Managing Multi-Species Forests To Minimize The Risk of Biodiversity Loss

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Abstract

The design and implementation of forest management systems affects the risk of biodiversity loss. Using a well-known competition-colonization metapopulation model of multiple competing species along with optimal control theory, we investigate both analytically and numerically the design of forest management system in an implicitly spatial context. We focus on the two major approaches to forest management: uniform and specialized. Under uniform management the whole forest estate is jointly managed for the production of timber and the conservation of biodiversity. In contrast, under specialized management the forest is divided into more or less exclusive management zones for timber production or biodiversity conservation.

When the model is parameterized to mimic the management of a diverse Malaysian tropical rainforest, the nonlinear dynamic relationships among species, along with interactions between economic and ecological factors, strongly influence the relative superiority of the two management approaches. In the sense of minimizing risks to floral diversity for a given level of timber harvest, the results indicate that in communities where biological trait differences between species are small, specialized management is superior to uniform management for the vast majority of situations. In contrast, in floral communities where biological traits vary between species, uniform management is often superior to specialized management. In addition, small changes in the discount rate or collateral harvesting damage can reverse the superiority of one management approach compared to the other.

Keywords: competition-colonization model, extinction debt, metapopulation, optimal harvesting, specialized forest management, sustainable forest management, uniform forest management
1. **Introduction**

Biodiversity conservation strategies in tropical rainforests have traditionally emphasized the creation of protected areas. Opportunities to conserve biodiversity in timber production forests are attracting increased attention, however. For example, the Global Environmental Facility recently revised its biodiversity objective to include the conservation of biodiversity in timber production forests. One reason for this expansion of the tropical conservation agenda is obvious: the vast majority of remaining forested area in tropical regions is managed for the production of timber and lies outside of countries’ protected area systems. The design of timber management systems affects the amount of biodiversity conserved in production forests. In this paper, using a simple mathematical model of multi-competing species we explore the impact of timber harvesting on the risk of biodiversity loss.

We investigate this question in an implicitly spatial context by focusing on the two major approaches to forest management: uniform and specialized. Under uniform management the whole forest estate is jointly managed for the production of timber and the conservation of biodiversity. In practice, this approach mainly takes the form of reduced impact logging, which may involve reduced harvesting intensity and the adoption of directional felling methods or cable logging to reduce damage to residual trees and the forest soil. In contrast, under specialized management the forest is divided into more or less exclusive management zones, some for timber production and others for biodiversity conservation. Within production zones the forest is managed solely for timber, while in the protection zones the forest is managed solely for the conservation of
biodiversity. Colloquially this approach may be thought of as “parks and plantations,” although it also includes intensively managed natural forests.

Ecological-economic models of timber harvesting in multi-species forests that incorporate both species extinction risks and spatial features are at an early stage of development. Existing harvesting models for multiple species tend to refer mainly to the management of multi-trophic fisheries and/or are aspatial (May et al. 1977; Clark 1990; Flaaten 1991; Finnoff and Tschirhart 2003; Crépin 2004). However, the floral component of forests, which tracks overall biodiversity quite well and is the source of timber harvests, is better described as a set of competing species at a single trophic level. Spatial ecological models of multiple competing species within a single trophic level do exist. Although many of these models incorporate habitat loss or disturbance, they have not been constructed or placed in an economic context (Tilman et al. 1994; Gyllenberg and Hanski 1997; Tilman et al. 1997; Huxel and Hastings 1999; Hanski 2000; Nakagiri et al. 2001; Ohsawa et al. 2002).

To remedy this shortcoming we modify Tilman’s (1994) competition-colonization metapopulation model to include timber harvesting under specialized and uniform management. Using optimal control theory, for a given social discount rate and timber price, we analytically find the optimal equilibrium harvest rate and the resulting species abundances for the harvesting of a single species group under uniform management. We then determine the area under specialized management that must be set aside as a monoculture to produce the equivalent amount of timber as the uniform case. We then compare the extinction risks under the two different approaches.

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1 In metapopulation models, species dynamics are modeled across a set of habitat patches with patch occupancy determined jointly by species’ dispersal abilities and mortality rates.
We parameterize the model to mimic the management of a biologically diverse Malaysian tropical rainforest containing one group of species that is harvested (the red meranti group, which includes closely related species of the genus *Shorea*) and 169 other genera, which we assume are not harvested. We find that the nonlinear dynamic relationships among species, along with interactions between economic and ecological factors, strongly influence the relative superiority of the two management approaches. The results indicate that in floral communities where biological trait differences between species are small, specialized management is superior to uniform management for the vast majority of situations. In contrast, in floral communities where biological traits vary between species, uniform management is often superior to specialized management. In addition, small changes in the discount rate or collateral harvesting damage and changes in monocultural inefficiency all can lead to changes in the superiority of one management approach over the other. These results indicate that ecological nonlinearities and the life-history characteristics of species have important implications for decisions about harvest strategies in multi-species forests where minimizing the risk of biodiversity loss is an important management objective.

The paper is organized as follows. We begin with a detailed description of the competition-colonization metapopulation model, noting how habitat destruction affects species extinction risk. Next we describe how we incorporated the two different forms of harvesting into the model and present the analytical solution to the optimal harvesting problem. We then calibrate the model to empirical data from a large-scale tropical forestry research plot in Malaysia in order to measure the magnitude of the predicted
differences. We conclude the paper by summarizing our findings and making a connection to the literature on sustainable forest management.

2. **Analytical Model**

Trees are sessile organisms. In the simplest terms their population dynamics are governed by the rate at which they colonize unoccupied sites and the rate at which they die and sites become unoccupied. A wealth of complexity underlies this statement, related to species’ intrinsic traits and extrinsic factors such as the presence of other species and variation in the physical environment. Metapopulation models, which we define and describe below, will allow us to describe species dynamics across a spatially implicit\(^2\) set of habitat patches in terms of these factors as well as to incorporate the effects of species-specific differences in these factors.

2.1 **Single- and Two-Species Metapopulation Models**

Levins (1969) invented the metapopulation model as way to characterize the dynamics of site occupancy of a single sessile species. The beauty of Levins’ model is that it is the spatially implicit analog to the logistic growth equation and has a globally stable equilibrium\(^3\) (Hastings 1980). The model assumes that the habitat is made up of distinct sites that are the size of an adult individual. Rather than explicitly keep track of the dynamics of each habitat site the model tracks the proportion of sites occupied.

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\(^2\) Spatially implicit models integrate the effects of spatial heterogeneity without explicitly accounting for the physical location of individual organisms.

\(^3\) Globally stable means that the model converges to a unique equilibrium abundance value for any starting value greater than zero and returns to the equilibrium value for any perturbations that do not lead to extinction.
Colonization and death determine this proportion. Death leads to the opening of sites, while colonization leads to their occupation.

If $p$ denotes the fraction of sites occupied, $c$ denotes the colonization rate of open sites, and $m$ denotes the mortality rate in occupied sites, then the dynamics of the system can be modeled as follows:

$$\frac{dp}{dt} = cp(1-p) - mp$$

(1)

The first term of Eq. (1) gives the colonization of new sites. $cp$ is the total number of propagules created while $1-p$ is the fraction of unoccupied sites. The second term, $mp$, is the density-independent rate at which sites become unoccupied.

The equilibrium proportion of sites occupied, $\hat{p}$, which can be found by setting Eq. (1) = 0, is:

$$\hat{p} = 1 - \frac{m}{c}$$

(2)

From Eq. (2) it is clear that the colonization rate must be greater than the mortality rate in order for the species to persist. In addition, unless the species has an infinite colonization rate or is immortal, it never fully occupies all the available sites.

The last sentence of the proceeding paragraph has an important implication. Namely, since a single species can never fully occupy the entire habitat, it may be possible under certain conditions for other species to invade and survive in the unoccupied portion of habitat. A number of researchers (Levins and Culver 1971; Horn and MacArthur 1972; Hasting 1980; and Nee and May 1992) recognized this and extended Levins’ model to include two species that differed in competitive ability. In these formulations one species is the superior competitor, whose dynamics are
completely unaffected by the other species, the inferior competitor. The superior competitor does, however, affect the inferior competitor. The inferior competitor can only colonize vacant sites and may be displaced from sites it occupies by the superior competitor. Conditions can be derived for the stable coexistence of the species in terms of the species’ colonization and mortality rates. In the case of equal or nearly equal mortality rates a tradeoff in colonization and competitive ability is needed for coexistence: the inferior competitor must be the superior colonizer.

2.2 **Tilman’s Multi-Species Model**

Tilman (1994) took the work of these researchers further and extended Levins’ metapopulation model to a community of an arbitrary number of competing species. Tilman extends the concept of inferior and superior competitors in the two-species model to a linear hierarchy of competitive abilities where individuals of higher-ranking species displace individuals of lower-ranking species from occupied patches. Competition in the model is both asymmetric and nonlinear.

Mathematically the model may be formulated as follows. Let $p_i$ be the proportion of sites occupied by species $i$, $m_i$ be the mortality rate of species $i$, and $c_i$ be the colonization rate of species $i$. The total number of species is $I$, ranked from the most competitive ($i = 1$) to the least competitive ($i = I$). The dynamics of species $i$ are governed by the following differential equation:

$$\frac{dp_i}{dt} = c_i p_i \left(1 - \sum_{j=1}^{i} p_j\right) - m_i p_i - p_i \sum_{j=1}^{i-1} c_j p_j, \quad \forall i$$  

(3)
Eq. (3) is similar in form to Eq. (1) except for two additions. The first term on the right hand side now includes all species that are superior competitors to species $i$ as species $i$ cannot colonize sites occupied by these species. The second addition is the last term on the right hand side. It incorporates the displacement of species $i$ from occupied sites by superior competitors.

The equilibrium proportion of sites occupied by species $i$, $\hat{p}_i$, can be found by setting Eq. (3) = 0:

$$\hat{p}_i = 1 - \frac{m_i}{c_i} - \sum_{j=1}^{i-1} \hat{p}_j \left( 1 + \frac{c_j}{c_i} \right), \forall i$$  \hspace{1cm} (4)

Eq. (4) is recursive: the equilibrium proportion of sites occupied by each species is found by starting from the top of the competitive hierarchy and working down through it.

Tilman (1994) proves the existence and local stability of a unique equilibrium in which all species occupy a positive proportion of the sites. In addition, he demonstrates that it is possible to find colonization and mortality rates that allow for the stable coexistence of an arbitrary number of competing species. Finally, he shows in the case of all species having equal or nearly equal mortality rates that coexistence requires a tradeoff between species’ colonization and competitive abilities: less competitive species must be better colonizers.

Ecological studies of tree communities support the existence of such tradeoffs. Howe et al. (1985) and Liberman and Liberman (1994) found differences in the dispersal and longevity of tropical trees. More recently, Kohyama et al. (2003) looked at the tradeoff between size-dependent growth rate (a proxy of light competition) and fecundity in tropical trees. They found that short-stature species with strong negatively size-
dependent growth rates coexist with taller species with less sensitive size-dependent growth rates, provided that the shorter species out-recruit taller species.

In an extension that is relevant to our analysis of specialized forest management, Tilman et al. (1994, 1997) extended the multi-species metapopulation model to incorporate the effects of habitat destruction on species diversity. They incorporate habitat destruction into their model by assuming that a proportion of the sites, \( D \), are permanently destroyed and cannot be colonized by any species. With the incorporation of habitat destruction, Eq. (4) becomes:

\[
\frac{dp_i}{dt} = c_i p_i \left(1 - \sum_{j=1}^{i} p_j - D \right) - m_i p_i - p_i \sum_{j=1}^{i-1} c_j p_j, \forall i
\]

The equilibrium proportion of sites occupied, \( p^D_i \), is now:

\[
p^D_i = 1 - D - \frac{m_i}{c_i} - \sum_{j=1}^{i-1} p^D_j \left(1 + \frac{c_j}{c_i}\right), \forall i
\]

Habitat destruction decreases the equilibrium proportion of sites occupied, and if large enough, may lead to the extinction of species. From (6), it is clear that a sufficient condition for the extinction of species \( i \) is \( D \geq 1 - \frac{m_i}{c_i} \). In communities where species have equal or nearly equal mortality rates this leads to the counterintuitive conclusion that the best competitor and perhaps the most abundant species may be most susceptible to extinction (Tilman et al. 1994, 1997). In communities of this type the best competitors have the lowest colonization rates. Habitat destruction reduces the total number of available sites and thus has the largest impact on the species least able to find available sites. In addition, the relationship between the number of species driven to extinction and the amount of habitat destroyed is nonlinear (Tilman et al. 1994).
Finally it should be noted that species extinctions do not occur immediately, as the species take time to die out after habitat loss. Tilman et al. (1994) coined the word “extinction debt” to refer to this delayed, deterministic loss of species after habitat destruction.

While Tilman’s competition-colonization metapopulation model provides a powerful, elegant, and analytically tractable way to explain the coexistence of multiple competing species, it is not without its deficiencies. Kinzig et al. (1999) point out a number of deficiencies that emerge when analyzing extremely diverse communities. In particular, when applied to such communities the model exhibits pathologically slow dynamics. This deficiency led us to focus on steady-state harvesting equilibria rather than on transition dynamics.

2.3 Incorporating Harvesting Under Uniform Management Into Tilman’s Model

As described in the introduction, uniform management involves managing the entire forest estate for the production of timber. In practice, a harvest rotation length is set and each year some proportion of the entire forest is harvested. For example, under a classic sustained-yield forest management system, if the harvest rotation length is set for 30 years then 1/30 of the forest estate is harvested each year.

Since the metapopulation model keeps track of the proportion of sites occupied it is easy to incorporate the concept of cyclically harvesting a proportion of the whole forest each year. The harvesting of a species involves removing the species from all the sites it occupies in some proportion ($h^U$) of the total forest area in each time step. In addition, the harvesting process usually damages trees adjacent to the tree being harvested. We
incorporate collateral damage due to harvesting by assuming that harvesting increases the mortality rates of all species by some percentage ($d^U$). Mathematically these changes involve incorporating $h^U p_i$ and $d^U$ into Eq. (3) and $d^U$ into Eq. (4), where ($h^U$) is implicitly the rotation length. We consider only the case of a single species (or group of ecologically similar species) being harvested. $i'$ indicates the harvested species. The state equation for species $i'$ becomes:

$$\frac{dp_i'}{dt} = c_i p_i \left(1 - \sum_{j=1}^{i} p_j \right) - m_i \left(1 + d^U \right) p_i - p_i \sum_{j=1}^{i-1} c_j p_j - h^U p_i$$  \hspace{1cm} (7)$$

and the state equations of the all the other species $i$ ($i \neq i'$) become:

$$\frac{dp_i}{dt} = c_i p_i \left(1 - \sum_{j=1}^{i} p_j \right) - m_i \left(1 + d^U \right) p_i - p_i \sum_{j=1}^{i-1} c_j p_j, \ \forall i \neq i'$$  \hspace{1cm} (8)$$

The equilibrium proportion of sites occupied can again be found by setting Eq. (7) and Eq. (8) equal to zero and solving them recursively by moving down the competitive hierarchy. The equations for these proportions now include $h^U$ (for species $i'$) and $d^U$ (for all species). For species $i'$ at equilibrium the proportion of sites it occupies, $p_i'$, is now:

$$p_i' = 1 - \frac{m_i}{c_i} \sum_{j=1}^{i-1} p_j \left(1 + \frac{c_j}{c_i} \right) - \frac{m_i d^U h^U}{c_i^2}.$$  \hspace{1cm} (9)$$

The equilibrium proportions of sites occupied by other species ($i \neq i'$) are:

$$p_i' = 1 - \frac{m_i}{c_i} \sum_{j=1}^{i-1} p_j \left(1 + \frac{c_j}{c_i} \right) - \frac{m_i d^U}{c_i}, \ \forall i \neq i'$$  \hspace{1cm} (10)$$

It is clear from Eq. (9) and and Eq. (10) that under uniform management, the harvesting of species $i'$ affects the persistence of other species as a result of the increase in mortality of species $i'$, which releases lower-ranking competitors, as well as the
collateral harvesting damage, which has a negative impact on the populations of species, including \( i' \) itself.

### 2.3 Optimal Harvesting Under Uniform Management

Having described how we incorporated single species harvesting under uniform management into the metapopulation model, we now turn to the determination of the optimal harvest rate, \( h^U^* \). We define \( h^U^* \) for a given discount rate, \( \delta \), and stumpage value, \( P \), to be the harvest rate that maximizes the net present value of the harvest over an infinite time horizon. \( P \) is the difference between the price of timber and the cost of timber harvesting.

Mathematically, we want to maximize:

\[
\int_0^\infty e^{-\delta t} Ph^U p_i \, dt
\]  

We find \( h^U^* \) using the current value Hamiltonian based on Eq. (11) and Eq. (7).

The current value Hamiltonian (\( \mathcal{H} \)) is:

\[
\mathcal{H} = Ph^U p_i + \lambda \left( F(p_i) - h^U p_i \right)
\]  

where

\[
F(p_i) = c_i p_i \left( 1 - \sum_{j=1}^{i-1} p_j^U - p_i \right) - m_i (1 + d^U) p_i - p_i \sum_{j=1}^{i-1} c_j p_j^U
\]  

The inclusion of only \( p_j^U \)s with \( j < i' \) in Eq. (13) is a direct result of the asymmetric nature of competition in this model. While species \( i' \)'s abundance is affected by species that are superior competitors, its abundance has no effect on theirs. Similarly, species that are inferior competitors to species \( i' \) are affected by species \( i' \) but do not affect it and
therefore do not enter into $\mathcal{H}$ or $F(p_i)$. At equilibrium the proportion of sites occupied by superior competitors can be viewed as fixed since species $i'$ cannot affect or alter the populations of these species.

Since we only interested in the system at equilibrium we look for the singular control. For $h^{U*}$ to be optimal at equilibrium (Clark 1990):

$$F(p_i) = c_i p_i \left(1 - \sum_{j=1}^{i-1} p_j - p_i\right) - m_i(1 + d_i) p_i - p_i \sum_{j=1}^{i-1} c_j p_j - h^U p_i = 0 \tag{14}$$

$$\frac{\partial \mathcal{H}}{\partial h^U} = P p_i - \lambda p_i = 0 \tag{15}$$

$$\dot{\lambda} = \delta \lambda - \frac{\partial \mathcal{H}}{\partial p_i} = \delta \lambda - \left[Ph^U + \lambda c_i \left(1 - \sum_{j=1}^{i-1} p_j\right) - 2\lambda c_i p_i - \lambda m_i(1 + d_i) - \lambda \sum_{j=1}^{i-1} c_j p_j - \lambda h^U \right] = 0 \tag{16}$$

The solutions of Eqs. (14-16) imply that:

$$p_i^{U*} = \frac{1}{2} - \frac{m_i(1 + d_i)}{2c_i} - \sum_{j=1}^{i-1} \frac{p_j^U}{2} \left(1 + \frac{c_j}{c_i}\right) - \frac{\delta}{2c_i} \tag{17}$$

$$h_i^{U*} = \frac{c_i - m_i(1 + d_i) - c_i \sum_{j=1}^{i-1} p_j^U \left(1 + \frac{c_j}{c_i}\right) + \delta}{2} \tag{18}$$

$$\lambda = P \tag{19}$$

The equilibrium proportions of sites occupied by the rest of the species can then easily be found using a combination of Eq. (10) and Eq. (17) as necessary.

We obtain the standard result that the optimal economic harvest is obtained when the natural rate of increase equals the discount rate (Clark 1990, p. 57-58). This is easily shown by taking the derivative of $F(p_i)$ with respect to $p_i$ and evaluating it at $p_i^{U*}$:
\[
F'(p_i) = c_i - 2c_i p_i - m_i (1 + d^U) - \sum_{j=1}^{i-1} (c_j + c_i) p_j^U
\]  (20)

and

\[
F'(p_i^*) = c_i - 2c_i \left( \frac{1}{2} - \frac{m_i (1 + d^U)}{2c_i} - \sum_{j=1}^{i-1} \frac{p_j^U}{2c_j} \left( 1 + \frac{c_j}{c_i} \right) - \frac{\delta}{2c_i} \right) - m_i (1 + d^U) - \sum_{j=1}^{i-1} (c_j + c_i) p_j^U
\]  (21)

which simplifies to

\[
F'(p_i^*) = \delta.
\]  (22)

2.5 Incorporating Harvesting Under Specialized Management

In contrast to uniform management, specialized management involves placing a proportion \(D\) under intensive management (a monoculture) for species \(i'\), with the remaining \(1-D\) of the forest left undisturbed. Harvesting now affects the proportions of sites occupied by species in the undisturbed area through the reduction in available habitat. From the perspective of biodiversity conservation the proportion under intensive management should is viewed as “destroyed”.

Since the focus of this paper is on determining which management approach, specialized or uniform, leads to a lower risk of biodiversity loss we do not find the optimal \(D\) for a given \(\delta\) or \(P\). Rather, we choose the \(D\) that produces the same stream of timber as uniform management (i.e. \(p_{i'}^U h_{i'}^U\) in each period).

Under specialized management, if each tree in the monoculture occupies a site of the same size as in the natural forest, then the area of the monoculture must also equal \(p_{i'}^U\) in order to generate the same stream of timber. Experience with monocultures of native timber species has been more disappointing in the tropics (Hartshorn 1983;
Appanah and Weinland 1993) than in the temperate and boreal zones where plantations account for a substantial portion of harvests of native species. Increased risk of disease and pathogens is one reason. To allow for the possibility that monocultures of native tropical timber species might not be able to sustain given harvest levels at the high stocking densities used in temperate and boreal plantations, we introduced a monoculture inefficiency multiplier, $M_i$, which increases the area that must be placed under intensive management. The area under intensive management is thus $M_iD$.

From Eq. (6), the proportion of the sites at equilibrium occupied by each species in the undisturbed portion of the forest being conserved becomes:

$$p_i^S = 1 - M_iD - \frac{m_i}{c_i} - \sum_{j=1}^{i-1} p_j^S \left(1 + \frac{c_j}{c_i}\right), \forall i$$  (23)

Except for the addition of $M_i$ and the change in the superscript on $p$ from $D$ to $S$, this is the same as Eq. (6).

### 2.6 Section Summary

In this section we described a well-known competition-colonization metapopulation model of multiple competing species. We then demonstrated how single species harvesting under uniform and specialized management could be incorporated into the model, and we derived analytical expressions for the optimal equilibrium harvest rate and species abundances at that rate.

For given assumptions about the relative magnitudes of the biological and economic parameters, it might be possible to determine analytically the conditions under which specialized management is superior to uniform management in terms of reducing biodiversity loss. At this point in our research we have not pushed the analysis this far.
Instead, we explore these issues using a numerical approach, described in the remaining sections of the paper.

3 Model Parameterization

We now describe how we parameterized the competition-colonization metapopulation model with harvesting to determine the impact of specialized and uniform management on risk of biodiversity loss in a highly diverse Malaysian tropical rainforest.

3.1 Defining Biodiversity and Site Occupancy

We drew data from the Center for Tropical Forest Science Pasoh Forest Dynamics Plot (Manokaran and LaFrankie 1991). The plot is located in the Pasoh Forest Reserve, Negri Sembilan, Peninsular Malaysia and is situated in mixed dipterocarp forest with an aseasonal climate of high and relatively evenly distributed rainfall. The plot is 50 ha (1000 x 500 m) in size. The method of plot establishment followed a standardized protocol (Manokaran et al. 1990; Condit 1998). All stems ≥1 cm dbh were tagged, mapped, identified to species, and measured for diameter at breast height (dbh). In 1996, the Pasoh plot contained 817 species and 320,903 stems.

Although the Pasoh data set provides a wealth of information on the abundance and performance of tropical tree species over decadal time scales, we still faced a number of decisions and challenges in using it to parameterize the metapopulation model. The first decision involved deciding at what level or resolution should we measure biodiversity. In Malaysian tropical rainforests the majority of timber income is derived
through the harvesting of species in the family Dipterocarpaceae. The most important commercial group is red meranti. Red meranti is composed of several species in the genus *Shorea*. We decided to simulate the harvesting of red meranti and therefore grouped all other species (including all other *Shorea*) to the genera level. We used the number of genera as our measure of biodiversity. Nearly three hundred (296) genera are found in Pasoh. Although in practice several of these genera are also harvested in timber production forests in Peninsular Malaysia, in this paper we consider only the harvesting of red meranti.

The next challenge involved deciding what the proper definition of an adult tree was. A tropical forest includes trees of different ages, but in the metapopulation model the site occupancy proportions (the *p’s*) refer to those reproductive individuals of the same age (it is a single-cohort model). Since we were modeling the harvesting of trees we used the lower size limit for commercial harvesting in Malaysia, which is 30 cm dbh as the size of an adult tree. At Pasoh, 170 genera, of which the red meranti group was considered to be one and all other *Shorea* to be another, had at least one individual with this minimum diameter.

Having defined what an adult tree was, we were then faced with the challenge of defining the size of a site occupied by an adult. The model does not keep track of the number of individuals of a given species but rather the proportion of sites occupied. The canopy area of a tree best describes the amount of habitat space an individual takes up.

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4Red meranti includes individuals of the following species found at Pasoh: *Shorea acuminata, Shorea dasyphylla, Shorea leprosula, Shorea macroptera, Shorea ovalis, Shorea parvifolia*, and *Shorea pauciflora*. 
We used an allometric relationship to relate canopy area to tree diameter\(^5\). Using the Pasoh data, we calculated the proportion of sites occupied by genus \(i\), \(p_i\), as the sum of the crown-projected area of all the trees in that genera divided by the total area of the plot (500,000 m\(^2\)). Figure 1 illustrates the dominance-diversity curve for the 170 genera in Pasoh. The sum total proportion of available canopy area occupied by trees greater than 30 cm diameter was 0.296, with red merantis making up 0.041. While trees greater than 30 cm only occupy approximately 1/3 of the total plot area, this is not to say the rest of the available sites were empty. They were in fact occupied by trees less than 30 cm, which are accounted for in the model only implicitly.

We made the simplifying assumption that the distribution we observed in the 1996 data was an old-growth equilibrium. While three complete censuses of the plot have been conducted over a 15-year period, this time scale is small when compared to the average lifetime of tropical trees. This fact precluded us from rigorously testing this assumption, but changes in the distribution over the three censuses have been small.

### 3.2 Calibrating the Colonization and Mortality Parameters

The main challenge involved choosing the species’ competitive hierarchy and using this, along with the proportional abundance distribution, to estimate genera-specific colonization and mortality rates. The Pasoh data provides no indication of the species’ competitive hierarchy. We chose to create a multitude of competitive hierarchies by

\(^5\) Köhler (2000) using data drawn from a rainforest in Sabah, Malaysia determined that crown diameter \((C_{dbh})\) is related to diameter \((dbh)\) in the following way \(C_{dbh} = (f_0 + f_1dbh^{f_2})dbh\) where \(f_0 = 0.132, f_1 = 0.933,\) and \(f_2 = -0.6615\). Crown area \((C_A)\) is thus \(\frac{\pi}{4}C_{dbh}^2\).
randomly permuting the competitive rankings of the genera. For a given, randomly assigned competitive hierarchy, we then determined genera-specific colonization and mortality rates that yielded the observed proportional abundance distribution. While the plot data do allow for estimating mortality rates (the death of trees > 30 cm dbh) and colonization rates (the in-growth emergence of trees > 30 cm), these observed rates are not the same as the colonization and mortality rates in the model. The colonization and mortality rates in the model encapsulate the whole dynamic process by which seeds are dispersed from the mother tree, sprout, grow from seedlings into samplings into adults, and eventually die.

We calibrated these rates as follows. First, in line with Malaysian forest management guidelines, we assumed that the optimal rotation for red meranti was approximately $T = 30$ years. Following Weitzman (1999, 2000), we assumed a long-run discount rate (the social rate of timber preference, not the market return on investment) of 2%. In addition, we assumed, as others have done (Tilman et al. 1994), that the mortality rates for tropical trees are equal or nearly equal. These two assumptions, along with Eq. (18), allowed us to calculate $c_i$ for red meranti. Using the fact that $h^{\prime \prime} = T^{-1}$ and assuming $d^{\prime \prime} = 0$, it is easy to show that Eq. (18) simplifies to:

$$T^{-1} = \frac{\delta + c_i \hat{p}_i}{2}$$

(24)

Thus for a given $\delta$, $T$, and $\hat{p}_i$, we can solve for $c_i$:

$$c_i = \frac{2T^{-1} - \delta}{\hat{p}_i}$$

(25)
This estimate is consistent both with the actual abundance of red meranti at Pasoh ($\hat{p}_r$) and with the assumption that a rotation length of $T$ (30 years in Peninsular Malaysia) is optimal for a discount rate of $\delta$ (2%, per Weitzman).

After finding $c_r$, we still needed to find values of $c$ for the other genera as well as determine the mortality rate $m$ for all the genera to produce the observed proportional abundance distribution. Tilman (1994) derived the following equation relating $c_i$, $m_i$, and $p_i$:

$$
c_i = \frac{\sum_{j=1}^{i-1} (\hat{p}_j m_j) + \left(1 - \sum_{j=1}^{i-1} \hat{p}_j\right) m_i}{\left(1 - \sum_{j=1}^{i-1} \hat{p}_j\right) \left(1 - \sum_{j=1}^{i} \hat{p}_j\right)}, \forall i
$$

Equation (26)

Assuming equal mortality rates it is easy to use Eq. (26) to solve for $m = m_i$ for all $i$. Once $m$ has been found, the observed proportional abundance distribution (the $p_i$s) can be inserted into Eq. (26) to find the rest of the $c_i$s.

The assumption of equal mortality rates is strong. Life history traits are known to vary among genera. We therefore also created floral communities where mortality rates varied across genera. In these communities, mortality rates were normally distributed. The mean mortality rate was set equal to the mortality rate found when parameterizing an identical community where genera were assumed to have equal mortality rates. The variance of the normal distribution was chosen to produce a specified coefficient of variation. Once the $m_i$s were chosen the $c_i$s were again calculated using Eq. (26).

### 3.3 Numerical Simulations
Using the methodology outlined above, we created a number of communities with permuted competitive hierarchies. These communities allowed us to explore the impact of variation in the discount rate (\(\delta\)), the collateral damage rate (\(d^c\)), and the monocultural inefficiency multiplier (\(M_i\)) on biodiversity when harvesting the red meranti group under uniform and specialized management. We measured changes in biodiversity by comparing the expected number of eventual local extinctions for the two strategies. A genus was defined to be locally extinct (extirpated) if the proportion of adult sites occupied was less than the equivalent of one adult tree per fifty ha. We also examined the number of rare genera and the number of genera of higher rank than red meranti that were lost.

We looked at three values of \(\delta\), 1.5%, 2% and 2.5%. We varied \(d^c\) between 1% and 5%\(^6\) and \(M_i\) between 1 and 5. The values of \(M_i\) are arbitrary. For every possible combination of these three variables we created 10,000 random communities of two types. One community where genera had equal mortality rates and the other where mortality rates varied. In communities where mortality rates varied, the mortality rates were calculated using the procedure described above. The distributions had a coefficient of variation of 0.01. We calculated the mean and variance of the number of genera lost for each case under each management strategy. Below we report on the means, as the variances were tiny due to the large number of simulations (10,000) that we ran.

4. **Results**

\(^{6}\) According to Pinard & Putz (1996) ~60% of unharvested trees in diameter classes ranging from 1-60 cm are "uprooted and crushed" or "snapped off below the crown" during harvesting. Little difference across diameter classes was noted. Thus if 1/30th of the area is harvested each year, then the damage rate would be about 2% per year, about the median of the range we considered.
Figures 2-6 display our main results. Harvesting under either management regime led to substantial reductions in biodiversity. Figure 2 compares the two regimes in the base case of no collateral damage, no monocultural inefficiency (i.e., the multiplier is equal to one), and a discount rate of 2%. Specialized management was slightly superior when genera had equal mortality rates (panel a), as only 25 genera were extirpated (became locally extinct) under that regime, compared to 28 under uniform management. The types of genera lost differed in the two cases, with the rarest genera being most at risk under specialized management and more abundant genera facing a greater risk under uniform management. In both cases, however, the most abundant genera were sometimes lost in particular simulation runs.

A simple explanation exists for the differential impact of the two management strategies on rare and common genera. In our randomly constructed hierarchical communities, rare and common genera are equally likely to be more or less competitive than red meranti. Under specialized management, rare genera face greater extirpation risk due to the fact that habitat destruction affects genera throughout the competitive hierarchy and, all things being equal, rare genera are more susceptible to extirpation in the face of habitat loss. However, under uniform management, only inferior competitors are only at risk of extirpation. Rare genera that are superior competitors to red meranti face no extirpation risk.

The introduction of variability in the mortality rate across genera (panel b) did not affect the number of genera lost under uniform management that much, but it did in the case of specialized management, where the total number lost nearly doubled to 46. Under uniform management, the changes in the abundance of genera that are inferior
competitors to red meranti far outweighed the effect of small changes in genera life history traits. In contrast, under specialized management, mortality rate variation greatly increases extirpation risk of genera through the possibility of lower-ranking genera going extinct before higher-ranking genera (Tilman et al. 1997). This is in stark contrast to the case of equal mortality rates where genera go extinct in order of decreasing competitive ability.

Figure 2 thus illustrates that the relative superiority of the two approaches depends on the life history traits of the genera in the forest. The greater the variability in those traits (specifically, in natural mortality rates), the more likely that uniform management will be the superior conservation strategy for a given volume of timber harvested.

Figures 3-4 provide more detail on the effects of the harvesting damage rate (Figure 3), monocultural inefficiency (Figure 4), and the discount rate (both figure) in the case where genera had equal mortality rates. In this case, regardless of the damage rate, specialized management led to fewer genera extinctions than uniform management (Figure 3a). The addition of harvesting damage to the model sharply increased the number of genera lost under uniform management, and the higher the damage rate, the greater the number lost. Given the structure of the model, the damage rate had little impact on the number lost under specialized management.

Figure 3a also shows that for a given damage rate, the discount rate had differing effects between the management strategies. Under uniform management, a higher discount rate was associated with more genera lost, while under specialized management the opposite association occurred. A straightforward explanation exists for this result.
Under uniform management, a higher discount rate reduces the optimal stock of red meranti. The larger the reduction in the abundance of red meranti, the larger the number of other less competitive genera that go locally extinct under uniform management. However, the smaller the equilibrium stock of red meranti, the smaller the area that must be put under specialized management; and the smaller the area under specialized management, the lower the number of genera loss. The impact of the discount rate was relatively small in both cases, however.

Figure 3b shows that the relative proportion of the types of genera lost changed with increasing damage rates. In the absence of logging damage, under uniform management the unidirectional competitive hierarchy prevents genera that are more competitive than red meranti from being driven extinct through direct harvest effects. However, harvesting damage affects all genera regardless of their competitive rank. As the collateral damage rates increased, the loss of higher-ranking genera increased. This loss in higher-ranking genera explains most of the additional genera loss at higher damage rates under uniform management. This effect was so strong that for damage rates above 2% uniform management caused more extinctions of high-ranking genera than specialized management.

Figure 4 shows that just as the collateral damage rate increased the number of genera lost under uniform management, so did the monocultural inefficiency multiplier increase the number of genera lost under specialized management. However, the multiplier had to be two or greater to make uniform management superior to specialized management. Moreover, for some values of the multiplier the relative superiority of the two approaches depended on the discount rate. For example, when the multiplier had a
value of 3 or 4, uniform management was superior for discount rates of 1.5% and 2% but was inferior for a discount rate of 2.5%. This result is due to the impact of reduced habitat area under specialized management on the number of higher ranking genera lost (Figure 4b). As noted by Tilman et al. (1994) “the number of superior competitors driven extinct by habitat destruction increases sharply with habitat destruction.” The impact of the discount rate is thus amplified under specialized management when the monocultural inefficiency multiplier is large.

We now turn to the case where the mortality rates varied slightly between genera. Figures 5 and 6 are the complements to Figures 3 and 4 for this case. Looking at the effect of collateral harvesting damage, two effects of mortality-rate variation are immediately obvious (Figure 5a). First, specialized management is inferior to uniform management when the damage rate is zero. Figure 2 showed this result for the 2% discount rate; Figure 5a shows that it holds for the 1.5% and 2.5% discount rates as well. The second effect is that the total number of genera lost increases substantially under both management strategies for nonzero damage rates. For example, for a damage rate of 2%, specialized management leads to the loss of approximately 38 genera while uniform management leads to the loss of approximately 60 genera; the corresponding losses in Figure 3a are 22 and 42, respectively. The number of higher-ranking genera lost also increased (Figure 5b vs. Figure 3b). As in Figure 3b, uniform management leads to fewer high-ranking genera being lost than does specialized management when the damage rate is low but more when the damage rate is high.

The effect of variation in mortality rates is most evident when looking at the effects of the monocultural inefficiency multiplier (Figure 6 vs. Figure 4). Uniform
management is now superior to specialized management for all values of the area multiplier and all discount rates, not just for larger multipliers and lower discount rates. For large values of the multiplier, a third to nearly a half of the genera were lost under specialized management (Figure 6a). About two-thirds of the genera lost in those cases were higher ranking competitors (Figure 6b).

5 Discussion and conclusions

Incorporating harvesting under uniform and specialized management into a spatially implicit metapopulation model of multiple competing species provided some surprising results. One is the importance of relatively small differences in life history traits. In ecological communities where natural mortality rates are the same across genera, the risk of local extinctions (for a given level of timber harvest) is lower under specialized management than uniform management for the vast majority of situations, except when monocultures are very inefficient and thus require relatively large areas. The conservation advantages of specialized management are less in communities where mortality rates vary across genera. The two management strategies also have differential impacts on the types of genera lost (i.e., better competitors vs. better colonizers). These results highlight the need for a better understanding of species’ life history traits in order to determine how to balance biodiversity conservation with timber production in tropical forests. Developing this understanding remains a great challenge in tropical ecology.

The results also indicate that small differences in the discount rate can affect the relative superiority of the two management approaches. In the case of specialized management, we found that the discount rate interacts in a significant way with the
degree of inefficiency of monocultures: the difference in the number of genera lost between the highest and lowest discount rates rises as monocultures become more inefficient. Even though the difference in the range of discount rates considered was just a single percentage point, in the extreme case of a monocultural inefficiency multiplier of 5 the number of genera lost rose from 58 (for the 2.5% discount rate) to 73 (for the 1.5% rate).

Similarly large impacts were found for the logging damage rate in the case of uniform management. An increase from zero to a 1% damage rate roughly doubled the number of genera lost. In the case of a forest with natural mortality rates that varied across genera, this slight increase reversed the order of superiority of the management strategies from uniform to specialized management.

Some of our results echo conclusions being reached by forest ecologists (e.g., Fredericksen and Putz 2003), that producing timber in small, intensively managed areas may be the most efficient means to conserve biodiversity while also maintaining a production of timber. Others, however, provide support for findings that the superiority of this specialized management approach depends on economic and ecological factors. For example, Potts and Vincent (2005) demonstrate that the superiority of specialized management depends both on the relative values of timber and biodiversity and on the extent to which individuals of the same species are spatially aggregated (clumped) within the forest. In our view, the current state of knowledge indicates that neither strategy, specialized or uniform management, is always superior in terms of minimizing risks to biodiversity in tropical forests subject to timber harvesting.
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Figure captions

1. Genera dominance-diversity curve for trees greater than 30 cm dbh located in the Center for Tropical Forest Science Pasoh Forest Dynamics Plot. The total number of genera inclusive of treating red meranti as its own genera is 170.

2. Impact of mortality rate variation on extirpation of genera (2% discount rate, no harvesting damage, no monocultural inefficiency).

3. Impact of logging damage on extirpation of genera (model with identical mortality rates). Monocultural inefficiency multiplier set equal to one. Panel a: All genera. Panel b: Genera with higher competitive rank than red meranti.


5. Impact of logging damage on extirpation of genera (model with varying mortality rates). Monocultural inefficiency multiplier set equal to one. Panel a: All genera. Panel b: Genera with higher competitive rank than red meranti.

Figure 1
Abundance distribution in ecological equilibrium (virgin forest)

- Red Meranti

Genera Abundance (no. of trees > 30 cm dbh in 50 ha)

Genera Rank in Abundance
Figure 2. Impact of mortality rate variation on extirpation of genera
(2% discount rate, no harvesting damage, no monocultural inefficiency)

- Uniform Management
- Specialized Management

a. Model with Identical Mortality Rates
b. Model with Varying Mortality Rates
Figure 3. Impact of logging damage on extirpation of genera: model with identical mortality rates

a. All genera

![Graph a. All genera](image)

Symbols: open = uniform management, solid = specialized management
Discount rates: ◦ ● = 2%; ▲ ■ = 1.5%; □ ■ = 2.5%

b. Genera with higher competitive rank than red meranti

![Graph b. Genera with higher competitive rank than red meranti](image)

Symbols: open = uniform management, solid = specialized management
Discount rates: ◦ ● = 2%; ▲ ■ = 1.5%; □ ■ = 2.5%

All genera
Figure 4. Impact of monocultural inefficiency on extirpation of genera: model with identical mortality rates

a. All genera

Symbols: open = uniform management, solid = specialized management
Discount rates: ○, ■ = 2%; △, ▲ = 1.5%; □ = 2.5%

b. Genera with higher competitive rank than red meranti

Symbols: open = uniform management, solid = specialized management
Discount rates: ○, ■ = 2%; △, ▲ = 1.5%; □ = 2.5%
Figure 5. Impact of logging damage on extirpation of genera: model with varying mortality rates

a. All genera

b. Genera with higher competitive rank than red meranti
Figure 6. Impact of monocultural inefficiency on extirpation of genera: model with varying mortality rates

a. All genera

Symbols: open = uniform management, solid = specialized management
Discount rates: • = 2%; △ = 1.5%; ■ = 2.5%

b. Genera with higher competitive rank than red meranti

Symbols: open = uniform management, solid = specialized management
Discount rates: • = 2%; △ = 1.5%; ■ = 2.5%