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Consequences of Species Introductions and Removals on Ecosystem Function — Implications for Applied Ecology

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Abstract

Species may be added to or removed from ecosystems without greatly affecting ecosystem function. Popular assumptions about delicate balance of ecosystem processes relative to plant species composition when examined in terms of: (1) paleoecological; (2) historical; and (3) current biochronological and biogeographical sequences are found lacking. Species composition of vegetation is shown to vary continuously in time as well as space. Natural ecosystems exhibit greater stability (inertia) in physiognomic structure and functional processes than in species composition. Characteristics of vegetation dynamics have important implications in applied ecology and the use of biological control in vegetation management.

The above generalizations are based on studies summarized as follows: (1) Creosotebush is a recent addition to the vegetation of the Chihuahuan, Sonoran and Mojave Deserts. In a short period of 11,000 yrs it has become a dominant component of the vegetation over many millions of hectares. The macrofossil record indicates a dynamic invasion from south to north with a continuing trend toward proportional increase over time. Some clones in the southern Mojave have reached great age (> 5000 yrs) and may represent members of the initial establishment population. A limited number of generations preclude the possibility of co-evolution proceeding to the point of establishing highly integrated and biologically regulated communities. (2) Similar dynamic changes are evident in paleoecological chronologies obtained from pollen stratigraphic profiles of the eastern deciduous forests of North America. The northward migration of the principle tree species (oaks, maples, hickories, etc.) has varied in rate (100–400 m/yr) and direction, and as a consequence, arrival times (as recent as 2000 yrs ago) in extant forest stands. Natural changes in modern forests indicate that shifts in species composition have continued into the present. (3) Similar kinds of dynamic changes are noted in the constant assembling and reassembling of species comprising the purportedly 'ancient forests' of the tropics. (4) Modern changes in the flora of California through introductions and extinctions have netted a substantial increase in species richness and probably diversity. Introduced species approximate 16% of the flora. Many aliens are primary contributors to ecosystem productivity and may be considered 'new natives'. Few extinctions are evident. Many indigenous species are only minor components of the ecosystem in which they are found. (5) Accidental and/or purposeful biological control episodes have seldom resulted in the complete removal of plant species from ecosystems. Worse case scenarios featuring American chestnut, American elm and eastern hemlock, show that biological control agents have the capacity of greatly altering the roles particular species play in natural ecosystems. Other species responded quickly to fill the gaps and maintain functional structures and processes. Similar responses resulted from purposeful application of biological control to both native (manuka and prickly pear) and introduced (Klamath weed and prickly pear) rangeland weeds.

Conséquences de l'Introduction et du Retrait d'Espèces sur l'Écosystème — Répercussions sur l'Écologie Appliquée

Certaines espèces peuvent être ajoutées à des écosystèmes ou en être retirées sans modifier sensiblement la fonction de l'écosystème. Les hypothèses populaires au sujet de l'équilibre délicat des mécanismes de l'écosystème appliqués à la composition des espèces végétales examinées en termes de successions paléo-écologiques, historiques, ainsi que biochronologiques et biogéographiques, s'avèrent plutôt rares. En effet, la composition spécifique de la végétation varie continuellement dans le temps et dans l'espace. Les écosystèmes

naturels affichent une plus grande stabilité (inertie) dans leurs structures physiognomiques et leurs mécanismes fonctionnels que dans leur composition spécifique. Les caractéristiques de la dynamique de la végétation ont des répercussions importantes en écologie appliquée et sur l'utilisation de la lutte biologique dans le'aménagement de la flore.

Les généralisations précédentes s'appuient sur des études qui se résument comme suit: (1) le creosotebush (*Larrea tridentata*) est une récente addition à la végétation des déserts du Chihuahua, Sonora et Mojave. En l'espace d'une brève période de 11 000 ans, le creosotebush est devenu une composante dominante de la végétation et occupe maintenant plusieurs millions d'hectares. Le répertoire des macrofossiles révèle une invasion dynamique du sud vers le nord avec une tendance continue vers un accroissement proportionnel dans le temps. Certains clones dans le sud du Mojave ont atteint un âge avancé (plus de 5 000 ans) et pourraient être des représentants du premier peuplement établi. Un nombre limité de générations écarte la possibilité d'une co-évolution vers l'établissement de communautés végétales hautement intégrées et biologiquement contrôlées. (2) On peut observer une évolution dynamique analogue dans les chronologies paléo-écologiques tirées de profils stratigraphiques de pollens des forêts cadugues de l'est de l'Amérique du Nord. La migration vers le nord des principales espèces arborescentes (chênes, érables, caryers, etc.) a varié en vitesse (100 à 400 m/année) et en direction, et par conséquent, dans l'époque d'arrivée (aussi récente qu'il y a 2 000 ans) dans les peuplements forestiers existants. Les variations naturelles rencontrées dans les forêts modernes révèlent que certaines transitions dans la composition spécifique se poursuivent encore aujourd'hui. (3) Le même genre d'évolution dynamique apparaît dans le groupement et le regroupement constant des espèces qui composent les soi-disante 'anciennes forêts' tropicales. (4) L'évolution moderns de la flore de la Californie par des introductions et des extinctions a entraîné un accroissement net substantiel de la richesse des espèces, et probablement de leur diversité. Les espèces introduites composent environ 16% de la flore et de nombreuses introductions contribuent essentiellement à la productivité de l'écosystème et peuvent donc être considérées pour cette raison comme 'nouvelles espèces indigénes'. On n'observe que de rares cas d'extinction. Beaucoup d'espèces indigènes ne forment que des composantes secondaires de l'écosystème dans lequel on les retrouve. (5) Aucun épisode de lutte biologique, qu'il soit accidentel ou intentionnel, n'a pu entraîner le retrait définitif d'espèces végétales des écosystèmes. Le châtaignier d'Amérique, l'orme d'Amérique et la pruche du Canada sont de tristes exemples qui rélèvent que les agents de lutte biologique sont capables de modifier considérablement le rôle que certaines espèces jouent dans les écosystèmes naturels. D'autres espèces réagissent alors rapidement pour combler les trous et maintenir des structures et des mécanismes fonctionnels. En effet, l'application préméditée de la lutte biologique à des mauvaise herbes indigènes (leptosperme et figuier de Barbarie) et introduites (millepertuis commun et figuier de Barbarie) de parcours a produit des réactions analogues.

Introduction

The relationship of the title of this paper to the biological control of weeds may not be immediately self-evident. At the outset then perhaps it is worthwhile to assert its presumed relationship to a major theme of the VI International Symposium on Biological Control of Weeds, i.e. 'conflicts of interest'. A tie with conflict bears directly on questions such as the propriety of *introducing* exotic insects to *remove* or reduce the abundance of native plants that are behaving as weeds on rangelands.

Questions of propriety in this regard usually revolve around assertions about the effects that such actions will have on other parts of the biological system and in particular on the ecosystem as a whole. Changes in ecosystems can be framed in terms of shifts in structure and function as reflected by stability, diversity, and productivity measures. Our attention will be directed toward stability, which has several conceptual components and in theory is often linked closely with diversity and productivity. Ecosystem stability has at least two principle aspects: (1) that related to the toughness of the system, i.e. how much force is required to change its structure and/or function; and (2) that related to its response after an alteration has occurred. Westman (1978) discusses the first aspect in terms of inertia and its measurements and the second under the heading resilience, which he separates into the purportedly measureable components of elasticity, amplitude, hysteresis and malleability. The usual perception of inertial stability is in terms of species structure, i.e. the number, size, age, etc., of individual

species, which in the proverbial 'balance of nature', constitute a self-sustaining system. An alternative view of a self-sustaining system may also be held in terms of physiognomic structure and functional processes in which various species with similar physiognomy and function are interchangeable. In the latter case a system may have high inertial stability even with the coming and going of species. The idea is that a steady state condition in terms of processes can be maintained in the absence of species population equilibria. As for the resilience of altered ecosystems, consideration of elasticity (the capacity for recovery) and malleability (the capacity for establishing a new structural or functional balance) are perhaps the two most significant parts of the concept for our discussion.

The ecosystems envisioned for purposes of this presentation are those that constitute native rangelands. Westman (1977) speaks of the structural components of such ecosystems as comprising nature's free 'goods' (e.g. forage, timber, fish, etc., that are marketable products), and the functional processes which drive them as providing nature's free 'services' (i.e. fixation of atmospheric nitrogen, energy capture through photosynthesis, breakdown of pollutants, maintenance of oxygen levels in the air, binding of the soil, etc.), which in short are those things that insure 'clean air, pure water and a green earth'. Westman asks the question, 'How much are nature's services worth' and Pimental *et al.* (1980) try their hand at calculating some of the values for the United States in economic terms and conclude that they are enormous.

Now, in terms of the biological control of weeds, which is one aspect of applied plant ecology, there is a common sentiment abroad, particularly in the United States, that organisms that are exotic (in this case insects) should not be used to control organisms that are native (in this case weeds). This sentiment seems to depend in large part on the assumptions that: (1) native species are essential pieces of delicately balanced co-evolved ecosystems that are stable through time and replicated in space (Andres 1981*a*, *b*; Pemberton 1985); and (2) native species and introduced species are fundamentally different in the roles they play in ecosystems (Howarth 1983). Indeed Andres (1981*b*) maintains that 'Ecological conflicting interests arise in the belief that all elements of an ecosystem are interrelated and that removal of a plant species from an area, especially a native species, will trigger some unknown and unwanted reactions.' and Howarth (1983) speaks of 'biological pollution' defined as 'the establishment in the wild of foreign or non-native organisms' and challenges the biological control method in terms of its 'environmental compatibility' which is often used as a principle argument in favor of the method (Harris 1977). Both Andres and Howarth ascribe much higher 'environmental value' to organisms with native status than to those that are alien.

The views just presented are most easily understood in terms of ecological theory formalized by Frederic Clements and his followers in the first half of this century. Clements perceived vegetation units as being highly integrated and regulated entities serving as the matrix for biotic assemblages representing discrete steps of biological organization, i.e. super organisms. As such, vegetation units arose, grew, and matured through processes of ecological succession and reproduced themselves by perpetuating the more or less final stable climax state. Stability in structure came to be viewed primarily in terms of species, i.e. each species in its proper proportion was important in making the climax what it was. Climax vegetation was considered ancient in age. Climatic change resulted in death of the climax organism or its shift to a new location trailing the climate (Clements 1916, 1920; Weaver and Clements 1938; Dyksterhuis 1946, 1949).

The formalized climax concept has had enormous appeal through the years particularly to animal ecologists and those working in applied fields of biology (e.g.

animal populations ecology and range management) where there is a need to relate vegetation dynamics to other considerations (Allee *et al.* 1949; Price 1975; National Range Handbook 1976; Meeker and Merkel 1984). Clementsian climax theory has not been nearly so readily accepted in its home discipline of plant ecology, although it is without doubt one of the most discussed subjects in plant ecological literature. The antithesis of the Clementsian climax theory is Gleason's individualistic hypothesis on the origin of plant communities (Gleason 1926). I have no intention of rehashing the differences in the two points of view here since it has been done many times by others. I would observe, however, that from my perspective, current theoretical research on the nature of vegetation, a very active field, leans much more strongly in the direction pointed by Gleason than that by Clements (Miles 1979; McIntosh 1980; Vale 1982). Theoretical questions on this matter should not be dismissed lightly as having significance only in academia. It must be realized that the generally accepted vegetation dynamic theory plays a crucial role in setting the mood for enactment of public policy and law in essentially all matters concerning our environment.

My perspective is presented from the position of a plant ecologist and not as a technical expert in biological weed control as are most of the contributors to this Symposium, including my colleagues from the USDA, ARS Laboratory in Temple, Texas. The latter have more than a casual interest in the stated subject matter since their primary research mission is to develop biocontrol technology for the management of southwestern North American rangeland weeds, most of which are native species and structural components of natural ecosystems. The critical assertions concerning balanced, co-evolved systems and biological pollution cited above seem to presuppose certain things about species, communities, and ecosystems that need to be examined more closely in terms of current knowledge and theory, particularly in regard to the origin and distribution of species, community structure and vegetation development, and ecosystem equilibria. I do not presume to have the expertise needed to give complete coverage to these matters here but will present some personal observation, examples from the literature and thoughts in these regards that may bear on the assessment of risks involved in attempts to manipulate native rangeland weeds using biological control agents.

The Case of Creosotebush

First I will consider some aspects of the natural history of creosotebush, *Larrea tridentata* (Ses. & Moc. ex DC.) Cov. (Zygophyllaceae), in particular how it came to occupy its present position in the warm deserts of North America. Furthermore, it has been identified as a possible candidate for biological control (DeLoach 1981). Today *L. tridentata* is *the* plant, i.e. the principle component of the vegetation, of the Chihuahuan, Sonoran and Mojave deserts (Fig. 1). It is certainly a nominee for the world record for the shrub species dominating the largest geographical area on earth. On each desert it is represented by a different chromosome race, i.e. diploid on the Chihuahuan, tetraploid on the Sonoran and hexaploid on the Mojave (Yang 1970); the races are not readily distinguished except on the basis of chromosome number. *L. tridentata* has close taxonomic affinities with *L. divaricata* Cav. of the Argentine desert in South America and has in fact been considered conspecific with it by some investigators (Hunziker *et al.* 1972). *L. divaricata* in South America is diploid, matching the race of *L. tridentata* of the Chihuahuan desert. The generally accepted interpretation of events connecting them and leading to the present distribution pattern is that the *L. divaricata* type from South America (more than one species of *Larrea* occurs there)

was introduced through processes of long distance dispersal to the Chihuahuan Desert in North America. From there it spread northwestward to the Sonoran and Mojave desert undergoing cytogeographic differentiation in the process (Wells and Hunziker 1976). The thing most significant about this spread for our consideration is the time frame in which it occurred.

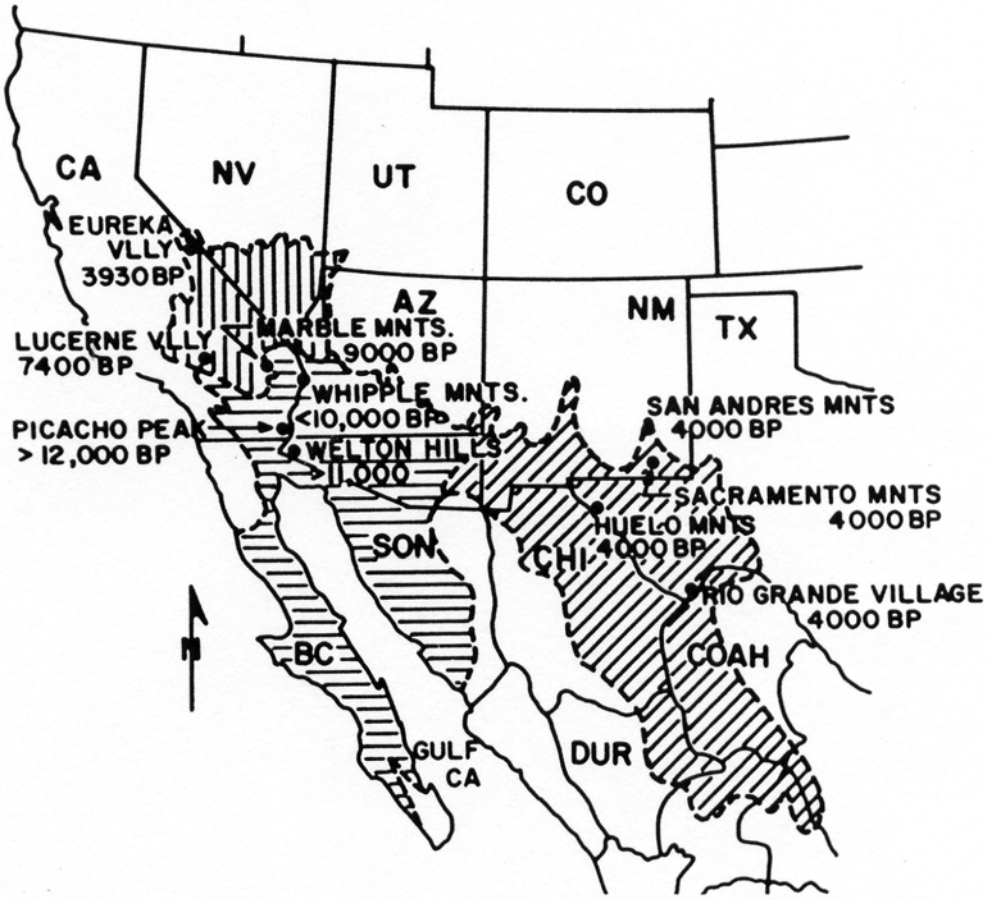

Fig. 1. The Deserts of southwestern United States and Mexico: ▥ = Mojave Desert; ▤ = Sonoran Desert; ▨ = Sonoran Desert; Named locations are places with appropriate series of ^{14}C dated packrat middens. The numerals indicate the approximate date that *Larrea tridentata* (Ses. & Moc. ex DC.) Cov. arrived at that point. AZ = Arizona, BC = Baja Calif., CA = California, Chi = Chihuahua, Coah = Coahuila, NM = New Mexico, NV = Nevada, TX = Texas, Son = Sonora, Dur = Durango.

A method of dating the expansion phase has been fortuitously provided through the peculiar activities of some attractive small rodents belonging to the genus *Neotoma*, known variously as packrats or woodrats, and the innovative perception of Dr. Philip Wells, who recognized a unique opportunity for paleoecological investigations (Wells and Jorgensen 1964). Packrats, long time residents of the deserts, have an apparent fetish for collecting and stockpiling in their nests samples of all manageable objects that occur within their home ranges, including the plant life. Nests or middens constructed from these materials can attain sizeable proportions when inhabited by

successive generations of rodents and when located in sheltered places can persist almost indefinitely. Dr. Wells recognized that the resulting deposits provided a chronological record of the plant life that had occupied the home range areas through the rats' generations of time. Carbon-14 dates of *Neotoma* nests span the period from present to over 40,000 yrs ago (Wells and Berger 1967). Many middens from all three deserts have now been located and analyzed. The focus of the research effort has generally been directed at utilizing fossil middens for timing the disappearance and elevational shifts in conifer woodlands as a surrogate measure of climatic change (Wells and Berger 1967; Wells 1976; Van Devender and Spaulding 1979). In keeping with this emphasis, middens containing fragments of juniper, pine and other conifers were particularly sought out for plant composition analysis and ^{14}C dating, especially in those areas now occupied by desert shrubs, the most abundant of which is, as stated earlier, creosotebush.

Today modern midden deposits in creosotebush-dominated areas contain an abundance of *Larrea* fragments (Wells 1974, 1976; Cole and Webb, *in press*). Yet in the fossil middens older than 11,000 yrs, there is essentially a dearth of creosotebush even though some other modern desert species' macrofossils (e.g. agaves, yuccas, and opuntias) do occur (Wells 1983; Van Devender 1984). This pronounced pattern was central to Wells and Hunziker (1976) suggesting the intriguing possibility of a relatively late introduction of *Larrea* from South America. The actual date of introduction is difficult to establish but the rate and direction of spread after its confirmed presence in North America can be determined.

The oldest macrofossils of *Larrea* reported so far are from low rainfall, low elevational portions of the Sonoran desert not far distant from the path followed by the Colorado River as it follows its course through the desert to the Gulf of California (Fig. 1). *Larrea* begins to appear consistently and in quantity in middens of this region about 11,000 years ago (Table 1); younger ages are associated with deposits toward the northwest, e.g. Marble Mountains $\approx$ 9000 yrs, before present (B.P.), Lucern Valley $\approx$ 7400 yrs B.P., Eureka Valley $\approx$ 4000 yrs B.P. An invasion time series from the mouth of the Colorado River in the Sonoran Desert to the northern limit of the present *Larrea* distribution in the Mojave Desert is thus evident (Fig. 1). In the Chihuahuan Desert creosotebush arrived at its northern limit at about the same time as in the Mojave, i.e. approximately 4000 years ago (Table 1). I have found no reports of macrofossils of *Larrea* from the central or southern Chihuahuan Desert areas, even though cytogeographic patterns strongly suggest that this is the area where the oldest ancestral fossils should be sought.

Although the 'thousands of years' time frame of this discussion may at first seem irrelevant to the usual time scale of concerns of our modern society (i.e. years, decades, and centuries), I submit that in view of the enormous expanses and long linear distances involved it does have immediate relevance. The present north–south range of creosotebush from approximately 23° to 37° latitude spans a diagonal distance of about 2000 km. The area of the three deserts invaded is estimated at around 100 million ha. Using a time frame of 7000 yrs (i.e. 11,000–4000 B.P.) the rate of movement required to attain the distribution evident in the macrofossil record, assuming a south to north expansion, would be on the order of 280 m/yr or 2.8 km/decade. The occupancy of newland area would need to proceed at a rate of about 16,000 ha/yr. Such dynamic change casts serious doubt on popular suppositions about long-term balance and delicate equilibria in the natural landscape before the advent of modern man.

Another significant point in the saga of creosotebush concerns its longevity. Plants in the Mojave desert have been found to develop clonally and live to great age (Vasek *et al.* 1975; Sternberg 1976). Clones are readily distinguished on aerial photographs by

irregular donut-shaped growth patterns (Fig. 2). Ages are extrapolated on the basis of clone size and measured rates of clone growth. Growth rates have been estimated using a variety of techniques, including time-lapse photographs, radio carbon dates of dead

Table 1. Dates of plant macrofossil assemblages preserved in packrat middens from localities in the Mojave, Sonoran and Chihuahuan Deserts currently dominated by creosotebush, *Larrea tridentata* (Ses. & Moc. ex DC.) Cov. (LATR). Data selected from localities where concentrated sampling provides extended chronological sequences of ^{14}C dates that permit reasonable bracketting of the time period of LATR arrival.

Location	Years Before Present LATR Time Bracket Absence	Presence	Comments	Source[1]
Mojave				
Eureka Valley, CA	6795	3930	LATR in low abundance after first appearance but increases markedy in time.	(1)
Mojave Northern Limit	5595 5435 (?)[2]	2635 1580		
Ord Mnt., CA	9140	7400	Sites located in close proximity.	(2)
Lucerne Valley, CA (South-Central Mojave)	7800	5880		(3)
Marble Mnts., CA Transition from	10465 10210	8925 (?) 7930	LATR low abundance at first appearance.	(1)
Mojave to Sonoran	9515 (?) 8905	5520 4475	Increases to position of dominance.	
Sonoran				
Whipple Mnts., CA Northern Sonoran	9980	(—)[3]	Presence of LATR not reported.	(4)
New Water Mnts., AZ Northern Sonoran	7870	10800	Some sites evidently continued longer without LATR than others.	4, 5
Welton Hills, AZ Southwestern, AZ	(—)	10580		2
Picacho Peak, CA Southeastern, CA	(—)	12730	Most arid part of Sonoran Desert. Has oldest fossils.	6
Chihuahuan				
San Andres Mnts., NM (near Northern Limit)	6330	4340	Presence dates for LATR from this desert indicates a recent occupation.	7
Sacramento Mnts., NM (Southcentral, NM)	4200	3300		8
Hueco Mnts., TX (Northwest, TX)	6360	3650	North to South Age difference not evident.	9
Rio Grande Village (Southwest, TX)	5500	4300		9

[1]Sources: (1) Spaulding (1980); (2) Wells and Berger (1967); (3) King (1976); (4) Van Devender (1977); (5) Van Devender and Spaulding (1979); (6) Cole and Van Devender (unpubl. data); (7) Van Devender *et al.* (1984); (8) Van Devender and Toolin (1983); (9) Van Devender (*in press*).

[2](?) indicates places where LATR was reported as trace but may be a contaminant.

[3](—) indicates no data available.

clonal segments and radial growth-ring increment determinations (Johnson and Vasek 1975; Vasek 1980). Clone diameter growth rates vary with substrates but are generally on the order of 2 mm/yr. Clones up to 21 m across are known. Extrapolated ages for the older individuals in the vicinity of Lucern Valley, California (Mojave Desert), range from 6000 to 11,000 yrs depending on the growth rate increment used (Sternberg 1976;

Vasek 1980). Radio carbon dates of packrat middens from the same vicinity show *Larrea* present at 5800 yr B.P. (King 1976) and 7400 yr B.P. but absent earlier than 7800 yr B.P. (Table 1). This strongly suggests that the older individual plants may represent the initial establishment of creosotebush in this part of the Mojave Desert (Johnson 1976), i.e. there is a strong possibility that members of the first generation are still present. This would seem to have a bearing on the extent to which the process of co-evolution might be regarded as a factor for establishing an integrated community functional equilibrium.

The concept of co-evolution relies on the idea that compensating adjustments occur in successive generations between, or among, interacting species to allow them to coexist.

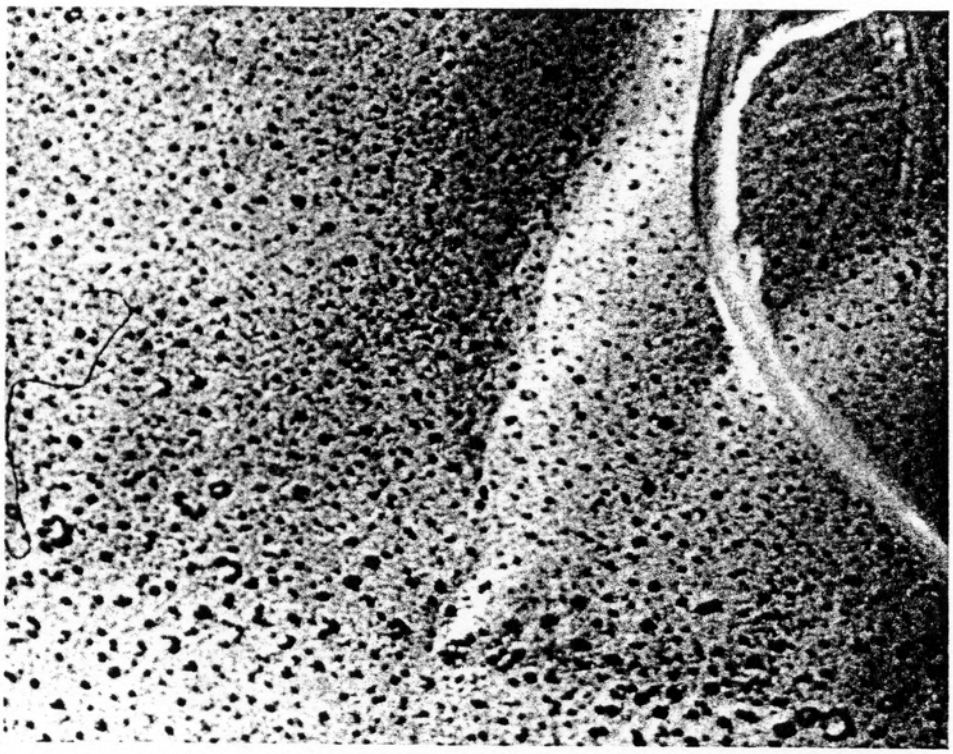

Fig. 2. Verticle aerial view of a stand of creosotebush, *Larrea tridentata* (Ses. & Moc. ex DC.) Cov., (dark globular objects) in the Mojave Desert. All stages in the development of hollow-centered vegetative clones are present, i.e. single-stemmed plants to multiple-stemmed clumps with dead centers. The large, doughnut-shaped clone on the lower left side is about 10 m in diam. and is estimated to be on the order of 5000 yrs old.

In this case there has been limited opportunity for such integration to take place due to a limited number of creosotebush generations. Indeed an argument for the recency of *Larrea* in North America is suggested by observations of relatively fewer obligatory dependent organisms and less plant consumption by insects than in Argentina where *Larrea* is purported to have originated (DeLoach, pers. comm.). I would suggest that the success of *Larrea* is due more to preadaptation than to co-evolution and that preadaptive characteristics are more often attuned to the physical environment than to biotic associates.

Other evidence for continuing change in desert vegetation up through modern times is also available. Cole and Webb (*in press*) sampled eight fossil and five modern packrat

middens in the central Mojave in an elevational belt that included the upper limit of creosotebush and the lower limit of blackbrush (*Coleogyne ramosissima* J. Torr.; Rosaceae). Creosotebush was present in all samples, the oldest dating back 2235 yrs. Blackbrush on the other hand was not present in middens older than 270 yrs, even in areas where today it is clearly the most dominant species. This provides conclusive evidence that shifts in species composition were occurring up through the period just prior to European settlement. In the Chihuahuan Desert, the invasion of creosotebush has continued into historical times. Buffington and Herbel (1965) have documented an extensive increase in the area occupied by woody species of brush, primarily creosotebush and mesquite, on the Jornada Experimental Range in New Mexico over the past century, as have York and Dick-Peddie (1969) for scattered localities all across the southern part of New Mexico. The increase in the area occupied by creosotebush to a large extent has involved the encroachment on desert grassland, or other shrub-dominated vegetation. Some original mesquite stands, have been replaced by *Larrea* (York and Dick-Peddie 1969).

The usual explanation for the increasing abundance of brush is that grazing of the desert grassland by introduced livestock upset a 'balance' which in turn triggered brush invasion. An alternative view is that a balance never existed in the first place and that the introduction of domestic livestock just added another environmental factor that tended to modify the rate rather than the direction of changes that were already in progress. Smeins (1983) emphasizes the importance of a long-term historical perspective, for understanding the current 'brush problem'. The region of documented brush invasion in New Mexico is near the northern limit of creosotebush's distributional range and may be interpreted as the leading front of the wave of *Larrea* invasion in the Chihuahuan Desert that has been proceeding since the mid-Holocene, or about 5000 yrs (Fig. 1, Table 1).

The documented dynamics for creosotebush in the ecosystems of the three deserts indicate low inertial stability both in terms of dominant species composition and functional processes. The former is implied by the rapid invasion of creosotebush and the latter is implied by shifts in physiognomic structure, from woodland to scrub in the Mojave and Sonoran Deserts and from grassland to scrub in the Chihuahuan Desert. In terms of resilience, these systems would rank low in elasticity but high in malleability, although the observed malleableness may reflect the lack of initial and subsequent biological integration more than the disturbance of an old equilibrium and the establishment of a new one.

The question might be asked as to how representative the dynamic history of creosotebush may be of plant species in other ecosystems. After all, *Larrea* is relatively new in North America, maybe not even 'native' according to some standards. Furthermore it occupies desert habitats notorious for extremes of both moisture and temperature and the irregularity with which they are imposed. Do other species of more equable ecosystems exhibit similar dynamics?

Forest Stability

Forests are generally thought to represent the highest form of integrated vegetation development on earth. A brief assessment of the past and present dynamics of selected forest species and forest types will be presented to provide a perspective for comparison with what has been shown for *Larrea* and deserts. The principal paleoecological tool for forests is palynology, the study of pollen. Chronologically stratified sediments from forested areas, such as lake bottoms, contain pollen that permit the restructuring of

the regional vegetation for periods when the sedimentation occurred. In contrast to the record preserved in packrat middens, which contain intensive samplings of all local flora, the pollen record is regional in scope and weighted heavily toward species producing relatively large amounts of wind-borne pollen.

Deciduous Forest of Eastern North America

A remarkable picture of the dynamics of tree species of the eastern deciduous forest since the last glaciation is now emerging. Three recent publications synthesize much of the available data (Davis 1981*a*, 1983*a*, *b*). Davis presents maps with isopleths circumscribing study sites with similar dates for the first appearance of pollen for each of the major tree genera or species in the eastern third of the United States. The invasion of trees, generally from south to north, after the glaciers melted is thus depicted (Fig. 3).

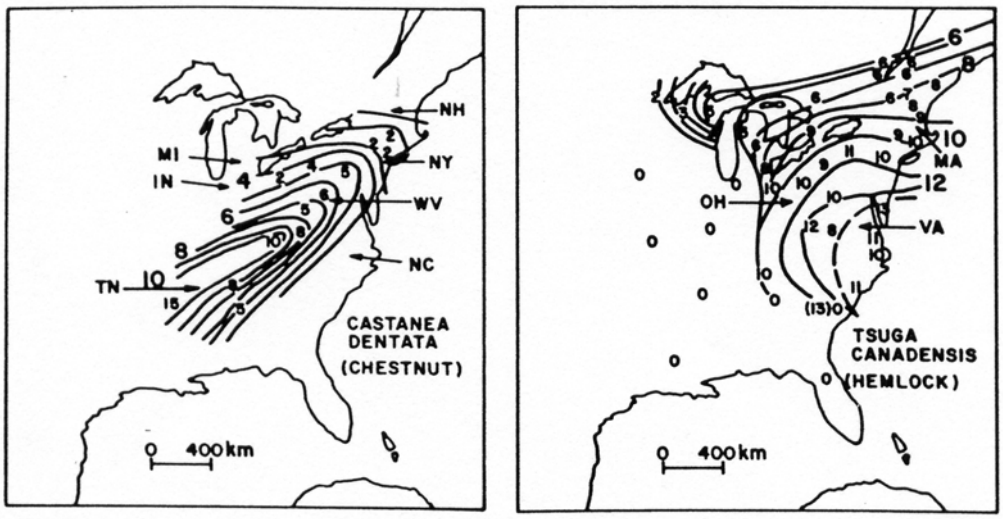

Fig. 3. Pollen isopleths of *Castanea dentata* (Marsh) Borkh. (chestnut) and *Tsuga canadensis* (L.) Carr. (hemlock) showing migration of these species through time and the approximate range attained by them in the eastern deciduous forest of North America by the time of the discovery of the New World. Small numerals represent time in thousands of years before present for the first appearance of pollen of the species in the pollen profile at that location. Large numerals apply to the curved lines that circumscribe areas of equal arrival times. The shape and orientation of the lines indicate the direction of migration, i.e. northwest for hemlock and northeast for chestnut. The distance between the lines and the time interval designation give indication of the rate of migration. IN = Indiana, MA = Massachusetts, MI = Michigan, NC = North Carolina, NH = New Hampshire, NY = New York, OH = Ohio, TN = Tennessee, VA = Virginia, WV = West Virginia. Modified from Davis (1983*b*) (*cf.* Table 2).

When maps of all contributing tree are considered, three points are strikingly evident: (1) direction of migration was different for each species/genus; (2) time of arrival at a given point was markedly different among species and/or genera; and (3) rates of movement were surprisingly fast (Fig. 3, Table 2). Documented changes in distribution and abundance spanned the entire time period between melting of the last continental glacier and the present. Rates of movement based on time increments between isopleths calculated by Dr. Davis range from 400 m/yr for jack/red pine to 100 m/yr for chestnut (Table 2). These rates are similar to those estimated for creosotebush in the desert.

The following conclusions drawn by Davis (1983*a*) are pertinent to our initial questions about balance and stability:

> '... various species of trees moved northward invdividualistically. Forest communities have represented fortuitous combinations of species during the Holocene. Many modern communities are very young; they include dominate species that have grown locally for only a few thousand years ... Evolutionary processes that may have adapted cooccurring species to one another have had very little time in which to take effect.'

The scope of short-term dynamic change in forests at the local scale is well illustrated in a novel study by Henry and Swan (1974). They considered the vegetational history of '... one of the rare old growth stands still undisturbed by man in central New England'. This site located in southwestern New Hampshire covers 8.1 ha of which 0.04 ha were investigated in detail. The forest history since the mid-1600s was reconstructed from the meticulous analysis of data on age and relative positions of tree

Table 2. Time span of first occurrences (years before present) of the main tree species/genera of the forests of eastern North America along a south to north gradient (*cf.* Fig. 3) and the rate of speed in m/yr (compiled from Davis 1981*a*, 1983*a*).

Species	Time span of first occurrences South North	Rate m/yr
Boreal elements		
Picea spp.	25000 to 7000	250
Larix laricina (Duroi) K. Koch	23000 to 7000	250
Pinus banksiana Lamb. and *P. resinosa* A.T.	23000 to 7000	400
Abies balsamea (L.) Mill.	21000 to 7000	200
Deciduous forest elements		
Pinus strobus L.	14000 to 2000	300–350
Quercus spp.	12000 to 7000	350
Ulmus spp.	17000 to 6000	250
Tsugu canadensis (L.) Carr.	13000 to 2000	200–250
Carya spp.	15000 to 4000	200–250
Acer spp.	14000 to 6000	200
Fagus grandifolia Ehrh.	15000 to 4000	200
Castanea dentata (Marsh.) Borkh.	15000 to 2000	100

parts by species in terms of standing trees, dead trees (down but unburied) and buried tree fragments. They found that three different forests had occupied the site over the last 300 yrs. A fire completely destroyed a forest made up principally of white pine (*Pinus strobus* L.; Pinaceae), white oak (*Quercus alba* L.; Fagaceae) and hemlock (*Tsuga canadensis* [L.] Carr.; Pinaceae) in approximately 1665 A.D. The forest that followed was dominated by white pine and hemlock until it was destroyed by a series of four wind storms commencing in 1897 and culminating in a hurricane in 1938. The young forest that developed following the hurricane is dominated by hemlock, beech (*Fagus grandifolia* J.F. Ehrh.; Fagaceae), red maple (*Acer rubrum* L.; Aceraceae) and black birch (*Betula lenta* L.; Betulaceae). Although the three forests have some elements in common, the differences among them suggest that the out-of-balance dynamics recorded in the palynological record persisted in the forests of eastern North America into the historical period on a local scale.

A question on the validity of extrapolating the imbalance of forests of eastern United States to other vegetation types in the world may arise on the basis of their initial proximity to the Wisconsin ice sheet and the opportunity for invasion afforded tree species by the exposure of bare surfaces as the ice melted. A measure of the dynamics of tropical forests would provide a test for such an objection since no such available void recently freed from ice is hypothesized for the lower latitudes.

Tropical Forests

Tropical forests are notorious in their reputation for complex physiognomy and floristic diversity, which to many are synonymous with antiquity and balance. The seemingly ancient qualities of these magnificent forests were, in the days of my student indoctrination in the theory of Clementsian ecology and the dogma of climax communities, often regarded as representing a sort of end point in an ultimate plant succession; i.e. a world climax. Studies testing such notions in the tropics are not abundant, but current investigations are providing some surprising results.

A recent interpretive report of the current understanding of the dynamics of tropical forests was presented by Lewin (1984). Lewin's discussion indicates that the pollen record from tropical Central America shows much the same lack of forest species stability as was shown above for the temperate forests to the north. The work of Graham in the lowlands of Mexico is cited as concluding that tropical forests should be regarded as '... dynamic and ephemeral rather than stable and ancient'. Work reviewed from the lowlands of Guatemala, a region known as the Peten, suggests that the '... lush, moisture-loving, semievergreen, seasonal forest that now carpets the lowland' was not evident 11,000 yrs ago. Instead, the area was occupied by a juniper scrub. Lewin (1984) notes that the rate of change needed to transform the juniper scrub into the 'age-old looking modern forest' is impressive by itself but even more so in light of the probability that large portions of the presently forested areas must have regrown after having been cleared by the Mayan peoples between 3000 and 400 yrs ago.

The search for ice age refugia (i.e. places where present-day tropical forests spent the Pleistocene glaciations) have been in vain. The absence of contemporary plant species assemblages in the fossil record at particular sites requires a dynamic movement of species from different places to those sites today. Lewin (1984) sees this as casting doubt on popular concepts of community identity. 'This repeated reassembly as opposed to repeated regrowth of pristine communities, forces one to view the tropical forest as less of a cohesive natural unit than previous theory implied.'

The intuitively appealing equation that diversity results in stability has little if any support in current literature (Connel 1978; McIntosh 1980). In fact, Lewin (1984) maintains that 'high diversity through instability not stability is how the equation [now] reads'. In matters pertaining to our questions about balance and biotic integration, the tropical forests appear similar to temperate forests in lacking abstract identities that are faithfully replicated in either time or space.

Plant Species Introductions and Extinctions in California

Another perspective on the dynamics of plant diversity and the stability of species composition in the landscape may be gained from analyses of local and/or regional floras and the changes in them that occur over time. The State of California is a prime candidate for such consideration since it is relatively well known floristically and has a continuing eager cadre of amateur and professional botanists conscientiously making

field observations. Even though the State political boundaries are not coincident with boundaries of recognized naturally occurring floristic units, one such unit, the California Floristic Province, falls mostly within the State (Gleason and Cronquist 1964). This gives a measure of coherence to 'political California' as a somewhat natural biotic unit to serve as framework for the floristic considerations that follow.

The earliest indications of foreign species becoming established in the State comes from the identification of plant fragments found as part of the binding material used in making adobe brick for the construction of the first Spanish mission in San Diego in 1769. Filaree (*Erodium cicutarium* [L.] L'Her. ex W. Ait.; Geraniaceae), curley dock (*Rumex crispus* L.; Polygonaceae), and sow thistle (*Sonchus asper* [L.] J. Hill; Compositae) are three introduced species so identified (Hendry 1931). These remarkable early records which date from the first European settlement, foreshadow a series of continuing waves of introductions and naturalizations of exotic plant species. As early as 1864 Bolander listed 109 species of grasses from the Central Valley of which 29 were foreign (cited by Burchann 1957). In more recent time the trend can be followed in more comprehensive floristic treatments (Table 2).

Two excellent State floras have been published: (1) 'A Manual of Flowering Plants of California' by Jepson (1925); and (2) 'A California Flora' by Munz and Keck (1959) with a supplement by Munz (1968). Three different increments of time are thus represented. Statistical summaries of these works show that 7% of the species were considered as introduced in 1925, 14% in 1959 and 16% in 1968 (Herrott and Noldeke 1956; Smith and Noldeke 1960; Howell 1972). Although differences among the tallies for the different time periods indicate changing taxonomic interpretations as well as advancing knowledge of both the native and introduced floristic components, it is most significant that the proportional increase for introduced species continues in an upward trend with time (Table 3).

Table 3. Numerical summary of reported plant species introductions to the vascular flora of California through time.

Year	No. introduced species	% of all species	Source
1925	298	7	Herriott and Noldeke (1956) from Jepson (1925)
1940	526	(?)	Robbins (1940)
1959	800	14	Smith and Noldeke (1960) from Munz and Keck (1959)
1968	975	16	Howell (1972) from Munz (1968)
1981	1022	17	Incorporation CNPS list of escapees (1981) with Howell (1972)

The very rapid encroachment of new species at the beginning of the historical period indicates the absence of initial stability in the system and perhaps what in Clementsian terms would be called a 'postclimax' situation; i.e. a condition where changes in vegetation have lagged markedly behind changes in climate. The idea is that the existing vegetation at the time of settlement was not well equilibrated with the associated physical environment and that this marked disequilibrium resulted in an increased opportunity for invasion and naturalization by new species fortuitously preadapted to the prevailing conditions. Many such species in the California Central Valley grassland should, perhaps, be considered 'new natives' because they exhibit a measure of ecological stability that ensures their continuance in face of the natural processes of vegetational

change (Heady 1977). Today it is estimated that over 50% of the vegetational cover of 'native' (unimproved) rangeland in the Central Valley is made up of exotic species (Burchann 1957; Heady 1977). Introduced species such as wild oats (*Avena fatua* L.; Poaceae), soft brome (*Bromus mollis* L.; Poaceae), and filaree (*Erodium* spp.) are major contributors to rangeland productivity. Of course, others such as Klamath weed (*Hypericum perforatum* L.; Clusiaceae), medusahead (*Elymus caput-medusae* Boiss.; Poaceae), and goatgrass (*Aegilops triuncialis* L.; Poaceae) are considered rangeland weeds that reduce forage yield.

The current makeup of the California flora in terms of the introduced and native taxa show proportional differences according to rank in the classification hierarchy (Table 4). The number of introduced families is low (6.8%) in comparison to the number of introduced species (16.2%), and the number of introduced genera is high (24.8%). The high incidence of new introduced genera, around one-fourth of the total, suggests that the introduced taxa have phylogenies divergent enough from the native taxa to cause a substantial increase in the breadth of the biological diversity of the flora as a whole.

The over 1000 species of adventive and naturalized plants can further be generally divided into two types: (1) those that arrived by accident as contaminants of crop seed,

Table 4. Statistical summary of the vascular flora of California in terms of native and introduced taxa according to classification hierarchy. Figures in ( ) indicate number of California endemics in category (prepared from Smith and Noldeke 1960, Noldeke and Howell 1960 and Howell 1972 as based on Munz and Keck 1959 and of Munz 1968).

Taxonomic level recognized	No. native		No. introduced	Total no.	% introduced
Families	155		12	167	6.8
Genera	857	(29)	282	1139	24.8
Species	5027	(1510)	975	6002	16.2
Specific and subspecific	6658	(2633)	1017	7675	13.2

etc.; and (2) those that were brought in intentionally for the purpose of being cultivated and escaped. This latter group of 'escapees' have been the focus of a special project being carried out by the California Native Plant Society (CNPS) over the past few years (Smith 1979). The project is directed at cataloging and evaluating escaped exotics with regard to the threat they might pose to native species through the process of competitive exclusion. The first list of 'escapees' compiled contained 326 species. Although most of the 326 were among the 1000 introduced species considered in the references mentioned above, 44 were not, and evidently represent recent naturalization supplying the ongoing invasion. The proportion of 'escapees' relative to the total number of cultivated species in California is not known since no accounting of the numerous kinds of plants (probably several thousand) grown in fields, orchards, aquaria, gardens and nurseries has been attempted. It should be supposed that, with the high commercial activity in gardening and landscaping and the large number of species involved, the flood of new exotics to the wilds will continue.

The documentation of exotics becoming adventive or naturalized is a much easier task than determining the degree of threat they might pose to native species. Evaluations by CNPS of the 326 escapees in this regard have been toward first identifying the most obvious offenders. The list of 326 was shrunk to 100, then to 37 and finally to 6 species

that appear aggressive enough to assume dominance in certain areas of native vegetation. The final six are: *Cortaderia jubata* (Lem.) Stapf. (Poaceae) (Andean pampas grass); *Cytisus monspessulanus* L. (Papilionaceae) (French broom); *C. scoparius* (L.) Link (Scotch broom); *Ulex europaeus* L. (Papilionaceae) (gorse); *Carpobrotus edulis* (L.) Bolus. (Aizoaceae) (ice plant); and *Tamarix ramosissma* LEDEB. (Tamariaceae) (salt cedar). Information is being sought on other species. A threat to native species is presumed if roles of dominance are assumed by 'escapees', especially if their potential habitat includes those occupied by native species that are considered rare and/or endangered (E. McClintock, pers. comm.).

Another primary effort of CNPS has accordingly been devoted to identifying, mapping and evaluating the status of the less common or threatened native plants in the State (Smith *et al.* 1980). Presently, 1394 species and subspecies, more than $\frac{1}{5}$ of the natives, have been categorized under this designation. The group has been further characterized as follows: (1) those presumed extinct (list one, 44 species); (2) those rare and endangered (list two, 680 species); (3) those rare but not endangered (list three, 430 species); and (4) those rare in California but more widely distributed outside the State (list four, 240 species).

Those classified as 'presumed extinct' are of particular interest in this discussion since they represent probable examples of species removed from ecosystems. Since the list was last published in 1980 (2nd edition revised), 10 of the 44 species have been located alive in California, 6 have been determined to still exist in adjoining states or regions, 5 are described as subspecies of more generally occurring species and several others initially collected from remote locations are thought by specialists to have a high probability of still existing there. The case against any chance of recovery appears strong for about 6 species of the initial 44 presumed extinct (A. Howard, pers. comm.). In general none of the initial group were ever abundant, and most were known only from a single location and in some cases as a collection from one or two individual plants. In view of their beginning rarity it is unlikely that any of the probable extinct species ever played significant roles in the structure and function of the ecosystems of which they were/are a part. On the balance sheet of current species richness, one aspect of diversity, the probable six extinctions, is far overshadowed by the documented 1000 species introductions.

The plant species listed as endangered and/or rare (CNPS lists two and three, respectively) are also, as might be surmised from the designations, only minor structural components of the ecosystems where they occur. There is little indication that any were ever major components of any extensive vegetations. In particular it appears that essentially all those designated as endangered have always been rare. Most are endemic, probably of recent origin, i.e. neoendemics, that belong to genera and families that exhibit a high degree of evolutionary activity. Examples from lists two and three are: (1) members of the genus *Eriogonum* (Polygonaceae), 51 rare species and varieties out of approximately 104 species and 50 varieties in the flora; (2) the genus *Arctostaphalus* (Ericaceae), 37 species and subspecies out of approximately 43 species and 18 subspecies or varieties in the flora; and (3) the genus *Astragalus* (Leguminosae), 37 species and varieties out of approximately 94 species and 32 varieties in the flora. The pattern calls to mind discussions on speciation from years ago in graduate school at the New York Botanical Garden, during which I remember the noted field botanist, taxonomist and plant systematist, Arthur Cronquist, expressing the opinion that incipient species were constantly being 'spewed off' of established species and that most of these 'new species' failed to increase beyond one or a few individuals. The point is that field collectors must be discriminating to obtain specimens that are generally representative of

successfully established populations. It seems probable that many of the species listed as rare are more or less on the fringe of successful establishment. In this regard, it is apparent that what taxonomists decide to call a species is of great significance.

The general ecological profile of the rare native species contrasts sharply with that of the naturalized exotics. The latter have already passed through the screen of successful establishment. In comparing the future potential of the two groups, the rare natives and the naturalized exotics, I audaciously opt for the latter as possessing qualities most suggestive of ecological significance and economic worth. This idea is related to Edgar Anderson's often cited hypothesis on the dump heap origin of Agriculture in which he suggested that weedy plants associated with rubbish piles (i.e. 'kitchen middens of fisher folk'), gave rise to the first and some of our most important domesticated crops (Anderson 1952). I am not aware of any established links between threats of extinction to natives and competition from naturalized exotics in California other than in theory although such cases are purported to have occurred in Australia (Bell 1983). At this juncture it appears that species have been more readily added than removed from the flora of highly industrialized California.

Biological Control and Ecosystem Structure and Function

Inadvertant Biological Control

The common objective in the biological control of weeds on rangeland is the reduction or removal of a targeted weed species through the action of an attacking organism. The introduction of attacking organisms for this purpose is customarily approached with great caution to avoid a mistake whereby non-target species are also attacked. The kinds of risks involved in introducing an attacker may be partly understood from results gleaned from some selected rather extensive 'experiments' that were performed inadvertently. Three such 'experiments', chestnut blight on American chestnut, Dutch elm disease on American elm and an unknown suspect on eastern hemlock will be briefly considered as 'worst case' scenarios.

The American chestnut (*Castanea dentata* [H. Marsh] Borkh.; Fagaceae) was until recently a dominant tree of the eastern deciduous forest of North America extending over a range of *c.* 80 million ha (200 million acres). It was a tree valued for lumber, fruit, chemicals (used in the leather tanning industry) and aesthetic appeal. In 1904, chestnut blight, a fungal pathogen (*Endothia parasitica* [Murr.] P.J. & H.W. And.; Sphaeriales), was discovered on chestnut trees in Bronx Park, New York City (Gravatt and Parker 1949). It proved to be highly lethal to mature tree stems. It spread rapidly and in < 50 yrs, 80% of the chestnut tree boles in the eastern deciduous forest were dead. This has been termed '... perhaps the greatest single natural catastrophe in the annals of forest history' (MacDonald *et al.* 1978). An appraisal of the current status of chestnut and its ecosystems is in order.

Granting the catastrophic dimensions of the American chestnut die off, it seems important to point out that the species has by no means been eliminated. It still persists over most of its original range albeit, in most instances, in a highly modified form. Chestnut sprouts vigorously from the base of the dead boles, and as such, it is now an understory shrub in many places where it once was a major component of the tree canopy. Data in a recent report by McCormick and Platt (1980) shows that in 1970 chestnut (stump sprouts) ranked seventh in IV (importance value) among 26 woody species of a forest in Virginia that was devastated by chestnut blight around 1920. Stump sprouts exhibit some juvenile resistance at first but then become susceptible to the blight

and after persisting for a few years succumb once more to fungal infections; then they sprout again and so on indefinitely. Almost pure stands of chestnut resprouts are observed in some areas of West Virginia where present-day forests have been recently clearcut (M. Double, pers. comm.). The pattern of chestnut as an understory shrub is a common one throughout the deciduous forest region today.

Perhaps of equal, or maybe greater, significance is the survival of some large individual trees of *C. dentata* throughout the length and breadth of its original range. Living trees are reported from North Carolina on the south (Stambaugh and Nash 1982) to New York on the east (Dietz 1978) to Michigan on the northwest (Brewer 1982) and West Virginia in the middle (Given and Haynes 1978). Tree survival has been attributed to: (1) disjunct distributions, wherein isolation has permitted evasion of the blight; (2) resistance, wherein the trees are purported to be tolerant of the blight; and (3) blight hypovirulence, wherein the blight organism itself has been reduced in its pathogenicity. All three of these survival mechanisms, especially the latter, are currently being actively studied. Together they provide ample evidence of a resurgent interest and optimism in the prospect of restoring *C. dentata* to a place of prominence in the American landscape. Two symposia have recently been held on the subject after a long period of apparent discouragement and dwindling interest (MacDonald *et al.* 1978; Smith and MacDonald 1982).

A matter of relevance to biological control is that the blight fungus (*E. parasitica*) is not specific to chestnut but has been reported on some 24 other tree species in eastern North America, particularly oaks (16 species) (Stipes *et al.* 1978). It appears innocuous in most cases but is accorded a role in the decline of eastern live oak on the Atlantic seaboard, while another fungus (*Cephalosporium* sp.; Hyphomycetes) is associated with live oak decline in central Texas (Stipes *et al.* 1978).

The aftermath of chestnut blight on the total forest ecosystem has not been a dramatic long-term disruption of ecosystem functional processes. The immediate consequence of death of American chestnut was development of gaps or holes in the energy-accumulating forest canopy. Ecosystem 'goods' in terms of chestnut fruits (nuts) and available chestnut timber declined markedly. The spread of the disease was so rapid that the decrease was essentially synchronous over the eastern forest region. The demise of chestnut was followed by a surge of growth by associated species which closed the gaps and holes in the forest canopy in 10–20 yrs. Oaks (*Quercus* spp.) responded most quickly in the south, e.g. Tennessee and Virginia (Woods and Shanks 1959; McCormick and Platt 1980), and cherry birch (*B. lenta*) in the north, e.g. New Jersey and Connecticut (Good 1968; Davis 1981*b*). Through the years hickory (*Carya* spp.; Juglandaceae) has increased in the south to the point of codominance with oaks (McCormick and Platt 1980), while in the north, oaks have continued to increase at the expense of birch (Davis 1983*a*). Other forest tree species, e.g. maples (*Acer* spp.), ashes (*Fraxinus* spp.; Oleaceae) and birches (*Betula* spp.) have also undergone population changes in the blight areas, as elsewhere.

Although projection of 'recovery' to some presumed new climax is a common practice (Wood and Shanks 1959; McCormick and Platt 1980), the results must be viewed as illusionary if the expectation extends beyond the generation time of the longest lived dominants. After all, chestnut had occupied the forest in New York for a brief 2000 yrs before the blight struck (Fig. 3). Based on probable life history considerations, 2000 yrs is equivalent to only three or four generations, hardly enough cycles to establish much integration. Still the system as a whole does not appear erratic but regulated in terms of functional processes.

The functional stability of the eastern deciduous forest ecosystem is not dependent on a definite species composition but that the species comprising the system have the capacity for the performance of essential processes. In arguing a point similar to this, Slobodkin *et al.* (1967) noted that the demise of the American chestnut '... has not left holes in our forests' and that 'Not one mature chestnut can be put back without displacing plants of other species', i.e. the processes once performed by chestnut are now being carried out by other tree species. In terms of ecosystem 'goods and services', the 'goods' of oak, birch, beech, maple, etc., have been substituted for the 'goods' of chestnut, and the 'services' have remained about the same.

The Dutch elm disease (DED) 'worst case' number two may be of more international interest since it has been said to have '... created more worldwide environmental concern than any other tree disease' and '... has proven to be one of the most devastating tree diseases known to mankind' (Karnosky 1979). The case of the American elm, *Ulmus americana* L. (Ulmaceae), in relation to DED caused by the fungus, *Ceratocystis ulmi* (Buismam) C. Moreau (Microascales), is similar to the case presented for the American chestnut. *U. americana* was a major component of the eastern deciduous forest at the time of European settlement. It was particularly abundant in low-lying lands along streams and rivers throughout almost all of the deciduous forest region. In addition to being a major forest species, its stately appearance led to its being selected as a favored choice for shade tree plantings in cities and towns all across the country, especially in the northeast. It has been called 'nature's noblest vegetable' (Karnosky 1979).

DED was unwittingly introduced to North America around 1930. It was first reported from Ohio where it is believed to have arrived via diseased elm logs from Europe. Soon after it was found in New Jersey and New York (Karnosky 1979). By 1949 it was reported from natural forests and shade tree plantings from Massachusetts in the northeast to Virginia to the south and Indiana to the west (Swingle *et al.* 1949). Unlike the chestnut blight, its spread is closely tied to insects: four species of elm bark beetles (Coleoptera: Scolytidae), three introduced (*Scolytus multistriatus* [Marsh.], *S. scolytus* F., and *S. pygmaeus* F.) and one native (*Hylurgopinus rufipes* Eichhoff) act as vectors (Karnosky 1979). Shade trees planted in parks and lining streets of many northeastern cities and towns have been particularly devastated. In areas where the DED has struck, tree death estimates range from 75–95% of the elm population.

As in American chestnut, resprouting in American elm is prolific. Of course stump and root sprouts cannot be tolerated as substitutes for living trees in streetside plantings but they do have considerable significance in the continuance of the species as part of the forest ecosystem. After reviewing the literature for both Europe and America in this regard Karnosky (1979) concludes that 'millions of root-sprouts are now developing in the original outbreak area, indicating that elms will continue to inhabit much of their original range — but not as dominant components which they once were.' and further

> '... resprouting of diseased elms will ensure that elms will continue to be important components of forest stands in north-temperate regions around the world. Thus, the major environmental impact of DED on elm forests will be the community structure changes resulting from the remaining and persisting elms being shrubby, understory trees rather than the major overstory trees that their progenitors once were.'

American elm also continues to be perpetuated by seed. Young trees apparently possess an age-related resistance that allows them to reach seed bearing size even though the average life span is greatly reduced over predisease times. Older resistant individuals

also persist, especially in mesic uplands (Richardson and Cares 1976). The opportunity for developing future resistant populations through genetic selection thus appears even more favorable for American elm than for American chestnut (Barnes 1976; Richardson and Cares 1976).

Five to ten yrs following the demise of canopy size American elm in deciduous swamp communities in Michigan, black ash (*Fraxinus nigra* H. Marsh.), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis* N.L. Britt.) became dominant in the tree layer and were expanding to fill the holes left by the dead elms (Barnes 1976). Twenty-six years after DED struck a mesic upland site in the same State, American elm still ranked first in importance value among forest trees but was declining relative to the oaks (*Quercus* spp.) and red maple (Richardson and Cares 1976). The rate of canopy hole closure was not indicated but this was implied to be proceeding.

In terms of ecosystem 'goods and services', the same kinds of trends as observed for the former chestnut forests are evident here though fewer data are available. The 'goods' are changing but the 'services' are remaining about the same.

The third 'worst case' concerns eastern hemlock (*T. canadensis*). Its story is less well known than that of American chestnut and American elm. It is an evergreen conifer that has exhibited a consistent association with deciduous trees through time (Table 2, Fig. 3). In parts of its range it forms almost pure stands and exhibits vigorous growth. Today there is no apparent unusual threat to hemlock's health. The case for hemlock involvement in a biological control episode is based on suggestive patterns in the pollen record (Davis 1981*b*, 1983*a*). Like other deciduous forest trees it migrated north after the last glaciation, but followed a distinctive northwesterly path (Fig. 3). About 5000 yrs ago it was widely represented as a major species in the regional vegetation. Then approximately 4800 yrs ago there was a sudden and large decrease in the rate of hemlock pollen deposition. The change appears synchronous throughout the entire deciduous forest. Pollen rain from other tree species remained high or increased. There was an immediate increase in birch pollen in the north followed by an increase in oak. In other parts of the range, pollen deposition rates increased for various combinations of beech, hickory, maple, oak and pine (Davis 1983*a*).

The decrease in deposition in hemlock pollen at the 4800-yr level and the subsequent compensating shifts in the pollen of associated species match closely the kinds of changes in chestnut pollen and the pollen of its associates in modern time as related to chestnut blight. This suggests strongly the involvement of some biological agent, possibly a pathogen or an insect, in the prehistoric demise of hemlock. It should be noted that hemlock did not disappear completely during this episode but remained at low levels for about 1000 yrs and then started to increase so that by about 3000 yrs B.P. it had returned to a position of major importance in the regional vegetation (Davis 1983*a*). Thus, here again in terms of ecosystem 'goods and services' the system appears to have regulated the 'goods' supply by substituting the 'goods' of other species for the 'goods' of hemlock while maintaining ecosystem processes or 'services' at a nearly constant level.

Biological Control of Weeds

A review of successful biological control programs fostered or carried out to remove undesirable plants on rangelands indicate results similar to the accidents or fortuitous case histories just discussed. Four selected examples, two representing native weeds, manuka (*Leptospermum scoparium* Forst.; Myrtaceae) in New Zealand and prickly pear (*Opuntia* spp.; Cactaceae) on Santa Cruz Island, California, and two representing

introduced weeds, Klamath weed (*H. perforatum*) in northwestern North America and prickly pear (*Opuntia* spp.) in Australia and other places, will be briefly considered in this regard.

Manuka, a native shrub of New Zealand, is an aggressive invader of established grassland on both the North and South Islands. The acreage it occupies has greatly increased in historical times, particularly in areas cleared of forests to establish pastures. Estimates of hectares infested, 2.8 million on the North Island and 0.6 million on the South Island, amount to 25% and 4% of the respective island areas (Hoy 1961). Dense stands of manuka suppress production of associated grasses and herbs. Such infestations diminish forage yield and pose vegetation management problems (Sewell 1949). Biological control of manuka was considered as a possible remedy only after the chance introduction of the mealy bug, *Eriococcus orariensis* Hoy (Homoptera: Eriococcidae), from Australia was discovered on the South Island (Hoy 1949, 1961). *E. orariensis* was observed to be effective in killing infected plants over a period of years and acquired the designation 'manuka blight' (Sewell 1949). Starting in 1946 the use of manuka blight was popularized in newspapers and was advertised for sale to farmers in 1948 (Hoy 1961). Its spread was fostered by man on both the North and the South Island at least up through 1953. Thereafter opposition to its use developed from those who feared eradication of the target native plant and possible damage to the affected watersheds as a result of its elimination (Hoy 1961). Distribution of the mealy bug soon became essentially coincident with that of the host plant. Manuka die-off was striking throughout its entire range at first but diminished markedly in places, particularly the North Island, where the debilitating insect became parasitized by a fungus. In fact, Hoy (1961) concluded in this connection that 'the recovery of *L. scoparium* in the North Island has been as spectacular as the initial control achieved by *E. orariensis*'. The fungus had little affect in reducing the efficacy of the mealy bug on the drier South Island or in the drier parts of the North Island. Effective control of manuka continued to be observed in these drier areas up through 1960 (Hoy 1961). Concern over possible eradication of *L. scoparium* in New Zealand proved premature since its continuance in the moister portions of its range now seem assured.

A series of significant vegetation structural changes during the manuka episode are related to shifts in both the goods and services (processes) provided by the ecosystem. Forest trees were removed initially to increase grass forage production which, in turn, was suppressed by the invasion of native manuka shrubs, but restored when the shrubs were killed by the introduced manuka blight (changes in goods). Physiological processes of trees, shrubs and herbs are sufficiently different as to represent substantial shifts in ecosystem services as the dominant life form changed from one to another.

Two species of native prickly pear (*Opuntia littoralis* [Engelman] Cockerell and *O. oricola* Philbrick) on Santa Cruz Island, just off the coast of southern California, increased to pest proportions during the early part of this century. Beginning in the late 1930s biological control efforts were undertaken using native mainland *Opuntia* insects not found on the island (Goeden *et al.* 1957). Although introduction of several different insect genera was attempted, the primary success was attained with *Dactylopius opuntiae* Cockerell (Homoptera: Dactylopiidae), a cochineal insect from Mexico via Australia and Hawaii. After successful establishment of a strain of *D. opuntiae* in 1951, prickly pear decreased markedly in abundance and livestock grazing conditions improved greatly (Goeden *et al.* 1967; Goeden and Ricker 1981). However, scattered clumps of prickly pear are still found throughout the island and in some places in quantity (R.D. Goeden, pers. comm.). In recent years the prickly pear mortality rate has decreased which may in part be due to changes in capacity of *Dactylopius* to inflict

damage since appearance of some of its predators on the island (R.D. Goeden, pers. comm.). The initial greater effectiveness of *D. opuntiae* in killing prickly pear on Santa Cruz Island as opposed to the adjacent mainland was largely ascribed to absence of cochineal insect predators in the island situation. Over the years there has been a shift in relative amounts of the two *Opuntia* species present in favor of *O. oricola*, which is less susceptible to damage by *Dactylopius*. Still, there appears to be little chance that either species will be eliminated from the island. Under current conditions prickly pear should be projected as a continuing conspicuous constituent of the vegetation.

The increase in density of native prickly pear to pest proportions and their latter demise is indicative of shifts in the goods and services provided by the ecosystem. Not only does it represent changes in vegetation structure due to the increase and decrease of different lifeforms but also alterations in the basic mode of photosynthetic production. Prickly pear exhibit crassulacean acid metabolism which has direct implications on how water and other plant growth resources from the environment are processed.

Klamath weed, or St. Johnswort (*H. perforatum*), a native of Europe and Asia, was introduced into the rangelands of northwestern North America in the early 1900s. It spread rapidly and by 1940 had become a prominent component of rangeland vegetation throughout an area covering an estimated 2 million ha (Goeden 1978). It was an undesirable addition to northwest rangelands because, besides being unpalatable, it exhibited certain toxicities to livestock (Huffaker and Holloway 1949). A perennial herb, it exhibited a particularly aggressive characteristic of not only invading new territory but of persisting indefinitely in the acquired spaces once gained. Affected areas could not be readily restored to productive status by conventional range vegetation management techniques.

Biological control efforts were undertaken in the early 1940s and by 1945 a leaf-feeding beetle (*Chrysolina quadrigemina* Suffrian; Coleoptera: Chrysomelidae), a native of France, that had been partially screened for biocontrol work in Australia, was, after further testing, released in northern California. The results were phenomenal. Within a decade the amount of Klamath weed was reduced an estimated 99% (Huffaker and Kennett 1959). The greatest influence of the leaf beetle appears to have been in the central area of the Klamath weed infestation. Weed populations toward the margins of its range northward in Canada and southward in California have been less affected.

The ecological position occupied by Klamath weed in the natural landscape changed under the influence of its insect predator from full-sun, open habitat to partial-shade understory habitat (Huffaker and Kennett 1959). It seems significant that the target species still persists throughout the range it attained during the period of its rapid invasion. Thus *H. perforatum* even in its reduced state is still more abundant than many native species in the flora. Its success should qualify it for the designation 'new native' since it now appears to be a permanent member of northwestern rangeland vegetation even in the presence of its imported enemies and the competition of associated plant species. The initial invasion of Klamath weed brought about a change in the specific goods and services provided by the ecosystem. Structural changes, though not as great as for manuka and prickly pear (see above), were associated with a shift in the quality of herbaceous plants for grazing. Klamath weed, an undesirable perennial forb, tended to replace more desirable grasses. The introduction of exotic insects for biological control reduced Klamath weed and shifted goods and services back toward grass goods and grass processes.

Biological control of prickly pear in Australia must be the most publicized biological control episode ever carried out. It is a favored example of the biological control concept used in biology textbooks as well as in technical publications of related fields (Heady

1975). The principal organisms involved are two closely related species or varieties of prickly pear, *Opuntia inermis* (DC.) DC. and *O. stricta* (Haworth) Haworth from the Gulf Coast in North America, and the moth *Cactoblastis cactorum* (Berg.) (Lepidoptera: Pyralidae) from Argentina in South America (Dodd 1940; Mann 1970). The campaign against prickly pear was undertaken in response to an enormous and alarming infestation that occurred about the turn of the century. The major pest species were brought into Australia between the early and mid-1800s. They were grown as hedges and were distributed widely for that purpose from about 1840–70. Their ability to spread naturally started to cause serious apprehension in the 1880s. By 1900 an estimated 4 million ha were affected. Following a serious drought in 1902 in which prickly pear was 'freely fed' to livestock the invasion rate accelerated. At its peak in 1925 it was estimated that an area of 24 million ha had been invaded and that the rate of spread was *c.* 0.5 million ha/yr (Dodd 1940). In 1925 *C. cactorum* was successfully introduced and started to be distributed through the infected area. Results of the insect killing the cactus were dramatic and Dodd (1940) indicates that after the first three years (i.e. in 1928), it was evident that prickly pear would be controlled. Most of the large pure stands of the pest prickly pears were effectively reduced to scattered plants as he predicted. *C. cactorum* continues to be effective in controlling *O. inermis* and *O. stricta* population levels in much of the area. It is significant, however, that the pest prickly pears still persist throughout most of the area they once dominated (Mann 1970; White 1981) and that they are still spreading, albeit at a slower rate (Haseler 1981). Haseler also points out that satisfactory control was never realized in central and southern New South Wales or coastal Queensland. The evidence suggests that prickly pear is well enough suited to the physical and biotic environments of Australia to persist indefinitely as a part of natural spontaneous vegetation. Perhaps it is a 'new native'. Changes in ecosystem goods and services in the case of invasion and control of prickly pear in Australia are obvious in terms of changes that took place in physiognomic structure and physiological processes, and parallel quite closely to those noted for Santa Cruz Island. A difference stands out in that prickly pear and its associated fauna have now established a new place in the Australian landscape as has Klamath weed in northwestern North America.

Australia is just one of a number of places where biological control efforts on various species of prickly pear using insect enemies has been declared a success (Table 5). In none of the instances examined does it appear that weedy prickly pears, foreign or native, have been eliminated through biological control. In fact no instance has been found in which biological control, either purposeful or accidental, has eliminated a plant species completely. The reoccurring suggestion that this might be the case for *Tribulus cistoides* L. (Zygophyllaceae) in Hawaii is in error (G. Funasaki, pers. comm.), although in animals such a case has recently been reported for an endemic snail on Moorea, an island in French Polynesia (Clarke *et al.* 1984). That is not to say that it has not occurred for plants. It probably has in view of all the plant species that have gone extinct in the past. But historical evidence suggests that the likelihood of a predator insect bringing about extinction of a plant host successful enough to be labelled 'weed' is quite remote; i.e. low risk.

Discussion and Conclusions

Now what does all the above have to do with applied ecology, and more specifically biological control of weeds on rangelands, as intimated in the introduction? It is simply this. The picture of vegetation dynamics that emerges from information presented on

Table 5. Summary of selected successful biological control efforts of prickly pear from different parts of the world using *Dactylopius* spp. and *Cactoblastis cactorum* (Berg.) (from Goeden 1978).

Opuntia species	Location	Insect species	Results[1]	Weed status[2]
O. aurantiaca Lindley	Australia	*Dactylopius* spp.	Good	Low density
O. aurantiaca	South Africa	*Dactylopius* spp. and *C. cactorum*	Poor	Pest levels
O. dillenii (Ker-Gaw.) Haw.	India and Ceylon	*D. opuntiae* (Cockerell)	Good	Low density
O. elatior Miller	India and Ceylon	*D. opuntiae*	Fair	Common
O. elatior	Celebes	*D. opuntiae*	Good	Low density
O. imbricata (Haw.) DC.	Australia	*D. newsteadii* Cock.	Good	Low density
O. inermis DC.	Australia	*C. cactorum*	Good	Low density
O. littoralis (Eng.) Cock.	Santa Cruz Is., USA	*D. opuntiae*	Good	Low density
O. megacantha Salm-Dyck	Hawaii	*C. cactorum*	Fair[3]	Low density
O. megacantha	Hawaii	*D. opuntiae*	Fair[4]	Low density
O. megacantha	South Africa	*D. opuntiae* (*C. cactorum*)	Good	Low density
O. oricola Philb.	Santa Cruz Is., USA	*D. opuntiae*	Fair	Low density[5]
O. streptacantha Lemaire	Australia	*D. opuntiae*	Partial	?
O. tomentosa Salm-Dyck	Australia	*D. opuntiae*	Good	Low density
O. triacantha (Will.) Sweet	LeeWard Is.	*C. cactorum*	Good	Low density
O. tuna (L.) Miller	Mauritius	*C. cactorum* then *D. opuntiae*	Good	Low density
O. vulgaris Miller	India–Ceylon	*D. ceylonicus* (Green)	Good	Low density
O. vulgaris	Australia	*D. ceylonicus*	Good	Low density
O. vulgaris	South Africa	*D. ceylonicus*	Good	Low density

[1]Usually judged relative to the degree of reduction in places of highest infestations — results may differ in other parts of range.
[2]Relative to abundance attained during height of infestation.
[3]Effective in intermediate elevational range of infestation.
[4]Effective in lower elevational range of infestation.
[5]Relatively more resistant and abundant than the associated *O. littoralis*.

creosotebush and creosotebush deserts, eastern deciduous forests, tropical forests, California floristics and episodes of biological control, is strikingly different from that which is commonly envisioned by many, if not most, practitioners of vegetation management, including those who would be such by employing or withholding biological control. The contrast to the seemingly ubiquitous, Clementsian climax (super organism — ancient in age — all parts essential — delicately balanced) view is that: (1) natural vegetation systems reviewed here exhibit ongoing change in species composition in time and space, i.e. both paleoecological and historical data show that plant communities are continually being assembled and reassembled in terms of species makeups; (2) vegetation (ecosystem) stability factors are more associated with physiognomy and functional processes than species persistence; (3) the flux rate in major plant species has been too fast to allow for the myriad of generations usually postulated as necessary for the refined development of co-evolutionarily integrated, biologically regulated and delicately balanced ecosystems of landscape scale; (4) some systems appear highly susceptible to invasion by introduced species, which then persist as major fluctuating components of the vegetation; and (5) the relative importance of species in ecosystems can be changed markedly and quickly by biological control type agents.

The meaning of vegetation dynamics as just summarized in relation to the specific query, 'should exotic insects (or other exotic biological agents) be used to control weedy native plants?' is that this individualistic view which the data presented supports tends to minimize or negate the concerns giving rise to the questions in the first place; i.e. the collapse of ecosystems is not an imminent prospect of biological control. Even in the case of dominant species being decimated by exotic biological agents, as in the examples of chestnut, elm, and perhaps hemlock, the ecosystem appeared to adjust rapidly in restoring productive capacity and functional processes. This is not to say that the short-term effects of biotic agents are not dramatic from a societal point of view, as was clearly the case for chestnut, where emotional and aesthetic attachments are evidently stronger for chestnut than for the ecosystem of which it is a part. In cases like this, the point of concern should be clearly identified and not generally perceived as a whole ecosystem disaster.

I conclude that:

(1) The sanctity attributed to 'climax vegetation' because it is 'ancient in age' and 'stable in species composition' is without merit. The label 'native' does not make a species sacrosanct. Clearly the status of nativity for plant species making up today's natural vegetation is relative (Figs. 1, 2; Tables 1, 2).

(2) Plants that are behaving as weeds on rangeland, whether designated native or introduced, obey similar principles as exemplified by manuka in New Zealand, Klamath weed in North America, and prickly pear in Australia, Santa Cruz Island and elsewhere.

(3) The chance of causing extinction of weedy plant species (either native or introduced) through the introduction of biological control agents is nil. The threat to non-target rare plant species needs to be evaluated on a case-by-case basis, but because of the minor role such plants play in the ecosystem any possible effect would be small at the ecosystem level.

(4) Biotic agents may rapidly alter prevalence of specific plant species without significantly affecting long-term structural and functional characteristics of the ecosystem, as with chestnut blight on American chestnut and Dutch elm disease on American elm, or conversely they may cause substantial shifts in both structure and function (goods and services), as found with *C. cactorum* and *Dactylopius* spp. on prickly pear, *C. quadrigemina* on Klamath weed and *E. orariensis* on manuka.

(5) The approach used in classical biological control provides a viable option for reducing undesirable plant species, introduced or native, that are interfering with the productivity of more desirable plants on rangelands. Contrary to a common assumption that the dominance of undesirable plants on rangelands always serve as evidence of overgrazing by livestock and that a reduction in grazing pressure will result in the reduction of the undesirable species, the evidence presented indicates that other environmental and biological factors weigh heavily in determining vegetation composition. Indeed, Harris (*in press*) contends that pure or nearly pure plant stands, whether native or introduced, are indicative of low herbivore pressure and that the introduction of appropriate insect herbivores will result in the decrease of dominance and an increase in plant species diversity.

The individual roles played by chestnut, elm, hemlock, manuka, Klamath weed, and prickly pear in their respective ecosystems were greatly altered through the action of biotic agents. Similar responses should be expected from purposeful biological control efforts directed at dominant native weed species like creosotebush and mesquite. After all, the whole intent of a biological control effort would be to bring about a notable shift in productive capacity and functional processes toward more favored species. Furthermore, if a species, native or non-native, is identified as a weed problem it may be assumed to be acting in an expansive mode that if not checked will result in ecosystem changes equal in magnitude but opposite in direction to those deemed desirable. The question as to whether or not biological control should be used in any given case seems to hinge mostly on the results of an evaluation of the positive and negative attributes of the weed itself and not on fears of postulated dire consequences to the ecosystem. This assumes of course that appropriate care is exercised in: (1) screening the designated biocontrol agent(s) for specificity, to prevent the decimation of some other species of high value; and (2) establishing reasonable assurance that the decrease in the target will result in an increase of more desirable species.

I realize that more basic philosophical questions are involved in the matters under consideration than has yet been alluded to. It goes to the heart of the question as to what man's place in nature is. Some question his right and capacity to manipulate the 'natural environment'. Nevertheless, the role man has played in contributing to dynamic change in vegetation has been on a grand scale and is of unquestionable significance. It is doubtful if there is a patch of vegetation on earth that does not bear some imprint of man's influence. Whether this is good or bad is a matter of both perspective and of the specific results realized. I fear that the viewpoint I have presented on the dynamics of natural vegetation may be misunderstood as support for disregarding ecological considerations. This is not intended, but instead, is meant to underscore the importance of relating theory and facts. Dr. Frank Egler (1984), a respected critic of contemporary plant ecology and a nemesis of traditional climax–successional theory, in speaking out for the Idea, and great value, of Natural Areas (i.e. areas of various sizes kept as free as possible from human influence) includes some salient comments in relation to vegetation dynamics and how man fits into the picture:

> '... I add a few comments about an Idea which has been understandably underplayed in Europe and Mediterranea, where man has man-handled the entire landscape for at least ten millenia; and underplayed in the Americas, where the pre-European Indian-influenced landscape has always been considered to be 'pristine,' 'virgin,' or 'climax.' It is also underconceived by those who consider the landscape of our hunter-gatherer ancestors of a million years ago to be 'natural'. (A hungry hunter-gatherer, territorially limited, will eat the last bulb or the last

> live meat, even as a hungry sailor ate the last dodo, all blissfully unaware of Rare and Endangered Species.) And the idea is underconceived by the present fashionableness of the preservationists, despite the extraordinary worthiness of all their accomplishments to date. They have preserved, too often with no interest in further knowledge of the changing nature of what they have preserved, at the highest level of holistic integration of that Nature.' ...
>
> 'A Natural Area, be it one hectare or a million hectares, is thus a control, a standard, a common denominator, essentially a non-human area, which by comparison with all managed areas, urban, farm, forest, and range, allows us to judge and separate the role of man himself in the man-and-his-total-environment ecosystem. It is not to be supposed that a Natural Area can be entirely free of the influence of man. Air pollution and winds, water pollution and aquifers and streams, and all the past influences of man leave their fingerprints and their footprints. But without Natural Areas, used by man, we have no logical grounds for evaluating the influence of man. Nor should we emotionally assume that Natural Areas are always bigger, better, finer, more Edenesque, and more ideal than what man has done. Man-less nature never did produce the ethics, the esthetics and the logic of a civilization.'

The above quote is not intended to shift our emphasis from vegetation dynamics to an augment for natural areas but to demonstrate that even in the ecology conservation enterprise of establishing natural areas the reality of vegetation interplay needs to be recognized. The impact of man has continued to increase through time. He now ranks as a primary force in shaping the environments of the globe and should be recognized in that context (Naveh and Lieberman 1984).

We must now be bold enough to accept the challenge of shaping and synthesizing new ecosystems even in the 'natural' environment. We can improve on nature with the guidance of what we can learn, or have learned, from Natural Areas. Biological control is one of the tools that needs to be employed. The structuring and restructuring of ecosystems will involve the visualization of appropriate arrangements of functional processes in time and space. Suites of plant species exhibiting the needed physiognomical, phenological, physiological, and phytosociological characteristics would need to be mixed with the appropriate microbes, invertebrates and higher animals. This is not an easy task, especially in light of present traditions and practices. An important step in this direction can be taken through more careful utilization of current information and theory on the dynamics of today's natural vegetation. Whether a correct single, simple theory on vegetation dynamics will be developed or not is open to question. What is clear is that many of the ideas associated with the species-constant climax concept are incorrect. The popular perception of balance in nature is a damnable heresy that persists in most fields of applied ecology and resource management to the detriment of establishing realistic goals and guides. It has been and is the basis for the formulation of much environmental policy and law, as can be attested to by many charged with meeting mitigation stipulations specified for environmental impact statements and/or regulations for inventorying natural biological resources. This socio-political involvement tends to make the task ahead more difficult but also more challenging.

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