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Ecological dynamics of *Quercus* dominated woodlands in California and southern Spain: a state-transition model

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Abstract

There are many similarities between Spanish and Californian *Quercus* woodlands and savanna. Both are located in Mediterranean climate zones, and are used predominantly for livestock grazing. The Californian overstory is dominated by one or a combination of five *Quercus* species and their hybrids: *Quercus douglasii* H.&A., *Q. agrifolia* Nee., *Q. wislizenii* A.DC., *Q. lobata* Nee., and *Q. englemannii* Greene (blue, coast live, interior live, valley, and Englemann oaks). In southern Spain and Portugal, *Quercus* woodland overstory is predominantly one or a combination of two *Quercus* species, *Quercus ilex* L. (holm oak) and *Quercus suber* L. (cork oak). The underlying natural and semi-natural ecological dynamics of the *Quercus* woodlands of Spain and California are different, and it follows that the management practices employed also differ. The greatest point of contrast between California and Spain is in the intensity and diversity of management goals and practices. A state-transition model for comparing the ecological dynamics of *Quercus* woodlands and savanna in California and southern Spain is developed and examined. The highly simplified model is an analytic tool of use in organizing research and developing management practices. States are reached and maintained in different ways in Spain and California, but their appearance and their function in each landscape are quite similar.

Introduction

This paper compares and contrasts the ecological dynamics of *Quercus* woodlands and savanna in California and southern Spain using a state-transition model. We propose that sustainable management and conservation of these woodlands depends on better knowledge of likely vegetation states and the transitions affecting those states. State-transition models, while highly simplified, provide a framework for acquiring and testing ecological information (Westoby 1989). The objective of this paper is not to describe fully the ecological dynamics of either the Californian or Spanish *Quercus* woodland, but to present an analytic tool of use in organizing research and developing management practices. The state-transition model is an alternative to more traditional and widely used succession-based models, the assumptions of which have been difficult to

verify in many ecosystems (Nobel 1986; Foin 1986; Anderson 1986; Mentis 1986).

There are many similarities between Spanish and Californian *Quercus* woodlands. Both are located in Mediterranean climate zones, and are used predominantly for livestock grazing. Spanish woodlands have been managed longer and for more diverse products, including cork, forage, acorn-fattened hogs, charcoal, milk, mushrooms, cereal crops, and lucrative hunting (Parsons 1962). Californian *Quercus* woodland landowners profit primarily from livestock, wildlife, and firewood.

The ecological dynamics of the Spanish and Californian woodlands vary in some important ways. The Spanish savanna, while visually almost identical to the Californian savanna, is to a large extent an artificial construct deliberately maintained by over 1,000 years of human intervention. It mimics a natural system and confers many of the benefits one expects from a natural woodland, including providing habitat for threatened and endangered species (Marañon, 1988; Huntsinger *et al.* 1991). Californian *Quercus* woodlands provide a refuge and breeding area for more than 300 vertebrate wildlife species (Block *et al.* 1990). The woodlands are remnants of a much larger pre-settlement woodland that over the last hundred years has been to a large extent replaced by crop production and urban development. Remaining woodlands have been greatly disturbed by changes in human activity, largely the introduction of livestock grazing and European annual grasses, and changes in fire frequency. But the role of human intervention in the structure and distribution of Californian *Quercus* woodlands remains little understood. Here we have used a state-transition model to simplify these two complex systems, and to describe and compare the natural and human-caused changes in vegetation that maintain or disrupt each.

Study areas

Climate in the woodlands of California and Spain is typical Mediterranean, with the Californian woodlands generally having a slightly warmer and drier summer (Jackson & Roy 1989). The majority of Spanish and Californian *Quercus* woodlands are in private ownership: 82 percent private in California (Ewing *et al.* 1988) and 98 percent private in Spain. In both Spain and California, *Quercus* woodland soils tend to be shallow and infertile, ill-suited for intensive crop production. In Spain, soils are limestone or granitic. In California, the woodland soils are of diverse metamorphic and sedimentary origins.

California's *Quercus* woodland and savanna covers approximately 3 million hectares of what is generally rolling foothill topography (Ewing *et al.* 1988). The overstory is dominated by one or a combination of five *Quercus* species and their hybrids: *Quercus douglasii* H.&A., *Q. agrifolia* Nee., *Q. wislizenii* A.DC., *Q. lobata* Nee., and *Q. englemannii* Greene (blue, coast live, interior live, valley, and Englemann oaks). In southern Spain and Portugal, *Quercus* woodland overstory is predominantly one or a combination of two *Quercus* species, *Quercus ilex* L.[1] (holm oak) and *Quercus suber* L. (cork oak). These two species together cover about 5.5 million hectares in southern Spain and Portugal, including the Andalusian uplands, and extending north toward Madrid and Lisbon (Marañon 1988; Campos Palacín 1984; Ruiz 1986).

In California, the characteristic *Quercus* savanna understory is annual grasses and forbs, most of which have emigrated from other Mediterranean regions, including Spain (McClaran & Bartolome 1989). The *Quercus* savanna type is considered a stable community that, in the absence of human intervention, changes slowly or not at all (Griffin 1977). Establishment of woody plants is uncommon (Bartolome *et al.* 1988). Stable grass-dominated vegetation, rare in the central Mediterranean (Jackson & Roy 1989), is more common in Spain (Pineda *et al.* 1981). But without repeated human intervention, most often the understory of Spanish *Quercus* savanna quickly becomes dominated by shrubs, characteristically

[1] Sometimes considered a separate species, *Quercus rotundifolia*.

Cistus (rockrose) species (Nuñez *et al.* 1986; Martin Bolaños & Guinea 1949). The open *Quercus* savannas of southern Spain are carefully maintained by land managers (Joffre *et al.* 1988). *Quercus* woodlands are managed to maintain an open savanna understory as part of the sylvopastoral system known as the 'dehesa'[2] (Marañon 1988). Spanish *Quercus* woodland ranches, or fincas, are sometimes called dehesas themselves.

Methods

State-transition models help organize information about vegetation change and its causes. These simple models have proven useful in range science and are quickly replacing traditional succession-based rangeland condition models (Westoby *et al.* 1989; Bartolome 1991). To develop the model a set of discrete vegetation 'states' are described for a representative location, and then a set of discrete 'transitions' between states are defined. Transitions may be triggered by natural events such as fire and weather, by human activity including management practices, or by a combination of the two. Transitions may occur swiftly or over a long period of time, but the system does not come to rest halfway through a transition (Westoby *et al.* 1989). The factors driving transitions between states, and shaping the state characteristics of interest, are identified and cataloged.

To develop a model that allows generalized comparison of Spain and California, we have used *Quercus* woodland types characteristic of each. In California, we have selected a *Quercus douglasii* savanna with a potential *Ceanothus* spp. (ceanothus) understory; for the Spanish counterpart, we have selected a southwestern Spanish *Quercus ilex* site with the typical *Cistus* spp. understory. Because of the greater diversity of *Quercus* woodland vegetation types in California, the *Quercus/Ceanothus* type cannot be considered as representative of the entire woodland as can the Spanish *Quercus/Cistus* type, however this complex is characteristic of several thousand hectares of foothill woodlands on the southern Sierran west slope (Allen-Diaz *et al.* 1991). At the same time the Spanish site is also not representative of all *Quercus ilex* woodlands in Spain, but instead is an example of typical dehesa woodland.

Definition of states

'States' should not be considered analogous to 'climax' vegetation, but instead are vegetative complexes that remain the same or change only slowly for the duration of a management-oriented time horizon. Four vegetation states can be defined for the Californian and Spanish woodland sites (Table 1). State I is annual grassland; State II is shrubland. On the California site, the shrubland or 'chaparral' would be dominated by *Ceanothus* shrubs, on the Spanish site, where it is termed 'matorral', by *Cistus* shrubs. State III is an overstory of either *Quercus douglasii* or *ilex* with understory shrubs; State IV is a *Quercus* savanna, a *Q. douglasii* or *ilex* overstory with an annual herbaceous understory. Each state is similar in appearance to its counterpoint in the other location, but the processes that affect the transitions among them differ between Spain and California. Fitting them into a transition matrix allows examination of these transitions (Fig. 1). The states, transitions, and forces that drive the transitions described below should be considered hypotheses.

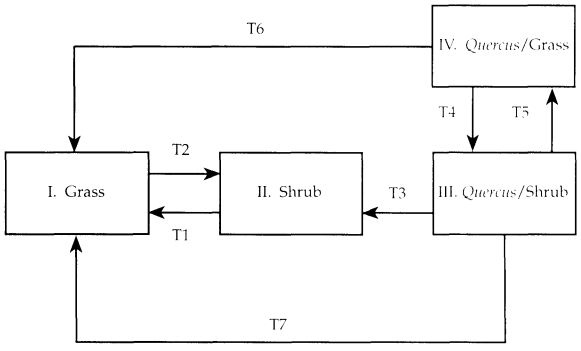

Fig. 1. Transition matrix for *Quercus* savanna.

[2] In Portugal the term montado is used.

Table 1. Catalog of states for Californian and Spanish oak savanna.

State	California	Spain
I. Grass	Annual herb dominated. Historically considered most economically valuable state.	Annual herb dominated.
II. Shrub	*Ceanothus* dominated, referred to as chaparral. Economic returns minimal.	*Cistus* dominated, referred to as matorral. Hunting may produce some significant economic returns.
III. Oak/Shrub	*Quercus douglasii* overstory, *Ceanothus* spp. understory. *Ceanothus* spp. valuable for wildlife forage and cover, also browsed by livestock.	*Quercus ilex* overstory, *Cistus* spp. understory. *Cistus* species useful for wildlife cover but limit other uses.
IV. Oak/Grass	*Quercus douglasii* overstory, annual herb understory. As long as tree cover is low, most desirable for economic return from combination of wildlife, firewood, and grazing.	*Quercus ilex* overstory, annual herb understory. Most desirable for economic return. Tree cover often controlled to maximize returns from wildlife, grazing, charcoal, milk, acorns, cork, and mushrooms.

The state-transition model

Transitions 4 (T4) and 5 (T5) are those between *Quercus*-grassland (State IV) and *Quercus*-shrubland (State III). In California, T4, the transition from *Quercus*-grassland to *Quercus*-shrubland, occurs slowly, over decades, if at all. *Quercus*-grassland, or State IV, is a highly stable vegetation state (Holzman & Allen-Diaz 1991). Moderate grazing or even infrequent, low intensity fires, is sufficient to suppress the potential shrub understory (Schultz *et al.* 1955). In Spain, on the other hand, State IV is often unstable, and the transition to the more stable State III, *Quercus*-shrubland, is rapid, often occurring in 2 to 5 years (Martin Bolaños & Guinea 1949). Transition 4 occurs in the absence of human intervention such as cultivation every 4 to 6 years, or regular weeding (Table 2) (Joffre *et al.* 1988).

Transition from *Quercus*-shrubland to *Quercus*-grassland (T5) is possible in California through managed grazing or fire. A fire followed by moderate livestock or wild herbivore grazing may extend the life of the conversion indefinitely (Biswell 1974). In Spain, the dehesa system of management is needed to convert *Quercus*-shrubland to

Table 2. Catalog of transitions for Californian and Spanish oak savanna.

	California	Spain
Stable states	I, II, III, IV. States with annual grass understory are often stable.	II, III. Maintaining states with grassy understory (I, IV) commonly requires human intervention.
Transition 4 (T4–shrub invasion):	slow, 10–15 years if at all in the absence of fire or grazing.	rapid, 2–5 years in the absence of fire and/or cultivation.
Transition 5 (T5–to grass undersotry):	promoted by grazing, prescribed or low intensity fire.	actively promoted by 'dehesa' system of cultivation, weeding, and grazing.
Transitions 3, 6, and 7 (T3, T6, T7–*Quercus* loss):	lead to permanent absence of States III and IV; can be promoted by wildfire, overharvest, lack of attention to oak regeneration.	lead to permanent absence of States III and IV; can be promoted by wildfire, overharvest, lack of attention to oak regeneration.

open woodland (Montoya Oliver 1989). This implies cultivation, or shrub removal by hand or machine, followed by grazing and cultivation or weeding for maintenance. Typically, woodlands are disked every 4 to 6 years (Jackson & Roy 1989). An examination of the difference in value between State III and State IV will shed some light on why this expensive, high-intensity effort has historically been worthwhile in Spain.

State III (*Quercus* with shrub understory) in both Spain and California has some wildlife value. In Spain, the relatively low value of the understory shrubs as wildlife forage, and the relatively high value of the multiple outputs possible with dehesa management, drives the transition (T5) to State IV. In California, the relatively low value difference between the two states, due to comparatively high utilization of *Ceanothus* shrubs for wildlife and livestock browse and the comparatively low value of savanna products such as cattle forage, would seem to make investment in this transition (T5) less likely (Sampson & Jesperson 1963; Standiford 1991). This is compensated for, however, by the comparatively low cost of effecting this transition through controlled burning and/or grazing, and the need for little or no maintenance beyond moderate grazing once the conversion to the highly stable State IV is completed.

Transitions 3 (T3), 6 (T6) and 7 (T7) all involve the loss of *Quercus* from the woodland. These transitions are most often driven by human intervention: over-harvest for firewood, clearing for increased forage or crop production, and arson are all possible causes. Natural causes include long-term climatic change, catastrophic fire, and insects and diseases. There are no return transitions, as in general, once the *Quercus* component is lost, there is no economical means of returning *Quercus* to the system (Bartolome *et al.* 1986), and natural regeneration is sporadic. In Spain, this most often results in a stable shrubland, in California, in a stable grassland or shrubland, depending site conditions. Loss of trees severely reduces management options and the diversity of products that can be derived from the land.

In California, all four stages most often are naturally stable, or at least changing so slowly that for management purposes they can be considered stable (Holzman & Allen-Diaz 1991). In Spain, on the other hand, only the shrub (State II) and *Quercus*-shrub (State III) states are commonly stable (Table 2) with out human intervention.

Conclusions

The natural and semi-natural ecological dynamics of the *Quercus* woodlands of Spain and California are different, and it follows that the management practices employed also differ. The greatest point of contrast between California and Spain is in the intensity of management. To maintain the open savanna, considerable effort is needed in Spain to control shrubs. Disking is the most common practice today. Lands may be disked every 4 to 6 years, either solely to control shrubs or as part of periodic crop production. Hand weeding may be used as follow-up control, and intensive livestock grazing may delay the need for the next disking.

Shrub invasion of Californian *Quercus* savanna is relatively rare. Even where it occurs, light grazing and infrequent understory fires maintain a grassy understory. California ranchers commonly use prescribed burning. With burning done at a low intensity under controlled conditions, damage to overstory *Quercus* spp. is uncommon. In any case, the financial risk in California to the system is less serious, since little direct profit is realized from the trees. Burning reduces shrubs and excess dry matter, and may also improve forage. Spanish land managers do not use fire as a tool because they believe that fire will damage the bark of *Quercus suber*. *Quercus* spp. are also valued because of direct annual returns from acorn production. In addition, fire is discouraged because arson is a serious problem in Spain.

The Spanish *Quercus* savanna as modeled is an artificial construct, but it is a construct that can be considered stable when the human component is included. The dehesa system of management has persisted for at least 1,000 years. The diversity of products and vegetation contributes both

to ecological stability and to economic stability for the landowner. However, a decreasing labor force and changing demand for livestock products threaten the labor-intensive dehesa system (Joffre *et al.* 1988). While the maintenance investment required of Californian *Quercus* woodland landowners is far lower, so are the returns. As California's swift growing population continues to drive the rapid conversion of *Quercus* woodlands to housing, the future of the marginal woodland grazing industry is most dependent on maintenance of a suitable land base and development of economic incentives for the livestock producer.

In California, we like to think that human intervention in *Quercus* woodland ecosystems has been brief, about 200 years. We think of ourselves as interlopers in a pristine system, as exploiters. It follows that we consider the open, stable *Quercus* savannas to be a completely natural state. But we know little about the long term ecological dynamics of Californian *Quercus* woodlands. Acorns were the dietary staple of a large population of Native Americans in California. It is possible that Californian *Quercus* spp. have been managed for thousands of years, and that present distributions and characteristics of species and vegetation stages are a function of that management to some degree (Heady & Zinke 1978).

As opposed to succession-based models, the state-transition model better fits the ecological dynamics of *Quercus* woodlands in California and Spain, and permits a more useful analysis and comparison of the effects of natural events and human activity in determining vegetation structure. Stable states that do not necessarily fit the definition of 'climax' conditions exist in both woodlands, either naturally or as a result of current or past management practices. States are reached and maintained in different ways in Spain and California, but their appearance and their function in each landscape are quite similar. Sustainable management depends on better knowledge of likely vegetation states and the transitions affecting those states. State-transition models provide a framework for acquiring and testing that knowledge.

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