Simulating anthropogenic impacts to bird communities in tropical rain forests

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Abstract

We used an aggregated modelling approach to simulate the impacts of anthropogenic disturbances on the long-term dynamics of faunal diversity in tropical rain forests. We restricted our study to bird communities even though the approach is more general. We developed a model called BIODIV which simulated the establishment of hypothetical bird species in a forest. Our model was based on the results of a simple matrix model which calculated the spatio-temporal dynamics of a tropical rain forest in Malaysia. We analysed the establishment of bird species in a secondary forest succession and the impacts of 60 different logging scenarios on the diversity of the bird community. Of the three logging parameters (cycle length, method, intensity), logging intensity had the most servere impact on the bird community. In the worst case the number of bird species was reduced to 23% of the species richness found in a primary forest.

Keywords: Diversity; modelling; tropical rain forest; bird species; disturbance

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1   Introduction

Recently, several models which analyse the spatio-temporal dynamics of tropical rain forest have been published (e.g. Liu and Ashton, 1999; Ditzer et al., 2000; Chave, 2001). These models are important for understanding how natural and anthropogenic disturbances influence and alter tropical rain forest ecosystems. Typical disturbances include El Niño events (Holmgren et al., 2001), hurricanes (Vandermeer et al., 2000), droughts and fires (Leighton and Wirawan, 1986), forest fragmentation (Riitters et al., 2000) and logging (Laurance, 2000). Models are useful tools for testing ecological theories (e.g. Alonso and Solé, 2000), developing forest management plans (van Gardingen and Phillips, 1999) and estimating forest carbon pools and fluxes when investigating climate change (Pinard and Cropper, 2000). However, all the dynamic tropical rain forest models known to the authors deal with plant communities and changes in the vegetation cover in tropical regions. There has not yet been a spatio-temporal model which simulates effects of these vegetation changes in tropical forests on animal populations or fauna diversity.

Attempts have been made to simulate the responses of bird communities to forest dynamics for a temperate forest in North America (Seagle and Shugart, 1985, Urban and Smith, 1989). Other modelling concepts have been restricted to the landscape matrix and approximated habitat dynamics or habitat quality of various fauna communities (Smith et al., 1981a, 1981b, Pausas et al., 1997). On a regional scale impacts of ongoing deforestation in the tropics on bird communities have been estimated (Brooks et al., 1999a, Manne et al., 1999). The population persistence of marshland birds based on the combination of species distribution data, population viability analyses and landscape indices was recently assessed (Verboom et al., 2001).

Many field studies on the responses of wildlife (e.g. Johns, 1985; Lawton et al., 1998; Cosson et al., 1999) and especially bird communities to anthropogenic disturbances in tropical rain forests have been undertaken in the last decade (e.g. Lambert, 1992, Kofron and Chapman, 1995, Canaday, 1996, Danielsen, 1997, Estrada et al., 1997, Thiollay, 1997, 1999, Raman et al., 1998, Whitman et al., 1998, Brooks et al., 1999b, Robinson, 1999, Robinson et al., 2000). However, they are beset by the general problem that field studies reveal short-term dynamics. The now established globally distributed 50 ha rain forest research plots are a first aim to generate longer time series of field data covering various aspects of rain forest ecology systematically (Condit, 1995, 1998). Even there the observsation time now spans only about two decades. Therefore, computer simulations validated with the available short-term data are an important tool for estimates of long-term trends.

In this study we simulate the long-term impacts of two anthropogenic disturbances — forest clearing and tree logging — on birds in a tropical rain forest in Malaysia. We want to enrich current discussion of these disturbances on the diversity by focusing not on individual bird species populations but on a whole community of bird species. We calculated bird species dynamics based on a description of the habitat structures in the forests. These habitat structures are mainly determined by the trees in the forest.

To simulate the dynamics of a tropical rain forest we used a simple Markovian matrix model (e.g. Acevedo et al., 1996), which was parametrised with results of the well-tested

mixed forest simulator FORMIX3 (Ditzer et al., 2000, Huth and Ditzer, 2000, 2001). We developed a model called BIODIV which simulates the population dynamics of hypothetical bird species and the diversity of the whole community based on the dynamics of our vegetation model (modified from Seagle and Shugart, 1985). The modelled species were characterised by species-specific niche requirements defined by the age and type of habitat necessary for survival.

We try to answer the following questions: (1) Models of habitat quality (e.g. Pausas et al., 1997) cannot reveal population dynamics or changes in species richness. Will the species composition in mature forests be stable and fixed, or will further species extinction occur in a primary forest? How high are the fluctuations in population sizes of different bird species in these forests? (2) On cleared and abandoned areas, secondary succession starts forest regrowth. How fast can birds recolonise these habitats and is species richness comparable with that in primary tropical rain forests? (3) Tree logging is a major disturbance in tropical rain forests (Putz et al., 2001). Based on 60 logging scenarios we aim to identify those with the least and the worst impacts on species richness.

2 Methods

2.1 Study site

The study area for which the rain forest simulator FORMIX3 (Huth and Ditzer, 2000) was first parametrised is the Deramakot Forest Reserve (DFR) situated in Sabah (North Borneo, Malaysia, 117°30' E, 5°25' N, 130–300 m asl.). Deramakot has a per-humid climate typical of the inner tropics. The mean annual temperature is 27° with little seasonal variations. The average annual precipitation is about 3500 mm, with no pronounced dry season. The geology of Deramakot is characterised by tertiary sediments, mostly sandstone. The soils are low in nutrients and prone to erosion once left devoid of tree cover. The prevailing forest type is lowland dipterocarp forest (Schlensog, 1997).

2.2 The vegetation model

We chose the rather simple approach of a Markov model for the simulation of the vegetation and its dynamics on which our diversity model was based (cf. Acevedo et al., 1995, 1996, Osho, 1995, 1996, Favrichon, 1998, Riéra et al., 1998).

We used the well-tested mixed forest simulator FORMIX3 to parameterise the Markov model (Ditzer et al., 2000, Huth and Ditzer, 2000, 2001). FORMIX3 is a process-based model which simultaneously calculates tree growth in a landscape matrix of neighbouring patches, which interact through tree fall processes. The more than 400 tree species found in the study area are aggregated into five species groups based on potential maximum tree height and successional growth behaviour of trees. Tree growth is mainly driven by incoming radiation and shading processes which control a detailed carbon cycle calculation. The simulation results of FORMIX3 were validated and compared with field data for several forest sites in Malaysia. In detail, individual tree growth was driven by measured

Table 1: Different habitat types h and the defining maximum tree heights used in the FORMIX3 simulator (Huth and Ditzer, 2000).

Parameter	Habitat type	Maximum tree height h
h_1	Gap	$0 < h \leq 25$ m
h_2	Transition	$25 < h \leq 36$ m
h_3	Climax	$h > 36$ m

diameter-increment data, forest canopy and light distribution and logging damages were compared with forest inventories (Ditzer, 1999).

In our Markov model we simulated the age a_k and the type of habitat h_k in a forest patch k of 20 m × 20 m. A mosaic of neighbouring patches ($k = 1, ..., 20000$) was simulated simultaneously. The patch size corresponded well to typical gap sizes in tropical rain forests (Shugart, 1998) and was also used in the FORMIX3 model.

For each time step dt and each patch k a probability matrix $\mathbb{P}$ determined transitions between different habitat types. If no transition occurred, the patches simply grew older. We distinguished between three different habitat types h: (1) gap, (2) transition and (3) climax. These habitat types described the successional stage in which the forest patch actually was and were defined by the maximum heights of trees in the patch in FORMIX3 (Table 1).

The straight-forward implementation of the transition matrix $\mathbb{P}$ bore some ecological problems. For example, it allows direct transition from a gap phase directly to a climax phase. Therefore we used an age-dependent approach with minimum ages for transition given in $\mathbb{M}$ (Acevedo et al., 1996).

$$\mathbb{M} = \begin{bmatrix} 0 & 0 & 0 \\ 10 & 0 & 0 \\ \infty & 50 & 0 \end{bmatrix} \text{years.} \tag{1}$$

Thus, the principle transition matrix $\mathbb{P}$ still had five independent variables $(p_{12}, p_{13}, p_{21}, p_{23}, p_{32})$:

$$\mathbb{P} = \begin{bmatrix} 1 - p_{21} & p_{12} & p_{13} \\ p_{21} & 1 - p_{12} - p_{32} & p_{23} \\ 0 & p_{32} & 1 - p_{13} - p_{23} \end{bmatrix}. \tag{2}$$

The parameter values p_{kl} were gained from the analysis of simulation results of the FORMIX3 model:

Table 2: Parameters of the BioDiv model. The values of most parameters (I, a, r, R, U) are averages $\pm$ SD of a normal distribution, from which the individual value of each species was chosen stochastically. The immigration rate I varied not for species but for each time step. Most values were taken from the approach of Seagle and Shugart (1985). Further explanation of the parameters is contained in the text.

Parameter	Unit	Value	Description
s		100	Size of species pool
I	y	12 ± 2	Immigration rate
a	y	15 ± 2	Age of habitat
h		1^a	Type of habitat
r	y^{-1}	3 ± 0.05	Reproduction rate per capita
S	patches	20 ± 5	Territory size of each individual
U		5 ± 1.5	Resource use efficiency

^{a}The type of habitat was chosen randomly and did not follow normal distribution. Only one type of habitat was considered for each species.

$$\mathbb{P} = \left[\begin{array}{ccc} 0.667 & 0.006 & 0.002 \\ 0.333 & 0.827 & 0.006 \\ 0 & 0.167 & 0.992 \end{array} \right] \text{years}^{-1}. \tag{3}$$

The reciprocal values of p_{kl} can be understood as average residence times of habitat types, before they transit to other types.

2.3 The BioDiv model

The BioDiv model simulated the dynamics of hypothetical animal populations (modified from Seagle and Shugart, 1985). In principle, the dynamics of every possible species can be simulated. In the following we only applied the model to bird species.

Out of a pool of s species, the different species-specific characteristics of each species i were generated (Table 2; niche conditions essential for species establishment: type of forest habitat h_i and age of forest habitat a_i; reproduction rate per capita r_i; resource use efficiency U_i; territory size of each individual S_i). For this first approach the parameter values for different species follow a normal statistical distributions from given averages and standard deviations. This was chosen to keep the model formulation as general as possible. However, in special cases one might adapt single parameters to different distributions found in the field. Two examples of niches and possible overlap for the
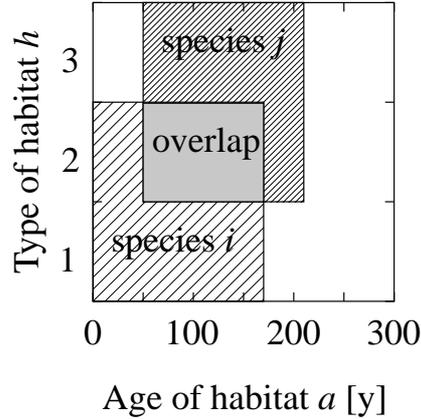
Fig. 1: An example of niches for two species i and j in the 2-dimensional parameter space determined by the type of habitat h and the age of habitat a.

species i and j were shown in Fig. 1.

To simulate the dynamics of our bird populations we needed information on the structure of the forest. Thus, for each time step a habitat–age matrix $\mathbb{R}$ was calculated from the vegetation model (Fig. 2).

The population growth with time $\mathrm{d}N_i/\mathrm{d}t$ of each species i was calculated using a logistic function:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = r_i N_i \left(1 - \frac{N_i}{K_i} \right), \tag{4}$$

where K_i: carrying capacity of the landscape.

We developed a competition process which used a matrix of competition pressure $\mathbb{Q}$ to be able to allow overlaps of niches. This process reflects the competition for the same resources. The competing resource might be interpreted differently, depending on the species. Example are competition for food and space. Without competetion it is assumed that different species use totally different resources with no overlap (e.g. different food or occupy different height layers of the canopy). With competition they share some resources which automatically leads to a lower carrying capacity for the concerned species.

$$\mathbb{Q}_{ha} \quad := \quad \sum_{i=1}^{n} (\chi_i(h,a) \cdot U_i \cdot N_i) \tag{5}$$

$$\chi_i(h,a) \quad = \quad \begin{cases} 1 & : \quad \text{if } h \in [h_{i,\min}, h_{i,\max}], \text{ and } a \in [a_{i,\min}, a_{i,\max}] \\ 0 & : \quad \text{else} \end{cases} \tag{6}$$

where n: number of patches, $h_{i,\min}$, $h_{i,\max}$, $a_{i,\min}$ and $a_{i,\max}$: lower and upper boundary of the parameters characterising the type of habitat h and age of habitat a needed by species i.
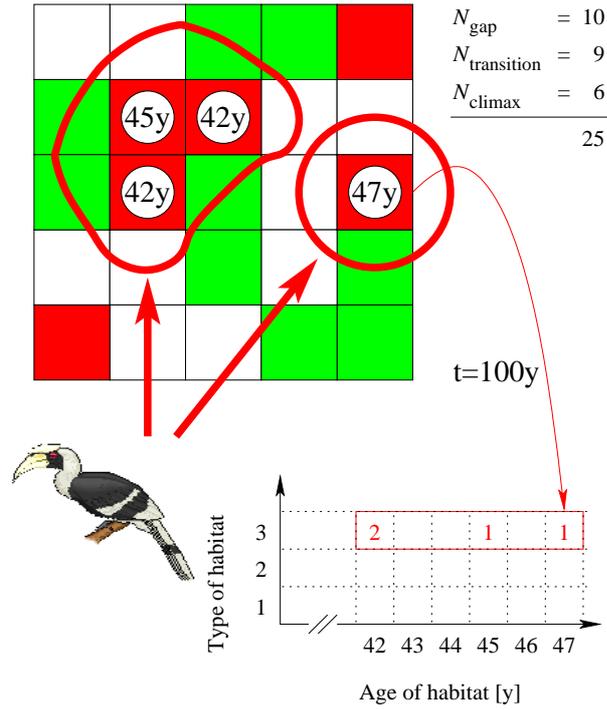
Fig. 2: The transition from a vegetation model to the diversity model BIODIV is demonstrated using a response matrix of habitat–age–correlation for a given time step $t = 100$ y. Here, the vegetation model simulates $5 \times 5 = 25$ patches. Each patch is represented by the type of habitat of a certain age. The necessary habitat conditions of a bird species are shown by way of example. They need a climax vegetation (habitat type 3) of 42–47 years old.

The carrying capacity of the species i without competition was given by

$$K_i = \frac{1}{S_i} \left(\sum_{h=h_{i,\min}}^{h_{i,\max}} \sum_{a=a_{i,\min}}^{a_{i,\max}} \mathbb{R}_{ha} \right). \tag{7}$$

$\mathbb{R}_{ha}$: element of the habitat–age matrix.

The use of the competition pressure matrix $\mathbb{Q}$ led to the following modified calculation of the carrying capacity K_i:

$$K_i = \frac{1}{S_i} \left(\sum_{h=h_{i,\min}}^{h_{i,\max}} \sum_{a=a_{i,\min}}^{a_{i,\max}} (\xi_i(h,a) \cdot \mathbb{R}_{ha}) \right) \tag{8}$$

$$\xi_i(h,a) = \begin{cases} U_i \cdot N_i / \mathbb{Q}_{ha} & : \quad \text{if } \mathbb{Q}_{ha} \neq 0 \\ 1 & : \quad \text{else} \end{cases} \tag{9}$$

$\xi_i(h,a)$ corresponded to the fraction of patches of $\mathbb{R}_{ha}$ occupied by the species i.
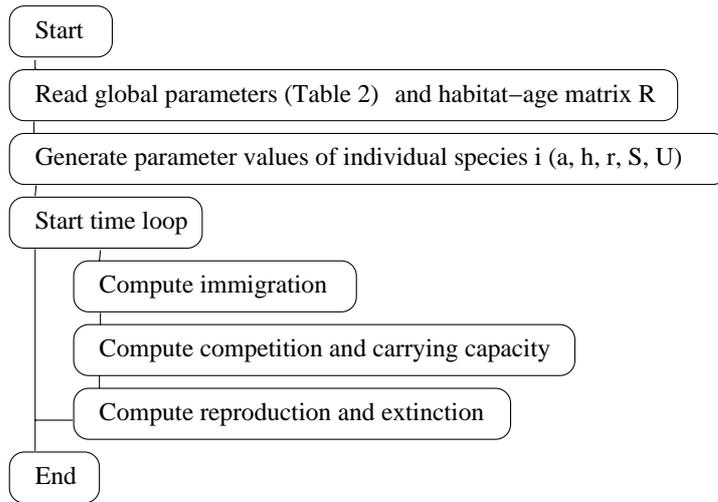
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│ Read global parameters (Table 2)  and habitat–age matrix R │
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│ Generate parameter values of individual species i (a, h, r, S, U) │
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Fig. 3: Process of a model run is illustrated for the BioDiv model. Note that all anthropogenic disturbances are not modelled in BioDiv, but are included in the results of the habitat-age-matrix calulated by the vegetation model.

The annual immigration rate I of new species did not depend on the area size (Table 2). I represented the number of attempts to establish a randomly chosen species out of the species pool. The immigration of the species thus selected was possible if the niches necessary for the survival of the species existed in the present vegetation structure and the species was not already found in the landscape. For each immigrated species, two individuals entered the simulation area.

To model the probability of extinction W_i due to demographic noise (e.g. Wissel et al., 1994) we calculated W_i as

$$W_i = \frac{1}{2^{N_i - 1}} \, \mathrm{d}t \tag{10}$$

which describes the probability of unavailing mate finding. We assume environmental noise – except for the local changes in habitat quality and composition – can be ignored in tropical rain forests. Extinct species were allowed to immigrate again.

For clarification, the conceptualn process of a model run was illustrated in a diagram (Fig 3).

To understand the dynamics of our diversity model BioDiv, we performed a sensitivity analysis of all parameters. For this purpose the vegetation model simulated a primary forest in its steady state for 300 years. Each parameter of BioDiv was varied several times in a given range. Additionally, five different simulations with different random numbers were performed for each parameter set. The results of the final 50 years were averaged.

2.4 Scenarios

We analysed three different scenarios in our study:

1. Primary forest: The Markov model simulated a primary forest. For this purpose the long-term results of the vegetation model ($t > 1000$ y) were taken as a basis for further simulations with BioDiv. The distribution of habitat types and ages of patches was at equilibrium here. The immigration of bird species into this forest formerly uninhabited by birds was simulated. This scenario was mainly used to analyse the model behaviour.

2. Secondary succession: Forests are cleared for various purposes in the tropics. The secondary succession of a forest on such a cleared area was simulated here (e.g. Aide et al., 1995, Raman et al., 1998). Thus, at the start of the simulation ($t = 0$ y) all forest patches were gap type habitats of the age $a = 0$ y.

3. Logging: We analysed the impacts of 60 different logging scenarios on the bird community. The scenarios differed in logging intensities, cycle lengths and methods, and were performed over a time period of 300 years. In a logging event timber extraction took place in randomly selected patches of the climax habitat which were older than a required minimum age. The logging intensity L_I defined the fraction of patches with climax habitats in which trees were felled ($L_I = 0, 25, 50, 75, 100\%$). Those patches were set to a gap habitat of the age $a = 0$ y afterwards. The length of a logging cycle L_L (time period between two logging events: $L_L = 0, 20, 40, 60, 80, 100$ y) influenced the number of logging activities. Two logging methods with different damage regimes L_D to the residual stands and different minimum ages of the logged patches L_A were investigated: conventional logging ($L_D = 50\%$, $L_A = 0$ y) and reduced-impact logging ($L_D = 20\%$, $L_A = 75$ y). The modelling of logging damage in the vegetation model was realised by setting the fraction L_D of randomly selected patches to the habitat type gap of the age $a = 0$ y.

3 Results

3.1 Dynamics of the vegetation model

In the simulation of a secondary succession (Fig. 4), the distribution of different habitat types reached a stable state after 100 years (gap/transition/climax: 4/34/62%). However, the habitat–age–distribution only reached its equilibrium after about 300 years. From this time on we called the dynamics of our vegetation model that of a primary forest.

3.2 Species dynamics in a primary forest

The colonisation of a primary forest without bird species was chosen to analyse the principle dynamics of the diversity model. After just five years the numbers of species
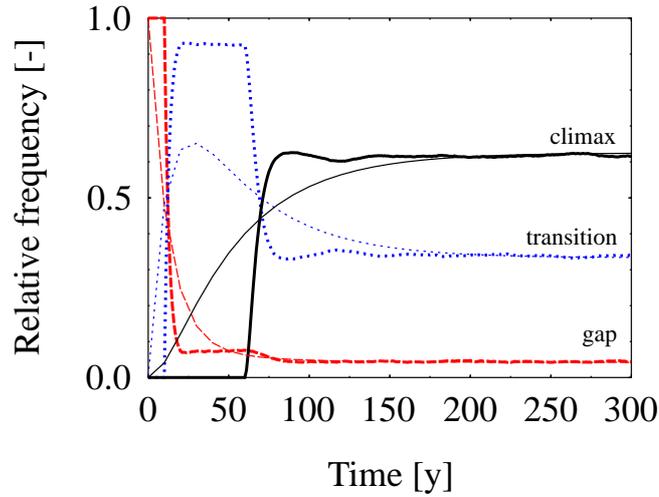
Fig. 4: Time series of the distribution of different habitat types (gap, transition, climax) in the simulation of the Markov model. Scenario secondary succession. Bold lines: distribution with the use of minimum ages for transition (see text); normal lines: distribution without use of minimum ages approach.

had reached its final level of 30–40 species. The number of individuals stabilised in the same time period at 1200 birds (Fig. 5 top).

In the ranking of species abundances for different times (Fig. 5 bottom), it can be seen that the species distribution at $t = 10$ years was quite similar to that of later times. Thus, the equilibrium in species diversity was reached very rapidly in a primary forest.

To understand the population dynamics of individual species, the average numbers and standard deviations of individuals of each species and the specific times of existence were analysed (Fig. 6). Only 22% of the species in the species pool never became established in the forest, because the niches essential for their establishment were never represented in the landscape. Of those species established at least once (78% of the species pool), only about half of them were found simultaneously in the forest landscape. Thus, the species composition changed throughout the whole simulation time, leading to high fluctuations in the numbers of individuals of each species.

The resulting relationship between the species number and the size of the simulated area (Fig. 7) saturated at approximately 50 species and followed the theoretical expectations of a saturation-type relationship (MacArthur and Wilson, 1967). The relationship between species number and area can be described by a power function ($S = cA^z$, where S: the number of species, A: the area, c, z: fitting constants). We gained an exponent $z = 0.4$ ($r^2 = 95\%$), which is in the upper range of z–values determined in various field studies (MacArthur and Wilson, 1967, Conner and McCoy, 1979, Begon et al., 1990, Rosenzweig, 1995). A function fitting our data even better was proposed only recently ($S = cA^z e^{kA}$, $r^2 = 99\%$; Plotkin et al., 2000).
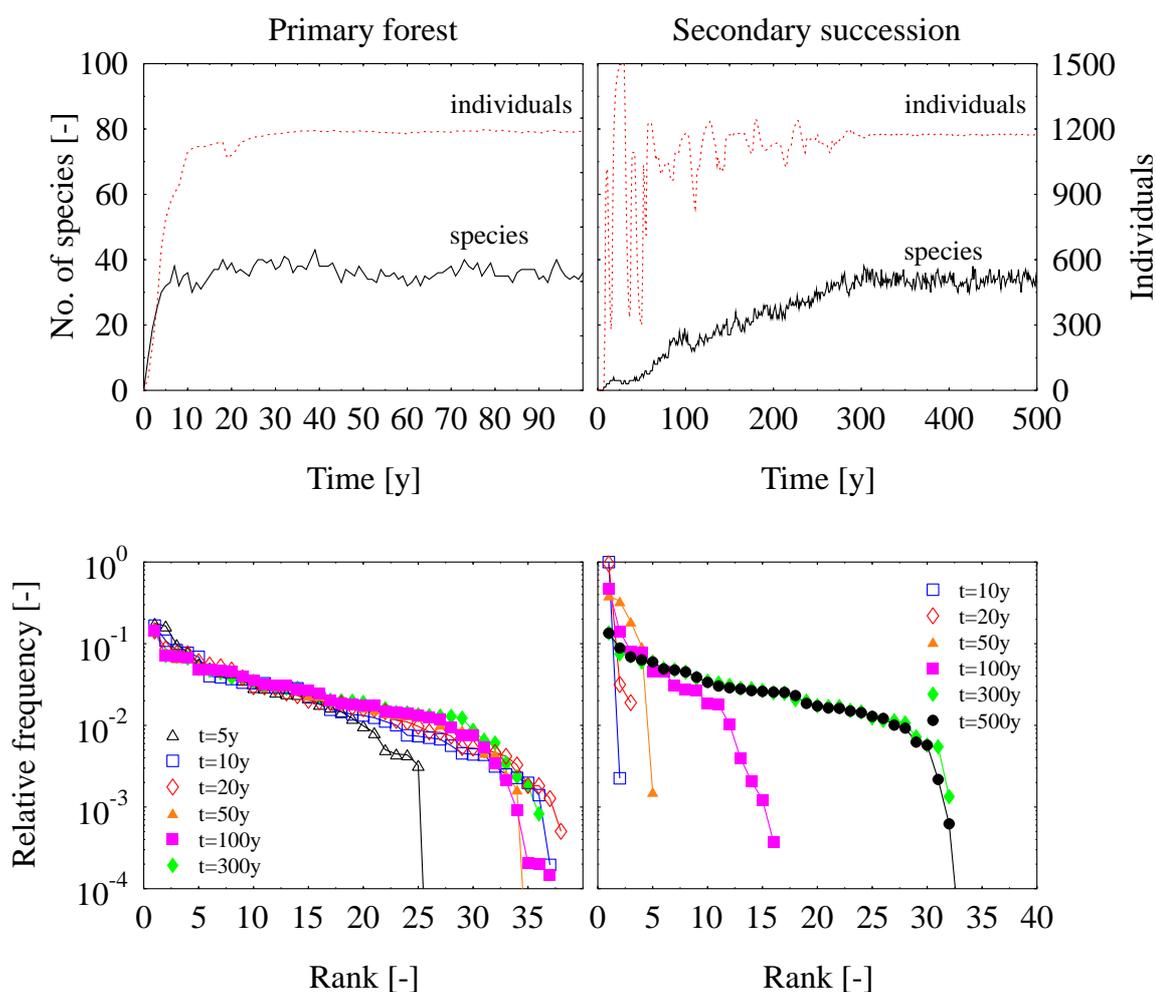
Fig. 5: Results of BIODIV for the two scenarios primary forest and secondary succession. Top: Time series of the numbers of established species and individuals. Bottom: Ranking of species abundance for different times.

3.3 Species dynamics in a secondary succession

In a regrowing secondary forest the number of individuals fluctuated highly in the first 300 years before stabilising at 1200 individuals. The fluctuations were mainly driven by the changing vegetation structure. Especially the sharp de-/increases in the years 10 and 60 induced by the age-dependent transition processes of the Markov model (Fig. 4) affected the carrying capacity of the species and thus the number of individuals.

The number of species increased slowly and reached its final level of about 30–40 species after 300 years, when the forest was comparable to a primary forest. The increase in species number with time was more or less linear, with about 1 new bird species appearing every 8–10 years (Fig. 5 top).
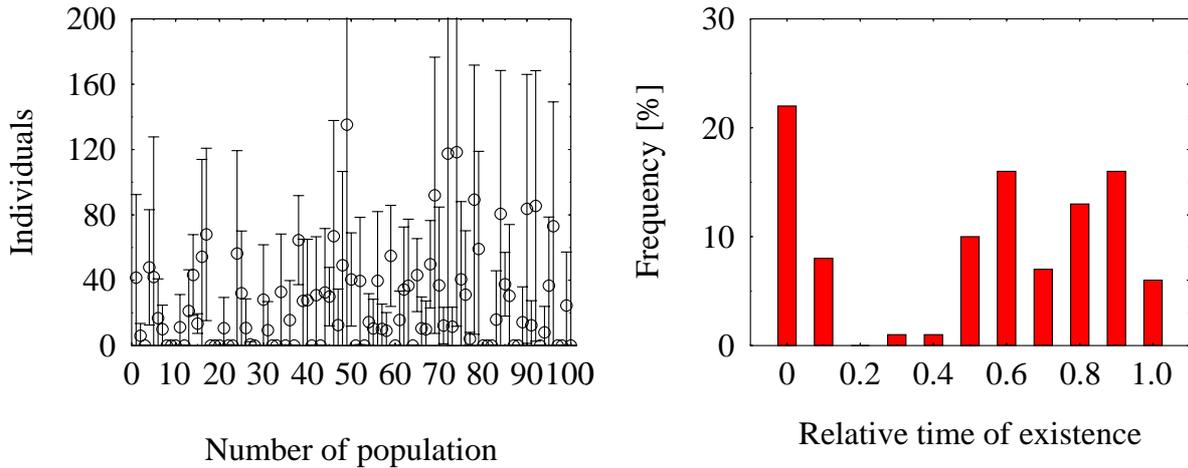
Fig. 6: Primary forest scenario. Population dynamics of individual species. Left: Time averaged ($\pm$ 1 SD) numbers of individuals of each species. Right: Frequency distribution of relative existence times. Results are based on a single run of 300 years.

In contrast to the primary forest scenario, the abundance of species changed and species richness increased to its equilibrium at $t = 300$ y (Fig. 5 bottom). However, even in this equilibrium the population dynamics of individual species were subject to high fluctuations including species extinction and immigration processes (not shown).

3.4   Sensitivity analysis of the diversity model

The variation of most parameters did not lead to significant changes in species diversity. This was especially the case for the resource use efficiency U and the reproduction rate r.

We found an increase in species richness for rising values of the average immigration rate I (Fig 8). For high values of I ($I \geq 1000$ y^{-1}) the composition of the bird species used the available landscape optimally and all species whose niche requirements were represented were found in the forest. The time until the species number saturated declined for increasing immigration rates. For our standard value ($I = 12$ y^{-1}) it still took about 10 years until saturation.

Sensitive results were achieved when varying the average width of niche concerning the habitat age a (Fig. 9 top). Thus, the number of bird species sustained by a forest depended critically on the habitat conditions essential for the establishment of the bird species. Species richness reached its maximum at small mean niche widths ($a = 5$ y). Thus, the model calculated higher species richness for specialists than for generalists. Two different effects influenced species richness. On the one hand small niches reduced the niche overlap and thus competition between different species. On the other hand communities with too small species niches ran the risk of parts of the available habitat space not being used at all. As the average niche width increased, the overlap of niches increased as well while the unused areas in the habitat space decreased (Fig. 9 bottom). The maximum number of
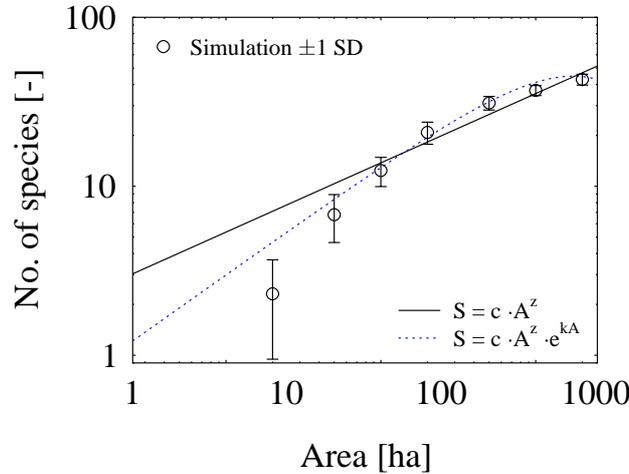
Fig. 7: Time series of species richness for different average immigration rates I (primary forest scenario).

established species was obtained for niche widths which maximised the product of niche overlap and unused area in the habitat space.

The maximum in species richness for small niche widths was mainly a result of the competition process included in the model. In simulations without competition (Fig. 9 top), species richness increased to 85% of species covered in the species pool – compared to 50% with competition – and a maximum was not detectable .

3.5 Species dynamics in a logged forest

The effect of specific logging scenarios on the mean number of bird species was significant (ANOVA: $P < 0.001$ for all main and all 2-dimensional interactive effects of cycle length, logging method and intensity, Table 3). After a single event of reduced-impact logging (Fig. 10), the number of bird species was reduced by less than 10% (reductions were of the order of magnitude of stochasticity and thus not clearly identified), whereas in conventional logging species number decreased by 75%. The length of time necessary for the regeneration of the bird community at the level of an unlogged forest also differed widely (conventional: 300 y; reduced-impact: < 100 y).

Results of all 60 logging scenarios were shown in detail in Fig. 11 (absolute values) and Table 4 (species diversity relative to primary forest values). Without logging (logging intensity $L_I = 0$) the simulations showed the dynamics in a primary forest and about 37 bird species were established. For low logging intensities ($L_I = 25\%$) and the use of conventional methods, the species number decreased to 25% (cycle length $L_L = 0$ y) of the numbers observed in primary forests. By applying longer logging cycles ($L_L = 80–100$ y) the losses could be minimised. However, for conventional logging with high intensities and
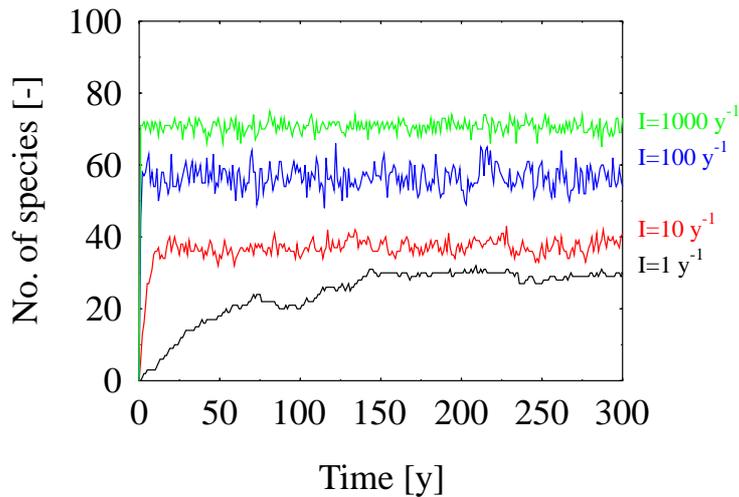
Fig. 8: The number of established species as a function of the size of the simulated area. Averages (± 1 SD) of five simulations of primary forest for 300 years were plotted. Two theoretical models were tested on the simulated data. $S = cA^z$, where $c = 0.81, z = 0.41, r^2 = 95\%$; $S = cA^z e^{kA}$, where $c = 0.15, z = 0.65, k = -3.71 \cdot 10^{-05}, r^2 = 99\%$. Note the logarithmic scales of both axes.

short cycles ($L_I = 75$–100%, $L_L \leq 40$ y) the established species ranged between 23–39% of primary forest values. Here, the influence of logging cycles was only minor. Similar dependencies of species richness on logging intensity and cycle length were observed for the reduced-impact logging scenarios, but species loss was always lower than in the conventional case. For example, in the worst case ($L_I = 100\%$ and $L_L = 0$ y) the number of established species increased from 23% to 42% (of species richness in primary forests) if the logging method was changed.

If the same scenarios were performed in a model version without competition process, the relative decrease in species number stayed the same.

4   Discussion

In ecosystems it is important to understand the interacting processes between fauna and flora. Fruits and seeds are important food sources for herbivores, and many plant species are zoochorous (Estrada and Fleming, 1986). Thus, strong disturbances of the animal communities have severe impacts on plant recruitment (da Silva and Tabarelli, 2000). Future studies must take such feedback processes between disturbances and regeneration into account.

For this study we used a Markovian forest growth model to describe habitat dynamics based on the results of a complex forest simulator. We restricted the habitat request to the age and the type of the forest stand. This restriction seems to be reasonable as in a recent study in temperate forests stand age and maximum canopy height were found
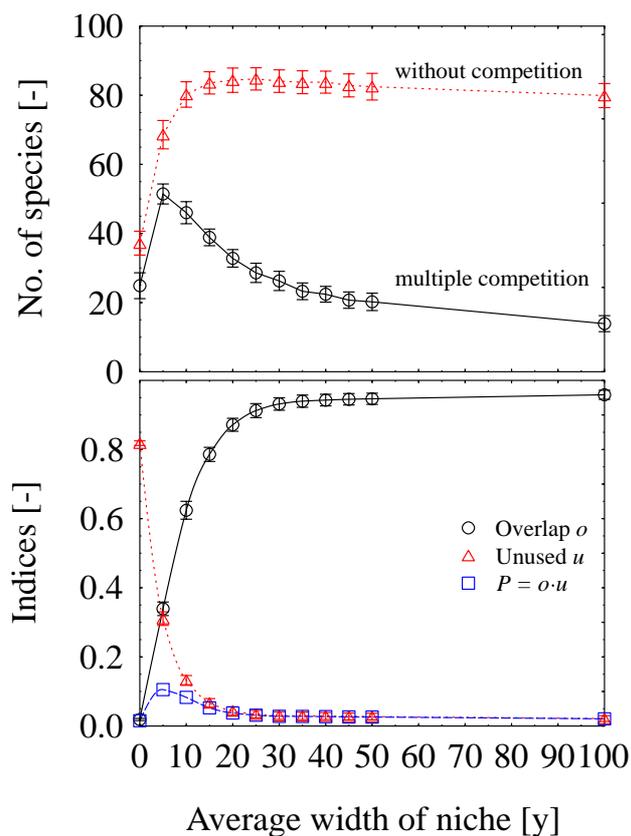
Fig. 9: Sensitivity analysis of the average width of niche for the age of the habitat a and its effect on the (top) species richness (comparing scenarios with multiple and without competition among different species) and (bottom) its effect on overlap and unused areas in the parameter space of the habitat age. Five simulations over 300 years with different initialisation of a random number generator were performed. The results were averaged over the last 50 years.

most important in determine the species-specific habitat requirements for birds (Kirk and Hobson, 2001). For further analyses it might be useful to couple the BIoDIv model directly to the complex forest simulator. By doing so, the habitat request of the bird species could be modelled in more detail. Other structural characteristics of the forest could be used to define the niche space such as present tree species or foliage height of trees. MacArthur and MacArthur (1961) showed that the index of foliage-height diversity is a good predictor for the diversity of bird species in a variety of habitats. Other studies used canopy height and stem-diameter distribution as indices, and showed that they were related to the foliage-height index (Aber et al., 1979, Smith and Urban, 1988). This might be valueable as bird inventories in Borneo show species–specific foraging heights (Lambert, 1992)

Using two model versions with and without competition processes increased our understanding of model behaviour (Fig 9). Thus, without any competition processes individuals
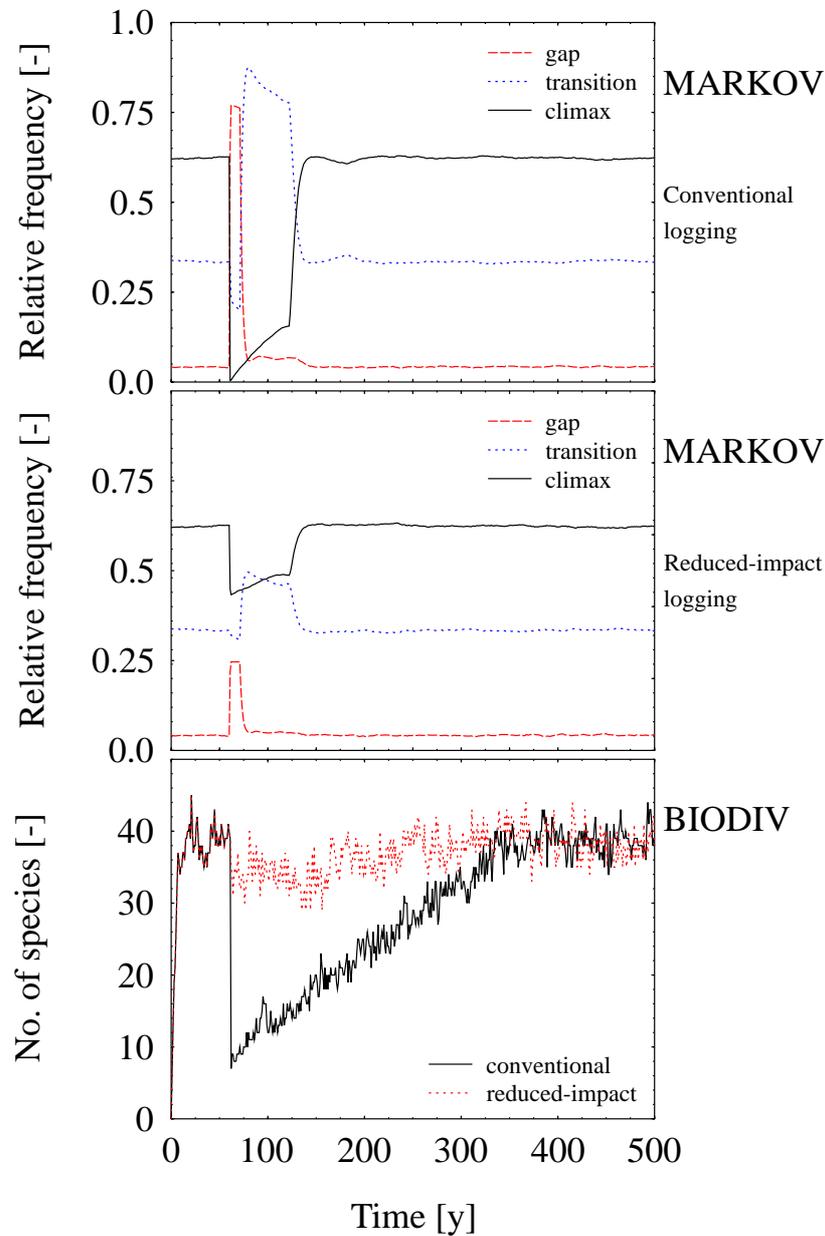
Fig. 10: Comparison of two different logging events. Conventional logging with high logging intensity ($L_I = 100\%$). Reduced-impact logging with moderate logging intensity ($L_I = 30\%$). Top, middle: Time series of the distribution of different habitat types (gap, transition, climax) in the simulations of the Markov model. Bottom: Times series of the number of species calculated by BioDiv based on the above scenarios.

Table 3: ANOVA on main and interactive effects of length of logging cycle, logging method and logging intensity on bird species richness. SS: Sum of squares, df: degrees of freedom, MS: mean of squares.

Effects	SS	df	MS	F ratio	P
Cycle	2817	5	563	44.93	< 0.001
Method	966	1	966	77.04	< 0.001
Intensity	9205	4	2301	183.52	< 0.001
Cycle × method	26.11	5	5.22	0.42	< 0.001
Cycle × intensity	1010.50	20	50.52	4.03	< 0.001
Method × intensity	264.38	4	66.09	5.27	< 0.001
Cycle × method × intensity	13.87	20	0.69	0.06	> 0.5
Error	1504.73	120	12.54		

of various bird species were using the same resources without restrictions. The competition procees can be understood as a limitation of resource availability. Therefore, the numbers of individuals increased sharply in the non-competing version, also allowing a higher number of species to become established. We believe reality to be somewhere in between. A more detailed description of the vegetation structure and thus a more complex habitat definition would enable the model to simulate various different habitats in the same patch and thus allow the coexistence of more species on the same area.

We believe the advantages of our approach lie in the analysis of the qualitative differences between various scenarios and the possibility to analyse population dynamics. Models which simulated potential habitats, habitat quality or which modelled only vegetation dynamics (Smith et al., 1981b; Pausas et al., 1997) could not resolve the dynamics of species richness. One result of our study was that even within the fixed habitat distribution of a primary forest, the population dynamics of individual bird species still fluctuated strongly and the species composition changed over time (Fig. 6).

We would like to highlight the generality of our approach which is applicable not only for avifauna but also for other animal species. There exists a huge body of literature on habitat disturbances and tropical rain forest mammals (cf. Cuarón, 2000). However, when considering non-airborne species, a spatially-explicit formulation of the landscape matrix is essential. In particular, the immigration process will need to be rebuilt in more detail.

This immigration process is also important if impacts of logging in fragmented forests on species diversity are analysed (Ney-Nifle and Mangel, 1999, 2000) as forest fragmentation is reducing the immigration rates. Yet even without logging the fragmentation process leads to high losses of animal species (Lovejoy and Bierregaard, 1990, Turner, 1996, Zuidema et al., 1996, Didham et al., 1998). In Bukit Timah (Singapur), a forest

Table 4: Logging scenario: Effects of tree logging in the vegetation model on the numbers of established bird species. Species numbers are shown as fraction of established species number n in a primary forest ($n = 37$). The two logging methods (CON: conventional, RIL: reduced-impact) differed in damage to the residual stand and in the minimum age of logged patches.

Lenght of logging cycle [y]	Logging method	Logging intensity [%]				
		0^a	25	50	75	100
0	RIL	101	42	42	42	42
	CON	100	25	24	24	23
20	RIL	100	64	53	48	48
	CON	101	47	34	29	28
40	RIL	100	76	62	55	54
	CON	100	63	45	38	35
60	RIL	100	84	69	60	61
	CON	99	74	54	44	42
80	RIL	100	88	74	66	65
	CON	100	79	61	50	48
100	RIL	100	91	80	72	71
	CON	100	86	69	57	55

[a]Values differ from 100% due to stochasticity.

fragment of 71 ha which was separated from larger forest areas a century ago, the number of mammal and bird species has been halved (Corlett, 1988, Turner and Corlett, 1996).

It is well known that intensity and frequency are important parameters of disturbances determining their impacts (Connell, 1978, Huston, 1979, Turner et al., 1993, Hunter-Jr., 1999). Our model led to high loss of species at all logging intensities. These losses could be reduced mainly by reducing logging intensity. A reduction of the logging damage or of the frequency of logging by prolonging the logging cycle benefited species richness but could not compensate for losses caused by high logging intensities.

The effect of logging on bird species diversity was investigated in various field studies. Johns (1985, 1992, 1997) showed that in a lightly logged tropical rain forest, the losses of bird and mammal species were rather small. The species number reached its original level ten years after the disturbance. Selective logging had no effect on birds in a rain forest in Belize (Whitman et al., 1998). However, this study was undertaken in a forest with a high percentage of natural occuring gaps and very small logging intensities (extraction of $\leq 2\mathrm{m}^3$ ha^{-1}). In other studies in Indonesia and French Guiana the bird species diversity was significant lower in logged forests (Thiollay, 1992; Marsden, 1998). In a secondary
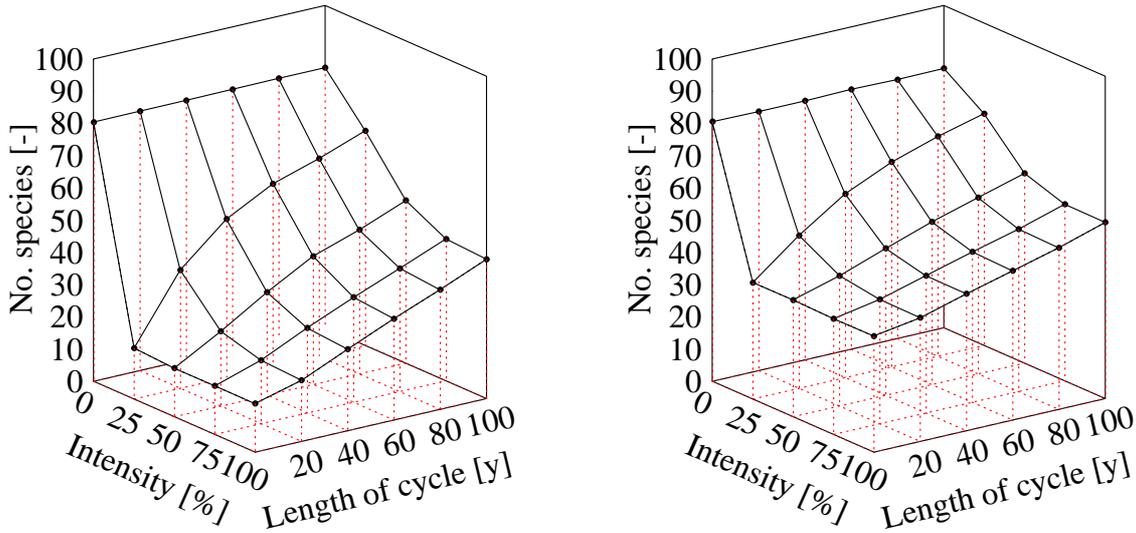
Fig. 11: Logging scenario: Effects of tree logging in the vegetation model on the numbers of established bird species. The two logging methods (left: conventional, right: reduced-impact) differed in damage to the residual stand and in the minimum age of logged patches.

succession in India (Raman et al., 1998) bird species diversity increased throughout the whole succession period. Nevertheless, it must be pointed out that such fast regeneration is only possible if a larger area of undisturbed forest is situated in the neighbourhood and acts as a species pool for immigration.

The number of species found in field survey depend on location, sampling area and technique. They range between 100–500 bird species in various studies (Johns, 1985, 1992, 1997; Thiollay, 1992; Marsden, 1998; Raman et al., 1998; Whitman et al., 1998). If the species pool was increased in our model the changes of bird species as function of disturbances stay the same.

We do not compare our results directly with field studies for various reasons. The species numbers of a birds survey might differ widely from those existing in the forest depending on technique (Whitman et al., 1997). We think our integrated approach is only valid to show trends and tendencies. For more quantitative results the parametrisation need to be revised for a specific location. Furthermore, for this first approach our parameter values were kept to those chosen by Seagle and Shugart (1985). In that way our analysis is compareable with their results. Some of the parameters found in Table 2 are only difficult to compare with field data. For example, the immigration rate is more a technical parameter for the attemps to establish new species. It is not compareable with immigration rates measured in the field. From our sensitivity analysis we know that the results are rather independent on the values of r (reproduction rate) and U (resource use efficiency) and to a wide respect from S (territory size). Thus, their exact knowledge is of minor importance for the simulation results and furthermore U can not be gained straightforward from field inventories. The parameters which determine the habitat re-

quirements (a, h) reflect a rather simple definition of habitats due to the used vegetation model. However, in a revision single tree species might be modelled and thus the habitat definition might be more special and validated with field data including an analysis of the statistical distribtion of parameters.

Although diversity is one main topic in ecological research, comprehensive investigations on this topic are rather limited. Investigations for tropical rain forests focus mainly on trees or selected animal species due to the complexity of these ecosystems. Field investigations can normally only reveal the short-term dynamics of species diversity. To analyse long-term dynamics, the use of simulation models might be a promising approach. Metapopulation models have been used successfully to analyse the survival of individual populations (e.g. Hanski and Ovaskainen, 2000). However, ecosystem management and conservation need more general results. It would be important to predict and analyse for example the impact of habitat destruction on whole animal groups. The traditional way of modelling complex ecosystems by adding up models for single populations is in many cases not applicable because the informations gained in field studies are not sufficient to parametrise such complex models. We also need models which describe the species diversity on an aggregated level.

In this paper we have presented a model which is a useful tool for analysing the long-term dynamics of species diversity. Since this aggregated approach has only been used in a few studies further elaboration and application are desirable.

Acknowledgements

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