Modelling survival of plant populations with differing mobility and sensitivity to climate change over real and simulated terrain types

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Abstract Scenarios of predicted climate change are expected to impact many biological populations independently of their current equilibrium-level community affiliations. A model is presented that uses environmental response surface, dispersal potential, plant longevity, and climate change vectors to predict the survival of various plant species populations with differing terrain types. These types include actual GIS cases from southern Africa with multiple levels of landscape permeability and discontinuity. Examples include terrain slope configurations that satisfy survival requirements of different plant populations with expected climate change.

1. INTRODUCTION

Development of models to predict change over landscapes is driven by availability of types of data at that level. High diversity of biotic species coupled with a high level of species specific behaviour places severe demands on developing the information base [Turner, et al., 1995] needed for modelling representative ranges of metapopulations in real space and time. Broadscale plant-related models have tended to concentrate on more easily generalised processes, such as primary productivity [Rutherford, 1993], or on units of plant form [Mackey, 1993], plant formation or biome [Prentice, et al., 1992; Neilson, 1995]. Systematic assessment of the behaviour, traits and response to environment of comprehensive sets of plant species through, for example, experimental screening programmes, have enjoyed little support outside forestry and intensive agriculture. This, in turn, has encouraged the use of surrogate behaviour data derived from both the occurrence (and absence) of species recorded in various forms of spatial survey and their apparent relations with environment. The application of these correlative data in space and time is inherently circular but potentially testable.

Many regions, including southern Africa, are likely to experience unprecedented rates of change in climate within the next century [Tyson, 1993]. Sufficient evidence suggests that species may respond independently to future climate change [Huntley, 1991]. This paper develops a modelling framework to predict the survival of plants at the species level under projected climatic conditions in South Africa. Advantage is taken of the recent availability of relatively high resolution and appropriate spatial databases for the region. Species are modelled independently of vegetation type affinity [see Sanderson et al., 1995].
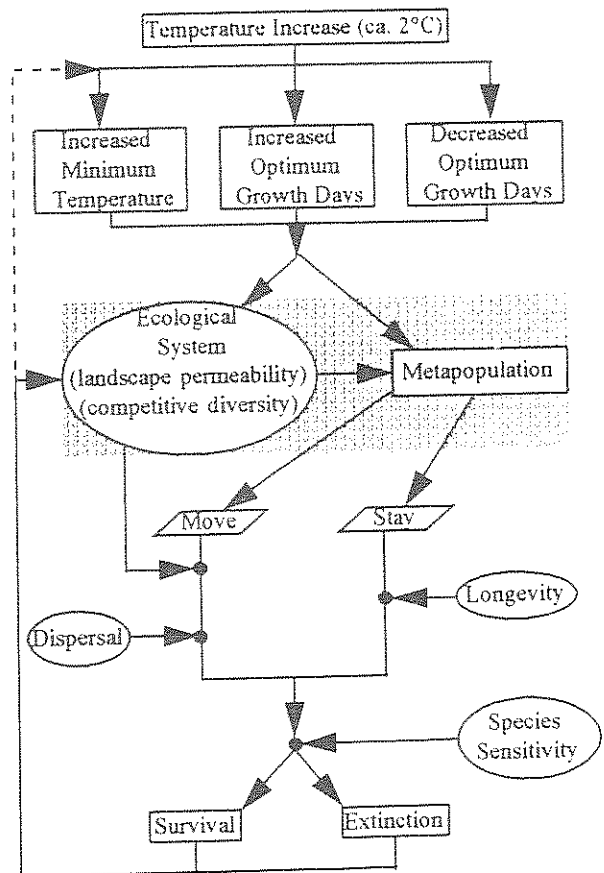

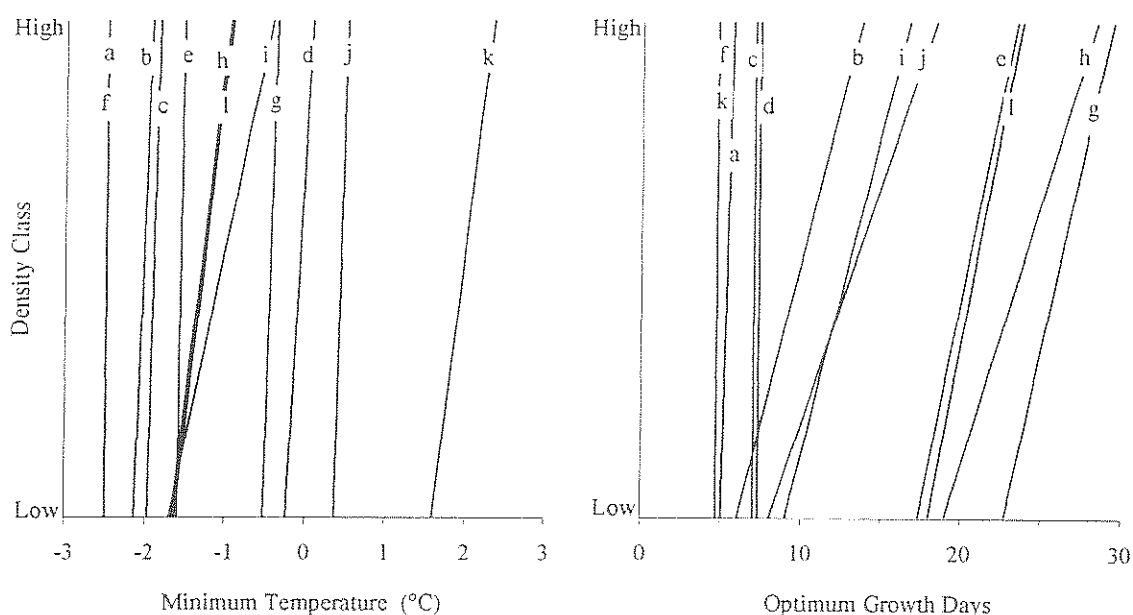Figure 1: Broad-scale rule-based model of the survival of metapopulations

Figure 2. Species sensitivity to minimum temperature and optimum growth days. (a) *C. tenuifolia*; (b) *A. congesta*; (c) *T. terrestris*; (d) *G. africana*; (e) *T. minuta*; (f) *E. rhinocerotis*; (g) *S. verticillata*; (h) *B. bipinnata*; (i) *D. stramonium*; (j) *N. glauca*; (k) *O. pes-caprae*; (l) *S. vulgaris*.

2. METHODS: APPROACH AND MODEL ELEMENTS

The model's bioclimatic foundation extends the approach applied by, for example, Booth [1990], Busby [1991] and Sindel and Michael [1992]. Essentially, the environmental limits of a selected species are determined by matching the comprehensive species distribution records and environmental (often climatic) records at a spatial resolution adequate to avoid ambiguity caused through local heterogeneity. This provides an estimate of the realised niche of the species [Cao, 1995] and is often expressed in the form of an environmental envelope [Carpenter et al.,

1993] or, where relative abundances are available, as an environmental response surface [Westman, 1991]. Rutherford et al., [In press] summarise the assumptions and some limitations of this approach.

We used the newly available ACKDAT data-base which reflects comprehensive plant abundance records of a total of about 12000 species at over 3500 sites well distributed throughout South Africa [Rutherford. et al., In press]. A climatic data-base at a corresponding spatial resolution of 1 x 1 minute provided temperature and water availability data for the close to half a million grid cells that cover the large climatic ranges found in South Africa.

Table 1. Species properties and climate-induced changes in potential area

| Species	Samples	Dispersal Rate Index	Longevity Index	Relative Sensitivity Rank MINT	Relative Sensitivity Rank OGD	Area (x 10^5 km²) Present Total	Area (x 10^5 km²) Present High Density	Area (x 10^5 km²) Future Meth. 1 Total	Area (x 10^5 km²) Future Meth. 1 High Density	Area (x 10^5 km²) Meth. 2 Total	% Change from present to future (Method 1) High Density	% Change from present to future (Method 1) Total
C. tenuifolia	1095	5	<10	1	3	9.53	8.71	8.23	7.16	6.33	-17.8	-13.6
A. congesta	1026	10	<1	5	7	11.42	10.57	10.54	8.31	10.53	-21.4	-7.7
T. terrestris	647	1	<1	3	1	10.28	8.50	8.50	6.32	3.74	-25.7	-17.3
G. africana	387	3	<20	3	2	4.95	4.54	5.04	4.76	3.13	4.9	1.7
T. minuta	371	1	<2	2	5	10.58	9.85	8.38	7.25	1.66	-26.4	-20.8
E. rhinocerotis	363	1	<50	1	1	6.70	5.72	5.99	5.29	1.37	-7.5	-10.6
S. verticillata	284	3	<5	4	6	8.45	6.85	5.66	4.10	3.16	-40.1	-33.1
B. bipinnata	223	1	<1	7	8	10.05	7.79	7.20	4.79	1.03	-38.5	-28.4
D. stramonium	196	3	<5	9	7	10.05	0.65	8.45	0.01	4.18	-98.9	-16.0
N. glauca	185	1	<20	6	9	8.18	7.26	7.19	4.94	1.35	-31.9	-12.1
O. pes-caprae	168	1	<100	8	1	3.84	2.83	5.00	4.87	0.56	72.1	30.3
S. vulgaris	119	5	<50	7	4	9.72	8.66	6.88	5.96	2.55	-31.1	-29.2
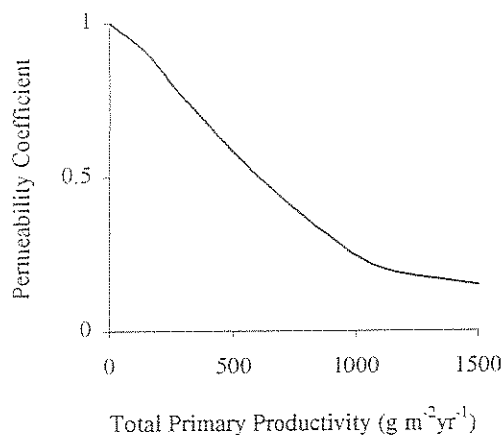
Figure 3. Dependance of landscape permeability on net primary productivity.
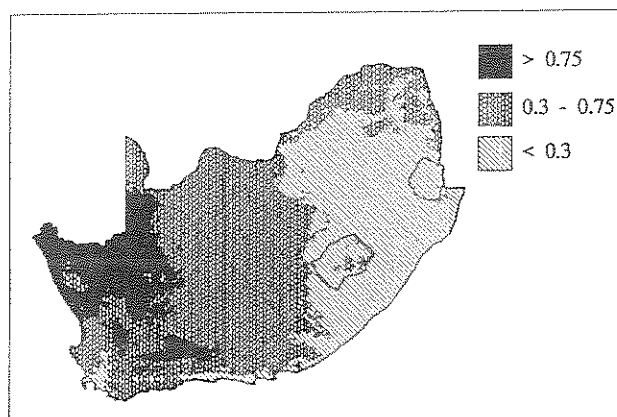

Figure 4: Distribution of classes of landscape permeability coefficients.

All plant species selected were "weedy" opportunists in disturbed areas and well represented in South Africa. Therefore, each realized niche was expected to more closely approximate the fundamental niche, competitive effects with other plant species should be reduced, and a short generation time (juvenile period to reproductive maturity - not plant age) would allow sensitive response to climate change. It has been shown that, at regional scale, scarce species often predict poorly [Cherrill, et al., 1995] and that broad-niched, generalist species are better able to track environmental change than specialist species [Bowers and Harris, 1994]. The species employed were *Aristida congesta, Bidens bipinnata, Chysocoma tenuifolia, Datura stramonium, Elytropappus rhinocerostis, Galenia africana, Nicotiana glauca, Oxalis pes-caprae, Setaria verticillata, Stoebe vulgaris, Tagetes minuta and Tribulus terrestris* and are listed in Table 1 together with various estimated properties.

Two primary and independent climatic determinants of plant establishment and growth were used. The first was a low temperature factor expressed as minimum temperature of the coldest month (monthly mean of daily values). The

second was number of optimum growth days expressed as the number of days when the actual evapotranspiration is more than half the potential evapotranspiration for the topsoil horizon and when monthly mean temperature exceeded 24°C. Growth days were calculated from daily soil water budgeting routines using actual soil properties and assuming hydrological vegetation characteristics. Optimum growth days fell to zero in a few high altitude areas which contained very few plant record sites and occurred outside the current area of model application. Climatic envelopes were established for each species using the mean of the three minimum and three maximum extremes for each climatic parameter. The procedure was repeated for higher density occurrences to obtain a nested "core" population in contrast to the "marginal" lower density populations. These provided the minimal requirements to approximate unimodal type response surfaces for use in the model of climate change.

The model structure is summarised in Fig. 1. The initial perturbation applied corresponded to a 50 year scenario of a 2°C increase at 30° latitude South but with temperature change increasing at higher latitudes. No change in precipitation is assumed for the region. The temperature increase results in reduced frost and a decrease in number of optimum growth days in more arid parts owing to increased evapotranspiration and to an increase in number of optimum growth days in the more mesic areas owing to longer growing seasons. These changes impact a species metapopulation and the parameters (for example, landscape permeability) of the rest of the ecological system (habitat) which in turn affects, *inter alia*, the effective mobility of metapopulation. The survival or extinction of the metapopulation is governed further by dispersal rates, plant longevity and intrinsic sensitivity level to environmental change. Resultant changes in metapopulations feed back to the ecological system and ultimately to the climate systems, although these feedbacks are not incorporated in the current model.

Dispersal rate indices given in Table 1 are largely based on the morphology of the diaspore and a factor of about 30 was used for conversion to linear kilometre distance over 50 years in the present model. This is a function of both dispersal jumps and generation length. Extreme rates rather than mean rates are important for rate of migration. The likely increase in landscape disturbance will also promote a more rapid movement of species that colonize disturbed areas. Noble [1989] has asserted that humans are already the dominant vector of plant dispersal.

Individual longevity indices reflect maximum expected perenniality in years but owing to paucity of data is subject to non-linear rescaling. Levels of precision may approximate those of Jurado, et al., [1991]. Relative sensitivities of species in terms of range of critical thresholds are indicated in Fig. 2. The slope of the response indicates the sensitivity of the whole population to climatic change and is ranked in Table 1. For example, in terms of growth days, species with less steep response slopes (e.g. *A.*

congesta) have the potential to survive as low density populations whereas steep sloped response species (such as *G. africana*) do not.

The movement of diaspores across the landscape was subjected to a landscape permeability coefficient which was inversely related to the changing production of plant biomass (Fig. 3) both as a physical barrier and possible competitive establishment resistance. Net primary productivity was estimated at the 25 year point through application of the simple empirical Miami Model (Esser, 1991). This form of landscape permeability is in keeping with relationships indicated by Cremer [1965] and differs

from that proposed by Dyer [1995]. The distribution of landscape permeability is indicated in broad classes (Fig. 4).

Net migration was effected using two methods. Method 1: applying the climatic change to the entire climatic envelope which is probably an over-estimate since current climatic potential ranges tend to be under-saturated. Method 2: applying the change to only the actual positions where the species was recorded (using the rook's move rule) which is almost certainly an under-estimate owing to incomplete sampling. The best estimate should lie between the two approaches.
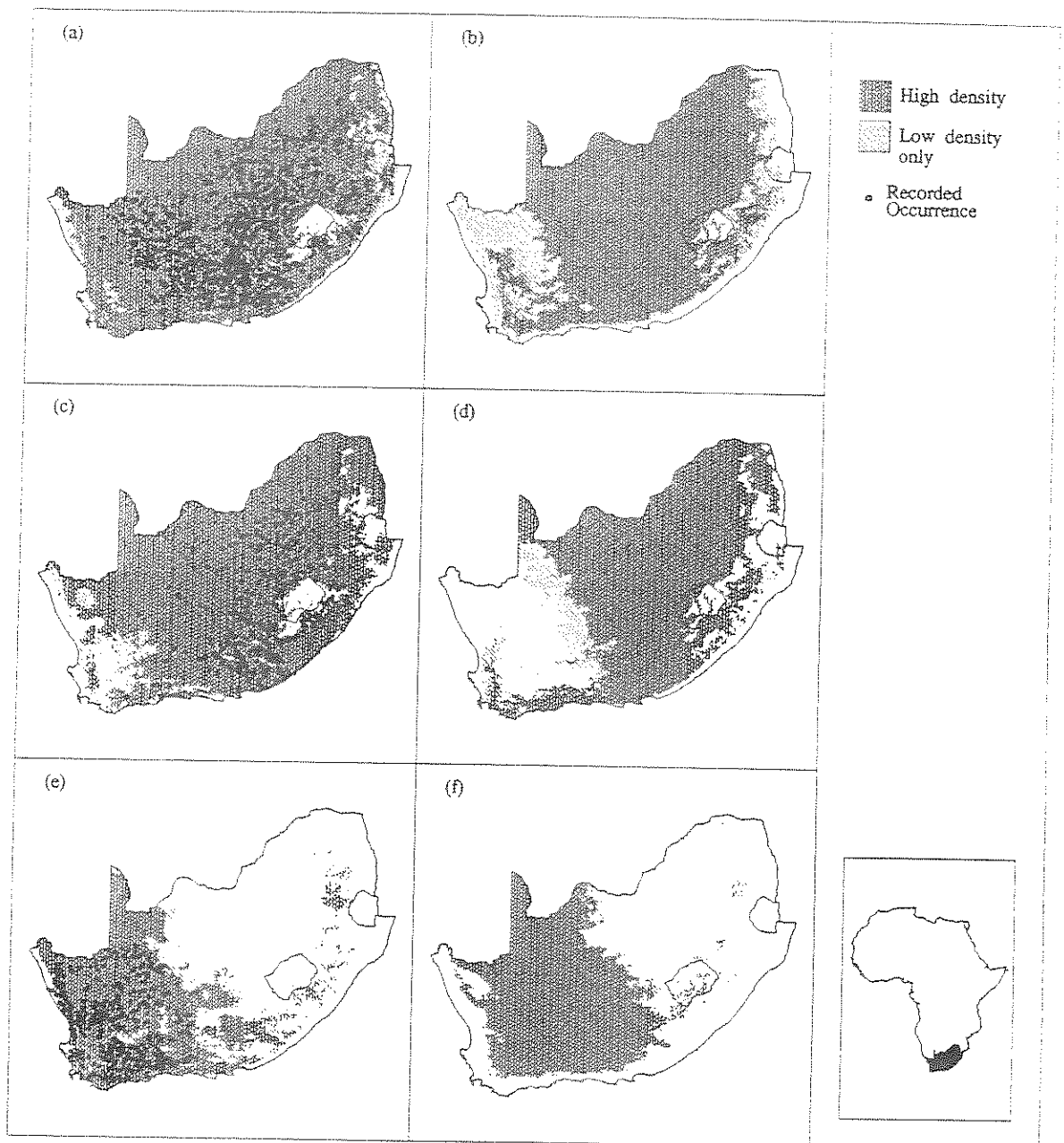

Figure 5: Current and future potential distributions for *A. congesta* (a,b), *T. minuta* (c.d) and *G. africana* (e.f).
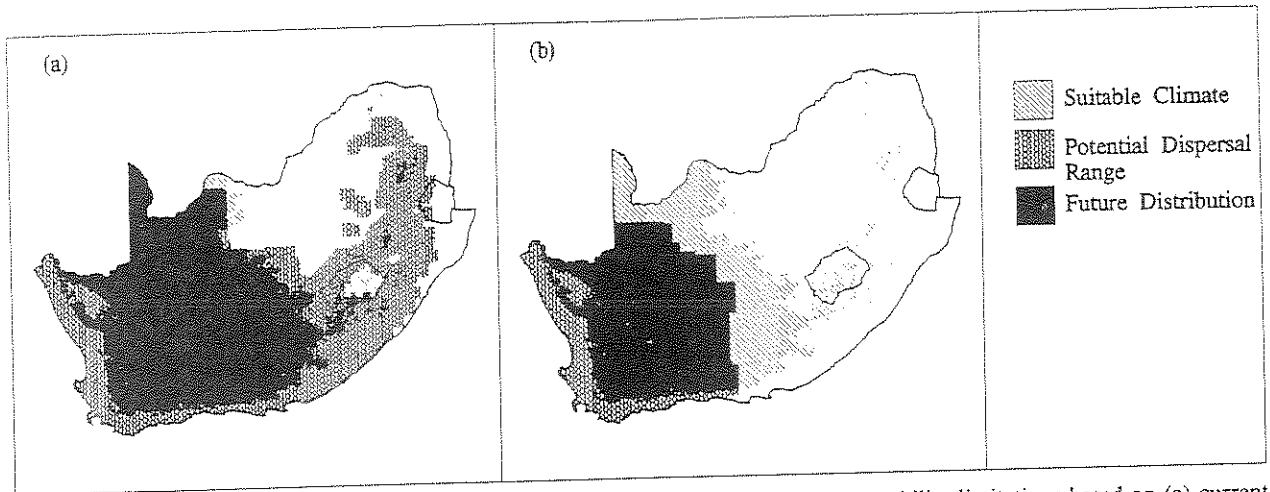
Figure 6: The future distribution of G. *africana* subject to dispersal and landscape permeability limitations based on (a) current potential distribution (shaded in Figure 5(e)), and (b) spread from recorded occurrences (dots in Figure 5(e)).
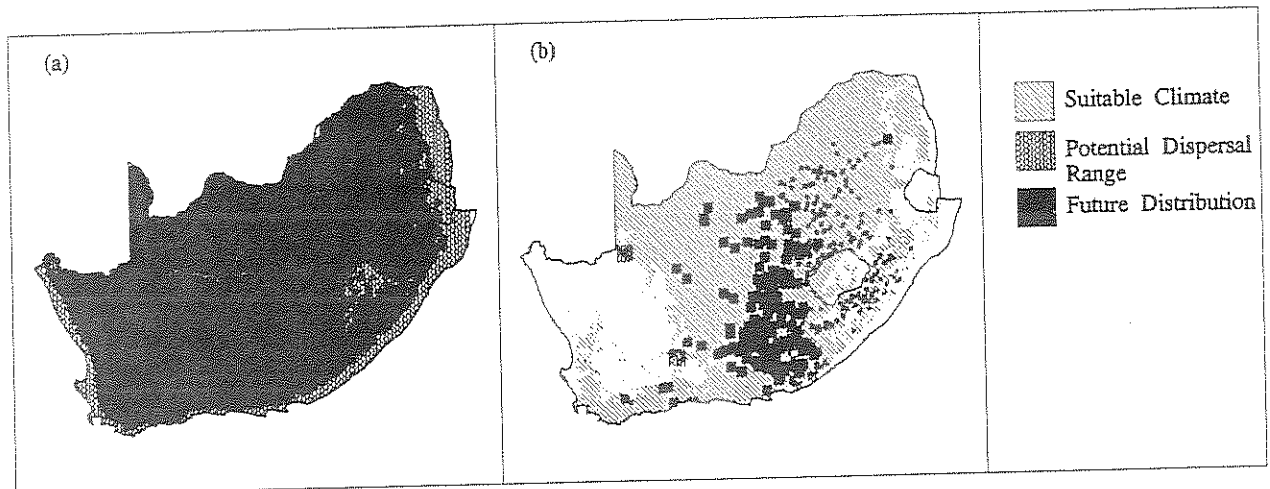

Figure 7 Future distributions of species with (a) a high dispersal rate index (*A. congesa*) and (b) a low dispersal rate index (*T. minuta*).

3.   RESULTS AND DISCUSSION

The climatic change scenario results in a decrease in areal extent in most species and an increase in a few (Table 1). Greater relative changes occurred in the high density class than for the metapopulation as a whole.   There is a significant inverse relationship between the difference between the results of Methods 1 and 2 and the species sample size. Both *A. congesta* and *T. minuta* decrease in area owing to reduced optimum growth days whereas *G. africana* increases primarily through a rapid displacement in the maximum constraints (Fig. 5). This may be related to the effect of very gentle landscape slope in this region (see below). Also illustrated here is an apparent lower current level of saturation of current climate space in *T. minuta* than in *A. congesta*. The effect of the two methods of estimating migration is contrasted for *G. africana* (Fig. 6) where Method 1 allows potential spread from a hypothetical archipelago of patches, whereas Method 2 is probably more

realistic in a more conservative combination of suitable climate and potential dispersal range. Using Method 2, the effect of fast and slow dispersal is clear (Fig. 7) despite the difference in sample size. Also in *T. minuta* the effect of differential landscape permeability is particularly evident. This gives rise to certain areas of coalescence while, especially in areas of lowest landscape permeability, the population is predicted to remain fragmented using this approach. Species with relatively long-lived plants can persist outside their future suitable climate area by year 50 (Fig. 8) since already established plants are far less sensitive to environmental perturbation than establishing plants. These cases are not incorporated in the calculation of areal change in Table 1.

The projected functioning of the identified marginal low density populations needs to be assessed in terms of hypothesized lower fecundity [Carrey et. al., 1995] and phenotypic plasticity [Cheplick, 1991].
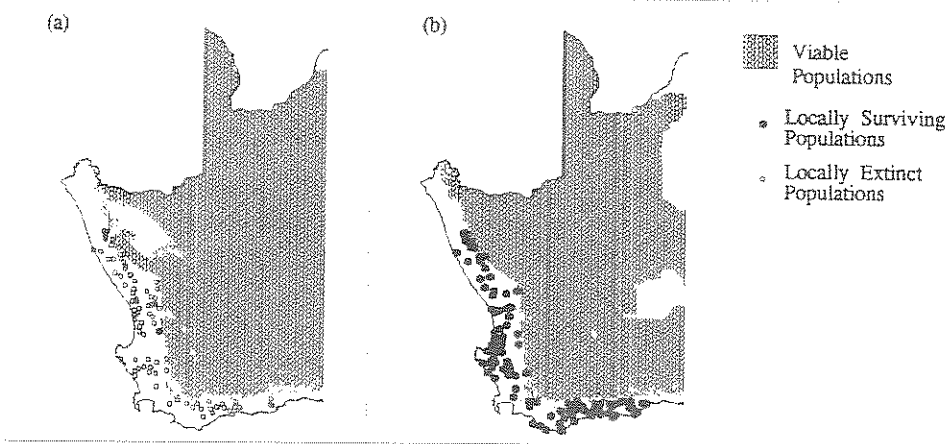
Figure 8   Population survival after climatic change of species with (a) low longevity (*G. africana*) and (b) high longevity (*O. pes-caprae*).

4.   LANDSCAPE SLOPE RELATIONS

Rates of migration relative to the rate of movement of a retreating edge of suitable climate may be crucial for survival of the species. Real landscape variation indicates a generalization in which slope is a critical component. This relationship is illustrated for temperature change according to latitude using a calculated lapse rate for the interior of South Africa and with the higher extremes smoothed by the 1 x 1 minute scale (Fig. 9). The critical landscape slopes for each of the four dispersal rate groups in Table 1 show (Fig. 10) the points below which a specific group may be expected to fail to keep up with the retreating climatic front.

By assuming constant rate of climate change in annual time steps, each of these groups was subjected to a simulated terrain slope with an unlimited fine-grained environment

(Fig. 11). Species groups were permitted, subject to their dispersal rate, to run ahead of the receding climatic edge along the variable slopes. The group with a dispersal rate index of 1 failed to maintain contact at 7 km from the start, whereas the group with dispersal rate index of 10 went extinct at only 241 km across the simulated landscape. This latter group managed to pass the impending climatic break in habitat connectivity of 62 km (corresponding to the landscape depression) shortly before it formed. Three-dimensional landscape applications are envisaged.

5.   CONCLUSIONS

The model shows how very simple approaches can provide useful insights into the possible consequences of climate change in southern Africa. There is nevertheless a need to
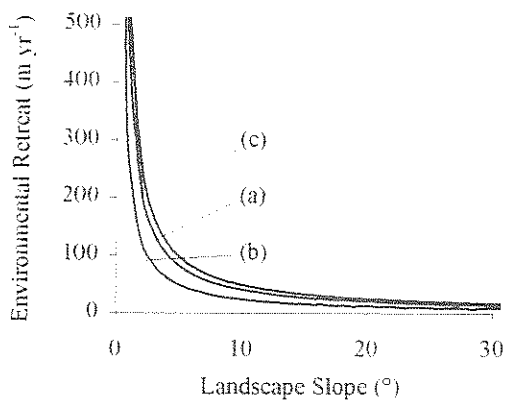

Figure 9.   The distance the temperature environment will retreat as a function of landscape slope: (a) Mean for the country (2°C), (b) northern extreme (1.2°C) and (c) southern extreme (2.4°C).
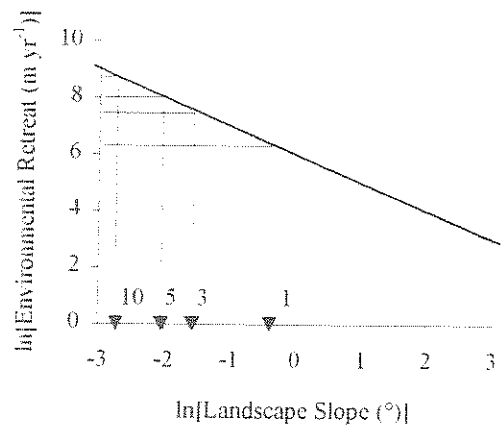

Figure 10.   Critical landscape slopes for species with four Dispersal Rate Indices (with a 2°C increase in temperature).
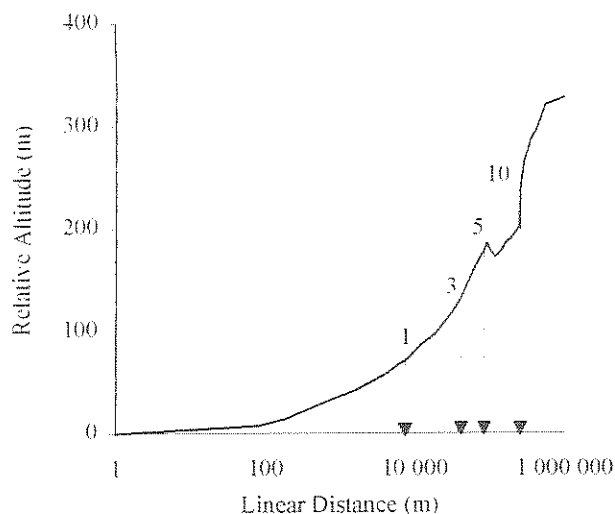
Figure 11. Points of extinction on an artificial landscape for species with four Dispersal Rate Indices (with a 2°C increase in temperature).

incorporate other landscape-level dynamics such as changes in land use and fire frequency, to develop stronger links with explanatory and mechanistic sub-models and to incorporate more explicit feedback routes by modelling through smaller time steps in stochastic environments.

6. ACKNOWLEDGEMENTS

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