Spatial modelling of landscape-scale vegetation dynamics, Mont Do, New Caledonia

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The coniferous tree *Araucaria laubenfelsii* forms a key component of vegetation structural assemblages on ultramafic substrate at Mont Do, New Caledonia. It is the sole species to be found both as an emergent in maquis and as a common canopy species in adjacent rainforest patches. This paper describes a spatially explicit, landscape-level model developed to investigate the vegetation pattern on Mont Do and provides preliminary results of model analyses. Results indicate that the interaction between fire, terrain and the long residence times of fire-prone successional stages may be largely responsible for the landscape patterns visible. Maquis is found predominantly on hillsides where fire spread is likely to be most rapid, while maquis with emergent *A. laubenfelsii*, and *A. laubenfelsii* woodland, are restricted to rocky areas and rainforest margins of likely intermediate fire frequency. The model indicates that if fires were to become either more frequent or increase in size, maquis would become increasingly prevalent in the landscape. Pattern metrics, such as fractal dimension, indicate that as a result of such a change, the spatial complexity and fragmentation of the landscape may be reduced. Conversely, if fire frequency decreases or fire sizes become smaller, then rainforest becomes more dominant. Although the presence of *A. laubenfelsii* on Mont Do is not threatened under such a scenario, the persistence of certain 'transient' structural assemblages at their current abundances seems less certain. While the role that ultramafic soil conditions might play at the landscape level is not clear, several possible interactions between the plant-soil relationship and broader scale dynamics are identified. In particular, soil chemical constraints on plant growth may be responsible for the very long time-scales associated with succession from maquis to forest, and this slowed succession increases the potential role of fire as a major determinant of landscape-scale vegetation pattern relative to that on nearby non-ultrabasic substrates.

Introduction

Since human settlement of New Caledonia, the natural disturbance regime has been altered, leading to a number of changes in landscape composition and structure. In particular, the vegetation on ultramafic substrate has been greatly affected by fire and other human disturbances associated with logging and mineral exploration. It is therefore pertinent to ask how the landscape may respond to present and future disturbance regimes and how these changes might relate to the peculiarities of the serpentine environment. For example, if disturbance return intervals were to increase, or if the average size of individual disturbance events were to change, how would the landscape respond? Questions such as these are not amenable to the traditional experimental approach commonly used in ecology. Instead, it is necessary to resort to the use of simulation models (see ref. 1). Simulation modelling of landscape-level dynamics has rarely been attempted for regions characterized by ultramafic substrates, perhaps due to the overriding concern of workers to identify the more site-specific roles of unusual soil chemical conditions in determining floristic and structural patterns of vegetation. The only other landscape models considering the dynamics of serpentine landscapes that we are aware of are those of Moloney *et al.*,[2] Wu and Levin[3] and Moloney and Levin,[4] which simulate the dynamics of a serpentine grassland near Santa Cruz, California. It is of both scientific and management interest to ask how broader-scale processes might operate in serpentine landscapes, and whether interactions across scales may imply landscape-level outcomes that differ from those expected under equivalent circumstances on non-ultramafic substrates.

Patch type or landscape models are the most widely used modelling framework to simulate landscape dynamics over large spatial and temporal extents. Unlike gap replacement models such as JABOWA[5] or FORET,[6] tree demography is not modelled explicitly in such landscape models. Instead, changes in vegetation structure are indexed to time since disturbance. These models may be described as spatially implemented patch transition simulators. Landscape models have been developed that use stochastic approaches to examine the relationship between fire regimes and landscape heterogeneity as well as fire-affected landscape changes through time, many of which are described in detail in ref. 7. Although designed to explore a variety of issues in a wide range of systems, these landscape models share several common features. These include coarser temporal resolution than mechanistic models (usually 1–10 years as compared to time-steps of minutes), ability to simulate large spatial extents with multiple fire events, and the use of stochastic algorithms. Since the temporal resolutions used in such models are much coarser than those of mechanistic models, detailed processes such as the mechanics of individual ignition events or individual tree growth and mortality can not be simulated precisely over time. Thus, in landscape models, fine-scale processes are integrated across temporal scales not by simulating them directly, but by representing them as aggregated phenomena in time and space. The model that is described and tested here falls into this broad category. As noted above, the research of Moloney *et al.*,[2] Wu and Levin[3] and Moloney and Levin[4] aside, the development and application of landscape models to serpentine landscapes has been extremely limited.

The spatially-realistic (*sensu* ref. 8) landscape model presented here is designed to explore landscape dynamics on Mont Do, a small montane reserve in the southern part of New Caledonia. The primary aim of this paper is to explore the role of fire, and the ways that changes to the fire regime may affect landscape pattern (structure and composition). Three facets of the fire regime are considered: fire frequency (return interval), the average individual event size and the flammability of the vegetation.

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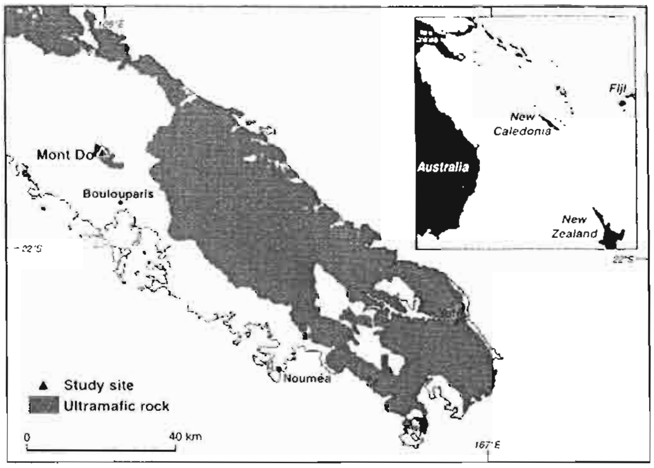

Fig. 1. Southern part of the Grand Terre of New Caledonia, illustrating the location of the Mont Do study site, and the extent of ultramafic substrate on the island.

Site description

New Caledonia is a small island group (~19 000 km^2), yet it contains an extremely diverse native flora of around 3000 species. Nearly 80% of these species are endemic, and New Caledonia is home to a large number (43) of conifer species, coming from four families.[9] Mont Do (see Fig. 1) is a Botanical Reserve (*Réserves Spéciales Minières et Botaniques*), established to preserve and protect the mountain flora and fauna associated with the ultramafic substrate predominant in the southern part of New Caledonia. Mont Do is part of the central mountain chain and is 1025 m a.s.l. at its highest point. The reserve occupies the top several hundred metres of the mountain, corresponding with the area of outcropping ultramafic bedrock and a relatively dense population of *Araucaria laubenfelsii*.[10]

The landscape on Mont Do is spatially complex, with the endemic conifer species *Araucaria laubenfelsii* being a key component of the unusual structural assemblages found in the landscape. These structural assemblages themselves form interesting spatial patterns in the landscape. *A. laubenfelsii* is the only tree species to be found both as an emergent in the maquis and as a canopy dominant in some patches of rainforest. Late in the successional sequence, however, *A. laubenfelsii* may be replaced in old forest patches by *Nothofagus codonandra*.[10,11] The density of *A. laubenfelsii* in the maquis is highly variable, ranging from areas where the species is locally absent, to areas where stem densities are very high. Patches of maquis without *A. laubenfelsii*, or with *A. laubenfelsii* emergents present at very low densities, are found on slopes on which fires may be expected to spread rapidly. Maquis containing higher densities of emergent *A. laubenfelsii* and *Araucaria* woodland are found on ridgelines where fire frequency may be reduced by the negative impact of rockiness on fire spread (see ref. 12). Rainforest patches are at present largely restricted to gullies and other fire-protected positions. The current structure of the landscape suggests interesting feedback (both positive and negative) between pattern and process, especially with regard to disturbance.

Jaffré,[9] Rigg *et al.*[10] and Rigg[11] suggest that a decrease in fire frequency since the establishment of the Mont Do reserve may have led to an increase in the recruitment of *A. laubenfelsii* in the maquis, and may lead ultimately to the expansion of rainforest. Factors relating to a combination of tropical weathering processes and ultramafic chemistry, influence fire frequency by affecting rates of biomass (fuel) accumulation, tree invasion and growth within the maquis.[13] Soil profiles may be excessively rocky due to the development of a surface iron hardpan (*sol cuirassé*), they have low concentrations of plant macronutrients, and potentially toxic concentrations of several metal elements including Ni, Mn and Cr. Although fire is the dominant disturbance structuring the landscape, other disturbance events are also evident. For instance, several recent treefalls of mature *Araucaria laubenfelsii* are attributable to the passage of tropical cyclones. Although these events undoubtedly play some role in generating pattern in the landscape they are not considered in the model presented here.

Model description

The model described here is designed to explore the way that patterns in the landscape may be attributed to the disturbance regime, and in particular, wildfires. It is evident that succession and disturbance operate across a number of scales in space and time. For the most part we will be concerned with temporal scales of decades and centuries (with the basic time-step of the model being one year), and spatial scales of hectares and above.

Figure 2 illustrates the basic design and structure of the model, which operates largely within a rule-based (IF-THEN) qualitative framework, with succession and disturbance events occurring in response both to simple rules and probabilistic tests. The model is stochastic and thus a number of replicate model runs are performed for each scenario explored. The model is built around four major components: (i) a vegetation dynamics module, (ii) a disturbance (fire) module, (iii) a climatic module, and (iv) a landscape metric/pattern analysis module for analysis of model output(s). The model results presented here are concerned largely with an analysis of the effects of the fire regime on the landscape composition and structure of Mont Do. Therefore, the fire component of the model will be described in

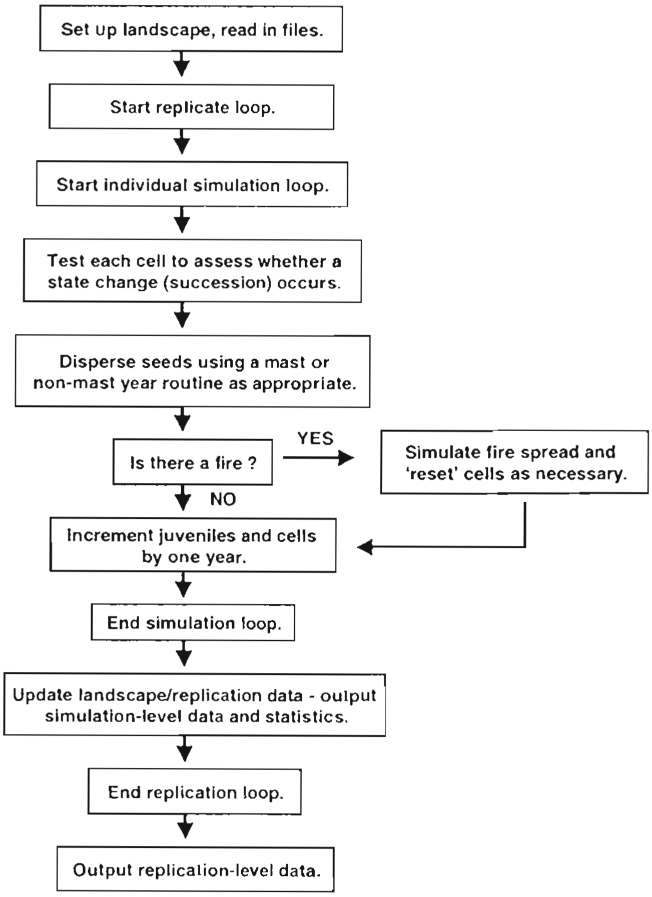

Fig. 2. Schematic representation of the spatial model described in this paper.

some detail and the three other components more briefly.

Within the landscape model fire frequency is simulated using the weibull distribution, whose hazard function is defined as:[14,15]

$$h(t) = \lambda^c t^{c-1}, \qquad (1)$$

where $h(t)$ = probability of a hazard (i.e. fire) occurring at time t, λ = 1/fire interval, and c = dimensionless shape parameter [if c = 1 then the hazard is constant, if $c > 1$ then the hazard increases with time (i.e. older stands have a greater chance of burning)].

The shape parameter may be altered to reflect the shape of the fire probability curve, and λ manipulated to change the average return interval of fire events.[16] A random number is tested against the probability of fire in each year and, if it is lower, then a fire event occurs. If a fire does occur, then another test is carried out to see whether the fire starts within the landscape, or spreads into the landscape from part of the adjoining area. If the fire starts within the landscape, then the ignition point is chosen at random; should the fire be spreading into the landscape, then the side from which it is spreading and the length of the front are randomly determined. Following ignition, the maximum potential size of the fire is calculated; this may either be set as a constant value, or may be selected stochastically from a negative exponential function. The probability of a fire event starting outside the landscape was set to five per cent for all of the simulations described here.

Fire spread is simulated as a simple percolation process[17,18] operating within a stochastic cellular automata framework.[19] Cells that contain flammable vegetation and are adjacent to ignited cells are tested to see whether they ignite. Flammability is modelled as a function of topography (slope), vegetation, fuel build-up (time since last fire), fire intensity and climatic conditions (wind speed and direction and rainfall). Fire may spread into any of the eight cells adjacent to the focal (burning) cell (i.e. the 'Queen's move'); a lag in spread is tested for those cells which share only a corner and not an edge. It should be emphasized that 'burning' is defined as fire sufficient to reset the successional sequence, and not low intensity fire events which may pass through the vegetation without causing any significant mortality. After a set number of iterations, the cell is assumed to burn out and fire may no longer spread from it. Fire spread continues in this manner until the maximum possible fire size is reached or until a time step occurs when the fire fails to spread into any new cells. For each fire event, a wind speed and direction are randomly generated and these act to bias the direction of fire spread. The general structure of the fire module of the model is illustrated in Fig. 3. This general framework for simulating fire spread is similar to that used by Ratz,[20] and Karafyllidis and Thanailakis.[21] Fine-scale variables such as temperature and humidity are not usually included in landscape models such as that described here because they are not designed to predict the exact location and behaviour of individual fire events.[22]

Vegetation dynamics are simulated in a quantitative manner. Four vegetation types are recognized in the model, representing (putative) successional stages (Table 1); a fifth vegetation class included in the model is a bare rock/soil class.

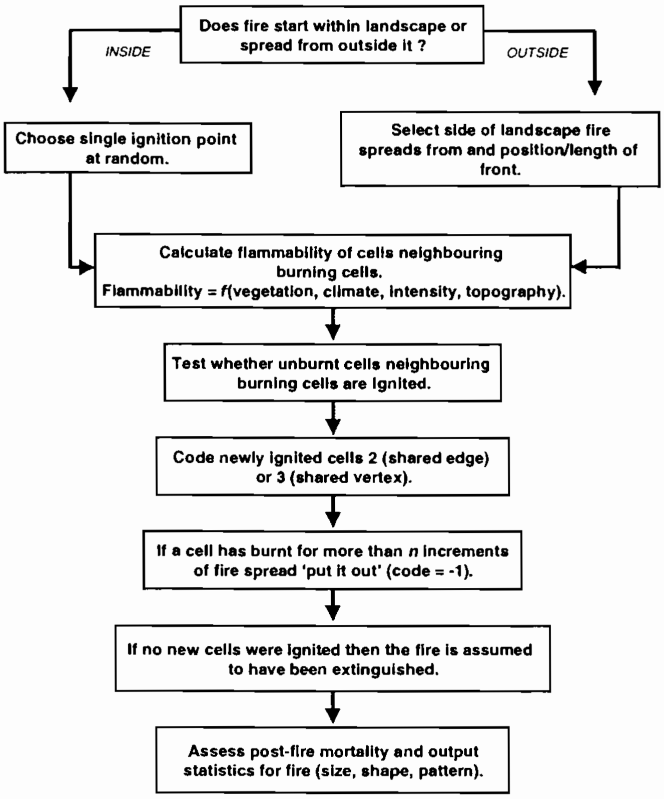

Fig. 3. Schematic representation of the fire module component of the spatial landscape-model.

The periods over which succession occurs in such ultramafic landscapes are very long.[10,13] Within the model, successional changes are simulated either simply as vegetation change taking place after certain time periods without fire burning a cell, or in some cases when fire has not occurred for a certain period of time and some other condition is met, such as the presence of a critical density of reproductively mature *A. laubenfelsii* (see Fig. 4). After a cell is burnt, it is assumed that the biomass in that cell is insufficient to carry fire for at least ten years (see refs. 13, 23). Critical stages in the life history of *A. laubenfelsii* are used for some of these stage changes. *A. laubenfelsii* becomes both reproductively mature and considerably less susceptible to fire-mortality at an age of around 120 years.[11] Thus, 'maquis with emergent Araucaria' is defined as any pixel with at least one reproductively mature (120-year-old) individual in it (this corresponds to a density of one mature individual per 100 m^2). The rate of succession is also influenced by landscape position, reflecting spatial variations in soil moisture across the landscape. Furthermore, the age to reproductive maturity is also high. It is probable that these long time periods reflect the harsh nature of the soil conditions which cause the extremely slow growth rates seen in *A. laubenfelsii* (and many other species) on Mont Do.

Table 1. Brief description of vegetation states included in the model.

State*	State description
Maquis (1)	Maquis miniers with no *A. laubenfelsii* present.
Maquis with emergent *Araucaria* (2)	Maquis with scattered *A. laubenfelsii* (at a density of at least one reproductively mature adult per 100m^2).
Araucaria woodland (3)	Increasing density of *A. laubenfelsii* — intermediate between 2 and 4.
Forest (4)	Mature forest dominated by *A. laubenfelsii* (as a canopy emergent) and *Nothofagus codonandra.*
Rocky (5)	Rocky outcrops – non-flammable.

*Number refers to the numeric code of the state.

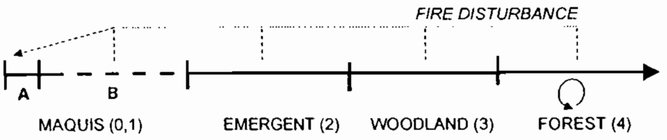

Fig. 4. Schematic diagram of the successional process as simulated in the model. The numbers refer to the code for each vegetation type within the landscape model, **A**, recently burnt maquis with biomass too low to support another fire; **B**, burnable maquis which will become maquis with emergent *Araucaria* when there is a reproductively mature *A. laubenfelsii* in the cell.

Araucaria laubenfelsii is known to mast seed, although the average period between masting events is not clear.[11] Within this model the probability of a year being a mast year is constant and each year is tested at random to see whether it will be a mast one, with the limitation that a mast year may not occur until three years after the previous such event. Seed production within each cell is calculated annually and individual seeds are then dispersed in a random direction and distance from each cell (seed source).

For each replicate of the model annual rainfall data are generated using one of four methods. Years are classified as abnormally wet, abnormally dry or normal, with the nature of the rainfall in the year affecting the fire dynamics (flammability, probability of an ignition event) in that year. These data are generated either as a constant type, as a random sequence (using set probabilities of each type of year), as a repeating cycle with a set period, or using a Markov chain approach using annual rainfall data from Mont Do and other nearby weather stations. The latter approach is the one used for all the simulations described in this paper. Wind speed and direction are generated at the time of each fire event.

The model is loosely-coupled with a geographic information system (GIS), which is used to store the spatial data input into the model, and subsequently for display and analysis of model output. This approach to hinging environmental models with GIS is described in more detail in Fedra.[24]

Description of model analysis

The results describe an initial analysis of the model with respect to some of the basic components of the fire regime. The primary question being asked is how the landscape structure and composition on Mont Do may respond to changes in the disturbance regime. The model results are not intended to be quantitatively predictive but rather to explore some of the outcomes of alternative scenarios. All the results presented below are based on 100 replicates of 500-year-long model runs. The terrain used in the model is that of Mont Do, while the base vegetation map is a synthetic one, of very similar nature to the contemporary Mont Do landscape, generated by a program specifically written for the task. The advantage of this approach is that specific hypotheses regarding initial landscape composition and structure may be tested, and that multiple landscapes fitting specified requirements may be generated and used as replicates. Furthermore, there are a number of problems involved with the interpretation and analysis of aerial photographs of the Mont Do region, including cloud cover and the accurate identification and discrimination of the various vegetation types. The size of the landscape in the model is 99 × 98 cells, with a cell size of 10 m, giving a landscape area of slightly less than 100 ha.; this corresponds to the size of the Mont Do reserve. Alongside the spatially explicit outputs generated by the model, and presented below, the analysis will also use a suite of landscape metrics designed to quantify various aspects of spatial heterogeneity. The use of such metrics is widespread in landscape ecology for the analysis of spatial simulation models, and their application provides a useful way of summarizing some of the results.[25–28]

Besides the relative abundance (proportion) of the different vegetation classes in the landscape, Shannon's diversity index will be used as a measure of dominance. This index may be defined as:

$$SHDI = -\sum_{i=1}^{m} (P_i . \ln P_i),\ \text{SHDI} \geq 0 \text{ without limit} \tag{2}$$

where P_i = proportion of the landscape occupied by patch type (class) *i*.

Fractal dimension (FD) will be used as a measure of landscape complexity. Fractal dimension measures landscape complexity in terms of deviation in the landscape mosaic from a Euclidean geometry, with values approaching 1.0 indicating the mosaic comprises patches with very simple shapes, and values approaching 2.0 indicating that the mosaic is made up of patches with highly-convoluted, plane-filling shapes. The final value for the fractal dimension is an area-weighted patch average. FD is defined as:

$$FD = \sum_{i=1}^{m}\sum_{j=1}^{n}\left[\left(\frac{2\ln(0.25 p_{ij}}{\ln a_{ij}}\right)\left(\frac{a_{ij}}{A}\right)\right],\ 1 \leq \text{FD} \leq 2 \tag{3}$$

where: $i = 1, \ldots, m$ patches, $j = 1, \ldots, n$ patches, a_{ij} = area (m^2) of patch *ij*, A = total landscape area (m^2), and P_{ij} = perimeter (m) of patch *ij*.

Landscape fragmentation is measured using the contagion index:

$$CONT = \left[1 + \frac{\sum_{i=1}^{m}\sum_{k=1}^{m}\left[(P_i)\left(\frac{g_{ik}}{\sum_{k=1}^{m} g_{ik}}\right)\right]\left[\ln(P_i)\left(\frac{g_{ik}}{\sum_{k=1}^{m} g_{ik}}\right)\right]}{2\ln(m)}\right],\ 0 \leq \text{CONT} \leq 1 \tag{4}$$

where $k = 1, \ldots, m$ patch types (classes), and g_{ik} = number of adjacencies (joins) between pixels of patch types (classes) *i* and *k*.

Contagion is a complex measure that may be summarized as a measure of the tendency for elements (classes or patches) of a given type to occur next to patches of another, or the same type, taking into account the relative abundance of the different vegetation types in the landscape.[29] Contagion approaches 0 when the distribution of adjacencies (at the level of individual cells) among unique patch types becomes increasingly uneven. Contagion approaches 1 when all patch types are equally adjacent to all other patch types. The algorithm used for calculating the contagion metric is that described by Li and Reynolds.[29] Although the model calculates these three metrics (and many more) at the individual patch, class and landscape levels, the analysis presented here is limited to the landscape level.

Results of the model analysis

Fire frequency

The first aspect of the disturbance regime to be explored is fire frequency. For the purposes of this analysis, return intervals of 10, 20, 33, 50 and 100 years were compared. Figure 5 shows that the frequency of fire events has a strong influence on the relative abundance of the different vegetation types in the landscape.

This is also illustrated by the average diversity (SHDI) values for each frequency, which are at a maximum for a return interval

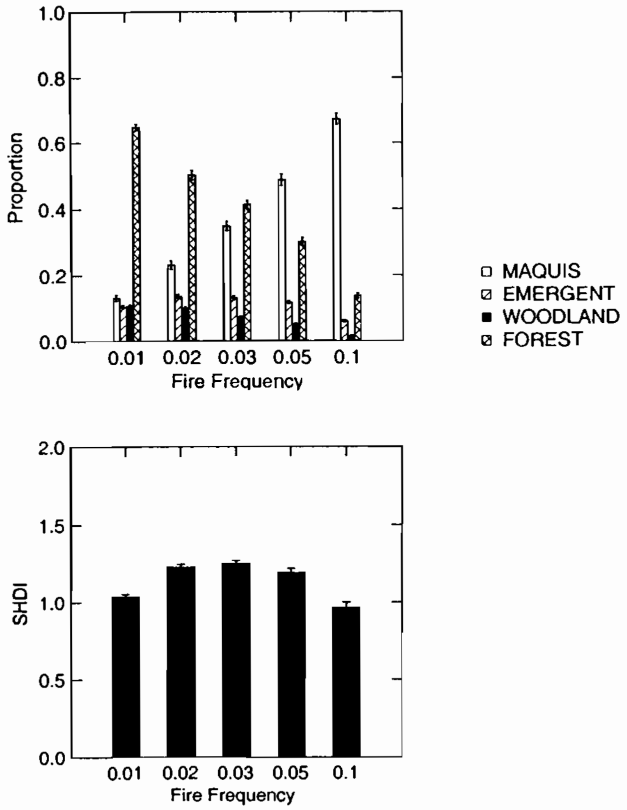

Fig. 5. Proportion of the landscape in each of the vegetation types and SHDI values under different fire frequencies; error bars are ±1 s.e.

of 33 years and at a minimum for the two extremes, where either forest or maquis dominates the landscape, respectively. In all of the frequencies examined both maquis with emergent *A. laubenfelsii*, and *A. laubenfelsii* woodland maintain their presence at low levels, although they decline as fire frequency increases. The SHDI values are statistically significantly different across all treatments (Kruskal-Wallis $H = 82.72$, $P < 0.0001$, d.f. $= 4$) with diversity highest at intermediate fire frequencies.

The effects of fire frequency are not limited to landscape composition. In terms of landscape complexity and fragmentation, different fire frequencies lead to landscapes of different structures. The complexity of the landscape mosaic (as measured by fractal dimension) changes as a function of fire frequency (Fig. 6).

Fractal dimension decreases from the lowest to the highest fire frequency. The fractal dimension of simulated landscapes usually falls between 1.1 and 1.6[30] and so the values reported here are quite low. This is probably due to the conservative fractal dimension formulation (area-weighted mean patch) used. Complexity is likely to be lowest at high fire frequencies as maquis becomes increasingly dominant and smaller patches of maquis aggregate to form large single patches. Differences between scenarios for fractal dimension are statistically significant when compared using Kruskal-Wallis tests ($H = 135.8$, $P < 0.0001$, d.f. $= 4$).

Contagion is highest at the maximum and minimum fire frequencies and lowest at intermediate fire frequencies. As described above, this is probably because intermediate disturbance frequencies promote more patchy landscapes (low contagion), whereas very low or very high disturbance frequencies lead to large patches of either maquis or forest, with fewer small patches present (high contagion). Again the between-scenario differences in contagion are statistically significant ($H = 115.1$, $P < 0.0001$, d.f. $= 5$) (Fig. 7).

Fire size

The size of individual disturbance events may be set either as a constant or as a randomly selected number from a negative exponential distribution within specific bounds. For the purposes of the analysis here, sizes of 500, 1000, 2000, 4000 and from a negative exponential with a maximum bound of 9702 cells (i.e. the whole landscape) were used. To repeat, this parameter specifies the maximum potential size of a fire event. In many cases the fire will not reach this size as it may either be extinguished or spread out of the landscape. For example, fire starting in forest may only burn a single cell as the fire fails to propagate into the extremely low flammability vegetation surrounding the ignition point. Size is a key component of the disturbance regime, since where individual disturbances are of large size relative to the landscape, it seems improbable that the landscape will ever be able to attain any sort of equilibrium.[31,32] Figure 8 illustrates changes in the proportion of the landscape in each of the vegetation types for each of the disturbance size scenarios tested.

The general trend is for the abundance of forest to decrease and the abundance of maquis to increase as fire size increases. Again, the two intermediate vegetation types persist in all scenarios at low densities. When fire size is selected from a negative exponential distribution (with a maximum of the entire landscape), the average fire size is around 640 pixels (6.4 ha.). It is interesting, therefore, to compare the abundance of maquis when disturbance size is selected from a negative exponential distribution to when it is limited to either 500 or 1000 (the values closest to the mean fire size for the negative exponential scenario). The negative exponential scenario leads to a more even landscape than is the case when fire size is restricted to

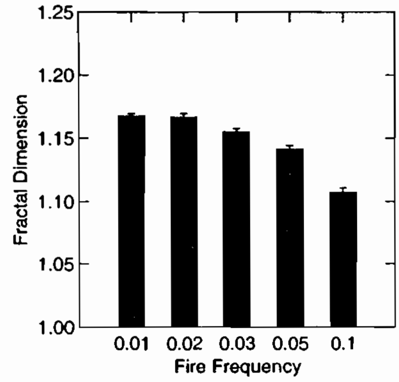

Fig. 6. Fractal dimension values for the different fire frequencies tested; error bars are ±1 s.e.

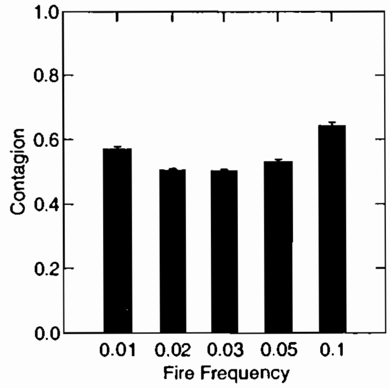

Fig. 7. Contagion values for the different fire frequencies tested; error bars are ±1 s.e.

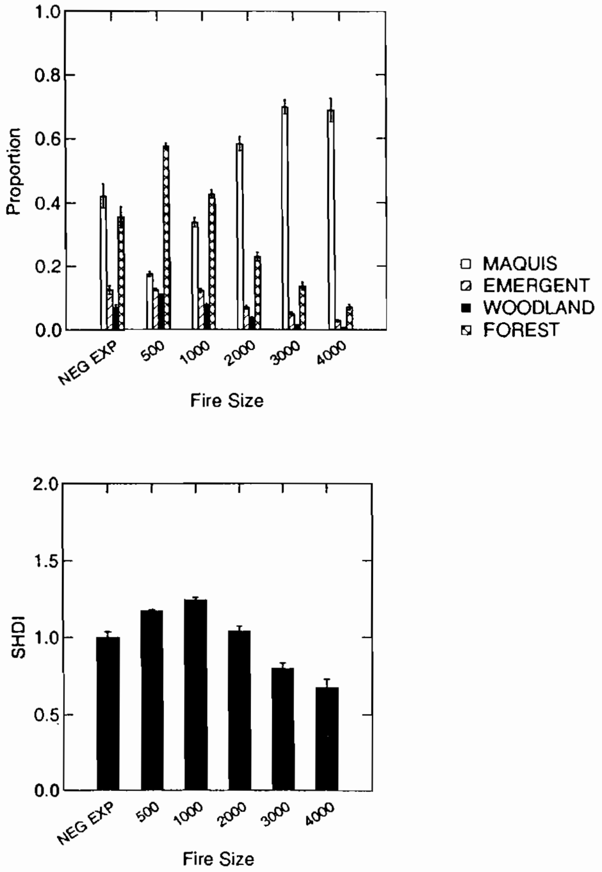

Fig. 8. Proportion of the landscape in each of the vegetaion types and SHDI values under different fire size scenarios; error bars are ±1s.e.

either 500 or 1000 cells. This result indicates that very rare but very large disturbance events may be of crucial importance in structuring the Mont Do landscape. Similar results have been found in studies elsewhere (e.g. see ref. 33).

Fractal dimension decreases as fire size increases (Fig. 9). Presumably, this is a similar response to that described for Fig. 6 in that recurrent, very large fires act to homogenize the landscape into large patches of maquis vegetation with forest retreating to fire-protected gullies and so forth.

Contagion responds in a similar manner, being at a minimum when fire size is restricted to 1000 pixels. As the maximum fire size expands, contagion increases as the landscape becomes more homogeneous (less fragmented) as described above (Fig. 10).

It is interesting to note that when the landscape is proportionately more dominated by forest (as in the scenario when fire is limited to 500 pixels in size), the landscape is at its most complex. This may be a result of small patches of vegetation being in different stages of succession with less likelihood of large areas being burnt and becoming maquis. Over very long periods with small fires, however, it is probable that the landscape would become less complex as large areas of forest formed through aggregation of patches. These large areas of forest may also act to make the landscape significantly less prone to fires, further reducing patchiness in the landscape. The way in which the landscape may become dominated by forest under low fire size regimes, or in which fire may retreat to fire-protected patches under high fire size regimes, is illustrated in Fig. 11.

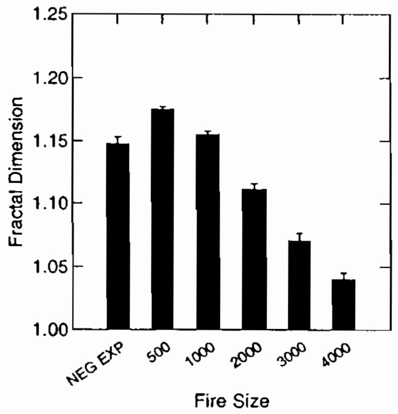

Fig. 9. Fractal dimension values for the different fire size scenarios tested; error bars are ±1 s.e.

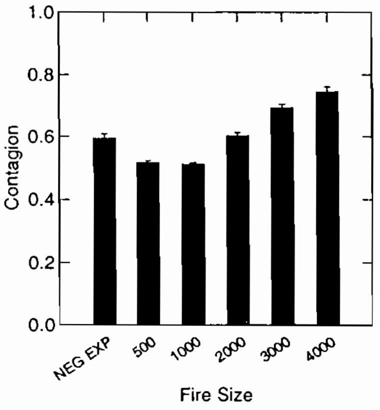

Fig. 10. Contagion values for the different fire size scenarios tested; error bars are ±1 s.e.

Flammability

Five different flammability 'treatments' were explored: a baseline flammability (i.e. that used for all the other simulations presented here) and treatments ±10 and ±20% of these values. An increase in flammability may have two effects. First, a higher amount of low flammability vegetation may burn, and, second, fire size may increase (within the bounds allowed by the size parameter) as fewer fires go out early in their development. The composition of the landscape does not vary greatly with changes in flammability (Fig. 12). Differences in SHDI between the different flammability scenarios are not statistically significant ($H = 4.24, P = 0.375$, d.f. = 4). Similarly, no significant differences were found for the other landscape metrics used. This lack of response to what are biologically large changes in flammability suggests that the two parameters tested above (size and frequency), and especially size, may act to constrain the behaviour of individual fires more than flammability does.

Discussion

The results presented above indicate the potential importance of changes in the size and frequency components of the disturbance regime to landscape composition and structure on Mont Do. However, changes in the flammability of the vegetation do not appear to have a large effect on the landscape. This may either be because the dynamics of individual fires are already constrained by other parameters (e.g. size), or because the range of values over which the sensitivity analysis was conducted was too small. Quantitative assessment of the flammability of the different vegetation types on Mont Do would certainly be valuable both in improving our understanding of the dynamics of the landscape and in future development of the spatial model. Furthermore, considering changes in fire size, fire frequency and flammability independent of each other is simplistic, since it is likely that a significant change in flammability would act to

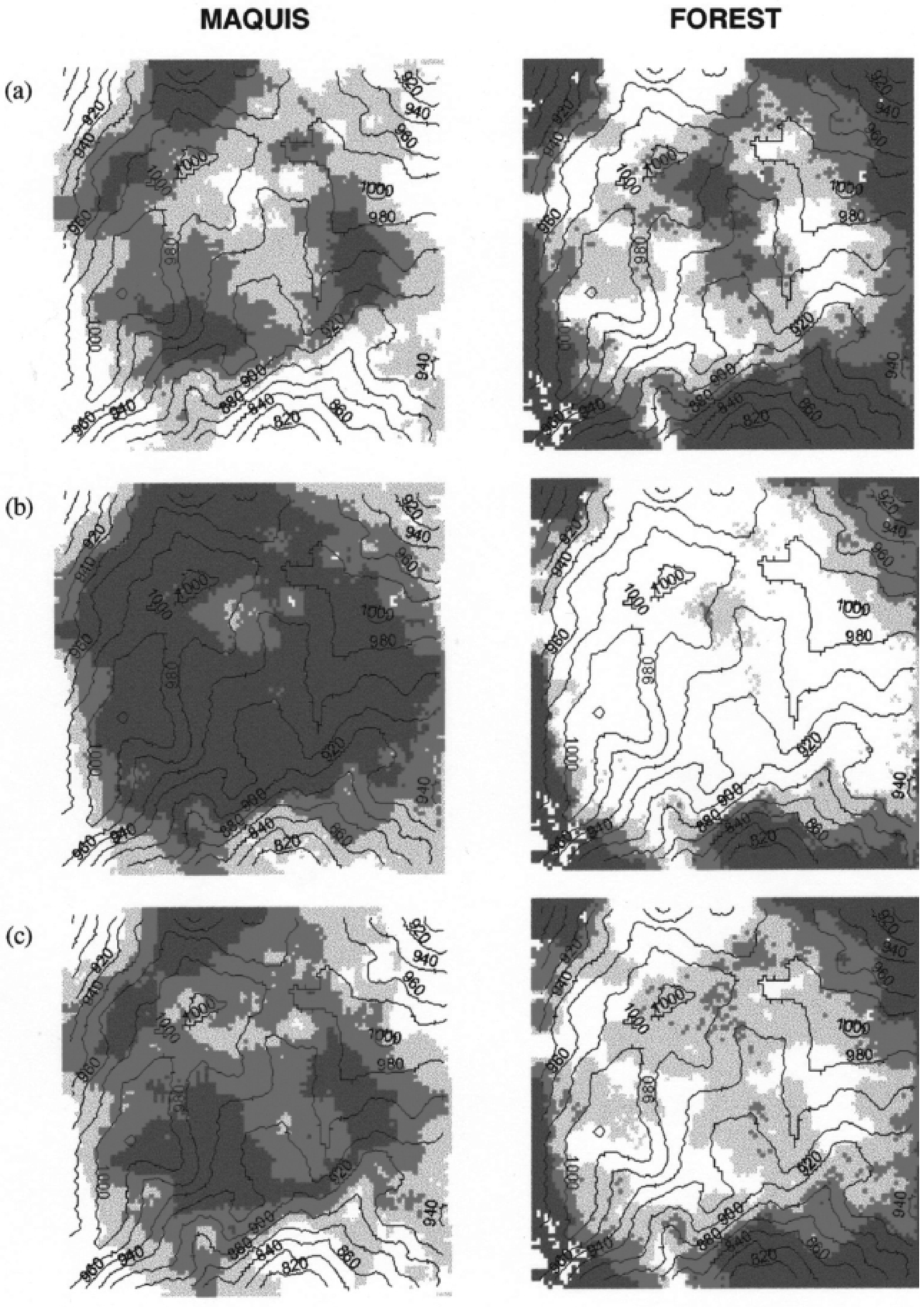

Fig. 11. Probability of maquis (left) or forest (right) vegetation occupying different parts of the landscape under different fire scenarios (**a**, size = 1000, **b**, size = 2000, **c**, size from negative exponential distribution). Contours are at 20-m intervals.

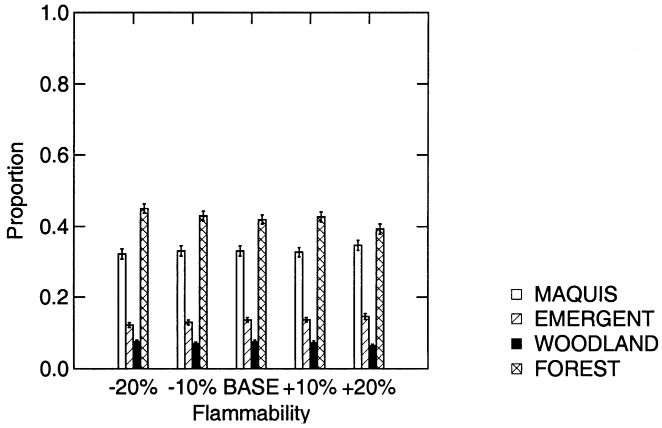

Fig. 12. Proportion of the landscape in each of the vegetation classes under different flammability scenarios; error bars are ±1 s.e.

increase either (or both) frequency and size. The relationship between serpentine substrate and sclerophylly is well documented,[34] as is that between sclerophylly and flammability,[35] suggesting an increased role for fire in serpentine landscapes so long as biomass production (fuel accumulation) does not limit fire spread. Other leaf properties associated with serpentine substrate (e.g. presence of oils in conifers and sclerophyllous angiosperms) might also influence flammability and may be worthy of further investigation.

The model indicates that at the landscape level the vegetation patterns seen on Mont Do are primarily driven by the disturbance regime (non-disturbance mediated approaches to seeking explanation for the distribution of maquis and forest are considered by Enright *et al.* elsewhere in this issue[36]). However, at broader spatio-temporal scales other factors such as long-term climate change may be superimposed, and at smaller scales factors such as local-scale edaphic variations leading to differences in growing conditions or safe sites for recruitment may be important. Furthermore, at different scales, disturbance events other than fire may become more significant. For example, in a dendroecological analysis of the influences of landscape on fire regime in the boreal forest, Bergeron[37] suggests that fire regime is controlled by long-term climate change at the regional scale, and by a strong interaction with landscape at the local scale. Both of these components may have a great impact on the distribution and dynamics of vegetation in the landscape.

Botkin and Nisbet[38] and Franklin *et al.*[39] believe that if global warming does occur, then fire frequency is likely to increase alongside a rise in fire intensity. How the fire regime on Mont Do may change in response to projected global climatic changes is uncertain. However, that temperature increases have occurred over the last century in the South Pacific seems indisputable (e.g. Salinger and Jones[40] suggest that average yearly temperatures have increased by ~0.6°C since 1860). Should these changes lead to an increased fire frequency (and possibly a coincident increase in disturbance size as a function of changes in flammability), then it seems likely that maquis will become increasingly abundant on Mont Do, and that fire-sensitive vegetation types such as forest will retreat to fire-protected sites such as gullies. The contemporary landscape of Mont Do suggests that this may have already taken place, possibly as a result of increased fire frequency since the time of human colonization of the islands. It seems probable that the occurrence and nature of ENSO events is also an important factor influencing the disturbance regime experienced by Mont Do.

Irrespective of the direction of any future changes in the disturbance regime, it does not appear that *A. laubenfelsii* is likely to disappear from the Mont Do landscape. There are two possible means through which the species may become extinct as a result of changes in the disturbance regime. First, if the occurrence or size of fire events was to increase significantly then the abundance of maquis in the landscape would increase and the abundance of the other vegetation types would correspondingly decrease (e.g. Figs 5 and 8). Alternatively, under very low fire frequencies, the abundance of late-successional forest in which *Nothofagus codonandra* might replace *A. laubenfelsii* may increase. However, the model suggests that this is unlikely to happen to the extent necessary to cause the local extinction of *A. laubenfelsii.* Even at low frequencies fire disturbance is sufficient to cause a patchy, mosaic landscape containing elements dominated by *A. laubenfelsii.* The complex mosaic on Mont Do at present is susceptible to small changes in fire regime in either direction. This susceptibility is possibly indicative of a transient landscape which appears stable at the scales at which humans tend to view ecological systems (see ref. 41), and because rate of successional change from maquis to forest is slow on these ultramafic soils.[13] Increased fire disturbance since human settlement of the islands may have caused the forest to retreat to the positions where it is seen today, while the reduced fire frequency over the last 30 years may be responsible for the increased evidence of regeneration of *A. laubenfelsii* in some parts of the maquis. Those areas of maquis where *A. laubenfelsii* is absent may be those that have either been recently subjected to fire, or which are more fire-prone. The very slow rates of successional change evident in the Mont Do landscape mean that the system will not recover rapidly from single fire events, and that two (or more) fire events happening in a relatively short time could lead to changes which take centuries to recover from. Recent evidence (N.J. Enright, pers. comm.) on the age of New Caledonian Araucariaceae for individuals growing on ultramafic substrates (e.g. *Araucaria muelleri,* estimated tree-ring age ~350 yr, radiocarbon date UWA33: 650±100 yr,) indicates that tree-ring counts may underestimate tree ages by up to half. This further emphasizes the likely role of slowed successional rates on ultramafics as a factor in the interplay between vegetation and fire in the expression of landscape-scale vegetation pattern.

The discussion above is based on results produced from a model designed to explore the dynamics of the Mont Do landscape. It seems appropriate, therefore, that some of the assumptions and limitations of the model be discussed. Within the model, the interactions between the disturbance regime and climate are very simplistic, reflecting the paucity of long-term climate data for New Caledonia. Development of this component of the model would allow more detailed investigation of landscape response to climate change, for example. Fire spread is modelled in a probabilistic, rather than mechanistic, manner. To understand how the landscape might respond to changes in the disturbance regime, and in particular changes in variables such as fuel flammability, a more detailed mechanistic approach to modelling fire spread might be valuable. However, most mechanistic models of fire spread operate at spatial and temporal resolutions (both inputs and outputs) far finer than is appropriate for landscape modelling.[22] Nevertheless models such as that presented here are useful tools for investigating the dynamics of large-scale landscape pattern — this, rather than the quantitative prediction of specific events, is the purpose of the model. Many of the assumptions and limitations reflect both its purpose and the lack of ecological data available for the Mont Do landscape.

While the results do not indicate a clear and important role for the special properties of ultramafic substrates in the outcomes of landscape-level dynamic processes, several potential interactions are recognized. Slow rates of biomass accumulation in maquis and slow succession to forest are outcomes of limiting soil conditions. This means that there may be a longer time lapse following fire before another fire can be sustained, and a longer mean interval between fires than would be the case on non-ultramafic sites with similar vegetation (e.g. some Mediterranean shrublands). In addition, flammability may generally be higher for vegetation of ultramafic substrates due to increased sclerophylly relative to vegetation on adjacent non-ultramafic substrates. We speculate that the landscape-scale vegetation pattern on adjacent, non-ultramafic substrates in New Caledonia should show a higher proportion of forest (relative to maquis) and higher levels of landscape diversity (SHDI), reflecting more rapid rates of succession to forest following disturbance, and smaller fire sizes.

Conclusion

The work presented here illustrates the manner in which landscape-level models may be used to explore the consequences of environmental change at scales not amenable to experimental approaches. The model demonstrates that if fire frequency or extent were to increase on Mont Do, then the amount of rainforest is likely to decrease. Conversely, if fire frequency or extent decreased, the amount of rainforest will increase as it invades the fire-dependent maquis. Changes in landscape structure (patch complexity, fragmentation) would accompany these shifts in landscape composition. Changes in the flammability of the vegetation in the landscape were found to have little impact on either landscape composition or pattern. This is an intriguing result, somewhat at odds with other similar models and one worthy of further investigation. Under none of the fire regimes explored did the unusual intermediate assemblage of maquis with an aborescent stratum of *A. laubenfelsii* disappear from the landscape. However, shifts in the fire regime in either direction would reduce the abundance of this striking vegetation type.

Further landscape modelling work on Mont Do will focus on how human-induced changes in the fire regime may have influenced the current landscape pattern, the temporal stability of the current landscape pattern, and how the Mont Do landscape may change in the future. As more data become available for the site the model can be improved — key areas for development are the seed production and dispersal routines and the fire spread algorithm. In addition, a key issue to be addressed concerns how landscape-scale vegetation dynamics in ultramafic landscapes might differ from that for vegetation on adjacent non-ultramafic substrates. The present modelling results suggest that slowed rates of plant growth due to limiting soil conditions may lead to feedback effects between vegetation and fire that ultimately control the landscape scale vegetation pattern.

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