

## A FOREST SIMULATION MODEL FOR PREDICTING EUCALYPT DYNAMICS AND HABITAT QUALITY FOR ARBOREAL MARSUPIALS

JULI G. PAUSAS,<sup>1,3</sup> MIKE P. AUSTIN,<sup>1</sup> AND IAN R. NOBLE<sup>2</sup>

<sup>1</sup>CSIRO Division of Wildlife and Ecology, PO Box 84, Lyneham, A.C.T. 2602, Australia

<sup>2</sup>Research Schools of Biological Sciences, The Australian National University, Canberra, A.C.T. 0200, Australia

**Abstract.** A forest simulation model (called EDEN) of eucalypt dynamics in south-eastern Australia is presented to predict habitat quality for arboreal marsupials. The model is presented as a tool for testing alternative hypotheses of forest management in the study area. EDEN uses a forest gap simulation (JABOWA/FORET type) model as a pattern generator of habitat in different landscape positions and under different harvesting regimes and predicts the habitat quality of this habitat for arboreal marsupials.

Application of the model is illustrated by simulating four environmental scenarios (gullies and ridges, at low and at high soil nutrient levels) and three harvesting regimes for each environmental scenario (no harvesting, low-intensity harvesting, and high-intensity harvesting). The changes in tree species composition and diversity and the changes in habitat quality for the arboreal marsupials are presented for the 12 scenarios. The predicted vegetation composition is different in the different environmental scenarios and agrees with empirical studies, suggesting that EDEN is a useful pattern generator in the study area. The simulation results suggest that there may be a harvesting level for which the habitat quality is not significantly reduced, but this will depend on the landscape position. The decline in habitat quality with increasing harvesting is stronger on ridges than in gullies.

**Key words:** arboreal marsupials; diversity; Eucalyptus; forest dynamics; forest gap model; forest management; habitat quality; habitat suitability; harvesting; simulation.

### INTRODUCTION

In addition to creating natural reserves (Pressey et al. 1993), effective conservation of biological diversity requires management of biodiversity in nonreserved areas (Franklin 1989, Wilcove 1989, Hunter 1990, Hansen et al. 1991, 1993). It is difficult to examine the long-term ecological consequences of management actions, or to compare the impacts of different management alternatives, because of the lack of suitable tools and scientific information to test hypotheses. We present a model that can be used as a tool for this purpose for southeast Australian eucalypt forests (mixed-species forests). We use this model to examine the impact of forest management techniques on the tree species composition and on the guild of arboreal marsupials (possums and gliders).

Arboreal marsupials are relatively homogeneous, both taxonomically and functionally, and their occurrence is strongly dependent on the availability of food (leaves, gum, pollen, nectar, and arthropods) and the availability of nest sites (natural cavities in trees). Braithwaite et al. (1983, 1984) and Pausas et al. (1995) found the abundance and occurrence of arboreal mar-

supials to be positively correlated to forest species composition, structure, and site characteristics (e.g., topography, soil nutrient level), and especially to the quality and availability of foliage nutrient. Bark type and proneness to hollow formation are also important in predicting the occurrence of arboreal marsupials (e.g., Lindenmayer et al. 1991, 1993, Pausas et al. 1995). The size class structure of the forest is a critical factor in habitat suitability for arboreal marsupials, because it determines the availability of nest sites (Smith and Lindenmayer 1988, 1992, Lindenmayer et al. 1991, Pausas et al. 1995).

A dynamic habitat model (Shugart and Urban 1986, Smith 1986) is needed to study the habitat of arboreal marsupials and to predict the consequences of disturbance and management alternatives. A dynamic habitat model has two components: (a) the relationship between habitat and the animal population, which is usually studied by a nondynamic statistical approach (e.g., Pausas et al. 1995); and (b) the dynamics of that habitat (pattern generator). Several types of vegetation dynamic models have been used as a pattern generator in dynamic habitat models. We can simplify them into three categories.

1) *Large-scale, patch type dynamics* in which tree demography is not modelled explicitly; instead, changes in forest structure are simply indexed as time elapsed since disturbance. These models are often linked with Geographical Information Systems. This

Manuscript received 2 December 1996; accepted 23 December 1996; final version received 22 January 1997.

<sup>3</sup>Present address: Centro de Estudios Ambientales del Mediterraneo (CEAM), Carrer 4 Sector Oest, Parc Tecnològic, 46980 Paterna, València, Spain.

approach has been used to study fauna richness in landscape islands of different size (Seagle and Shugart 1985), North American avian communities (Hansen et al. 1992, Gustafson and Crow 1994), and the relationship between animal population dynamics (Bachman's Sparrow, *Aimophila aestivalis*) and economic yield from timber harvesting in loblolly pine forests (Liu et al. 1994). Possingham et al. (1994) studied the risk of extinction of the greater glider (*Petauroides volans*) in the montane ash forests of Victoria by linking the population dynamics of these marsupials with a coarse, large-scale vegetation patch model.

2) *Forest stand models*, also called forest growth models (e.g., forest yield models). These models are at a finer scale (forest level) than patch dynamic models, and are based on statistical equations or Markov processes. Examples include the habitat quality models for birds and cervids in North America (Benson and Laudenslayer 1986, Raedeke and Lehmkuhl 1986).

3) *Gap replacement models* (also called individual tree-based gap models or community dynamic models; Shugart 1984). These are mechanistic (process-based), and simulate the establishment, growth, and mortality of every tree on a small plot. An array of these models can simulate different parts of the landscape. Detailed descriptions of these models are given by Shugart (1984), Shugart et al. (1992), and Urban and Shugart (1992). Few examples of applications of this type of modelling to habitat quality have been published (Smith 1986, Urban and Smith 1989). Recently, Kruse and Porter (1994) and Holt et al. (1995) suggested the use of this type of model for predicting structural characteristics of wildlife habitat.

These three approaches differ in their scale of resolution: landscape, forest stand, and forest gap level. The first and second types of dynamic models are mainly for single-species stands, or where differences between tree species within the patch are not taken into account. There is a considerable body of information suggesting that, at fine scale (forest level), individual-based gap models are the best way to simulate mixed-aged, mixed-species forest dynamics (Shugart 1984, Dale et al. 1985, Huston and Smith 1987, Huston et al. 1988, Shugart et al. 1992, Urban and Shugart 1992), although Noble et al. (1988) have cautioned users about overinterpretation of the predictions from these models. Hansen et al. (1993) provide a good example of estimating habitat suitability for birds by linking a gap model and a large-scale patch dynamic model, thus simulating forest harvesting regimes in a gridded landscape.

Individual-based forest gap simulation models provide a powerful tool to investigate eucalypt dynamics and the quality of habitat for arboreal marsupials, because of the complexity of mixed-species, mixed-aged eucalypt forests and the strong dependence of arboreal marsupials on forest structure and tree species composition. Based on previous work on habitat require-

ments of arboreal marsupials (Pausas et al. 1995) and the dynamics of eucalypt forests (Shugart and Noble 1981), we developed a forest model (EDEN) that simulates forest dynamics and predicts habitat quality for arboreal marsupials of southeastern New South Wales (NSW), Australia. EDEN uses a forest gap simulator (JABOWA/FORST type) as a pattern generator of habitat in different landscape positions, and predicts the quality of this habitat (following Pausas et al. 1995) for arboreal marsupials. The JABOWA/FORST type of gap model makes no distinction between the fundamental and realized niche of tree species when estimating the growth response to temperature (Austin 1992, Malanson et al. 1992, Pacala and Hurtt 1993). This introduces a circularity into modelling the observed distribution of species. However, gap models are recognized as being successful at reproducing the landscape pattern of forest composition, and may therefore be used to investigate dynamics of forests and of faunal habitat quality, provided that the general species composition remains unchanged.

Timber harvesting is the major human-induced disturbance in the study area. It affects both the composition and structure of forest communities, and thus has important consequences for forest-dependent animals such as arboreal marsupials. We simulate different harvesting scenarios in different landscape positions in order to investigate the effect of timber harvest on habitat quality for arboreal marsupials.

We use habitat quality (HQ, also called habitat suitability) for arboreal marsupials as a measure of the potential occurrence of arboreal marsupials, based on forest and site attributes (Pausas et al. 1995). The actual occurrence of arboreal marsupials will also depend on other factors such as animal mobility, predation, and the habitat quality of the surrounding forests. Spatial arrangement of forest patches and the mobility of arboreal marsupials are not considered in the present work.

The aims of this paper are (1) to test the overall performance of the EDEN model; (2) to predict the response of tree species composition to harvesting; and (3) to predict the response to harvesting of the habitat quality for arboreal marsupials. Objectives (2) and (3) were investigated by means of simulation in different landscape positions.

## METHODS

### *The model*

All simulations were made using the EDEN model. EDEN is an individual-based gap model (JABOWA type model; Botkin et al. 1972, Shugart 1984) of eucalypt forest dynamics, which was developed on the basis of BRIND (Shugart and Noble 1981). The main features distinguishing EDEN from its predecessor are that EDEN simulates forest dynamics in different topographic positions and at different soil fertility levels,

and predicts habitat quality for arboreal marsupials. EDEN was developed on the basis of data from the Eden area (south coast of NSW, Australia), and includes 43 tree (and large shrub) species. Tree growth equations and estimation of the growth rates were as in BRIND and most JABOWA type models (see details in Botkin et al. 1972, Shugart 1984). Large shrubs were simulated using the same algorithms as for trees. Maximum size and maximum age of the tree species, which are used to estimate growth rate parameters, were obtained from Boland et al. (1984) and from the CSIRO (Commonwealth Scientific and Industrial Research Organization) forest database. We will briefly describe the new features of the EDEN model.

*Nutrient and drought response.*—Indices of tolerance to low nutrient levels and tolerance to drought were developed for each species, based on the statistical models developed by M. P. Austin and collaborators relating the probability of occurrence of tree species to environmental parameters (Austin et al. 1990b, 1994; M. J. Gaywood, C. R. Margules, M. P. Austin, A. O. Nicholls, and J. A. Meyers, unpublished data), and based on nutrient concentrations in leaves (data from Pausas et al. 1995).

The drought tolerance index (DroTol) ranges from 1 (low) to 5 (high), and takes into account the influence of topographic position and aspect. For example, a drought tolerance index of 5 represents a species that has a maximum frequency of occurrence on exposed topographic positions (e.g., ridges), whereas an index of 1 represents a species with a maximum in protected topographic positions (e.g., gullies). The index of tolerance to low nutrients (NutrTol) ranges from 1 (low) to 3 (high). Species that have a maximum frequency of occurrence at low soil nutrient levels and have low foliage nutrient concentration were assigned a high tolerance (NutrTol = 3), and species with maximum occurrence at high soil nutrient levels and high foliage nutrients were assigned a low tolerance (NutrTol = 1). Species for which soil nutrients were not significant in predicting their occurrence, and species that showed apparent inconsistencies between soil nutrient response and foliage nutrient concentration, were assigned to intermediate tolerance (NutrTol = 2).

The optimal growth of each species is reduced by using the growth modifier function, depending on the nutrient level and topographic position of the simulated site and the nutrient and drought tolerance index of the species. These growth modifier factors range from 0 to 1 and are calculated by the following functions:

$$\text{NutrGMF} = \begin{cases} 2.15 \times \exp(-3.04/\text{Nutr}) & \text{if NutrTol} = 1 \\ 1.25 \times \exp(-0.92/\text{Nutr}) & \text{if NutrTol} = 2 \\ 1 & \text{if NutrTol} = 3 \end{cases}$$

and

$$\text{DroGMF} = \min(1, 0.2 \times (\text{DroTol} + 5 - \text{Dro}))$$

where NutrGMF and DroGMF are the nutrient and drought growth modifier factors, respectively, Nutr is the site nutrient level index (from 1 to 4 in the Eden area), and Dro is the site drought index (1, gully; 2, flat; 3, lower slope; 4, south slope; 5, ridge or north slope). These equations imply that on sites with "better" conditions (high nutrients and high moisture), all species would grow optimally (DroGMF = 1, NutrGMF = 1), and that the displacement of some species is due to other factors, such as competitive ability and temperature response.

*Habitat quality for arboreal marsupials.*—The quality of habitat (HQ) for the arboreal marsupials is determined by availability of food (leaves, gum, pollen, and arthropods) and nest sites (holes in trees). It is measured as the probability of occurrence of arboreal marsupials, based on forest and site attributes, following the statistical model developed by Pausas et al. (1995) for the Eden region:

$$\text{HQ} = f(\text{FNI}, \text{BarkI}, \text{HoleI}, \text{PTN}, \text{Topo}, \text{SNutr})$$

where HQ is the probability of occurrence of arboreal marsupials, FNI is the foliage nutrients index, BarkI is the amount of decorticing bark (as a measure of availability of arthropods), HoleI is an index of the susceptibility of trees to defects, PTN is the number of potential nesting trees (>60 cm in diameter), Topo is the topographic position, and SNutr is the soil nutrient level. FNI, BarkI and HoleI are computed following Pausas et al. (1995), and their values depend on the tree species composition. The main variable determining the occurrence of arboreal marsupials was the foliage nutrients index. HQ was positively related to FNI, BarkI, HoleI, and PNT. HQ was also higher at high soil nutrient levels than at low soil nutrient levels, and higher in gullies and on flat sites than on slopes and ridges (for more details, see Pausas et al. 1995).

*Treefall rate.*—The number of dead trees is an important component of HQ. Most gap models predict only the death of individual trees, but EDEN includes the probability that dead trees will fall, based on Lindenmayer et al. (1990a), who derived a transition probability matrix of treefall in eucalypt forests of Victoria, Australia. We reanalyzed these data to estimate the probability of a treefall assuming a Markov process for a period of 100 yr. From these values, we obtained the following function of the annual probability of a treefall:

$$y = \exp(-15.18/t)$$

where  $t$  is the time since death. This results in an average of 10 yr between the death of a tree and its fall

*Fire response.*—Most eucalypts in the study area resprout after fire. Resprouting in the EDEN model is based on a model from Strasser et al. (1996) that predicts the probability of trees surviving fire by simu-

lating the production of epicormic buds or lignotuberos sprouts, as well as the amount of recovery. According to this model, after a fire trees may: (1) be killed outright; (2) have their aboveground parts killed but resprout from basal lignotubers; or (3) continue to grow from undamaged and epicormic aboveground buds. Thus, the EDEN model includes not only random mortality and mortality due to stress (reduction of growth due to competition, etc.), as most forest gap models do, but also mortality from fire and sprouting failure.

**Temperature.**—The temperature response of each tree species is assumed to be parabolic between growing degree days (GDD) limits, as in most forest gap models (see Botkin et al. 1972, Shugart 1984). GDDs were estimated from the mean monthly temperatures for 98 meteorological stations in NSW, using the sine wave method (Allen 1976). From these data, the following function was obtained to estimate GDD from mean annual temperature:

$$\text{GDD} = 153.1T + 7.138T^2$$

( $R^2 = 98.88\%$ ;  $P < 0.0001$ ) where GDD is the growing degree-days (days at degrees Celsius), with a baseline of 4.44°C, and  $T$  is the mean annual temperature (in degrees Celsius).

We parameterized 43 species of trees and large shrubs of the Eden area, based on the temperature limits (transformed to GDD) from a CSIRO database. The EDEN model has many more species and a much greater overlap between species for the temperature range than do other forest gap models.

**Harvesting.**—EDEN allows the simulation of logging of a given proportion of trees, of a given minimum diameter, and at a given logging interval.

**Shade tolerance.**—The original BRIND model treated all species as shade tolerant, but two shade-tolerant classes were added to the EDEN model. In EDEN, rain forest species are treated as tolerant, whereas eucalypt species are treated as intolerant or intermediate, depending on the species' response to light in the statistical models developed by M. P. Austin and collaborators (Austin et al. 1990b, 1994; M. J. Gaywood, C. R. Margules, M. P. Austin, A. O. Nicholls, and J. A. Meyers, unpublished data). The response function for each shade-tolerant class was the same as in most of the JABOWA type models (equations in Botkin et al. 1972 and Shugart 1984).

**Climatic variability.**—The interannual climatic variability was increased from the original BRIND model, on the basis of data from 98 meteorological stations with a mean of 20 years of observations for each station. GDD was computed for each station and each year, and the mean of the standard deviations of all stations was 230 degree-days. There was no clear relationship between the mean and the standard deviation of GDD in the study area ( $r = -0.09$ ). Therefore, the climatic variability of a given site is simulated assuming a nor-

mal distribution around the mean degree-days for this site, with a standard deviation of 230 degree-days.

### Scenarios

First, four environmentally based scenarios were run for 1000 yr, starting from bare soil, to ensure that the models were approximately in equilibrium before we investigated the simulated treatments. The scenarios were chosen for environmentally contrasting conditions of topography and soil nutrients at an altitude of 600 m, which is midaltitude for the study region. These scenarios were (mnemonic names in parentheses): ridges under very low soil nutrient level (RL) and under high soil nutrients level (RH), and gullies under very low soil nutrients (GL) and under high soil nutrients level (GH). The annual probability of fire was set to 0.025 for ridges and 0.012 for gullies.

Three harvesting scenarios were run for each environmentally based scenario, making 12 scenarios. These scenarios were applied from year 1000 until year 2000. The harvesting scenarios were: no harvesting (GH0, GL0, RH0, and RL0); low-intensity harvesting (GH1, GL1, RH1, and RL1); and high-intensity harvesting (GH2, GL2, RH2, and RL2). Low-intensity harvesting was simulated as harvesting 80% of the trees with dbh > 50 cm every 100 yr. High-intensity harvesting was simulated as harvesting 90% of the trees with dbh > 20 cm every 40 yr. If, in a particular harvesting year, there were no trees of the required size, no harvesting was done until the next scheduled harvesting date. Low- and high-intensity harvesting scenarios were meant to mimic the two main harvesting regimes carried out in the study area, i.e., sawlog harvesting and woodchipping, respectively. The possible damage to trees during the harvesting was not taken into account.

All scenarios were run 20 times (i.e., 20 forest patches) with different seeds for the random number generator, and the results were averaged. For all scenarios, the initial number of species was 43 (i.e., the main species found in the study area), and the model started with a bare plot and a random seeding of all species. For each scenario, Shannon-Weiner's diversity index ( $H' = -\sum p_i \ln p_i$ ;  $p$  = proportion of total biomass) and Pielou's evenness index ( $J' = H'/H'_{\max}$ ) were computed (Pielou 1966, Margalef 1980, Magurran 1988).

## RESULTS

### Vegetation

The average predicted species composition in 20 simulated patches in each of the environmentally based scenarios (RH, RL, GH, GL) is shown in Fig. 1. Comparison with field data will be discussed later.

At 600 m elevation in gullies with high soil nutrients (GH; Fig. 1a), the predicted vegetation was dominated by *Eucalyptus fastigata* (65% of total plot biomass), followed by *E. obliqua* (17%) and *E. cypellocarpa*

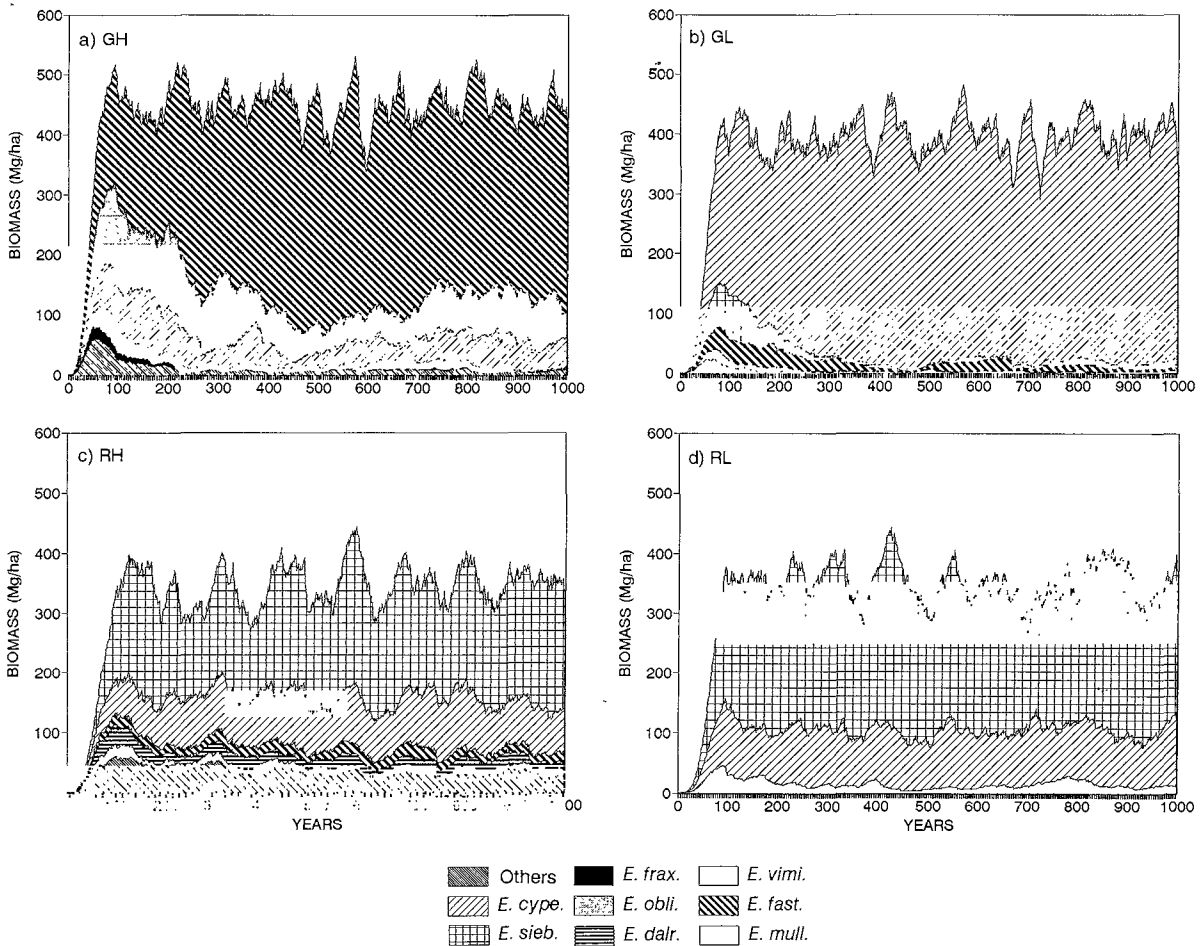


FIG. 1. Predicted biomass for different tree species in the four environmentally based scenarios: (a) gullies at high soil nutrient levels (GH); (b) gullies at very low soil nutrient levels (GL); (c) ridges at high soil nutrient levels (RH); and (d) ridges at very low soil nutrient levels (RL). Full species name are: *Eucalyptus cypellocarpa*, *E. dalrympleana*, *E. fastigata*, *E. fraxinoides*, *E. muelleriana*, *E. obliqua*, *E. sieberi*, and *E. viminalis*.

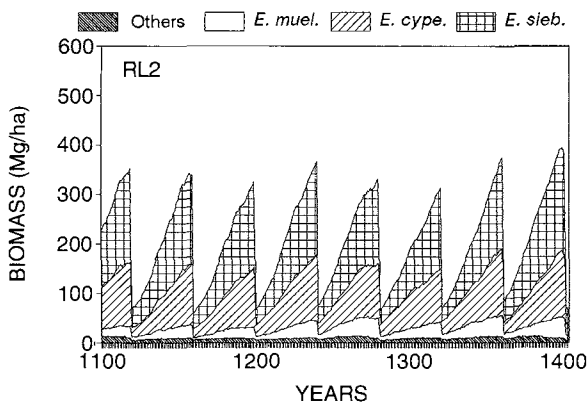


FIG. 2. Predicted biomass for different tree species in a high-intensity harvesting scenario on ridges at low soil nutrient levels (RL2). See Fig. 1 for full species names.

(10%). In the same topographic position, but under very low soil nutrient levels (GL; Fig. 1b), the predicted vegetation was dominated by *E. cypellocarpa* (90%), with a very low contribution from other tree species (*E. sieberi*, *E. fastigata*, *E. obliqua*, and *E. muelleriana*).

The predicted vegetation on ridges with high soil nutrients (RH; Fig. 1c) was a forest dominated by *E. sieberi* (49% of total plot biomass), with *E. cypellocarpa* second in importance (21%). Other species with less biomass were *E. fastigata*, *E. muelleriana*, and *E. dalrympleana*. At low nutrient levels, the vegetation predicted on ridges (RL; Fig. 1d) was *E. sieberi* (70%), followed by *E. cypellocarpa* (26%) and *E. muelleriana* (4%).

Comparing the predictions of the model in these four scenarios (Fig. 1), we observe that the model predicts higher tree species richness at high nutrient levels, and higher dominance (lower evenness) at low nutrient lev-

TABLE 1. Mean plot biomass and mean tree density in the 12 harvesting scenarios for eucalypt forests in southeastern Australia.

Scenarios†	Harvesting intensity‡		
	0	1	2
<b>GH</b>			
Biomass (Mg/ha)	443.6	426.6	298.9
Density (no. trees/ha)	1309	1550	2442
<b>GL</b>			
Biomass (Mg/ha)	397.7	377.9	257.8
Density (no. trees/ha)	1204	1428	2553
<b>RH</b>			
Biomass (Mg/ha)	364.2	330.0	219.2
Density (no. trees/ha)	2305	2521	3547
<b>RL</b>			
Biomass (Mg/ha)	356.1	346.9	199.6
Density (no. trees/ha)	1670	1769	2353

† G, gullies; R, ridges; H, high soil nutrients; L, very low soil nutrients.

‡ 0, no harvesting; 1, low-intensity harvesting; 2, high-intensity harvesting.

els (see also the nonharvesting scenarios in Figs. 3 and 4). EDEN also predicted different forest structure in different landscape positions (see nonharvesting scenarios in Table 1). It predicted higher biomass in gullies than on ridges, and higher biomass at high soil nutrient levels than at low soil nutrient levels. The tree density was predicted to be lower in high soil nutrient levels than in low nutrient levels, and lower on ridges than in gullies.

Simulated harvesting did not change the dominant tree species, but did change the presence and relative abundance of the minor tree species and the forest structure. Figure 2 shows an example of one of these harvesting scenarios (RL2). Figures 3 and 4 and Table 1 summarize the changes in abundance of tree species and forest structure for the 12 harvesting scenarios. Harvesting increases simulated tree species diversity (Figs. 3 and 4a) and evenness (Figs. 3 and 4b) in the four simulated environmental conditions. It also increases tree density and reduces plot biomass (Table 1). All these changes are particularly clear in high-harvesting scenarios.

To compare the biomass harvested in the different harvesting scenarios, we computed the annual biomass harvested (average rate) from the total biomass harvested during the whole simulated period (Fig. 5). Annual biomass harvested was higher in gullies than on ridges, for both low- and high-intensity harvesting scenarios. The difference between low- and high-intensity scenarios was larger on ridges (4.5 times more biomass in high-intensity harvesting) than in gullies (3.3 and 3.8 times more biomass in high-intensity harvesting, under high and low nutrient status, respectively).

#### Habitat quality

Figure 6 shows the average HQ for arboreal marsupials of 20 simulated vegetation patches under each

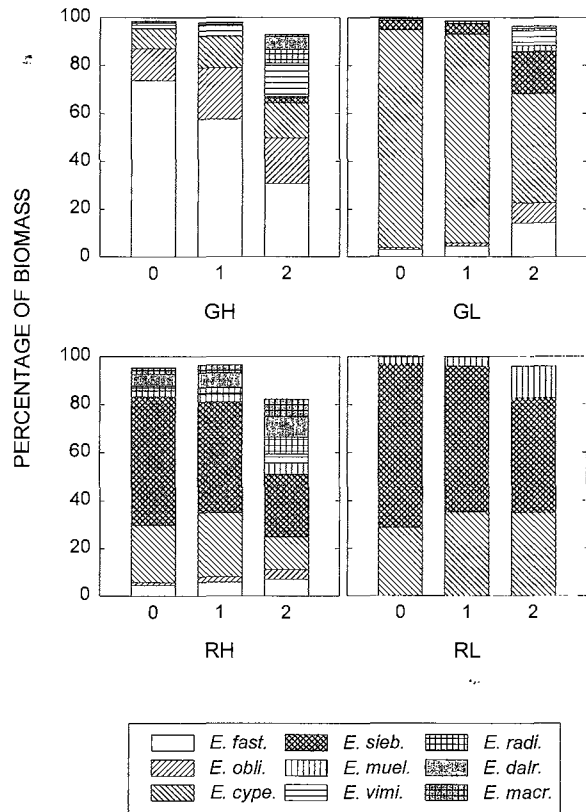


FIG. 3. Summary of the percentage of biomass of the different tree species in the 12 harvesting-based scenarios (average of 1000 years). The species shown are contributing >5% to the total biomass in at least one scenario. Note that some column bars do not reach 100%, because of the presence of other species with a contribution to the total biomass of <5%. Species names and scenario types are as in Fig. 1, with the addition of *Eucalyptus macrorhyncha* and *E. radiata*. Tree harvesting scenarios in the x-axis are 0, nonharvesting; 1, low-intensity harvesting; and 2, high-intensity harvesting.

of the 12 harvesting-based scenarios. For clarity, only 300 years are shown in the figure, starting from 1100 years to avoid the transition period.

Without harvesting, HQ is higher in gullies than on ridges, and higher in high soil nutrient forests than in very low soil nutrient forests. Variations in HQ due to soil nutrients (compare RL0 vs. RH0 and GH0 vs. GL0; Fig. 6) are higher than those due to topography (compare RL0 vs. GL0 and RH0 vs. GH0; Fig. 6). Low-intensity harvesting did not reduce HQ in any of the four simulated environments, whereas high-intensity harvesting greatly reduced HQ for arboreal marsupials.

The decline in HQ with increasing harvesting was stronger on ridges than in gullies (Fig. 6). After intense harvesting, HQ recovered more quickly in gullies than on ridges, and reached levels of HQ similar to non-harvesting scenarios, although for very short periods. On ridges, the recovery was slower and did not reach the non-harvesting level of HQ. This effect can also be observed by averaging the HQ values during the

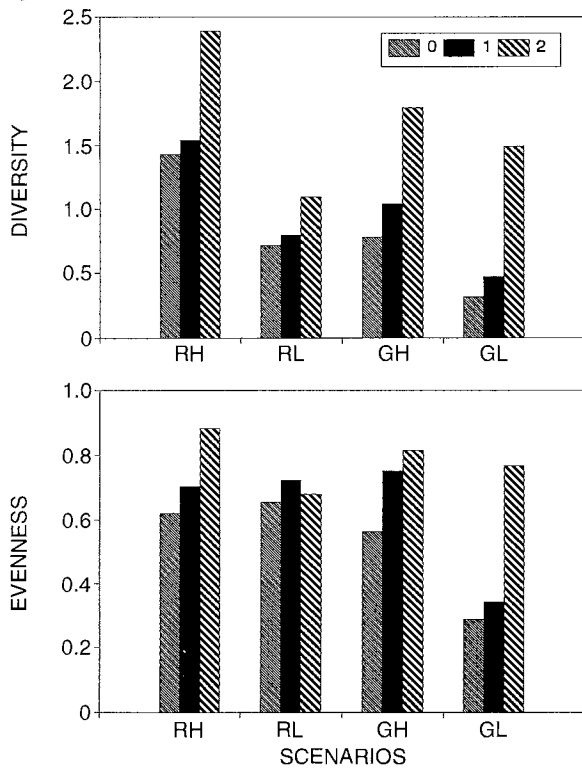


FIG. 4. Average diversity (a) and evenness (b) of tree species for the 12 harvesting scenarios (GH, GL, RH, RL, 0, 1, and 2 are defined as in Figs. 1 and 3).

simulated period (Table 2). On average, high-intensity harvesting with high and low soilnutrients reduces the HQ by 47% and 42% in gullies, and by 80% and 77% on ridges, respectively.

If we express the changes in HQ with time (turnover or variability of HQ) as the standard deviation of the HQ during the 1000 years of harvesting scenarios, we observe (Table 2) that the variability through time is higher in high-nutrient forests than in low-nutrient ones. In the gullies, the variability increases with logging, whereas on ridges it does not.

DISCUSSION

*Vegetation*

The EDEN model predicts different combinations of tree species in different topographic positions and different soil nutrient levels at the same altitude (Fig. 1). This pattern is consistent with empirical work in the study area (Austin 1978, Fanning and Mills 1989, Austin et al. 1990b, 1996). Lambert and Turner (1983) showed a close relationship between eucalypt species composition and soil nutrient status, whereas Keith and Sanders (1990) explained the vegetation in terms of soil moisture and soil fertility. Both studies were undertaken in the Eden region. Austin et al. (1990b) also showed the importance of topography (or incident radiation) in explaining the occurrence of different eu-

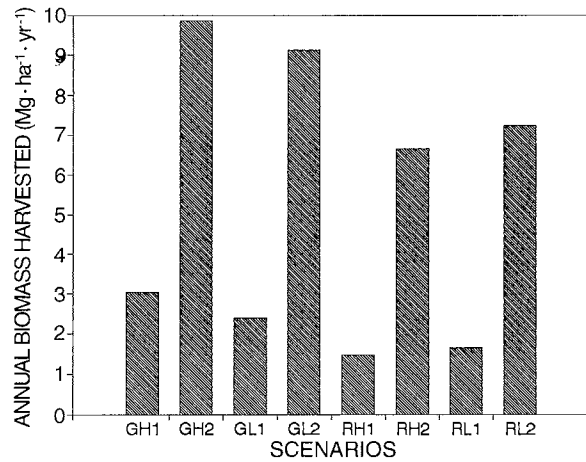


FIG. 5. Average annual biomass harvested for different harvesting scenarios.

calypt species in southeastern New South Wales. Austin et al. (1996) have shown the greatest eucalypt species richness at intermediate to high soil nutrient levels. Results of the EDEN simulations are consistent with this finding. Because the BRIND model did not take into account topography and soil nutrient level, EDEN is a significant improvement over BRIND as a pattern generator in the study area.

EDEN deals with a large number of species over a relatively small range of temperatures. This implies a large environmental overlap between species, reflecting the great diversity of trees in the coastal forests of NSW (Austin et al. 1996). A comparison with other published forest models (Botkin et al. 1972, Shugart and Noble 1981, Shugart 1984, Bonan 1989, Prentice and Helmissaari 1991) has shown that EDEN has the highest number of species and the highest overlap index in relation to temperature (J.G. Pausas et al., unpublished data).

An exact test of the validity of the predicted vegetation would require output from a model run with the disturbance specified to closely approximate the disturbance regime at the Eden area. However, complete characterization of the disturbance (e.g., fire and logging) regime at Eden is not available. In the absence of an exact test, a general evaluation of the model can be obtained by comparing the predicted community compositions with those described in independent studies of similar forests in the Eden area. Unfortunately, there is no standard, well-defined classification system of the coastal forest communities of NSW, so some interpretation of the real and predicted categories is needed. Several approximations have been made, based on numerical classification systems (Austin 1978, Austin et al. 1990a, Keith and Sanders 1990). The Forestry Commission of New South Wales (FCNSW 1986) has also provided a forest classification for the study area. This lack of consensus reflects the complexity of species distribution in the area, and suggests that the spe-

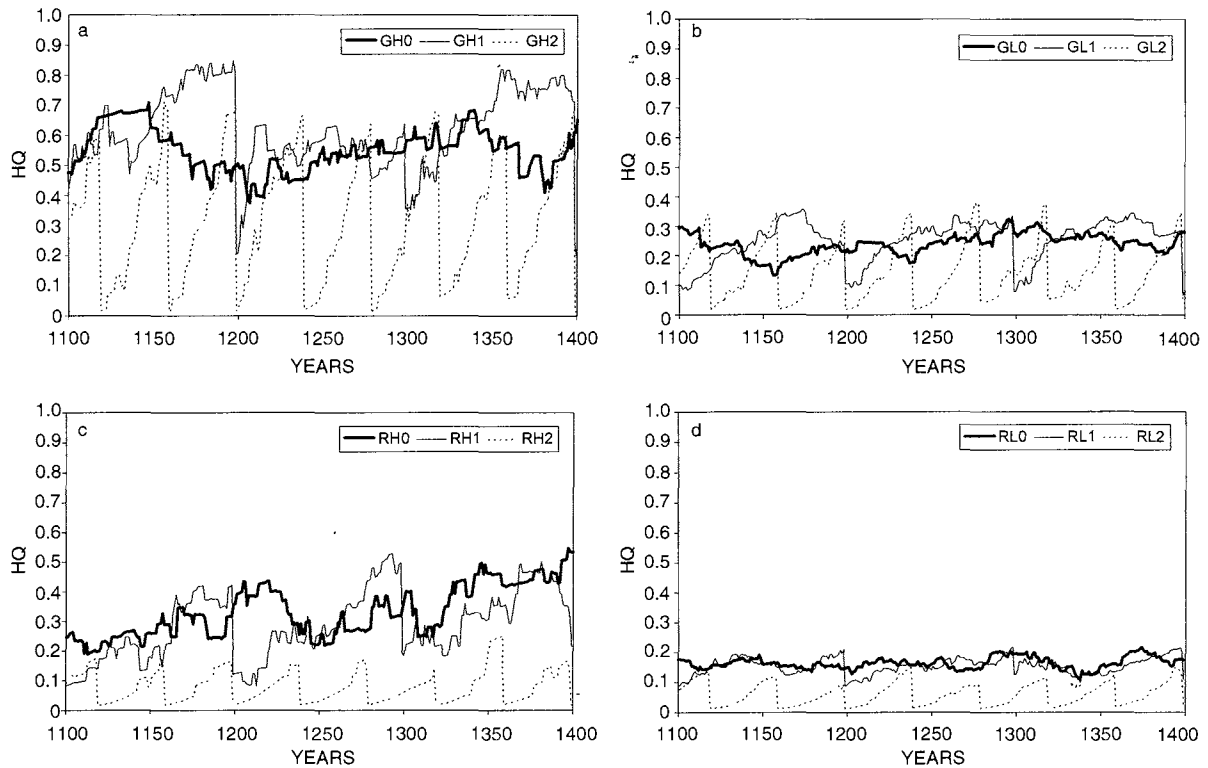


FIG. 6. Predicted habitat quality for arboreal marsupials under three harvesting scenarios (0, no harvesting; 1, low-intensity harvesting; 2, high-intensity harvesting) under four different environmental conditions: (a) gullies under high soil nutrient levels (GH0, GH1, GH2); (b) gullies under very low nutrient levels (GL0, GL1, GL2); (c) ridges under high nutrient levels (RH0, RH1, RH2); and (d) ridges under very low nutrient levels (RL0, RL1, RL2).

cies reflect a continuum with constantly changing composition in relation to environmental gradients (Austin et al. 1990b).

The species mix predicted in gullies is clearly differentiated from that on ridges at both nutrient levels, and can be related to two previously described community types. The community predicted in GH corresponds to Community 5 (*Eucalyptus fastigata/Olearia argophylla*) of Keith and Sanders (1990), and to the *E.*

*fastigata* group (group 33) of Austin et al. (1990a). The vegetation predicted in GL agrees with Community 9I (*E. cypellocarpa/Indigofera australis*) of Keith and Sanders (1990), and *E. cypellocarpa* group (group 9) of Austin et al. (1990a). Keith and Sanders (1990) describe the habitat of their Community 5 as "sheltered plateau slopes and gullies at 600–950 m elevation, generally on moist, fertile, granitic soils," and the habitat of community 9I as "moist, sheltered gullies and slopes

TABLE 2. Mean and standard deviations of habitat quality (HQ)<sup>†</sup> during the years 1000–2000 in the four simulated environments (high and very low soil nutrients on gullies and on ridges) and for nonharvesting and intensive harvesting scenarios. The percentage of reduction of HQ due to harvesting is shown in parentheses.

Habitat	High soil nutrients		Very low soil nutrients	
	No harvest	Intense harvest	No harvest	Intense harvest
<b>Gullies</b>				
Mean ± 1 SD	0.55 ± 0.12	0.29 ± 0.21	0.25 ± 0.04	0.14 ± 0.10
HQ reduction (%)		47		42
<b>Ridges</b>				
Mean ± 1 SD	0.36 ± 0.10	0.07 ± 0.05	0.16 ± 0.03	0.06 ± 0.04
HQ reduction (%)		80		77

<sup>†</sup> Habitat quality, the probability of occurrence of arboreal marsupials is defined as  $HQ = f(FNI, BarkI, HoleI, PTN, Topo, SNutr)$ , where the first three terms are indices of foliage nutrients, decorticing bark, and susceptibility to tree defects, respectively, and the last three terms are the number of potential nesting trees, topographic position, and soil nutrient level, respectively.



with sandy soil, mostly of granitic or alluvial origin at elevations up to 700 m." Both communities correspond in composition and environment to the communities simulated in gullies.

On ridges, for both nutrient levels, the main dominant tree species predicted was *E. sieberi*, and the second was *E. cypellocarpa*. At low nutrient levels, *E. muelleriana* was the only other eucalypt, together with the dominant *E. sieberi* and *E. cypellocarpa*, whereas at high nutrient levels, species characteristic of high soil nutrients appeared. In the classification systems reviewed, the communities on dry sites (with *E. sieberi*) are not clearly segregated for different soil nutrient levels or geologies. The differences between the *E. sieberi* communities in the classification Keith and Sanders (1990) are mainly related to understory species composition. The communities predicted by EDEN for ridges were similar to Community 22 (*E. sieberi*/*E. cypellocarpa*/*Daviesia ulicifolia*) of Keith and Sanders (1990), and to group 8 (*E. sieberi* group) of Austin et al. (1990a), although the presence of *E. globoidea* is also expected, but was not predicted. The EDEN-predicted community for RH was also similar to Community 26II (*E. sieberi*/*E. muelleriana*/*Exocarpus cupressiformis*), and RL was similar to community 24 (*E. sieberi*/*Oxylobium ilicifolium*) of Keith and Sanders (1990).

EDEN reproduces the landscape patterns in the study area reasonably well, and can be used as a pattern generator for this area. However, because it has not established cause-effect relationships between topographic position or nutrient availability and plant performance, EDEN cannot be applied to novel conditions. The main weakness of EDEN is that it does not predict the occurrence of *Eucalyptus globoidea*, although field observations show that this species may occur together with *E. sieberi* on ridges (Fanning and Mills 1989, Keith and Sanders 1990). Research on the ecological traits of this species is needed. Few data on the biology and life history are available for eucalypts, and more research on the autoecological parameters of eucalypts, including noncommercial species, needs to be done.

The values for plot biomass obtained in the simulations (mean values between 356 and 444 Mg/ha) are within the intervals of biomass values estimated from field measurements of basal area (CSIRO database; Austin et al. 1990b) in the study area (mean = 574 Mg/ha,  $n = 692$ ) and in the adjacent region of Batemans Bay (mean = 328 Mg/ha,  $n = 376$ ).

An important shift in the vegetation under simulated harvesting was an increase in tree species diversity and evenness with an increase in harvesting intensity (Figs. 3 and 4). The intermediate disturbance hypothesis of species diversity suggests that the highest levels of diversity are found at some "intermediate" level of disturbance, whereas species diversity decreases at lower and higher disturbance regimes (Connell 1978, Huston 1979). Most experimental and comparative studies sup-

port this hypothesis in a variety of different ecosystems (e.g., Sousa 1979, Fox 1981, Padiak 1993). However, experimental evidence from eucalypt forests is required to test the increase in tree diversity with an increasing harvesting rate. Tree diversity increased with an increase in the harvesting intensity in a long-term experimental cutting study in northeastern Wisconsin (Niese and Strong 1992), and tree diversity also increased after harvesting operations in the coastal forest of Florida (Swindel et al. 1984). Elliott and Swank (1994) reported some experimental evidence of decreasing tree diversity and evenness in the absence of harvesting in the southern Appalachian forests. Increase in harvesting and overstorey heterogeneity has also been associated with an increase in understory plant species diversity in different ecosystems, attributed to the increase of microsite richness (e.g., Woods and Whittaker 1981, Pausas 1994).

Although some theoretical and experimental studies support the finding of increasing diversity with moderate harvesting, some warnings must be given. The EDEN model is not spatially explicit, and it does not include realistic seed dispersion parameters. Instead, new individuals are selected from a pool of all the species in the model, with a bias toward those species with adults present on the simulated plot (Shugart and Noble 1981). Experience with these models has shown that they produce an overly diverse composition in the early stages of succession after a disturbance (Shugart and Noble 1981, Noble et al. 1988). Furthermore, incorporation of seedling dispersion parameters in a spatially explicit, individual-based forest model has caused substantial changes in species abundance (Ribbens et al. 1994).

Fire is an important factor structuring eucalypt ecosystems. In the present work, the probability of wildfire was fixed at different rates, depending on the topography (see *Methods*). The effect of fire on vegetation is not discussed here, but has been addressed in Austin et al. (1997), using the EDEN model. They showed an important change in relative abundance of tree species when they simulated eucalypt dynamics with or without fire. Variations in fire probability also led to variations in the abundance of tree species. The possible interaction between harvesting and fire has not been addressed in the present work, but could be investigated using the EDEN model.

#### *Habitat quality*

The pattern of HQ predicted without harvesting (i.e., higher in gullies than in ridges, and higher under high soil nutrient levels) agrees with data on eucalypt forests. Arboreal marsupials are more abundant in gullies than on ridges in the forests of Victoria and New South Wales (Lunney 1978, Lindenmayer et al. 1990b, Pausas et al. 1995). Lunney (1987) and Kavanagh and Bamkin (1995) reported on the number of arboreal marsupials occupying logged and unlogged forests within our

study area. Both studies found most species of arboreal marsupials to be associated with forests in gullies, and with unlogged sites. Many studies have emphasized the importance of unlogged gullies as refuges for arboreal marsupials and other forest animals, and as wildlife corridors in forest ecosystems (Thomas 1979, Lunney 1987, Recher et al. 1987, Hunter 1990, Kavanagh and Bamkin 1995).

The importance of nutrients in determining the HQ for arboreal marsupials has been recognized (Braithwaite et al. 1983, 1984, Kavanagh and Lambert 1990, Jones et al. 1994, Pausas et al. 1995). Braithwaite et al. (1983, 1984) found that the abundance of arboreal marsupials in the Eden area was correlated with those forests communities having tree species with high concentrations of foliage nutrients. These forests also grew mostly on high-fertility soils derived from Devonian intrusive bedrock. This positive relationship between soil nutrients and foliage nutrients has been reported elsewhere (Lambert and Turner 1983).

The differential reduction of HQ by the different harvesting scenarios reflects the importance of forest structure in predicting HQ. The difference in HQ, when testing different alternative management strategies (i.e., the relative effectiveness), may be more important than the value of HQ itself. Smith and Lindenmayer (1988, 1992) and Lindenmayer et al. (1990b, 1991, 1993) provide extensive evidence of the importance of forest structure for predicting the occurrence and abundance of arboreal marsupials in eastern Victorian forests. The main effects of logging on HQ are the removal of den trees, and variations in the abundance of tree species with different values for arboreal marsupials (Pausas et al. 1995). The simulation results suggest that there may be a harvesting level for which the HQ is not reduced, but this will depend on the landscape position.

The EDEN model predicts the HQ for arboreal marsupials based on forest and site attributes. This value is independent of the surrounding area and the mobility of the animals. After logging, the HQ recovery depends only on forest attributes, and not on the HQ of the surrounding area or possible immigration from this area. It is a question for the manager to know if the HQ obtained in the simulation model can be "filled" by animals. For example, in an isolated forest patch, the HQ (the potential occurrence) may recover after logging, but the arboreal marsupials may not be able to recolonize the patch (actual occurrence) if the next patch of suitable habitat is a long distance away. This needs to be considered when managing highly fragmented forests. Tyndale-Biscoe and Calaby (1975) have shown that several arboreal marsupial species (e.g., greater glider and mountain brushtail possum) do not migrate away from logged areas to adjacent suitable areas. The spatial arrangement of the forest patches is not considered in the current version of EDEN, but this could be the next step for improving the model (Pulliam

et al. 1992, Holt et al. 1995, Turner et al. 1995). The impact of the Powerful Owl (*Ninox strenua*), a predator of arboreal marsupials, on the survival of local populations (Kavanagh 1988) has also been ignored. Habitat quality defines the potential of a plot to support arboreal marsupials, but is only one component of the comprehensive model needed to investigate all aspects of managing animal populations in forestry areas.

Possingham et al. (1994) also provide a tool for testing alternative forest management techniques on the viability of marsupial populations, taking into account the size of the forest patch and life history traits of the marsupial species. However, they do not consider differences between tree species, and cannot deal with the complexity and diversity of the coastal forests of New South Wales. Tree species composition and forest structure have been considered crucial factors in the occurrence of marsupials in these forests.

We used the guild approach for arboreal marsupials because of the lack of specific information, especially for endangered species with low abundance. However, this approach is still useful for management purposes (Chapin et al. 1992, Hansen et al. 1993). More work needs to be done before we can include all individual marsupial species in the EDEN model, but some of the most abundant species can be incorporated in the near future.

The results of predicting habitat quality for arboreal marsupials cannot be extrapolated to other fauna groups. For example, Catling and Burt (1995) found that forest structure is more important than foliage nutrient contents for predicting the abundance of small, ground-dwelling mammals in eucalypt forests, and that the abundance of these mammals was negatively correlated with foliage nutrients. This pattern contrasts with our results for arboreal marsupials.

#### CONCLUSIONS

EDEN can be used to investigate the potential trade-offs between conservation and management in a mixed-species eucalypt forest. The model is useful for investigating alternative hypotheses and comparing the outcome in vegetation and habitat quality for the arboreal marsupials. It can be improved as more detailed data become available. The simulation results suggest that ridges are more susceptible to losing quality of habitat after harvesting than are gullies, and that there may be a level of harvesting that may sustain the quality of habitat for arboreal marsupials. We believe that the approach used here, which links a forest gap dynamic model with a habitat quality model to obtain a dynamic habitat quality model, is a useful way to develop tools for improving decision making processes in forest ecosystems.

#### ACKNOWLEDGMENTS

The present work was partially supported by The Spanish Government (Ministerio de Educación y Ciencia) with a post-doctoral fellowship to the first author. We thank I. Davies for

writing the code for the EDEN model with a very friendly interface, M. D. Doherty for several discussions on eucalypt species, E. M. Cawsey for her work on database management, and L. W. Braithwaite for comments on the biology of the arboreal marsupials and for making his data available. Useful comments on the manuscript were provided by B. H. Walker, A. O. Nicholls, M. D. Doherty, S. J. Cork, and K. Hogan.

## LITERATURE CITED

- Allen, J. C. 1976. A modified sine wave method for calculating degree days. *Environmental Entomology* **5**:388–396.
- Austin, M. P. 1978. Vegetation. Pages 44–67 in M. P. Austin and K. D. Cocks, editors. Land use on the South Coast of New South Wales. Volume 2. Biophysical Background Studies. Commonwealth Scientific and Industrial Research Organization (CSIRO). Melbourne, Australia.
- . 1992. Modelling the environmental niche of plants: implications for plant community response to elevated CO<sub>2</sub> levels. *Australian Journal of Botany* **40**:615–630.
- Austin, M. P., E. M. Adomeit, and J. A. Meyers. 1990a. Classification of the available vegetation data in the Eden Region. Consultancy Report for the Joint Scientific Committee on Southeast Forests, CSIRO Division of Wildlife and Ecology, Canberra, Australia.
- Austin, M. P., A. O. Nicholls, M. D. Doherty, and J. A. Meyers. 1994. Determining species response functions to an environmental gradient by means of a beta function. *Journal of Vegetation Science* **5**:215–228.
- Austin, M. P., A. O. Nicholls, and C. R. Margules. 1990b. Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. *Ecological Monographs* **60**:161–177.
- Austin, M. P., J. G. Pausas, and A. O. Nicholls. 1996. Patterns of tree species richness in relation to environment in southeastern New South Wales, Australia. *Australian Journal of Ecology* **21**:154–164.
- Austin, M. P., J. G. Pausas, and I. R. Noble. 1997. Modelling environmental and temporal niches of eucalypts. In J. E. Williams and J. C. Z. Woinarski, editors. *Eucalyptus ecology: from individuals to ecosystems*. Cambridge University Press, Cambridge, UK.
- Benson, G. L., and W. F. Laudenslayer, Jr. 1986. DYNAST: simulating wildlife response to forest management strategies. Pages 351–355 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Boland, D. J., M. I. H. Brooker, G. M. Chippendale, N. Hall, B. P. M. Hyland, R. D. Johnston, D. A. Kleinig, and J. D. Turner. 1984. *Forest trees of Australia*. Nelson and CSIRO, Melbourne, Australia.
- Bonan, G. B. 1989. Environmental factors and ecological processes controlling vegetation patterns in boreal forests. *Landscape Ecology* **3**:111–130.
- Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *Journal of Ecology* **60**:849–872.
- Braithwaite, L. W., M. L. Dudzinski, and J. Turner. 1983. Studies on the arboreal marsupial fauna of eucalypt forests being harvested for wood pulp at Eden, New South Wales. II. Relationships between the faunal density richness and diversity, and measured variables of habitat. *Australian Wildlife Research* **10**:231–247.
- Braithwaite, L. W., J. Turner, and J. Kelly. 1984. Studies on the arboreal marsupial fauna of eucalypt forests being harvested for woodpulp at Eden, New South Wales. III. Relationships between faunal densities, eucalypt occurrence, and foliage nutrients, and soil parent materials. *Australian Wildlife Research* **11**:41–48.
- Catling, P. C., and R. J. Burt. 1995. Studies of the ground-dwelling mammals of eucalypt forests in southeastern New South Wales. The effect of habitat variables on distribution and abundance. *Wildlife Research* **22**:271–288.
- Chapin, F. S. III, E.-D. Schulze, and H. A. Mooney. 1992. Biodiversity and ecosystem process. *Trends in Ecology and Evolution* **7**:107–108.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**:1302–1310.
- Dale, V. H., T. W. Doyle, and H. H. Shugart. 1985. A comparison of tree growth models. *Ecological Modelling* **29**:145–169.
- Elliott, K. J., and W. T. Swank. 1994. Changes in tree species diversity after successive clearcuts in the Southern Appalachians. *Vegetatio* **115**:11–18.
- Fanning, F. D., and K. Mills. 1989. Natural resource survey of the southern portion of Rockton Section, Bondi State Forest. Forest Resource Series Number 6. Forestry Commission of New South Wales, Sydney, Australia.
- FCNSW. 1982. Eden native forest management plan. Forestry Commission of New South Wales, Sydney, Australia.
- Fox, J. F. 1981. Intermediate levels of soil disturbance maximize alpine plant diversity. *Nature* **293**:564–565.
- Franklin, J. 1989. Toward a new forestry. *American Forestry* **Nov/Dec**:37–44.
- Gustafson, E. J., and T. R. Crow. 1994. Modeling the effects of forest harvesting on landscape structure and the spatial distribution of Cowbird brood parasitism. *Landscape Ecology* **9**:237–248.
- Hansen, A. J., S. L. Garman, B. Marks, and D. L. Urban. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. *Ecological Applications* **3**:481–496.
- Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests: lessons from natural forests. *BioScience* **41**:382–392.
- Hansen, A. J., D. L. Urban, and B. Marks. 1992. Avian community dynamics: the interplay of landscape trajectories and species life history. Pages 170–195 in A. J. Hansen and F. di Castri, editors. *Landscape boundaries*. Ecological Studies 92, Springer-Verlag, New York, New York, USA.
- Holt, R. D., S. W. Pacala, T. W. Smith, and J. Liu. 1995. Linking contemporary vegetation models with spatially explicit animal population models. *Ecological Applications* **5**:20–27.
- Hunter, M. L. 1990. *Wildlife, forest, and forestry: principles of managing forests for biological diversity*. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81–101.
- Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. *BioScience* **38**:682–691.
- Huston, M., and T. Smith. 1987. Plant succession: life history and competition. *American Naturalist* **130**:168–198.
- Jones, B. A., R. A. How, and D. J. Kitchener. 1994. A field study of *Pseudocheirus occidentalis* (Marsupialia: Petaurialia). I. Distribution and habitat. *Wildlife Research* **21**:175–187.
- Kavanagh, R. P. 1988. The impact of predation by the Powerful Owl, *Ninox strenua*, on a population of the greater glider, *Petauroides volans*. *Australian Journal of Ecology* **13**:445–450.
- Kavanagh, R. P., and K. L. Bamkin. 1995. Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in Southeastern New South Wales, Australia. *Biological Conservation* **71**:41–53.
- Kavanagh, R. P., and M. J. Lambert. 1990. Food selection by the greater glider, *Petauroides volans*: is foliar nitrogen a determinant of habitat quality? *Australian Wildlife Research* **17**:285–299.
- Keith, D. A., and J. M. Sanders. 1990. Vegetation of the Eden Region, Southeastern Australia: species composition,

- diversity, and structure. *Journal of Vegetation Science* **1**: 203–232.
- Kruse, R. L., and W. F. Porter. 1994. Modeling change in habitat conditions in northern hardwood forests of the Adirondack Mountains of New York. *Forest Ecology and Management* **70**:99–112.
- Lambert, M. J., and J. Turner. 1983. Soil nutrient–vegetation relationships in the Eden area, New South Wales. III. Foliage nutrient relationships with particular reference to *Eucalyptus* subgenera. *Australian Forestry* **46**:200–209.
- Lindenmayer, D. B., R. B. Cunningham, C. F. Donnelly, M. T. Tanton, and H. A. Nix. 1993. The abundance and development of cavities in *Eucalyptus* trees: a case study in the montane forests of Victoria, southeastern Australia. *Forest Ecology and Management* **60**:77–104.
- Lindenmayer, D. B., R. B. Cunningham, M. T. Tanton, and A. P. Smith. 1990a. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, southeast Australia. II. The loss of trees with hollows and its implications for the conservation of Leadbeater's possum *Gymnobelideus leadbeateri* McCoy (Marsupialia: Petauridae). *Biological Conservation* **54**:133–145.
- Lindenmayer, D. B., R. B. Cunningham, M. T. Tanton, A. P. Smith, and H. A. Nix. 1990b. Habitat requirements of the mountain brushtail possum and the greater glider in the montane ash-type eucalypt forests of the Central Highlands of Victoria. *Australian Wildlife Research* **17**:467–478.
- Lindenmayer, D. B., R. B. Cunningham, M. T. Tanton, A. P. Smith, and H. A. Nix. 1991. Characteristics of hollow-bearing trees occupied by arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, southeast Australia. *Forest Ecology and Management* **40**:289–308.
- Liu J., F. W. Cabbage, and H. R. Pulliam. 1994. Ecological and economic effects of forest landscape structure and rotation length: simulation studies using ECOLECON. *Ecological Economics* **10**:249–263.
- Lunney, D. 1987. Effects of logging, fire, and drought on possums and gliders in the coastal forests near Bega, New South Wales. *Australian Wildlife Research* **14**:263–274.
- Magurran, A. E. 1988. *Ecological diversity and its measure*. Princeton University Press, Princeton, New Jersey, USA.
- Malanson, G. P., W. E. Westman, and Y. Yeuh-Lih. 1992. Realized versus fundamental niche functions in a model of chaparral response to climate change. *Ecological Modelling* **64**:261–277.
- Margalef, R. 1980. *Ecologia*. Editorial Omega, Barcelona, Spain.
- Niese, J. N., and T. F. Strong. 1992. Economic and tree diversity trade-off in managed northern hardwoods. *Canadian Journal of Forest Research* **22**:1807–1813.
- Noble, I. R., A. D. Moore, and M. J. Strasser. 1988. Stand structure and the prediction of vegetation dynamics. Pages 263–275 in H. J. Doring, M. J. A. Werger, J. H. Willems, editors. *Diversity and pattern in plant communities*. SPB Academic Publishing, The Hague, The Netherlands.
- Pacala, S. W., and G. C. Hurtt. 1993. Terrestrial vegetation and climate change: integrating models and experiments. Pages 57–74 in P. M. Kareiva, J. G. Kingsolver, R. B. Huey, editors. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Padisak, J. 1993. The influence of different disturbance frequencies on the species richness, diversity, and equitability of phytoplakton in shallow lakes. *Hydrobiologia* **249**: 135–156.
- Pausas, J. G. 1994. Species richness patterns in the understory of Pyrenean *Pinus sylvestris* forest. *Journal of Vegetation Science* **5**:517–524.
- Pausas, J. G., L. W. Braithwaite, and M. P. Austin. 1995. Modelling habitat quality for arboreal marsupials in the South Coastal forests of New South Wales, Australia. *Forest Ecology and Management* **78**:39–49.
- Melou, E. C. 1966. The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* **13**:131–144.
- Possingham, H. P., D. B. Lindenmayer, T. W. Norton, and I. Davies. 1994. Metapopulation viability analysis of the greater glider *Petauroides volans* in a wood production area. *Biological Conservation* **70**:227–236.
- Prentice, I. C., and H. Helmisaari. 1991. Silvics of north European trees: compilation, comparisons, and implications for forest succession modelling. *Forest Ecology and Management* **42**:79–93.
- Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-Wright, and P. H. Williams. 1993. Beyond opportunism: key principles for systematic reserve selection. *Trends in Ecology and Evolution* **8**:124–128.
- Pulliam, H. R., Jr., J. B. Dunning, and J. Liu. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* **2**:165–177.
- Raedeke, K. J., and J. F. Lehmkuhl. 1986. A simulation procedure for modeling the relationships between wildlife and forest management. Pages 377–381 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Recher, H. F., J. Shields, R. Kavanagh, and G. Webb. 1987. Retaining remnant mature forest for nature conservation at Eden, New South Wales: a review of theory and practice. Pages 177–194 in D. A. Saunders, G. W. Arnold, A. A. Burbidge, and A. J. M. Hopkins, editors. *Nature conservation: the role of remnants of native vegetation*. Surrey Beatty and Sons, Chipping Norton, Australia.
- Ribbens, E., Jr., J. A. Silander, and S. W. Pacala. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* **75**:1794–1806.
- Seagle, S. W., and H. H. Shugart. 1985. Faunal richness and turnover on dynamic landscapes: a simulation study. *Journal of Biogeography* **12**:499–508.
- Shugart, H. H. 1984. *A theory of forest dynamics*. Springer-Verlag, New York, New York, USA.
- Shugart, H. H., and I. R. Noble. 1981. A computer model of succession and fire response of the high-altitude *Eucalyptus* forest of the Brindabella Range, Australian Capital Territory. *Australian Journal of Ecology* **6**:149–164.
- Shugart, H. H., T. M. Smith, and W. M. Post. 1992. The potential for application of individual-based simulation models for assessing the effects of global change. *Annual Review of Ecology and Systematics* **23**:15–38.
- Shugart, H. H., and D. L. Urban. 1986. Modeling habitat relationships of terrestrial vertebrates: the researcher's viewpoint. Pages 425–429 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Smith, A. P., and D. B. Lindenmayer. 1988. Tree hollow requirements of Leadbeater's possum and other possums and gliders in timber production ash forests of the Victorian Central Highlands. *Australian Wildlife Research* **15**:347–362.
- Smith, A. P., and D. B. Lindenmayer. 1992. Forest succession and habitat management for Leadbeater's possum in the State of Victoria, Australia. *Forest Ecology and Management* **49**:311–332.
- Smith, T. M. 1986. Habitat simulation models: integrating habitat classification and forest simulation models. Pages 389–393 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of*

- terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. *Ecology* **60**:1225–1239.
- Strasser, M. J., J. G. Pausas, and I. R. Noble. 1996. Modelling the response of eucalypts to fire in the Brindabella Range, Australian Capital Territory. *Australian Journal of Ecology* **21**:341–344.
- Swindel, B. F., L. F. Conde, and J. E. Smith. 1984. Species diversity: concept, measurement, and response to clear-cutting and site preparation. *Forest Ecology and Management* **8**:11–22.
- Thomas, J. W., editor. 1979. Wildlife habitat in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service Agricultural Handbook Number. 553. Washington, D.C., USA.
- Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit population models in land management. *Ecological Applications* **5**:12–16.
- Tyndale-Biscoe, C. H., and J. H. Calaby. 1975. Eucalypt forest as refuge for wildlife. *Australian Forestry* **38**:117–133.
- Urban, D. L., and H. H. Shugart. 1992. Individual-based models of forest succession. Pages 249–291 in D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. *Plant succession: theory and prediction*. Chapman and Hall, London, UK.
- Urban, D. L., and T. M. Smith. 1989. Microhabitat pattern and the structure of forest bird communities. *American Naturalist* **133**:811–829.
- Wilcove, D. S. 1989. Protecting biodiversity in multi-use lands: lessons from the U.S. Forest Service. *Trends in Ecology and Evolution* **4**:385–388.
- Woods, K. D., and R. H. Whittaker. 1981. Canopy–understory interactions and the internal dynamics of mature hardwood and hemlock–hardwood forests. Pages 305–323 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest succession: concepts and applications*. Springer-Verlag, New York, New York, USA.