Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees

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The belief that canopy gaps are important for the maintenance of tree species diversity appears to be widespread, but there have been no formal theoretical models to assess under what conditions gap phase processes allow coexistence. Much of the empirical research on niche differentiation in response to gaps has focused on evidence for an interspecific tradeoff between low light survival and high light growth. The objectives of this study are first to distinguish the possible mechanisms allowing coexistence based on this tradeoff, and second, to explore their limitations. We present a theory of forest dynamics driven by small-scale disturbances as a special case of the theory of coexistence in variable environments. We demonstrate that temporal and spatial heterogeneity in light conditions that results from canopy gaps can allow stable coexistence as a result of three previously documented general mechanisms: 'relative non-linearity', 'the successional niche' and the 'storage effect'. We find that temporal fluctuations in light availability alone allow the stable coexistence of only two species. Spatial variation in disturbance synchronicity and intensity allows three species to coexist in a narrow parameter space. The rate of extinction is, however, extremely slow and there is transient coexistence of a larger number of species for a long period of time. We conclude that while the low light survival/high light growth tradeoff may be ubiquitous in forest tree species, it is unlikely to function as an important mechanism for the stable coexistence of several tree species.

In closed forest ecosystems, light availability is a major constraint on tree growth and survival, and an important axis for differentiation of the ecophysiology, architecture, and demography of tree species. There have been extensive efforts to document canopy disturbance regimes and the resulting heterogeneity of light availability in forests worldwide (Runkle 1981, Brokaw 1982, Canham et al. 1990, Yamamoto 1992, Kneeshaw and Bergeron 1998, Nicotra et al. 1999). Many studies have documented a tradeoff in the demography of juvenile trees along gradients in light levels. At one extreme are shade tolerant species with juveniles that have elevated survival rates under low light conditions but only moderate response to canopy openings. At the other extreme are shade intolerant species with juveniles that experience high mortality under low light but have a strong growth response to canopy openings (Canham 1989). This tradeoff between low light survival and high light growth has been reported in tropical, temperate and boreal forests worldwide (Hubbell and Foster 1992, Pacala et al. 1996, Kobe and Coates 1997, Kobe 1999, Gilbert et al. 2006, Kneeshaw et al. 2006, Poorter et al. 2008).

The idea that canopy gaps contribute to the maintenance of tree species diversity has a long history in forest ecology (Ricklefs 1977, Denslow 1980, Poulson and Platt 1989, Runkle 1989, Hubbell et al. 1999, Brokaw and Busing

2000). Its generalization to forests around the world makes it extremely powerful and appealing. It is unclear, however, by which mechanisms canopy gaps maintain diversity. The 'gap theory' of forest dynamics (Yamamoto 1989) comprises a mix of different, largely intuitive, hypotheses on the maintenance of species diversity. In one sense, canopy gaps are thought of as small-scale disturbances that reset community dynamics before competitive exclusion is achieved by the most shade tolerant species (the R* rule, Tilman 1982). More generally, coexistence could be maintained by a wide range of gap-phase related processes, including the generation of a mosaic of small-scale patches at different phases in succession (Jones 1946, Watt 1947, Forcier 1975, Connell 1978), species sorting along a gradient of gap size (Kohyama 1993, Busing and White 1997), within gap partitioning (Ricklefs 1977, Denslow 1980), the regeneration niche (Grubb 1977), or different temporal strategies to access the canopy (Canham 1990, Poulson and Platt 1996, Messier et al. 1999).

Despite the enormous amount of empirical research on gap-phase dynamics in forests worldwide, there are no formal theoretical studies that rigorously identify the mechanisms and conditions under which small-scale disturbances promote species coexistence. The lack of a formal theory of forest dynamics based on canopy gaps and shade tolerance

differentiation may explain conflicting results of studies testing the role of canopy gaps in maintaining species diversity (Hubbell et al. 1999, Brokaw and Busing 2000, Molino and Sabatier 2001, Schnitzer and Carson 2001). Thus, a clear understanding of the mechanisms involved in coexistence of tree species is essential to allow formulation of testable predictions in the field.

Our objectives in this study are to identify the formal mechanisms of coexistence of forest trees based on the low light survival/high light growth tradeoff and heterogeneity in light availability created by canopy gaps, and to highlight their limitations. We do not attempt to address a full list of all potential mechanisms; our focus is specifically on the survival/growth tradeoff and the heterogeneity in light availability created by canopy gaps. Other mechanisms could operate through small-scale disturbances, some that could even be correlated with shade tolerance (e.g. competition/colonization tradeoffs), but these are not treated here. We first present three possible mechanisms that could promote tree species coexistence via the survival/growth tradeoff, with a particular emphasis on their essential parameters and predictions. Those mechanisms are derived from general theories of coexistence in variable environments. These theories are based on very general models, and we thus assess their limitations for forest dynamics with a simple simulation model of forest dynamics. The model is intentionally a simplification of more complex simulation models such as SORTIE (Pacala et al. 1996), as it uses the same functions for juvenile dynamics but simplifies the spatial structure, in order to track the sources of heterogeneity in light availability and avoid other confounding coexistence mechanisms (e.g. tradeoffs in canopy light transmission, Canham et al. 1994, or tree size at maturity, Adams et al. 2007).

The first mechanism we consider is known as 'relative non-linearity' (Chesson 1994), which relies on temporal heterogeneity in light availability. Under this mechanism, coexistence is achieved through a tradeoff in competitive abilities under variable versus constant competitive conditions. The second mechanism is the 'successional niche' (Pacala and Rees 1998), which is based on the capacity of fast growing species to exploit transient pulses of abundant resources immediately after disturbances. The third mechanism is the 'storage effect' (Chesson and Warner 1981), and is based on spatial heterogeneity generated by spatial variability in the disturbance regime. The spatial storage effect is also explored in the context of spatial variation in shade tolerance related to soil heterogeneity. The last two mechanisms rely on spatial dynamics, and thus we will also consider the impact of dispersal limitation in those two cases. Dispersal limitation usually enhances already existing coexistence mechanisms by a process termed 'growth-density covariance' (Chesson 2000b).

Theory of coexistence in a variable environment

The theory we present is an interpretation in the context of forest dynamics of three models of species coexistence in variable environments developed by Chesson (1994, 2000b) and Pacala and Rees (1998). Here, we interpret those models for the special case of forest dynamics, and later we illustrate them by simulations.

Coexistence via relative non-linearity
Following the work of Armstrong and McGehee (1980), Chesson (1994) showed that stable coexistence could result from variation in the limiting resource when at least one species has a non-linear response to it. This situation occurs because one species is a superior competitor for the resource when it is stable, while the other species is superior when it is fluctuating. This results from Jensen's inequality (Ruel and Ayres 1999). Coexistence might occur given an appropriate tradeoff between the non-linearity of the species response to resource availability and the variance of it when it dominates.

In terms of forest dynamics, the limiting resource most affected by canopy disturbances is light availability, although canopy gaps also alter soil resource availability (Marthews et al. 2008). By definition, the most shade tolerant species will tolerate lower light availability, largely because of greater low light survival. Since both survival and growth of individuals are usually non-linear functions of light availability (Pacala et al. 1996), we should expect that per capita population growth rate as a function of light availability is also a non-linear function. If the variance in light availability is superior when the tolerant species is dominant, these factors together would provide the necessary conditions for the relative non-linearity mechanism to operate (we will assess these conditions by simulations in the following section). Although the R* rule predicts that the shade tolerant species will be the competitive dominant, sufficient temporal variance in light availability due to canopy gaps will reduce the recruitment rate of the tolerant species more than the intolerant one, and promote coexistence. This theory predicts that the difference in shade tolerance (e.g. low light survival) of coexisting species will increase with the difference in the variability of light availability they experience when they dominate. One consequence of this mechanism, however, is that it also predicts that only two species could coexist through temporal variability in light availability (Chesson 1994).

Coexistence via successional niche differentiation
The second mechanism of coexistence in variable environments, and perhaps the one with the most intuitive application to forest dynamics, is the successional niche (Pacala and Rees 1998). The R* rule of competitive exclusion assumes that all species have access to the resource (i.e. access is not limited by any spatial or temporal constraint). In a disturbed community, because it takes a finite period of time for populations to recover to equilibrium densities where the resources are scarce, there is a window of time when resources are underexploited. If an inferior competitor is successful at colonizing recently disturbed locations, this transient resource pulse provides an opportunity for temporal partitioning of the resource.

The successional niche mechanism has two simple parameters (Pacala and Rees 1998): the disturbance rate (return interval and intensity) and the successional rate (speed of succession). A high disturbance rate and a low successional rate will promote coexistence. In terms of forest dynamics, the disturbance rate is the well-documented frequency of canopy disturbance and average gap size (Runkle 1981). The successional rate integrates all of the processes that lead to

gap-filling, including traits related to fecundity, dispersal, survival and growth. Essentially, this theory predicts that the likelihood that a shade intolerant species will coexist with a shade tolerant species will increase with the disturbance rate and the high-light growth rate of the shade intolerant species, and will decrease with the growth rate of the shade tolerant species. Dispersal limitation of either or both species will also promote coexistence by reducing the successional rate. It also predicts that a shade intolerant species could not competitively exclude a shade tolerant species.

Coexistence via the storage effect
The third coexistence mechanism we consider is the storage effect. This is a mechanism of coexistence based on the storage of the benefits that accrue during periods of high recruitment (Chesson 2000a). This process prevents dramatic population losses during periods of low recruitment. The same reasoning applies to spatial variation in recruitment. The storage effect applies when species response to competition (e.g. competition for light among forest trees) is affected by an environmental factor that varies temporally (e.g. temperature) or spatially (e.g. soil fertility). The strength of the storage effect depends on how different species respond to variability in the environment, the buffer against population growth (i.e. any factor increasing the capacity to withstand unfavourable conditions, e.g. a seedbank or spatial refuges) and the variance in the environment.

There are a number of ways in which storage effects can occur in forests. Perhaps the most intuitive example – temporal variation in light availability resulting from canopy gaps – however, does not meet the requirements for a formal storage effect. The storage effect needs variation in the environment, while canopy gaps are variation in the intensity of competition (density dependence). For the storage effect to apply in this context, there would need to be variation in the environmental factors that define the response of each species to fluctuating light availability in gaps.

There are several potential forms of spatial heterogeneity that could generate a storage effect. One example would be spatial variation in species demography due to soil heterogeneity (John et al. 2007, Gravel et al. 2008). If the survival of only one species is sensitive to soil pH, then this will create spatial variation in the response to disturbance. Another source of spatial variability would be the spatial variation in the disturbance intensity and frequency (the species sorting hypothesis – Hubbell et al. 1999). The storage effect theory thus predicts that the difference in shade tolerance of coexisting species will increase with the difference in their response to environmental heterogeneity and the amount of heterogeneity. As was the case with the successional niche, dispersal limitation will favour the strength of the storage effect because it buffers the gains a species could make in a favourable environment.

The simulation model

We use a simulation model to explore the effects of these three mechanisms in the specific context of forest dynamics. Forests are obviously far more complex than the general models used to develop the theory of coexistence we have presented here. Our goal is to see whether predictions from the general theory will hold in a more complex community. More generally, we hope that translating the processes into terms more easily interpretable by field ecologists will lead to the generation of new and empirically-testable hypotheses.

Structure of the forest community
The model simulates the survival and growth of populations of juvenile and adult trees in spatially homogeneous localities, called cells, on a lattice (all parameters are listed in Table 1 and the functions illustrated at Fig. 1). The model structure allows us to distinguish between the various sources of heterogeneity in light availability created by canopy gaps. Every individual within a cell experiences the same light availability. Cells are independent from each other except through dispersal. Simulated this way, we discretize the spatial structure of a forest into cells corresponding conceptually to a few canopy trees. The spatially discrete nature of the model allows us to determine if coexistence could occur in the presence of only temporal variation in light availability (through tests performed in a single cell). However, because cells are also connected by dispersal, we can also ask if the parameter space of the low light survival/high light growth tradeoff allowing coexistence is affected by the spatial dimensions of disturbance and dispersal.

Population growth
Competition for light is mechanistic. Light availability (L, in % of full sun) for juveniles in a cell follows an exponentially declining function of adult density (trees cell^{-1}):

$$L = 100e^{aN}$$

The parameter a depends on the carrying capacity of the cell K (trees cell^{-1}), defined as the number of adult

Table 1. List of the model parameters.

| Symbol	Description
Light availability	
K	Carrying capacity, i.e. the number of adult stems required to reduce light availability to 1% (trees cell^{-1})
Sapling dynamics	
b_i	Slope of the soil fertility-low light mortality relationship (year^{-1} S^{-1})
m_{0i}	Intercept of the soil fertility-low light mortality relationship (year^{-1})
m_{1i}	Low light mortality rate (year^{-1})
m_{1i} m_{2i}	Shape of the light-mortality relationship (unit less)
h_i	Asymptotic high light radial growth for saplings (mm year^{-1})
g_i	Low light increase in growth (year L mm^{-1})
Adult mortality	
m_3	Baseline adult mortality rate (year^{-1})
m_4	Disturbance mortality rate (disturbance^{-1})
l	Disturbance return interval (year disturbance^{-1})
Reproduction	
d	Dispersal limitation (year^{-1})
r_S	Initial seedling diameter (mm)
r_A	Threshold diameter for reproduction (mm)
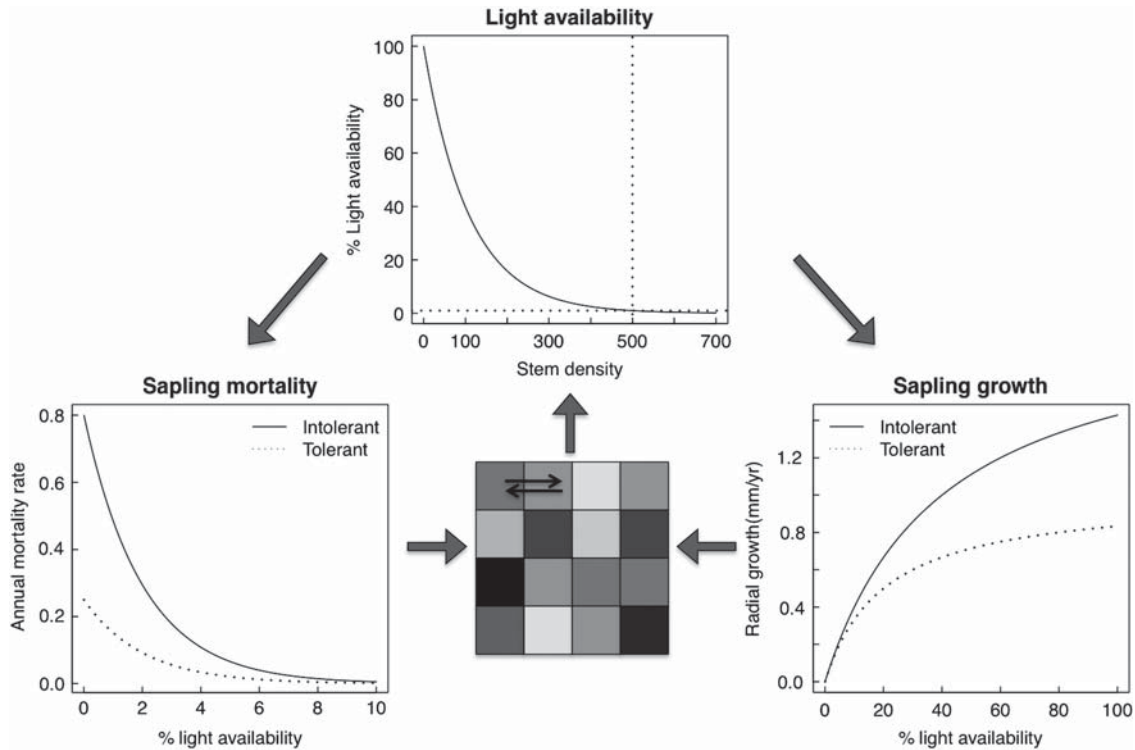
Figure 1. Schematic representation of the forest simulation model for a shade tolerant 3 ($m_{1A} = 0.5$ and $h_A = 1.0$) and a shade intolerant ($m_{1B} = 0.8$ and $h_B = 2.0$) species. The forest community consists of a lattice of cells connected by dispersal. In each cell, light availability (depicted by the color of the cell) depends on the number of trees per cell. The model simulates the mortality and growth of populations of juveniles, which depend on light availability. Adult mortality occurs because of a constant annual mortality and disturbances creating canopy gaps. Recruitment to the canopy occurs once saplings reach a threshold size.

trees to obtain 1% of light availability, and is given by $a = \log(0.01)/K$. For simulations, K was fixed at 50 trees cell^{-1} (note the value of K has no qualitative impact on community dynamics and on coexistence).

The mortality rate of juveniles of species i (M_i, year^{-1}) is a function of light availability:

$$M_i = m_{1i}\, e^{-m_{2i}L}$$

The parameter m_{1i} (year^{-1}) is the low light mortality rate and m_{2i} (unit less) shapes the decline of the relationship with light availability ($m_{2i} = 0.5$ for every species).

Soil conditions are allowed to vary from one cell to another. To simplify the representation of soil heterogeneity, we considered a soil fertility index S with an average value of 0 for the lattice, with negative values representing poor soil conditions and positive values better than average conditions. The parameter m_{1i} is a linear function of soil fertility:

$$m_{1i} = m_{0i} + b_i S$$

where m_{0i} is the intercept of the soil fertility-low light mortality relationship (year^{-1}) and b_i is the slope of the soil fertility-low light mortality relationship (year^{-1} S^{-1}).

Juvenile tree growth (G_i, in mm year^{-1} of diameter growth) is also a function of light availability:

$$G_i = \frac{h_i L}{(h_i/g_i) + L}$$

The parameter h_i (mm year^{-1}) is the asymptotic high light growth (species-specific) and g_i (year L mm^{-1}) is the low light rate of increase in growth ($g_i = 0.05$ for every species). New seedlings are initialized with a stem diameter (r_s) of 2 mm. Juveniles grow until they reach the threshold diameter (r_A) of 100 mm and then become adults. Adults have a fixed size for simplicity.

Disturbance
Adult mortality occurs in two ways. First, a baseline mortality rate (m_3, in year^{-1}) kills a fraction of adult trees each year (we fixed it a 0.005 year^{-1}). Second, disturbance occurs at regular intervals (I, year disturbance^{-1}) and kills a fraction of adult trees (m_4, in year^{-1}). The total average ($m_3 + \overline{m}_4$) adult mortality rate is fixed at 0.01 year^{-1} (which gives life expectancies similar to those reported for tropical (Brokaw 1982) and temperate (Runkle 1981) forest trees). We varied the disturbance mortality rate as a function of the return interval to keep the global mortality rate constant ($m_3 + m_4/I$) = 0.01 year^{-1}).

Dispersal
The parameter d (year^{-1}) specifies the fraction of the seeds produced in one cell that will be dispersed to regional seed pool and then redistributed among all cells. The remaining fraction $(1 - d)$ germinates in the cell it was produced. Dispersal among cells is spatially implicit, i.e. seeds dispersed from one cell are distributed uniformly across all cells of the lattice. Fecundity is set to 0.1 seeds tree^{-1} year^{-1} and all seeds germinate.

Simulation experiments
Relative non-linearity
We first tested if the growth/survival tradeoff allowed coexistence with only temporal variation in light availability. For these simulations, only one cell was simulated to assure pure temporal variation in light availability. We also conducted monospecific simulations with a gradient of shade tolerance and recorded the statistics of light availability (average and variance) to investigate further the factors necessary for coexistence by relative non-linearity.

The successional niche
We assessed if coexistence was promoted by spatial variation in the occurrence of disturbances. We simulated the extreme situation where disturbances are perfectly asynchronized across the 10 cells of the lattice. Preliminary simulations showed the results did not change for larger lattices. The return interval was 75 years. We varied dispersal limitations from low (d = 1) to high (d = 0.1).

The spatial storage effect
We also assessed if coexistence was promoted by spatial variability in the disturbance return interval. In this scenario, the 10 cells had different and independent return intervals, ranging from 30 to 120 years (mean = 75 years). Again, we varied dispersal limitation from low to high.

We also assessed if coexistence was promoted by spatial variability in soil fertility. In this scenario, light availability was spatially uniform, but soil fertility varied across the 10 cells. The average soil fertility was always 0, but we increased the range of S from 0 to 5 (with a uniform distribution). Soil fertility only affected survival of species B (b = –0.05). Again, we varied dispersal limitation from low to high.

Criteria for coexistence
We first conducted simulations with two species to assess the general predictions of the model. For convenience, the shade tolerant species (high m_{1i}, low h_i) was species A and had fixed parameters. The intolerant species B had varying parameters. To assess stable coexistence, we ran two simulations for each set of parameters to test if both species had a positive growth rate when at low abundance (sensu Chesson 2000a). The first simulation starts with species A at 99% (the dominant species) of relative abundance and species B at 1% (the rare species). The second simulation is opposite with species A being rare and species B abundant. We ran the simulations for 1000 years to remove transients and then recorded the average abundance over the next 200 years. We considered that coexistence was stable when both species increased their relative abundance (by any amount) when starting as rare. Unstable coexistence occurred when none of the species could increase in relative abundance when rare (meaning the resident species wins the competition). Competitive exclusion occurred when one species could increase when starting as rare and the other could not.

Simulations with three species were also conducted in the same manner to assess multi species coexistence for the scenarios with pure temporal heterogeneity, asynchronized disturbances and variability in disturbance return interval. The three species (A, B and C) were ranked by their high light

growth and low light survival. High light growth was fixed (h_B=1.6), but low light survival varied for species B and C to find combination of parameters allowing coexistence. The disturbance return interval was 75 years. Time to fixation at three species was longer than in the two species trials, so coexistence with the invasibility criterion was assessed after 2000 years, following an initial period of 5000 years to remove transient dynamics.

Sensitivity analysis
To assure that the observed coexistence was not restricted to a narrow set of parameters, we performed a series of additional simulations. We ran 10^6 simulations with values for all parameters selected at random from a uniform distribution (all parameters were random draws with the mean values corresponding to the set of parameters used in this study). This strategy allowed us to explore a very wide parameter space. We report in the Supplementary material Appendix 1 the range of values for each parameter under which stable coexistence was observed and the structure of this parameter space. We assumed that if the simulations showed coexistence for a portion of parameter space at a given location, the corresponding parameters would allow coexistence for a spatially-structured community as well. The results showed coexistence was possible under a wide range of parameter values. Consequently, we are confident that our conclusions are not restricted to a narrow parameter space.

Results

A typical run is illustrated for a shade tolerant and a shade intolerant species in Fig. 2. As we would expect, the shade intolerant species reached its peak of abundance much quicker than the shade tolerant species because of faster high-light growth. Once the disturbance occurred, saplings initially increased in abundance because of higher survival, but sapling density subsequently decreased because they were recruited to the adult stage. Once the adult population increased, it produced more offspring and the sapling layer started to build-up again. The range of densities encountered depended on the species parameters and, as we will see in the next section, it had considerable influence on the mean and the variance in light availability and thus the likelihood of coexistence.

Relative non-linearity

Simulation results were consistent with the predictions from the general theory. First, the low-light survival/high light growth tradeoff allowed stable coexistence of two species through temporal variation in light availability alone (i.e. even in the absence of spatial variation) (Fig. 3A). The shape of the survival/high light growth tradeoff allowing coexistence is thus not only a result of evolutionary/physiological constraints, it is also necessary for coexistence since a faster growing species must have a lower survival to coexist with a species with slow growth/high survival (Fig. 3A). The parameter space allowing coexistence was affected by the disturbance return interval (Fig. 3B). Coexistence was maximized
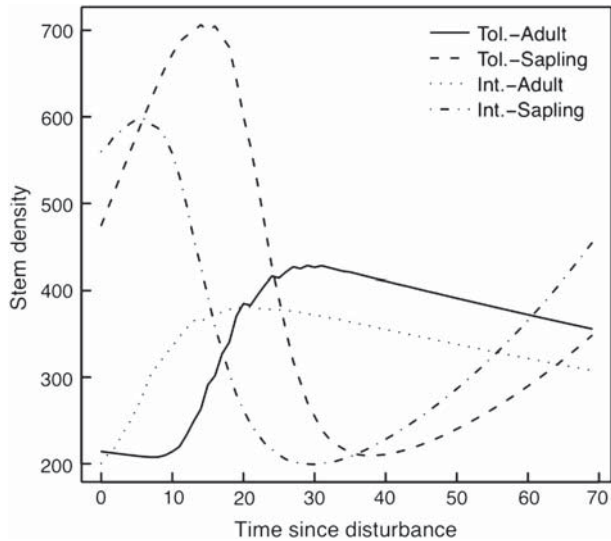
Figure 2. Illustration of a typical simulation for a shade tolerant (m_{1A} = 0.5 and h_A = 1.0) and a shade intolerant (m_{1B} = 0.8 and h_B = 2.0) species and a disturbance return interval fixed at 75 years. The light availability is spatially uniform for the purpose of the illustration (i.e. only one cell is simulated and K is fixed at 500).

at an intermediate disturbance return interval, as indicated by the range of the survival rate for species B allowing coexistence. The intermediate disturbance return interval also corresponded to the highest variability in light availability (not shown).

At some disturbance return intervals, community dynamics were unstable (Fig. 3B), meaning none of the species could successfully invade when at low abundance. We believe this instability is the result of a deterministic return interval since we did not observe unstable dynamics when the return interval was stochastic (coexistence was stable also for these return intervals - results not shown). This situation could have arisen from the interaction between the community dynamics (it takes approximately 30–40 years for a sapling

to reach the canopy, creating intrinsic population fluctuations) and the deterministic return interval. At shorter return interval, the mortality rate is perhaps too low, while at longer intervals disturbances dominate the dynamics. The synchronization of a fluctuating community dynamics and an external disturbance could alter both community properties and coexistence (Guichard and Steenweg 2008).

We explored the structure of the parameter space allowing two-species coexistence for a wide range of parameter values with the sensitivity analysis (the results are presented in the Supplementary material Appendix 1). We were interested to learn how the different parameters would tradeoff in this multidimensional space. We found no consistent pattern, however, as coexistence was observed for a wide range of parameter values and there was no significant correlation between parameters. The only exception was between parameters that were constrained by default (because species A is defined as shade tolerant and species B is intolerant, it implies a correlation between survival and growth parameters). This situation arises from the multidimensional structure of this parameter space. For instance, we should expect a correlation between mortality and the disturbance return interval. This relationship was not observed however because it was blurred by the simultaneous variation of high light growth. As a result, it is very difficult to reduce the parameter space to a few variables: the principal component analysis of the parameter space yielded very low scores for the first (26.2%) and the second axis (17.7%).

Numerous lines of evidence suggest the coexistence we observed, based on temporal heterogeneity in light availability, results from the relative non-linearity mechanism. To our knowledge, this is the first time this mechanism has been shown to operate in a system other than a predator-prey interaction. Several arguments support the role of relative non-linearity in the observed coexistence. First, the ratio between the species' recruitment rates is non-linear (Fig. 4), the essential condition for this mechanism. Because the Figure is on a log-log scale, the slope of the relationship is a measure of the strength of the relative non-linearity.
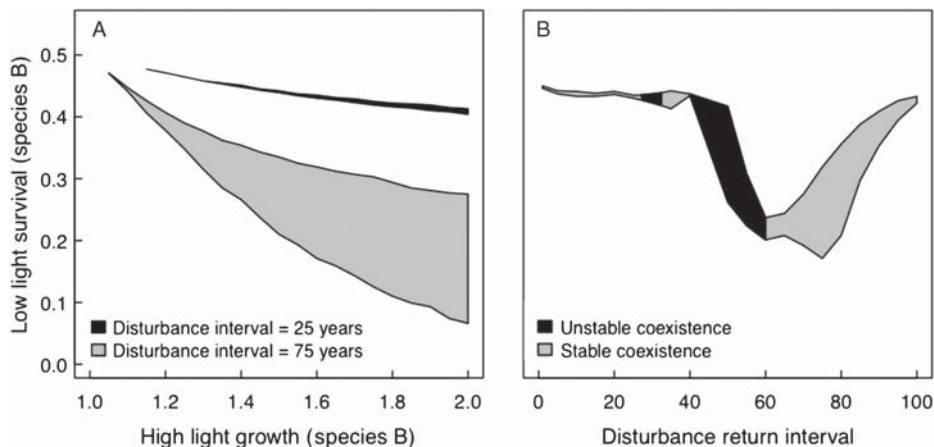

Figure 3. Parameter space allowing coexistence with spatially uniform light availability. For both panels are presented the lower and upper limits of the low light survival parameter of species B (m_{1iB}) allowing coexistence with species A. For all simulations, m_{1A} = 0.5 and h_A = 1.0. (A) the critical low light survival of species B is inversely related to its high light growth. (B) the low light survival for species B allowing coexistence with species A varies with the disturbance return interval (h_B is fixed at 1.6).

The higher recruitment of species A compared to B, observed in most cases, corresponds to the prediction that the most shade tolerant species (here species A) is the strongest competitor. Second, the non-linearity of the recruitment function depends on the average light availability and shade tolerance. Third, the average light availability is lower under shade tolerant species, and the variance in light availability is higher for the most shade tolerant species (Fig. 5). Lower variance in light availability when the shade intolerant dominates occurs because shade intolerant species take less time to fill the gap (Fig. 2). Thus, although the shade intolerant species is negatively affected by low light availability when it is an invader, its growth rate is promoted by the variance in light availability it experiences. As predicted by Chesson's (1994, 2000b) general models, only two species can coexist stably according to this mechanism (Table 3). Competitive exclusion is, however, extremely slow because of the long life spans of trees, leading to transient coexistence for extended periods of time (not shown). Over the long term, however, only the two most dissimilar species coexist at equilibrium.

The successional niche

The simulation results are also consistent with the predictions of the successional niche theory. The simultaneous occurrence of sub-populations at different successional phases in the community (as a result of variation in the time of occurrence of disturbances) slightly increases the range of parameters allowing coexistence (Table 2). Coexistence was promoted by dispersal limitation. These simulations where characterized by very low spatial variability in relative abundance of the species, which might explain the small effect of this mechanism on coexistence.
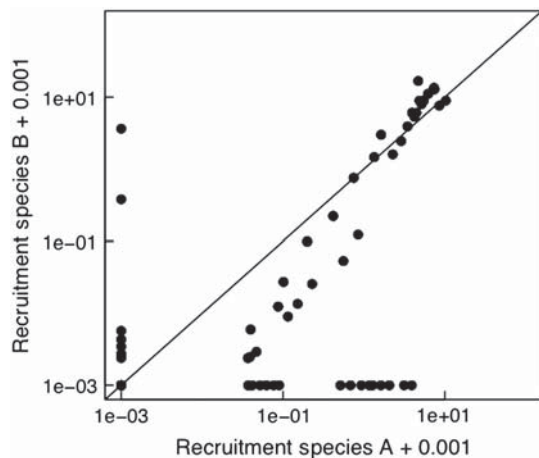

Figure 4. The non-linear relationship between recruitment of species A and species B. Each point represents the number of new individuals recruiting to the adult stage, per time step, of species A and B. Points represent recruitment in each of the last 250 years of a single 1000 years simulation with species A and B coexisting. Because of the log–log scale, any relationship that is not on the 1:1 slope demonstrates relative non-linearity. Disturbance return interval is 75 years; low light survival of species B is 0.2 and high light growth is 2.0. The simulation was initiated with equal abundances of each species.

The shade tolerant species has a lower gap-filling rate (successional rate) than the shade intolerant species (Fig. 2). Note however that random occurrences of disturbance events, instead of perfectly asynchronized occurrences, reduced the likelihood of coexistence (Table 3).

The storage effect

Spatial heterogeneity in the environment does favour coexistence as a result of the storage effect (Fig. 6, Table 2). Increasing soil heterogeneity can allow the coexistence of species that are increasingly dissimilar in their low light survival (Fig. 6). The presence of strong dispersal limitation also promotes coexistence. Soil heterogeneity and dispersal limitation increase spatial variation in relative abundance (not shown) in a manner consistent with the storage effect.

Spatial variability in the disturbance return interval also promotes coexistence, especially when dispersal limitation is
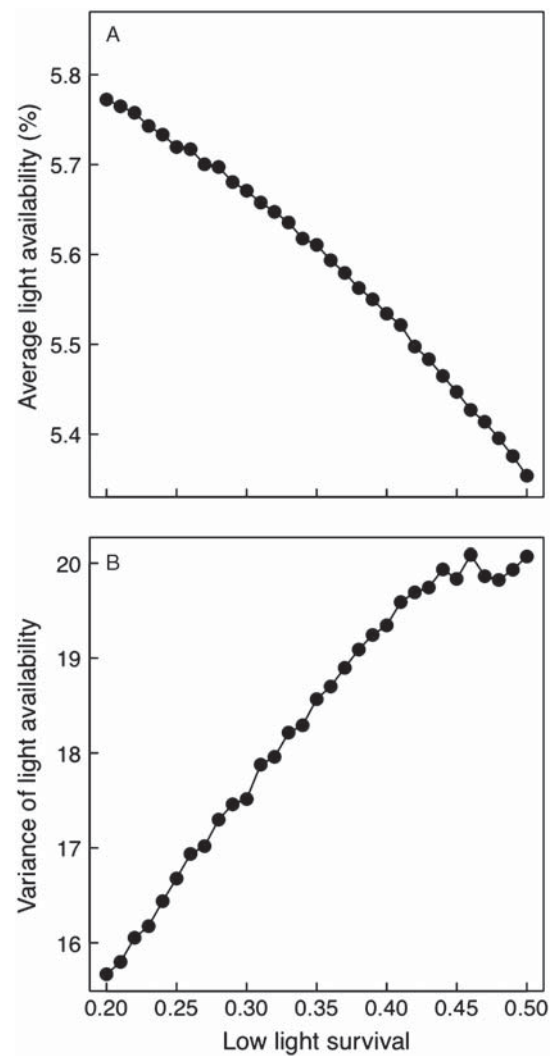

Figure 5. The average (A) and variance (B) of light availability (%) varies with species shade tolerance. Disturbance return interval fixed at 75 years. The statistics are recorded over 250 years for simulations with only one species, after the transients have been removed. We varied the low light mortality (m_1) and scaled hA linearly with m_{1A} between the most shade tolerant ($m_{1A} = 0.5$ and $h_A = 1.0$) and shade intolerant ($m_{1B} = 0.8$ and $h_B = 1.6$) species.

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Table 2. Lower and upper limits of the low light survival parameter of species B ($m1_B$) allowing coexistence with species A (see parameters below) with spatial heterogeneity in disturbance. Simulations included 1) no spatial variation (only temporal variation in resource availability – for reference); 2) spatio-temporal variation resulting from asynchrony in the occurrence of disturbance across the 10 simulated cells (but with a fixed return interval of 75 years), and 3) spatio-temporal variation resulting from spatial heterogeneity in the disturbance return interval (mean = 75 years, range is from 30 to 120). Default parameters: species A low light survival (m_{1A}) = 0.5 and high light growth (h_A) = 1.0, species B high light growth (h_B) = 1.6. Only extreme cases of dispersal limitation are represented. na = not available.

Source of heterogeneity		With dispersal limitation	No dispersal limitation
Only temporal	lower limit	na	0.171
	upper limit	na	0.319
Spatially asynchronized disturbances	lower limit	0.102	0.164
	upper limit	0.290	0.317
Spatial variability in disturbance return interval	lower limit	0	0
	upper limit	0.376	0.414

Table 3. Results of the tests for three species coexistence. The high light growth parameter (h) was set to 1.0, 1.6 and 2.0 for species A, B and C, respectively; the low light survival (m_1) was fixed at 0.5 for species A, but varied from 0.5 to 2.0 for species B and C to find combinations of parameters allowing coexistence. Disturbance return interval was 75 years. Dispersal limitations: d = 0.1. Three species coexistence (YES) is achieved when all three species could invade a mixture of the other two species. na = not available.

Source of heterogeneity	With dispersal limitation	No dispersal limitation
Temporal	na	NO
Spatial – asynchronized disturbances	YES	NO
Spatial – heterogeneity in disturbance return interval	YES	NO
Spatial – random occurrence of disturbance events	NO	NO

important (Table 2). Spatial variability in light availability allows stable coexistence of more than two species over the long term (Table 3). Three species coexistence was not observed when disturbance occurred at random (Table 3).

Discussion

We have shown that coexistence among forest trees based on the low light survival/high light growth tradeoff is made possible by three different mechanisms: relative non-linearity, the successional niche, and the storage effect. Variation in the intensity and return interval of disturbances, spatial asynchronicity in the occurrence of disturbances, spatial variability in disturbance frequency and soil properties are all sources of heterogeneity contributing to coexistence.

Nonetheless, our results suggest that the low light survival / high light growth tradeoff may play only a minor role in the stable coexistence of tree species. We found that with only temporal variability in light availability, only two species could coexist via this tradeoff. Three species coexistence was possible with spatial variation in light availability, but the parameter space allowing coexistence was considerably smaller than for two species coexistence, suggesting it is very unlikely that four or more species could stably coexist under this mechanism. This is not to deny the ubiquity of the tradeoff in nature, because it could still contribute to transient coexistence. Nor does it deny the importance of the tradeoff in determining the successional status of species (Pacala et al. 1996) and the successional dynamics of communities. However, the presumption that the tradeoff plays a major role in coexistence of many tree species is not supported by our study.

Our model illustrates the specific processes and mechanisms that underlie hypotheses relating coexistence to shade tolerance differentiation and spatio-temporal fluctuations in light availability created by canopy gaps. Perhaps the most common and intuitive prediction is that diversity should peak at an intermediate level of disturbance (Hubbell et al. 1999), the so-called intermediate disturbance hypothesis (IDH, Connell 1978). It is now recognized that IDH is a conceptual framework involving both relative non-linearity and the storage effect as coexistence mechanisms (Roxburgh et al. 2004). We found that the mechanism of relative non-linearity predicts that the parameter space allowing coexistence is largest at an intermediate level along the disturbance interval/severity axis.

However, the mechanism of relative non-linearity allows for stable coexistence of only two species. The formal mathematical argument to justify why relative non-linearity allows only two species to coexist is given in Chesson (1994). Basically, this mechanism creates a maximum of two temporal niches: one for the species having the highest per capita growth rate under constant intensity of competition, the other for the species having the highest per capita growth rate under varying competition. In communities of three or more species, competition selects the two species that will maximise the relative non-linearity. This result is in sharp contrast with the widely held view that the low light survival/high light growth tradeoff allows coexistence of multiple species (Hubbell et al. 1999, Rees et al. 2001).

The contrast between our results and other models of successional diversity (including the IDH) might arise from the consideration of space and the way colonization occurs. Models of successional diversity, such as the competition/colonization and successional niche models (Tilman 1994, Pacala and Rees 1998), do not explicitly decompose the temporal and spatial mechanisms of coexistence. Such models usually either explicitly or implicitly assume some sort of a competition–colonization tradeoff (which we did not here). Pioneer species differ from late successional species in many life-history traits, including their typically high fecundity, large dispersal and early age at reproduction (Pacala et al. 1996, Rees et al. 2001). A correlation between disturbances and some competitive responses such as germination of seed banks (Roxburgh et al. 2004) and fecundity (Kelly and Bowler 2002) also shapes the response to competition. All of these traits contribute to a storage effect.
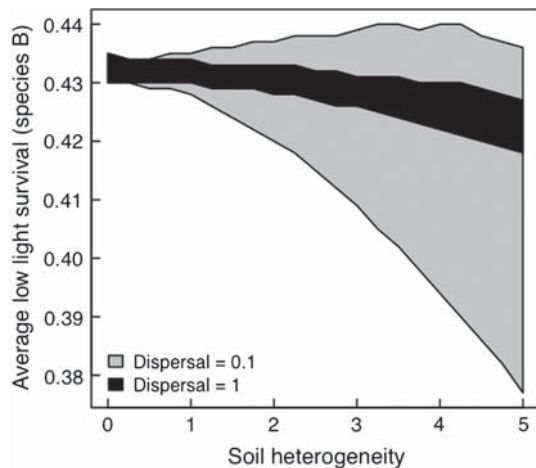
Figure 6. Soil spatial heterogeneity promotes species coexistence. The critical low light survival of species B for coexistence varies with the soil heterogeneity (mean S = 0, range increases from 0 to 5). The low light mortality rate of species B varies with S as: $m_{1B} = 0.8 + 0.05 \times S$.

In other models that do not include explicitly a competition–colonization tradeoff, a colonizing advantage is often implicitly assumed in the way initial recruitment occurs following disturbances. Disturbances are commonly viewed as extreme events that reset the community, eliminating all species from the site. Prior to a disturbance, the late successional species should be expected to be more abundant. After a disturbance, if every species is recruited in equal proportion (the niche model of Pacala and Rees 1999) or in proportion to the regional abundance (the shifting mosaic hypothesis; Jones 1946, Watt 1947), then disturbance will be most beneficial to pioneer species. The net effect is an implicit competition–colonization tradeoff, which allows very a high number of coexisting species (Tilman 1994).

Our results show that spatial variation in light availability promotes coexistence. We simulated extreme cases where spatial heterogeneity of disturbances was minimal and maximal to facilitate the analysis. As predicted, the range of parameter values that allowed coexistence was positively related to the heterogeneity of disturbance occurrence. Increasing dispersal limitation also reinforces the spatial storage effect by enhancing spatial variability in species distribution.

The effect of a varying return interval was much more substantial than the effect of asynchronicity. In contrast to the situation with pure temporal fluctuations in light availability, both forms of spatial variability in disturbance allowed stable coexistence of three species.

The simple simulation model of forest dynamics we presented here is an alternative to much more complex simulation models such as SORTIE (Pacala et al. 1996) or FORMIND (Köhler and Huth 2007). The simplification of the light environment in our model involved a simpler definition of the adult cohort structure and neglected shading by understory individuals. We believe however that the results we presented here would hold under more complex simulations of light availability. The limits on the ability of canopy disturbances to support coexistence is likely due to the fact that canopy gaps do not disturb completely the community, as some trees and saplings remain after a disturbance. The coexistence mechanisms

we presented all require strong variation in light and in relative abundance following disturbance, but the simulations show that canopy gaps did not significantly alter composition. A better representation of canopy structure would simply strengthen this, as canopy closure would be more rapid (by horizontal growth of trees and saplings, Beaudet et al. 2004, 2007a, 2007b) and thus reduce spatio temporal variability in the light environment. The way we simulated spatial variation in disturbances also maximises variation in light availability, suggesting that coexistence would be even less likely with more realistic simulation of the disturbance regime. For instance, by simply making the occurrence of disturbance random events instead of deterministic in the lattice impeded coexistence of even three species.

Our results suggest that while the high light growth/low light survival tradeoff may be ubiquitous in forest tree species, it is not as strong a mechanism for tree species coexistence as was previously thought. It could however contribute to other coexistence mechanisms by reducing the fitness inequality between species. Further work should be done with more realistic models of forest dynamics to explore the coexistence criteria under a more realistic and operational set of parameters. Moreover, forest ecologists have noted a wide range of traits associated with species responses to canopy disturbances. The high light growth/low light survival tradeoff is only one of the many possible strategies for trees to differentiate along a disturbance gradient (Pacala et al. 1996, Loehle 2000). Consequently, further studies should investigate how other traits related to shade tolerance interact with the growth/survival tradeoff to promote coexistence.

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Supplementary material (available online as Appendix O17441 at www.oikos.ekol.lu.se/appendix). Appendix 1.