

BIODIVERSITY OF AUSTRALIAN DESERT LIZARDS

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ABSTRACT

At both local and regional scales, the Australian deserts house by far the most diverse lizard assemblages in the world. More than a dozen different factors contribute to this high diversity; one of the most important is the high frequency of natural wildfires, which generate a patchwork of habitats in different states of recovery, each of which favors a different subset of lizard species. The inland Australian desert is one of the last remaining places where natural wildfires are a regular and dominant feature of an extensive landscape largely undisturbed by humans. In this region, the fire succession cycle generates spatial and temporal heterogeneity in microhabitats and habitats. Habitat-specialized species can become locally extinct, but persist in the overall system by periodic reinvasions from adjacent or nearby patches of suitable habitat (fire scar) in a different stage of recovery. Such regional processes facilitate local diversity. This system is currently being studied at the local level in the field in Western Australia and at the regional level at the University of Texas at Austin using aerial photography and multispectral satellite imagery. Satellite imagery offers a powerful new way, heretofore underutilized by biologists, to acquire regional-level data on the frequency and phenomenology of wild fires, and thus the system-wide spatial-temporal pattern of disturbance. Several different approaches to modeling fire succession are outlined.

Key Words: Australia; Biodiversity; Desert lizards; Fire succession.

Introduction

The Australian deserts house the most diverse lizard assemblages on earth. No where else do so many different kinds of lizards live together — at least 47 different species occur at a sandridge site in the Great Victoria desert. The “thorny devil” *Moloch horridus* and the gigantic perentie *Varanus giganteus* are familiar forms, but there are also a dozen species of exquisitely beautiful nocturnal geckos and another dozen-plus of wary and secretive skinks, as well as many other species, including snake-like flap-footed legless pygopodid lizards.

Why are the Australian deserts so rich in lizard species? The challenge of explaining this high diversity, and of understanding what goes on between and among component species, is awesome.

Compared to Australia, North American deserts are impoverished, with a mere dozen different species of lizards. In the Kalahari semi-desert of southern Africa, only 20 species occur. How do so many lizard species avoid competition and manage to coexist in the Australian desert? How do they partition resources such as food and microhabitats? What historical and ecological factors have led to the evolution and maintenance of such high biodiversity? Ecologists still know surprisingly little about exactly how diverse natural ecological systems function—such ecological understanding is much needed and will obviously be critical to our own survival and that of other species of plants and animals. In fact, the Australian deserts may well offer the last opportunity to study the regional effects of disturbance on local diversity.

In the Great Victoria desert, sands are rich in iron, usually a delicate pale rusty-red, almost flesh colored. Long undulating sandridges provide attractive curves to create a sensuous image of mother Earth. Equally curvaceous, evergreen Marble gum trees (*Eucalyptus gongylocarpa*) with their smooth white bark adorn this splendid landscape. The dominant ground cover is porcupine grass or spinifex (*Triodia basedowi*), a perennial grass that grows in hummocks or tussocks, a plant growth form found only in Australia. Rain is infrequent and blue skies prevail most of the time. Taken together, the Great Victoria desert is a clean, spectacular, and most enchanting place, an extensive wilderness area of government-owned Crown land containing largely pristine habitats, still relatively undisturbed by human activities aside from the introduction of exotics, which include camels, cats, foxes, and of course, European rabbits.

Resource Partitioning

Lizards divide up environmental resources in three major ways: by being active at different times, by spending time in different places, and by eating different foods. Such ecological differences reduce competition, hence facilitating coexistence. Many lizard species are food generalists, eating a wide variety of arthropods. However, some other species of lizards are dietary specialists, with certain species eating only ants, others termites, and still others almost nothing except other lizards. One species, *Pygopus nigriceps*, preys heavily on scorpions. Lizards differ in their choice of microhabitats: some climb, others are terrestrial, while still others are fossorial, swimming through the sand. Some species frequent the open spaces between spinifex tussocks, whereas others seldom leave the protective cover of spinifex.

Considerable fidelity in microhabitat utilization is evident among various species of lizards. Many species separate out on fifteen very crude microhabitat categories (Pianka, 1973, 1975, 1986): for example, some species frequent open spaces between plants, to the virtual exclusion of other microhabitats, whereas other species stay much closer to cover.

Desert lizards vary widely in their modes of thermoregulation. Regulation is never perfect, but there is a continuum between the two extremes of perfect conformity and perfect regulation. Because thermoregulation clearly has costs and risks as well as profits, an emerging conceptual framework envisions an optimal level of regulation that depends on the precise form of the constraints and inter-

actions among costs and benefits arising from a particular ecological situation (Huey and Slatkin, 1976). In an analysis of the costs and benefits of lizard thermoregulatory strategies, Huey and Slatkin (1976) identified the slope of the regression of body temperature against ambient environmental temperature as a useful inverse measure of the degree of passivity in regulation of body temperature. On such a plot of active body temperature versus ambient temperature, a slope of zero reflects one extreme (perfect thermoregulation), whereas a slope of one indicates the other extreme of true poikilothermy or totally passive thermoconformity (air temperature and body temperature are perfectly correlated).

Some lizard species, particularly nocturnal ones such as most geckos, exhibit relatively passive "thermoconformity," with their body temperatures mirroring ambient thermal conditions. Other species, particularly active diurnal heliotherms, control their body temperatures with considerable precision by behavioral means. Various species can be placed on a unidimensional, linear, thermoregulation continuum (Pianka, 1985, 1986). The remarkably good fit to a transcendent straight line does not seem to be a statistical artifact, but rather reflects an innate physiological design constraint on the vertebrate body plan. Positions of different species along this thermoregulatory spectrum reflect a great deal about their complex activities in both space and time, and are correlated with patterns of microhabitat utilization (Pianka, 1986). This thermoregulation axis can also be exploited as a convenient unidimensional surrogate to represent multidimensional spatial and temporal niche dimensions (Pianka, 1993).

Considerable consistency in diet is also evident among lizard species. For example, some species eat virtually nothing but termites, whereas others never touch them. Moreover, diets of many species change little in space or time. Indeed, using just twenty very crude prey categories allows reasonably clean separation of many pairs of lizard species on the basis of foods eaten (Pianka, 1986). When prey items are analyzed by either numbers or size, separation is substantially less than when the proportional representation of each food category by volume is used.

Only a relatively few foods dominate the diets of these lizards. Prey resource spectra are broadly similar between continents (Pianka, 1986), although some notable quantitative differences are evident. Beetles, termites, and insect larvae dominate in the diets of North American lizards, whereas termites, beetles, and ants form the bulk of the diet of Kalahari lizards. In Australia, the five most important food categories, in decreasing order of volumetric importance, are: vertebrates, termites, ants, grasshoppers plus crickets, and beetles. Three prey categories, termites, beetles, and ants, constitute major foods in all three continental desert-lizard systems. Termites assume a disproportionate role in the Kalahari, as do vertebrate prey in Australia (this is largely a reflection of the diets of saurophagous varanid lizards). Somewhat surprisingly, the overall diversity of foods consumed by all species of lizards is actually greatest in the least diverse North American saurofauna, lowest in the Kalahari lizards, and intermediate in Australia (Pianka, 1986). Estimates of prey diversity for different study areas correlate with various measures of the variability in average annual precipitation, and presumably, primary productivity (Pianka, 1986).

The impact of prey taxa on the composition of saurofaunas is illustrated by the conspicuous and diverse termite fauna of southern Africa, which has apparently facilitated the evolution of termite-specialized species of skinks, lacertids, and geckos. Indeed, termites comprise a full 41% by volume

of the diet of Kalahari lizards, but only about 16% of the overall diet of the entire saurofauna in western North America and only about 18.5% of the diet of Western Australian lizards (Pianka, 1986).

Niche breadths, for both diets and microhabitats, are not correlated with sample size, indicating that samples are adequate to characterize patterns of resource utilization among species. Frequency distributions of niche breadths for diet and microhabitat demonstrate a spectrum from specialists to generalists (Figure 1). Intercontinental variation in niche breadth is slight and seldom statistically significant. Food-specialized species tend to exhibit narrow microhabitat niche breadths.

Numbers of species with different modes of life differ among sites within continents and between continental systems. More than twice as many species of diurnal ground-dwelling lizards occur on a typical Australian site than on an average site in the North American and Kalahari deserts; however, when expressed as a percentage of the total lizard fauna, diurnal ground-dwelling species constitute a full 74% of the North American saurofauna, compared with only 43% of the Kalahari lizard fauna and 51% of the lizard species on a typical Great Victoria desert site (Pianka, 1986). Intercontinental variation in the absolute number of species that forage by sitting and waiting for their prey is slight, but the absolute number of widely-foraging species increases rather markedly from North America to the Kalahari to Australia. When expressed as a percentage of the total lizard fauna, only about 16% to 18% are diurnal sit-and-wait foragers in the southern hemisphere deserts (an average of 2.4 species in the

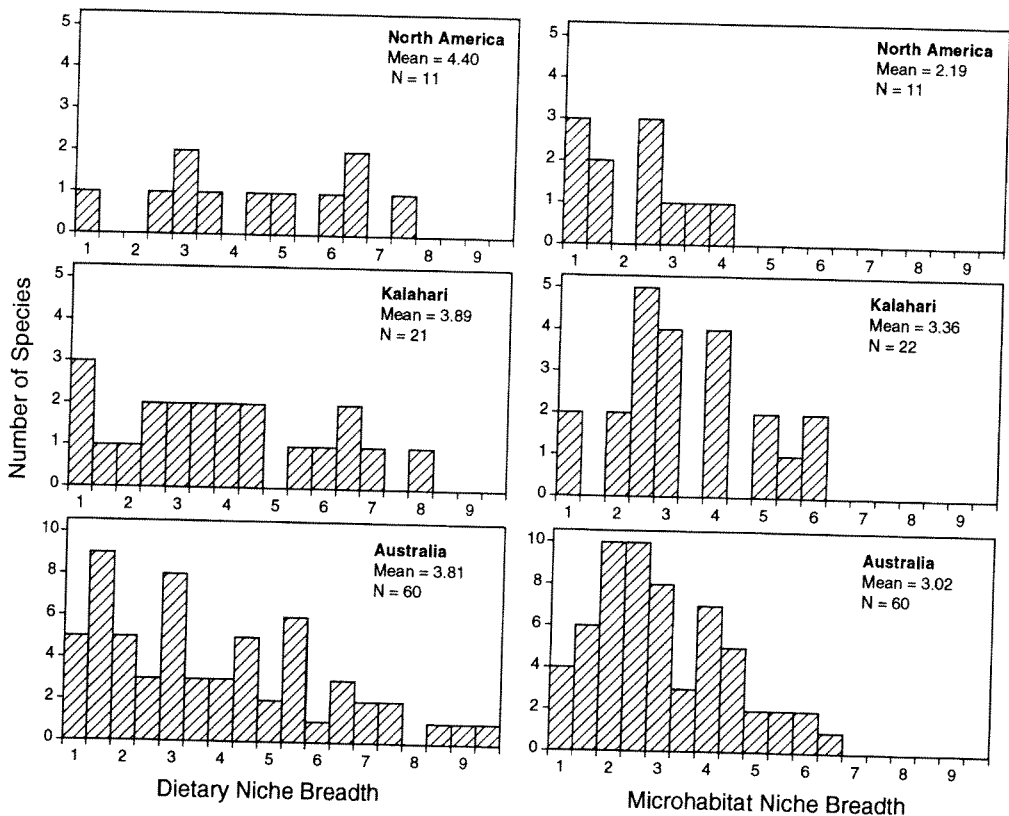


Figure 1. Dietary and microhabitat niche breadths for 11 species of North American desert lizards, 21 and 22 species of Kalahari lizards, plus 60 species of Australian lizards from the Great Victoria desert.

Kalahari and 5.3 species in Australia), whereas a full 60% of the North American lizards (average 4.4 species) fall into this category due to the low diversity of the latter desert-lizard system (Pianka, 1986).

The percentage contribution of all nocturnal species to the total fauna increases (i.e., diurnality declines) as the number of lizard species increases. Arboreal, subterranean, and nocturnal species are all conspicuously more prevalent in the two southern hemisphere deserts than they are in North America; subterranean lizards and arboreal nocturnal species are entirely missing from North American lizard faunas, yet contribute three or four species to an average site in the two southern hemisphere deserts. Numbers of species of arboreal lizards and their percentage contribution to total lizard faunas tend to increase with number of lizard species. Arboreal lizard species are, however, less well represented on structurally simple sites with low lizard diversity, even within the very diverse Australian lizard faunas.

Historical Factors

The heightened relative importance of nocturnality among lizards in the Kalahari and Great Victoria deserts could be a consequence of any or all of at least three different historical factors: 1) In North America, other taxa such as spiders could fill the ecological role of arboreal nocturnal lizards. Differences in species numbers and/or densities of insectivorous and carnivorous snakes, birds, and mammals might also play a crucial role. 2) Various desert systems could differ in diversity and abundance of available resources at night, such as nocturnal insects. 3) Effects of the Pleistocene glaciations are generally acknowledged to have been stronger in the northern hemisphere, and must certainly have influenced the evolution of nocturnal lizards. However, in at least the southernmost parts of the Sonoran desert of North America, present-day climates are easily adequate for nocturnal lizards. The eublepharine gecko *Coleonyx* thrives as a nocturnal terrestrial lizard in the Sonoran and Mojave deserts, occurring as far north as latitude 37 degrees (some geckos reach comparable southern latitudes in Australia). As expressed so forcefully by G. E. Hutchinson (1959) in a slightly different context, "if one . . . species can" (exist in the nocturnal terrestrial niche), "why can't more?"

The absence of a climbing gecko in the flatland deserts in the southern Sonoran desert is puzzling, particularly since the rock-dwelling climbing gekkonid *Phyllodactylus xanti* occurs nearby. A tree or shrub-climbing gecko species might well be able to invade this desert region if given an opportunity. Without such an introduction, either accidental or deliberate, such interpretations must unfortunately remain speculative.

Various historical factors, such as degree of isolation and presence of available biotic stocks (particularly those of potential prey, predators, and competitors) have clearly shaped these lizard faunas as well. There is a paucity of geckos in the New World (Duellman and Pianka, 1990). Certain ecological roles occupied by non-lizard taxa in North America and the Kalahari have been usurped by Australian desert lizards. Thus, Australian pygopodid and varanid lizards clearly replace certain snakes and mammalian carnivores, impoverished taxa in Australia. The number of species in various vertebrate taxa found on study sites were summarized by Pianka (1986). More species of snakes occur on sites in the

North American deserts than on other continents, although species richness of Australian “snakes” becomes similar when adjusted by addition of legless snake-like pygopodid lizards to the real snakes. Just as pygopodids appear to replace snakes, varanid lizards in Australia are clearly ecological equivalents of carnivorous mammals such as the kit fox and coyote in North America. Mammal-like and snake-like lizards contribute from one to eight (usually only four) species to various Australian study sites and thus represent a relatively minor component of the overall increase in numbers of lizard species on that continent. Nonetheless, such usurpation of the ecological roles of other taxa has clearly expanded the variety of resources (or “overall niche space”) exploited by Australian desert lizards.

The impact of history on these desert-lizard systems has clearly been profound, but it is overly facile, even glib, to assert that the Australian deserts have a greater diversity than other deserts simply by virtue of their antiquity. The Namib desert in southwestern Africa is even more ancient and supports an extremely rich beetle fauna, but supports only a moderate diversity of lizards. Clearly, ecological factors promoting coexistence, such as resource diversity and climatic predictability, are of vital importance.

Numerous more elusive interactions between taxa doubtlessly occur. For instance, one reason that the Australian deserts support such rich lizard faunas could involve reduced predation pressures from snakes, raptors, and/or carnivorous mammals on that isolated continent (many Australian lizards, both varanids and pygopodids, do, however, prey upon other lizards). Similarly, the higher incidence of arboreal and nocturnal lizard species in the Kalahari and Australia compared to North America could well be related to fundamental differences in the niches occupied by other members of these communities, including potential competitors among arthropods, snakes, birds, and/or mammals.

Vegetation Structure

The physical structure of the vegetation exerts a profound influence on the composition of lizard faunas. In North America, sites with greater spatial heterogeneity of vegetation support more species than do sites with simpler vegetation (Pianka, 1967). The mere existence of the unique hummock grass plant life form in Australia is a major factor contributing to the high lizard diversity on that continent (Pianka, 1969). Two pure “spinifex” (*Triodia*) grass flat study sites support 20 and 27 species of lizards, including 7-8 species of *Ctenotus* skinks. These grass tussocks are extraordinarily well-suited for lizard inhabitants, providing protection from predators and the elements, as well as an insect food supply. Certain lizard species appear to spend almost their entire lives within dense *Triodia* clumps, whereas other lizards exploit their edges. Still other species forage in the open spaces between tussocks, but rely on spinifex clumps for escape cover in emergencies. The latter species tend to have longer hind legs than the former and are faster runners - a trade off exists, however, since long-legged open-dwelling species move clumsily through dense vegetation, whereas short-legged species literally “swim” through it with ease.

Lizard faunas of shrub desert sites on each of the three continents were compared by Pianka (1986). The structure of the vegetation, consisting of low microphyllous chenopod shrubs, is virtually identi-

cal on these three sites, which were chosen to control vegetative structural complexity (plants of the ancient globally-distributed Gondwanaland genus *Atriplex* occur on all three areas).

The Kalahari shrub site supports 13 lizard species, whereas an Australian shrubby area in a dry lakebed sustains a full 18 species. Major differences between continents are traceable to non-lizard-like lizards and to nocturnal species. Four gecko species are nocturnal in the Kalahari, while eight species of geckos and skinks are active at night on the Australian site (only one nocturnal lizard species occurs on southern North American sites). Tiny, insect-like species (*Mabuya variegata* and *Menetia greyi*), a mammal-like lizard (*Varanus gouldi*), and a “worm-like” subterranean skink (*Lerista muelleri*) further expand the species lists in the southern hemisphere. Numbers of species of truly lizard-like lizards that are both diurnal and terrestrial (or semi-arboreal) are much more comparable among the three continents: North America (5 species, with a sixth species added in the south), Kalahari (8 species), and Australia (7 species).

Organisms that fill similar ecological niches in different, independently-evolved, biotas are termed “ecological equivalents” (Grinnell, 1924). Some such convergent evolutionary responses of lizards to the desert environment, although imperfect, are evident among continents Pianka (1985). For example, Australian and North American deserts both support a cryptically-colored and thornily-armored ant-specialized species: the agamine *Moloch horridus* exploits this ecological role in Australia, while its counterpart, the iguanian *Phrynosoma platyrhinos*, occupies it in North America. No Kalahari lizard has adopted such a life style. Interestingly enough, a morphometric analysis demonstrates that *Moloch* and *Phrynosoma* are actually anatomically closer to one another than either species is to other members of their own lizard faunas (Figure 2). North America and Australia also have long-legged species that frequent the open spaces between plants: *Ctenophorus scutulatus*, *C. cristatus*, and *C. isolepis* in Australia; *Callisaurus draconoides* in North America. These two continents also each support a medium-sized lizard-eating lizard (*Varanus eremius* in Australia and *Crotaphytus wislizeni* in North America). Active, widely-foraging lizards occur in all three deserts: teiids (*Cnemidophorus*) in North America, skinks (*Ctenotus*) in Australia, and lacertids (*Eremias*, *Heliobolus*, *Nucras*, and *Pedioplanis*) in the Kalahari. A few Kalahari-Australia species pairs are also crudely convergent: for example, the subterranean skinks *Typhlosaurus* and *Lerista* are roughly similar in their anatomy and ecology, as are the semi-arboreal agamine lizards *Agama hispida* and *Pogona minor*. The Australian knob-tailed geckos (genus *Nephrurus*) could be considered to be crude counterparts of the large terrestrial Kalahari gecko *Chondrodactylus angulifer*.

Although pairs of approximate ecological equivalents can thus be identified based on similar patterns of resource utilization, relatively few convergences among the faunas of all three continents are apparent. Ecologies of putatively convergent species pairs inevitably differ when scrutinized closely. In fact, the differences in the ecologies of most lizard species among the three continental desert-lizard systems are much more striking than are the similarities. It is easy to make too much out of convergence, and one must always be wary of imposing it upon the system under consideration.

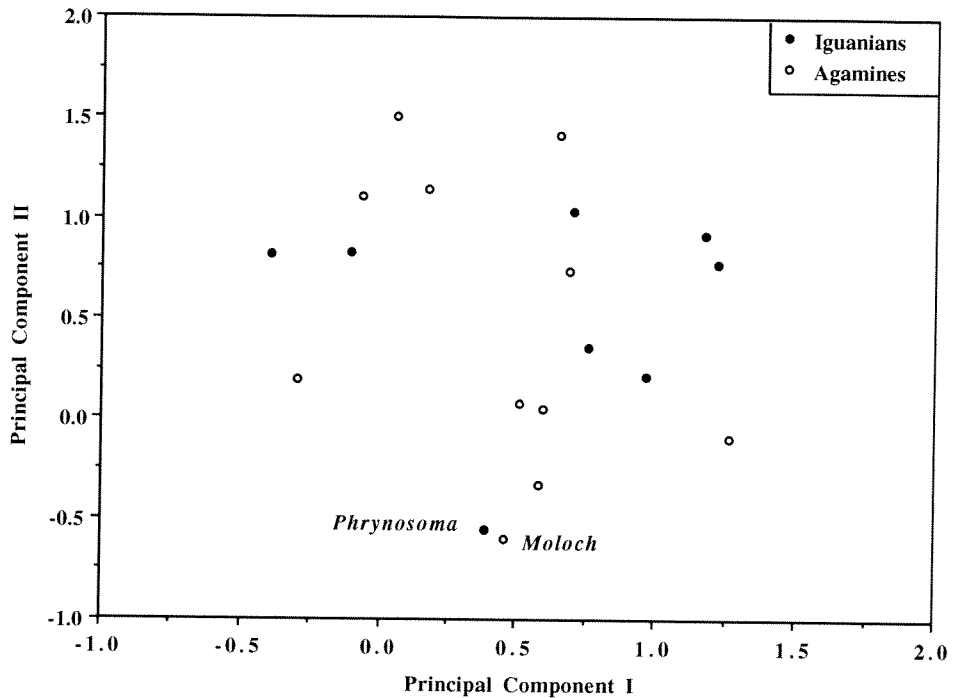


Figure 2. Plot showing scores on the first two principal components of a ten-dimensional morphometric space for eight sympatric North American iguanian lizards and eleven Australian agamine lizards. The North American desert horned lizard *Phrynosoma platyrhinos* is closer to the Australian agamine, the “thorny devil” *Moloch horridus*, than it is to any other sympatric iguanian. Likewise, *Moloch* is closer to *Phrynosoma* than it is to other agamines, indicating that these two species have undergone convergent evolution and are ecological equivalents.

Factors Influencing Lizard Diversity

In sum, at least a dozen different factors contribute to the exceedingly high diversity of lizards in arid Australia. These include 1) unpredictable rainfall, 2) nutrient poor soils, 3) the unique hummock life form and physical structure of spinifex grasses, 4) the low nutrient content of spinifex, 5) abundant and diverse termite faunas, 6) nocturnality, 7) fossoriality (sand swimming), 8) arboreality, 9) habitat specificity, 10) usurpation of ecological roles occupied by other taxa elsewhere, 11) biogeographic and historical factors, and 12) a complex fire succession cycle that creates and maintains habitat variety via disturbance (*see next section*). Morton and James (1988) put most of these mechanisms together in a mega-hypothesis (*see also* Pianka, 1989). Figure 3 summarizes their proposed causal network, with some of my own additions. Unpredictable precipitation, nutrient-poor soils, and wildfires are the driving physical variables. Primary productivity is scant and erratic, favoring spinifex grasses that are poor in nitrogen and relatively unusable fodder for most herbivores except termites, which in turn constitute a particularly suitable food resource for ectothermic lizards. Moreover, aperiodic heavy rainfall promotes woody vegetation (*Acacia* shrubs, mulga and marble gum trees), therefore supporting arboreal and litter-dwelling species of lizards. Although fire and fire-induced spatial heterogeneity were not included in their scheme, they are easily added (Pianka, 1992).

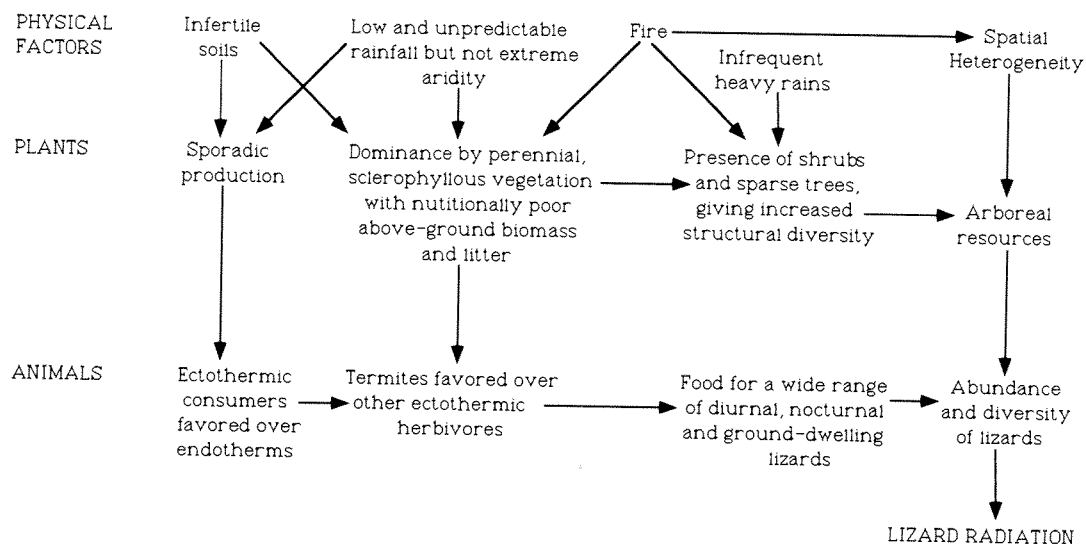


Figure 3. Morton and James' (1988) megahypothesis explaining the high lizard diversity in arid Australia (with modifications as suggested by Pianka [1989]).

Fire Succession Cycle

Satellite imagery offers scientists a powerful tool for studying a wide variety of large-scale phenomena, ranging from geology to oceanography to meteorology. Unfortunately, this potent new methodology comes a bit too late for large-scale biology since extensive areas remaining undisturbed by human activities are few. In some regions of the world, such as chaparral, the North American tall grass prairies, African savannas, and Australian bush, natural wild fires were once so frequent as to be a regular and dominant feature of the landscape before human control. Inland desert areas of Australia constitute one of the last remaining areas where natural wild fires are still allowed to burn themselves out, hence offering a final opportunity for study. Excellent imagery is the rule, greatly facilitating analyses, because cloud cover is low or non-existent most of the time. The sizes and geometry of fires can be readily measured and fire scars can be traced through time. In such a large natural region, habitat patches at different stages of post-fire recovery can reach a dynamic quasi-equilibrium, with new burns continually arising via the "death" of more combustible and more vulnerable older stages of succession. A two dimensional frequency distribution of the states and sizes of fire scars can be estimated and examined to see if it approximates a stationary distribution. Reflectance properties recorded from space allow inference of the present state of habitats and biotas on the ground, as well as the climate during the immediate past. The extent to which temporal changes in multispectral reflectance patterns at a given site can be extrapolated to geographic patterns in space still needs to be ascertained by careful field work. Although a great deal more remains to be known, monitoring habitats and biotic diversity from satellites could ultimately prove to be possible, at least in arid regions.

Spatial scale has been neglected in traditional ecology, although not in the emerging field of landscape ecology. Quantitative methods have recently been exploited to study the influence of landscape on ecology. In the past, ecologists, including myself, have focused on local-level processes. Larger scale regional factors also exert powerful influences on local phenomena (Ricklefs, 1987, 1989; Ricklefs and Schluter, 1993). Relatively little empirical attention has been given to the interaction between these two levels. Unfortunately, few areas, unfragmented by human activities, remain where regional and local phenomena can still be studied simultaneously. I am undertaking such a study in the uninhabited Great Victoria desert of Australia, an area with an extremely high lizard diversity.

Do independently-evolved ecological systems converge? Convergences suggest that generalizations are possible (Orians and Paine, 1983; Orians and Solbrig, 1977). Lack of convergence arising from historical differences is equally intriguing, but more difficult to study and understand. Criteria for studies of convergence, as well as existing studies of it, were reviewed by Schoener (1988) and Schluter and Ricklefs (1993), who noted that about half the studies failed to demonstrate convergence. Intercontinental comparisons of desert lizard assemblages have elucidated a challenging unsolved problem: the phenomenally high diversity of lizards in arid Australia. Understanding the impact of regional processes of disturbance on local diversity should help to resolve intercontinental differences in diversity.

Community ecologists have slowly but surely come to recognize disturbance as a critical cornerstone controlling biotic diversity, largely as a result of experimental studies in the space-limited, rocky, marine intertidal zone. Models have been developed that relate local disturbance to spatial heterogeneity and diversity. Intertidal marine ecologists have focused on wave action. Floods, hurricanes, and fires are terrestrial analogues. Biotic disturbances are important, particularly so-called "keystone" predators, and phenomena such as epiphyte load. The idea that intermediate levels of disturbance result in highest diversity has become known as the "intermediate disturbance hypothesis" (Levin and Paine, 1974; Menge and Sutherland, 1976). More generally, the precise temporal pattern, or "phasing", of disturbance has been suggested as a major determinant of species diversity (Abugov, 1982). These hypotheses can be tested using quantitative information on precise temporal patterns of disturbance obtained from satellite images, the "macrographs" of community ecology.

Fires are a particularly tractable agent of disturbance. They are readily quantified and lend themselves to tidy mathematical analysis. Their timing, shape, and extent are readily obtained from aerial photographs and satellite images. Excellent imagery is commonly obtained in arid regions because cloud cover is usually low. In the near-infrared ash is highly absorptive, whereas unburned vegetation is very reflective. Even after rains or wind wash or blow away ash, reflectance properties of burned and unburned areas differ markedly, allowing sharp delineation of fire boundaries. Fires are easily detected and delineated by simply subtracting reflectance values of one scene from those of another registered scene recorded one year earlier or later.

I have surveyed the lizard fauna at a site located about 38 km east of Laverton, Western Australia three times over the last 25 years, once in 1966-68, again in 1978-79, and most recently during 1989-1991. This study area (the L-area) supports 37 different species of lizards. I have studied the lizard fauna of another site, Red Sands, located about 100 km ENE of the L-area, for 15 years.

Spinifex Grasslands in Arid Australia

Spinifex tussocks are perfectly designed for combustion, consisting of hemispherical clumps of numerous match-stick sized blades of dry curled grass filled with flammable resins, loosely interpenetrating one another and laced with ample air spaces. Spinifex is an "ideal pyrophyte," nearly optimal tinder (Burrows et al., 1991; Pyne, 1991). Spinifex grasses give off dark smoke which can be seen from afar. Most early explorers and historians of Australia commented on the extent to which the aborigines exploited fire. Australian aborigines used fire to send long distance smoke signals, to manage habitats and keep terrain open, as well as to facilitate capture of various animals for food. Some think that the extensive grasslands in Australia were formed and maintained by regular aboriginal burning and that over many thousands of years aborigines acted to select members of plant communities for resistance to fire or for an ability to come back quickly following a fire.

As indicated above, the hummock grass plant life form is unique to Australia and is exceedingly flammable. Deserts in other regions, such as the Sonoran desert of North America, do not usually accumulate enough combustible material to carry fires. However, fires do occur regularly in the Kalahari semi-desert of southern Africa, an open savanna woodland. Fires are a predictable event in arid Australia, particularly in spinifex grasslands. Bush fires are usually started by lightning, raging completely out of control for weeks on end across many square kilometers of desert. Thunderstorms and lightning are regular during summer. Lightning-induced fires are most frequent during the months of November and December (Ralph, 1984). Over the 35 year period from 1950 through 1984, approximately 60% of natural wildfires in the Northern Territory were estimated to have been caused by lightning (Griffin et al., 1983, 1988). During that same period of time, Australian aborigines moved out of the bush, reducing the numbers of fires started by humans. Recently, aborigines are increasingly moving back to reside on their tribal lands, except that now aborigines seldom walk, preferring to ride in vehicles. They still set fires, but rarely very far from tracks and roads.

Winkworth (1967) suggested that all spinifex communities are in a state of cyclic development from fire to fire. He estimated that in the Northern Territory, only about 20% of some 150,000 square kilometers of spinifex habitat is in a "mature" climax state, with the other 80% either in regenerative stages following fires or in a degenerative state caused by drought. A single fire in this region covered about 10,000 square kilometers or about 7% of the total area of spinifex habitat. An even larger fire in 1982-83 burned 30,000 km², (about 20% of the spinifex habitat). Over the 35 year period from 1950 through 1984, there was an average of 143 fires per year in this region, most set by lightning (Griffin et al., 1988). With such an exceedingly high level of disturbance, one might expect a fairly rapid rate of recovery. Fire return intervals are short: some areas will carry another burn within 4-5 years. Burned plots converge on their original state quickly; in 7 years, dry weight production of spinifex totalled 823 kilograms per hectare, approximately one quarter of the standing crop of "mature" stands at a nearby site. Time required for a burned stand to reach maturity is a function of precipitation, probably often requiring as long as 20-25 years, sometimes even longer. The probability of a burn presumably increases with the time since the last burn.

Extensive analyses of spinifex fires in the Northern Territory have been undertaken recently by Griffin and his colleagues (Allan and Griffin, 1986; Griffin et al., 1983, 1988). Mapping every identifiable fire in the southern half of the Northern Territory between 1950 and 1984 (more than 5,000 fires in some 750,000 km²), these workers discovered certain informative relationships between fire patch dynamics and rainfall. At wetter, more productive areas, fires are not only more frequent but also patches are more variable in size and tend to be younger on average. Following periods of low rainfall, fires are both less frequent and homogeneously smaller. Fuel load recovery is a function of time and total rainfall: cumulative millimeters of precipitation is a useful temporal productivity metric against which to measure fires and vulnerability to fire. These authors estimate that approximately 63 cm of rain are necessary for a site to accumulate sufficient fuel to burn again under extreme summer conditions.

I have undertaken preliminary examination of the phenomenology of wild fires in the uninhabited western part of the Great Victoria desert in remote interior Western Australia over a period of more than a quarter of a century, using aerial photographs and satellite images to study and to quantify both the spatial pattern of burns and the dynamics of the recovery process. Data collated for each fire include: date, area, perimeter, compass direction (of burn and prevailing wind), as well as the extent of reticulation, which can be measured by perimeter/area ratio and/or fractal dimensionality (Milne, 1988; Sugihara and May, 1990). Over a period of just 25 years, some areas in the Great Victoria desert have burned three times. The average time between fires is about a decade. Few areas escape burning for much longer than 25-30 years, although some areas appear not to have burned for 40-50 years (N. Burrows, pers. comm.). In this part of the Great Victoria desert, prevailing surface winds blow from west to east during most months (Maher and McRae, 1964).

Fire Geometry

Bush fires generate a spatial mosaic of patches of habitat at various stages of post-fire succession (Recher, 1981). The geometry of burns is not only rich in detail, but also exceedingly varied. As a regular agent of disturbance, fires contribute substantially to maintaining a spatially heterogeneous patchwork of habitats, hence facilitating the biodiversity of Australian desert lizards (Pianka, 1986, 1989, and next section). Fires vary considerably in intensity and extent. *Eucalyptus* trees are fire resistant (Gardner, 1957), often surviving a hot but brief ground fire carried by the exceedingly combustible spinifex (*Triodia* and *Plectrachne*).

In grasslands, fires burn along two "fronts" that are essentially unidimensional, each at an approximate right angle to prevailing winds, and burning away from one another in opposite directions. The "backfire" burns slowly into the wind, whereas the much hotter "headfire" burns faster racing with the wind. Backfires typically die out more easily than headfires, leaving a single front. Airborne flaming materials, termed "firebrands," may jump over unburned areas to rekindle new fires on the downwind side of a fire, sometimes resulting in establishment of multiple fire fronts (these can extinguish one another when one runs into another's swath).

Fires frequently reticulate, missing an occasional isolated grass tussock or even large tracts embedded in or immediately adjacent to burns. Upon ignition, an isolated grass tussock generates an egg-shaped thermal field around it. At low wind velocities, isotherms for such fields are symmetric and close to the combustibles, but as wind speed increases, thermal fields become asymmetric and extend farther out, especially downwind (Figure 4). If other tussocks are within such a field's threshold temperature for ignition, they too are lighted and the fire spreads. Due to the geometry of the thermal fields, fires tend to burn along broad continuous fronts at low wind velocities, whereas at higher wind velocities, elongate narrow tongues of flame are produced. Fires are more likely to reticulate at higher wind velocities.

Previously burned areas have sparser vegetation and act as gigantic fire breaks. Sandridges and termitaria create smaller vegetationless areas that also act as local fire breaks, but with fundamentally different geometries and at very different spatial scales. "Sleepers", embers created from burning hard wood of *Eucalyptus*, lie dormant in burned areas; some of these hot coals at the edges re-ignite days or even weeks later when new strong winds come up. New secondary bush fires begin that take off at an angle to the immediately previous primary burn, resulting in an interesting reticulating pattern that generates a qualitatively and spatially different sort of refuge.

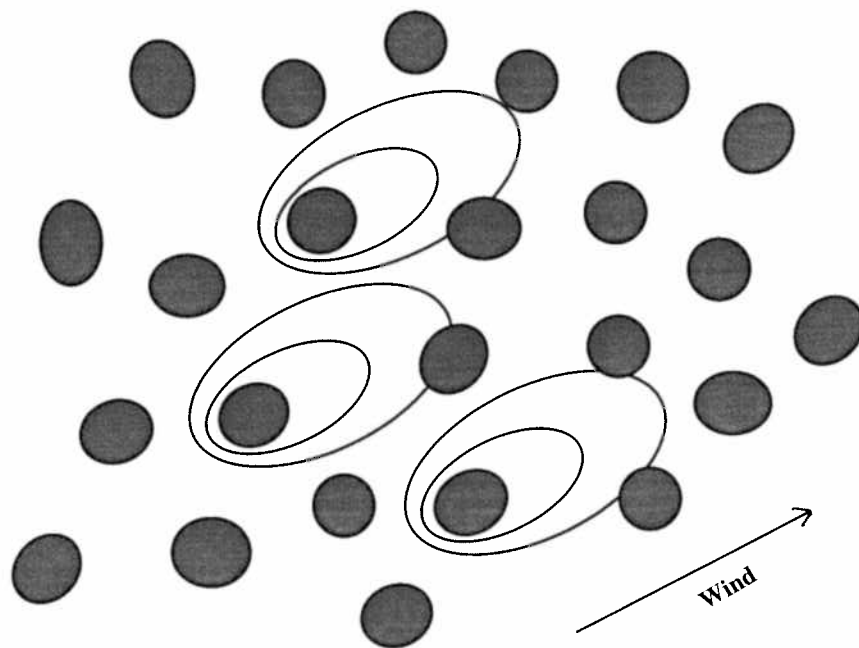


Figure 4. Grey ovals represent spinifex tussocks. Isotherms are shown for three burning tussocks at an intermediate wind speed. Burning tussocks are more likely to light other tussocks downwind than those to the side. At higher wind velocities, thermal fields are more elongate, resulting in long fire tongues.

Major factors that determine the frequency, extent and geometry of grassfires include temperature, combustibility, plant biomass and spatial distribution, natural firebreaks, and of course, winds, which as explained above, are of paramount importance. If the density of combustible material is high, fire fronts can burn virtually everything in their path, leaving behind an almost completely burned swath. However, if grass is green or wet and therefore less flammable and/or if tussocks are widely spaced and/or if winds are weak, a fire may falter and die out. Strong winds, by supplying oxygen, “feed” a fire making it burn both faster and hotter. With sufficient wind, even a relatively uncombustible area can burn, whereas with little or no wind, a fire may not “take” even in a fairly combustible situation. Headfires will burn even when backfires will not. Studies of thousands of forest fires have shown that the extent of such fires is directly proportional to wind velocity (Barrows, 1951), allowing area to be used as an after-the-fact indirect estimate of wind speed at the time of a burn.

The extent to which grassfires reticulate appears to vary among geographic regions with differences in vegetation structure. In the savanna woodland of the Kalahari semi-desert in Botswana, southern Africa, for example, fires are frequent but continuous, seldom reticulating (plate 342, page 377 in Short et al., 1976). Because Australian spinifex habitats are relatively more open and because they contain various sorts of natural firebreaks, fires reticulate more than they do in other, more homogeneous areas (the unique growth form and extreme flammability of spinifex doubtlessly contributes to fire reticulation in Australia). Intercontinental differences in winds could also be crucial in the generation of different fire geometries.

Biodiversity

Combined effects of these forces on animals and their microhabitats are drastic, yet exceedingly heterogeneous in space. Certain lizard species are arboreal and/or associated with trees. These are relatively unaffected by fire. Many or even most individual lizards sometimes survive such burns (Christensen et al., 1981; Longmore and Lee, 1981; Greer, pers. comm., as reported by Recher, 1981), although survivorship is doubtlessly reduced for some time afterwards (Newsome et al., 1975). Fires attract hawks and crows, which feed on fire-killed animals and take advantage of the lack of cover to catch survivors. Their ectothermy allows many lizards to become inactive and stay underground for a month or more until the vegetation and insect fauna recover.

Population densities of certain species of lizards, such as *Ctenophorus fordi* and *Ctenophorus isolepis*, are actually greater on recently burned areas (Caughley, 1985; Cogger, 1969, 1972; Griffin et al., 1988). Burrowing species are often more abundant on recently burned areas than they are on nearby unburned sites (Caughley, 1985; Fyfe, 1980). Many other desert lizard species, including *Ctenophorus inermis* and *Ctenotus calurus*, with open habitat requirements, presumably reinvade and/or repopulate burned areas rapidly, quickly reaching high densities in their “preferred” open habitat (such species usually persist at very low densities even in mature stands of dense closed in spinifex). Other lizard species, such as *Delma butleri*, *Omolepida branchiale*, and/or *Diplodactylus elderi* require large spinifex

tussocks for microhabitats, and nearly vanish over extensive open areas following a burn. However, such “climax” species can continue to exist in the isolated pockets and patches of habitat that escaped burning.

Following a fire caused by lightning, sands are frequently wetted by thundershowers, facilitating rapid regeneration of spinifex from live roots and by seedling establishment (Burbidge, 1943). Newly-burned areas are quite open with lots of bare ground and tiny, well-spaced, clumps of *Triodia*. Unburned patches, in contrast, are composed of large ancient tussocks, frequently quite close together with little open space between them. As time progresses, *Triodia* clumps grow, which simultaneously increases the amount of combustible material and reduces the gaps between tussocks, both increasing the probability that a fire will be carried.

Throughout this process, cover, microhabitats, and associated food resources change gradually along with reflectance properties. Through succession, the relative abundances of various animal species fluctuate along with such changes in available resources, with some common species becoming quite rare and vice versa. A particular species can go extinct within a given area, but by surviving in an adjacent patch of habitat, still survive in the region. Periodic dispersal from such “source” habitats and recolonization of other habitats allows such species to continue to persist in the overall landscape (Pulliam, 1988; Pulliam and Danielson, 1991). An appropriate mix of spatial patchiness coupled with disturbance and dispersal can promote coexistence in competitive systems (Kareiva, 1991; Levin and Paine, 1974).

For both lizards (Table 1) and birds (Pianka and Pianka, 1970), the species present on recently burned areas represent a subset of those present on more mature climax sites. As noted above, relative abundances fluctuate substantially through succession, with some common species becoming quite rare. Rare species do not always remain rare and may be vitally important to hold a system together (Main, 1982), allowing the system to respond to changing environmental conditions. The prey spectrum for a recently burned area differs from those of less recently burned areas with relatively fewer termites but comparatively more spiders (Pianka, 1989). Presumably, by destroying litter and spinifex, fires reduce cellulose availability, hence reducing food supplies for termites.

More than a dozen species of mid-sized marsupial mammals, including hare wallabies, have become extinct in the Australian interior during the past half century. Burbidge et al. (1988) discovered this only recently, by taking museum skins into the desert and interviewing older aborigines about their youth. Approximate dating was accomplished by recalling airplane traffic over Australia during the second world war. Aborigines not only remembered many species now extinct as being abundant during the 1940s, but were also able to provide localities. Theories about the causes of the disappearance of these mid-sized marsupials include competition with introduced rabbits and camels, predation by introduced feral cats and foxes, and the removal of aboriginal human populations, with a consequent reduced incidence of set fires. Australian authorities are eager to mimic aboriginal burning patterns to create a spatial mosaic of fire-disturbed habitat patches of differing ages and sizes (small burns act as fire breaks and prevent extensive burns which homogenize the landscape) (Minnich, 1983).

Table 1. Estimates of the relative abundances (percentages) of various species of lizards on a recently burned site (N-area), on the long-unburned B-area, and on the L-area.

	N-area	B-area	L-area
<i>Ctenophorus clayi</i>	–	0.41	–
<i>Ctenophorus inermis</i>	2.74	0.41	0.44
<i>Ctenophorus isolepis</i>	24.66	11.26	20.31
<i>Moloch horridus</i>	–	–	0.56
<i>Pogona minor</i>	–	0.69	0.59
<i>Varanus brevicauda</i>	–	2.20	–
<i>Varanus eremius</i>	1.37	2.20	0.64
<i>Varanus gouldi</i>	1.37	–	0.42
<i>Varanus tristis</i>	–	–	0.68
<i>Ctenotus ariadnae</i>	–	8.38	1.27
<i>Ctenotus calurus</i>	6.85	19.78	11.18
<i>Ctenotus grandis</i>	4.11	21.02	2.47
<i>Ctenotus greeri</i>	–	0.14	–
<i>Ctenotus helenae</i>	1.37	0.41	2.56
<i>Ctenotus leae</i>	–	0.14	–
<i>Ctenotus pantherinus</i>	2.74	10.17	1.81
<i>Ctenotus piankai</i>	6.85	10.85	1.29
<i>Ctenotus quattuordecimlineatus</i>	1.37	2.20	15.72
<i>Ctenotus schomburgkii</i>	–	0.14	3.20
<i>Egernia inornata</i>	8.22	0.14	0.17
<i>Egernia kintorei</i>	–	–	0.02
<i>Egernia striata</i>	5.48	2.06	4.57
<i>Lerista bipes</i>	–	0.55	5.37
<i>Lerista muelleri</i>	–	–	0.66
<i>Menetia greyi</i>	4.11	3.71	2.15
<i>Morethia butleri</i>	–	–	0.07
<i>Tiliqua multifasciata</i>	–	0.14	–
<i>Tiliqua occipitalis</i>	–	–	0.05
<i>Delma butleri</i>	–	0.96	0.27
<i>Delma nasuta</i>	–	0.14	0.02
<i>Lialis burtonis</i>	–	–	0.22
<i>Pygopus nigriceps</i>	–	–	0.37
<i>Diplodactylus conspicillatus</i>	–	0.14	2.32
<i>Diplodactylus damaeus</i>	–	0.28	–
<i>Diplodactylus elderi</i>	–	–	0.17
<i>Diplodactylus stenodactylus</i>	–	–	0.07
<i>Gehyra purpurascens</i>	–	–	10.57
<i>Gehyra variegata</i>	–	0.28	0.24
<i>Heteronotia binoei</i>	4.11	1.10	0.10
<i>Nephrurus laevissimus</i>	–	0.14	–
<i>Nephrurus levis</i>	10.96	–	1.66
<i>Rhynchoedura ornata</i>	13.70	0.14	4.18
Total number of lizards	73	729	4,092
Lizard Species diversity		8.5	7.7

Models of Fire Succession in Spinifex Habitats

Elements discussed above can be exploited to develop dynamic models of fire succession incorporating disturbance probabilities, flammabilities, fuel load recovery curves, and various fire break geometries and the resulting patchwork of habitats. The major challenge is to invent ways of incorporating important biological processes, such as species-specific habitat requirements and colonization and dispersal abilities, into models. Properly constructed models should generate testable predictions, such as frequency distributions of sizes and states of fire scars, and changing vectors of relative abundances of various animal species. Such models do not constitute an end in themselves, but rather primacy should be placed on the data that give models a quantitative basis. At least three very different types of models hold promise, although each has its own strengths and weaknesses. Each will be briefly outlined and considered in turn. Ultimately, these varying models will have to be amalgamated into a more realistic one that incorporates biological processes.

Projection matrices or markov chain models

In principle, this approach is quite simple and basically descriptive. The aim is not to simulate mechanics of disturbance, which are better left to process oriented models (next section), but to identify and describe spatial and temporal elements of heterogeneity. An ecosystem is categorized into a series of discrete states or cells. For example, any given state might represent the size of a spinifex tussock, combustibility, a given state of recovery (age, time since burned, or cumulative precipitation since last burn), some particular mixture of species, or even an entire study area. Any given unit cell of the landscape is wholly in one or another of these given states at any particular time. Each later stage in succession is related to earlier stages by some probability of transition. These probabilities are placed into a transition matrix, which describes probabilities that a cell in any given state will move to a new state during the next time step. The probability of transition of each cell is assumed to be independent of all other cells (Abugov, 1982; Horn, 1976).

In the Markov approach, the overall state of a large area (the landscape, or system) is represented by a vector giving the fraction of cells in each state at some time. The state of the system at any future time is readily computed in terms of the initial state and the matrix of transition probabilities. This approach has been used successfully by Horn (1976), Usher (1979), Noble and Slatyer (1981), Abugov (1982), Seagle and Shugart (1985), and others. If succession is unidirectional, all elements below the diagonal in the transition matrix are zero. With disturbances, some transition probabilities below the diagonal are positive, reflecting the likelihood that a cell in a given state will revert to an earlier state. Fires are typically all-or-none, taking the system back to state zero (bare sand), although some fraction of cells in the overall landscape will "escape" disturbance and persist as refuges.

Computer simulation models

The primary goal of this research is to understand the effects of fire on the biota. This can be accomplished without studying fire dynamics per se. While somewhat tangential to the present project, mechanisms of fire spread are of interest to the extent that they generate reticulation. A large two dimensional grid can be set up in a computer's memory with "grass tussocks," trees, and other combustibles distributed across the grid according to the spatial characteristics measured in aerial photography and satellite imagery. As time passes, spatially-autocorrelated rainfall patterns can be superimposed to mimic observed conditions so that "tussocks" are allowed to grow and become increasingly more vulnerable to carrying a fire. The exact rate of closure is not essential to develop a realistic model because the time axis can simply be expanded or compressed without qualitative change. Prevailing surface "winds" can also be simulated (again, wind velocity can be scaled without altering qualitative results). A series of local firebreaks, both aerial and linear as detected from maps, photographs, and imagery, can be superimposed on the grid. A computer generated "fire" can then be started and allowed to burn itself out. The geometries of such simulated "fires" can be compared with those of real fires.

It should also prove fruitful to make a detailed map of combustibles over a large real area using low level aerial photography both before and after a burn. Digital computer images can be "burned" on the computer, making a variety of assumptions about the shapes of thermal fields produced by burning tussocks as a function of various wind "velocities." Although the real ground cover in a given area can be burned only once, such a computer image can be "burned" as many times as required to develop a realistic model. The variety of fire geometries that can be generated for the same basic vegetation structure will be informative. Fire dynamics can also be studied on computers by allowing spinifex to grow and close in to see how burn geometry changes (denser stands will presumably burn more continuously than more open stands). A predictable theory of fire spread in spinifex grasslands seems within grasp. More elaborate computer simulation models of larger-scale regional phenomena, incorporating multi-disturbance patch dynamics with local extinctions and dispersals, will also be developed.

Analytic models using differential equations

As just one example, a simple analytic model of patch dynamics can be constructed based on the Von Foerster equation (Von Foerster, 1959; Sinko and Streifer, 1967; Levin and Paine, 1974; Oster and Takahashi, 1974). Let $\rho(a,s,t)$ be the density function for the frequency of patches of state a and size s at time t . For small Δa and Δs , the number of patches that fall in the state interval a to $a+\Delta a$ and with size between s and $s+\Delta s$ is given approximately by $\rho(a,s,t)\Delta a\Delta s$. The density function is assumed to be continuously differentiable.

Unlike patches in the intertidal, burns do not change in size as they recover unless a new burn partially destroys an older one. Hence $\partial\rho/\partial s$ is zero. Indeed, part of the beauty of this system is the fact

that patches do not grow or shrink, but stay the same size for many years. Since fire scars do not change in size, the governing equation for $\rho(a,s,t)$ is

$$\frac{\partial \rho}{\partial a} + \frac{\partial \rho}{\partial t} = -\rho c(a,s) \tag{1}$$

where $c(a,s)$ is the combustibility of a patch of state a and size s . Empirical considerations suggest that c is zero below a threshold value and that it increases monotonically with both a and s .

This equation can be solved if both the initial and boundary distributions can be specified. The initial distribution is $\rho(a,s,0)$, the frequencies of fire scars of various states and sizes at some particular early point in time (such as in 1972, when satellite images first became available). The boundary distribution, $\rho(0,s,t)$, represents the state-size specific birth rate of new patches, or the probability that fire disturbance will produce a patch of size s . New patches, $\rho(0,s,t)$, are generated according to a given input function,

$$\rho(0,s,t) = b(s) \tag{2}$$

where $b(s)$ represents the probability of a burn of size s , or the size distribution of newly-burned patches, a distribution readily estimated from imagery.

Since the total area of spinifex habitat must remain constant, creation of new patches of state zero must always occur by destruction of older patches (i.e., “births” arise from and equal the sum of all “deaths” of varying state and size classes). The total area burned (LHS) must be equal to the total area of newly formed patches (RHS):

$$\int_0^\infty \int_0^\infty \rho c(a,s) s da ds = \int_0^\infty b(s) s ds \tag{3}$$

To solve for the stationary distribution of ages of patches, $\rho(a,s)$, set $\partial \rho / \partial t$ equal to zero in equation (1):

$$\frac{\partial \rho}{\partial a} = -\rho c(a,s) \tag{4}$$

Integrating

$$\rho(a,s) = b(s) e^{-\int_0^a c(x,s) dx} \tag{5}$$

Such a stable state and size distribution of fire scars should be approximated provided that underlying burning parameters have not varied greatly over the time interval of interest. This model is, however, limited in that it does not incorporate fire geometry, which will require its own independent analysis.

Future Prospects

Field work has been undertaken to map vegetation structure, to determine which lizard species are present, and in what abundance, at three sites with old spinifex before burns. Low-level aerial photographs have been acquired and will be digitized, georeferenced, and analyzed to make detailed maps of vegetation structure for use in computer simulations of fire dynamics. Vertebrate faunas and arthropods, particularly foods eaten by lizards, will be compared at recently burned sites with those at various stages of post fire recovery to collect data for modelling various aspects of the dynamics of the fire succession cycle. The three mature spinifex sites will be monitored over the long-term after being burned under known wind conditions. Fire scars will be photographed and “burns” will be simulated on the computer to mimic observed fire geometry. Precipitation, rates of accumulation of combustibles, and the arthropod and vertebrate faunas of these study sites will be monitored roughly every other year, funding permitting, over the next decade to collect more precise data on the fire succession cycle.

Empirical study of lizard metapopulations in the Great Victoria desert is exceedingly difficult due to the long temporal and extensive spatial scales of this dynamic habitat mosaic and the infrequency of local extinction and dispersal-colonization events. Detailed analyses of satellite imagery should enable us to describe the actual spatial-temporal phasing of the fire succession cycle, which will then be used as a realistic habitat mosaic background in computer simulation studies of metapopulation dynamics. Given various degrees of extinction proneness, we plan to explore what reproductive capacities and dispersal abilities are required for various habitat specialists to persist in this ever-changing landscape. For example, one would predict that habitat specialists must have higher powers of dispersal than habitat generalists. Moreover, because of the dynamic habitat mosaic and local extinctions, populations will be below their respective carrying capacities to varying degrees that will depend upon their relative abilities to track their habitats. To what extent do such landscape dynamics impose particular biological properties on component species?

This report is on research still in progress. A major goal of this study is to obtain baseline data on temporal patterns, spatial structure, and distribution of disturbances. These data will form the backdrop for a more detailed study of the population dynamics and dispersal abilities of species. Animals with active habitat selection, such as Australian desert lizards, should reach ecological and evolutionarily stable equilibria between “source” and “sink” habitats, with dispersal from the former metapopulations to the latter maintaining the species locally. Such data on the component species will be fitted into the overall spatial-temporal patchwork mosaic in an effort to explain the persistence of this diverse desert fauna. Ultimately, I plan to model the entire Great Victoria desert region as a dynamic habitat mosaic to understand mechanisms of coexistence of its component species and the effects of fire disturbance in maintaining lizard biodiversity in this region. Faunas of unstudied sites will be predicted by extrapolation, thus allowing models to be subjected to direct test. It should also be feasible to exploit controlled burns to test some aspects of such fire succession models.

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