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Understanding height-structured competition in forests: is there an R^* for light?

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Tree species differ from one another in, and display trade-offs among, a wide range of attributes, including canopy and understorey growth and mortality rates, fecundity, height and crown allometry, and crown transmissivity. But how does this variation affect the outcome of interspecific competition and hence community structure? We derive criteria for the outcome of competition among tree species competing for light, given their allometric and life-history parameters. These criteria are defined in terms of a new simple whole life-cycle measure of performance, which provides a simple way to organize and understand the many ways in which species differ. The general case, in which all parameters can differ between species, can produce coexistence, founder control or competitive exclusion: thus, competition for light need not be hierarchical as implied by R^* theory. The special case in which species differ only in crown transmissivity produces neutral dynamics. The special case in which species differ in all parameters except crown transmissivity gives hierarchical competition, where the equivalent of R^* is Z^* , the height at which trees enter the canopy in an equilibrium monoculture.

Keywords: biomechanics; succession; community ecology; forest dynamics; pairwise invasibility; SORTIE

1. INTRODUCTION

The major current debates in plant community ecology are about the nature and consequences of interspecific life-history trade-offs, which can be defined generally as negative correlations between different aspects of performance, and can take a wide variety of forms (e.g. Canham *et al.* 1994; Loehle 2000; Nishimura *et al.* 2005). According to niche-based theories, these trade-offs maintain diversity by giving each species (or functional group) a fitness advantage when it becomes rare (stabilizing trade-offs; Chesson 2000). Neutral theory, which does not allow such density-dependent regulation, nonetheless needs to invoke trade-offs to explain why species with very different vital rates (e.g. mortality and fecundity) can co-occur for long time periods (equalizing trade-offs; Chesson 2000). And at larger scales, the marked correlations among species, climate and soils are difficult to explain without recourse to trade-offs between performance in different environments.

This theoretical background has contributed to the current interest in life-history trade-offs in forest communities (Gilbert *et al.* 2006). For example, fast-growing tree species have been found to survive poorly in the shade (e.g. Pacala *et al.* 1996; Hubbell 2001, p. 324; Poorter & Aerts 2003) and in cold climates (Loehle 1998). Species that can survive well in deep shade have been found to be shorter for a given diameter (Poorter *et al.* 2006), less tolerant of drought and waterlogging (Niinemets & Valladares 2006), and to produce denser foliage (Canham *et al.* 1994). Additional potentially important trade-offs in forest communities

include the competition–colonization (C–C) trade-off (e.g. Dalling & Hubbell 2002); specialization to different soils and climatic conditions, which is evidenced by the marked species–environment correlations observed at all spatial scales (e.g. Woodward 1987; Pelissier *et al.* 2002; Phillips *et al.* 2003); and various interspecific trade-offs among, or involving, various physiological and demographic attributes (e.g. Kohyama *et al.* 2003; Craine & Reich 2005; Poorter & Bongers 2006).

However, the implications of these trade-offs for species coexistence and community structure remain almost completely obscure, for the simple reason that there has been no way to translate interspecific differences in allometric and life-history parameters into predictions about the relative competitive abilities of species, and hence the outcome of competition at the community scale (Aarssen & Keogh 2002). Classical population dynamic theories, such as the Lotka–Volterra equations and their recent extensions, provide a general framework for addressing such questions of interspecific competition, but their level of abstraction makes them fundamentally disconnected from life-history parameters that can be measured in the field. For example, the Lotka–Volterra equations have no way to represent the dynamics of individual growth, and biomass and height distributions, and asymmetric competition for light, which are fundamental to forest dynamics. At the other extreme, detailed stochastic individual-based forest simulators have been successful in mimicking, and in some cases predicting, the dynamics of particular communities (Kohyama 1993; Pacala *et al.* 1996; reviewed by Busing & Maily (2002)). But the complexity of these models has precluded general results about the nature of interspecific competition and community composition. Thus, the rich history of forest ecology, including intensive studies of tree physiology and growth, the development of forest simulators, enormous efforts of forest inventory

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Table 1. Notation.

	description	units
i, j	indices for species: for two-species problems, i denotes resident, j denotes invader	n.a.
$G_{L,i}, G_{D,i}(L)$	diameter growth rate of canopy and understorey trees, respectively	cm yr^{-1}
$\mu_{L,i}, \mu_{D,i}(L)$	mortality rate of canopy and understorey trees, respectively	yr^{-1}
F_i	fecundity of species i	$\text{m}^{-2} \text{yr}^{-1}$
H_i, β_i	height allometry parameters for species i	m, n.a.
α_i	crown radius parameter for species i	m cm^{-1}
L_i	canopy transmissivity: the incident light level (fraction of full sunlight) in the understorey of a monoculture of i	n.a.
Z^*	canopy height	m
\hat{Z}_i^*	equilibrium value of Z^* for a monoculture of i	m
$\hat{Z}_i^*(L)$	equilibrium value of Z^* for a monoculture of i , with imposed understorey light level L	m

programmes and the recent interest in interspecific trade-offs, has not led to the kind of analytical theoretical advances that have been so valuable elsewhere (e.g. R^* and resource ratio theory for belowground competition, Tilman (1980), Tilman & Wedin (1991); the Levins model for metapopulation dynamics, Levins (1969) and standardized incidence ratio (SIR) models in epidemiology, Anderson & May (1991)). And, therefore, it has not provided a route towards general conclusions about the ecological forces structuring forest communities.

In this paper we present a simple theory for understanding interspecific competition for light in forest communities. We derive the conditions for the invasion of a monoculture by a second species, given the key allometric and life-history parameters of both species (including growth, mortality, crown transmissivity, fecundity, and height and crown allometry). This allows us to determine the conditions necessary for competition between the species to be characterized by deterministic coexistence, founder control or dominance by one species; and to uncover the general processes that drive these outcomes. We show how two special cases of the model lead to perfectly hierarchical competition, analogous to R^* theory; and to neutral dynamics, allowing ecological drift. Surprisingly, we find that the outcome of pairwise competition can be described in terms of a simple index of the relative whole lifetime performance of two species, defined as a particular nonlinear combination of all of the allometric and life-history parameters. This provides a possible theoretical foundation for interpreting and guiding fieldwork on interspecific trade-offs in forest communities.

Any such analysis can only be as good as the model on which it is based. How do we know that the model bears a close relationship to the dynamics of real forest communities? Crucially, the model we employ here (which was derived only recently; Strigul *et al.* submitted) has been shown to reproduce the average behaviour of complex forest gap models (Strigul *et al.* submitted), which themselves have a proven ability to reproduce observed forest dynamics (Pacala *et al.* 1996; Coates *et al.* 2003). It has been proven analytically that the model formulation naturally reproduces important, well-documented behaviours of tree monocultures, including self-thinning and the law of constant final yield (Strigul *et al.* submitted). Perhaps most importantly, when parameterized from individual-level forest inventory data from the Lake States of the USA, the model accurately reproduces the 100-year dynamics of basal area and biomass versus

time; the identities of the early and late successional species; the size distribution of 100-year-old stands; and how each of these change across soil types (D. W. Purves, N. Strigul, J. W. Lichstein, S. W. Pacala 2007, unpublished data). Although the literature contains other analytical and computational examinations of height-structured competition, and its implications for community dynamics (e.g. Kohyama 1993, 1994; Nakashizuka & Kohyama 1995; Perry *et al.* 2003; Vance & Nevai 2007), we are not aware of any other model formulation that has been compared with the dynamics of real forest communities to this extent.

2. MATERIAL AND METHODS

The analysis builds on the recent development of a simple set of equations that describe forest dynamics in terms of temporal changes in the density of the individuals of each size and species (macroscopic equations; Strigul *et al.* submitted). Crucially, these equations are explicitly derived from the rates of individual growth and mortality, which themselves are subject to height-structured asymmetric competition for light. Thus, the equations scale directly from the properties of individual trees of different species, to dynamics and properties of the stand, including changes in densities, size distributions and species composition. The equations are subject to the assumptions of the forest gap models from which they are ultimately derived, along with the additional assumption of perfect plasticity in canopy structure (see below; figure 1). For the formal derivation of the macroscopic equations, we refer the reader to Strigul *et al.* (submitted).

Using the macroscopic equations, we seek to define and understand the conditions for the invasion of an equilibrium population of a resident species i by a second species j introduced at low density (table 1). This condition is fundamental to understanding the long-term outcome of competition between two species (Turelli 1978; Chesson & Ellner 1989). The steps in the analysis are given in detail below, and consist of (i) calculation of the equilibrium state of the resident species, in particular, the aspects of the state that affect the population growth rate of the invading species j , (ii) calculation of the initial population growth rate of the invading species j , given the equilibrium state of the resident species i , and (iii) consideration of the pair of invasion criteria, $i \rightarrow j$ and $j \rightarrow i$, resulting from a given set of differences in the allometric and life-history parameters between species i and j . We then consider two special cases—where crown transmissivity is the only difference between species, and where crown

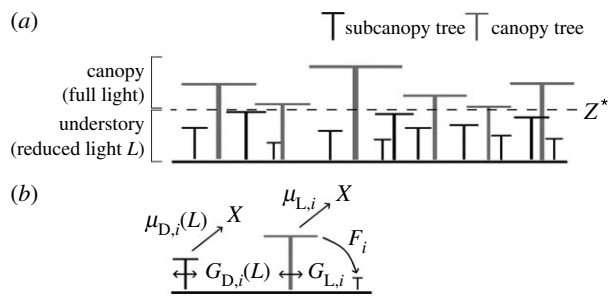


Figure 1. A simple model formulation to capture height-structured competition for space in forest stands. (a) An assumption of perfect plasticity of horizontal growth, together with a simplification to flat-topped crowns, reduces canopy structure to a simplified form where each tree is entirely within the canopy, in which case it receives full light; or entirely within the understory, which has a homogeneous, reduced light level L . The understory light level is determined by the transmissivities of the canopy trees crowns. (b) The dynamics for species i are determined entirely the five rates shown: mortality $\mu_{D,i}(L)$ and $\mu_{L,i}$; growth $G_{D,i}(L)$ and $G_{L,i}$; and fecundity F_i ; together with parameters to set height allometry (height given DBH), crown allometry (crown radius given DBH) and the understory light level (L). For the invasion analysis, a species j is introduced at low density into an equilibrium monoculture of species i , in which case it experiences an understory light level L_i determined solely by species i canopy trees, and the equilibrium canopy height for species i in monoculture, Z_i^* .

transmissivity is the only parameter that does not differ between species—before examining the general case where all parameters are allowed to differ between the two species.

(a) Model description

The macroscopic equations derived by *Strigul et al.* (submitted) describe the average behaviour of an individual-based forest gap model similar to SORTIE, which is known to be capable of reproducing the dynamics of a wide variety of forest communities (Pacala *et al.* 1993, 1996; Coates *et al.* 2003). Individual-based forest simulators predict the fates of thousands of individuals, by predicting each tree's growth, mortality, fecundity and dispersal. These rates are determined by the amount of light intercepted by the tree. The complex three-dimensional light ray tracing used in these models is discarded when deriving the macroscopic equations; this is known to have only a small effect on dynamics (*Deutschman et al.* 1999). In addition, a critical failing of SORTIE is addressed, by including plasticity in the growth and locations of crowns (after *Purves et al.* 2007; see below). Crown plasticity increases the complexity and realism of the simulator but, in conjunction with the removal of ray tracing, leads to a simple mean-field approximation—the macroscopic equations—that shows a remarkably close match to the dynamics of the individual-based simulator (*Strigul et al.* submitted).

The key to the mean-field approximation is a new model of canopy structure, which assumes perfect plasticity in the horizontal growth of tree crowns. This model, which we refer to as the ideal tree distribution (ITD; referred to as the perfect plasticity approximator, PPA, in *Strigul et al.* (submitted)) predicts the canopy status (in or out of canopy), crown depth and total and exposed crown area (ECA) of the trees in stand, given their stem size and given their potential three-dimensional crown shapes. The ITD has been parametrized and verified for a wide variety of North American

forests (*Purves et al.* 2007). According to the ITD, canopy structure reduces to a simple form where foliage above a critical canopy height Z^* from the ground is exposed to sunlight, and other foliage is in the understory. Thus, an individual tree is assigned to the canopy if its height exceeds Z^* , and is assigned to the understory otherwise (figure 1). Canopy trees are assigned an ECA. The value of Z^* is set to ensure that the canopy area is perfectly filled, and therefore depends in a simple way on the species, size, spatial densities and crown shapes of the trees in the stand (*Purves et al.* 2007; *Strigul et al.* submitted; see below). Crown plasticity also ensures that all trees in the understory experience the same light level, determined solely by the crown transmissivity of the canopy trees.

The ITD requires, for each species i , parameters to set the height allometry (height given stem diameter D : parameters H_i and β_i) and crown shape parameters (in this case, a single parameter α_i ; see below). We use the 'flat-top' version of the ITD (figure 1), where trees have a potential crown of a flat disc with height equal to the tree height, and with radius proportional to stem diameter D (i.e. crown area = $\pi(\alpha_i D)^2$) and fixed canopy transmissivity L_i (i.e. species i creates an understory light level L_i).

Given these parameters, all that is necessary to completely specify a model of forest dynamics is to specify individual growth, mortality and fecundity, as a function of canopy status (in or out of the canopy), ECA (canopy trees only) and incident light level (understorey trees only). Here we make the simplest possible choices for these functions. However, *D. W. Purves et al.* (2007, unpublished results) show that the model with these simplifications predicts the dynamics of real forests in the Lake States of the USA. For species i , we assign a constant diameter growth rate for canopy trees, $G_{L,i}$ (cm yr⁻¹); and a diameter growth rate for understorey trees, $G_{D,i}(L)$, as a function of the understory light level L . Similarly, we assign a mortality rate for canopy trees, $\mu_{L,i}$ (yr⁻¹); and a mortality rate for understorey trees in the understory $\mu_{D,i}(L)$ as a function of the understory light level L . Fecundity is set to proportional to ECA for trees in the canopy, and zero for understorey trees. The flat top assumption means that canopy trees express their full potential crown, such that fecundity is equal to $F_i \pi(\alpha_i D)^2$. Since perfect plasticity makes the light environment equal for all locations in the understory, the choice of global versus local seed dispersal becomes moot (local dispersal has small effects on dynamics even without this plasticity; *Deutschman et al.* 1999).

(b) Macroscopic equations

Under the assumptions given above, the dynamics of the system—measured by the evolution through time of the size distribution of each species i —can be described by the following macroscopic equations (von Foerster equations, 1959):

$$\frac{\partial N_i(D, t)}{\partial t} = \begin{cases} -G_{D,i}(L) \frac{\partial N_i(D, t)}{\partial D} - \mu_{D,i}(L) N_i(D, t) & D < D_i^*(t) \\ -G_{L,i} \frac{\partial N_i(D, t)}{\partial D} - \mu_{L,i} N_i(D, t) & D \geq D_i^*(t) \end{cases}, \quad (2.1)$$

where $N_i(D, t)$ is the density (ha⁻¹) of individuals of species i and diameter D (cm) at time t ; $\partial N_i(D, t)/\partial t$ is the rate of change of this density (ha⁻¹ yr⁻¹); and $D_i^*(t)$ is the diameter at breast height (DBH) at which trees of species i reach the height required to enter the canopy, $Z^*(t)$. New individuals of size 0

are added to the community via reproduction from canopy trees. This process is described by the r.h.s. of the boundary condition

$$G_{D,i}(L)N_i(0,t) = \int_{D_i^*(t)}^{\infty} N_i(D,t)\pi(\alpha_i D)^2 F_i dD, \tag{2.2}$$

which integrates over the canopy area of all members of cohorts with DBH > $D_i^*(t)$. equation (2.2) ensures that the rate at which trees leave size class 0, due to growth, is equal to the total rate of reproduction. Note that (2.2) assumes a closed canopy; if the canopy were open the $G_{D,i}(L)$ on the l.h.s. would be replaced by $G_{L,i}$.

This minimum DBH required by species i for entry into the canopy ($D_i^*(t)$) is represented by an integral condition

$$1 = \sum_{i=0}^n \int_{D_i^*(t)}^{\infty} N_i(D,t)\pi(\alpha_i D)^2 dD, \tag{2.3}$$

for a stand consisting of species $i=0, \dots, n$. This reflects the assumption that, at any time t , the canopy is perfectly filled by trees with DBH > $D_i^*(t)$.

Finally, at the instant cohorts reach a size sufficient to be part of the canopy, they undergo an immediate change in growth/mortality regime (the boundary between understorey and overstorey; figure 1). This leads to a continuity condition on the flux at the boundary

$$\lim_{D \rightarrow D_i^*} N_i(D_i^*(t), t)G_{D,i}(L) = \lim_{D \rightarrow D_i^*} N_i(D_i^*(t), t)G_{L,i}, \tag{2.4}$$

such that the total rate at which cohorts ‘arrive’ at size $D_i^*(t)$ must equal the rate at which they ‘leave’, as canopy trees.

(c) Equilibrium state of the resident species

The key to the invasion analysis is to calculate the value of those metrics of the equilibrium state of a monoculture of a resident species i , which affect the population growth of an invading species j . In this case, there are only two such metrics. The first is the understorey light level created by i , L_i . Since by definition the canopy of a monoculture of species i is entirely composed of crowns of species i , L_i is determined entirely by the light transmission of crowns of species i and L_i can be treated simply as a structural parameter of species i .

The second metric is the canopy height \hat{Z}_i^* , i.e. the height of trees when they enter the canopy, in the equilibrium stand structure of a monoculture of i (equilibrium denoted by \wedge). The value of \hat{Z}_i^* is determined solely by the equilibrium size distribution of the resident, which occurs when the rate of density change of each size class is equal to zero. This is obtained by setting the l.h.s. of the equations to zero, and solving for $N_i(D_n, t)$,

$$\hat{N}_i(D) = \begin{cases} \frac{F_i}{G_{D,i}(L_i)} \exp\left(-\frac{\mu_{D,i}}{G_{D,i}(L_i)} D\right) & D < \hat{D}_i^* \\ \frac{F_i}{G_{L,i}} \exp\left(-\left(\frac{\mu_{D,i}}{G_{D,i}(L_i)} - \frac{\mu_{L,i}}{G_{L,i}}\right) \hat{D}_i^*\right) \exp\left(-\frac{\mu_{L,i}}{G_{L,i}} D\right) & D > \hat{D}_i^*. \end{cases} \tag{2.5}$$

Equilibrium canopy closure height for the system is defined implicitly by an integral that describes lifetime reproductive success

$$1 = \int_0^{\infty} \exp\left(-\frac{\mu_{D,i}}{G_{D,i}(L_i)} \hat{D}_i^*\right) \exp(-\mu_{L,i}\tau) F_i \pi \alpha_i^2 \left(\hat{D}_i^* + G_{L,i}\tau\right)^2 d\tau. \tag{2.6}$$

The first exponential term inside the integral gives the proportion of a cohort that reaches the canopy. The remaining terms give the total reproduction of the

cohort while in the canopy. At equilibrium, the lifetime reproductive success is equal to one (the canopy is at such a height that on average, each individual exactly replaces itself over its lifespan). Solving the integral

$$\frac{\mu_{L,i}}{2\pi\alpha_i^2 F} \exp\left(\frac{\mu_{D,i}}{G_{D,i}(L_i)} \hat{D}_i^*\right) = \left(\left(\hat{D}_i^*\right)^2 + 2\frac{G_{L,i}}{\mu_{L,i}} \hat{D}_i^* + 2\left(\frac{G_{L,i}}{\mu_{L,i}}\right)^2 \right), \tag{2.7}$$

while \hat{D}_i^* remains on both sides, we can simplify the solution by noting the relative order of each of the three terms on the r.h.s. Because $\mu_{L,i}$ is small (typically 1/50 or 1/100 yr) and because open grown trees will grow to canopy height in a few tens of years or less, the third term on the r.h.s. is of larger order than the other two. Thus, a very close approximation of \hat{Z}_i^* can be calculated (ignoring lower-order terms)

$$\hat{D}_i^* = \left[\frac{G_{D,i}(L_i)}{\mu_{D,i}(L_i)} \right] \cdot \ln \left[\frac{2\pi\alpha_i^2 F_i G_{L,i}^2}{\mu_{L,i}^3} \right] \text{ and } \hat{Z}_i^* = H_i [\hat{D}_i^*]^{\beta_i}, \tag{2.8}$$

where H_i and β_i are the height allometry parameters for species i : H_i is the height (m) of a 1 cm DBH tree and β_i sets the curvature of height versus DBH. For the monoculture system, \hat{D}_i^* (and consequently \hat{Z}_i^* and $\hat{N}_i(D)$) is locally stable when $D_i^*(\mu_D/G_D) > 2$ (Strigul *et al.* submitted). That is, the proportion of seedlings that survive to reach the canopy is less than $e^{-2} = 0.135$, a condition satisfied for all reasonable parameter values.

(d) Invasion criterion

The invasion of species i by species j is successful if and only if, on average, an individual of species j , subject to the environment imposed by the resident species i , can produce more than one offspring in its lifetime. Call the number of offspring produced by an average individual of j in an equilibrium monoculture of species i , $r(j, i)$, where r denotes relative per generation population growth, i.e. the lifetime reproductive success of an individual. Then

$$r(j, i) = P_{\text{mat}}(j, i) \int_{\tau=0}^{\infty} F_j \pi \alpha_j^2 \exp(-\mu_{L,j}\tau) [D_{j,i}^* + \tau G_{L,j}]^2 d\tau, \tag{2.9}$$

where $P_{\text{mat}}(j, i)$ is the fraction of individuals of species j , in an equilibrium monoculture of species i , which survive long enough to become a canopy tree and where the integral in equation (2.9) is the total reproductive output of a tree, given that it survived to reach the canopy. This latter term includes the effects of canopy tree mortality of j (the exponential term, which includes the canopy mortality rate $\mu_{L,j}$) and the effects of canopy tree growth $G_{L,j}$. Here, $D_{j,i}^*$ is the trunk radius at which species j attains sufficient height to reach the canopy height \hat{Z}_i^* , of the stable resident, i , calculated via the allometry for species j (and consequently its initial size upon commencement of reproduction).

Importantly, as equation (2.9) shows, the lifetime reproductive output of a canopy tree of j does not depend in any way on the identity of the resident species i (subject to the mathematical approximation used to generate equation (2.8), which corresponds to setting the term in square brackets in equation (2.9) to $\tau G_{L,j}$: numerical tests show that this approximation is very close; Adams 2006). Thus, the dependency of $r(j, i)$ on the resident i is contained almost

entirely within $P_{\text{mat}}(j, i)$, the fraction of trees of species j reaching the canopy.

$P_{\text{mat}}(j, i)$ is simply the fraction that survive the time required to grow from the initial size of a sapling (assumed to be height zero) to the canopy height determined by the resident species, \hat{Z}_i^* (see above). During this time, the saplings of j die at a rate $\mu_{D,j}(L_i)$, and grow in trunk diameter at rate $G_{D,j}(L_i)$, both of which are determined by the understorey light environment created by i . Thus,

$$P_{\text{mat}}(j, i) = \exp \left[-\frac{G_{D,j}(L_i)}{\mu_{D,j}(L_i)} D_{j,i}^* \right] = \exp \left[-\frac{G_{D,j}(L_i)}{\mu_{D,j}(L_i)} \left(\frac{\hat{Z}_i^*}{H_j} \right)^{1/\beta_j} \right]. \quad (2.10)$$

As equation (2.10) shows, there are exactly two ways in which the resident species i can reduce the value of $r(j, i)$, and hence make invasion by j less likely. It can reduce the understorey light level L_i , thereby reducing $G_{D,j}(L_i)$ and increasing $\mu_{D,j}(L_i)$. Or, it can increase the canopy height \hat{Z}_i^* , thereby raising the required height to reach the canopy.

The criterion for successful invasion of j is $r(j, i) > 1$. Evaluating the integral in equation (2.9), taking logarithms of both sides and rearranging gives

$$H_j \left(\left[\frac{G_{D,j}(L_i)}{\mu_{D,j}(L_i)} \ln \left[\frac{2\pi\alpha_j^2 F_j G_{L,j}^2}{\mu_{L,j}^2} \right] \right)^{\beta_j} > \hat{Z}_i^*. \quad (2.11)$$

Substituting in for \hat{Z}_i^* then gives the invasion criterion

$$H_j \left(\left[\frac{G_{D,j}(L_i)}{\mu_{D,j}(L_i)} \ln \left[\frac{2\pi\alpha_j^2 F_j G_{L,j}^2}{\mu_{L,j}^2} \right] \right)^{\beta_j} > H_i \left(\left[\frac{G_{D,i}(L_i)}{\mu_{D,i}(L_i)} \ln \left[\frac{2\pi\alpha_i^2 F_i G_{L,i}^2}{\mu_{L,i}^2} \right] \right)^{\beta_i}, \quad (2.12)$$

Equation (2.12) provides a simple direct way to compare the life-history parameters of species j with those of i , to decide whether j can invade i from low density. Note that this depends on all of the parameters of i and j , except for the understorey light level created by j . This is because the condition refers to whether j can invade from an infinitesimal density, in which case the canopy would be composed solely of species i , creating an understorey with light level L_i .

(e) Special case 1: does understorey light level act like R^* ?

When applied to competition in nutrient-limited communities, between, for example, different species of plants, R^* theory states that the species a that reduces the limiting nutrients to the lowest level in monoculture—call this R_a^* —will outcompete the other species when grown in mixture (Tilman & Wedin 1991). It has been suggested previously that an equivalent to R^* (or component in a resource ratio theory) for aboveground competition might be the understorey light level (Tilman 1985; Oliver & Larson 1996; Perry *et al.* 2003). If so, this would mean that the species a that reduced understorey light level to the lowest level in monoculture, i.e. L_a in the notation used here, would outcompete the other species in aboveground competition (see Vojtech *et al.* (2007) for an experimental test of this idea in grasslands).

To evaluate this assertion, we consider a special case where the two species i and j are identical except in crown transmissivity, i.e. all parameters are shared between i and j except for L_i and L_j . In this case, the invasion criterion for j

into i (equation (2.12)) can be rewritten as

$$\left[\frac{G_{D,j}(L_i)}{\mu_{D,j}(L_i)} \right] > \left[\frac{G_{D,i}(L_i)}{\mu_{D,i}(L_i)} \right] \quad (2.13)$$

(since $0 < \beta_i = \beta_j$). Because the parameters governing the functions describing understorey growth and mortality, $G_{D,i}(L_i)$ and $\mu_{D,i}(L_i)$, are shared between the species, the two sides of equation (2.13) are always exactly equal, and vice versa for i invading j . This means that the lifetime reproductive success (per generation population increase) of either species, introduced at low density to the other, is neither negative nor positive, but exactly zero. This is the characteristic of neutrality, which leads to ecological drift (Hubbell 2001). Thus, the analysis presented here does not support the notion that understorey light level necessarily acts like R^* in height-structured competition for light. Rather, in the absence of correlated differences in other life-history parameters, it does not carry any significance for the long-term outcome of interspecific competition. In fact, in the general case, it is possible for the species that casts less shade to exclude the other species (see below; figure 2).

(f) Special case 2: Z^* as an equivalent to R^*

A second special case considered here is where species differ in all parameters except crown transmissivity. In this case, the species-specific understorey light levels L_i and L_j can be replaced with a single value L

$$H_j \left(\left[\frac{G_{D,j}(L)}{\mu_{D,j}(L)} \ln \left[\frac{2\pi\alpha_j^2 F_j G_{L,j}^2}{\mu_{L,j}^2} \right] \right)^{\beta_j} > H_i \left(\left[\frac{G_{D,i}(L)}{\mu_{D,i}(L)} \ln \left[\frac{2\pi\alpha_i^2 F_i G_{L,i}^2}{\mu_{L,i}^2} \right] \right)^{\beta_i}, \quad (2.14)$$

which, following equation (2.8), simply translates to

$$\hat{Z}_j^* > \hat{Z}_i^*. \quad (2.15)$$

Importantly, the left and right sides of equations (2.14) and (2.15) are equal for both $i \rightarrow j$ and $j \rightarrow i$ only in the non-generic case where both species have identical \hat{Z}^* . Otherwise, therefore, species that do not differ in crown transmissivity can be ranked into a competitive hierarchy, according to their threshold canopy heights in monoculture, \hat{Z}^* . In spirit, this is exactly equivalent to the R^* theory, namely a measurable emergent property of a species in monoculture (\hat{Z}^*) predicts the outcome of competition in polyculture. As we see below, however, height-structured competition for light need not be hierarchical in the general case.

(g) General case: coexistence and founder control

The general case is given by allowing all species parameters—growth and mortality, allometry, crown transmissivity and fecundity—to differ between the species. We show here that this can lead to coexistence, founder control or the dominance of one species by the other.

To understand how these results come about it helps to define, for a species i , a new quantity

$$z_i(L) = H_i \left(\left[\frac{G_{D,i}(L)}{\mu_{D,i}(L)} \ln \left[\frac{2\pi\alpha_i^2 F_i G_{L,i}^2}{\mu_{L,i}^2} \right] \right)^{\beta_i}, \quad (2.16)$$

which has an obvious connection with the formula for \hat{Z}_i^* (equation (2.8)) and the invasion criterion (equation (2.12)). In fact, $z_i(L)$ is simply the equilibrium canopy height that a

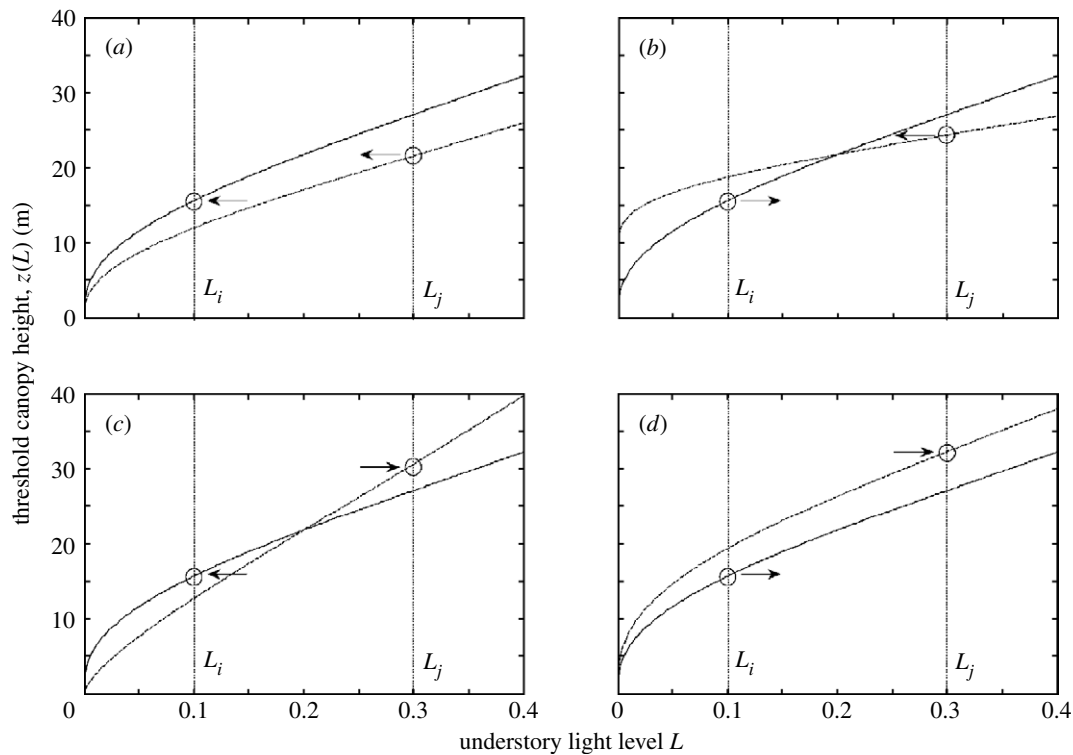


Figure 2. Understanding the outcome of height-structured competition for light. (a–d) An example of a pair of $z(L)$ curves (see equation (2.10)), for species i (parameters estimated for RED MAPLE, *Acer rubrum*, in Wisconsin, Minnesota and Michigan, USA, D. W. Purves 2007, unpublished data), and a second species j (parameters obtained by altering the parameters of i). Circles indicate the equilibrium light level and canopy closure height of each species in monoculture. Arrows pointing into or away from the circles indicate whether these points are locally attracting, or repelling in a community consisting solely of the two species. Therefore, both arrows heading inwards indicates coexistence; both outwards indicates founder control; one inwards and one outwards indicates dominance by one species. (a) Dominance by species i , (b) coexistence, (c) founder control and (d) dominance by species j .

monoculture of species i would reach, if its understorey light level was set at L . Thus, by definition, $z_i(L_i) = \hat{Z}_i^*$. Then, from equation (2.12), we can then write out a compact form for the pair of invasion criteria for i and j :

$$j \text{ invades } i \text{ if } z_j(L_i) > z_i(L_i) \quad \text{and} \quad (2.17a)$$

$$i \text{ invades } j \text{ if } z_i(L_j) > z_j(L_j), \quad (2.17b)$$

and, depending on which of equations (2.17a) and (2.17b) are true, the interaction between i and j can be classified simply into coexistence (both true), founder control (neither true) or dominance by one species (only one true; table 2). Although we have not performed a global analysis, numerical solutions of (1–3) support table 2.

Equations (2.17a) and (2.17b) has a very simple interpretation. Consider $z_i(L)$ as a measure of the whole life-cycle performance of species i in the environment (i.e. light level) L . Then, species j can invade i only if species j outperforms i in the environment created by i and vice versa for i invading j . This allows a simple visual understanding of the conditions for coexistence, founder control and dominance (figure 2).

Coexistence requires that species i and j can invade each other (table 2). Consider a mixed community of species i and j . The understorey light level L in this community must be between those of the two monocultures, i.e. $L \in [L_i, L_j]$, assuming $L_i < L_j$. For mutual invasibility, both of the terms in equations (2.17a) and (2.17b) must be true, such that j outperforms i under L_j (i.e. in a pure community of i) and i outperforms j under L_i (i.e. in a pure community of j). This means that a plot of the two species performance

Table 2. Competitive outcomes based upon invasion criteria (equation (2.11)).

	(11.1) satisfied	(11.1) not satisfied
(11.2) satisfied	coexistence	dominance by i
(11.2) not satisfied	dominance by j	founder control

functions z against understorey light level L must cross between L_i and L_j (figure 2b). Thus, for coexistence there must be a light level L , corresponding to a canopy with a particular mix of i and j , at which the two species have equal whole life-cycle performance. Coexistence also requires that, as one species becomes more common, it makes the environment more favourable to the other species: this imposes a directionality on the way the two z functions cross (contrast figure 2b with figure 2c). By contrast, if the two z functions do not cross between L_i and L_j , then one species outperforms the other at all possible light levels, and competitive exclusion of the inferior species must occur (figure 2a,d).

The third possibility occurs where the functions cross, but they do so in the wrong direction for coexistence (figure 2c). In this case, a small perturbation of the community away from the composition where the two species perform equally, will alter the relative performances in such a way as to amplify the perturbation, resulting in the exclusion of one species. This is the signature of founder control, where either species can outcompete the other in the long term, depending on the initial state (in this case, the initial state includes the size

distribution and density of each species in way that has yet to be explored). Finally, equation (2.17*a*) and (2.17*b*) reveals the general requirements for neutral dynamics and ecological drift: for this to occur, the two z functions must be exactly equal at *all* understorey light levels between L_i and L_j .

3. DISCUSSION

(a) *Competition and life-history trade-offs*

What are the practical implications of these conclusions for understanding the community ecology of forests? First, the analysis provides a whole life-cycle measure of the competitive ability of a species, in the form of the z function. This is a particular nonlinear combination of all of the parameters of the species, including canopy growth and mortality rates, understorey growth and mortality rates and their dependency on understorey light, crown allometry, height allometry and fecundity (equation (2.16)). The appearance of all of these parameters in the function is not surprising, since they all affect different aspects of performance. But the exact way in which they affect competitive ability would not have been clear without the kind of explicit modelling presented here (see also Strigul *et al.* submitted). For example, the sensitivity of the z functions to life-history parameters falls out as height allometry (coefficient H_i) > understorey growth and mortality \gg canopy mortality > canopy growth > fecundity = crown allometry (equation (2.16)), with the effect of crown transmissivity, and the height allometry slope curvature parameter (β_i), being less clear. This ordering has obvious implications for guiding field-work, and in interpreting trade-offs between particular pairs of these parameters.

For two species to coexist in the long term, their z functions must cross, in the right direction, at an understorey light level intermediate between those of the two monocultures (figure 2*b*). The fact that the z functions involve many different life-history parameters suggests that the trade-offs enabling coexistence could be multi-dimensional (e.g. fecundity versus height allometry versus canopy mortality, understorey growth versus canopy growth versus crown allometry and so on), such that they might not be revealed in pairwise plots of one parameter against another (e.g. canopy growth versus understorey survival). But this requires careful qualification. Specifically, coexistence requires a change in the rank of the performance of the species in different understorey light environments, such that each species outcompetes the other species under its 'own' light level (figure 2); and the change in the z function with light depends only on understorey performance and height allometry. Therefore, we can conclude that trade-offs enabling coexistence (stabilizing trade-offs) must involve interspecific variation in understorey growth and mortality, and/or height allometry, coupled with variation in crown transmissivity. The other parameters simply scale the z functions up and down, but do not affect their dependency on light. Thus, trade-offs between these other parameters (fecundity, canopy growth, canopy mortality and crown allometry) can only reduce the average competitive difference between species (equalizing trade-offs). Overall then, we can conclude that (i) trade-offs among any of the major life-history parameters in trees can be equalizing, (ii) the strength of this effect depends strongly on the parameters

being traded off, and (iii) stabilizing trade-offs, the only kind that cause long-term coexistence, must involve differences in crown transmissivity, coupled with differences in understorey performance and height allometry.

However, it is important to realize that the analysis presented here deals with only one form of coexistence (or exclusion or founder control), namely that within homogeneous stands that are not subject to disturbance events larger than those created by the random deaths of canopy trees. Furthermore, we here consider only *pairwise* coexistence (invasibility) of species; the possibility of multiple species existing along a trade-off axis requires further investigation. Other forms of coexistence, which the analysis does not rule out and which almost certainly act in reality, include habitat specialization, and specialization on large disturbances. Habitat specialization can enable coexistence in the landscape, even where no two species can coexist within a single stand. The z functions may point the way to understanding some aspects of this form of coexistence: specifically, according to this analysis, if two late successional species are to coexist due to this mechanism, their z functions must change rank across different habitats. Since the z function involves all life-history parameters, changes in any of these parameters with habitat could be involved. However, the differential sensitivity of the z functions to different parameters implies that habitat-dependent height allometry and understorey performance have the greatest potential to enable this form of coexistence. This is in line with the findings of a study of coexisting rainforest species by Kohyama *et al.* (2003).

Implications for understanding specialization on large disturbances are less easily discerned. This is because, when disturbances are sufficiently large, the equilibrium assumption inherent to the analysis breaks down. In reality, this implies that, in effect, the overall community breaks into separate stands, each at different stages of recovery from disturbance. The study of this process has a rich history in forest ecology and is known to be able to support coexistence of so-called 'pioneer' and 'late successional' species (e.g. Grime 1979; Tilman 1982; Oliver & Larson 1996; Pacala & Rees 1998). Finally, we note that there is every reason to expect these different forms of coexistence—the mechanism in table 2, habitat specialization and successional niches—to interact, providing a higher-dimensional niche space, and hence higher species diversity, than any mechanism alone.

(b) Z^* versus R^*

At a local scale, there is abundant evidence of species that do not coexist long term, without repeated stand-destroying disturbances. Almost universally, recently disturbed sites become dominated by pioneer species, which in turn become excluded by late successional. This pattern suggests that at a local scale many tree communities are structured, at least partly, as a competitive hierarchy. But a major challenge to date has been to identify how to measure the position in this hierarchy at the individual level, i.e. which features of a species' biology make for late successional dominance? As shown by this analysis, this problem has no fundamental solution, for the simple reason that competition need not be hierarchical at all. However, the special case of equal crown transmissivity did lead to hierarchical competition, with species ranked

according to their \hat{Z}^* values. In reality, could within-stand competition be closer to this special case than to the general case, thus explaining the ubiquity of succession dynamics in forest communities? Given our current state of knowledge, this seems a possibility. First, as figure 2 shows, for competition to be hierarchical, species need not have identical crown transmissivity. Rather, all that is required is that their z functions do not change rank within the range of light levels generated by the crown transmissivities of the different species. This seems possible, especially because these transmissivities fall within a fairly narrow range within most communities. Thus, interestingly, whereas the similarity of crown transmissivities of co-occurring species makes hierarchical competition according to the previously proposed R^* criteria (understorey light) less plausible, it makes hierarchical competition according to Z^* more likely. As a consequence, we might expect forest communities with large numbers of coexisting species, such as rainforests, to be more fully explained by additional mechanisms (e.g. understorey specialists are not considered). Second, parameters for the special case of equal crown transmissivities were estimated recently for the dominant species within Michigan, Minnesota and Wisconsin, USA (D. W. Purves *et al.* 2007, unpublished results). Late successional species have significantly greater estimated \hat{Z}^* values than the early successional species. Thus, assuming hierarchical competition according to \hat{Z}^* appears to be able to provide correct predictions for forest dynamics on the ground, at least in this one case; although it is much too early to conclude whether this might be true in general.

(c) Caveats and extensions

The analysis necessarily makes a number of simplifying assumptions, and this calls for caution in applying the results to real forest communities. Some of these assumptions have little or no effect on the dynamics of forest gap models, and so are of limited interest (e.g. no light tracing, Deutschman *et al.* (1999); sharp differentiation between canopy and understorey, Strigul *et al.* (submitted)). More important are the assumptions of a homogeneous physical environment, lack of interannual variation, no reproduction until the canopy is reached, no allelopathy or nutrient retention effects, no resprouting and no species-specific pathogens or herbivores. Identifying which of these processes are critical to the dynamics of which plant communities remains a major challenge in ecology. It is probable that, in principle, each can create opportunities for interesting population dynamics, including those identified here (coexistence, exclusion and founder control) and more complex possibilities (e.g. new kinds of interactions involving three or more species). Whether they do this in practice remains to be seen.

However, we do know that, despite ignoring these additional effects, forest gap models can capture the dominant signals in the population dynamics of at least some forest communities (e.g. Pacala *et al.* 1996; Coates *et al.* 2003). And since the analysis presented here is ultimately derived from these models (Strigul *et al.* submitted), it is hoped that we have provided an appropriate starting point for developing theory to deal with more complex biological scenarios.

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