The use of GIS and modelling approaches in squirrel population management and conservation: a review

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We review modelling approaches in relation to three key areas of sciurid ecology: management, disease risk assessments and conservation. Models enable us to explore different scenarios to develop effective management and conservation strategies. They may also assist in identifying and targeting research needs for tree and flying squirrels. However, there is a need to refine techniques and assure that data used are applicable at the appropriate scale. Models allow managers to make informed decisions to help conserve species, but success requires that the utility of the tool be evaluated as new empirical data become available and models refined to more accurately meet the needs of current conservation scenarios.

Keywords: Geographic information system, habitat suitability index, modelling approaches, population management, Sciuridae.

Introduction

MODELS have been described as simplifications of reality that are used to help us understand complex systems[1]. Therefore, models can assist as tools in the management and conservation of many species. An examination of the literature on tree and flying squirrels (Mammalia: Sciuridae) for application of modelling and geographic information system (GIS) techniques reveals an abundance of approaches (Table 1). Their uses range from statistical approaches such as generalized linear models (GLM) or principal component analysis (PCA) relating presence of tree or flying squirrels to distribution and quality of habitat[2,3], to spatially explicit population dynamics models (SEPMs) predicting eastern grey squirrel (*Sciurus carolinensis*) range expansion[4]. In this article, we present a targeted review of key GIS and modelling studies in relation to three areas of sciurid ecology: management, disease risk assessments and conservation.

Management

Tree and flying squirrels are viewed as a natural resource or threat to natural resources in many regions of their cosmopolitan distribution. Squirrels are managed as game or fur-bearers that provide considerable subsistence and economic value[5], especially in Holarctic species[6]. Tree squirrels are also viewed as pests in many regions, attacking crops, trees and electrical systems or competing with native species[6–8]. Modelling in a natural resources management context has usually focused on habitat-based methods and harvest dynamics.

Habitat-based models have been applied to two common species of North America, eastern fox squirrels (*S. niger*) and eastern grey squirrels[9–11]. Models identify habitat in terms of two relatively simple components: winter food availability and cover requirements. Similar approaches were applied to identify and model habitat quality of native Japanese squirrels (*S. lis*) and introduced Pallas's squirrels (*Callosciurus erythraeus*) from empirical data in Japan; the results of the modelling efforts predict marked overlap between the species[12,13]. Similar attempts have been made for northern flying squirrels[14–16] (*Glaucomys sabrinus*), Siberian flying squirrels[17] (*Pteromys volans*) and Abert's squirrels[18] (*S. aberti*). Increasingly, these approaches incorporate data from satellite imagery to develop predictive models of patch occupancy, habitat use and suitability[16,19–24].

Human influence on population persistence has also been examined using a theoretical approach. Habitat suitability index (HIS) models have been applied successfully to assess distribution of urban populations of eastern grey squirrels by identifying the most important tree species and size classes, and provide guidance for urban foresters[25]. Impacts of deforestation on eastern fox squirrels, eastern grey squirrels, Eurasian red (*S. vulgaris*), and red squirrels (*Tamiasciurus hudsonicus*) were assessed with regression models to identify responses to habitat fragmentation and effect thresholds[26–29]; Eurasian red squirrels appear particularly sensitive to fragmentation, whereas red squirrels in North America are less impacted[2,29]. Spatially explicit models applied to population persistence in fragmented landscapes verify that red squirrels of North America are least sensitive to fragmentation, whereas southern flying squirrels (*Glaucomys volans*) are most sensitive[30]. The potential for modelling approaches to assist in 'softening' human impacts on tree and flying

Table 1. Examples of modelling approaches and applications to conservation and management of tree and flying squirrels

Approach	Description	References
Statistical models	Relating habitat and other variables to presence/absence or population data using, for example, regression analysis or GLMs.	2, 14, 17, 53
Principal components analysis	Summarized trends of species habitat measurements. Identifies important variables in selection and reduces data dimensionality.	3
Habitat suitability index	Hypothesis of species–habitat relationships describing the landscape in which a species could occur. Examines requirements of habitat.	26, 27, 28
Spatially explicit dynamic population models	Individually based population dynamics models linking the spatial composition of a landscape with life-history processes of mortality, reproduction and dispersal. Require an understanding of the species and life-history data.	4, 20, 32, 39, 42, 51, 53
General programs, e.g. RAMAS, VORTEX	General population modelling tools, requiring basic life-history inputs. Have many extra abilities like metapopulation analysis, genetic effects, habitat analysis, etc.	46, 54

squirrels appears to be substantial (see 'Conservation' below).

Modelling has been used to track populations due to economic necessity or to develop viable economic strategies. Pelt production of Eurasian red squirrels is predicted by seed crops of a single tree species, two years in advance[5]. Economic value of conservation of native Eurasian red squirrels in the United Kingdom was examined using regression techniques to identify the amount residents would pay to conserve the species[31]. Dynamics of introduced populations of eastern grey squirrels outside their native range has been modelled to assess their implications for native fauna[4,32–34]. Similarly, researchers used regression approaches to develop means of combining timber harvest and tree squirrel persistence[17,35,36]. The use of models in evaluating management schemes has thus often succeeded in the formulation of large-scale management plans, suggesting the promise of using such approaches[37–39].

Disease risk assessments

SEPMs predict distribution of species in the landscape on the basis of interactions between landscape structure and life-history processes such as dispersal, reproduction and mortality[20]. These models are inevitably more complex than statistical methods but allow for investigating species with dynamic expanding distributions, especially where squirrels may act as a vector for disease. They can be used to investigate the likely spread of disease such as in the case of the introduced eastern grey squirrel, which is linked to squirrel poxvirus outbreaks in Eurasian red squirrels in the UK[40,41].

Rushton et al.[42] integrated a SEPM with a disease model and investigated Eurasian red squirrel decline in Norfolk, UK. Their results indicated that the virus, like interspecific competition, could have led to the observed decline and suggested that interaction between the two squirrel species and the virus represented a system of competition mediated by an infectious agent. Subsequent work applied the approach to Eurasian red squirrel decline in the north of England. The studies used modelling and records of field observations to quantify the impact of the disease and to assist in the development of landscape-scale strategies for conservation[43,44].

Conservation

Tree squirrels are imperiled worldwide[8] and several modelling approaches have been used to aid in their conservation. Unfortunately, few life-history data exist for many tree squirrels[45] and in such cases a general approach may be useful. Generic averages have been used to fill life-history gaps and predict populations needed for the successful introduction of six tree squirrel species[46]. These modelling efforts and empirical data reviewed therein demonstrate that tree squirrels can establish from low numbers, provided introductions occur into quality habitat and small populations can recover if factors implicated in their decline are managed[46]. Validation of modelling results through examination of empirical data, field experiments and sensitivity analyses are a necessary step to determine the utility of candidate models and to further modify and enhance the model value.

For endangered Delmarva fox squirrels (*S. niger cinereus*), HSI models are used to identify release sites[47] that have led to successful translocations[48]. However, recovery requires evaluation of the HSI models along with mapping of habitat[47]. One approach to mapping habitat used LiDAR (laser imaging detection and ranging or light detection and ranging) airborne laser to screen for appropriate vertical structure[24]. Sites identified as potential habitat were visited after a HSI model was used to predict if it matched release-site criteria. A stand-level HSI was also used for Siberian flying squirrels and moose (*Alces alces*). Although the general aim was to manage both species effectively, the intention, more specifically, was to increase the boundaries between neighbouring stands suitable for breeding and foraging for the squirrels, and to increase the amount of edge between winter foraging habitat and other areas for the moose[49].

Another specific case is that of endangered Mt Graham red squirrels (MGRS: *T. h. grahamensis*), that are restricted to <12,200 ha of forest in the Pinaleño Mountains, Arizona, USA. Buenau and Gerber[50] incorporated multiple analytical techniques to identify the fact that although overall population growth rate was >1, variation between years was high and posed the main threat to MGRS. They then examined a demographic model, based on general red squirrel data, and identified survival as more important than reproduction to population growth rate. SEPMs were utilized for MGRS wherein their conspicuous larder-hoards (middens) serve as centres of activity with individual interactions based on these points[51]. The availability of conifer seeds, the primary MGRS food source, is variable between years with poor cone crops between occasional mast years. Middens are stocked with cones and provide a buffer to minimize reductions in fecundity and juvenile survival when no cones are available on trees; the authors thus included a variable in their model reflecting cone availability at a given midden. The model predictions indicated the potential large effect of competition from introduced Abert's squirrels as well as predation. Furthermore, the peripheral population of MGRS was driven by factors different from those affecting core populations, illustrating the need for population-specific data and management actions.

The future of the MGRS is uncertain, as recently large fires and insect damage[51] have degraded their habitat extensively. New modelling approaches combining multiple thread scenarios with technological advances in remote sensing will be imperative for evaluating and creating management strategies. For example, while habitat distribution has previously been mapped for MGRS[19,52], an update is needed to account for current conditions and the availability of new technologies[53]. This project thus serves to highlight new technologies, such as high-resolution satellite imagery, that can be used to conduct a fine-scaled analysis of individual trees. Additionally the resultant habitat quality map will be incorporated into SEPMs to predict changes in population size due to disturbance. Effects of resource limitation can then be evaluated to inform management decisions.

Combining assessments of habitat quality with population models has been employed in Greece with the vulnerable Caucasian squirrel (*S. anomalus*)[54]. Using satellite-derived land-cover and life-history parameters of the closely related Eurasian red squirrel as inputs into RAMAS[55], the researchers were able to identify deviations from a baseline scenario due to the two greatest threats to Caucasian squirrels, namely fragmentation from roads and illegal poaching[54]. While the responses of the two closely related species to these threats may be similar, care has to be taken when using life-history parameters even within a species for different populations. Endangered fringe populations may have significantly different life-history parameters than populations found in the core of a species range[51].

Developing habitat models and predicting patch occupancy and population viability in relation to landscape structure has been conducted for several tree and flying squirrels[2,17,56]. Woodland habitats of squirrels are relatively well defined and easily mapped by techniques such as remote sensing[57]. However, relating species abundance to landscape structure may need to consider isolation measures in urban landscapes and how easy it is for squirrels to move across different habitats (e.g. based on cost distance factors[58]) or take into account that critical variables for some species such as understorey complexity, microclimate and food availability may not be available in large-scale digital map datasets[16].

Conclusions

Modelling of mammals in real landscapes offers both opportunities and challenges[59]. With the increase in economic value of the world's forests[60] and the anthropogenic and ecological pressures faced by forested ecosystems worldwide[61], managers and foresters may have to weigh conservation objectives with often conflicting economic, social and conservation demands. Modelling shows promise in enabling us to explore different scenarios to soften human impacts, and to develop effective management and conservation strategies (Figure 1).

Often multiple modelling approaches exist and the decision of which to use is dependent on the questions asked and the availability of appropriate ecological and geographic data at the right temporal and spatial resolution and scale. Multiple approaches can be used in synergistic fashion to develop long-term conservation strategies (Figure 1). In addition, different levels of experience are needed for 'off-the-shelf programmes' like VORTEX[62] and RAMAS[55] in comparison to models specifically developed or adapted to target populations.
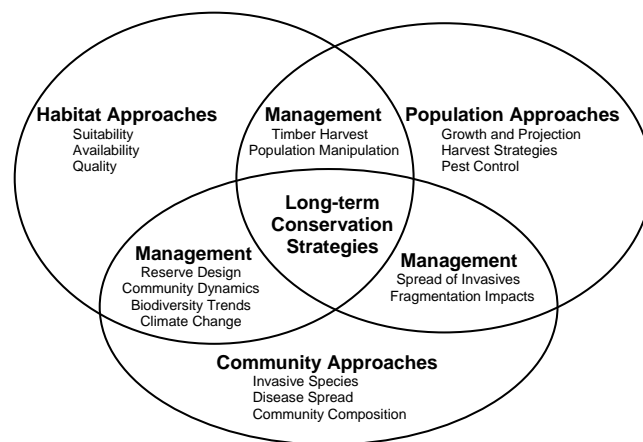

Figure 1. Venn diagram illustrating the ecological aspects of modelling approaches and their applications to tree and flying squirrels. Note that management and conservation implications of efforts increase with the use of multiple approaches.

SEPMs appear particularly useful in predicting the expansion of introduced species and their likely impact on local populations. Many introduced species threaten tree squirrels with expanding distributions and this modelling approach is adaptable to investigating many systems with similar species interactions. However, SEPMs require an understanding of basic life history processes and data that are not always available, especially when dealing with rare species and populations at the range periphery.

Despite the use of HSI and other modelling approaches for endangered species, further work needs to be done to refine techniques and ensure that the data used are applicable at the appropriate scale[16]. Our knowledge of tropical squirrel species is generally poor and the application of sophisticated ecological models is limited. However, there is an urgency to understand the ecological requirements of these species[8] and modelling approaches may assist in identifying and targeting research needs as well as the ecological variables needed to study and offer management and conservation advice. For example, the use of sensitivity analyses linked to SEPMs can identify the key life-history parameters for populations, help target ecological and epidemiological studies and inform on the levels of management needed to control pest populations[32,42,44,51].

The future of modelling will be driven by new approaches and effective utilization of current knowledge (Figure 1). There is a need for continual modification of techniques, making use of whole ranges and combinations of approaches, and continued monitoring to integrate new knowledge, update and validate assumptions and uses of models, especially in cases where available data are scarce. Management situations should involve multiple stakeholders to help foster cooperation, involve local site-specific knowledge and expertise to reach decisions supported by all parties. Experience in the UK and the USA has shown that models allow managers to make informed decisions to help conserve species[39]. Ecologists and stakeholders must remember that models are simplified versions of reality that can provide useful tools to evaluate a variety of options; however, success requires that the utility of the tool be evaluated as new empirical data become available and models are refined to more accurately meet the needs of current conservation scenarios.

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