

# Application of ecological models to landscape planning: the case of the Mediterranean basin

M.A. Zavala<sup>a,\*</sup>, T.V. Burkey<sup>b</sup>

<sup>a</sup> Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA

<sup>b</sup> University of Oslo, S.U.M. Center, (Center for Development of the Environment), P.O. Box 1116, Blindern N-0317, Oslo, Norway

---

## Abstract

Landscapes in the Mediterranean basin have been modified by human exploitation for ages. Currently, European Community (EC) agricultural policies are reshaping land use patterns and vegetation disturbance regimes. It is uncertain how vegetation and animal population dynamics will be modified by the novel spatial patterns of habitat fragmentation and disturbance. Therefore, landscape planners need diagnostic tools to evaluate the impact of alternative management schemes on habitats and wildlife. In this contribution, we discuss the possible role of ecological models in describing how animal and plant community dynamics are affected by anthropogenic processes. First, we review models of landscape change and their applicability to habitat modeling in the Mediterranean basin. Second, we discuss different approaches to investigate the effect of habitat spatial structure on the long-term persistence of animal populations. © 1997 Elsevier Science B.V.

*Keywords:* Mediterranean basin; Land use; Natural and cultural influences; Habitat fragmentation; Habitat modeling

---

## 1. Introduction

Ecology investigates the relationship of organisms with their environment (Begon et al., 1986). Scientists dealing with both theoretical and applied ecological problems come from a variety of backgrounds and address a diverse set of problems related to organisms and their environment. Ecological processes are strongly impacted by activities generated by human economic motives and social interests. Ecologists are thus hard-pressed to separate 'natural' from 'cultural' influences on the relationships between organisms and its environment.

Landscape ecology can help to make sense of this complex situation by offering an interdisciplinary

forum where to integrate the biological, economical and geographical aspects of ecological problems (Naveh and Lieberman, 1984). The complexity of landscapes has been approached by Grossman (1991) following a system analysis perspective that considers landscapes as three-layered hierarchical systems. Briefly, the bottom layer consists of a template defined by data such as topography, property boundaries or soil type distribution and other spatial detail usually incorporated into a GIS. The intermediate layer or layer of complex dynamics includes structures and their dynamics, like vegetation, timber prices or climate. The dynamics of these structures can be described by models of forest succession, supply–demand models or global climate models. Finally, the highest or strategic layer describes processes that modify the structures of the intermediate layer, for example changes in fire control policy,

---

\* Corresponding author. Tel.: +1-609-258-3987; fax: +1-609-258-1334; e-mail: mazavala@phoenix.princeton.edu

political events like the Middle East oil crisis that increase the demand of plant biomass or atmospheric events like 'El Niño' that turn global circulation patterns.

This approach provides a powerful perspective to integrate biological and economical processes. Nevertheless, its applicability can be limited by the degree of uncertainty associated with the complex dynamics layer. In this contribution, we discuss how to model the dynamics of the structures of the intermediate layer in order to decrease the degree of uncertainty associated with these dynamical predictions. We focus on Mediterranean landscapes because they are a unique system to investigate the effects of repeated historical strategic changes on biological structures. In Section 2, we discuss different approaches to describe forest habitat dynamics under the Mediterranean climate. In Section 3, we discuss different methods that can contribute to evaluate the effects of habitat configuration on animal populations' persistence.

## 2. Anthropogenic habitats: the case of the Mediterranean basin

It has been estimated that humans occupy 38% of the global terrestrial surface for their own devices—habitation, cultivation, transportation, extraction and commerce—and that most of the 30% that is still forested is exploited to some degree by agroforestry (Vitousek et al., 1986; Ehrlich and Ehrlich, 1990). The impact of humanity in what we call natural landscapes has been different for each continent and its intensity and extension is open to debate (e.g., Naveh, 1975; Nakagoshi et al., 1987; Minnich, 1988; Abrams, 1992; Denevan, 1992). In some regions, this pressure is becoming more intense and extensive than ever before. For example, annual habitat loss in tropical forests has been estimated at 170,000 km<sup>2</sup>, or 0.9%, over the period from 1981 to 1990 (Groombridge, 1992). But these changes can be qualitatively very different in other parts of the world. For example, the Mediterranean basin has experienced a remarkable succession of civilizations each possessing their own economic systems. Each of these civilizations has contributed to the structure of the present-day landscape. Therefore, the landscape we observe

today is the result of subtle interaction between ecological and anthropogenic processes occurring at each successional stage. Human influence, however, is not only an attribute of the past. These landscapes are currently undergoing important structural changes (Antrop, 1993; Fernández-Alés et al., 1992; Gómez-Sal et al., 1993). Given the strong association between human activities and ecological processes, and the variety of spatial and temporal scales at which these interactions operate, the Mediterranean region is a point of reference for considering human dominated habitats.

The influence of humans on biological systems in the Mediterranean basin has been so intense and extensive that different authors have pointed out the 'anthropogenic' structure of plant communities (Naveh and Whittaker, 1979; Ruiz de la Torre, 1985; Gómez-Sal et al., 1992; Montalvo et al., 1993). This structure is characterized by a characteristic patchiness (Ruiz de la Torre, 1990) derived from the interaction at different scales of multiple land-use patterns with a physically heterogeneous environment (Di Castri and Mooney, 1973; Pineda et al., 1981). These interacting processes have apparently resulted in high values of  $\alpha$ - and  $\beta$ -diversity associated or even dependent upon traditional land-use systems (Naveh and Whittaker, 1979; Ruiz de la Torre, 1985; Mooney, 1988).

The structural changes associated with the rural exodus during the 1960s, and more recently land abandonment resulting from European Community (EC) agricultural policies, have modified traditional land-use systems and have altered patterns of biological diversity (Naveh and Kutiel, 1990; González-Bernáldez, 1990; Pineda, 1992). These changes are markedly different in Euro-Mediterranean countries than in Northern Africa. In the former, market economy seems to promote woodland and forest extension in some localities (Fernández-Alés et al., 1992; Gómez-Sal et al., 1993), while in the latter habitats are under intense pressure related to exponential human growth and traditional farming techniques (Blondel and Aronson, 1995). As a result, the Mediterranean landscape is comprised of stands at different stages of development that vary in space and time according to ecological and economic factors (Hutsinger and Bartolome, 1992; Fernández-Alés et al., 1992). Ecological factors include environmen-

tal variability, disturbance gradients and the colonizing and competitive ability of different taxa. Relevant socioeconomic factors include the profitability of firewood versus fossil fuel, timber market economy and ownership patterns. Therefore, original vegetation has been modified to a variety of 'states' such as agroforestry systems with local varieties (e.g., Spanish 'dehesa') or woodlands subjected to different silvicultural treatments (e.g., pollarding, coppicing or thinning). Current structural changes will impose important qualitative changes in the dynamical behavior of these systems. The interaction between pattern and process has been widely documented in ecological literature (e.g., Watt, 1947; Turner, 1989), however the underlying mechanisms have been investigated only for a few biological systems. Possible feedbacks in the Mediterranean region have been recently reviewed by Blondel and Aronson (1995) (also see Naveh and Kutiel, 1990). These authors have emphasized the critical role of spatial pattern in maintaining structures and their dynamics at the intermediate layer, e.g., between biodiversity and ecosystem function. For example, changes in the spatial and temporal distribution of fire regimes could lead to soil erosion and even desertification. Similarly, the spatial pattern in land abandonment can collapse regional diversity by eliminating species that depend on patches of traditional land use. Understanding the biological mechanisms driving the dynamical behavior of ecological systems is necessary in order to design resource management policies that consider economic as well as ecological factors at regional scales.

### *2.1. An overview of patterns and processes in Mediterranean forests*

Ecologists have long investigated the mechanisms underlying forest dynamics. It is widely accepted that at global scales, climate controls vegetation types, while at local scales species-distribution boundaries are determined by competition, with tolerance to climatic stresses setting limits to these boundaries (Whittaker, 1975). Human and natural disturbances can also alter species distributions by affecting species' demographic processes at different stages. The effects of human activities on forest processes are poorly understood. One possible reason

is that ecologists have traditionally conducted their research in pristine systems and have rarely addressed the effect of human activities on forest ecosystems (but see Ledig, 1992; Bormann and Likens, 1994). However, it seems difficult to imagine how we could study Mediterranean forests without taking into consideration the effects of human social systems.

Mediterranean forests have been grazed, burned and exploited in a variety of ways for ages, and therefore many of the patterns that we observe today depart from what could be expected from climatic influences alone (Naveh and Kutiel, 1990). For example, in large regions of the Mediterranean basin humans seem to have maintained forest composition at a certain state that was more profitable to them, either directly by eliminating competitors or by changing the competitive regime and favoring species that benefit from disturbance. E.C. reunification initiates an important strategic change (Grossman, 1991). Novel agricultural policies will result in management abandonment in some regions and new management practices in others. Accordingly, important changes in forest species composition could take place in the near future as silvicultural regimes are released, with new species outcompeting the existing dominant ones (Pons and Vernet, 1971; Barbero et al., 1990). Nevertheless, stand trajectories as defined by species composition and their relative abundance are uncertain (Romane et al., 1992). To complicate things further, it is not generally possible to study chronosequences to infer stand trajectories because the influence of humans could be as old as the Mediterranean climate itself (Naveh and Whittaker, 1979; Ruiz de la Torre, 1990), and may have extended across the entire climatic region (Thirgood, 1981).

Forest composition and dynamics are strongly affected by environmental features such as exposure, slope, soil and elevation that reflect underlying patterns in water and nutrient availability. Therefore it is possible to imagine the variety of dynamical behaviors that can be obtained if we superimpose the 'complex dynamics layer' over the 'bottom layer.' The former consists of a dynamical description of the population interactions that govern stand dynamics and the latter is a GIS database that incorporates the remarkable spatial variability in topography and

soils that can be found in Mediterranean habitats. If such a dynamical model is perceived in the absence of management and fragmentation, different dynamical scenarios could be imagined. For example, stands could enter into a self-thinning stage mediated by competition that would ultimately lead to cyclic behavior (Schaeffer and Moreau, 1958; Ducrey, 1992). The landscape could also behave as a catastrophe-driven system, with large-scale disturbances such as fires and droughts resetting the system to pioneer stages (Naveh, 1987) and ultimately converging to a shifting mosaic of monospecific stands. In this last scenario, species could also self-replace locally after disturbance (autosuccession), maintaining multiple stable states across topographic gradients.

Models of stand dynamics have been extensively used to explain and to predict forest succession in temperate forests. These models rely on the reasonable biological assumption that species distributions are to a first approximation determined by climatic stresses and competition. Therefore, stand dynamics can be investigated if we know how species-specific population processes such as growth, mortality or recruitment are affected by climate and competition. In Section 2.2, we discuss the potential role of these models to simulate habitat dynamics in the Mediterranean region.

## 2.2. *Models of habitat change: constraints in Mediterranean habitats*

Models of habitat change have been reviewed by different authors (e.g., Shugart, 1984; Baker, 1989; Turner, 1989). These models differ in their state variables, the level of aggregation of input and output variables and the mathematical details of the model itself (Baker, 1989). Landscape models usually consider land use or vegetation types as the input variable and therefore encapsulate all the underlying biology in these units. We will refer to these models as top-down models. In vegetation models, input variables can refer to much lower scale mechanisms like the physiological details that control species' differential performance (see Tenhunen et al., 1987). Given the limited data on species' life history, simple top-down correlational models can be as effective as much more sophisticated models for applied purposes. For example, in order to predict

forest basal area or productivity, a simple regression between basal area and water balance can challenge the predictions of more complicated mechanistic physiological models.

Mediterranean landscapes can be described by the statistical distribution of smaller units called states that reflect different land-use and vegetation types (Fernández-Alés et al., 1992; Gómez-Sal et al., 1993). Habitat dynamics can therefore be defined by the processes that regulate transitions between these states, mainly management and environmental variables (Hutsinger and Bartolome, 1992). Therefore, we need to estimate transition rates among habitat types in order to implement a model of landscape change. Depending on the kind of model, transition probabilities can be assumed stationary over time (e.g., Drewett, 1969), defined as explicit functions of time or dependent on the state of proximal neighbors (Turner et al., 1995). Generally, these models can be calibrated from present and past patch distributions (see review in Baker, 1989).

Top-down models can be accurate for short-term predictions, but they alone cannot provide long-term predictions of habitat change in Mediterranean landscapes. As we have pointed out, these landscapes are undergoing 'strategic changes' at the top layer that are not only modifying the dynamics of the structures at the intermediate layer (e.g., land use units), but the structures themselves (e.g., new types of states), therefore it is not possible to calibrate a standard landscape model based on a temporal series of 'state' distributions. Considering this, we need to understand the underlying mechanisms of patch formation and turnover in these systems.

Over the last decades, significant advances have been made in models of forest dynamics (for details, see Shugart, 1984; Pacala et al., 1996). Among these, individual-based simulators of temperate forests have played a predominant role. Commonly, these models are spatial stochastic formulations that track the fate of each tree throughout its life cycle. They summarize the underlying physiological detail with regression functions that describe the species' demography, e.g., growth or mortality. The parameters that define these functions can be obtained from forestry literature (Shugart, 1984) or directly estimated from field data (Pacala et al., 1996). Another subroutine describes resource dynamics, generally

light, water and nitrogen, as a function of tree uptake and environmental supply. In this way competition is modeled through the effect that neighboring trees have on the resource levels that in turn determine individual tree performance. These models can be fundamentally different in the way that parameters are linked to data, the scale of spatial detail in resource and dispersal functions, complexity of the model and uncertainty estimates. Nevertheless, a complete description of these differences goes beyond the scope of this paper (for details refer to Shugart, 1984; Pacala et al., 1996).

These models have several advantages over physiological simulators, both from a theoretical and an applied perspective point of view. First, they incorporate variables like growth that are observable and exhibit less variability than physiological measurements. Secondly, by describing population dynamics they can help to bridge physiological- and community-level approaches. A major challenge of these models is to keep them simple enough so that predictions can be mathematically and biologically interpretable. Mathematical understanding usually requires models to be solved in a closed form, at least for some special cases. Simulation has generally a wider applicability to practical problems than it has to theoretical problems, where analytical approaches are generally required. A modeling program integrated with empirical work is a powerful tool to sharpen our questions and point out relevant ecological mechanisms.

As we discussed earlier, modeling habitat dynamics in the Mediterranean region may require an understanding of the mechanisms that link population dynamics to stand structure. Given that fundamental processes distinguish Mediterranean forests from temperate forests, it is not generally possible to directly use models of forest dynamics developed for temperate systems. Water limitation seems one of the most important determinants of species distributions in Mediterranean forests, (Pigott and Pigott, 1993) yet the effects of soil moisture availability and its interaction with radiation have not been empirically incorporated in previous models of stand dynamics. Similarly, disturbance regimes in Mediterranean habitats can be very different from those in temperate forests. In Mediterranean vegetation, fire, drought, herbivory and agrosilvicultural systems provide re-

cruitment opportunities at very different spatial and temporal scales than the forest gaps that typically occur in temperate forests. This difference is critical because the most widespread type of forest simulators have a built-in gap dynamics structure (Shugart, 1984).

Implementing biologically-based models that scale up from observable variables and are biologically realistic require interdisciplinary research between landscape planners, foresters, field ecologists and modelers. Landscape planners and foresters should state clearly what it is we need to model and what degree of uncertainty that we can afford. Foresters and field ecologists usually have valuable knowledge of the processes we are trying to understand that can help us to distinguish between biologically essential and superfluous phenomena. Taking these as simplifying assumptions, modelers can derive simple models and test them against independent data, which in turn can lead to new hypotheses. These assumptions can then be formally tested by experimentation or can lead to detailed parameter estimation by ecologists.

### **3. Effects of landscape structure on animal populations**

The dependence of animal communities on vegetation structure has been widely documented (Wiens, 1976; Blondel et al., 1992). Indeed, much of what is meant by habitat refer to the spatio-temporal patterns of plant communities. Therefore, understanding which structural habitat features are most important for multispecies animal assemblages is a major issue to wildlife management on a regional basis. The interactions between wildlife and habitats are spatial and dynamic (Blondel et al., 1992; Turner et al., 1994; Holt et al., 1995) and spatial models might be the only feasible way of exploring these relationships across different scenarios (Turner et al., 1995).

Our understanding of the mechanisms underlying the observed correlations between habitat structure and animal communities is poor (Holt et al., 1995). Studies from the Mediterranean region indicate that at biogeographical scales, factors explaining bird species composition turnover along habitat gradients are not likely to be explained uniquely by adaptive

processes, but also by historical and anthropogenic processes related to habitat structure (Blondel and Vigne, 1993). At shorter spatial and temporal scales, habitat patch structure and regional fragmentation (e.g., different types of forests) can have dramatic effects on animal metapopulation dynamics and the evolution of life history trait (Blondel et al., 1992; Santos and Tellería, 1992). Evaluating the effect of habitat structure on animal community structure at different scales is beyond the scope of this review. We will focus instead on the effect of habitat fragmentation and patch size on animal populations' persistence. These factors are not the only ones to which animal populations respond. However, given our limited knowledge of biological mechanisms, measurements of landscape spatial patterns may be an acceptable metric to summarize the effect of habitat structure on animal communities. Moreover, it is a variable that landscape planners can easily take into account in short-term decision-making.

We therefore consider that as a first approximation, landscape structure can affect population dynamics through two main interacting factors: habitat loss and habitat fragmentation (Wilcox and Murphy, 1985; Groombridge, 1992). We will refer to the reduction in area available to a population as habitat loss and to the subdivision of the remaining habitat area into isolated or semi-isolated patches (without further loss of area) as habitat fragmentation. This is somewhat different from the most common usage, where fragmentation encompasses both habitat loss and subdivision of the remainder into multiple patches. We make the distinction here, however, under the assumption that reducing a phenomenon into its component parts may aid in the understanding of its effects.

### 3.1. Fragmentation and population persistence

Much of what we know about habitat structure and population persistence has been motivated by the single-large-or-several-small (SLOSS) debate about reserve design. The claim that several small reserves are a worse conservation strategy than a single large was first raised by Diamond (1975) and Wilson and Willis (1975) (see Fig. 1a–f). Most of their recommendations follow from island biogeography theory (MacArthur and Wilson, 1967). For instance, Fig. 1a follows from the realization that the risk of extinc-

tion decreases with area, and Fig. 1c from the realization that proximity increases the probability that dispersers may recolonize fragments where the species has gone extinct (the 'rescue effect' in Brown and Kodric-Brown, 1977). However, Fig. 1b does not follow from island biogeography theory, at least not without further analysis.

In Section 3.2, we will focus on the effects of habitat fragmentation on the probability of extinction for a focal species. When a landscape is fragmented, it becomes more heterogeneous to residents of the original habitat, which become more patchily distributed at the landscape scale. There seems to be a consensus in the ecological literature that habitat heterogeneity can be stabilizing (e.g., Levins, 1970; Levin, 1974; Nisbet and Gurney, 1982; Hastings, 1990; Kareiva, 1990), and that a predator–prey system that would break down rapidly in a homogeneous, continuous environment may persist in a patchy environment (Huffaker, 1958; Atkinson and Shorrocks, 1981). The focus here, however, is on systems that had a high probability of persistence prior to some form of (anthropogenic) habitat loss and fragmentation. That is, systems where the species in their various predator–prey and competitive interactions were relatively persistent in the habitat texture as it was before the disturbance and as it may still remain at a smaller scale within the new fragments.

### 3.2. Factors affecting species persistence in fragmented landscapes: a modeling approach

There are likely to be two broad classes of mechanisms affecting fragmented populations. First, there are mechanisms which break down in isolated communities when the isolate drops below a certain size. This means that more isolates of the same size will not enhance persistence. Second, there are mechanisms whereby a system in a small isolate has a certain risk of breaking down, greater than that in a large system, but where the existence of several such isolates may bring the risk that they all break down below the risk in the large continuous system. This dichotomy is partially captured by the distinction between deterministic and stochastic processes. It is important to understand under what circumstances a metapopulation will survive in a set of small frag-

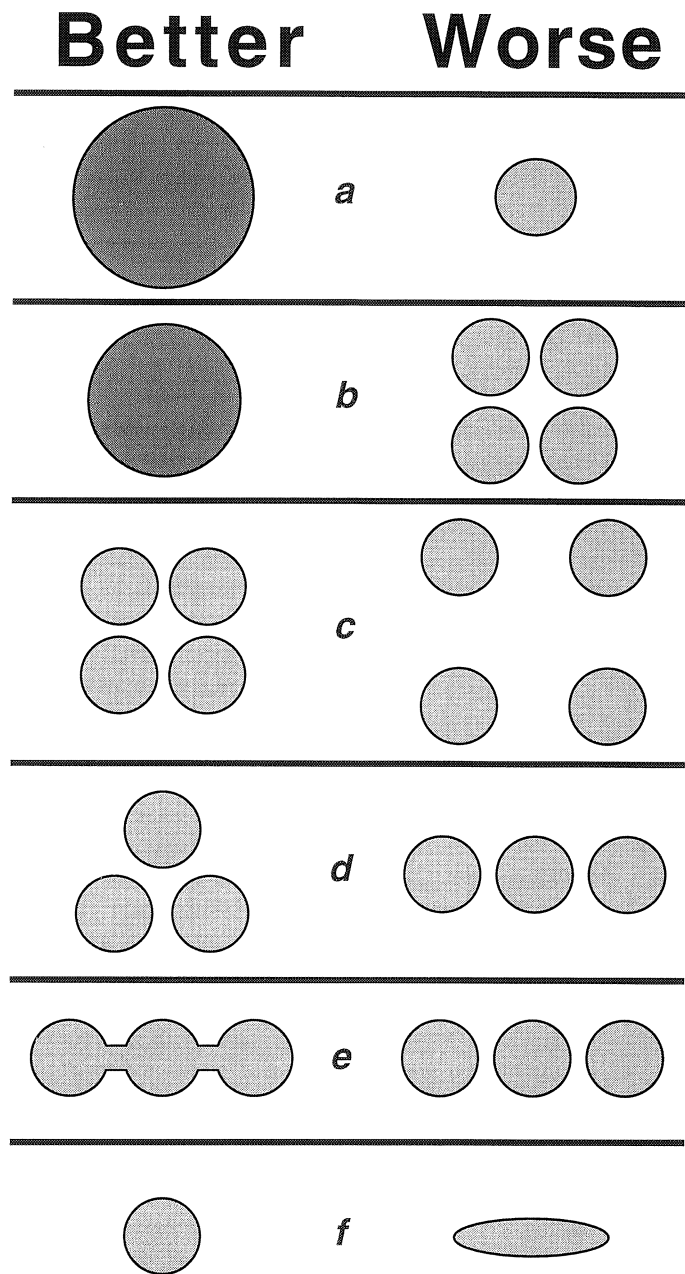


Fig. 1. Recommendations for reserve design after Diamond (1975) and Wilson and Willis (1975). These suggestions have still not been adequately tested. The positive effect on species diversity of increasing size and decreasing distance is well documented (MacArthur and Wilson, 1967). The influence of connectivity and edge effects, however, remains poorly understood.

ments and when each small fragment will have to contain a functioning system within itself, and how these predictions can be affected by disturbance regimes of different spatial and temporal architectures.

### 3.2.1. *Density dependence and demographic stochasticity*

Density dependence is critical to the study of fragmented populations, because it is one way of introducing a dependence of the fate of one individual on that of another. If individuals are completely independent of one another, they might as well be in separate reserve fragments. If that is the case, habitat fragmentation should have little effect on the fate of the population. Without density dependence, the concept of area as in classic island biogeography has little meaning, since density dependence determines how individuals perceive the area available to them.

For example, Järvinen (1982) used a density-independent model proposed by Pielou (1977) to show that it is 'not obvious a priori whether one large or several small populations can be maintained more securely.' Following Bailey (1964), the probability of extinction by time  $t$ , for a density-independent birth–death process with birth rate  $b$ , death rate  $d$  and initial population size  $N$  is  $P_e(t) = \{[d(e^{(b-d)t} - 1)]/[b(e^{(b-d)t} - d)]\}^N$ ,  $b \neq d$  and  $P_e(t) = \{(bt)/(bt + 1)\}^N$ ,  $b = d$ . The probability of extinction for  $n$  populations of initial size  $N/n$  is identical for all  $n$ , since under the assumption of independent populations  $(P_e(t)|N = x/n)^n = P_e(t)|N = x$ .

The inclusion of density dependence in these models can change the predictions for the relative persistence of fragmented and unfragmented populations (Burkey, 1989). Solving a stochastic birth–death process with linear density dependence in per capita birth and death rates numerically, we see strong detrimental effects of fragmentation even without any loss of area (Burkey, 1995). Wright and Hubbell (1983) modified the Markov process studied by MacArthur and Wilson (1967) and Richter-Dyn and Goel (1972) by including recolonization from outside the system, and by introducing a version of diffuse competition between species. They concluded that for closed systems, extinction takes longer in a single large than in two small fragments. For open systems, the difference was usually negligible. They

suggested that the coefficient of variation of abundance is the best predictor of species persistence for a focal species.

Quinn and Hastings (1987) borrowed a result from reliability theory to calculate the mean time to extinction for fragments of different degrees of subdivision. From some simple models of demographic and environmental stochasticity, they concluded that the mean time to extinction decreases with increasing subdivision under the former, and increases under the latter.

Goodman (1987a,b) introduced environmental variance in a birth-and-death-process model by letting the fates of individuals be correlated. He concluded that mean extinction times go up exponentially with carrying capacity under demographic stochasticity, but less than linearly under environmental stochasticity. Hence, if environmental variance is high enough and spatially uncorrelated enough, and there is at least some recolonization of extinct islands, multiple reserves may be preferable to single large reserves. He pointed out that when we incorporate environmental fluctuations into our models, extremely large population sizes may be necessary to confer reasonably long persistence times. Mere demographic stochasticity plays a relatively slight role when population sizes stay above some moderate (model-dependent) value. Consequently, it may be that environmental variance may override the effects of demographic stochasticity. In this scenario, the pivotal issue is whether environmental variance is great enough and spatially uncorrelated enough in nature to really make subdivision a viable option. More complicated dynamics and more biological realism than has currently been incorporated into theoretical models (notably the existence of 'threshold values') may yet impose limits on the applicability of this view. Furthermore, the 'correct answer' may well turn out to be scale-dependent, both spatially and temporally, as well as species-specific.

Models based on demographic stochasticity yield exponentially increasing mean times to extinction with increasing carrying capacity (MacArthur and Wilson, 1967; Richter-Dyn and Goel, 1972; Goodman, 1987a,b). The implication is that such models are only relevant to extinction and fragmentation events for very small populations (e.g., 20 or less).



However, these models are devoid of any time lags (they are derived from Markov processes as  $\Delta t \rightarrow 0$ ), predator–prey dynamics, or other factors that might bring the population back down after they have passed the reputed ‘critical population size.’ The importance of demographic stochasticity in determining the fate of real populations may therefore be seriously underestimated (see Burkey, 1995).

### 3.2.2. Environmental stochasticity

Habitat fragmentation accelerates the extinction process in populations subject only to demographic stochasticity (Burkey, 1989). This still holds true when large-scale environmental stochasticity is added (Burkey, 1995). Small-scale environmental stochasticity which is at least partially uncorrelated spatially can counteract the effect of demographic stochasticity if it is severe enough. Thus, the effect of a given landscape configuration on population persistence hinges on actual level of disturbances and their correlation structure. This is an empirical matter, though one which is difficult to observe, and should be explored with various modeling approaches.

Burkey (1989) developed a simulation model for a single population that incorporates migration between reserve fragments, spatial and temporal variance in carrying capacity, and ‘catastrophes’ that can be spatially correlated. Simulation runs of relatively small reserve systems show that the probability of extinction in a population subjected to demographic stochasticity goes up exponentially with habitat fragmentation. With frequent catastrophes that are spatially uncorrelated less likely to hit a smaller area, and expected to kill the same proportion of the individuals in a patch regardless of its size, it is possible to reverse this effect. The model however is biased in favor of a fragmented system; migration between fragments can partially alleviate the effect of fragmentation, but can never reverse it and even with extremely high migration rates, the fragmented reserves have higher extinction rates. Migration between reserve fragments complicates analysis by dynamically coupling fragments. However, it adds little to the conceptual framework.

If habitat patches/islands are isolated completely from each other, the effect of subdivision is still not trivial. If the probability of extinction,  $P$ , as a func-

tion of island size ( $K$ ) is described by a negative exponential function  $P(K) = \exp(-cK)$ , then fragmentation does not affect  $P$ , (where  $n$  is the number of fragments into which the area is subdivided). If  $P(K)$  declines more rapidly than a negative exponential, then fragmentation is detrimental. But if  $P(K)$  declines less rapidly, then fragmentation is beneficial. Specifically, if isolated fragments are independent and  $x$  is a positive constant such that, the probability of archipelago-wide extinction is  $P_e(n, K) = \exp(-cK^x n^{1-x})$ , where  $n$  is the number of fragments. For  $x = 1$ , fragmentation is neutral; for  $x > 1$ , fragmentation accelerates extinction; and for  $x < 1$ , fragmentation decelerates extinction (Burkey, 1995). Fig. 2a,b shows three types of extinction curves that yield different results for SLOSS. We should take a closer look at different extinction models to see what shapes they dictate for  $P(K)$ ,

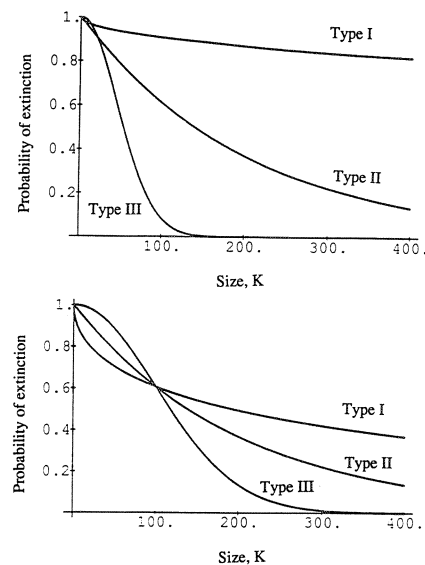


Fig. 2. Three types of extinction curves. (a) and (b) Assume  $P_e(A) = \exp(-cK^x)$ , then a type I curve is obtained for  $x < 1$ , a type II for  $x = 1$  and a type III for  $x > 1$ . If extinction probability declines with area as in the type I extinction curve, fragmentation is beneficial (the probability of extinction for a set of small reserves is lower than that in a single large). For type II extinction curves, there is no effect of fragmentation. For type III extinction curves, fragmentation is detrimental.

and at organisms to see what kind of biology give the different scenarios. In general, if  $P(K)$  is log convex, fragmentation increases the risk of extinction (a function  $f$  is log convex if  $\log(f)$  is convex). This result is generalizable to  $n$  patches of any size distribution using Jensen's inequality.

Simulation models by Possingham et al. (1992, 1993) have yielded viability estimates for a variety of populations in different sized habitat areas under demographic stochasticity and fire regimes. This can be used to calculate the probability of extinction with and without subdivision of such areas, under the assumption that isolated fragments are entirely dependent. For instance, they estimate the extinction risk for a single species after 300 yrs in single patches of different sizes, with and without fires (Fig. 3a). Assuming independence, we can calculate from these numbers the probability that two populations in 30-ha areas go extinct and compare with the viability of a single population in a 60-ha area, etc. Fig. 3b shows the result of such comparisons under demographic stochasticity only (no fires) based on the data in Fig. 3a. The fragmented systems go extinct sooner than the unfragmented systems. Even in this implementation the effect of fragmentation is conservative since any correlation between the fate of isolated populations will increase the risk that they both go extinct. In a similar calculation based on the simulations with fires, this concern is even more evident since fires may spread from one patch to the other (although we may not know the correlation structure of such events), and the assumption of independence is likely to cause an underestimation of the effect of fragmentation if fires are important.

Fig. 3c shows the extinction risk of a single large population and a pair of small populations based on the fire simulation data of Possingham et al. (1992, 1993). Note the spatial scale dependence in the effect of fragmentation that emerges from this treatment of their data. Assuming independence, fragmentation appears to increase overall extinction if the available area is small, but reduce the risk of extinction at larger spatial scales (Burkey, 1995). For a comprehensive analysis of the effects of habitat fragmentation on extinction risk, including predator-prey interactions, demographic and environmental stochasticity at different spatial scales and different spatial contagion, see Burkey (1995).

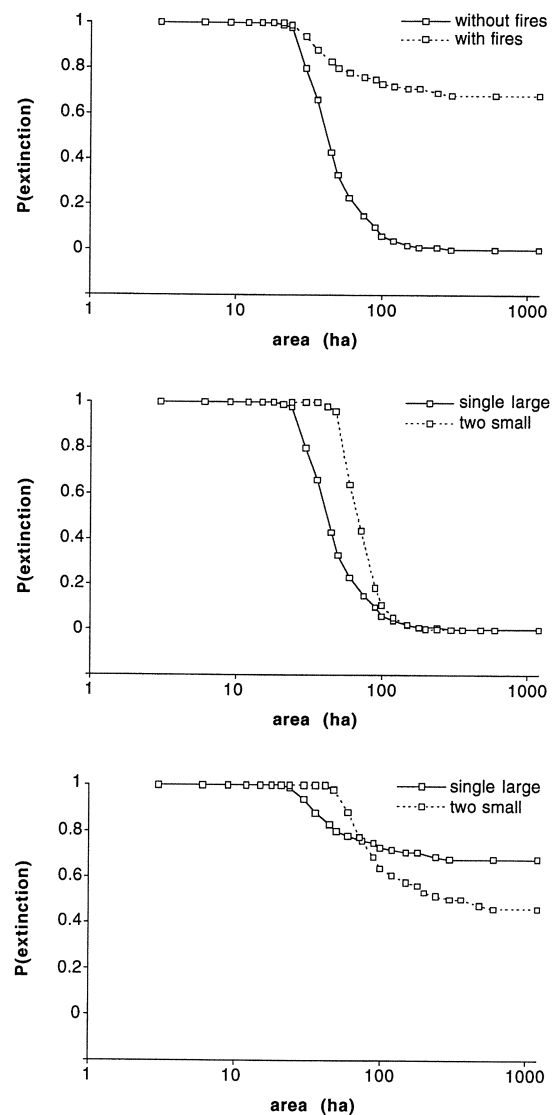


Fig. 3. (a) The population viability of Leadbeater's possum, with and without fires, calculated by Possingham et al. (1993) using the model ALEX. Assuming that individual subpopulations in a patchy landscape are independent of each other, we can calculate from (a) the probability of extinction in a single large patch of a given area and in a set of two patches each half that size, without fires (b) and with fires (c). The annual probability of wildfires used for the simulation was 1%. The calculation with fires is biased in favor of fragmented systems, because it assumes that a fire burns a constant proportion of a forest patch regardless of its size (in this case, 75%), and because it assumes that the occurrence of fires is independent in a set of small patches (e.g., fires do not spread from one patch to another and the incidence of fire is in no way correlated).

#### 4. Conclusions

Di Castri and Hadley (1986) have argued that most achievements in ecology have not been relevant to landscape planners. Together with other authors (e.g., Peters, 1991), they have raised concern about the state of ecology as a rigorous science, based on its lack of predictability and the rarity of interactions between ecologists and planners. In this contribution we have discussed a framework in which these interactions could be fruitful. Generally, landscape planners need to evaluate the consequences of different management strategies. Therefore, in order to integrate the biological, economical and geographical aspects of landscapes, we need models that can evaluate and extrapolate the effect of human activities across spatio-temporal scales (Levin, 1992; Turner et al., 1995). We have discussed the example of southern EC regions, where novel agricultural policies have shifted silvicultural regimes and patterns of land fragmentation. Stand dynamics under these new management regimes and land abandonment, are unknown. Therefore land managers need predictive tools that can assist them in decision making, under the complex settings defined by economic and ecological conditions in this region.

Models that explain and predict plant community dynamics at different scales are under development (Moffat, 1994). An important feature of successful models is that they have been implemented according to integrated programs of empirical and theoretical research (Kareiva, 1989). They are therefore system-specific and rely on the biological mechanisms of the modeled system. These models have been mainly motivated by the need to understand patterns of community structure in an evolutionary context and their ultimate goal is to focus on the

generalities across systems rather than on the specifics. Applied models in turn cannot sacrifice detail at the cost of generality because the scope of their predictions is usually limited to local aspects of the modeled system. There is no reason to think that similarly, biologically realistic and useful models cannot be developed to address specific applied questions providing integrative research programs among managers, field ecologists and modelers.

In addition to forest products, wildlife is another important resource in wildland management. It is generally correct to assume that patterns in animal communities are linked to vegetation structure. For some species, population dynamics takes place at much shorter scales than vegetation dynamics, while for others long-term habitat dynamics are critical. Animals also respond to specific habitat features not necessarily considered by vegetation models. We have circumvented this problem by using the degree of fragmentation as a surrogate variable, but clearly more research is needed in order to identify habitat structural factors that affect animal communities.

One of the reason why the SLOSS debate has not had much success in improving our understanding of wildlife populations, and has not had much impact on managers, is that we have not emphasized the mechanisms behind our observations. Only when we understand the ecological, behavioral, statistical and genetic mechanisms that link population dynamics to habitat structure will models be explanatory as well as predictive. In the following, we suggest directions in which our knowledge needs to be improved. Tables 1 and 2 list potential mechanisms that make populations and communities vulnerable to habitat fragmentation. Many of them require an occasional skew in population densities between fragments to affect fragmented populations disproportionately.

Table 1  
Stochastic mechanisms making species vulnerable to fragmentation

- 
- (1) Allee effect (reduced ability to find mates, etc.—notably when densities, sex ratios, or age distribution are nonuniform across patches)
  - (2) Inbreeding depression and loss of rare alleles in local populations
  - (3) Individuals unequally distributed in isolated patches
  - (4) Demographic stochasticity: 'sampling variance,' uneven sex ration or age structure, uneven distribution of individuals between fragments
  - (5) Fragmentation causes a breakdown of regional density dependence, which may be destabilizing
  - (6) Low carrying capacity in patches
  - (7) 'The extinction ratchet'—in the absence of recolonization, the extinction of a fragment is an absorption point. Small fragments contain smaller populations and go extinct more easily, one after the other until the species has disappeared from all the fragments.
-

Table 2

Deterministic mechanisms making species vulnerable to fragmentation

(1) *Migration / dispersal*

- (a) Old migration routes disrupted
- (b) Restricting movement among different required patch types
- (c) Fluctuating environments may make some habitat patches temporarily unsuitable (fragmentation would make it difficult to track suitable patches)
- (d) Reduced dispersal to suitable sites yields reduced recruitment (e.g., fewer available light gaps in the forest—inherently an edge effect)

(2) *Interspecies interactions*

- (a) Loss of predator makes prey explode, then crash (or in any other way destabilize prey)
- (b) Loss of top predator releases other smaller predators from predation, increasing predation on seeds, eggs, young, etc.
- (c) Loss of top predator increases interspecies competition
- (d) Loss of refugia from predators
- (e) A discontinuous prey population is less likely to attain reproductive synchrony, hence suffering higher predation
- (f) Patch too small to maintain a population of mutualists (pollinators/dispersal agents)
- (g) Destabilization of mutualistic interactions (pollination, dispersal)

(3) *Intraspecific interactions*

- (a) Cooperative behavior breaks down (too few wolves to form a pack)
- (b) Primary social unit needs a large foraging area to persist
- (c) Threshold number—minimum breeding colony size (passenger pigeon)
- (d) Allee effect—social facilitation, information centers, group defense, mate search, social interaction necessary for reproduction or survival

(4) *Edge effects*

- (a) Increased predation/disturbance by man with increased edge:area ratio
- (b) Microhabitat changes in edge zones
- (c) Increased colonization/interference from species of neighboring habitat
- (d) Increased dispersal to uninhabitable areas (or suboptimal habitats)
- (e) Edge avoidance

(5) *Negative population growth*

- (a) Patch is a sink
- (b) Isolated from essential resources
- (c) Resources are sparsely distributed
- (6) Patch smaller than home-range or territory
- (7) Packing (fewer home-ranges/territories can be packed into a fragmented reserve—another edge effect)
- (8) Critical resources not protected, or unavailable to the entire metapopulation, within the reserve (e.g., watershed, critical winter grazing grounds, etc.)

Table 3 lists some mechanisms from which subdivided communities may benefit relative to continuous ones. The lists are by no means exhaustive, and their effect on fragmented populations have typically not been documented in the field or in any experiments.

We also consider that ecology as a whole would greatly benefit from a landscape planning perspective. Ecologists need also to address the effect of humans in ecological systems simply because humans are an intrinsic part of them. Quoting Blondel and Vigne (1993): “The real ecological world is no longer the orderly, predictable and deterministic world of the sixties, but a world where factors such

as population phenomena share their roles in the shaping of biodiversity, with disturbances, patchiness, historical processes and the impact of humanity.” Therefore theories attempting to explain and predict the main features of ecological systems should be based on stochastic and spatial formulations that consider historical events and the impact of humanity.

Managers should be aware of the spatio-temporal dynamical features of ecosystems. It is generally neither appropriate nor possible to manage ecosystems towards an assumed status quo (Naveh, 1971; Sinclair, 1979; Westmann, 1990). In most ecological systems, patterns of community structure and diver-

Table 3  
Mechanisms by which species may gain from fragmentation

*Stochastic phenomena*

- (1) Bet hedging—disease, spatially uncorrelated environmental variation, catastrophes
- (2) Could increase genetic diversity on a regional scale (drift, different selection pressures, etc.)
- (3) Wright's shifting balance theorem. May allow more rapid evolutionary response to environmental changes if some migration between fragments is enabled. Favorable genes can be fixed more rapidly in subpopulations, and exported to other subpopulations (populations with the 'best' genes will produce more migrants)
- (4) Greater chances of surviving transients in unstable community interactions

*Deterministic phenomena*

- (1) Persistence if predator–prey system
  - (a) Enhanced by prey hiding out in a different patch
  - (b) Overshoot reduced by predator dispersal between patches
- (2) Refugia from competitors
- (3) Patches can be selected in high-resource areas or center of local endemism

sity are associated in one way or another to disturbances. If this structure is to be preserved, remnant fragments should be large enough to encompass the regime of disturbances and the scale of environmental patchiness within them. If political priorities preclude this, fragments should at least be linked so as to emulate this patch structure and disturbance regime as much as possible within reserve systems. In the particular case of Mediterranean woodlands, the importance of large-scale disturbances like fires and of traditional anthropogenic activities must be investigated further before this issue is resolved, and the spatial correlation structure is of special concern in such an endeavor.

It is also necessary to consider that management objectives depend on societal demands. Until recently, forestry has dealt with the problem of achieving a sustained yield of a few products. Scientists and managers will need to work together to understand how economic and ecological costs and benefits trade off for different management strategies. Some components of ecological systems are crucial to the maintenance of human populations (e.g., crops for human food, the hydrological cycle or timber). Others such as patterns of biological diversity in pristine systems are not as clearly related to first-order human needs and their benefits are indirect. Ecology should help to disentangle how effectively interconnected these components are for each particular system and their relevance to human societies. Ultimately, the balance between direct and indirect benefits that will determine landscape structure may be more a sociological issue or a matter of political will.

What we do to it reveals our priorities, our view of ourselves and our view of the other species on Earth.

### Acknowledgements

The first author was supported by a grant from I.N.I.A. (Instituto Nacional de Investigaciones Agrarias), Ministry of Agriculture, Spain. We thank Anna Prats for her assistance in typing the manuscript. We also acknowledge John Caspersen, Jon Rodieck and the review committee for critical comments that helped improve an earlier version of this manuscript

### References

- Abrams, M.D., 1992. Fire and the development of oak forests. *BioScience* 42, 346–353.
- Antrop, M., 1993. The transformation of the Mediterranean landscapes: An experience of 25 years of observations. *Landscape Urban Plan.* 24, 3–13.
- Atkinson, W.D., Shorrocks, B., 1981. Competition on a divided and ephemeral resource: A simulation model. *J. Anim. Ecol.* 50, 461–471.
- Bailey, N.T.J., 1964. *Elements of Stochastic Processes with Applications to the Natural Sciences*. Wiley, New York.
- Baker, W.L., 1989. A review of models of landscape change. *Landscape Ecol.* 2, 111–133.
- Barbero, M., Bonin, G., Loisel, R., Quezel, P., 1990. Changes and disturbances of forest ecosystems caused by human activities in the western part of the Mediterranean basin. *Vegetatio* 87, 151–173.
- Begon, M., Harper, J.L., Townsend, C.R., 1986. *Ecology: Individuals, Populations and Communities*. Blackwell, Oxford.

- Blondel, J., Aronson, J., 1995. Biodiversity and ecosystem function in the Mediterranean basin: Human and nonhuman determinants. In: Davis, G.W., Richardson, D.M. (Eds.), *Mediterranean-Type Ecosystems: The Function of Biodiversity*. Springer, Berlin, pp. 43–119.
- Blondel, J., Vigne, J.D., 1993. Space, time and man as determinants of diversity of birds and mammals in the Mediterranean region. In: Ricklefs, R.E., Schluter, D. (Eds.), *Species Diversity in Ecological Communities*. Univ. Chicago Press, Chicago, pp. 135–146.
- Blondel, J., Perret, P., Maistre, M., Dias, P.C., 1992. Do harlequin Mediterranean environments function as a source sink for blue tits (*Parus caeruleus* L.)?. *Landscape Ecol.* 6, 213–219.
- Bormann, F.H., Likens, G.E., 1994. *Pattern and Process in a Forested Ecosystem*. Springer, New York.
- Brown, J.H., Kodric-Brown, A., 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* 58, 445–449.
- Burkey, T.V., 1989. Extinction in nature reserves: The effect of fragmentation and the importance of migration between reserve fragments. *Oikos* 55, 75–81.
- Burkey, T.V., 1995. Extinction in fragmented landscapes: Demographic mechanisms and predator–prey interactions. PhD thesis, Princeton University, NJ.
- Denevan, W.M., 1992. The pristine myth: The landscape of the Americas in 1492. *Ann. Assoc. Am. Geographers* 82 (3), 369–385.
- Diamond, J.M., 1975. The island dilemma: Lessons of modern biogeography studies for the design of natural reserves. *Biol. Conserv.* 7, 129–145.
- Di Castri, F., Hadley, M., 1986. Enhancing the credibility of ecology. Is interdisciplinary research for land planning useful?. *Geojournal* 13, 299–325.
- Di Castri, F., Mooney, H.A., (Eds.), 1973. *Mediterranean-Type Ecosystems*. Springer, Berlin.
- Drewett, J.R., 1969. A stochastic model of the land conversion process. *Regional Studies* 3, 269–280.
- Ducey, M., 1992. Quelle sylviculture et quel avenir pour les tallis de chêne vert (*Quercus ilex* L.) de la région Méditerranéenne française. *Rev. For. Fr.* 154, 12–34.
- Ehrlich, P.R., Ehrlich, A.H., 1990. *The Population Bomb*. Simon and Shuster, New York.
- Fernández-Alés, R., Martín, A., Ortega, F., Alés, E., 1992. Recent changes in landscape structure and function in a Mediterranean region of SW Spain (1950–1984). *Landscape Ecol.* 7 (1), 3–18.
- Gómez-Sal, A., Rodríguez, M.A., De Miguel, J.M., 1992. Matter transfer and land use by cattle in a dehesa ecosystem of Central Spain. *Vegetatio* 67, 345–354.
- Gómez-Sal, A., Alvarez, J., Muñoz-Yanguas, Rebollo, S., 1993. Patterns of change in the agrarian landscape in an area of the Cantabrian Mountains (Spain)—Assessment by transition probabilities. In: Bunce, R.G.H., Ryszkowski, L., Paoletti, M.G. (Eds.), *Landscape Ecology and Agroecosystems*, Lewis Publisher, Boca Raton, LA, pp. 141–152.
- González-Bernáldez, F., 1990. Consideraciones ecológico-políticas acerca de la conservación y regeneración de la cubierta vegetal en España. *Ecol. Fuera Ser.* 1, 439–445.
- Goodman, D., 1987a. The demography of chance extinction. In: Soulé, M.E. (Ed.), *Viable Populations for Conservation*. Cambridge Univ. Press, Cambridge, pp. 11–34.
- Goodman, D., 1987b. Consideration of stochastic demography in the design and management of biological reserves. *Nat. Res. Model.* 1, 205–234.
- Groombridge, B. (Ed.), 1992. *Global Biodiversity Status of the Earth's Living Resources*. Chapman & Hall, London.
- Grossman, W.D., 1991. Model- and strategy-driven geographical maps for ecological research and management. In: Risser, P.G. (Ed.), *Long-Term Ecological Research*, Wiley, Chichester, pp. 241–256.
- Hastings, A., 1990. Spatial heterogeneity and ecological models. *Ecology* 71, 426–428.
- Holt, R.D., Pacala, S.W., Smith, T.W., Liu, J., 1995. Linking contemporary vegetation models with spatially explicit animal population models. *Ecol. Appl.* 5 (1), 20–27.
- Huffaker, C.B., 1958. Experimental studies on predation: Dispersion factors and predator–prey oscillations. *Hilgardia* 27, 343–383.
- Hutsinger, L., Bartolome, J.W., 1992. Ecological dynamics of *Quercus*-dominated woodlands in California and southern Spain: A state transition model. *Vegetatio* 99–100, 299–305.
- Järvinen, O., 1982. Conservation of endangered plant populations: Single large or several small reserves?. *Oikos* 38, 301–307.
- Kareiva, P., 1989. Renewing the dialogue between theory and experiments in population ecology. In: Roughgarden, J., May, R.M., Levin, S.A. (Eds.), *Perspectives in Ecological Theory*. Princeton Univ. Press, Princeton, NJ, pp. 68–88.
- Kareiva, P., 1990. Population dynamics in spatially complex environments: Theory and data. *Philos. Trans. R. Soc. London, Ser. B* 330, 175–190.
- Ledig, F.T., 1992. Human impacts on genetic diversity in forest ecosystems. *Oikos* 63, 87–108.
- Levin, S.A., 1974. Dispersion and population interactions. *Am. Nat.* 108, 207–228.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73 (6), 1943–1967.
- Levins, R., 1970. Extinction. *Lect. Math. Life Sci.* 2, 75–107.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton Univ. Press, Princeton, NJ.
- Minnich, R.A., 1988. The biogeography of fire in San Bernardino Mountains of California. A historical study. *Geography*, 28, Univ. California Press, Berkeley.
- Moffat, A.S., 1994. Theoretical ecology: Winning its spurs in the real world. *Science* 263, 1090–1092.
- Montalvo, J., Casado, M.A., Levassor, C., Pineda, F.D., 1993. Species diversity patterns in Mediterranean grasslands. *J. Veg. Sci.* 4, 213–222.
- Mooney, H.A., 1988. Lessons from Mediterranean-climate regions. In: Wilson, E.O. (Ed.), *Biodiversity*. National Academy Press, Washington, DC, pp. 157–165.
- Nakagoshi, N., Nehira, K., Takahashi, F., 1987. The role of fire in pine forests of Japan. In: Trabaud, L. (Ed.), *The Role of Fire in Ecological Systems*. Academic Publishing, The Hague, pp. 91–119.
- Naveh, Z. 1971. The conservation of ecological diversity of Mediterranean ecosystems through ecological management. In:

- Duffey, E., Watt, A.S. (Eds.), *The Scientific Management of Animal and Plant Communities for Conservation*. Blackwell, London, pp. 605–622.
- Naveh, Z., 1975. The evolutionary significance of fire in the Mediterranean region. *Vegetatio* 29 (3), 199–208.
- Naveh, Z., 1987. Biocybernetic and thermodynamic perspectives of landscape functions and land use patterns. *Vegetatio* 1 (2), 75–83.
- Naveh, Z., Kutiel, P., 1990. Changes in the Mediterranean vegetation of Israel in response to human habitation and land use. In: Woodwell, G.M. (Ed.), *The Earth in Transition: Pattern and Processes of Biotic Impoverishment*. Cambridge Univ. Press, Cambridge, UK, pp. 259–299.
- Naveh, Z., Lieberman, A.S., 1984. *Landscape Ecology. Theory and Application*. Springer, Berlin.
- Naveh, Z., Whittaker, R.H., 1979. Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean areas. *Vegetatio* 41 (3), 171–190.
- Nisbet, R.M., Gurney, W.S.C., 1982. *Modelling Fluctuating Populations*. Wiley, New York.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecol. Monogr.* 66, 1–43.
- Peters, R.H., 1991. *A Critique for Ecology*. Cambridge Univ. Press, Cambridge, UK.
- Pielou, E.C., 1977. *Mathematical Ecology*. Wiley, New York.
- Pigott, C.D., Pigott, S., 1993. Water as a determinant of the distribution of trees at the boundary of the Mediterranean zone. *J. Ecol.* 81, 557–566.
- Pineda, F.D., 1992. Conservation of the biological diversity and traditional systems of land use in the Mediterranean. *Management of Natural and Agrarian Ecosystems: I. Ethnobotanical Garden Symposium 6*, Botanical Garden, Cordoba, Spain.
- Pineda, F.D., Nicolás, Ruiz, M.B., Peco, B., González-Bernáldez, F.G., 1981. Succession, diversite et amplitude de niche dans les paturages du centre de la peninsule iberique. *Vegetatio* 47, 267–277.
- Pons, A., Vernet, J.L., 1971. Une synthese nouvelle de l'histoire du chêne vert (*Quercus ilex* L.). *Bull. Soc. Bot. Fr.* 118, 841–856.
- Possingham, H.P., Davies, I., Noble, I.R., Norton, T.W., 1992. A metapopulation simulation model for assessing the likelihood of plant and animal extinctions. *Math. Comput. Simulation* 33, 367–372.
- Possingham, H.P., Lindenmayer, D.B., Norton, T.W., 1993. A framework for the improved management of threatened species based on population viability analysis (PVA). *Pac. Conserv. Biol.* 1, 39–45.
- Quinn, J.F., Hastings, A., 1987. Extinction in subdivided habitats. *Conserv. Biol.* 1, 198–208.
- Richter-Dyn, N., Goel, N.S., 1972. On the extinction of a colonizing species. *Theor. Pop. Biol.* 3, 406–433.
- Romane, F., Bacillieri, R., Bran, D., Bouchet, M.A., 1992. Natural degenerate Mediterranean forests: Which future? The examples of the holm oak (*Quercus ilex* L.) and chestnut (*Castanea sativa* Mill.) coppice stands. In: Teller, A., Mathy, P., Jeffers, J.N.R. (Eds.), *Responses of Forest Ecosystems to Environmental Changes*. Elsevier, London, pp. 374–380.
- Ruiz de la Torre, J., 1985. Conservation of plants within their native ecosystems. In: Gómez-Campo, C. (Ed.), *Plant Conservation in the Mediterranean*. J. Junk Publ., The Hague, pp. 197–219.
- Ruiz de la Torre, J., 1990. Distribución y características de las masas forestales españolas. *Ecol. Fuera Ser.* 1, 11–30.
- Santos, T., Tellería, J.L., 1992. Edge effects on nest predation in Mediterranean fragmented forests. *Biol. Conserv.* 62, 1–5.
- Schaeffer, R., Moreau, R., 1958. L'alternance des essences. *Bull. Soc. For.* 1, 3–297.
- Shugart, H.H., 1984. *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*. Springer, Berlin.
- Sinclair, A.R.E., 1979. Dynamics of the Serengeti ecosystem. In: Sinclair, A.R.E., Norton-Griffiths, M., (Eds.), *Serengeti: Dynamics of an Ecosystem*. Univ. Chicago Press, Chicago, pp. 1–30.
- Tenhunen, J.D., Catarino, F.M., Lange, O.L., Oechel, W.C. (Eds.), 1987. *Plant Responses to Stress-Functional Analysis in Mediterranean Ecosystems*. NATO Advanced Science Institute Series, Springer, Berlin.
- Thirgood, J.V., 1981. *Man and the Mediterranean Forest*. Academic Press, New York.
- Turner, M.G., 1989. Landscape ecology: The effect of pattern on process. *Annu. Rev. Ecol. Syst.* 20, 171–197.
- Turner, M.G., Wu, Y., Romme, W.H., Wallace, L.L., Brenkert, A., 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecol. Appl.* 4, 472–496.
- Turner, M.G., Arthaud, G.J., Engstrom, R., Hejl, T.S., Liu, Loeb, S., McKelvey, K., 1995. Usefulness of spatially explicit population models in land management. *Ecol. Appl.* 5 (1), 12–16.
- Vitousek, P.M., Ehrlich, P.R., Ehrlich, A.H., Matson, P.A., 1986. Human appropriation of the products of photosynthesis. *BioScience* 36, 368–373.
- Watt, A.S., 1947. Pattern and process in the plant community. *J. Ecol.* 35, 1–22.
- Westmann, W.E., 1990. Managing for biodiversity: Unresolved science and policy questions. *BioScience* 40, 26–33.
- Whittaker, R.H., 1975. *Communities and Ecosystems*. Macmillan, New York.
- Wiens, J.A., 1976. Population responses to patchy environments. *Annu. Rev. Ecol. Syst.* 7, 81–120.
- Wilcox, B.A., Murphy, D.D., 1985. Conservation strategy: The effects of fragmentation on extinction. *Am. Nat.* 125, 879–887.
- Wilson, E.O., Willis, E.O., 1975. Applied biogeography. In: Cody, M.L., Diamond, J.M. (Eds.), *Ecology and Evolution of Communities*. Harvard Univ. Press, Cambridge, MA, pp. 522–534.
- Wright, J.P., Hubbell, S.P., 1983. Stochastic extinction and reserve size: A focal species approach. *Oikos* 41, 466–476.

