

LINKING CONTEMPORARY VEGETATION MODELS WITH SPATIALLY EXPLICIT ANIMAL POPULATION MODELS¹

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Abstract. Spatially explicit models for animal populations (SEPMs) necessarily embody assumptions about plant community structure and dynamics. This paper explores the advantages and limitations of directly linking animal SEPMs with models for vegetation dynamics. Such linkages may often be unnecessary. For instance, in research focussed on questions with short time horizons, the spatial patterning of vegetation can be reasonably approximated as a fixed landscape templet for animal population dynamics. But if one needs to consider longer time scales (e.g., decades to centuries), landscapes will be dynamic. Models of vegetation dynamics provide useful tools for predicting landscape dynamics. We outline the sorts of output from vegetation models that might be useful in animal SEPMs. We discuss as a concrete example recent forest simulators, which predict with reasonable accuracy some variables (e.g., tree species composition), but which, to date, are quite poor for others (e.g., seed production). Moreover, because vegetation models target a restricted range of temporal and spatial scales, they may be more useful for certain consumer groups than for others. Despite these cautionary observations, we believe that the time is ripe for fruitful linkages between models of vegetation dynamics and animal SEPMs.

Key words: aggregation; forest simulators; gap models; habitat; landscape drivers; plant–animal interactions; scale; spatially explicit models; succession; vegetation dynamics.

INTRODUCTION

“Some of the most obvious patterns in [animal ecology] are those relating species to habitats” (Wiens 1989). A spatially explicit population model (SEPM) blends a specification of the location of organisms and habitat patches in a heterogeneous landscape with information on habitat-specific demography and dispersal behavior (Dunning et al. 1994). SEPMs are becoming increasingly useful in both basic and applied animal ecology, for example as management tools for evaluating the effects of altered land use patterns (Turner et al. 1995). Because the physical structure, species composition, and resource production of plant communities largely define what is meant by “habitat,” characterizing spatiotemporal variation in vegetation is central to describing landscape-level processes in terrestrial animal populations.

Thus, all animal SEPMs embody assumptions about plant communities. A necessary step in developing a SEPM is a descriptive, statistical submodel describing

animal–vegetation relationships in a landscape. For some questions, a quite crude habitat model (e.g., dividing landscape units into “suitable” vs. “unsuitable” habitat) may suffice; for other questions, more complex multivariate models describing demographic responses to vegetational axes are needed (e.g., James et al. 1984, Wiens 1989). Over the past several decades, sophisticated models have been developed aimed at predicting successional trajectories and equilibria in the physical structure and species composition of vegetation. The question we address is: When might a spatially explicit animal model benefit from linkage with dynamical vegetation models, complementing the usual sort of descriptive, statistical habitat model?

Here, we do three things. First, we discuss at a general level when linking animal and vegetation models might be useful—and when not. Then, we outline the sort of output variables from vegetation models desirable as potential inputs for animal SEPMs. Finally, we consider the most successful vegetation models to date, namely forest simulators (Shugart and Prentice 1992), and summarize their strengths and weaknesses as predictors of habitat variables needed in animal models.

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We ask whether one can take relatively complex plant dynamics models and abstract from them simpler, aggregated models potentially useful as drivers in animal models. There have been few attempts to use vegetation models in the way considered here; our remarks are provisional suggestions about potentially profitable research directions, rather than a definitive statement of proven results.

Why bother linking animal SEPMs with vegetation models?

The answer depends, among other things, on the time scale mandated by one's research agenda. It is useful to distinguish time scales and systems for which vegetational attributes can be viewed as fixed parameters, from those for which they must be considered to be system variables.

The time step in a typical SEPM for an animal population is one generation (or a fraction thereof). In terrestrial forest communities, the dominant plants defining the physical structure of the habitat usually have generation times greatly exceeding that of animal cohabitants. For short-term questions, one can sensibly assume the landscape to be a fixed spatial template, against which animal populations wax and wane in time, and ebb and flow in space. Year-to-year variability in animal numbers (Pimm 1991) may be enormous compared to any signal of change in the plant community. In such cases, explicitly linking a vegetation model to an animal SEPM would substantially increase the overhead of model analysis and parameter estimation (Conroy et al. 1995), without correspondingly enhancing understanding. The ecological world is complex and highly interconnected, but our goal as scientists is to seek simplicity, using models with just enough complexity and connections to answer the question in hand, but no more. In many circumstances, then, no linkage between SEPMs and vegetation models will be necessary or useful (beyond the usual descriptive habitat model already implicitly embedded in the SEPM).

However, many critically important ecological questions involve longer term processes, acting at time scales over which landscape structure itself can change. If one is concerned with how global climate change or habitat fragmentation influences animal species conservation over periods of several decades to centuries, an accounting of landscape dynamics must be integrated into the animal model. Vegetation dynamics are an important driving force in landscape dynamics. Vegetation models can help delimit landscape changes that are likely, out of the vastly greater number that are possible.

Consider, as a hypothetical example, the SEPM "BACHMAP" developed for the threatened Bachman's Sparrow (*Aimophila aestivalis*) in pinewoods of the southeastern United States (Pulliam et al. 1992). The spatial structure of the model is a landscape di-

vided into 2.5-ha cells (sparrow territories). BACHMAP incorporates a descriptive habitat use model for the sparrow. Each cell is classified into 1 of 22 vegetation classes: clearcuts, 20 1-yr age classes of pine plantations, and old growth (Pulliam et al. 1992). The vegetation attributes defining optimal breeding habitat include high light penetration, grassy ground cover, and scattered understory woody plants (Dunning and Watts 1990) typifying both very young and mature pine stands. Assessing birth, death, and movement rates as functions of vegetation type completes the SEPM.

In an entirely managed landscape (i.e., no old growth, and no disturbance other than clear-cutting), if one were concerned with year-to-year variation in sparrow numbers, adding a vegetation model to BACHMAP would surely be overkill. But imagine instead that old-growth stands are critical for sparrow breeding. Over time scales of a century or more, disturbances (e.g., fire, hurricanes, tornadoes) will pockmark old-growth stands with gaps of varying sizes and spatial arrangement, which then undergo succession back to mature pine. Golley et al. (1994) observe that succession toward mature pine woodland is rapid in small fields, and slow in large fields, most likely because of limited seed dispersal from the edges of large fields toward their interior. Predicting how optimal breeding habitat in a non-managed landscape shifts in areal extent and spatial arrangement over many generations requires a spatially explicit model of disturbance and plant dynamics, a model incorporating the spatial dynamics of seed dispersal for pine as well as local determinants of pine growth and survivorship. An adequate model of landscape dynamics will often (if not always) incorporate a spatially explicit model of plant dynamics, as a driver for transitions from one habitat type to another. For long-term sparrow conservation, one would want to predict changes in the landscape: vegetation models, we believe, can be used judiciously in refining such predictions.

An explicit consideration of vegetation dynamics may be particularly important when dealing with herbivores at longer time scales. There are numerous direct and indirect feedback loops through which herbivores affect plant community composition and dynamics and thereby (with a time lag) their own dynamics (Huntly 1991). Herbivores can limit the abundance of their food plants (Caughley and Lawton 1981) or influence the physical structure and competitive relationships of plants (e.g., Louda et al. 1990, Mopper et al. 1991). Accounting for such effects is an important desideratum in any mechanistic model of herbivore dynamics in a landscape context.

What is needed in animal SEPMs?

It has long been a commonplace of animal ecology that plant community structure influences species' distribution and abundance, and more generally the species composition of entire animal communities (e.g.,

Grinnell 1917, MacArthur and MacArthur 1961, James 1971, James and Wamer 1982, Rabenold and Bromer 1989, Wiens 1989, Brown 1991). One typical example of community-level effects comes from long-term studies at Manu National Park in southeast Peru, where along successional gradients from recently formed sandbars into progressively older forest, species richness of avian insectivores increases monotonically (Terborgh 1985). The literature of animal ecology is replete with comparable examples.

The mechanistic underpinnings of such correlations are often obscure (e.g., Willson 1974, Terborgh 1977, James and Wamer 1982, James et al. 1984, Wiens 1989: 317), but in some cases mechanisms have been determined; these are highly heterogeneous among species. Direct effects of plant community composition and physical structure on animal populations include: (1) the influence of plant architecture on tactics of food acquisition; (2) the provisioning of spatial resources, including nest sites and refuges from predation or inclement weather, and the determination of microclimate; and (3) the direct supply of food for herbivores.

As an example of (1), many spiders build webs for prey capture; specific architectural features associated with particular plant species may be needed for a web to be anchored (Riechert and Gillespie 1986, Uetz 1991). For (2), more complex, larger plants have a greater range of microclimatic conditions, permitting them to harbor a greater species richness of small-bodied ectotherms with narrow thermal niches (Claridge and Reynolds 1972). Category (3) is often patently obvious. For instance, host-specific insects cannot persist unless host plants are present, so insect abundance often reflects host plant abundance (Denno and Rodrick 1991).

In addition to direct effects, a plethora of indirect effects are possible. For instance, vegetation heterogeneity can modify indirect interactions between insect hosts via the numerical responses of shared parasitoids, for instance by affecting refuge availability and spatial flows of searching parasitoids (Holt and Lawton 1993).

It is thus clear what might be wished of a plant model used as a driver for an animal SEPM: its output should provide spatially referenced variables corresponding (possibly after transformation) to landscape descriptors used in the SEPM (i.e., Smith 1986). When available, a mechanistic understanding of habitat use patterns helps focus attention on causally important aspects of vegetation structure, an emphasis that should reduce the noise in model predictions.

What is available?

The most widely studied models of plant community dynamics are the menagerie of simulators developed for tree communities, particularly temperate forests (Botkin et al. 1972, Shugart and West 1977, Shugart 1984, Smith and Huston 1989, Huston 1992, Shugart and Prentice 1992). These simulators are called "gap"

models because they are scaled to the canopy gap left by the death of a large tree. Their complexity usually entails simulation, ideally guided by study of related tractable, analytic models (Pacala 1989).

The original gap models were individual-based, but not spatially explicit. They incorporated mechanistic functions predicting tree performance (growth, mortality, and fecundity) from local resource (e.g., light) availability, and submodels for how resource availability was affected by consumers (e.g., by shading) (Clark 1992). Two pragmatic decisions shaped their formulation. The first was to utilize functional forms and parameter values estimated from published data. This decision constrained the models in several ways. For example, a function relating light to growth rate was assigned using species' shade tolerance, as reported in published classifications (i.e., Baker 1949); it was assumed that all species in a given shade tolerance class have equal growth responses to light. Similarly, because species-specific data on resource-dependent mortality was not generally available, all species were typically given the same function relating mortality and growth rates. Finally, because of the small size of modeled plots, new recruits were drawn from a fixed species pool, rather than produced by the modeled trees themselves.

The second pragmatic decision was to produce model output matching data typically gathered in forestry practice, in particular tree diameters and growth increments (Huston 1992). The models have successfully predicted changes in species composition and woody stem size structure during succession (Shugart 1984, Horn et al. 1989, Shugart and Prentice 1992). Because the models output successional trajectories, they have on occasion been used to predict animal community responses to disturbance, by splicing these trajectories with previously known correlations between animal distributions and plant community composition (Smith et al. 1981, Smith 1986).

The current generation of simulators, such as SORTIE (Pacala et al. 1993) and ZELIG (Smith and Urban 1988), relaxes these pragmatically justified assumptions. Methods have been developed to estimate, from field data, parameters in species-specific submodels for growth, mortality, fecundity, dispersal, and establishment (as affected by local resource abundance), and in submodels of local resource availability (as affected by individual resource acquisition [see Pacala et al. 1993, and references therein]). The newer models are spatially explicit in three dimensions. Each individual tree has a specified spatial position and canopy geometry; mechanistic, spatially localized processes govern resource availabilities; recruits are produced endogenously; and, dispersal is spatially explicit. At present, these models predict some things with reasonable accuracy for northeastern US forests (Pacala et al. 1993) including: (a) structural (i.e., geometrical or architectural) forest features, particularly basal area, foliage

profile, and age structure, all by species; (b) species diversity patterns through time and space.

This brief overview highlights the kind of output currently generated by simulators, potentially usable as inputs for animal SEPMs. The first requirement, of course, is a set of empirical descriptors for habitats potentially occupied by a given animal species. It is better to have a mechanistic understanding of habitat use, but this is not strictly necessary, and is in any case often unavailable.

Predicting animal habitat distributions

Sometimes, the distribution of an animal species may be adequately predicted by simple structural features. If woody stem density (say, exceeding a given DBH) is correlated with a given animal species' presence, extant plant models can directly output an input parameter for the animal models (Smith 1986). Or, the simulators can be used to generate transition rules among cell states in landscape models such as BACHMAP (Pulliam et al. 1992) or OWL (Noon and McKelvey 1992), and the models can be run with the transition rules. At times, a simple transformation or model augmentation may be needed to forge a link between a vegetation model and an animal SEPM. For instance, combining the age structure of the forest with a mortality submodel allows one to estimate the rate that dead stems in different diameter classes are produced (Morrison and Raphael 1993). Together with additional information on decomposition rates as a function of stem diameter, one could predict the standing crop of resources (e.g., nest sites, foraging substrates) for a guild of woodpeckers. (For an example of this approach, see Garman et al. 1992.) Certain structural features of vegetation not currently produced by the simulators may be important. Consider again the Amazonian bird community example. Along the sandbar-to-forest gradient, average tree height and diameter increase. These variables may not directly matter to insectivorous birds, which instead respond to other, correlated structural variables. A dominant group in the insectivorous bird assemblage is the flycatching guild. Flycatchers sit on a perch and launch attacks after prey into open spaces, and different-sized species use different-sized spaces for turning and maneuvering (Leisler and Winkler 1985). To a flycatching bird, a forest has a "Swiss cheese" structure; the important aspect of the three-dimensional structure of the forest is the frequency distribution of "hole" sizes constraining the flycatching strategies mechanically feasible in a given forest. Current forest simulators do not directly predict such three-dimensional structural features (but see Urban et al. 1989). It is an open question as to how complex the models must be made to make such predictions directly. A simpler approach would be to carry out additional field studies and construct statistical response surface models that relate key structural fea-

tures to those vegetation attributes already well predicted by the models.

Along with predicting mean vegetation states, forest simulators predict with reasonable accuracy variances around the means and spatial autocorrelations. Given that different animal species differ in habitat requirements, variance estimates for structural measurements may be important outputs from plant models, for instance in estimating how animal diversity might scale with successional age, or in defining the spatial scale of variation in the plant community to which the animal community can respond (Urban and Smith 1989).

Predicting temporal fluctuations in resources

Current plant models adequately predict structural attributes and species composition, but rather poorly predict temporal patterns in the availability of certain key resources (e.g., seeds, flowers). For instance, seed production and survivorship exhibit considerable spatial and (especially) temporal variation because of masting and seed predation, among other factors. Most forest models do not capture this variability. This deficiency does not markedly affect the overall power of the model in predicting vegetation dynamics; for example, doubling the number of seeds that fall in a freshly opened site may have little effect on which tree species captures the resultant gap. Yet this same magnitude of variation in food supply could dramatically affect seed predator dynamics, with reverberating effects through the food web. We expect that current plant models will be more useful in providing inputs for some spatially explicit animal models (e.g., if vegetation structure is paramount in explaining animal distributional patterns), than for others (e.g., if resource availability drives animal population dynamics).

Scaling up models

Recently Shugart and Prentice (1992) discussed the problem of scaling up local, individual-tree-based ecosystem models to landscape, or even global, scales. The range of approaches they outline should also be useful in linking spatially explicit vegetation and animal models. Shugart and Prentice point out that with recent advances in supercomputers and massively parallel computing, it should soon be feasible to carry out gap model simulations for entire landscapes. Thus, one could take a brute force method to project landscape dynamics and how this is tracked by mobile animal populations.

However, it will often be more useful to devise simplifications and short-cuts for studies carried out at large spatial scales. This raises the problem of model aggregation (Rastetter et al. 1992). The two primary approaches to model aggregation are *formal* and *operational* aggregation. To complete a formal aggregation, one must find a way of omitting or averaging fine-scale information (a scheme of aggregation) for which the model *converges* mathematically to a simpler system at some larger scale (see Iwasa et al. 1987, 1989,

Levin 1992). To date, forest simulators have resisted attempts at formal aggregation (though admittedly, few such efforts have been made). For example, S. W. Pacala, S. A. Levin, and J. Saponara developed a version of SORTIE (*unpublished data*) containing a grid with user-specified cell size. They performed runs at a series of cell sizes in which either the positions of trees were randomly scrambled within each cell (in each iteration), or the position of each tree was rounded to the center of the cell containing it. They found that gap phase species, such as *Betula alleghaniensis* (yellow birch), were unable to persist in the scrambled treatment, even if cell sizes were considerably smaller than a canopy gap (all cell sizes <100 m²). This implies that very fine-scale spatial information is essential to maintain diversity. Alas, at such small scales, forest simulators such as ZELIG or SORTIE belong to a notoriously intractable class of mathematical models (stochastic nonlinear point or contact processes, see Durrett 1988, Durrett and Levin 1994). Though this is a discouraging observation, useful schemes of formal aggregation may yet be discovered for predicting forest species composition, or other forest characteristics important for animals (e.g., foliage height profiles across a landscape).

In contrast, to complete an operational aggregation one simply fits a simple dynamical model to output of a forest simulator. For example, gap models can be used to estimate probabilities of species replacements, or transitions among multivariate state classes used to classify animal habitats. These probabilities can then be used in Markov matrix models summarizing the entire pattern of transitions among vegetation-habitat classes (Horn 1975).

Alternatively, consider a system of finite difference equations of the form: $N_{i,t+1} = F_i(N_t)$, where $N_{i,t}$ is the abundance of species i at time t , and N_t is the vector of abundances of all species at time t . S. W. Pacala (*unpublished data*) fit systems of this form to the output of the simulator SORTIE. Excellent, predictive fits were obtained from:

$$N_{i,t+\Delta t} = \frac{r_i N_{i,t}}{1 + (r_i - 1) \left[\sum_{j=1}^Q \frac{\alpha_{ij} N_{j,t}}{K_i} \right]}, \quad i = (1, 2, \dots, Q), \quad (1)$$

where $N_{i,t}$ is the basal area (in hectares) of species i at time t , the time step is 50 yr, Q is the number of species (up to 10 in SORTIE), and the remaining parameters have the same meaning as in the Lotka-Volterra competition equations.

Fig. 1 provides one example showing that, when calibrated using one set of runs, system (1) predicts the behavior of the simulator in independent runs. Systems such as (1) provide neither good fits nor accurate predictions if the state variables summarize areas that are too small (i.e., 0.1 ha), essentially because stochastic

effects dominate at small spatial scales, or if the time step is too long or too short (i.e., 10 or 100 yr) (S. W. Pacala, *unpublished data*). We suspect that in this example, the 50-yr time step works because it is consistent with the time scale of the development of advance regeneration (a layer of suppressed saplings of shade-tolerant species in the understory). For many spatially explicit animal models, approximate models such as (1) may provide sufficient resolution and thus an easy-to-scale-up alternative to complex vegetation simulators that track each plant.

The problem of reconciling scales across models

The problem of scaling-up forest models is one facet of a larger problem: the range of spatial and temporal scales targeted by plant and animal models may differ. For instance, gap models traditionally use a unit of ≈ 0.1 ha (Huston 1992), yet spatial models for single vertebrate species typically use spatial units equal to one territory or home range. For example, BACHMAP uses an array of 2.5-ha cells, whereas OWL (Noon and McKelvey 1992) has much larger units (>0.5 km²). If organisms have nonlinear responses to resource availability or habitat characteristics (e.g., a bird may need only a single suitable nest site within its territory), simply averaging over multiple runs of the local plant models may give a misleading picture of habitat quality. This is particularly worrisome if one does not understand the mechanisms actually determining habitat quality and is instead using descriptive, correlative models. Conversely, invertebrates may be sensitive to small-scale heterogeneities that are only noise in the plant models. Successful linkages between animal and vegetation models will require not only direct correspondence between the output and input variables in each model, but also the judicious meshing of spatial and temporal scales.

We should emphasize that in addition to the class of models emphasized above, another major type of vegetation model comes from forestry models that use individual trees or stands as basic units (e.g., PROGNOSIS, Wyckoff et al. 1982; J. Liu and P. S. Ashton have carried out a comparative review [*in press*]). Using regression techniques and site-specific remeasurement data (e.g., forest variables and site quality), forestry models have as a primary aim projecting growth and yield of timber species in managed forests. However, such models may be useful beyond their primary purpose, because their outputs include variables that determine the structure of animal habitats, including: tree density (stems per area), heights, basal area, crown ratio, amount of cover and leaf biomass in the tree canopy by height class, height and cover of shrubs, forbs, and grasses in the understory, and overstory and understory cover, and stand biomass (Moeur 1986)—all standard descriptors of habitat for animal populations.

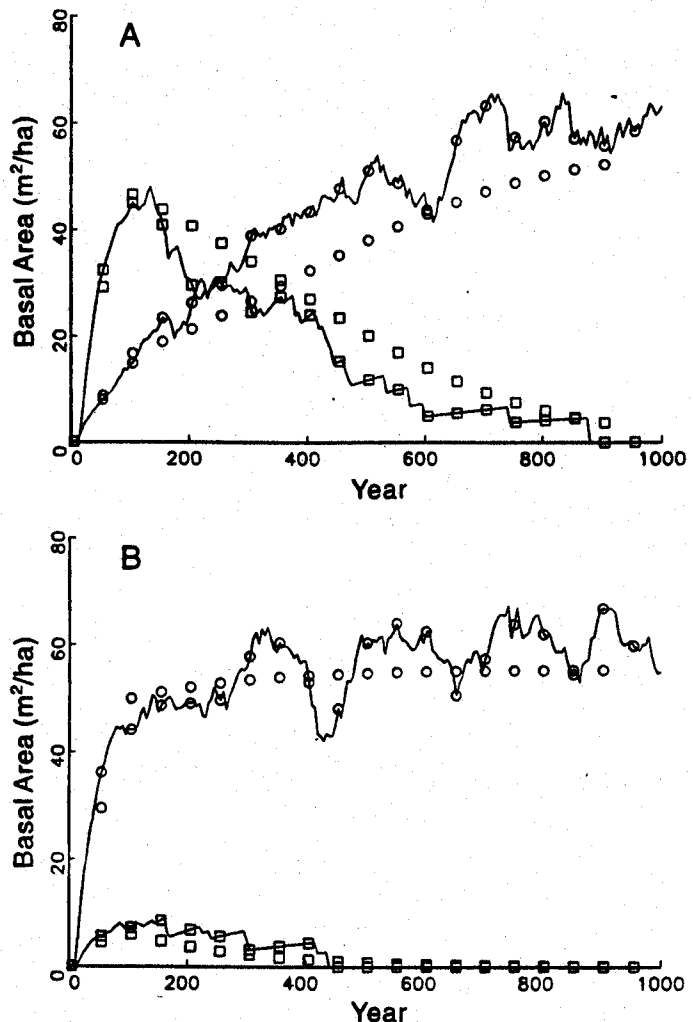


FIG. 1. The ability of the simple model (1) to predict the outcome of simulations of two-species communities; *Tsuga canadensis* (Canadian hemlock) is denoted by circles. The circles on the erratically rising line indicate output from the complex forest simulation; the unconnected circles, smoothly rising through time, are predicted from model (1) in the text. The squares similarly denote dynamics of *Fraxinus americana* (white ash) generated by the simulator (squares along erratic, peaked line), and the approximate model (1). Each run was initiated with 300 saplings/ha of 1 cm diameter. The initial ratio of ash to hemlock was 5 in (A) and 0.2 in (B). In all cases, the models had been previously calibrated on independent runs.

Gap models vs. forestry models

Gap models such as ZELIG and forestry models could play complementary roles in animal modeling. The former are developed for natural forests, the latter for managed forests or plantations. Gap models have typically dealt with the dynamics of an area ranging from 0.01 to 0.1 ha, and their output may be quite sensitive to simulated area (Shugart 1984). In contrast, forestry models deal easily with large tracts of forest, and so may be especially useful for animals with large territories such as the Spotted Owl (Noon and McKelvey 1992). With site-specific forest and/or environmental information, forestry models have the potential to provide spatially specific outputs for spatially explicit animal population models. For instance, Liu (1992) successfully used a stand-level forestry model (Borders et al. 1990) to simulate the habitat and population dynamics of the Bachman's Sparrow. A few gap models have been used to assess animal habitats. An early example was provided by Smith et al. (1981),

who developed two gap models to assess the impact of various management schemes on avian populations. Garman et al. (1992) modified ZELIG to evaluate the suitability of a Douglas-fir forest under different management schemes for 14 species of birds in western Oregon. Structural features such as tree density, basal area, snag, and log density were simulated for 500 yr. A notable feature of this work is that routines simulating snag and log dynamics were integrated into the generic version of ZELIG, along the lines of the woodpecker scenario sketched above.

CONCLUSIONS

Vegetation models are no panacea for animal SEPMs, even at long time scales. Animal communities are composed of species that both experience the world at vastly different spatial scales (Addicott et al. 1987, Holt 1993) and exhibit distinct, species-specific responses to vegetation. Because current vegetation models target a restricted range of spatial scales and output variables (viz.,

those pertinent to questions in plant community ecology or forestry), these models are likely to be more useful for some consumer groups than for others.

Despite these cautionary remarks, we believe the recently developed plant models alluded to above are ripe for direct linkage with spatially explicit animal models. Because vegetation structure is usually important for most members of animal assemblages, linkage to vegetation models provides one avenue for the development of more general, multi-species approaches to spatially explicit animal models. Such models, if successfully developed, could provide essential tools for assessing effects on the landscape of shifting land-use practices, natural catastrophes, and global climate change, and ultimately assist in mitigating the pernicious influence of such forces on renewable resources and the conservation of endangered species. Fostering these linkages will become increasingly important as ecologists try to understand and, if possible, mitigate the looming effect of processes operating over long time scales.

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