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Modelling the spatial dynamics of ground beetles (Carabidae) within landscapes

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A generalised matrix model for analysing the spatial dynamics of ground beetle populations in landscape is described. The model links simple population dynamics models for stage structured populations and their spatial distributions. The model assumes that individual populations have their own internal dynamics, but interact with each other through the dispersal of animals between them.The model consists of three components. i) age structured models describing dynamics of individual populations, ii) functional relationships linking life history characteristics to the underlying environments, and iii) a spatial process model linking populations in space.The utility of the model is assessed by analysis of the dynamics and spread of *Leistus rufomarginatus* through the United Kingdom over the last 30 years: the model was reasonably accurate in predicting the geographical spread of this species. Whilst the model provides only a general framework, and does not incorporate all biotic processes (e.g. inter-specific competition) it could readily be modified to model the distribution and spread of many other invertebrate species.

1. Introduction

Previous approaches to modelling the distribution of ground beetles have been based on the use of models developed from associative and correlative techniques (Rushton *et al.* 1994). All associative approaches link the distribution of the focal feature to explanatory variables, typically habitat, land use or environmental features. Once suitable explanatory variables have been identified the spatial distribution of these can be used to predict the distribution of organisms in other landscapes. The commonest associative techniques have been based on regression. Other approaches have been based on the use of ecological hierarchies. A matrix model was developed by Rushton (1992) which linked associations of species to the habitats in which they were found and this was used to predict the distribution of beetles in landscapes (Rushton *et al*. 1994, 1995). Whilst these approaches are valuable first steps they are not definitive models because the underlying temporal and spatial mechanisms that determine species responses to habitat structure and landscape have not been modelled explicitly. There is abundant evidence that ecological processes are not independent of the space in which they occur and that they are spatially articulated (Sklar & Constanza 1991). Thus, whilst associative models may be used within the time and space 'universe' from which the data were collected, there is no way of assessing the extent to which they can be used under other circumstances where the relationships and associations may not apply. In order to produce effective generalisable models for predicting the distribution of ground beetles we need to consider underlying ecological processes as well as the space in which they occur.

A species can be modelled at the level of the individual, population or meta-population. Clearly, attempting to model the effects of land use change on individual organisms is unrealistic. At a larger spatial scale organisms can be considered to be members of distinct populations. Individuals within populations interact in some way, usually through reproductive activity or through competition for resources. At a yet larger scale populations can be grouped into collections of populations (parts of a metapopulation) that occur in semi-isolated units of habitat separated by areas of non-habitat. Individual populations in metapopulations interact rather more loosely through dispersal. There have been extensive developments in metapopulation dynamics theory and modelling (Levins 1969, 1971, Gilpin & Hanski 1991) with extensions into the spatial domain. As metapopulation models analyse changes in the distribution of populations in terms of probabilities of extinction and colonisation of habitat patches these models are of some practical use in landscape scale research. Whilst the mathematical basis of metapopulation models is elegant and the concept has intuitive appeal, practical applications of it have been relatively few e.g. Thomas and Jones (1993) and Hanski and Thomas (1994). Furthermore, there is some debate as to whether or not species populations exist in a balance between extinction and colonisation (Harrison 1994). Realistic models should include the individual processes of birth, death and dispersal in the individual populations in real landscapes. Analytical modelling approaches in heterogeneous landscapes are effectively intractable (Fahrig 1991) thus simulation procedures would seem to be the most appropriate framework for modelling the distribution of species at the large scale. These approaches also have the advantage that metapopulation dynamics behaviour (if it exists) appears as an emergent property rather than an explicitly defined component of the model structure.

In order to model the dynamics of animal populations within landscapes it is necessary to have access to spatially referenced habitat information. Even for very small areas the data manipulation and storage requirements can be very large. Geographical Information Systems (Burrough 1986) have been developed which provide efficient data storage and handling routines. These systems when coupled to population dynamics models offer considerable potential for investigating the spatial ecology and distribution of ground beetles.

In this paper we outline a process-based simulation model that we have developed for investigating the dynamics of ground beetle species within defined landscapes. The model utilises a population modelling approach (Caswell 1989) generalised to model the spatial dynamics of semi-isolated individual populations which interact through dispersal. Whilst the model has been developed to investigate the dynamics of one species of ground beetle, it has general application for other species of plant and animals for which adequate life history data are available.

2. Methods

2.1. Study areas and studied species

The study area consisted of England and Wales: this comprised an area of land of 452 800 km^2. This is an area where the beetle *Leistus rufomarginatus* has colonised and spread over the thirty years to 1990. *Leistus rufomarginatus* is a recent introduction to Britain from Continental Europe (Crowson 1942) whose early range expansion was noted by Hammond (1974). It has now spread throughout England, north to south-Northumberland, and Wales, although it is more common in the south and east (Luff 1996). *L. rufomarginatus* occurs in woodlands, both deciduous and coniferous, although most British records are from deciduous woodland. It feeds on Collembola, using specialised mothparts as a setal trap (Bauer 1985). *L. rufomarginatus* is winged, and has been recorded in flight (Jobe 1990); its European distribution is also spreading, and now includes most of central and southern Europe, including the southern tip of Scandinavia. It is a summer breeder, but with overwintering larvae as in the remaining *Leistus* species.

2.2. The simulation model

2.2.1. Overall structure

The model for simulating the distribution of beetle populations in landscapes has two main components. First, a geographical information system (GIS) which stores environmental, habitat and population information. This system undertakes data manipulation and abstraction, providing inputs for the second component. This consists of modules simulating the population dynamics of the species and their dispersal within the GIS-held landscape. We used the public-domain raster-based GIS produced by the United States corps of Engineers, GRASS (Westervelt 1990). The population dynamics sub-modules were written in the programming language C and integrated with the GIS component through a UNIX-shell environment.

2.2.2. Habitat suitability and population dynamics

The land surface of England and Wales was divided into areas of habitat used by the beetle species and areas of non-habitat through which animals could move when dispersing. Identification of habitat suitable for occupation by the beetle within the landscape was undertaken using the GIS module. Suitable habitats were defined on the basis of the distribution of deciduous and coniferous woodland and scrub areas as recognised by categories of the Institute of Terrestrial Ecology classification of Landsat satellite imagery (Fuller *et al.* 1994). Beetles were assumed to utilise coniferous, scrub and deciduous woodland habitats.

Each 1 km square within the landscape was modelled as having one population if there was available habitat present. Each of the populations had its own dynamics which interacted with others through the processes of dispersal and an indirect form of interspecific competition. For each 1 km square, in each year, population size was modelled in terms of the net change due to four factors. These were, gains from recruitment from breeding and immigration of adults from other squares and losses due to mortality and emigration. Growth, survivorship and fecundity data were not available for *L. rufomarginatus* so data from similar forest inhabiting species were utilised in the model. Reproduction was assumed to occur once in each population in each year. Total egg fecundity was assumed to be 150 per individual (Heessen 1980). Mortality in the egg stage was assumed to be 50% similar to that recorded for *Calathus graminaceus* by Cardenas (1994) whereas that of the larval to pupal stages was 10% (Brunsting 1986).

Dispersal was modelled as a process occurring once a year. Animals were allowed to disperse to squares containing blocks of habitat that were at or below the carrying capacity for that species. The carrying capacity of the habitat was assumed to be 2.5 m approximating to the middle of the range of adult population densities recorded for the similar sized *P. oblongopunctatus* by Brunsting (1986). Beetles were allowed to disperse up to a fixed upper limit (plus associated standard deviation) from the site of their birth. Dispersal was modelled as a series of events from each km square. Since the potential number of dispersing adults from each square could in theory number millions, dispersal was not modelled for each beetle individually rather it was modelled as a series of stochastic dispersal events. The total number of dispersing beetles was divided into 15 groups. Distance dispersed and angular direction for each of the 15 groups were derived by sampling from a normal distribution and a uniform distribution for each respectively. The extent to which beetles were allowed to invade any square was weighted by the availability of suitable habitat within it. Thus if the available habitat constituted 50% of the area of the square then the proportion of beetles actually successfully colonising the square was 50% of those in the group that reached it. In addition if there were no suitable habitats available for occupation within squares then dispersers within any group were assumed to die.

2.3. Sensitivity analysis of the model to inputs and invasion dynamics

The sensitivity of the model to the population parameters of survivorship and maximum dispersal distance were investigated by simulating the spread of *L. rufomarginatus* in woodland habitats over 5 years in an 81 by 77 km rectangle of south-east England. The National Grid Co-ordinates for this area were eastings 545 000 to 626 000 and the northings 218 000 to 295 000. This corresponds to the block of land surrounding the most isolated record of *L. rufomarginatus* up to 1960.

The model was run for four scenarios: i) maximum adult dispersal of 10 km per year (standard deviation of 1.5 km) with a combined larval and pupal mortality of 90%; ii) the same but with survival increased to 55%; iii) maximum adult dispersal of 5 km per year (standard deviation of 1.5 km) with a combined larval and pupal mortality of 90%; iv) the same as iii) but with survival increased to 55%.

The simulation model was used to investigate the dynamics of the invasion of England and Wales. Records of the observed distribution of *L. rufomarginatus* in 1960 were used as invasion foci to start the model. 10 000 individuals were released at each of 11 points and the subsequent spread of beetles monitored over thirty years. The predicted distribution of the beetle was then compared with the observed distribution at 10 year intervals by comparing records for each 10 year period with those generated by the simulation model. Three model runs were undertaken. The first with adult dispersal at a maximum of 10 km (standard deviation of 1.5 km), the second with adult dispersal of 5 km (standard deviation of 1.5 km) and the third with adult dispersal of 20 km (standard deviation of 1.5 km).

The predicted distributions of *L. rufomarginatus* in England and Wales at the end of 10, 20 and 30 years were

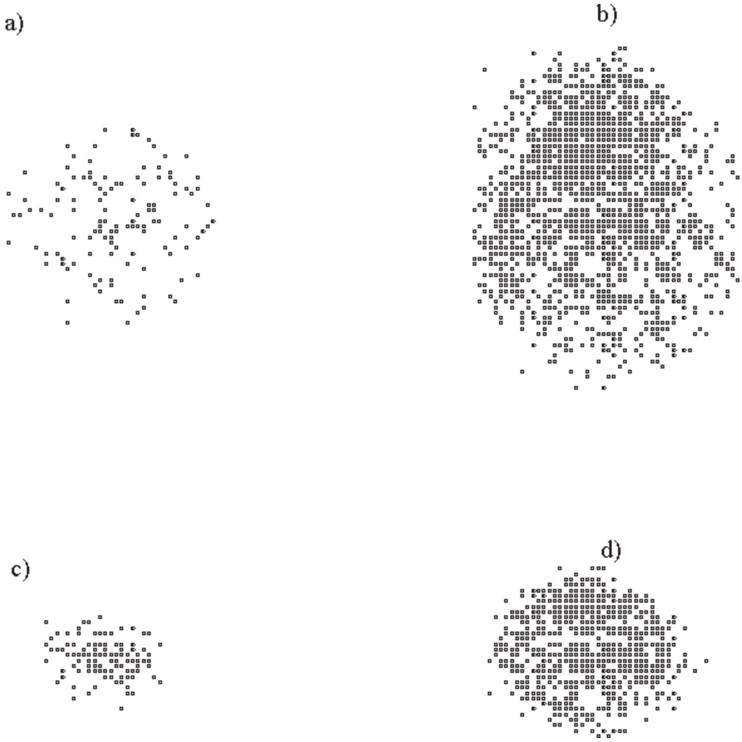

Fig. 1. The predicted distribution of *L. rufomarginatus* in a 77 by 81 km landscape after five years under four different larval-pupal survivorship and adult dispersal scenarios. a) 90% mortality 10 km adult dispersal; b) 55% mortality 10 km dispersal range; c) 90% mortality 5 km dispersal range and d) 55% mortality 5 km dispersal range.

compared with the observed distribution in 1970, 1980 and 1990 separately.

3. Results

3.1. Sensitivity analysis

Predicted spread of *L. rufomarginatus* in the 77 km by 81 km landscape after 5 years was greatest in the high survivorship-high dispersal scenario and lowest in the low dispersal-low survivorship scenario (Table 1, Fig. 1). In excess of 10 times as many squares were colonised in the high survivorship-high dispersal as in the high dispersal low survivorship scenario. Similarly, approximately 5 times as many squares were colonised in the high survivorship-low dispersal as in the equivalent low survivorship-low dispersal scenario. It is clear that survivorship and dispersal range interact in determining the overall results of the model.

3.2. The dynamics of invasion by *L. rufomarginatus*

The most obvious feature is the widespread distribution of suitable habitat for *L. rufomarginatus* in the East and West, few if any 1 km grid squares contained no woodland. The only areas where habitat was sparse

Table 1 Characteristics of the predicted spread of *L. rufomarginatus* under four different larval-pupal survivorship and adult dispersal scenarios

Maximum dispersal (km)	Larval-pupal survivorship (%)	Number of squares colonised (km)	Maximum range of colonisation (km)	Number of squares colonised
10	0.10	122	16.5	1148
10	0.55	1303	32.2	3244
5	0.10	99	13.5	342
5	0.55	540	16.2	1076

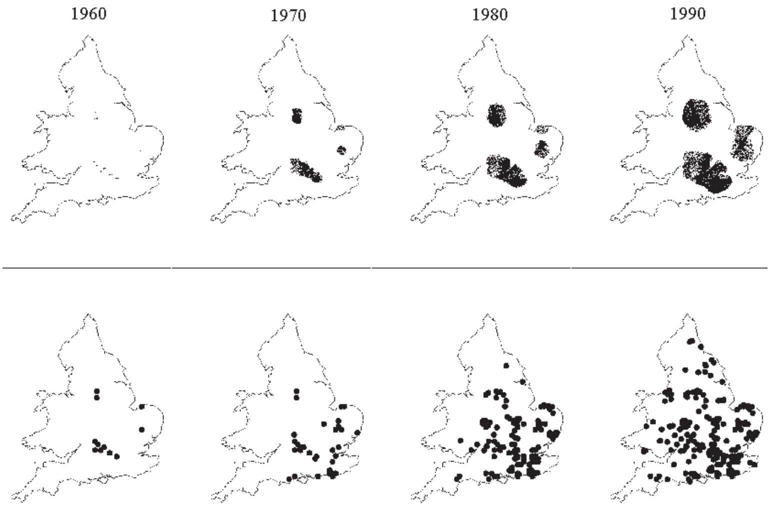

Fig. 2. The predicted distribution (top) of *L. rufomarginatus* in 1960, 1970, 1980 and 1990 with adult dispersal at 5 km maximum and the observed distribution (bottom) in each year.

were the lowland areas of East Anglia around the Fens where the land use was predominantly arable and the upland mountainous regions of the Pennines running north-south in northern England.

The predicted distribution of *L. rufomarginatus* in England and Wales 10, 20 and 30 years after releasing animals at the observed sites in 1960 are shown in Figs. 2, 3 and 4 for maximum dispersal ranges of 5 km, 10 km and 20 km respectively. Since each record constitutes a 1km square the scale of resolution for the observed records has been scaled up to 10 km to allow comparison. The most obvious feature of these results is that despite the inclusion of a stochastic component to dispersal the populations of beetle expanded from their initial position in a roughly circular pattern. Repeated runs produced the same pattern, and probably reflects the difference in scale between the population processes within the model and the mapped output. The proportions of 1km grid squares where observed records matched the predicted distribution are shown in Table 2 for each scenario. The closest match between observed and predicted distribution was for the 20 km dispersal where 76% of squares observed to have *L. rufomarginatus* up to 1990 were predicted to be colonised by this time. The equivalent figure for the 5 km dispersal scenario was only 33%

The most obvious differences between the observed data and model predictions are that the predicted spread was slower than that actually observed. Furthermore, the model predicted a smooth spread from the colonisation points of 1960 whereas the observed distribution was more fragmented. Finally, the observed distribution records suggest that there was a lateral spread along the south and east coasts of England and Wales that was not predicted by the model.

4. Discussion

Achieving ecological reality in any model is dependent on how the individual processes are modelled. In this study, we have used the stage-structured matrix approach developed by Caswell (1989) and extended it to the spatial domain. Each life history process was modelled at the level of the population mean for each population in the landscape. This approach makes the assumption that mean values for individual life history parameters such as fecundity

Table 2. Number of 1km grid squares where *L. rufomarginatus* was recorded up to 1970, 1980 and 1990 and the proportion predicted to have been colonised after 10, 20 and 30 years of simulated model runs.

	year					
	1970		1980		1990	
Maximum dispersal (km)	obs.	pred.	obs.	pred.	obs.	pred.
20	33	16	122	98	209	166
10	33	14	122	59	209	133
5	33	13	122	34	209	70

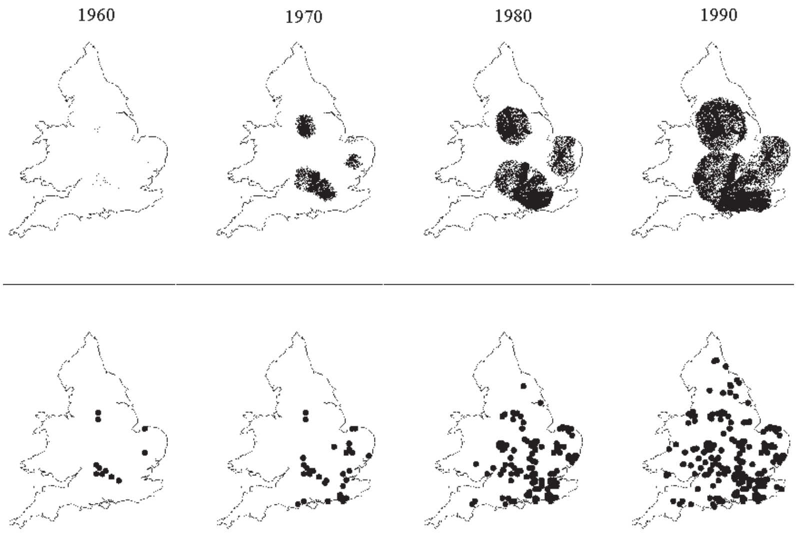

Fig. 3. The predicted distribution (top) of *L. rufomarginatus* in 1960, 1970, 1980 and 1990 with adult dispersal at 10 km maximum and the observed distribution (bottom) in each year.

and survivorship can be applied at the population level. There was no scope for individual variation. Where populations are small or there is considerable temporal stochasticity in the environment, models based on the simulation of processes for individuals (i-space configuration models) may be more appropriate because the net effect of variation in individuals may have considerable impact on the overall behaviour of the population (De Angelis & Rose 1992). This may be particularly important in dispersal models where population spread may depend on the chance colonisation of new habitat by few animals. Whilst individual based models have been developed to investigate dispersal in ground beetles (Vermeulen & Opsteeg 1994), this has been at comparatively small scale. The technological problems associated with modelling individual beetles at large-scales coupled with the lack of adequate life history data mean that an individual based approach may not be appropriate for this type of research problem.

Given that the model obviously lacks ecological reality at the level of the individual to what extent was it realistic at the population level? In the first instance only four population processes were effectively modelled; mortality, fecundity, intra-specific competition and stochastic dispersal. Population survivorship and fecundity were modelled as straightforward multiplicative functions derived from field estimates for another species. These estimates effectively subsumed all of the underlying processes affecting mortality and fecundity into simple parameters. There is abundant evidence that climate has considerable effects on the development of Carabidae (Butterfield 1986, Sota 1986) and also adult dispersal (Van Huizen 1990). Since climate varies spatially, factors such as temperature, rainfall and wind are likely to be important in determining the outputs of large-scale spatial models. In addition, interspecific interactions were not modelled. It is possible that the ability of *L. rufomarginatus* to invade new sites will be influenced by extant communities of ground beetles. Biotic resistance of this type could have implications for the accuracy of this modelling approach. Furthermore, even at the level of simplicity with which these processes were modelled, the sensitivity analyses suggested that interactions between these factors and dispersal could have marked effects on the predicted rate of spread of the beetle. This may have considerable implications for the application of this modelling approach to the study of ground beetles, because dispersal power is considered to be a major factor determining population spread and survival (Den Boer 1981). Whilst the simplifications made in this study are clearly unrealistic, they probably have little importance for the utility of the modelling approach. The framework could easily be extended to include specific life history or dispersal processes of significance to individual species if these were available and if it was necessary to pursue a more specific/tactical rather than general/strategic approach.

Whilst the modelling approach has considerable potential as a tool for investigating the spatial dynamics of animals, it is debatable whether the re-

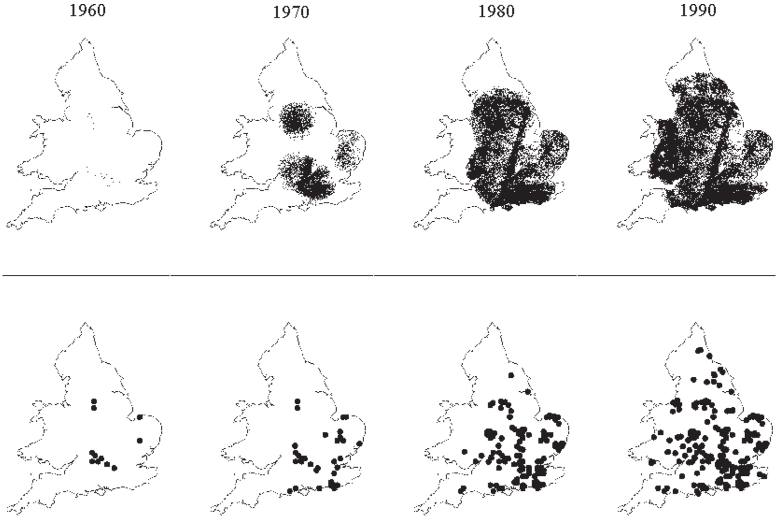

Fig. 4. The predicted distribution (top) of *L. rufomarginatus* in 1960, 1970, 1980 and 1990 with adult dispersal at 20 km maximum and the observed distribution (bottom) in each year.

sults present here increase our understanding of the spread of *L. rufomarginatus* in the United Kingdom. It is clear that the model was capable of predicting the geographical spread of *L. rufomarginatus* from 1960 to 1990 with reasonable accuracy. This may have arisen because of fortuitous selection of the basic life history parameters as model inputs or because the behaviour of the model matched that of the animal in the field. It is likely that the apparent goodness of fit of model predictions to observed spread was fortuitous, reflecting the structure and composition of the landscape in which the beetle was found. Fahrig (1989) demonstrated that the dynamics of dispersal in any dispersing organisms are strongly linked to the dispersing distance and the probability of the organisms finding suitable habitat. Consideration of the cover of habitat suitable for occupation by *L. rufomarginatus* in the UK indicates that there were few if any 1 km squares where suitable habitat was not present. Whilst there is some evidence that *L. rufomarginatus* favours some woodland types over others (Eyre & Luff 1994) it is clear that most habitat parcels in the UK suitable for occupation by the species are likely to be within the range of dispersal of the beetle. Furthermore, woodland habitats in this area are also likely to be temporally stable relative to the life history span of the beetle. Thus, the simple model of dispersal used in this study which, despite having a stochastic component was effectively a diffusion approach, probably accurately reflects what was occurring in the field, with beetles spreading out from central foci to utilise a widespread and stable habitat resource. It would be interesting to use this modelling approach to investigate the dynamics of species of ground beetle which utilises habitats that are less temporally and spatially homogeneous than woodland. This would be useful in evaluating the extent to which the results obtained here were real rather than purely fortuitous. *L. rufomarginatus* was chosen not to validate the model, but simply as an example of how this modelling approach could be applied.

The model did not predict the observed rapid spread of the beetle along the south and north-east coasts of England and Wales. There are at least two possible reasons why the model did not predict this spread. Firstly, the model assumed that only those 1 km squares observed to be occupied by *L. rufomarginatus* up to 1960 were invasion foci for the subsequent spread. It is by no means certain that these squares were the only ones occupied by the beetle in 1960. It is possible that many more sites supported *L. rufomarginatus* at this time. The data used as inputs for 1960 are likely to have been inadequate because they were not derived from systematic ecological surveys. The absence of systematic sampling is also possibly reflected in the patchy pattern of the spread of the species post-1960. The relative importance of this factor cannot be resolved. Secondly, the model did not allow for new invasions from areas external to the land mass of England and Wales modelled in this study. It is possible that the more rapid spread of *L. rufomarginatus* along the south coast reflects new invasion of the UK by animals dispersing or carried from the continent by human transport. Such transport within England and Wales was also not considered.

The simple combined GIS-population modelling framework outlined in this study provides a methodology for investigating the large scale dynamics of beetle populations. It is clear that this approach could readily be adapted and modified to investigate other issues of significance to ground beetle ecology. The model could be used strategically to investigate the consequences for ground beetles of changes in the temporal and spatial dynamics of habitats which could arise from factors such as land use change. By extending this model to individual species which utilise rare or fragmentary habitats and including model components unique to the species concerned this framework could be used tactically to investigate conservation or pest issues. In either case the inclusion of a GIS system with habitat and environmental information incorporates ecological realism that should enhance our understanding of the spatial ecology of this group of insects.

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