

# A Scaling Rule for Landscape Patches and How It Applies to Conserving Soil Resources in Savannas

John A. Ludwig,<sup>1\*</sup> John A. Wiens,<sup>2</sup> and David J. Tongway<sup>3</sup>

<sup>1</sup>*Tropical Savannas Cooperative Research Centre and CSIRO Wildlife and Ecology, PMB 44, Winnellie, Darwin, NT 0822, Australia;*

<sup>2</sup>*Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523, USA; and*

<sup>3</sup>*Tropical Savannas Cooperative Research Centre and CSIRO Wildlife and Ecology, GPO Box 284, Canberra, ACT 2601, Australia*

## ABSTRACT

Scaling issues are complex, yet understanding issues such as scale dependencies in ecological patterns and processes is usually critical if we are to make sense of ecological data and if we want to predict how land management options, for example, are constrained by scale. In this article, we develop the beginnings of a way to approach the complexity of scaling issues. Our approach is rooted in scaling functions, which integrate the scale dependency of patterns and processes in landscapes with the ways that organisms scale their responses to these patterns and processes. We propose that such functions may have sufficient generality that we can develop scaling rules—statements that link scale with consequences for certain phenomena in certain systems. As an example, we propose that in savanna ecosystems, there is a consistent relationship between the size of vegetation patches in the landscape and the degree to which critical resources, such as soil nutrients or water, become concentrated in these patches. In this case, the features of the scaling functions that underlie this rule have to do with physical processes, such as surface water flow and material redistribution, and the ways that patches of plants physically “capture”

such runoff and convert it into plant biomass, thereby concentrating resources and increasing patch size. To be operationally useful, such scaling rules must be expressed in ways that can generate predictions. We developed a scaling equation that can be used to evaluate the potential impacts of different disturbances on vegetation patches and on how soils and their nutrients are conserved within Australian savanna landscapes. We illustrate that for a 10-km<sup>2</sup> paddock, given an equivalent area of impact, the thinning of large tree islands potentially can cause a far greater loss of soil nitrogen (21 metric tons) than grazing out small grass clumps (2 metric tons). Although our example is hypothetical, we believe that addressing scaling problems by first conceptualizing scaling functions, then proposing scaling rules, and then deriving scaling equations is a useful approach. Scaling equations can be used in simulation models, or (as we have done) in simple hypothetical scenarios, to collapse the complexity of scaling issues into a manageable framework.

**Key words:** landscape ecology; land-use disturbances; resource conservation; resource patches; scaling equations; scaling functions; soil conservation; soil nitrogen.

Received 8 December 1998; accepted 17 August 1999.

\*Corresponding author; e-mail: john.ludwig@terc.csiro.au

## INTRODUCTION

Scaling issues are complex, yet they lie at the very heart of ecology. They are complex because of the vast array of scale dependencies and scaling thresholds that characterize the physical environment of landscapes and because of the diversity of ways in which the responses of organisms are scaled. They are at the heart of ecology because, ultimately, all ecological patterns and processes are sensitive to scale at some point and because our attempts to make sense of ecological data or to use our findings in management are constrained by scale.

Scaling issues are also ubiquitous in ecology and resource management. No matter which components of ecological systems are studied, which questions are asked, or which goals underlie management policies, the results depend on the time and space scales used. A documentation of the distribution and abundance of a particular species, for example, will reveal one pattern when viewed at a fine scale over a short time period, another when viewed broadly in time and space (Wiens and others 1985). Ecology, whether basic or applied, is a scale-dependent science.

Recognition of the importance of scale in ecology has grown dramatically in recent years (for example, Gardner and others 1989; O'Neill 1989; Wiens 1989; Holling 1992; Levin 1992; Schneider 1994; Pickett and others 1997; Gustafson 1998; Peterson and others 1998). However, this insight generally has not progressed much beyond the observation that the scale of investigation does make a difference. Scale often is viewed as a complex problem that constrains analysis and interpretation, rather than taking a view that scale-dependent "rules" are an inherent property of ecological systems, worthy of consideration in their own right. As Sale (1998) has observed, some ecologists "have begun to treat spatial scale as an object before which to genuflect rather than as an element in project design and analysis." Explicit incorporation of scale dependencies and scaling rules in management policies lags even farther behind.

Our aim in this article is to illustrate how consideration of a scaling rule can improve our understanding and management of scale-dependent processes in savanna landscapes. We approach this topic by first defining the "scaling problem" within the context of a conceptual framework involving landscape patterns and processes, and how scaling functions and rules relate these patterns to processes in space and over time. We then define a scaling rule for Australia's savannas, specifically how landscape patches of different sizes concentrate resources such

as soil nitrogen (N). A scaling equation for small patches in local landscapes then was derived from this scaling rule. This equation was used to illustrate how the scaling rule predicts the consequences of different landscape disturbances on soil N conservation in savannas.

Finally, this illustrative example was placed within a broader context of how well landscapes conserve vital resources—a continuum from highly functional "conserving" landscapes to highly dysfunctional "leaky" landscapes. We discuss the importance of maintaining patches when managing savanna landscapes. Our intent here is not to provide definitive scaling rules and equations for the conservation of resources in savannas—present data are too limited—but rather to provide a "proof of concept" for an approach that is based on a conceptual framework of scaling functions and how scaling rules and equations can be derived from this concept and applied to land management situations. Real world management applications require rigorously determined scaling equations, ideally embedded within simulation models to examine management strategies and tactics.

## THE SCALING PROBLEM—EXTRAPOLATION AND LANDSCAPE PATCHINESS

### Scaling—A Conceptual Framework

Scaling in ecology involves an interaction of three elements (Figure 1). First, there are scales at which landscape processes and patterns are expressed in the physical environment. For example, at fine, local landscape scales spatial patterns of soil moisture and nutrient concentrations affect activities of ants or termites, which in turn affect soil processes, such as water infiltration and litter breakdown rates (for example, Jones 1990; Eldridge 1993). At broad, regional scales, geological and hydrological processes dominate, producing different patterns of sediment deposition as one moves from the scale of hectares to catchment (Woodmansee 1990; Blöschl and Sivapalan 1995).

Second, organisms respond in a scale-dependent manner to this template of scale-dependent patterns and processes in the environment (Figure 1). Thus, species that differ in size, mobility, physiology, or life history may respond to the same physical setting not only in different ways but also at different scales (Addicott and others 1987; Kotliar and Wiens 1990; With 1994; With and Crist 1996). Beetles and ants occupying the same microlandscapes, for example, respond to landscape heterogeneity in different ways, and although different species of *Eleodes*

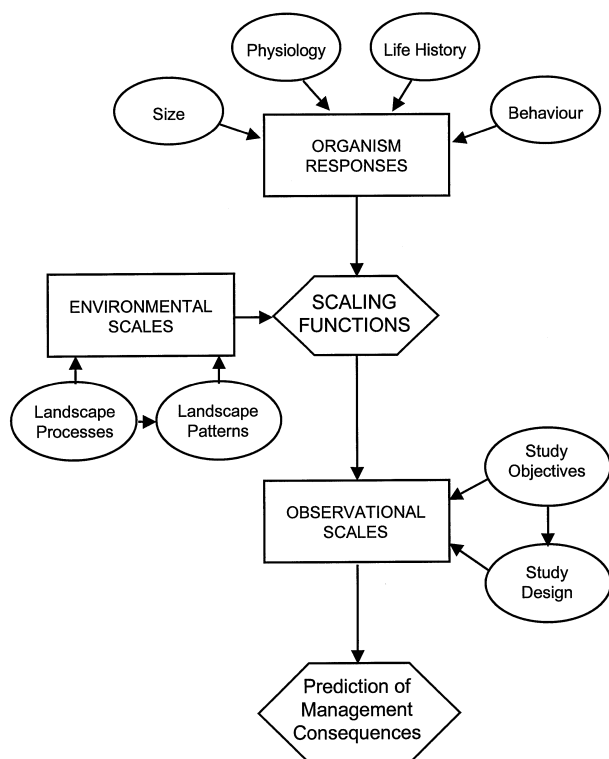


Figure 1. Key elements of scaling in ecology: (a) the environmental scales relating landscape patterns and processes, and (b) the scale-dependent responses of organisms. These elements are linked through scaling functions and the scale at which we observe this organism–environment system, which then allows one to predict consequences of different management actions on landscapes.

beetles may move in similar ways, they do so at different rates that correspond with size differences among the species (Wiens and others 1995). As a consequence, they may perceive the structure of the landscape at different scales (Ims 1995).

The combination of environmental scaling with the scaling of organism responses defines scaling functions (Figure 1; Southwood 1988; Wiens 1989, 1995). Scaling functions define the aggregate scaling dynamics of the environment–organism system. They enable us to determine at what scales the patterns and processes of the landscape coincide with the scales at which organisms are likely to respond to those patterns and processes, and therefore what scales may be most appropriate for observation or management.

But our observations of such functionally coupled environment–organism systems are themselves constrained by scale (Figure 1). As scientists and resource managers, we observe systems at a particular scale or range of scales. From these observations we

wish to predict how organisms will respond to environmental perturbations or the consequences of management actions. Observational scale acts as a “window” through which we view the scaling of the environment and the scale-dependent responses of organisms (Allen and others 1993). Observational scale therefore determines which patterns and processes are detected and which are missed; what we see through the observational window may be clear enough, but the view is limited, and the overall context of the observations may be incomplete. Usually, the observational scale is selected on the basis of the objectives of an investigation or management activity, the study design, and various logistical, financial, sociological, or political constraints. Obviously, the closer this observational window coincides with the scaling functions of the system under study, the more likely the resulting observations will portray real organism–environment interactions rather than artifacts. Ecologically based management requires that observations are appropriately scaled, and scaling functions define the conceptual framework for scaling such observations.

### Extrapolation

Of course, logistical constraints often dictate that ecological studies will be conducted at relatively fine scales (Kareiva 1990; Wiens 1995). Thus, our observation window for viewing scale-dependent organism responses (Figure 1) is really a narrow “slit.” Because our scientific or management objectives are often more general, however, we frequently wish to derive inferences and rules that can be applied at much broader scales. This raises the issue of extrapolation.

The fundamental premise of extrapolation is the assumption that pattern–process linkages do not change unexpectedly with changes in scale. So long as the factors that produce the patterns of environmental scaling or organismal response act in a consistent fashion with changes in scale, scaling functions will validly extrapolate from finer to broader scales. Because the scale dependency of environment–organism relationships is not linear, however, there are likely to be thresholds at which pattern–process responses change rapidly with small changes in scale (for example, Krummel and others 1987). There may be “domains” of scale, within which functional relationships remain relatively consistent and extrapolation is possible (Wiens 1989). At other points on the scaling spectrum, however, the pattern–process relationship suddenly changes profoundly, and extrapolation becomes difficult or impossible.

Proponents of hierarchy theory (Allen and Starr 1982; O'Neill and others 1988; Allen and others 1993; Ahl and Allen 1996) suggest that such domains may be represented as hierarchical levels. They argue that observations should be scaled to include not only the level of interest, but also the next lower level, because it contains the mechanisms acting to produce the patterns of interest, and the next higher level, because it incorporates the constraints on the patterns of interest. Unfortunately, it often is not clear where the boundaries between hierarchical levels or scale domains occur. Because scaling properties differ among different kinds of organisms (for example, small vs. large, herbivores vs. carnivores), different kinds of environments (for example, wet, productive vs. arid, unproductive), or different time periods (for example, wet vs. dry seasons), the limits to extrapolation are likely to be different for different features of a system. Such heterogeneity of scaling relationships may be especially troublesome for multispecies studies or for multiple-use management over broad landscapes or regions.

There is also a close relationship between landscape patchiness and scale (Wiens 1997). Ecologists (for example, Watt 1947; Usher 1975, Greig-Smith 1979) have long recognized that whether or not we regard a given environment as heterogeneous, and in what measurable ways (Kolasa and Pickett 1991; Wiens and others 1993), depends on both the scale of observation and the scale of pattern and process being studied. Whether patchiness is ecologically important, however, depends on how organisms respond to spatial patterns and physical processes at different scales (Figure 1). The research challenge is for the investigator to observe and measure landscape patches at scales relevant to the patterns and dynamics of the organisms or processes of interest. The challenge for the resource manager is to use the findings of such studies to define scaling rules at the appropriate scales of management, rather than forcing data to fit into preexisting management scales and thereby ignore scale-dependent response rules.

### Resource Concentration by Patches

The concentration of soil nutrients and runoff water to form enriched or fertile patches has been well documented for many semiarid landscapes in Australia (for example, Tongway and others 1989; Ludwig and Tongway 1995; Tongway and Ludwig 1997a), and for other arid and semiarid lands around the world (for example, Southwest deserts in the US: Schlesinger and others 1996; Whitford and others 1997; Negev Desert, Israel: Garner and

Steinberger 1989; Sahelian savanna, West Africa: Seghieri and others 1994). From these studies, it is evident that patches within many patterned landscapes do concentrate resources such as soil water, nutrients, and organic matter, and the differences in concentration of materials, such as soil N between versus within patches, reflects the long-term effects of landscape processes. What are these processes?

The primary process producing such spatial patterns in landscapes is redistribution (Risser and others 1984). In semiarid landscapes, excess water from rainfall usually is redistributed as runoff, which is captured as run-on by landscape patches that act as "traps" for runoff soil water, nutrients, and organic matter (Tongway and Ludwig 1997a). For example, when runoff encounters a grass clump (a small patch), the flowing water is slowed by this obstruction. This water has more time to infiltrate into the soils of the clump. Any rich topsoil sediments, litter, and seeds being carried in the runoff also may be trapped in this clump, leaving poor subsoils exposed on the surface of interpatches. The clump will grow and maintain itself as nutrients are assimilated into biomass by the plants and animals living in the clump. Microorganisms through death, decay, and fixation processes recycle and concentrate nutrients. For example, soil N is concentrated in vegetation clumps by N-fixing plants and by free-living N-fixing organisms.

As long as patches are physically intact, they will continue to grow and concentrate resources through enhanced capture of runoff. The generation of patches within local landscape systems is therefore (within limits) a self-reinforcing process. The positive feedback between patches and resource concentration processes creates self-organizing patterns in landscapes (for example, Holling and others 1996).

The actual patterns and processes of resource redistribution in landscapes are complex and difficult to measure. Landscape patches, on the other hand, may be relatively easy to measure at multiple scales, at least in semiarid and arid ecosystems. Is it possible to use simple landscape patch attributes as indicators or surrogates of resource conditions? Such landscape patch indicators could be quite useful in monitoring the consequences of changes in landscapes due to disturbance or changing land use (Ludwig and Tongway 1992; Tongway 1995). Because landscape indicators have received so little study, however, empirical support is scanty. Here we propose that developing scaling functions and rules may provide a means of relating landscape pattern to resource conditions.



## A SCALING RULE FOR PATCHES

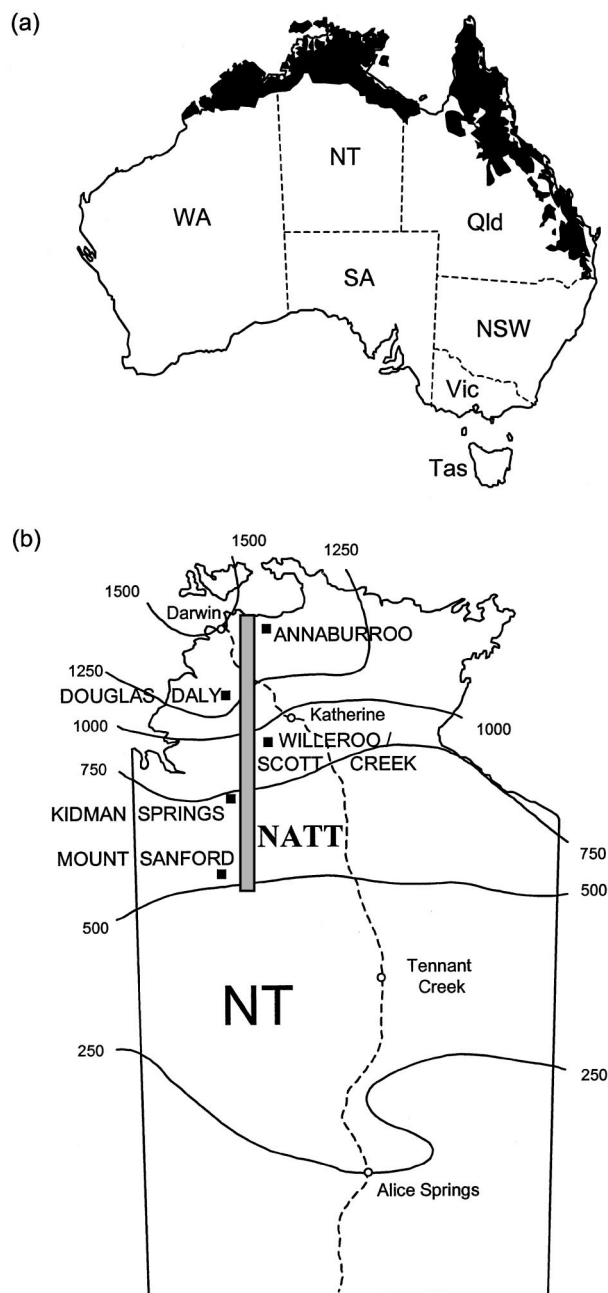
There is more to the story than just the concentration of resources to form enriched patches. Studies in the semiarid woodlands of eastern Australia indicate that differences in nutrient concentrations between open interpatch spaces and small patches (for example, grass clumps) are low compared with concentration differences between interpatch spaces and patches when the patches are intermediate sized (for example, shrub thickets) or large (for example, tree groves; Tongway and Ludwig 1994; Ludwig and Tongway 1995). This observation suggests a scaling rule: the concentration of resources into patches becomes increasingly greater as patch size increases. We define patch size in terms of its surface area ( $\text{m}^2$ ). Note that this rule defines a concentration effect: it is the amount of resource per unit of patch area, not the total amount for the patch as a whole that increases, which of course would increase as area increased. In other words, the increase in patch resource is not just a simple linear multiple of patch size, but is a nonlinear increase in the concentration of the resource in the patch.

## TESTING AND APPLYING THE PATCH SCALING RULE

To test this scaling rule, we used soil N and patch-size data from the savannas of northern Australia. A scaling equation was fit to this data and then used to predict the consequences of different landscape disturbances on the conservation of soil N.

### Australia's Savannas

Following Gillison (1994), we define savannas as vegetation with a grassy ground layer underlying a discontinuous tree layer. Several savanna types are recognized by Gillison: from types with a nearly closed tree canopy to types appearing as nearly open grasslands. These savannas are spread across the wet-dry, monsoonal tropics of northern Australia (Figure 2a) and occupy approximately  $1.5 \times 10^6 \text{ km}^2$  (Mott and Tothill 1984). The Australian continent occupies some  $7.6 \times 10^6 \text{ km}^2$ . Tropical rainforest and floodplains (for example, Mary River and East Alligator River floodplains) adjoin these savannas along coasts and rivers (Whitehead and others 1990; Russell-Smith 1992). At a regional scale, as in the north or Top End of the Northern Territory, Australia, savannas are divided into different vegetation types defined by the dominant *Eucalyptus* species in the overstory and the grasses in the understorey (Wilson and others 1990). These savanna



**Figure 2.** The location of: (a) savannas across the wet-dry tropics of northern Australia, and (b) five sites sampled along the rainfall gradient of the NATT. The distribution of savannas follows Moore and Perry (1970).

vegetation types are correlated with underlying geology, topography, hydrology, and soils (Isbell 1983). Within the Top End region, tree height, cover, and basal area decline on clay soils and with decreasing rainfall to the south (Williams and others 1996).

At broad landscape scales ( $1 \text{ km}^2$  and greater), savannas also vary with land-use history (for ex-

ample, cattle grazing), soil texture and depth (for example, deep sands and shallow loams), and local topographic position (for example, ridges, midslopes, toe-slopes) (Bowman and Minchin 1987; Fensham and Kirkpatrick 1992; Williams and others 1996). On steeper slopes, aspect also influences savanna composition (Kirkpatrick and others 1988). Fire is a dominant disturbance in these savannas, so fire frequency, intensity, and extent also cause variations within savannas at local to broad landscape scales (Morton and Andrew 1987; Lonsdale and Braithwaite 1991; Cook 1994). It has been estimated that most of the savannas in the Top End will burn every 1–2 years (Graetz and others 1992). In the entirety of Kakadu National Park, which includes floodplains, wetlands, savanna uplands, and rocky escarpments, 46% of the park is likely to burn each year (Russell-Smith and others 1997). It has been estimated that up to 70% of the savanna uplands burn annually (Gill and others 1996).

At finer, local savanna landscape scales (ha), patchiness is expressed as, for example, *Allosyncarpia* patches in Kakadu National Park (Bowman 1991) or patches of monsoon forest “islands” surrounded by savanna (Bowman and others 1991; Bowman 1992). At yet a finer scale (2–10 m<sup>2</sup>), patches occur in the form of tree islands and log mounds. Also, very fine-scale, ground-layer patches of less than 1 m<sup>2</sup> (for example, tussocks and clumps of perennial grasses) are important components of the structure of these savannas. The spacing and, hence, the size and cover of these very fine-scale patches vary with rainfall and soil type (Ludwig and others 1999b).

### Study Areas and Soil and Patch Sampling

Soil N data were derived for five locations along a 1000-mm rainfall gradient defining a North Australian Tropical Transect (NATT; Figure 2b). These five locations form part of other rainfall-gradient, soil-texture NATT studies on the landscape ecology of savannas (for example, Williams and others 1996; Ludwig and others 1999b). For this study, we only used soils collected on loam sites at these five locations.

On each loam site, soils were sampled from two patch types, smaller perennial grass clumps and larger woody patches. The latter are tree islands and log mounds formed by tree trunks, stems of saplings or postfire resprouts, and downed logs and fallen branches. Soils also were collected from interpatch spaces, which were either bare soil or partially covered with litter. Any litter on the collection surface was removed before soil coring. At each site, five replicate soil cores were collected for each of the two patch types and the interpatch zone. Each core

was partitioned into four samples by depth: 0–1 cm, 1–3 cm, 3–5 cm, and 5–10 cm. These soils samples then were air-dried, passed through a 2-mm sieve, and stored in sealed containers until analyzed for total N content (Twine and Williams 1967). Several other chemical analyzes were completed on these soils (pH, EC, OC, S, P, Na, K, Mg, and Ca), but, because our purpose was to simply illustrate the application of a scaling rule to the conservation of a soil resource, only the N data for the 0–5 cm depth were used. For each patch, mean soil N, weighted by sample depth, was computed.

Patch sizes for each site were estimated as elliptical areas from a sample of patch lengths and widths taken along a line transect as part of a general study on landscape patches (Ludwig and others 1999b). Where the data were available, 10 patch lengths and widths were used to compute an average patch size for the site. Mean patch sizes will tend to underestimate actual patch sizes because patch lengths along a line transect will not necessarily be the maximum lengths for patches. Furthermore, widths of patches were taken as “obstruction to flow” widths. These widths were measured at approximately 1 cm above the ground surface (see Tongway and Hindley 1995), which are not maximum widths. To reduce these length and width measurement biases as much as possible, we restricted the sample of 10 patches for a site to those larger grass and woody patches with nearly equal width to length ratios (approximately circular).

### Scaling Equation

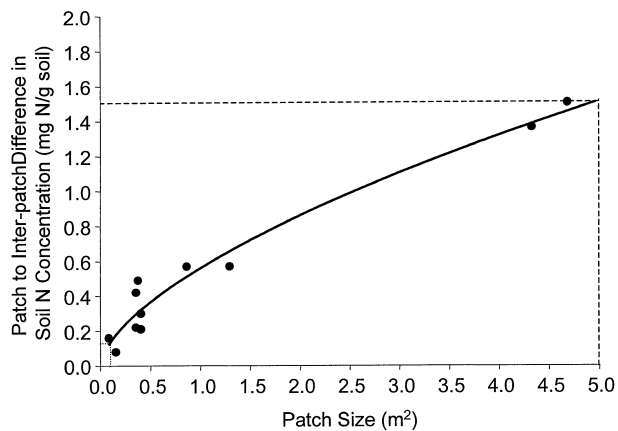
To express the scaling rule quantitatively, we used our patch data (Table 1) to generate a scaling equation relating the difference in soil N levels between patch and interpatch areas to patch size. Plots of this scaling-rule relationship data appear to be curvilinear (Figure 3), suggesting a simple power equation (for example,  $Y = aX^b$ ). Thus, a scaling equation was estimated by fitting this power equation to the data, which had a close fit ( $Y = 0.565X^{0.615}$ ;  $r^2 = 0.96$ ;  $P < 0.001$ ), even though we lacked patches in the 1.5–4-m<sup>2</sup> range. This equation expresses the scale-dependent consequences of the scaling functions and runoff/run-on processes producing an increasing concentration of soil N in patches as patch size increases.

### Two Examples

We can use this scaling equation to evaluate potential disturbance effects on soil N in local savanna landscapes. To illustrate such effects, assume that a 10-km<sup>2</sup> area of undisturbed savanna is fenced as a

**Table 1.** Concentration of Soil Nitrogen<sup>a</sup> in Local Landscape Patches of Different Sizes<sup>b</sup> in Comparison to Interpatch Zones for Loam Sites along the NATT

NATT Location	Patch Type	Dominant Patch Component(s)	Patch Size		Kjeldahl Nitrogen (mg N/g Soil)			
			m <sup>2</sup>	log <sub>10</sub>	Patch	Interpatch	Difference	log <sub>10</sub>
Mt Sanford	Grass	<i>Chrysopogon fallax</i> , <i>Heteropogon contortus</i>	0.35	-0.45	0.62	0.40	0.22	-0.66
	Woody	Trunks, logs of <i>Eucalyptus argillacea</i>	4.32	0.64	1.76	0.40	1.36	0.13
Kidman Springs	Grass	<i>Sehima nervosum</i> , <i>Chrysopogon fallax</i>	0.35	-0.45	1.60	1.19	0.42	-0.38
	Woody	Trunks, logs of <i>Eucalyptus pruinosa</i>	4.68	0.67	2.69	1.19	1.50	0.18
Willeroo	Grass	<i>Themeda triandra</i> , <i>Chrysopogon fallax</i>	0.37	-0.43	1.00	0.51	0.49	-0.31
Scott Creek 1	Grass	<i>Themeda triandra</i>	0.40	-0.40	1.37	1.07	0.30	-0.52
Scott Creek 2	Grass	<i>Chrysopogon fallax</i> , <i>Themeda triandra</i>	0.40	-0.40	1.28	1.07	0.21	-0.68
Douglas Daly	Grass	<i>Heteropogon contortus</i>	0.15	-0.82	0.75	0.67	0.08	-1.10
	Woody	Trunks, stems, logs of <i>Eucalyptus latifolia</i>	1.29	0.11	1.25	0.67	0.57	-0.24
Annaburroo	Grass	<i>Heteropogon triticeus</i> , <i>Chrysopogon fallax</i>	0.08	-1.10	1.04	0.88	0.16	-0.80
	Woody	Trunks, stems, logs of <i>Eucalyptus miniata</i>	0.86	-0.07	1.45	0.88	0.57	-0.24

<sup>a</sup>0–5 cm depth.<sup>b</sup>m<sup>2</sup> surface areas and log<sub>10</sub> transforms.**Figure 3.** Patch to interpatch differences in soil N in relation to patch size for small-scale, local landscape vegetation-soil patches. The estimated differences in soil N are 0.14 mg/g soil for 0.1-m<sup>2</sup> patches (dotted line) and 1.5 mg/g soil for 5.0-m<sup>2</sup> patches (dashed line).

paddock for cattle grazing. Let us also assume that the savanna vegetation is characterized by *Eucalyptus tetradonta* (stringybark) and *E. dichromophloia* (variable barked bloodwood), with grasses such as *Themeda triandra* (kangaroo grass) and *Chrysopogon fallax* (golden beard grass) in the understory. This vegetation is a common savanna type in the Top End of the Northern Territory, covering over 17 million km<sup>2</sup> (Wilson and others 1990). Furthermore, assume that the management aim is to sustain a stocking rate that will use the grasses such that their density is only reduced by 20% over the long term—allowing for fluctuations due to fire and prolonged dry seasons typical for the area.

First, if the grasses in this savanna paddock occur at an average density of 5/m<sup>2</sup>, a 20% grazing utilization in the long term could lead to a 20% loss of tussocks, reducing their density to 4/m<sup>2</sup>. Furthermore, if these grasses primarily occur as tussocks of approximately 0.1 m<sup>2</sup> patch size, the loss of 1 tussock/m<sup>2</sup> then could result in the loss of soil and N beneath the tussock, eventually reducing the level of soil N to that equal to the level in the interpatch spaces. From the scaling equation or Figure 3 (dotted line), we estimate that the loss of a grass patch (tussock) of 0.1 m<sup>2</sup> in size would produce a loss of 0.14 mg N/g soil, assuming a reduction of patch soil N down to that of the interpatch.

Next, we know that 0.14 mg N/g soil = 0.00014 kg N/kg soil, and that these savanna soils have a bulk density of 1.4 g/cm<sup>3</sup> (Stace and others 1968). This bulk density is equivalent to 14 kg soil/m<sup>2</sup> of surface area, assuming a 1-cm loss of soil from below each lost grass tussock. Given these facts and assumptions, we estimate that 1960 kg of N (approximately 2 metric tons) could be lost in total from the 10-km<sup>2</sup> paddock (see Appendix for calculation details).

Second, we apply similar calculations to a situation in which the same type of savanna landscape is impacted by another type of disturbance—tree thinning to form a more open paddock or improved pasture. The tree layer of this savanna is assumed to have a density of 1000 trees/ha, and the mean tree canopy area is assumed to be 5 m<sup>2</sup>. Then, with 1000 trees/ha and 5 m<sup>2</sup>/tree, we have 5000 m<sup>2</sup>/ha of total tree canopy cover, that is, a 50% cover (5000 m<sup>2</sup> per ha/10,000 m<sup>2</sup> per ha = 0.5). This canopy cover is

typical of savannas on sandy loam soils above 1000 mm rainfall in northern Australia (Williams and others 1996).

As before, we apply a 20% impact. In this case, tree density is reduced by 20% down to 800 tree/ha, or, in terms of tree canopy area, 800 trees/ha at 5 m<sup>2</sup>/tree is 4000 m<sup>2</sup>/ha—a 20% reduction in the original 5000 m<sup>2</sup>/ha tree canopy area. If we assume that the area of enriched soil (patch) is equal to the area defined by the tree canopy, then we have a 20% loss of patches, hence, a potential loss of soil from the paddock if 1 cm of this soil patch is eroded away. For comparison, we want to have the same total soil surface area impacted as in the previous example (that is, 1,000,000 m<sup>2</sup>/paddock; see Appendix). From the scaling equation or Figure 3 (dashed line), we estimate that the loss of a tree patch (island) 5 m<sup>2</sup> in size would produce a loss of 1.5 mg N/g soil. Given a soil bulk density of 1.4 g/cm<sup>3</sup>, this is a loss of 14 kg soil/m<sup>2</sup> when 1 cm of soil is eroded from below each island. From this, a total of 14,000,000 kg of soil and 21,000 kg of N (21 metric tons) would be lost from the 10-km<sup>2</sup> paddock (see Appendix).

## DISCUSSION

### Applying Scaling Rules

In Australian savanna landscapes with loamy soils, our data illustrates that soil N is increasingly concentrated into landscape patches as these patches increase in size. We quantified this scaling rule with a scaling equation by using patch N and size data. Then we applied this equation to hypothetical situations to examine how two different landscape disturbances might affect patches and, hence, determine how soil and the nutrients associated with these soils and patches might be lost. We believe such hypothetical situations should be realistic applications, not extreme scenarios. In the first example we only assumed a 20% utilization of perennial grass tussocks by cattle and a subsequent 20% death and loss of tussocks. Actual utilization and death rates of savanna grasses are often much higher (McIvor and others 1995). Thus, for our example, a predicted potential loss of approximately 2 metric tons of soil N is not extreme.

One can reasonably assume that downslope patches in the landscape would capture some of the soil lost from upslope tussocks, at least in the short term. In other words, soil N would not be immediately lost from the paddock. However, small patches such as grass tussocks have a finite capacity to capture soil and build mounds around them before they overload with sediment. There may be a

cascading effect in which sediments not captured by overloaded tussocks on midslopes in the landscape will cascade downslope and rapidly overload patches on lower slopes (Ludwig and Tongway 1997). In other words, there are limits to the scale-specific, “self-organizing” capacity of an ecosystem or landscape (*sensu* Holling and others 1996).

In the second example, we described a land management action commonly used in savannas—tree killing and thinning for pasture improvement (McIvor and Gardener 1995). We described a situation in which 20% of the trees were killed in a newly established 10-km<sup>2</sup> cattle paddock. In the long term, with soil erosion from beneath killed trees, we estimated that this erosion potentially could lead to the loss of approximately 21 metric tons of soil N from this paddock. This is a large potential loss of soil N due to the impacts of killing trees in patches compared with the 2 metric tons of soil N potential lost due to the impacts of grazing on small grass patches. In reality, this difference could be even greater because the soil mound formed by tree islands is usually higher than 1 cm—more than 1 cm of soil surface could be lost with erosion after tree thinning. Furthermore, if all the trees in the paddock were cleared for, say, cropping, the impact would be even greater.

Our predictions from these two examples seem realistic based on a few studies on the loss of soil from savanna paddocks (for example, Scanlan and others 1996). These studies confirm that runoff and sediment yields vary positively with rainfall amount and intensity but negatively with ground cover (for example, Gardener and others 1990). Savanna pasture and soil type also strongly influence soil loss (for example, Eldridge and Rotham 1992; McIvor and others 1995).

### Generality

We expect our scaling rule for how resources are concentrated into small landscape patches also is generally applicable to larger savanna landscape patches. We base this expectation on some data from the savanna literature. We looked for articles in which soil N was measured in various run-on patches within a matrix of upland savanna (taken as interpatch areas). These articles also had to describe their study areas in enough detail to allow us to estimate the approximate size of run-on lowland and floodplain patches. We found data for patches ranging in size from a few ha (for example, dry and wet monsoon savanna forest islands; Bowman 1992), to a few km<sup>2</sup> (for example, peninsula monsoon forests; Bowman and Fensham 1991; Bowman and Panton 1993), and to regional patches of several



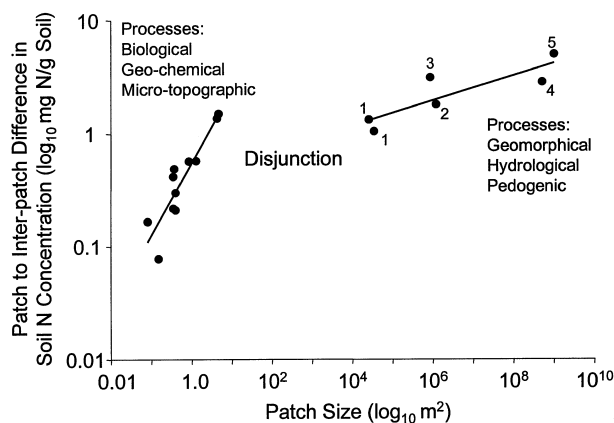


Figure 4. Use of  $\log_{10}$  transforms for patch to interpatch differences in soil N and for patch sizes shows that there is an apparent disjunction between the scaling relations for smaller, local landscape patches and for larger, regional lowland/floodplain patches. This disjunction probably is related to the landscape processes operating at these two scales (see text). Large patch data is from: 1 Bowman (1992), 2 Bowman and Fensham (1991), 3 Bowman and Panton (1993), 4 Day and others (1979), and 5 White (1984). Upland savanna soil N data is from Bowman (1991).

thousand  $\text{km}^2$  (for example, river floodplains; Day and others 1979; White 1984).

Although estimated patch sizes were pretty rough and some of the soil N data were limited to only a few samples collected from a very large area, concentration differences between these soil N data with that for surrounding upland savannas (Bowman 1991) support the scaling rule (Figure 4). Over the range of patch sizes from a few ha ( $10^4 \text{ m}^2$ ) to thousands of  $\text{km}^2$  ( $10^9 \text{ m}^2$ ), patch to interpatch soil N concentration differences increased with patch size. The scaling rule applies because differences in soil N concentrations between floodplains and surrounding savannas are greater than soil N concentration differences between smaller landscape patches (for example, monsoon forest islands) and surrounding savannas.

When these data for larger landscape patches are log-transformed and plotted with similarly transformed data for small local landscape patches (Figure 4), it is apparent that the scaling relations differ at these two scales—there is a disjunction—extrapolation is unwise. This sudden change in scaling relations reflects a scale-dependent threshold that is probably caused by the different landscape processes operating at the two scales. For local landscapes, biological, geochemical, and microtopographic redistribution processes largely influence the concentration of soil resources within small

vegetation patches, whereas for large regional landscape patches, vegetation and soils are largely structured by geological, hydrological, and pedogenic processes (also see The Scaling Problem section). For example, regional floodplain soils have higher concentrations of soil N and organic matter than surrounding upland savannas (White 1984), and lower bulk densities (for example, 1.2 vs. 1.4  $\text{g}/\text{cm}^3$ ; Stace and others 1968).

We also expect our patch scaling rule for wet-dry tropical savannas to be generally applicable to most arid and semiarid landscapes where the redistribution of scarce resources (for example, water and nutrients) is observed, for example, in deserts (for example, Noy-Meir 1981) and rangelands (for example, Tongway and Ludwig 1997a). However, scaling equations for different vegetation-soil types will likely differ because of inherent properties. For example, on fine-textured loams, infiltration rates can be very low and runoff can be very rapid (Greene and others 1994), but runoff is very slow on deep, coarse sandy soils and on deep cracking clays because infiltration rates are very high.

The patch scaling rule also may apply generally to other resources that are redistributed and concentrated in landscapes. In the examples presented here, for simplicity, we only derived scaling equations for soil N, but we also could have derived equations for other soil nutrients such as phosphorus. Scaling equations for the capture of runoff water by landscape patches of different sizes also could be derived if soil attributes, such as infiltration rates and soil-water storage capacities, along with landscape attributes such as terrain shape and slope, were available for large data sets. These scaling equations then could be used in simulation modeling studies to rigorously address a number of questions about the role of landscape patches in conserving soil resources in savannas. Such studies would add to those that have examined optimal patch area, shape, and configuration in conserving runoff in semiarid woodlands (Ludwig and others 1994, 1999a).

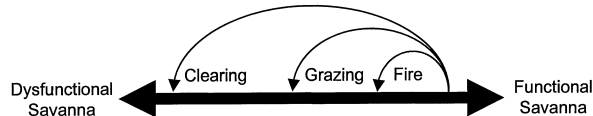
### Landscape Functionality—A Continuum

Our data for savanna landscapes demonstrate that patches concentrate soil resources. Patches in the semiarid woodlands of eastern Australia also function to capture, concentrate, and conserve water and the nutrients carried in runoff sediments and litter (Tongway and Ludwig 1997a). Patches also trap soil particles and litter being blown about by winds, often forming vegetation mounds. Such landscapes with patches that function to capture resources are termed “conserving” landscapes,

## (a) Continuum of Landscape Functionality



## (b) Shifts along the Continuum caused by Disturbances



## (c) Recovery from Disturbances with Time

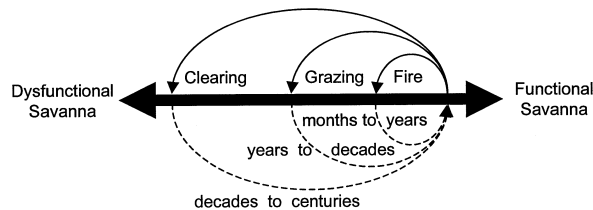


Figure 5. Landscape functionality in relation to: (a) a continuum from “leaky” dysfunctional systems to “conserving” functional systems, (b) shifts caused by fire, grazing, and clearing disturbances, and (c) approximate recovery times for these disturbances.

whereas landscapes that have been degraded and have lost some of their patches are termed “leaky” or partially dysfunctional (Tongway and Ludwig 1997b). These leaky landscapes no longer function to effectively capture scarce resources.

Conceptually, landscapes can be positioned along a continuum (Figure 5a). At one end of this continuum are fully functional landscapes that are highly patchy and, ideally, capture all resources (that is, no runoff and sediments are lost). At the other end are totally dysfunctional landscapes that do not trap or retain any of the resources made available to them (that is, all runoff, sediments, and litter are lost).

What causes a functional landscape to lose patches and become leaky, and thereby shift down the continuum toward becoming dysfunctional? Although many forces can disturb savanna landscapes, we focus on three: fire, grazing, and vegetation clearing (Figure 5b). We chose these three because they vary in their potential severity of

impact on savanna landscapes, from least severe (fire) to most severe (clearing).

Fire is a natural, regular feature of savannas in northern Australia (Gill 1975). As noted earlier, much of the savanna in the Top End of the Northern Territory burns every year or two (Graetz and others 1992). Fire also is used as a rangeland management tool in savannas (Tothill 1971; Mott and Tothill 1984). Fires, both natural and human caused, affect savannas by causing some tree mortality, but trees regenerate quickly (Bowman and others 1988; Lonsdale and Braithwaite 1991; Williams and others 1997). Thus, fire disturbances are likely to cause only small shifts down the continuum toward dysfunctionality (Figure 5b). Recovery from any shifts are likely to be rapid, occurring in months to a few years (Figure 5c).

In contrast to fire, the impacts of grazing on savanna landscapes are likely to be more severe (Mott and Tothill 1984), particularly because of the introduction of tropical zebu (*Bos indicus*) cattle breeds into northern Australia (Frisch and Vercoe 1977). These breeds are more resistant to heat stress and ticks and can more effectively forage and utilize tropical grasses than the British breeds of *Bos taurus* that were originally used in these savannas (Gardener and others 1990). Thus, long-term grazing impacts on landscape patches are likely to cause greater shifts down the continuum toward dysfunctionality (Figure 5b). These large shifts may cause a grazing impacted savanna to change to a different state, such as a savanna with mostly annual and exotic grasses (Ash and others 1994). Overgrazing savannas can collapse soil structure, cause surface sealing, and form bare areas within a few years (Bridge and others 1983). Recovery from degraded states back to more functional states, however, would likely take many years to decades (Figure 5c).

Grazing impacts may cause a change in vegetation state by shifting the scale (grain) and size of patches. For example, in the chenopod shrublands of Western Australia, grazing impacts and wind have changed areas of dense, small mounds of bluebush (*Maireana polypterygia*) into areas of sparse, large mounds of *Acacia* spp. (Tongway and Ludwig 1994). Similar impacts and processes have changed the fine-scale patchiness of desert grasslands occurring on the Jornada in southern New Mexico, USA, into coarse-scaled dunelands dominated by mesquite (*Prosopis glandulosa*; Schlesinger and others 1990). The soils beneath the mesquite dunes form “fertile islands” (Schlesinger and others 1996), and the primary productivity in these dunelands does not appear to be lower (degraded) compared with that in grasslands (Huenneke 1996). If soil is only redis-

tributed by winds into larger patches (for example, mesquite dunes), a loss of small landscape patches (for example, grass clumps) does not mean a net loss of nutrients from the broader landscape. The scale of resource concentration and production within the system is only changed from fine to coarse. However, if impacts are severe and prolonged, the broader landscape can become leaky and dysfunctional, leading to a desertified state with lower production (Schlesinger and others 1990).

If savannas are cleared for purposes of agricultural cropping, impacts on tree patches and soils obviously will be very severe, and landscapes can become very dysfunctional, no longer containing patches to trap resources (Figure 5b). Recovery to a functional state could take decades to centuries (Figure 5c). Such dysfunctional landscapes may require rehabilitation by rebuilding patches (Ludwig and Tongway 1996; Tongway and Ludwig 1996). However, a more common savanna land use is to improve pastures (that is, increase forage production) by killing trees but not clearing them (Mott and Tothill 1984; Burrows and others 1988). In the long term, production is likely to decline as soil nutrients are depleted on the areas where trees were killed, eventually approximating yields of the interpatch areas.

## ACKNOWLEDGMENTS

We gratefully acknowledge the Tropical Savannas Cooperative Research Centre (TSCRC) and CSIRO Wildlife and Ecology for supporting J.A.W. as a TSCRC visiting scientist in 1996. We thank Norman Hindley for assisting with soil sampling and soil N analyzes, and Garry Cook for leading us to other soil N data in reports. Robert Eager helped with compiling these data and preparing figures. We also thank Garry and Robert, and Alan Andersen, Dave Bowman, Dick Williams, and Bea Van Horne for debating issues on scaling in ecology and the pros and cons of scaling functions. These discussions, along with constructive comments from reviewers, clarified our thoughts and improved this article.

## REFERENCES

- Addicott JE, Aho JM, Antolin MF, Padilla MF, Richardson JS, Soluk DA. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos* 49:340–6.
- Ahl V, Allen TFH. 1996. Hierarchy theory. A vision, vocabulary, and epistemology. New York: Columbia University Press.
- Allen TFH, Starr TB. 1982. Hierarchy: perspectives for ecological complexity. Chicago: University of Chicago Press.
- Allen TFH, King AW, Milne BT, Johnson A, Turner S. 1993. The problem of scaling in ecology. *Evolutionary Trends Plants* 7:3–8.
- Ash AJ, Bellamy JA, Stockwell TGH. 1994. State and transition models for rangelands. 4. Application of state and transition models to rangelands in northern Australia. *Trop Grasslands* 28:223–8.
- Bloschl G, Sivapalan M. 1995. Scale issues in hydrological modelling: a review. *Hydrol Processes* 9:251–90.
- Bowman DMJS. 1991. Environmental determinants of *Allosyncarpia ternata* forests that are endemic to western Arnhem Land, northern Australia. *Aust J Bot* 39:575–89.
- Bowman DMJS. 1992. Monsoon forests in north-western Australia. II. Forest-savanna transitions. *Aust J Bot* 40:89–102.
- Bowman DMJS, Fensham RJ. 1991. Response of a monsoon forest-savanna boundary to fire protection, Weipa, northern Australia. *Aust J Bot* 16:111–8.
- Bowman DMJS, Minchin PR. 1987. Environmental relationships of woody vegetation patterns in the Australian monsoon tropics. *Aust J Bot* 35:151–69.
- Bowman DMJS, Panton WJ. 1993. Factors that control monsoon-rainforest seedling establishment and growth in north Australian *Eucalyptus* savanna. *J Ecol* 81:297–304.
- Bowman DMJS, Wilson BA, Hooper RJ. 1988. Response of *Eucalyptus* forest and woodland to four fire regimes at Munmarlary, Northern Territory, Australia. *J Ecol* 76:215–32.
- Bowman DMJS, Wilson BA, McDonough L. 1991. Monsoon forests in northwestern Australia I. Vegetation classification and the environmental control of tree species. *J Biogeogr* 18:679–86.
- Bridge BJ, Mott JJ, Hartigan RJ. 1983. The formation of degraded areas in the dry savanna woodlands of northern Australia. *Aust J Soil Res* 21:91–104.
- Burrows WH, Scanlan JC, Anderson ER. 1988. Plant ecological relations in open forests, woodlands and shrublands. In: Burrows WH, Scanlan JC, Rutherford MT, editors. Native pastures in Queensland—the resources and their management. Information Series Q187023. Brisbane, Australia: Queensland Department of Primary Industries. p 72–90.
- Cook GD. 1994. The fate of nutrients during fires in a tropical savanna. *Aust J Ecol* 19:359–65.
- Day KJ, Harrison CJ, VanCuylenburg HRM. 1979. Land resources of Wildman River Station, NT. Land Conservation Report LC 79/6. Darwin, Australia: Northern Territory Parks and Wildlife Commission.
- Eldridge DJ. 1993. Effects of ants on sandy soils in semi-arid eastern Australia: local distribution of nest entrances and their effect on infiltration of water. *Aust J Soil Res* 31:509–18.
- Eldridge DJ, Rotham J. 1992. Run-off and sediment yield from a semi-arid woodland in eastern Australia. I. The effect of pasture type. *Rangeland J* 14:26–39.
- Fensham RJ, Kirkpatrick JB. 1992. Soil characteristics and tree species distribution in the savannah of Melville Island, Northern Territory. *Aust J Bot* 40:311–33.
- Frisch JE, Vercoe JE. 1977. Food intake, entry rate, weight gains, metabolic rate and efficiency of feed utilisation in *Bos taurus* and *Bos indicus* crossbreed cattle. *Anim Prod* 25:343–58.
- Gardener CJ, McIvor JG, Williams J. 1990. Dry tropical rangelands: solving one problem and creating another. In: Saunders DA, Hopkins AJM, How RA, editors. Australian ecosystems: 200 years of utilization, degradation and reconstruction. Sydney, Australia: Surrey Beatty and Sons. p 279–86.
- Gardner RH, O'Neill RV, Turner MG, Dale VH. 1989. Quantifying scale-dependent effects of animal movement with simple percolation models. *Landscape Ecol* 3:217–27.



- Garner W, Steinberger Y. 1989. A proposed mechanism for the formation of "fertile islands" in the desert ecosystem. *J Arid Environ* 16:257–62.
- Gill AM. 1975. Fire and the Australian flora: a review. *Aust For* 38:4–25.
- Gill AM, Moore PHR, Williams RJ. 1996. Fire weather in the wet-dry tropics of the World Heritage Kakadu National Park, Australia. *Aust J Ecol* 21:302–8.
- Gillison AN. 1994. Woodlands. In: Groves RH, editor. *Australian vegetation*, 2nd ed. Cambridge, UK: Cambridge University Press. p 227–55.
- Graetz RD, Fisher RP, Wilson MA. 1992. Looking back: the changing face of the Australian continent. Canberra, Australia: CSIRO Wildlife and Ecology.
- Greene RSB, Kinnell PIA, Wood JT. 1994. Role of plant cover and stock trampling on runoff and soil erosion from semi-arid wooded rangelands. *Aust J Soil Res* 32:953–73.
- Greig-Smith P. 1979. Pattern in vegetation. *J Ecol* 67:755–79.
- Gustafson EJ. 1998. Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems* 1:143–56.
- Holling CS. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol Monogr* 62:447–502.
- Holling CS, Peterson G, Marples P, Sendzimir J, Redford K, Gunderson L, Lambert D. 1996. Self-organisation in ecosystems: lumpy geometrics, periodicities and morphologies. In: Walker B, Steffen W, editors. *Global change and terrestrial ecosystems*. Cambridge, UK: Cambridge University Press. p 346–84.
- Huenneke LF. 1996. Shrub and grasslands of the Jornada long-term ecological research site: desertification and plant community structure in the northern Chihuahuan Desert. In: Barrow JR, McArthur ED, Sosebee RE, Tausch RJ, editors. *Proceedings: shrubland ecosystem dynamics in a changing environment*. General Technical Report INT-GTR-338. Intermountain Research Station, Forest Service, US Department of Agriculture, Ogden, UT. p 48–50.
- Ims RA. 1995. Movement patterns related to spatial structures. In: Hansson L, Fahrig L, Merriam G, editors. *Mosaic landscapes and ecological processes*. London: Chapman and Hall. p 85–109.
- Isbell RF. 1983. Kimberley-Arnhem-Cape York (III), Chapter 14. In: CSIRO Division of Soils, editors. *Soils: an Australian viewpoint*. Melbourne, Australia: CSIRO Publishing. p 189–99.
- Jones JA. 1990. Termites, soil fertility and carbon cycling in dry tropical Africa: a hypothesis. *J Trop Ecol* 6:291–305.
- Kareiva PM. 1990. Population dynamics in spatially complex environments: theory and data. *Philos Trans R Soc Lond B Biol Sci* 330:175–90.
- Kirkpatrick JB, Fensham RJ, Nunez M, Bowman DMJS. 1988. Vegetation-radiation relationships in the wet-dry tropics: granite hills in northern Australia. *Vegetatio* 76:103–12.
- Kolasa J, Pickett STA, editors. 1991. *Ecological heterogeneity*. New York: Springer-Verlag.
- Kotliar NB, Wiens JA. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253–60.
- Krummel JR, Gardner RH, Sugihara G, O'Neill RV, Coleman PR. 1987. Landscape patterns in a disturbed environment. *Oikos* 48:321–4.
- Levin SA. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–67.
- Lonsdale WM, Braithwaite RW. 1991. Assessing the effects of fire on vegetation in tropical savannas. *Aust J Ecol* 16:363–74.
- Ludwig JA, Tongway DJ. 1992. Monitoring the condition of Australian arid lands: linked plant-soil indicators. In: McKenzie DH, Hyatt DE, McDonald VJ, editors. *Ecological indicators*, volume 1. Essex, UK: Elsevier. p 763–72.
- Ludwig JA, Tongway DJ. 1995. Spatial organisation of landscapes and its function in semi-arid woodlands, Australia. *Landscape Ecol* 10:51–63.
- Ludwig JA, Tongway DJ. 1996. Rehabilitation of semi-arid landscapes in Australia. II. Restoring vegetation patches. *Restoration Ecol* 4:398–406.
- Ludwig JA, Tongway DJ. 1997. Modelling scale-dependent processes and impacts of agricultural disturbances on tropical savanna ecosystems in northern Australia. In: McDonald AD, McAleer M, editors. *Proceedings, International Congress on Modelling and Simulation*, volume 4. Canberra, Australia: The Modelling and Simulation Society of Australia. p 1875–80.
- Ludwig JA, Tongway DJ, Marsden SG. 1994. A flow-filter model for simulating the conservation of limited resources in spatially heterogeneous, semi-arid landscapes. *Pacific Conserv Biol* 1:209–13.
- Ludwig JA, Tongway DJ, Marsden SG. 1999a. Stripes, strands or stipples: modelling the influence of three landscape banding patterns on resource capture and productivity in semi-arid woodlands, Australia. *Catena* 37:257–73.
- Ludwig JA, Tongway DJ, Eager RW, Williams RJ, Cook GD. 1999b. Fine-scale vegetation patches decline in size and cover with increasing rainfall in Australian savannas. *Landscape Ecol* 14:557–66.
- McIvor JG, Gardener CJ. 1995. Pasture management in semi-arid tropical woodlands: effects on herbage yields and botanical composition. *Aust J Exp Agric* 35:705–15.
- McIvor JG, Williams J, Gardener CJ. 1995. Pasture management influence run-off and soil movement in the semi-arid tropics. *Aust J Exp Agric* 35:55–65.
- Moore RM, Perry RA. 1970. Vegetation. In: Moore RM, editor. *Australian grasslands*. Canberra, Australia: Australian National University Press. p 59–73.
- Morton SR, Andrew MH. 1987. Ecological impact and management of fire in northern Australia. *Search* 18:77–82.
- Mott JJ, Tothill JC. 1984. Tropical and subtropical woodlands. In: Harrington GN, Wilson AD, Young MD, editors. *Management of Australia's rangelands*. Melbourne, Australia: CSIRO Publishing. p 255–69.
- Noy-Meir I. 1981. Spatial effects in modelling of arid ecosystems. In: Goodall DW, Perry RA, editors. *Arid-land ecosystems: structure, functioning and management*, volume 2. Cambridge, UK: Cambridge University Press. p 411–32.
- O'Neill RV. 1989. Perspectives in hierarchy and scale. In: Roughgarden J, May RM, Levin SA, editors. *Perspectives in ecological theory*. Princeton, NJ: Princeton University Press. p 140–6.
- O'Neill RV, Milne BT, Turner MG, Gardner RH. 1988. Resource utilization scales and landscape patterns. *Landscape Ecol* 2:63–9.
- Peterson G, Allen CR, Holling CS. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18.
- Pickett STA, Osfeld RS, Shachak M, Likens GE, editors. 1997. *Enhancing the ecological basis for conservation: heterogeneity, ecosystem function, and biodiversity*. New York: Chapman and Hall.



- Risser PG, Karr JR, Forman RTT. 1984. Landscape ecology: directions and approaches. Special Publication 2 Champaign, IL: Illinois Natural History Survey.
- Russell-Smith J. 1992. Classification, species richness, and environmental relations of Monsoon rain forest in northern Australia. *J Vegetation Sc* 2:259–78.
- Russell-Smith J, Ryan PG, Durieu R. 1997. A LANDSAT MSS-derived fire history of Kakadu National Park, monsoonal northern Australia, 1980–94: seasonal extent, frequency and patchiness. *J Appl Ecol* 34:748–66.
- Sale PF. 1998. Appropriate spatial scales for studies of reef-fish ecology. *Aust J Ecol* 23:202–8.
- Scanlan JC, Pressland AJ, Myles DJ. 1996. Run-off and soil movement on mid-slopes in north-east Queensland grazed woodlands. *Rangeland J* 18:33–46.
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological feedbacks in global desertification. *Science* 247:1043–8.
- Schlesinger WH, Raikes JA, Hartley AE, Cross AF. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77:364–74.
- Schneider DC. 1994. Quantitative ecology: spatial and temporal scaling. San Diego, CA: Academic Press.
- Seghier J, Floret C, Ponanier R. 1994. Development of an herbaceous cover in a Sudano-Sahelian savanna in North Cameroon in relation to available soil water. *Vegetatio* 114: 175–94.
- Southwood TRE. 1988. Tactics, strategies and templets. *Oikos* 52:3–18.
- Stace HCT, Hubble GD, Brewer R, Northcote KH, Sleeman JR, Mulcahy MJ, Hallsworth EG. 1968. A handbook of Australian soils. Adelaide, Australia: Rellim Technical Publications.
- Tongway DJ. 1995. Monitoring soil productive potential. *Environ Monitoring Assess* 37:303–18.
- Tongway DJ, Hindley N. 1995. Manual for soil condition assessment of tropical grasslands. Canberra, Australia: CSIRO Wildlife and Ecology.
- Tongway DJ, Ludwig JA. 1994. Small-scale resource heterogeneity in semi-arid landscapes. *Pacific Conserv Biol* 1:201–8.
- Tongway DJ, Ludwig JA. 1996. Rehabilitation of semi-arid landscapes in Australia. I. Restoring productive soil patches. *Restoration Ecol* 4:388–97.
- Tongway DJ, Ludwig JA. 1997a. The conservation of water and nutrients within landscapes, chapter 2. In: Ludwig J, Tongway D, Freudenberger D, Noble J, Hodgkinson K, editors. Landscape ecology, function and management: principles from Australia's rangelands. Melbourne, Australia: CSIRO Publishing. p 17–26.
- Tongway DJ, Ludwig JA. 1997b. The nature of landscape dysfunction in rangelands, chapter 5. In: Ludwig J, Tongway D, Freudenberger D, Noble J, Hodgkinson K, editors. Landscape ecology, function and management: principles from Australia's rangelands. Melbourne, Australia: CSIRO Publishing. p 53–65.
- Tongway DJ, Ludwig JA, Whitford WG. 1989. Mulga log mounds: fertile patches in the semi-arid woodlands of eastern Australia. *Aust J Ecol* 14:263–8.
- Tothill JC. 1971. A review of fire in the management of native pasture with particular reference to north-eastern Australia. *Trop Grasslands* 5:1–10.
- Twine JR, Williams CH. 1967. Determination of nitrogen in soils by automated chemical analysis. CSIRO Field Station Records 6:61–7.
- Usher MB. 1975. Analysis of pattern in real and artificial plant populations. *J Ecology* 63:569–86.
- Walker BH, Langridge JL, McFarlane F. 1997. Resilience of an Australian savanna grassland to selective and non-selective perturbations. *Aust J Ecol* 22:125–35.
- Watt AS. 1947. Pattern and process in the plant community. *J Ecol* 35:1–22.
- White LA. 1984. Dark cracking clays of the estuarine flood plains of the Northern Territory. In: McGarity JW, Hoult EH, So HB, editors. The properties and utilization of cracking clay soils. Reviews in Rural Science 5. Armidale, Australia: University of New England. p 29–35.
- Whitehead PJ, Wilson BA, Bowman DMJS. 1990. Conservation of coastal wetlands of the Northern Territory of Australia: the Mary River floodplain. *Biol Conserv* 52:85–111.
- Whitford WG, Anderson J, Rice PM. 1997. Stemflow contribution to the "fertile island" effect in creosotebush, *Larrea tridentata*. *J Arid Environ* 35:451–7.
- Wiens JA. 1989. Spatial scaling in ecology. *Funct Ecol* 3:385–97.
- Wiens JA. 1995. Landscape mosaics and ecological theory. In: Hansson L, Fahrig L, Merriam G, editors. Mosaic landscapes and ecological processes. New York: Chapman and Hall. p 1–26.
- Wiens JA. 1997. The emerging role of patchiness in conservation biology. In: Pickett STA, Osfeld RS, Shachak M, Likens GE, editors. Enhancing the ecological basis for conservation: heterogeneity, ecosystem function, and biodiversity. New York: Chapman and Hall. p 93–107.
- Wiens JA, Crawford CS, Gosz JR. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45:421–7.
- Wiens JA, Stenseth NC, Van Horne B, Ims RA. 1993. Ecological mechanisms and landscape ecology. *Oikos* 66:369–80.
- Wiens JA, Crist TO, With KA, Milne BR. 1995. Fractal patterns of insect movement in microlandscape mosaics. *Ecology* 76: 663–6.
- Williams RJ, Duff GA, Bowman DMJS, Cook GD. 1996. Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. *J Biogeogra* 23:747–56.
- Williams RJ, Cook GD, Ludwig JA, Tongway DT. 1997. Torch, trees, teeth and tussocks: disturbance in the tropical savannas of the Northern Territory (Australia). In: Klomp N, Lunt I, editors. Frontiers in ecology: building the links. Oxford, UK: Elsevier Science. p 55–66.
- Wilson BA, Brocklehurst PS, Clark MJ, Dickinson KJM. 1990. Vegetation of the Northern Territory, Australia. Technical Report No. 49. Darwin, Australia: Conservation Commission of the Northern Territory.
- With KA. 1994. Ontogenetic shifts in how grasshoppers interact with landscape structure: an analysis of movement patterns. *Funct Ecol* 8:477–85.
- With KA, Crist TO. 1996. Translating across scales: simulating species distributions as the aggregate response of individuals to heterogeneity. *Ecol Modelling* 93:125–37.
- Woodmansee RG. 1990. Biogeochemical cycles and ecological hierarchies. In: Zonneveld IS, Forman RTT, editors. Changing landscapes: an ecological perspective. New York: Springer-Verlag. p 57–71.

## Appendix Estimating Losses of Soil N from a Savanna Paddock

The estimate of 1.96 metric tons N being lost from a 10-km<sup>2</sup> savanna paddock (see text for setting) was calculated by: (0.14 mg N/g soil) x (1.4 g soil/cm<sup>3</sup>) x (1000 cm<sup>3</sup> soil lost/tussock) x (1 tussock lost/m<sup>2</sup>) x (1,000,000 m<sup>2</sup>/km<sup>2</sup>) x (10-km<sup>2</sup> paddock) x (1 kg/1,000,000 mg) = 1960 kg N/paddock.

This estimate also can be calculated from the total area of grass patches lost from the 10-km<sup>2</sup> paddock, which was 1,000,000 m<sup>2</sup> = (0.1 m<sup>2</sup> of tussock/m<sup>2</sup>) x (10,000 m<sup>2</sup>/ha) x (100 ha/km<sup>2</sup>) x (10 km<sup>2</sup>/paddock).

The amount of soil lost is then 14,000,000 kg/paddock = 14 kg soil/m<sup>2</sup> x 1,000,000 m<sup>2</sup>/paddock, and the amount of lost soil N is 1960 kg = 0.00014 kg N/kg soil x 14,000,000 kg soil/paddock.

The total area of tree patches impacted in the 10-km<sup>2</sup> paddock was also 1,000,000 m<sup>2</sup> = (5 m<sup>2</sup>/tree island patch x 200 patches/ha) x (100 ha/km<sup>2</sup> x 10 km<sup>2</sup>/paddock). Again, given the same soil bulk density of 1.4 g/cm<sup>3</sup>, or 14 kg soil/m<sup>2</sup> when 1 cm of soil is lost from below each thinned tree island, then the total soil loss from the 10-km<sup>2</sup> paddock is also 14,000,000 kg. Then, given that 1.5 mg N/g soil is 0.0015 kg N/kg soil, 21,000 kg N (21 metric tons N) would be lost from the paddock.