills all trees in the patch. Reproduction (red fruits) is proportional to crown area. When an individual is overtopped, it stops growing and reproducing (note that species 2 has no fruits in patch 4 of case I). **I**: the out vs. up growth tradeoff drives the competitive dynamics of three species with different allocations to crown expansion vs. stem height. Species with greater investment in height (1) grow faster but have a smaller crown. **II:** a tradeoff between survival in the shade and growth in the light. Here species have different maximum photosynthetic capacities (A_{max}). Species with higher A_{max} (1) grows faster when it has access to light. However, when light is limited, the greater cost of maintaining high-capacity photosynthetic machinery does not allow these species to make the necessary investments in defense to survive in the understory (note that there are no saplings of species 1 in patch 3 and 4). **III**: a tradeoff between growth and reproduction drives dynamics. Here species have the same allometry, but those with a greater allocation to reproduction (2) grow slower and are overtopped by taller competitors allocating less to reproduction. **IV:** a tradeoff between growth and maturation drives dynamics. Here also, species have the same allometry, but they differ in the threshold size at which they start diverting all resources to reproduction. Species that reach sexual maturation earlier (2) are overtopped by species that keep growing and delay reproduction.

Figure 2. The strategy axis illustrates the strict hierarchy of light competition. The axis stretches from k_0 to $k_{\max}$, the smallest and largest feasible values of the crown area growth rate. Strategies on the left invest more in height, strategies on the right invest more in crown area. Under a strict

hierarchy, species with lower k overtop species with higher k. The non-invasibility intervals ( ) define the strategies that cannot invade given a resident community of species with higher k's. The Δk's are independent exponential random variables with rate proportional to $k_{\max}/(S\text{-}1)$, where S is the number of available strategies. As S increases Δk's decrease, allowing coexistence of an infinite number of species.

Figure 3. Equilibrium density of coexisting species as a function of plant strategy in a system with strict hierarchy and periodic disturbance. **a**) forest mosaic with the out vs. up tradeoff (also equivalent to a community of annual plants with fecundity proportional to end-of-season mass) **c**) annual plants with the out vs. up tradeoff and in which plants continue to grow at a reduced rate in the understory for different values of the ratio between canopy and understory net photosynthesis per unit of crown area u, **e**) a forest with species-specific allocation to reproduction, and **g**) a forest with species-specific tradeoff between survival in the shade and growth in the light. The top panels show the simulations with uniform random draw of k's (**a** and **c**), allocation parameter φ's (**e**) and survival in the shade F's. The bottom panels show the same simulations normalized by Δk_i^*, $\Delta \varphi_i^*$ and $\Delta log(F_i^*)$. Analytical solutions for the continuous cases are shown as red lines (for all simulations $S = 150, \gamma = 1.5, t_0 = 1$).

Figure 4. Equilibrium species richness in the forest mosaic (S_c) depends on the number of species in the initial pool (S) and on the variability of the patch-age distribution. **a**) S_c as a function S for two patch-age distributions with the same mean (60 yr), uniform (blue) and modified power-law (red). The modified power-law allows generating distributions with the same mean but different variance (Appendix S1: section 3.5). **b** and **c**) S_c and k_0 as function of the coefficient of variation of the disturbance intervals for the modified power-law distributions with the same mean patch

age (60 yr) and initial pool of 200 species. Each Dot represents an individual stochastic realization; analytical solutions (Eq. (13)) are depicted with solid lines.

Figure 5.Two-species dynamics with a maturation vs. growth tradeoff (**a**-**b**) and a reproduction vs. growth tradeoff (**c**-**d**). Panels **a** and **c** show the LRS of the resident individual that is never overtopped, with an optimum at 0.4 and 90 yr (vertical dashed lines). Panels **b** and **d** are two species invasion plots. Invasion fails in the white and striped areas and succeeds in black and grey. Black areas also denote the combinations of strategies that result in the competitive exclusion of the species labeled as the resident by the species labeled as the invader. White areas denote the opposite – exclusion of the invader by the resident. Grey areas show combinations of strategies that coexist. Striped areas show combinations that produce founder control, in which neither strategy can invade the other. Results obtained with random disturbance (exponential patch-age distribution)

Figure 6. **a**-**b**-**c**) Invasibility plot and long-term dynamic: an equilibrium monoculture (resident) is invaded by an initially rare species with a different stem allocation, for three different values of the shape parameter θ ($\theta = \infty$ is the strict hierarchy). Invasion fails in the white areas and succeeds in black and grey. Black areas also denote the combinations of strategies that result in the competitive exclusion of the species labeled as the resident by the species labeled as the invader. White areas denote the opposite – exclusion of the invader by the resident. Grey areas show combinations of strategies that coexist. **d**) The ESS as a function of θ (black curve). An equilibrium monoculture of the ESS strategy cannot be invaded by any nearby strategy within the grey area shown, but the ESS can invade any other strategy. The ESS (normalized by k_0) approaches unity for (strict hierarchy). The non-invasibility interval is a limit to similarity, which decreases as θ. Note that below the ESS invasion is always prohibited

Figure 7. Shannon equivalent species richness ($\prod_{i=1}^{S} p_i{}^{-p_i}$, where p_i is the proportion of species-i) increases as a function of the parameter θ and the number of species in the initial pool S. Each point represents the average of 1000 simulations (±standard error) where the strategy k of each species is randomly drawn from a uniform distribution between k_0 and $k_{\max}$. The equilibrium densities are obtained by iterating the system 10,000 times (other parameters: $FG = 1, \gamma = 1.5, t_0 = 1$).

Figure 8. Within season dynamics at equilibrium of three annual species with the up-vs-out tradeoff. The solid portion of each curve depicts the portion of the growing season during which individuals are continually overtopped, at which point they reproduce and die. **a**) Plant height. The dashed portions show each species period before canopy closure. **b**) Lifetime reproductive success each individual would have if it were to die at that time (assuming that seed production is proportional to end-of-life mass). The horizontal dashed-line shows LRS=1, and its intersections curves given the values of t_{r1} (blue), t_{r2} (red) and t_{r3} (yellow). Other parameter values: $FG = 0.01$ seeds m^{-2} day^{-1}, $t_0 = 100$ day and $\gamma = 1.5$.