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SPECIAL FEATURE

Theoretical ecology

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The effect of patch demography on the community structure of forest trees

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Abstract The effect of patch demography on the structure of forest tree communities was examined using a patch-age and tree-size structured model of forest dynamics. Changes in abundance of species of different types (four different maximum tree-size classes each in two or three shade-tolerance classes) were numerically modeled in response to changes in the duration of the gap-formation-free lag phase. Average patch mortality was identical in all simulations. Tolerant species were more abundant without a lag phase due to larger variation in patch longevity, while subtolerant or intolerant species were successful when patch longevity was fixed with a long duration of lag phase. Variation in patch-age distribution facilitated species coexistence. Increasing 'advance regeneration', or surviving fraction at gap formation, brought about the exclusive dominance of the tolerant species. Results suggest that patch demography plays a significant role in the community organization of forest trees. In species-rich systems like tropical rain forests, longevity or canopy duration of large trees can differ among species, which brings about the variation in patch longevity, thus promoting further coexistence of species.

Keywords Advance regeneration · Coexistence · Gap dynamics · Lag phase · One-sided competition · Patch mortality · Shade tolerance · Simulation

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Introduction

Simon Levin (Levin and Paine 1974; Levin 1976) introduced the theoretical framework of patch mosaic dynamics creating heterogeneous spatial patterns in the organization of biological communities. A simplified model distinguishing two dichotomous states of patches as either occupied or vacant has been widely applied (Levin and Culver 1971; Levin 1974, 1976; Whittaker and Levin 1977; Tilman 1994) and has contributed to the concepts of meta-population and meta-community (Giplin and Hanski 1991). Meanwhile, it is possible to observe finer-scale resolution of the states of patches such as patch age and size. To study these dynamics, Simon Levin suggested the use of the continuity equation of fluid dynamics in physics. For instance, ignoring the patch-size dimension, the dynamics of the probability for a patch at age a at time t, $s(t, a)$, is described by

$$\frac{\partial s(t,a)}{\partial t} = -\frac{\partial s(t,a)}{\partial a} - \gamma(a)s(t,a), \tag{1}$$

where $\gamma(a)$ is the age-specific mortality of patches. If the total land area is conserved and 'dead' patches simultaneously contribute to the creation of 'newborn' patches, the boundary condition of Eq. 1 with respect to patch age a is described as

$$s(t,0) = \int_0^\infty \gamma(a)s(t,a)\,\mathrm{d}a. \tag{2}$$

The model of Eqs. 1 and 2 allows us to develop demographic analyses of patch dynamics in a landscape on which species migrate, persist, and reproduce. Patch mortality in ecological systems can be dependent on the state of the patches. For instance, in forest ecosystems prone to disturbances such as fire, prevailing wind, storm, and landslide, the probability of damage by disturbance is often dependent on the developmental stage of patches, and is usually higher at later stages of patch development where patches have higher fuel stock, higher canopy stature, and heavier deposition of topsoil with aboveground vegetation load (Heinselman 1973; Sprugel 1976; Kohyama and Fujita 1981; Johnson and Van Wagner 1984; Foster 1988; Clark 1989). It is not known how the pattern of patch survival influences tree community structure.

In this paper, I examine how patch demography affects the landscape pattern and tree community structure of forest ecosystems, applying a model of forest dynamics (Kohyama 1993) which combines patch demography model of Eqs. 1 and 2 and the dynamic model of tree-size structure regulated by patch-scale upper crowding (Kohyama 1992). Kohyama (1993) suggested by model analysis that the stable coexistence among tree species is enabled by one-sided competition among trees (vertical light-resource heterogeneity) and is further emphasized by among-patch variation in crowding (horizontal heterogeneity) through among-species trade-offs in demographic parameters, proposing 'forest architecture hypothesis' of tree species coexistence. Using the same model, Kohyama (1997) showed that the increasing growth rate of individual trees and the decreasing tree mortality and gap-formation rate, promote species coexistence by creating larger spatial light-resource heterogeneity. However, the effect of changing patch demography on tree communities has not been examined so far.

In this paper, using basically the same model of Kohyama (1993), I show how community structure is sensitive to patch demographic patterns even while keeping the average patch mortality identical. I also show how large the effect of advance regeneration, or the survived fraction through gap-formation process, on the community structure of forest trees.

Methods

The model

I assume that a forest is composed of patches of different ages since gap formation. Tree population dynamics are regulated at the local scale of the patch, and across-patch interactions occur through patch aging, patch mortality, and reproduction of populations with random seed dispersal across patches. Establishment and recruitment of tree populations are not restricted to gaps, or newborn patches, but occur in patches of any age. Furthermore, if there are survivors at gap formation, patches of age zero can contain variously aged trees. Therefore, patch age is not a good predictor of tree age in this model system, as well as in actual forests.

I employ the same model as in Kohyama (1993) for patch demography, where patch mortality, or gap-formation rate, is described by a function of patch age a, $\gamma(a)$ (year^{-1}). I assume that gap formation does not occur for the period from patch age zero to patch age a_c (lag-phase duration) and is constant afterward:

$$\begin{aligned}&\gamma(a) = 0 \quad \text{for } a \le a_c,\\ &\gamma(a) = 1/(L - a_c) \quad \text{for } a > a_c.\end{aligned} \tag{3}$$

From Eq. 3, the cumulative probability for a patch to survive from age 0 to a, $l(a)$, is 1 for $a \le a_c$, and is an exponential function

$$l(a) = \exp\left(-\int_0^a \gamma(\alpha)\,d\alpha\right) = \exp\left(-\frac{a - a_c}{L - a_c}\right) \quad \text{for } a > a_c, \tag{4}$$

of which average longevity from the age of a_c is $L-a_c$ (year). Therefore, L (year) is average patch duration, and $1/L$ (year^{-1}) is average patch mortality or gap-formation rate for the whole forest landscape irrespective of a_cs. Figure 1 shows the dependence of $l(a)$ on changing lag-phase duration, a_c. Variation in patch demography in this paper is introduced by changing a_c as in Fig. 1, setting L at 100 (years). Kohyama (1993) used $a_c = 40$ and $L = 100$ (years) as default, based on the analysis of basal-area dynamics of a warm-temperate rain forest (Kohyama 1987).

I define the word 'landscape' as a closed space, without any reproductive input from outside, consisting of patches of various ages. Distribution of tree population of species i in size in trunk diameter x (cm) and patch age a at time t (year) throughout the landscape is denoted by $f_i(t, a, x)$ (cm^{-1} m^{-2} year^{-1}). Dynamics of $f_i(t, a, x)$ is described by (cf. Kohyama 1993)

$$\frac{\partial f_i(t,a,x)}{\partial t} = -\frac{\partial f_i(t,a,x)}{\partial a} - \frac{\partial (G_i(t,a,x) f_i(t,a,x))}{\partial x} - (\gamma(a) + \mu_i(t,a,x)) f_i(t,a,x), \tag{5}$$

where $G_i(t, a, x)$ (cm year^{-1}) is the growth rate of tree size x of species i at a patch of age a at time t; while $\gamma(a)$ (year^{-1}), the same as in Eqs. 1, 2 and 3, is the mortality

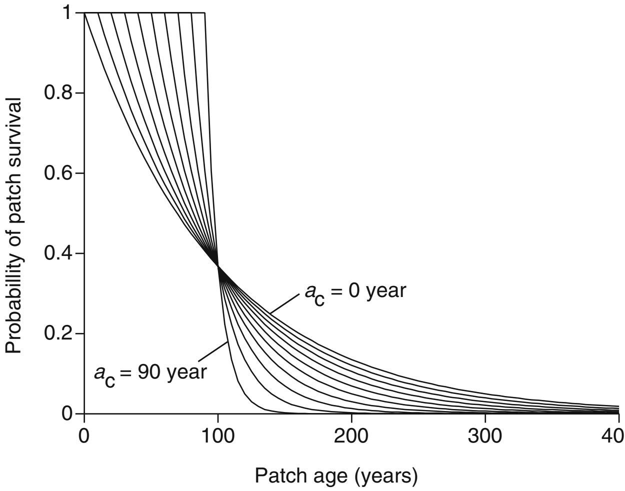

Fig. 1 Patch survivorship curve, Eq. 4, with the changing duration of lag phase, a_c, from 0 to 90 years at 10-year intervals. Average patch longevity L is set at 100 years

of a patch at age a due to gap formation; and $\mu_i(t, a, x)$ (year^{-1}) is the gap-formation-free mortality of the tree at size x at a patch of age a at time t. The dynamics is restricted by boundary conditions with respect to a (advance regeneration) and x (reproduction) given respectively by

$$f_i(t,0,x) = p(x)\int_0^\infty \gamma(a) f_i(t,a,x)\,\mathrm{d}a, \qquad (6)$$

$$G_i(t,a,x_0) f_i(t,a,x_0) = R_i(t) s(t,a), \qquad (7)$$

where $p(x)$ (dimensionless) is the tree-size-dependent probability of survival through a gap-formation event, $R_i(t)$ (m^{-2} year^{-1}) is landscape-level reproduction of species i, and $s(t, a)$ (year^{-1}) is the landscape-level probability for a patch at age a at time t as in Eq. 1, and x_0 is the minimum tree size for recruitment. The submodel of tree population dynamics, Eqs. 5, 6 and 7, is combined with the submodel of patch-age dynamics, Eqs. 1 and 2, sharing gap-formation rate $\gamma(a)$ (Kohyama 1993; Hurtt et al. 1998; Kohyama et al. 2001; Moorcroft et al. 2001).

A strong assumption of the model is that all of the three demographic processes of growth, mortality and reproduction for the tree at size x are regulated by the local upper basal area $B(t, a, x)$ (cm^2 m^{-2}), i.e., basal area per unit area of patch of age a above size x for all species:

$$B(t,a,x) = \frac{\pi}{4s(t,a)} \sum_i \int_x^\infty y^2 f_i(t,a,y)\,\mathrm{d}y. \qquad (8)$$

This assumption is based on the unique property of light competition among forest trees such that upper trees absorb light resources first, and lower trees exploit the leftovers that penetrate through the upper canopy. The other important aspect of this assumption is that there is no species-to-species specific factor that modifies the strength of inter-specific competition, which, on the other hand, is the basis for the stable coexistence of species in no-stage-structured models such as the Lotka–Volterra competition equations.

Size growth rate $G_i(t, a, x)$ is formulated by

$$G_i(t,a,x) = b_i x(1 - b_{1i} \ln x - b_{2i} B(t,a,x)), \qquad (9)$$

for non-negative $G_i(t, a, x)$; otherwise $G_i(t, a, x) = 0$ (Kohyama 1992, 1993). Three parameters of Eq. 9 characterize tree growth properties. Parameter b_i (year^{-1}) is the potential relative growth rate of a tree of species i, where potential means that for trees at $x = 1$ cm without upper crowding, $B(t, a, x) = 0$. Parameter b_{1i} (ln cm^{-1}) describes the degree of the size-dependent decline of the relative growth rate, and $\exp(1/b_{1i})$ (cm) characterizes the upper maximum size of species i where the growth rate is zero. The third parameter, b_{2i} (m^2 cm^{-2}), is the degree of sensitivity to upper crowding in relative growth rate.

Mortality in this model, as in Eq. 5, is composed of disturbance-caused mortality $\gamma(a)$ and thinning-caused mortality $\mu_i(t, a, x)$. Disturbance-caused mortality $\gamma(a)$ is linked with patch demography and is independent of tree size x in the case without advance regeneration. Gap formation is caused by the mortality of canopy trees and there may be a fraction of trees that survive through gap formation to form advance regeneration. Survival during gap formation is likely to decrease with increasing tree size. Probability of survival to form advance regeneration, $p(x)$ in Eq. 6, is expressed as a decreasing function with size x,

$$p(x) = \frac{k}{k + x} \qquad (10)$$

for non-negative k (cm). In this equation, $k = 0$ means no advance regeneration, and $k = 1$ and 4 allows, respectively, $p(x) = 1/3$ and $2/3$ survival for trees at the minimum size of $x = 2$ cm in the present simulation, while almost no trees survive (0.7 and 2.6%) at the model-parameter defined maximum size of $x = 150$ cm.

Mortality due to thinning by local crowding, $\mu_i(t, a, x)$, is assumed here to be proportional to $B(t, a, x)$, with species-specific parameter of sensitivity to upper crowding in mortality, c_i (m^2 cm^{-2} year^{-1}). To make results comparable across simulated systems with changing k, operational 'thinning' corresponding to advance regeneration, $p(x)\gamma(a)$, is added to the mortality by crowding as

$$\mu_i(t,a,x) = c_i B(t,a,x) + p(x)\gamma(a). \qquad (11)$$

Reproduction of a tree of species i at size x at a patch of age a, $r_i(t, a, x)$ (tree^{-1} year^{-1}) is proportional to its own basal area, $\pi x^2/4$ (cm^2), and is suppressed by the local upper basal area of the patch as

$$r_i(t,a,x) = d_i \frac{\pi}{4} x^2 (1 - d_{1i} B(t,a,x)) \qquad (12)$$

for non-negative $r_i(t, a, x)$; otherwise $r_i(t, a, x) = 0$. Parameter d_i (cm^{-2} year^{-1}) describes the annual seed reproduction rate per basal area of a tree of species i, while parameter d_{1i} (m^2 cm^{-2}) expresses the sensitivity to local upper crowding in the reproduction of species i. The landscape-level reproduction of species i, $R_i(t)$, is therefore

$$R_i(t) = \int_0^\infty \int_{x_0}^\infty r_i(t,a,x) f_i(t,a,x)\,\mathrm{d}x\,\mathrm{d}a, \qquad (13)$$

and is assumed to be randomly dispersed across patches over the landscape as in Eq. 7. This expression of reproduction is different from that in Kohyama (1993) where 'recruitment' rate as the combination of seed production process and seedling survival/upgrowth processes is expressed only by the total basal area of the patch due to the limitation of forest-plot census data. Here, more precisely, I employ Eq. 12 based on a single-tree reproduction process, where light availability, expressed by local upper crowding, determines reproduction rate of a single tree (cf. Kohyama 1982; Greene et al. 2002; Uraguchi and Kubo 2005).

Simulation

Eight or twelve species differing in potential maximum tree size in four layers and in two (or three) shade-tolerance classes of either tolerant, (subtolerant) or intolerant were modeled. Their demographic parameters, except reproductive capacity d_i, were arbitrarily chosen to reflect the observed values for a warm-temperate rain forest (Kohyama 1992, 1993), as shown in Table 1. Potential maximum size, or $\exp(1/b_{1i})$, is 148.8, 46.8, 22.8, and 12.2 cm for canopy, subcanopy, understorey, and treelet species respectively. Subtolerant and intolerant species are respectively twice and three times more sensitive to the crowding than tolerant species in growth (b_{2i}), mortality (c_i) and reproduction (d_{1i}), and are respectively two and three times higher in potential size growth rate (b_i) than tolerant species. The left parameter d_i was then tuned for the eight species (in two tolerance classes) or the 12 species (in three tolerance classes) to allow them to coexist in the three respective conditions of patch demography, namely 0, 40, and 90 years of lag phase defined by a_c.

Simulation runs using a finite-difference approximation method were carried out with 1-year time steps, Δt, up to 40,000 years (until the system attained steady state); 10-year intervals for patch age, Δa, up to 400 years with a pooled age class of above 400 years; and 2-cm for tree size,Δx, with the minimum size of $x_0 = 2$ cm. Initial condition at time $t = 0$ was 0.001 tree m^{-2} for each species at the minimum size class of each patch-age class from 0 to 100 years. Simulation suggests that the long-time steady state is independent of initial conditions. The source code of simulation in c+ + is available at http://www.hosho.ees.hokudai.ac.jp/~kohyama/Gmodel/.

I examined community sensitivity to a variety of situations by comparing steady-state community structure in species abundance after 40,000 years of simulation across situations. The examined situations were (1) changing reproduction capacity for a particular species, (2) changing patch demography, in terms of lag-phase duration a_c, from 0 to 90 years at 10-year intervals, and (3) changing the degree of advance regeneration in terms of k from 0 to 5 at intervals of 0.5.

Results

The case with eight species

Tuning and simulation for species coexistence

I tuned the reproduction parameters (d_i) left free with the fixed set of other parameters in Table 1 so that all of the eight species (four stature classes in each of two tolerance classes, without a subtolerant class) eventually coexisted over 40,000 years for each of the lag phases of 0, 40, and 90 years in patch demography without advance regeneration ($k = 0$) and with d_i of intolerant-treelet species identical throughout. The tuned d_i for coexistence, in the three columns on the left-hand side of Table 2, differed among scenarios of patch dynamics with different lag phases. Tolerant species with small reproductive capacity (defined by d_i) persisted and coexisted with intolerant species in patch dynamics with short lag phases while high reproductive capacity was required for persistence of tolerant species with intolerants in long lag-phase conditions. Low-stature intolerant species needed to have relatively higher reproductive capacity in short lag-phase patch demography to coexist with tolerant species. Each single species, without competitors, as defined by Tables 1 and 2, persisted in any patch demography with a changing lag phase ($0 \le a_c < L$) and changing fraction of advance regeneration ($0 \le k \le 5$). This is because the per capita reproduction rate exceeded mortality without thinning, and the intrinsic growth rate was positive.

Figure 2 illustrates the time course of the eight-species systems for $a_c = 0$, 40, and 90 years. Abundance of each species is expressed by landscape-level species basal area,

$$B_{0i} = \frac{\pi}{4} \int_0^\infty \int_{x_0}^\infty x^2 f_i(t, a, x)\, \mathrm{d}x\, \mathrm{d}a,$$

on vertical axes in Fig. 2, and in Figs. 4, 5, 6, 7 and 8 as well.

Irrespective of lag-phase difference, intolerant species occupied the landscape first and tolerant species

Table 1 Demographic parameters of tree species populations, except d_i, defining four stature classes by three tolerance classes

Species	b_i (year^{-1})	b_{1i} (ln cm^{-1})	b_{2i} (m^2 cm^{-2})	c_i (m^2 cm^{-2} year^{-1})	d_{1i} (m^2 cm^{-2})
Tolerant-canopy	0.04	0.20	0.005	0.0001	0.005
Tolerant-subcanopy	0.04	0.26	0.005	0.0001	0.005
Tolerant-understory	0.04	0.32	0.005	0.0001	0.005
Tolerant-treelet	0.04	0.40	0.005	0.0001	0.005
Subtolerant-canopy	0.08	0.20	0.010	0.0002	0.010
Subtolerant-subcanopy	0.08	0.26	0.010	0.0002	0.010
Subtolerant-understory	0.08	0.32	0.010	0.0002	0.010
Subtolerant-treelet	0.08	0.40	0.010	0.0002	0.010
Intolerant-canopy	0.12	0.20	0.015	0.0003	0.015
Intolerant-subcanopy	0.12	0.26	0.015	0.0003	0.015
Intolerant-understory	0.12	0.32	0.015	0.0003	0.015
Intolerant-treelet	0.12	0.40	0.015	0.0003	0.015

Table 2 Tuned reproduction parameter d_i (cm^{-2} year^{-1}) for 8 and 12 species coexisting at each demographic condition without advance regeneration; with respect to other parameters in Table 1

Species	d_i of 8 species for			d_i of 12 species for
	$a_c = 0$ (year)	$a_c = 40$ (year)	$a_c = 90$ (year)	$a_c = 0$ (year)
Tolerant-canopy	0.0001	0.0003	0.0006	0.0001
Tolerant-subcanopy	0.0005	0.001	0.0012	0.0005
Tolerant-understory	0.0012	0.002	0.002	0.0012
Tolerant-treelet	0.0024	0.0035	0.0032	0.0024
Subtolerant-canopy	–	–	–	0.00012
Subtolerant-subcanopy	–	–	–	0.0015
Subtolerant-understory	–	–	–	0.005
Subtolerant-treelet	–	–	–	0.011
Intolerant-canopy	0.00012	0.00015	0.0002	0.00012
Intolerant-subcanopy	0.0024	0.002	0.002	0.0024
Intolerant-understory	0.010	0.009	0.008	0.010
Intolerant-treelet	0.024	0.024	0.024	0.026

followed replacing intolerants (Fig. 2). The time required for the community to attain steady state changed from a few thousand years for $a_c = 0$ (Fig. 2a) to several thousand years for $a_c = 40$ (Fig. 2b), and to several ten-thousand years for $a_c = 90$ (Fig. 2c). Particularly for $a_c = 90$, such a long time as 40,000 years was not sufficient for the system to attain steady state, as the abundance of tolerant-subcanopy species was slowly but steadily declining until the simulation year 40,000 (Fig. 2c). At the ‘steady state’ (or exactly at the final simulation year 40,000), overall coverage increased with patch age, and local species abundance was dependent on patch age (Fig. 3). Intolerant species were more abundant in younger patches and persisted in aged patches. Tolerant species abundance increased in older patches. Within each tolerance class, canopy species increased their abundance in older patches as compared to lower-statured species.

Sensitivity to changing reproduction capacity

Demographic parameters of each species substantially affected the steady-state community structure. Figure 4 illustrates examples of changing the reproduction parameter d_i of tolerant-canopy species, for each of three lag-phase scenarios, from one fifth to 2 times the baseline figure in Table 2. Change in community structure with single-species reproduction parameter was most remarkable for the long lag-phase case (Fig. 4c); by contrast, it was less obvious for the no-lag-phase case (Fig. 4a). Decreasing d_i for tolerant-canopy species brought about the failure of not only the tolerant canopy, but also the tolerant understory, and increasing it resulted in the marked decline of the tolerant subcanopy and understory, more than the treelet class (Fig. 4a, b).

The change in the competitive ability of a particular species largely influenced the nearby-stature species of the same tolerance class, and was indirectly influenced more apart species in stature and tolerance. Interesting situations demonstrated in Fig. 4a, b are that the addition of one species (tolerant-canopy species, in this case) into the system that does not already have that species promotes the survival and coexistence of another species (tolerant-understorey species) that is excluded by competition with other species (tolerant-subcanopy and tolerant-treelet species), as seen on the left-hand side of Fig. 4a, b.

Sensitivity to changing lag phase

With an increase of the duration of lag phase in patch demography for each of the species parameter sets, the overall steady-state coverage decreased as did the abundance of tolerant species, from higher stature to lower in sequence (Fig. 5). A long lag phase with a small fraction of old patches (e.g. Figs. 1, 3) still offered habitats for shade-tolerant, low-stature species, as the upper canopy of intolerant species created shaded conditions underneath. Similar to changing species reproductive capacity (Fig. 4), the tendency for species with apart statures to coexist was observed for the intolerant subcanopy and treelet in Fig. 5a (right side), the tolerant canopy and treelet in Fig. 5b (left side), and the intolerant canopy and treelet in Fig. 5c (left side).

Sensitivity to changing advance regeneration

With increasing survival of trees at gap formation, intolerant species decreased their abundance (Fig. 6). The decline in abundance of the intolerant species group was emphasized by a long lag-phase case (Fig. 6c); intolerant species persisted even with high survival of small trees at gap formation for patch mortality of no lag phase (Fig. 6a). Demography without lag phase provided opportunity for four tolerant species differing in stature classes to coexist (Fig. 6a). Intermediate lag phase brought about the failure of tolerant-subcanopy species (Fig. 6b), and, when advance regeneration

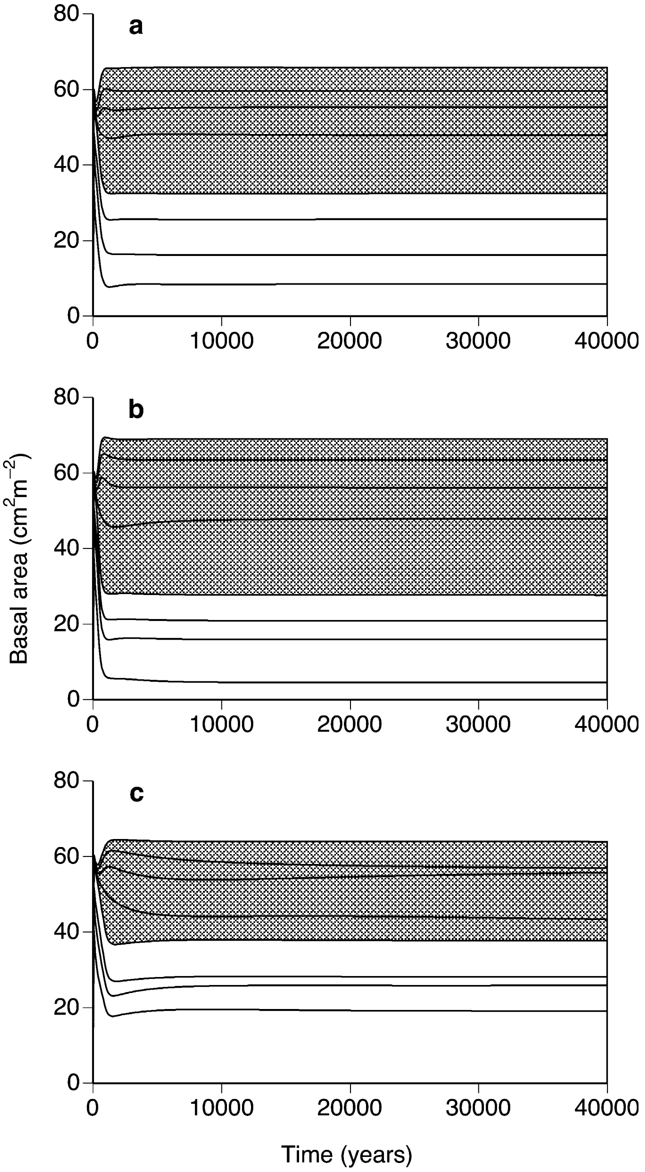

Fig. 2 Simulated time course of eight species abundance in basal area B_{0i}. Panels **a**, **b**, and **c** are for patch demography with lag phases of 0, 40, and 90 years respectively, using the corresponding reproductive capacity parameters in Table 2. The *shaded* and *open* areas correspond to tolerant and intolerant species respectively. The four species' stature classes of canopy, subcanopy, understory, and treelet, are arranged from *top to bottom* for each of tolerance classes. No advance regeneration at gap formation

increased, long lag-phase demography eventually wiped out all the others except for the tolerant-canopy species (Fig. 6c).

The case with 12 species

Tuning and simulation for species coexistence

When an intermediate tolerance class was added, 12 species characterized by four maximum stature classes

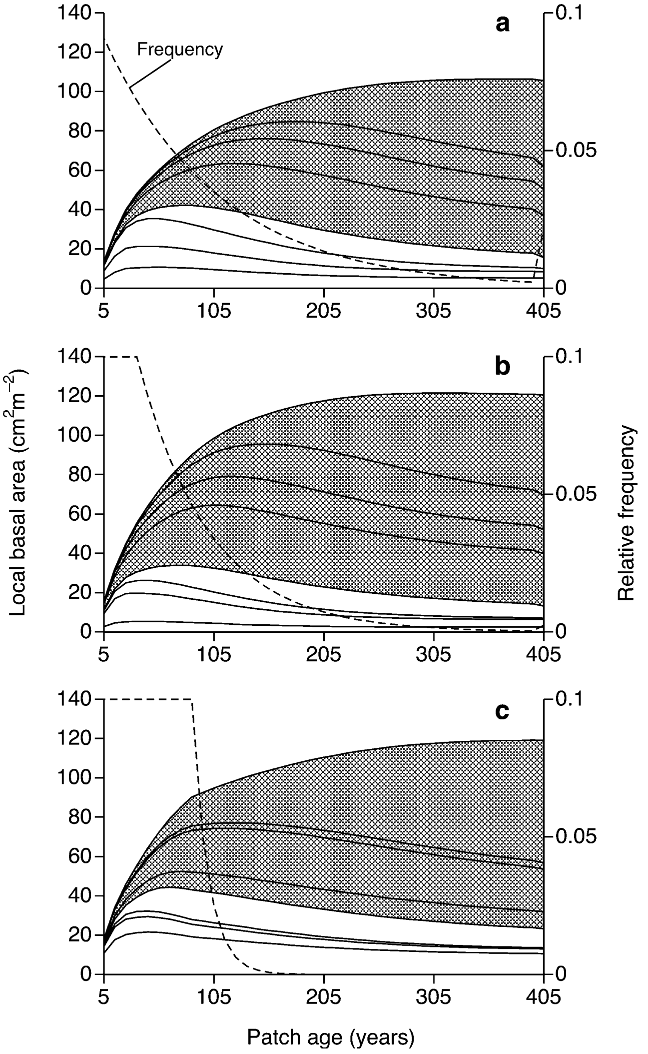

Fig. 3 Steady-state distribution of species across the age of patches. Panels **a**, **b**, and **c** are for patch demography with lag phases of 0, 40, and 90 years respectively, using the corresponding reproductive capacity parameters given in Table 2. The *shaded* and *open* areas correspond to tolerant and intolerant species respectively. The four species' stature classes, canopy, subcanopy, understory, and treelet, are arranged from *top to bottom*. Relative frequency of the patch at the 10-year age class is designated by the *broken line*. No advance regeneration at gap formation

and three tolerance classes (Table 1) coexisted in the patch demography of the no lag phase, with tuned d_is as given in the far right-hand column of Table 2. It was, however, too subtle, or too narrow in parameter range for their coexistence in a longer lag-phase demography. Therefore, only the case with zero lag phase is demonstrated.

Figure 7 illustrates the time change of the community structure of the 12-species system. Intolerant species first increased their abundance, followed by subtolerant species bringing about a temporal decline of intolerant abundance at around thousand years. The tolerant species finally increased, and the system converged in a stable community structure after around ten-thousand years.

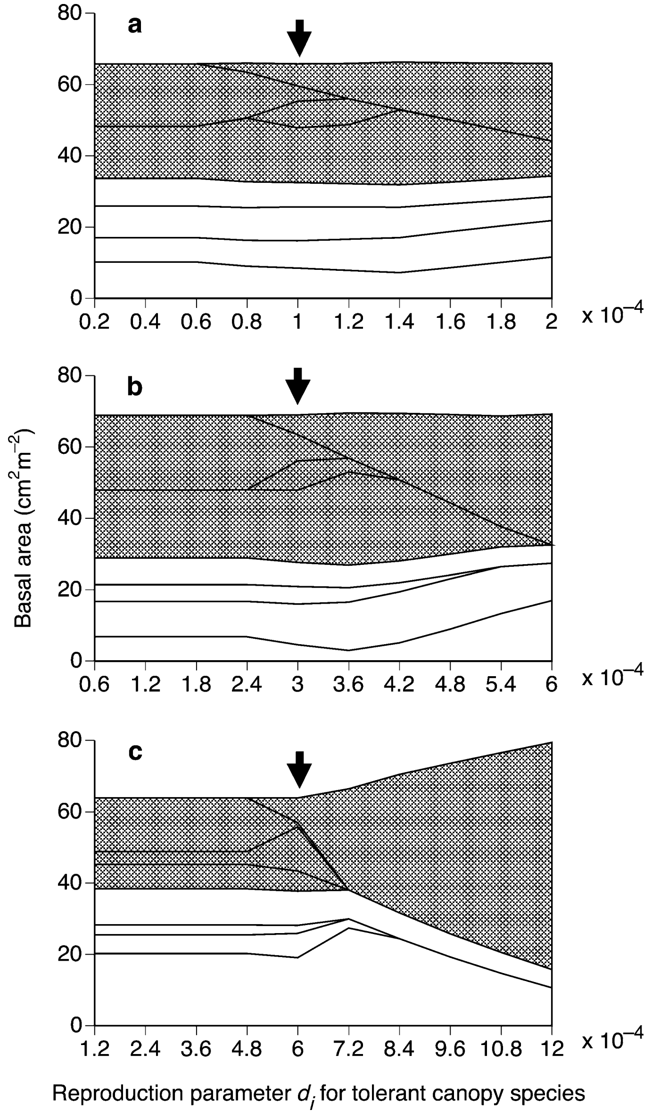

Fig. 4 Sensitivity of steady-state abundance of eight species to reproduction parameter d_i for tolerant-canopy species, fixing other parameters as in Tables 1 and 2. Baseline parameter d_i is marked by an *arrow*. Panels **a**, **b**, and **c** are for lag phase of 0, 40, and 90 years respectively, using the species parameter set given in Table 2. *Shaded* and *open* are respectively tolerant and intolerant species. The four species' stature classes of canopy, subcanopy, understory, and treelet, are arranged from *top to bottom*. No advance regeneration at gap formation

Sensitivity to changing lag phase and advance regeneration

Increasing lag-phase duration in patch demography brought about the decline of both the tolerant and intolerant species; and the forest, with 90 years of lag phase, was composed only of subtolerant-subcanopy, subtolerant-treelet, and intolerant-subcanopy species (Fig. 8a). The increasing survival of small trees at gap formation resulted in the decline of the intolerant species first, followed by the decline of subtolerant species. Within the same tolerance class, there was the tendency for lower-stature species to disappear prior to the decline of higher stature species (Fig. 8b).

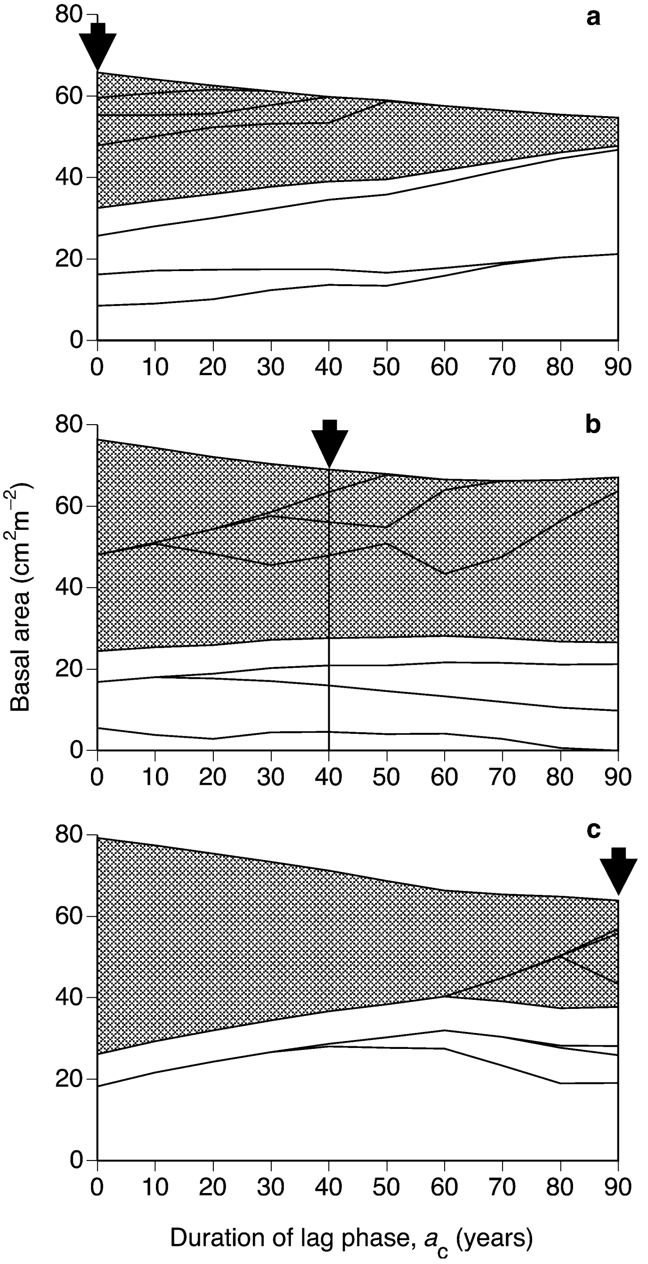

Fig. 5 Sensitivity of steady-state abundance of eight species to the changing duration of lag phase in patch demography, a_c of Eq. 3. Panels **a**, **b**, and **c** correspond to parameter sets of eight species for coexistence at a 0-, 40-, and 90-year duration of lag phase respectively, as shown in Table 2; default duration is marked by an *arrow*. *The shaded* and *open* areas correspond to tolerant and intolerant species respectively. The four species' stature classes of canopy, subcanopy, understory, and treelet, are arranged from *top to bottom*. No advance regeneration at gap formation

Discussion

The present results suggest that the pattern of patch demography in terms of variation of lag-phase duration

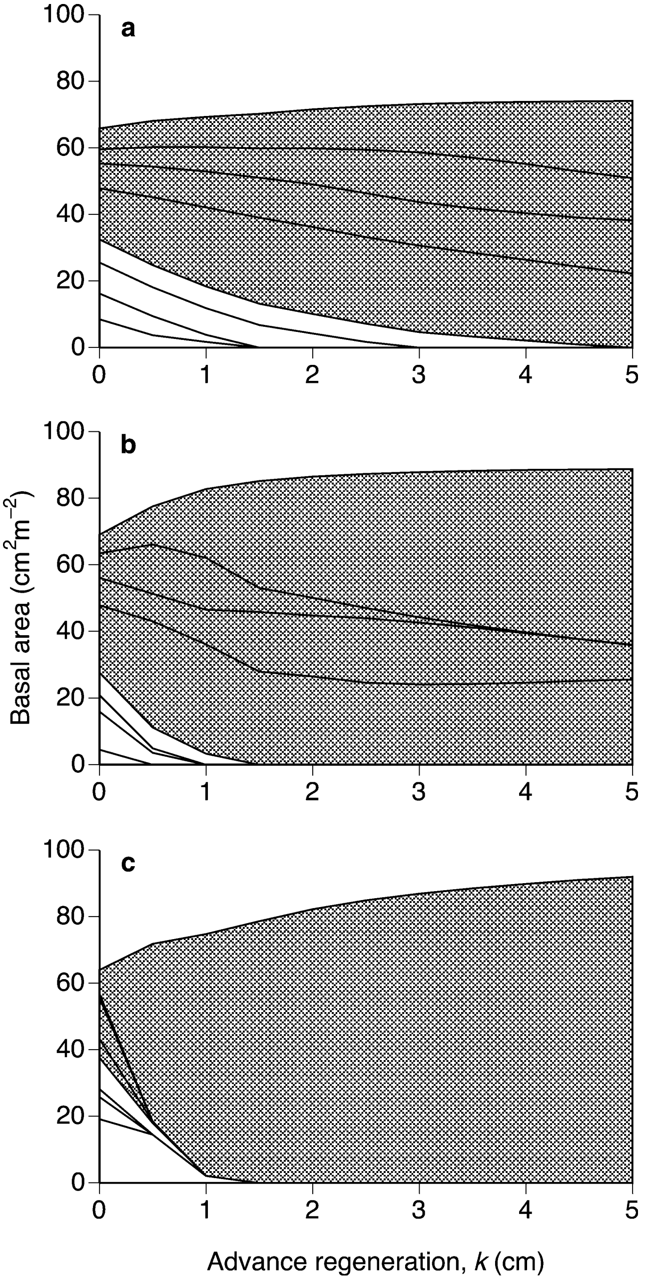

Fig. 6 Sensitivity of steady-state abundance of eight species to changing advance regeneration, *k* of Eq. 10. Panels **a**, **b**, and **c** correspond to lag phases of 0, 40, and 90 years respectively, with the species parameter set given in Table 2. *The shaded* and *open* areas correspond to tolerant and intolerant species respectively. The four species' stature classes are canopy, subcanopy, understory, and treelet from *top to bottom*

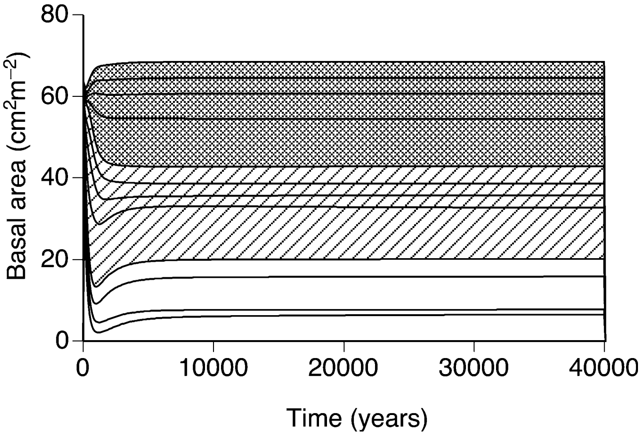

Fig. 7 Simulated time course of 12 species abundance in a basal area for patch demography with no lag phase, using the species parameters in Tables 1 and 2. *The shaded*, *hatched*, and *open* areas correspond to tolerant, subtolerant, and intolerant species respectively. The four species' stature classes of canopy, subcanopy, understory, and treelet, are arranged from *top to bottom* for each of tolerance classes. No advance regeneration at gap formation

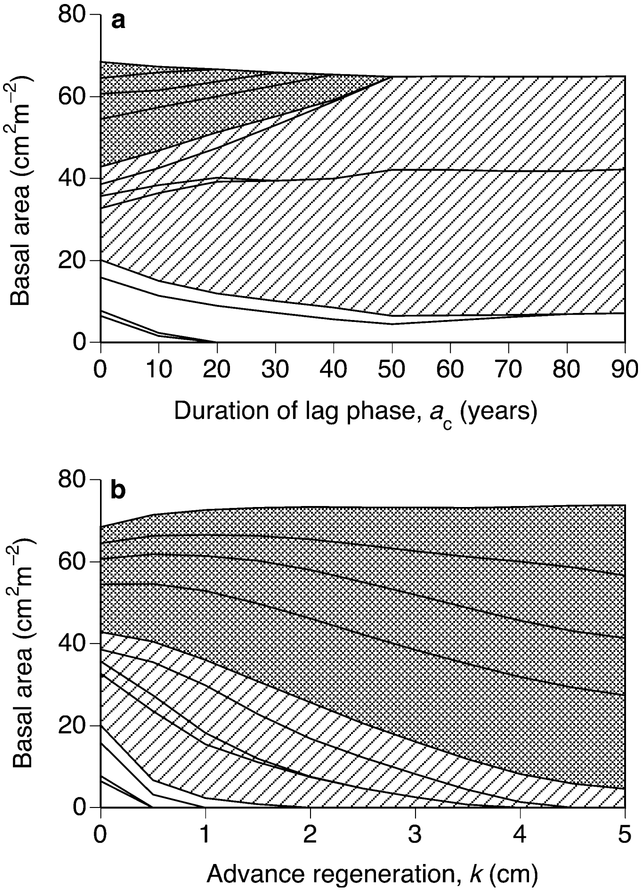

Fig. 8 Sensitivity of steady-state abundance of 12 species to **a** changing duration of lag phase (a_c of Eq. 3) without advance regeneration, and **b** changing advance regeneration (*k* of Eq. 10). The *shaded, hatched*, and *open* areas correspond to tolerant, subtolerant, and intolerant species respectively. The four species' stature classes are canopy, subcanopy, understory, and treelet from *top to bottom* for each tolerance class

of patch mortality substantially affects not only the overall ecosystem structure (in terms of total basal area) but also the composition and abundance of tree species. The case of patch-age independent patch mortality without lag phase provides a wider range of patch-age distribution than other cases with lag phases (Figs. 1, 3). Therefore, it is a reasonable result that tolerant species, particularly with large maximum stature, increased their abundance with decreasing duration of the lag phase. At the same time, in all the scenarios there were young patches that allow intolerant species to persist in these less-crowded conditions.

Kohyama (1993) pointed out the mechanisms of stable coexistence among species simulated in this model: partial vertical segregation of species with different maximum stature mediated by one-sided regulation of size-structured populations at local patch scale, and among-patch segregation of species with different shade tolerance at landscape scale. The present results additionally suggest that the demographic pattern without the lag phase provides the highest opportunity for species coexistence compared to that of long lag phase, because among-patch variation in crowding is highest for the no-lag-phase patch demography. Species difference in terms of reproductive capacity for coexistence was the largest (Table 2) and time for convergence in steady state was the shortest (Fig. 2) for the no-lag-phase scenario. The changing of species parameters least affected the community structure for the baseline no-lag-phase community (Fig. 4). Higher among-patch heterogeneity in structure provides greater opportunity for species to differentiate with respect to crowding conditions. Similarly, increasing advance regeneration least affected the coexistence of intolerant species with tolerant species in no-lag-phase demography. It is also the high among-patch heterogeneity that makes it possible for species partitioning among three tolerant classes (Fig. 7).

Kohyama (1997) suggested, in the patch-heterogeneity ignored model (cf. Kohyama 1992), that the possible range of the reproduction parameter for a species to coexist with others was narrower when maximum statures between species were closer, and when the number of species was increased. Similarly, the present results suggest that the possible range of the reproduction parameter is narrower in long-lag phase, less heterogeneous patch demography, and is particularly so when the number of species is increased.

It is noteworthy that the present results (Fig. 4) demonstrate examples caused by adding a new species A into the multi-species system—not only the failure of some other species but also the recovery of another species B that is otherwise excluded by competition in the system without species A. In such cases where a keystone species enables the coexistence of another two or more species has been recognized as the effect of third parties of community organization (Grubb 1986). The present results give the theoretical basis for the third party effect within autotrophs.

This study showed that the stable coexistence of 12 species, differing in their maximum stature and shade tolerance, was feasible in the no-lag-phase case; however, whether 12 is almost the realistic maximum of species packed along stature-tolerance axes or not is not yet known. This paper pre-assumed the Table 1 parameters systematically, where species of the same tolerance class with different stature had the identical response to crowding in terms of intrinsic growth rate and tolerances in growth rate, survival and reproduction. However, it is likely that there is some interaction between shade tolerance and stature.

Compared to high stature species, low stature species experience more shaded conditions. Also, what is unknown is whether the response to crowding is identical for growth rate, survival, and reproduction. For instance, from forest permanent-plot census, the relation to crowding is relatively easy to record for growth rate, while it is difficult in regards to survival, and is impossible in regards to individual-based reproduction. Identical maximum-stature parameters across tolerance classes, and identical survival parameters across maximum stature classes at the same tolerance class (Table 1) may also make it difficult for species to coexist. The present trial of adjusting a single parameter of reproductive capacity (Table 2) may increase the difficulty for species to coexist. Further numerical and theoretical examination of community consequences of the changing of six demographic parameters for each species is needed, together with reliable field data analysis (Clark et al. 2003).

There are studies suggesting that the high frequency of disturbance, or gap-formation rate, contributes to high species diversity in tropical rain forests (Connell 1978; Hartshorn 1978). The reported gap-formation rate is, however, not remarkably different between tropical and extra-tropical forests (Denslow 1987; Kohyama 1997). On the contrary, in an examination using the same model as this paper, Kohyama (1997) suggests that high tree growth rate promotes, while high tree mortality inhibits, species coexistence. The present results suggest that even with the same average gap-formation rate, the patch-age-specific pattern of gap formation greatly contributes to the capacity of species coexistence.

A variety in the probability of survival among canopy tree species in species-rich forests may bring about a variation in canopy duration. Therefore, it is possible for species-rich tropical rain forests to show higher variation in canopy duration. Opposite cases are observed in wave-regenerated high altitude fir forests with an almost fixed canopy duration (Sprugel 1976; Kohyama and Fujita 1981), and fire-regenerated sub-arctic forests (Heinselman 1973; Johnson and Van Wagner 1984), dominated only by a few canopy species. Variation in canopy duration and tree species diversity can be mutually interrelated.

The present model assumes that patch dynamics is dependent only on patch age, and is independent of the local community structure as a first-order approximation. However, patch mortality is likely to be dependent on local community structure. It is possible to improve the present model so that gap formation is not dependent on patch age but dependent on patch state, as expressed by the tree size structure of each species.

This paper suggests the importance of recording the patch-state specific gap-formation rate in field census, in addition to the conventional estimation of the landscape-average of the gap-formation rate. For instance, spatially explicit records from large-scale permanent plots enable the objective subdivision of patches into different coverage, or basal area, and the estimation of the coverage-specific gap-formation rate. Such information will contribute to the parameter estimation of patch demography, and to the further understanding of tree community organization.

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