An Individualistic Model of Vegetation Stand Dynamics

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FATE (Functional Attributes in Terrestrial Ecosystems) is a new, general model of vegetation dynamics which is based on a model of the functioning of individual plants in a stand. It has been designed to predict vegetation dynamics with a low resolution and from a simple parameter set. This makes it suitable for use by managers of extensive natural areas. FATE also provides age structure information about communities.

We have divided plant function into three main areas (life history, responses of plants to their immediate environment and their responses to natural disturbance), and built the FATE model by constructing a simple representation of essential features of each of these processes.

Examples from Australian forest and woodland communities are used to demonstrate the operation of the model and to compare it with other modelling approaches. The limitations of FATE and possible extensions are also discussed.

Keywords: vegetation, stand dynamics, modelling, functional attributes.

1. Introduction

In recent years, work on the theory of vegetation dynamics has utilized a wide variety of approaches and formalisms (Connell and Slatyer, 1977; Shugart, 1984; Tilman, 1985; Pickett *et al.*, 1987). Despite this diversity, nearly all discussion of the subject in the last fifteen years has shared an underlying conceptual framework which is remarkably consistent. The core of this research programme is the idea of H. A. Gleason (1926) that the best way of understanding the dynamics of plant communities is to work from a knowledge of how individual plants function in their environment.

Tied in with the Gleasonian approach is the idea that competition between plants takes place mostly through interference (Harper, 1977); that is, that the major interactions between plants are due to modification of the environments of the individuals concerned, especially through pre-emption of resources by competitively superior plants.

This paper presents a new, general model of vegetation dynamics. The model lies

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firmly within the Gleasonian research programme, having been constructed by explicitly considering the biology of individual plants. It is concerned with stands of vegetation of the order of 1 to 10^2 ha in extent and with time scales of 1 to 10^3 years. We will refer to it as FATE (an acronym for Functional Attributes in Terrestrial Ecosystems).

Our reasons for constructing FATE were both theoretical and practical. If one examines various general models of vegetation dynamics (Table 1), two related points become apparent. First, there is a gap between those models which operate at the level of populations and those which deal with the fates of individual plants. The relatively site-specific model of Kessell and Potter (1980) is a partial exception. Population models cannot capture the life history processes which are important in many successions (Noble and Slatyer, 1980; Legg, 1980; Peet, 1981), but it is not necessary to descend to the individual level to achieve a dynamically sufficient (Lewontin, 1974) description of vegetation: age structure information can be incorporated by modelling cohorts. The use of cohorts in plant community models has previously been restricted to the work of Malanson (1984), who used an extended Leslie matrix model to examine the dynamics of California coastal sage scrub.

The second point is that even models which are not especially complex in their formulation, for example the resource-ratio model (Tilman, 1985) and the Lotka–Volterra succession model presented in Huston and Smith (1987), are resistant to mathematical analysis. By this we mean that analytic techniques can extract only equilibrium solutions for these models, and sometimes not even those; since stands of vegetation rarely come to equilibrium (see papers in Pickett and White, 1985), such solutions do not provide us with useful predictive ability. Note that all the mathematically tractable models in Table 1 are analysed using techniques from probability theory.

Our theoretical motivation was paralleled by a practical one. Land managers have a need for predictive models of vegetation dynamics, especially in situations where natural disturbance is important. Constraints on time and funding mean that it is impossible to construct specialized models for every area of interest to land managers; generalized models are therefore needed.

The generalized predictive tools hitherto developed by ecologists are the vital attributes scheme (Noble and Slatyer, 1980) and especially the class of forest gap models (Botkin et al., 1972; Shugart, 1984; these in fact usually require considerable "tuning" before they can be used in a given situation). There is a need to predict vegetation change with more resolution than the presence/absence information which the vital attributes model provides; however, where extensive landscapes are concerned, the resolution (and consequent complexity) of forest gap simulators are often unnecessarily high and their use involves computational difficulties. There is also a need to use models in making strategic rather than tactical decisions. By *strategic* we mean especially that a model's predictions be made within the context of disturbance regimes rather than individual disturbances.

By far the most efficient way to achieve this goal is to deal with models that are mathematically tractable. The only way to obtain a strategic perspective with intractable models is to perform multiple simulations, which may well be expensive of resources.

FATE provides a *discrete quantitative* resolution, that is it uses ranked scales for abundance and for plant attributes; it can be used in conjunction with tractable mathematical models to provide predictions in a form useful for strategic decision making.

TABLE 2. *The division of plant function used in FATE, with the parameters required to describe each process. Cf table 1 in Pickett et al.* (1987)

Plant function	Process	Parameters	Parameter domain
Life history	Dispersal	Is functional group widely dispersed?	Yes/No
	Dormancy/ propagule storage	Does functional group have innate dormancy?	Yes/No
		If so, then: —longevity of dormant pool† propagule pool	
		—proportion of propagules moving from the dormant to the active pool as a result of each disturbance type	Proportion‡
		Longevity of active propagule pool	Age
	Germination/ enforced dormancy	Germination rates at each resource level	None/Low/ Moderate/High: see table 3
	Establishment	See environmental response	
	Growth	Size§ of immature plants as a proportion of the size of mature plants	Proportion
	Maturation	Maturation time	Age
	Senescence	Lifespan	Age
Environmental response	Tolerance of environmental conditions	Strata of plants in immature and mature life stages	Small integer
		Survival/death of germinants, immatures and matures	Yes/No
	Niche relationships	Maximum abundance at the site	Low/Medium/ High¶
Disturbance response	Escape Death	Proportions of each life stage meeting each of the three fates	Proportion‖
	Resprouting	Ages of resprouting plants	Age

† Ages are integer values which represent numbers of time steps. Usually the time step will be one year.

‡ Proportions are expressed on a scale of none/few/half/most/all. Arbitrary values are assigned to the intermediate levels, viz. 10% for "low" or "few", 50% for "half" and 90% for "most".

§ In internal calculations of resource availability, the consumption of resources by a cohort of immature plants is assumed to be this proportion of the consumption of an otherwise equivalent cohort of mature plants. This assumption is based on an extremely simple, discrete-stage model of the growth of individual plants.

¶ The highest level of maximum abundance implies that a functional group could capture all the resource entering a stand in the absence of the deleterious impacts of other functional groups. The other levels represent proportions of this highest value; they are set arbitrarily at 50% for "medium" and 10% for "low".

‖ Only two of the disturbance responses need be specified; the third may be inferred from those given.

We have simplified Harper's (1977) description of the propagule pool. In FATE, propagules in innate and induced dormancy form a *dormant* pool, while active propagules and those in enforced dormancy are combined as an *available* pool. (Not all functional groups have a dormant pool.) In the present version of FATE, propagules may move from the dormant to the available pool only as a result of a disturbance. The abundance of each propagule pool is measured on a discrete scale with three levels: nil, low or high abundance.

The *germinant* life stage corresponds to Harper's "seedlings". The germinant stage is assumed to last less than one time step. It corresponds to the period in which a plant

TABLE 4. Germination rates used in the FATE model, and the modification of germination rate by propagule bank size

Germination rate (discrete scale)	Functional groups with innate dormancy	Functional groups without innate dormancy
None	0·0	0·0
Low	$0·1/([S-1)/3]+1)$	$0·1/L$
Moderate	$0·5/([S-1)/3]+1)$	$1·0/L$
High	$1·0/([S-1)/3]+1)$	$1·0/\min((M+1),(S+1))$†

M, maturation age of a functional group; L, its lifespan; and S, the longevity of propagules in the active pool. [x], integer next below x; $[(S-1)/3]+1$ represents the number of time steps a functional group will retain a high propagule abundance in the absence of propagule input. The values given here are proportions of the maximum abundance of the functional group.

† For functional groups with widely dispersed propagules, the propagule longevity is ignored in the calculation of cohort size for the high germination rate.

2.3. COMPETITION SUBMODEL

The dominant environmental influence on survival of plants in a community is assumed to be the availability of a single resource, or at least several resources which follow the same trends. We differ here from Tilman (1982); also, if one follows the view of Yodzis (1986) that plants compete for generalized "space" then space may be considered to be the single resource and the model may be formulated in the same manner. Three discrete levels of resource availability are considered: high, medium and low. The internal calculations of resource availabilities described below are once again carried out in real arithmetic and then classified; the continuous scale of resource availability ranges from 1 (the level in the "global" environment, outside the canopy and rhizosphere) down to a minimum of zero.

Competitive relationships between plants are expressed by ordering the plants into discrete *strata*. All plants of the same functional group and life stage are assumed to fall in the same stratum; plants may move from stratum to stratum as they change life stage. We consider that even in structurally complex communities the competitive relationships between life stages and functional groups can be expressed in no more than five or so strata.

The amount of resource available to plants in a stratum is a function of the total abundance of plants in superior strata. If the plants of a life stage cannot tolerate the current resource level in their stratum, then they will all die. Competition between plants in different strata is therefore one-sided; plants in the same stratum are assumed not to affect one another's survival. Competition in FATE is also indirect, being mediated by the resource.

The term *abundance* of a cohort in FATE is taken to be the amount of the resource consumed by the plants comprising it. Thus, an abundance of 1 represents capture of all the available resource. Measurable surrogates for this conceptual abundance might be actively growing biomass (where nutrients are important) or leaf area (where light is important). It is assumed that the effects of density-independent and self-thinning mortality and growth of surviving plants roughly balance, so that the total amount of the resource consumed by a cohort of a given life stage and size at recruitment is constant. The amount of resource consumed by a cohort of immature plants need not be as great as the amount consumed by an otherwise equivalent cohort of mature plants, as detailed in Table 2.

initial community of sequences of disturbance types and disturbance intervals. Because such simulations can be performed in a matter of seconds on a microcomputer, they can be used by land managers to ask "what-if" questions about the responses of vegetation to different sequences of events. Simulations with FATE are deterministic; a single simulation run therefore suffices for prediction, in contrast with the multiple simulations required if one uses a forest gap model. FATE simulations covering several centuries generally take less than a minute on a microcomputer.

FATE can also be used to generate the *replacement sequence* for a landscape unit (Noble and Slatyer (1980) developed replacement sequences using the vital attributes scheme). A replacement sequence may be defined mathematically as a directed graph in which the nodes represent community types and the arcs denote changes of community type due to succession or disturbance (e.g. Figure 1). A stand's replacement sequence captures all its possible trajectories. Replacement sequences are created by dividing each successional sequence into stages which are sufficiently similar in composition, establishing the community arising from disturbance of each of these stages, and treating each of these as the starting point of a new succession; the process is continued recursively. Note that a replacement sequence derived in this way is strictly an approximation; how approximate it is, and the size of the sequence, depend upon the definition of "sufficiently similar".

Directed graphs lie at the heart of the mathematical theory of stochastic processes, including the Markov process familiar to vegetation ecologists. A stochastic process may be represented as a graph in which the nodes are states and the arcs the possible
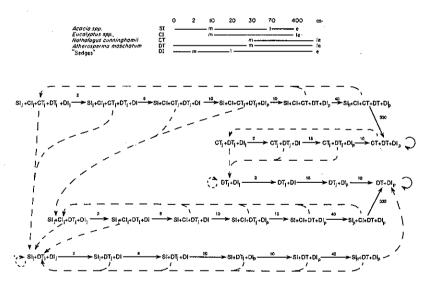

Figure 1. Vital attributes scheme and replacement sequence for a forest community in south-western Tasmania (adapted from Noble and Slatyer, 1980).

Functional groups with the "D" persistence attribute will have propagules available at any time a fire occurs; those with the "S" persistence attribute have long-lived propagules; those with the "C" persistence attribute have short-lived propagules, so that mature plants must be present immediately before a fire for the functional group to persist through the fire. Functional groups with the "T" establishment attribute continue to establish in the absence of fire, while those with the "I" vital attribute can only establish shortly after fire. "m" is the time after a fire at which a functional group reaches the mature stage, "l" the time at which it leaves the mature stage and "e" the time at which it becomes locally extinct.

Successional transitions are shown with solid arrows while transitions due to wildfire are shown by dashed arrows. The subscript "j" denotes the immature population stage; the subscript "p" denotes the propagule population stage. The numerals above arrows show the length of each successional stage.

TABLE 5. Functional attributes of plants in a forest community of southwestern Tasmania

	Eucalyptus	Nothofagus	Atherosperma	Acacia	"Sedges"
Maximum abundance	High	High	High	Medium	High
Maturation time	10	30	30	10	2
Lifespan	400	400	250	70	20
Size of immatures relative to adults	Low	Low	Low	Low	Low
Stratum of: immatures	2	2	2	1	1
adults	3	3	3	2	1
Widely dispersed propagules	No	No	Yes	No	Yes
Innate dormancy	No	No	No	Yes	No
Propagule lifespan: active	0	0		5	
dormant				200	
Proportion of propagules with dormancy broken by fire				High	

	Eucalyptus			Nothofagus			Atherosperma			Acacia			"Sedges"		
Resource level:	Low	Moderate	High	Low	Moderate	High	Low	Moderate	High	Low	Moderate	High	Low	Moderate	High
Germination rate:	Nil	No	No	Mod.	Mod.	High	Mod.	Mod.	Mod.	Nil	No	High	Nil	No	High
Survival of: Germinants	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes	Yes	No	Yes	Yes
Immatures	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes	Yes
Matures	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes

Disturbance: Fire

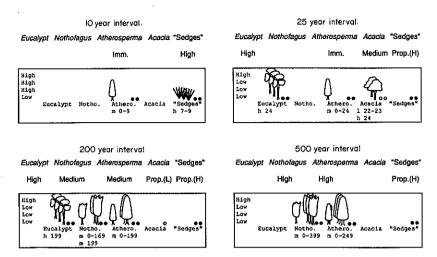|	Eucalyptus	Nothofagus	Atherosperma	Acacia	"Sedges"
Propagules unaffected:	All	All	All	All	All
Immatures unaffected:	None	None	None	None	None
Adults unaffected:	None	None	None	None	None
Immatures resprouting:	None	None	None	None	None
Adults resprouting:	None	None	None	None	None

Figure 3. The results (as predicted by FATE) of repeated fires at each of four intervals (10 years, 25 years, 200 years and 500 years) on the composition of a forest community in south-west Tasmania. The descriptions of communities are as in Figure 2.

4.2. INVASION BY BROOM CYTISUS SCOPARIUS AT THE BARRINGTON TOPS, NEW SOUTH WALES

English broom *Cytisus scoparius* is a shrub, native to western Europe, which has become naturalized in many places in south-eastern Australia. In the Barrington Tops region of New South Wales (151°30′E, 32°S), it has become a serious pest both in grazing land and a National Park (Waterhouse, 1988). Natural vegetation of the area consists of sub-alpine grasslands and woodlands dominated by *Eucalyptus* species, mainly *E. pauciflora*, *E. fastigata* and *E. dalrympleana*. The shrub layer is typically very sparse or absent.
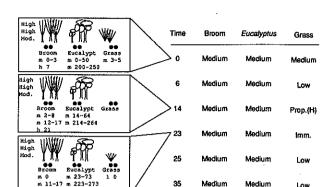
Functional attributes are presented in Table 6 for three functional groups: *C. scoparius*, the eucalypts, and grass species such as *Poa sieberana*. The two disturbance types considered are potential control measures, viz. low-intensity fire and spraying the broom plants with herbicide.

As shown in Table 6, seedlings of *C. scoparius* are observed to germinate even at low resource availabilities. There is some question, however as to whether any of the germinant *C. scoparius* can successfully establish at low overall resource levels (Waterhouse, 1988). While seedlings of *C. scoparius* cannot establish under a continuous canopy of mature plants, its high seed densities (c. 3000 ha^{-1}) mean that broom can successfully exploit small-scale gaps caused by, for example, the foraging of feral animals. The frequency of appearance of such gaps is unknown; we take both possibilities into account here.

Note also that both immature and mature *C. scoparius* plants are placed in the same stratum as the mature eucalypts. Since established broom plants seem to be very tolerant of low resource levels, the eucalypts cannot exert any competitive effect on their survival.

Our example deals with a woodland community in the process of being invaded by *C. scoparius*. Figure 4 shows the predicted results of 40 years succession in a woodland from the same stage of invasion assuming that germinant *C. scoparius* are intolerant (Figure 4(a)) or tolerant (Figure 4(b)) of low resource levels. If broom does in fact regenerate in small gaps, then *Poa* will not persist in the above-ground community. On the other hand,

(a)

Time	Broom	*Eucalyptus*	Grass
0	Medium	Medium	Medium
6	Medium	Medium	Low
14	Medium	Medium	Prop.(H)
23	Medium	Medium	Imm.
25	Medium	Medium	Low
35	Medium	Medium	Low

(b)

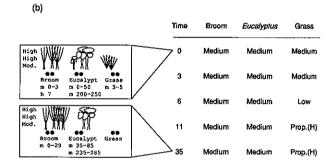| Time	Broom	*Eucalyptus*	Grass
0	Medium	Medium	Medium
3	Medium	Medium	Medium
6	Medium	Medium	Low
11	Medium	Medium	Prop.(H)
35	Medium	Medium	Prop.(H)

Figure 4. A simulation of 35 years succession in a woodland community at the Barrington Tops, New South Wales, which has been infested by broom (*Cytisus scoparius*). In (a) it is assumed that germinants of broom are intolerant of low resource levels, allowing a "window" in which grasses (*Poa* spp.) may recruit. In (b) it is assumed that germinant broom are tolerant of low resource levels; *Poa* is excluded from the above-ground community. The descriptions of communities are as in Figure 2.

4.3. SCLEROPHYLL WOODLAND NEAR CANBERRA

Our final example is taken from a dry sclerophyll woodland near Canberra, Australia (Purdie and Slatyer, 1976) dominated by *Eucalyptus macrorhyncha* F. Muell. ex Benth., *E. rossii* R. T. Baker et H. G. Smith and other lignotuberous eucalypts. It has been chosen to show how the FATE model overcomes one of the major inadequacies of the vital attributes model.

Noble and Slatyer (1977) presented the vital attributes of three functional groups in the community; we have included a further functional group representing the grasses (*Poa* spp.) and generated the replacement sequence given in Figure 6. Because all four functional groups have the "I" (intolerant) vital attribute, the result of a succession lasting more than 100 years is unrealistic.

The functional attributes of these four groups are given in Table 7 and the results of a simulated succession after fire shown in Figure 7. In the FATE model, canopy breakup is followed by a second period of recruitment which results in an even-aged eucalypt population, with a grassy understorey in its earlier stages.
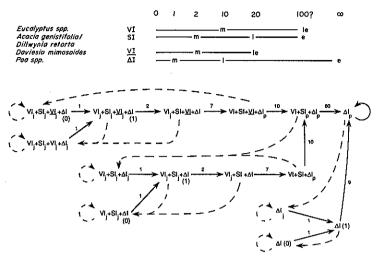
Figure 6. Vital attributes scheme and replacement sequence for a sclerophyll woodland community near Canberra, Australia (expanded from Noble and Slatyer, 1977). Symbols are as in Figure 1; the Δ persistence attribute indicates that the functional group will return to the mature population stage after a fire at any time. Note that 100 years without fire is predicted to produce a community with no plants except propagules.

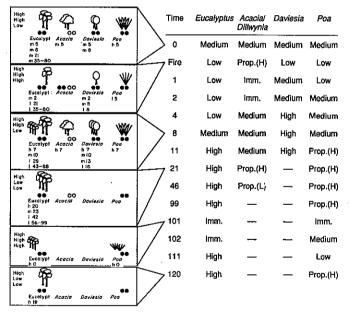| Time	Eucalyptus	Acacia/ Dillwynia	Daviesia	Poa
0	Medium	Medium	Medium	Medium
Fire	Low	Prop.(H)	Low	Low
1	Low	Imm.	Medium	Low
2	Low	Imm.	Medium	Medium
4	Low	Medium	High	Medium
8	Medium	Medium	High	Medium
11	High	Medium	High	Prop.(H)
21	High	Prop.(H)	—	Prop.(H)
46	High	Prop.(L)	—	Prop.(H)
99	High	—	—	Prop.(H)
101	Imm.	—	—	Imm.
102	Imm.	—	—	Medium
111	High	—	—	Low
120	High	—	—	Prop.(H)

Figure 7. Stages in the succession of a sclerophyll woodland community near Canberra after wildfire, as simulated by the FATE model. Symbols are as in Figure 2. This figure should be compared with the successional sequence running across the top of the replacement sequence in Figure 6.

5. Discussion

There has long been a dichotomy between ecological models constructed for the purpose of mathematical analysis and those constructed for the purpose of simulation (Pielou, 1969).

Frequently, models intended for the first category are found to fall within the second (e.g. Tilman, 1985), simply as a consequence of the limitations of mathematical techniques. FATE is a hybrid; the biological model is numerical in its formulation, but because the range of trajectories that it may follow is relatively small, and because the successional process and the responses to disturbance are deterministic, it can be used to construct a replacement sequence of analytically manageable proportions. This melding of approaches is novel.

Huston and Smith (1987) have argued that plant succession is driven by interactions between individual plants and that the appropriate level of aggregation for understanding forest succession is therefore that of the individual plant. We disagree with the exclusiveness of the second assertion: in fact, the crucial element missing from the population models criticized by Huston and Smith (1987) is competitive structure, and, as we have shown here, this may be captured while aggregating the vegetation into cohorts. The FATE model can, for instance, be used to generate mechanistically the five general patterns of two-species interactions presented in Figure 3 of Huston and Smith (1987).

Scale hierarchies are increasingly being regarded as of fundamental importance in understanding natural vegetation (e.g. White and Pickett, 1985). While the FATE model operates at the spatial scale of the landscape unit, the impacts of processes occurring at smaller scales on its operation should be appreciated. Growth and competition are conceived as being individual-scale processes, while disturbance operates at the landscape-unit scale. The question of scale must be borne in mind when parameterizing the model, especially the responses of propagules and germinants to resource availabilities. The resource levels in the model are average values at the stand scale; at the individual scale, there will be variation around this average, and a functional group which cannot germinate or establish at the notional level may be able to exploit the "gaps" to achieve partial success. The importance of local variation in disturbance severity has already been discussed; it may be thought of as occurring at an intermediate scale.

Although the strata in FATE are not physically defined, the physical sizes of mature and immature plants can be used with the FATE model to arrive at the physical structure of the communities predicted by the model. This information will be of use to those concerned with managing populations of animals which respond to vegetation structure rather than composition. It also means that FATE's community descriptions can be readily classified using structural systems such as that of Specht (1981).

By their very essence, all models are limited in their application. It is therefore important to recognize the limitations of the FATE model as well as its capabilities. Restrictions on the applicability of FATE arise from three sources: the assumption of a reasonably constant global environment, the use of qualitative scales for estimating parameters, and the fact that the model deals with a single, isolated stand. All these restrictions can be readily removed at the expense of an increase in model complexity.

The assumption that the environment outside the stand, and in particular that the rate of arrival of resources in each time step is reasonably uniform, renders FATE unsuitable for use in a number of ecosystems, for example deserts, where the most important resource (water) arrives unpredictably. We consider (with Bazzaz, 1983) that events such as rainfall in deserts are in fact a form of natural disturbance: the essential elements of natural disturbances are their stochasticity and the fact that they change resource availabilities suddenly (whether they destroy plant matter or not). The concept of "resource" used in FATE would have to be generalized in order to model such ecosystems.

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