# Simple rules underlie the complex and non-linear dynamics of terrestrial and aquatic ecosystems:

## Implications for catchment biogeochemistry and modelling



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**Table of Contents**

## Introduction

The Australian continent is old, flat and mainly arid, with a peculiar biogeography. Large areas of the continent have been cleared for agriculture and dry land salinity is a widespread problem (see e.g. Walker et al. 1999). Land use change and habitat fragmentation have also had major impacts on biodiversity (Saunders et al. 1991). This essay is an attempt to link these changes in land use, habitat fragmentation and loss of biodiversity to water quality and changes in Australian rivers.

Previous analyses and interpretations of Australian water quality data by Harris (1999b, 2001) and others—including information produced as part of the National Land and Water Resources Audit (<http://www.nlwra.gov.au>)—have shown clear relationships between land use, water quality and catchment exports. Water quality in many Australian surface waters is poor with increasing levels of salt, turbidity and nutrients. When compared to data from the rest of the world, the biogeochemistry of Australian catchments is in some respects peculiar, with strong evidence of low nitrogen concentrations, particularly in inland rivers (Harris 1999c, 2001).

The conclusion reached herein is that it is possible to relate changes in land use, and the consequent changes in biodiversity, directly to impacts on water quality. In this respect, biodiversity has a function in landscapes that goes well beyond its iconic value. These functions have been termed "ecosystem services" and much recent emphasis has been placed on the value of these services. A full understanding of the functional value of biodiversity requires an understanding of the processes that link the biology and ecology of catchments to their hydrology and biogeochemistry. This essay is an attempt to further that understanding.

## Catchment land use, hydrology and nutrient exports

Recent analyses by Harris (2001, 2002) and Bormans, et al. (2002) have shown a number of major impacts of land use change on catchment behaviour and water quality in Australian rivers and estuaries. Catchment hydrology has changed since clearing occurred in that both runoff and groundwater recharge have increased. Rates of groundwater recharge and downstream transport of materials have increased dramatically since western agriculture was introduced in Australia. This appears to be due to a reduction in the leaf area of the vegetation and therefore a decrease in evapo-transpiration (Holmes and Sinclair 1986, Hatton et al. 1994, Zhang et al., 1997, 1999). Compared to that observed under native bush, groundwater recharge has increased by at least an order of magnitude (Walker et al. 1999) and erosion and sediment transport to coastal waters have increased by at least one to two orders of magnitude (Wasson et al. 1996).

Conversion of land use to agriculture or grazing also commonly results in soil erosion and gullying and increased downstream transport of nutrients (Harris 2001) and suspended particulate material (Prosser et al. 2001). Similar patterns have been observed elsewhere (Caraco 1995, Caraco and Cole 1999, Cole and Caraco 2001). Clearing of native vegetation and conversion of land use to agriculture has also resulted in higher mobility of major ions (Cl, $SO_4$, Na, K, Ca) and salinisation of soils and catchments. These effects are now well documented and are widespread in Australia (see eg Jolly et al. 2001).

Nutrient exports from cleared Australian catchments have increased with greater delivery of C, N and P to coastal waters (Harris 2001, see also Caraco 1995, Caraco and Cole 1999, 2001). Likens and Bormann (1974, 1995) showed many years ago that nutrient and cation exports increased dramatically in clear-felled catchments. The overall ratio of C, N and P discharged from Australian catchments is in roughly Redfield proportions (106C:15N:1P by atoms, Redfield 1958, Harris 2001, 2002) and, despite large variations in flow, the ratio is quite stable. This is indicative of the fact that washout of nutrients from decay and diagenesis in the soil is a significant source of nutrients and cations (Markewitz et al. 2001). There is now good evidence for a close coupling between the state of the terrestrial ecosystems and water quality (Engstrom et al. 2000).

The observed relationships between catchment clearing and exports of nutrients and major ions are decidedly non-linear. All the available observations (Bott 1993, Walker et al. 1998, Eyre et al. 1999) indicate that the export of nutrients and major ions remains low as long as less than about 50% of the catchment is cleared of native bush. Once the clearing exceeds 50% of the catchment, horizontal and vertical movement of water through and across the landscape increases sharply and nutrient exports increase exponentially. Similar observations have been made in urban

catchments; catchment exports of N and P rise exponentially with increasing population density, and as the TN and TP exports increase more and more of the TN and TP exports are in available forms (Ferguson et al. 1994, Simeoni et al. 1995). In addition to increased loads of total N and P (TN and TP) sourced from cleared and agricultural land, the forms of N and P are changed so as to proportionally increase the loads of available forms of dissolved inorganic N and P (DIN and DIP) thus rendering it more biologically available (Harris 2001, Caraco and Cole 2001).

Harris (1999a) argued that many features of the ecology of aquatic systems could be explained in terms of some simple propositions. These propositions related the ensemble properties of aquatic ecosystems to the physiology and population dynamics of the major species and functional groups found in those aquatic ecosystems. Harris (1999b) then elaborated on this approach to explain features of the biogeochemistry of rivers, lakes and estuaries. Australian estuaries and coastal embayments show strong hysteresis effects when subjected to increased nutrient loads. When nutrient loads increase seagrasses are replaced by macrophytic algae and, finally, phytoplankton blooms – and the systems do not recover easily (Harris 1997, 1999b,c, Harris et al. 1996). Simple models of these systems (Harris 1999c) show that the strong hysteresis effects have their origin in the physiological responses of the major functional groups in these ecosystems. In short a study of "ecosystem physiology" can explain much (Harris 1999a). Simple models can have some very complex and realistic emergent properties.

What is now required is a fusion of this knowledge about aquatic impacts with information about the relationships between terrestrial biodiversity, ecosystem function and biogeochemistry so that some useful explanations of the complex linkages between terrestrial and aquatic systems may be achieved. In effect what is required is a definition of what Vollenweider (personal communication) called "catchment physiology" or the ways in which the ensemble properties of the constituent species together make up the catchment response. "Catchment physiology" is presumed to be the sum of the physiological activities of the constituent species in the catchment. Again we might expect there to be some emergent properties that arise from the complex spatial and temporal interactions.

## Body size, abundance and biodiversity in terrestrial ecosystems

Many aspects of the structure of ecosystems are predictable from simple models. Neutral and field theories of plant communities produce allometric distributions of individuals with a power law relationship describing the distribution of body size and abundance between large and small organisms (Walker and Dowling 1991, Enquist et al. 1999, Wu et al. 2000, Enquist and Niklas 2001). Simple models of interactions between plants can explain emergent properties of terrestrial ecosystems such as the allometric self-thinning rule and the distribution of biomass between the ranges of individuals in the community. Models that produce these kinds of statistical distributions of body size can be very simple – requiring only interactions between individuals also varying allometrically in growth rate, body size and dispersal (Pachepsky et al. 2001). Enquist and his co-workers (op. cit.) have elucidated a large number of such relationships. Gilooly et al. (2001) have shown that models of temperature and body size can explain most of the variability in metabolic rate between organisms and Valentini et al. (2000) have shown how such relationships control the overall metabolism of carbon in ecosystems. Such is the power of these physiological and allometric models of community structure and ecosystem process that some have argued for a neutral theory of macro-ecology (Brown 1995, 1999, Bell 2001).

Complex interactions between organisms in ecosystems also produce similar power law distributions of body size and abundance, and the statistical distributions are very like those produced in Complex Adaptive Systems (CAS, Harris 1999). Kaitala et al. (2001) and Wootton (2001) showed that there are self organised dynamics in populations distributed in patchy environments. The combination of internal dynamics and environmental perturbations in complex ecosystems produce similar results to the neutral models, so neither result is a true test of the underlying cause. Pattern cannot be used to unambiguously infer process, but it is interesting and highly suggestive that some parsimonious neutral models based on physiology and allometry can produce remarkably realistic distributions of body size, abundance and biodiversity (Mouillot at al. 2000, Pachepsky et al. 2001, West et al. 197, 1999a, 1999b, Whitfield 2001). Ritchie and Olff (1999) produced a synthetic theory of biodiversity from some simple structuring rules of allometry, dispersal and physiology.

So why might neutral models be so powerful? As opposed to aquatic ecosystems that are characterised by temporal fluctuations in fluid media, terrestrial systems are more usually characterised by strong spatial patterns and "patch dynamics" (Wu and Loucks 1995). Australian ecosystems are no exception and the patch dynamics of terrestrial ecosystems are a critical part of the overall functional dynamics (Ludwig et al. 1997). Dispersal of organisms across patchy environments weakens competitive interactions and seems to produce species distributions in space and time that are

largely determined (a) by the regional pool of species (and a source of immigrants to a particular patch) and (b) by the local physical and chemical environment. Habitat patchiness and environmental variability serve to weaken the strength of competitive interactions and lead to a more individual view of ecology (Walter and Hengeveld 2000). For example, Austin and his co-workers have shown that aspects of the physical environment (slope, aspect, temperature, water availability) are strong determinants of the distributions of Eucalypt species (Austin 1998, 1999, Austin et al. 1996, Anderson et al. 2000, Pausas and Austin 2001). Therriault and Kolasa (1999, 2000) have shown that physical determinants of ecosystem structure are very important and Kolasa (pers. comm.) has estimated that physical factors may, in patchy systems, determine as much as 70% of the species distribution patterns.

Many observations of species distributions in sampling areas of various sizes frequently produce what are called unsaturated (or Type I) distributions (Gaston 2000). i.e. when the biodiversity of smaller areas is compared to the biodiversity of regions there is a linear relationship. This may also be taken to be evidence of weak competitive interactions and the predominance of regional and contingent immigration (Cornell 1999, Fox et al. 2000, Blackburn and Gaston 2001). Again pattern may not be a reliable guide to process because various kinds of species interactions and differing relationships between scales of diversity (at patch, local and regional scales) can produce similar results (Loreau 2000, Shurin et al. 2000, Bartha and Ittzes 2001, Whittaker et al 2001). Even in patchy and dynamic environments there clearly are some competitive interactions that structure community processes (Symstad et al 1998). Trophic interactions in food chains are also powerful structuring processes but again some relatively simple models can produce highly realistic results (Williams and Martinez 2000).

Notwithstanding the practical and theoretical objections to simple neutral models, the overall impression that emerges is that there is considerable descriptive power in ecosystem models that incorporate allometry, physiology and biophysical environmental conditions (Harris 1999a). Despite the apparent complexity of the natural world, it certainly seems to be possible to explain many aspects of the overall biodiversity and functioning of both terrestrial and aquatic ecosystems (and many of the emergent properties of these ecosystems) by means of simple algorithmic models (Wootton 2001).

## Biophysical limits to biomass and production in catchments

There is ample evidence in the Australian landscape that the upper limit to plant biomass and production is set by biophysical parameters such as water, rainfall, soil moisture and evaporation. Work over many years by Specht and others had shown that many aspects of Australian terrestrial pant communities are set by such factors (Specht 1972, Specht and Specht 1999). In many respects it would seem that most basic biophysical properties of ecosystems are independent of species composition; for example, the Holmes-Sinclair relationship between rainfall, runoff and evapo-transpiration ($E_T$) is independent of species composition and dependent instead on the dominant plant growth forms in the catchment (Holmes and Sinclair 1986, Zhang et al. 1999). Biophysical constraints appear to set upper limits on evaporation from plant communities so that over sufficiently long time periods a form of equilibrium is reached (as suggested by Eagleson, see references and discussion in Hatton et al. 1997).

Recent work by Enquist and others has shown the importance of some simple structuring relationships between plant structure and function so that, for example, total xylem water flux of terrestrial plants is largely independent of species composition across a wide range of plant functional types and sizes (Enquist et al. 1998, 1999, Enquist and Niklas 2001, Niklas and Enquist 2001, West et al. 1998, 1999a, b). Many aspects of terrestrial plant communities may also be explained in terms of simple allometric and fractal properties of plant structure and function (West et al. 1999a, Mouillot et al. 2000). All of these observations indicate that there are some relatively simple features of plant physiology (eg transport networks; Banavar et al. 1999) that structure the responses of terrestrial communities to the physical environment..

Similarly, Raupach et al. (2001) have shown that the basic stoichiometry of living organisms – which, for microbiota, closely approximates to Redfield proportions – is responsible for the overall storage and metabolism of C, N and P in landscapes. In a broad sense the modelling has shown that when the biophysical limits of water and temperature are taken into account across the Australian continent, it is possible to produce realistic distributions of biomass, productivity and soil nutrients. So do the plants themselves determine soil nutrient levels or are the plants subservient to the underlying geology? This is not a new debate (see Beadle, 1968, Specht, 1996). The answer seems to be largely the former – and that the biophysical environment plays an important determining role (Adams 1996). Given that the basic stoichiometry of living organisms appears to be the determinant of soil nutrient stocks it is perhaps not surprising that the nutrient ratio of Australian catchment exports closely follow Redfield proportions.

These models and observations indicate that in the relatively arid Australian landscape climate, in the form of water availability and temperature, has an overall role in determining the structure of plant communities across the landscape (Specht and Specht 1999). Furthermore some simple functions of physiology and nutrient stoichiometry underlie and determine the overall response in terms of water balance and nutrient cycling. The native Australian bush is both biologically diverse and a highly efficient user of water and resources (Specht and Specht 1999, Pate and Bell 1999). Land clearing and deforestation fragments the native bush, reduces biodiversity and destroys the original hydrological equilibrium. Reduction in leaf area and water use efficiency leads to disruption of the hydrological balance and increases in runoff and infiltration (Burch et al. 1987, Specht and Specht 1999). The frequency and magnitude of peaks in runoff change and nutrient exports increase (Townsend and Douglas 2000).

## Habitat fragmentation, biodiversity and function in catchments

All the models and observations of habitat fragmentation indicate that as the patch size of fragments of intact ecosystems is reduced then overall species number and abundance declines. Biodiversity is lower in fragmented landscapes (Saunders et al. 1991). Intuitively this must be true in situations where immigration becomes less likely as patches become more and more isolated, and where mortality rates increase due to disturbance within patches. One further factor that reduces biodiversity is the reduction in habitat complexity that occurs in smaller patches due to grazing, logging, removal of dead wood etc. Species requiring complex habitats show proportionally greater reductions in abundance in smaller fragments (Freudenberger 2001, Lindenmeyer et al. 2001).

As biodiversity declines in fragments then ecosystem function will be compromised. Many studies now show that reduction in biodiversity leads to reduced biomass, productivity and nutrient use by plants (Risser 1995, Chapin et al. 1998, 2000, Tilman 1999, 2000, Tilman et al. 1996, 1997a, 1997b, 2001b). Both large-scale experiments (Hector et al. 1999) and literature surveys (Schlapfer and Schmidt 1999, Diaz and Cabido 2001) reveal statistically significant relationships between biodiversity and a number of aspects of ecosystem function. The relationship is decidedly non-linear indicating functional complementarity between species – more species give better total resource coverage and improved function. Tilman (2000) likens the effect to overlapping snowballs splattered on a barn door. Ecosystem function saturates at high biodiversity (as the snowballs overlap), but declines when species number is small (Chapin et al. 1998, 2000, Tilman 1999, 2000, Tilman et al. 1997a, b). Because function appears to saturate, some have therefore argued that to preserve ecosystem function it is not essential to preserve all the original, un-fragmented regional biodiversity (Schwartz et al. 2000). Tilman et al. (2001) have demonstrated that the longer plot scale experiments are run, the more ecosystem function continues to improve with species number.

Most importantly, perhaps, it is not just reduction in species number and biodiversity that is important; it is reduction in the number of functional groups that compromises ecosystem function (Bengtsson 1998, Hulot et al. 2000, Diaz and Cabido 2001, Loreau et al. 2001). Overall, reductions in plant biodiversity lead to increases in nutrient concentrations in soils, less efficient use of soil nutrients and lower productivity (Tilman et al. 1996, 2001b). While there are some individual and idiosyncratic effects of particular species on ecosystem function (Wardle et al. 1998, Emmerson et al. 2001), Wardle and his co-workers discovered precisely the expected relationships between a number of aspects of nutrient dynamics in small vegetated islands and variations in the sizes of those fragments (Wardle et al. 1997). Soil nutrient concentrations in particular are higher in smaller patches with fewer species. Forests normally cycle nutrients very efficiently

(Attiwill et al. 1996) but detailed work by Durka et al. (1994) showed that reductions in the growth rates of trees led to increased nitrate leaching from woodland soils. Tilman et al. (1996) showed the same effect from reduced biodiversity in artificially manipulated plots. Higher nutrient exports are to be expected when habitat fragmentation occurs and biodiversity is reduced.

Pate and Bell (1999) have done some of the most complete work on functional complementarity in Australian woodland ecosystems. They dug up and categorised the root systems of the main species in the *Banksia prionotes* woodlands of Western Australia. Species grew at different times of the year and had various rooting depths and distributions. Pate and Bell (1999) showed that the functional complementarity between the various rooting strategies was responsible for the high water use efficiency in these woodlands. Replacement of these highly diverse woodland ecosystems by a single crop growth form and physiology – that of annual grasses in the form of wheat reduces water use efficiency and increase recharge. The hydrological impacts of land clearing for agriculture in Australia have been well documented for about 100 years (see eg Walker et al. 1998). The resulting ground water rise and the mobilisation of salt has caused, and is causing, severe and widespread problems.

## Spatial patterns, patch dynamics, soil structure, hydrology, through-flow and nutrient mobility in catchments

Land use change, from native woodland ecosystems to crops or pastoral systems changes many aspects of the spatial patterning and patchiness of landscapes. Ludwig et al. (1997) gave an excellent example of the importance of species-specific spatial patterning in arid zone landscapes. The dominant open woodland species of the arid zone (eg tussock grasses and mulga, *Acacia aneura*) are highly patterned in unmodified bush so that runoff and runon zones are separated. Infiltration is highest under the mulga where the deep roots create networks of macropores. Clearing and ploughing or trampling destroys these macropore networks, rapidly decreasing the rate of infiltration of water and increasing runoff (Greene 1992). The entire functioning of these landscapes depends on the spatial patterns created idiosyncratically by the dominant species (Ludwig et al. 1997).

Other dominant species in the Australian landscape, such as termites, also create macropores and increase infiltration. Holt et al. (1996) found that increases in grazing pressure significantly decreased hydraulic conductivities through increased trampling and decreased abundance of termites in grazed areas. Holt and Coventry (1990) showed that termites were a very important part of the overall nutrient economy of Australian savannas, being responsible for more than 20% of the carbon cycling. When coupled with alterations in the fire regime, agricultural practices in tropical catchments cause marked changes in the catchment hydrology, nutrient cycling and exports. Nutrient exports increase and the frequency and magnitude of runoff events are altered (Townsend and Douglas 2000).

Land clearing and the removal of deep-rooted perennials have been shown to lead to reduced infiltration and increased runoff (Burch et al. 1987). The effect of fire is similar (Townsend and Douglas 2000). Forested and woodland catchments have higher infiltration rates than grassland catchments so that surface runoff and sheet flow are greater after clearing. Fire regimes also influence runoff characteristics (Townsend and Douglas 2000). There is a tendency for cleared catchments to have more impermeable areas and higher water tables so that they have larger areas that are quickly wetted up during rain (Burch et al. 1987). Even depressions in forest catchments were relatively permeable so that runoff is delayed and reduced in magnitude. Sources of increased nutrient loads to rivers are spatially distinct and the importance of saturated areas in catchments is well known because they lead to increased surface flows and higher runoff (Pionke et al. 2000).

Macropores have been shown to be very important in providing preferential flow pathways for infiltration and through-flow, thus connecting soil

processes and nutrients to water quality in receiving waters. Infiltration is higher and deep drainage is more rapid in soils with greater numbers of macropores, and the numbers of macropores decrease under tillage (McGarry et al. 2000). There are numerous literature accounts of the effect of macropores in ensuring rapid and effective connection between soil chemistry and water quality (Cox et al. 2000, Goss et al. 2000, Heathwaite and Dils 2000, Pampolino et al. 2000).

Elsenbeer et al. (1994) observed large differences in the water quality of streams depending on whether the water came from fast overland flow pathways or slower, shallow groundwater influences. In their rainforest system the rapid surface flows were more dilute than the slower pathways that connected to shallow perched water tables. In urban and agricultural catchments the more rapid pulses of surface sheet flows are usually more concentrated than some of the slower base flow components because they contain eroded materials and higher concentrations of fertilisers and animals wastes (Simeoni et al. 1994, Ferguson et al. 1995).

Chittleborough et al. (1992) and Smettem et al. (1991) have noted large differences in flow paths between winter and summer in Australian catchments. When the soil is wetter in winter most of the flow is via macropores in the B horizons. In summer (when the soil is drier and it might be expected that infiltration would be greater) the presence of dry, hydrophobic organic matter in the A1 horizon causes decreased infiltration, increased surface flows and erosion of the A horizon. These seasonal changes in the dominant pathways were visible in the dissolved organic carbon exports from the catchments. Over grazing and erosion in tropical catchments, which are dry between intense rainfall events, leads to complete stripping of the A horizons from these soils (Ludwig et al. 1997). Even in forests where infiltration may be expected to be high, a protective cover of dry hydrophobic litter and organic material may negate the effect.

Gullying is a common response to clearing of catchments in upland areas in Australia when increased surface flows result from land clearing (Prosser et al. 2000) and the source of much of the suspended sediment in Australian lowland rivers is erosion from gully walls (Wallbrink et al. 1998, Martin and McCulloch 1999). Most of the P in Australian systems is closely linked to the particulate fraction and is also sourced from gully walls (Caitcheon et al. 1995). Trampling and grazing by cattle in tropical catchments is sufficient to decrease infiltration and increase surface runoff to the point where gullying can occur (Ash et al. 1997, Roth, in prep.) Anecdotal evidence points to the fact that the introduction of cattle into tropical Australia in the 1860s led, as expected, to the drying up of perennial springs and creeks and an increase in flashy discharges from the Burdekin River.

## Catchment loads and receiving water quality

The combination of surface and through-flow sweeps nutrients, organic material and suspended solids from the soil into streams and rivers. Much evidence is now emerging to show that there is a close connection between land use, soil characteristics and water quality in receiving waters (Dillon and Molot 1997, Carpenter et al. 1998, Crosbie and Chow-Fraser 1999, Engstrom et al. 2000, Arbuckle and Downing 2001).

Land clearing and agricultural development has produced a global trend towards river nutrients loads having a stoichiometry which approximates the Redfield (1958) ratio (106C:15N:1P by atoms). Over time, C, N, P and Si in rivers have become more biologically available (Justic et al. 1995). We now realise that almost all macro- and micro-nutrient transformations in soils and water are microbially controlled and that events in catchments can be explained by a combination of the physiology of the macro- and micro-biota (Harris 1999b). There are great similarities between soils and water in the ways that major elements are processed (Wagener et al. 1998). The predominant approximation to the Redfield ratio in C:N:P ratios in water quality data (Harris 2001) is a good indication of the importance of microbial processes operating in catchments and their controls on nutrient ratios and cycling. We have speeded up the cycling of elements in catchments through land clearing, ploughing and agricultural development.

Harris (1999b) discussed the relationships between changes in land use and the rates of export and predominant forms of C, N and P. Catchment exports of N and P from diffuse sources are a strong function of land use, population densities, agricultural practices and urban development (Carpenter et al. 1998). In short, forested catchments export mostly dissolved organic carbon and little N or P. Agricultural and urban catchments show increased exports of C, N and P with more particulate organic carbon (from eroded A horizons), particulate P from gullying and more dissolved inorganic N and P from fertilisers and wastewater inflows. Howarth (1998) showed that export of N from cleared catchments is a function of agricultural N inputs (fertilisers etc) and atmospheric N deposition, where the deposited nitrate and ammonia comes from fossil fuel combustion and agricultural activity.

Aitkenhead and McDowell (2000) have shown that there is a very close relationship between soil C:N ratios and the export of dissolved organic carbon from catchments around the world. C:N ratios under forests and woodlands therefore determine the C exports from catchments and DOC concentrations in rivers. The dominant plant groups determine the forms and turnover of C in soils and structure biotic interactions in ecosystems (Wardle et al. 1998). In Australia surface soils C:N ratios are about 20-30 under open *Eucalyptus* forest (fresh litter may have C:N ratios as high as 100) so that N is consumed during the decomposition of the litter (Parnas 1975) and large amounts of DOC are exported (Hopkinson and Vallino

1995, Attiwill et al. 1996). This appears to be typical of subtropical systems and results in terrestrial and aquatic ecosystems high in C and poor in N. Organic matter entering rivers from catchments appears to be sourced primarily from vegetation in riparian zones close to the river (McClain et al. 1997) reinforcing the importance of connectance between the catchment and river channel and the need to understand the storage and mobility of dissolved and particulate organic matter off stream in catchments.

The result of land clearing in Australia has been to produce rivers which have higher concentrations of available nutrients, and which are more turbid and saline, than before the advent of agriculture and urban development (Bott 1993). Harris (2002) showed that the turbidity in Australian rivers has a geochemical signal very similar to the drainage from acidic and sodic soils that are frequent in agricultural areas. Turbid Australian systems can be thought of as dilute soil and sediment suspensions (Wagener et al. 1998) so that the microbial interactions between organic molecules, iron, C and S discussed by Froelich et al. (1979) and Roden and Edmonds (1997) come into play. It is reasonable to conclude that the Fe:P ratio is a key factor in the availability and speciation of P in these waters (Gunnars and Blomquist 1997, Gerritse 1999, Harris 1999b). Certainly interactions between particulate materials and sediment-water column interactions control the concentrations of soluble P in the water column (House and Denison 2000, Bowes and House 2001, May et al. 2001)

In turbid Australian rivers there are a series of microbial interactions between clay particles, organic coatings, iron concentrations and the speciation of P in the water (Harris 2001, 2002). The proportion of DIP to TP also stays roughly constant (10-30%) in concentration terms in the rivers, unless there are large wastewater inflows. P exports rise as a function of altered land use and urbanisation but the proportion of DIP to TP appears to be roughly constant across a range of land uses as long as there is a large surface area of clays and organic coatings. This differs from the situation in the more oligotrophic and less turbid waters of the northern hemisphere (Janus and Vollenweider 1981) where DIP rises as a fraction of TP as waters become more eutrophic.

Concentrations of nitrate and ammonia in Australian rivers are usually small in rivers draining forested catchments (Flinn et al. 1979, Harris 2001, 2002). This is a common observation world wide (Caraco and Cole 2001). The explanation for this lies in the close coupling of root uptake and microbial cycling of N in forest soils (Durka et al. 1994, Perakis and Hedin 2001). In agricultural soils, reduction in biodiversity and the addition of fertiliser leads to an uncoupling of microbial recycling and plant uptake. Soil nitrate and ammonia concentrations increase in fragmented and agricultural ecosystems (Wardle et al. 1997) and washout to rivers becomes greater (Carpenter et al. 1998, Caraco and Cole 2001). N may be flushed out of soils by fluctuating water tables and soil moisture levels (Creed et al. 1996, Creed and Band 1998). One certain influence on N exports is the density of cattle

and sheep in the catchment (Carpenter et al. 1998). Elser et al. (1996, 2000) and Elser and Urabe (1999) showed how the recycling of C, N and P in terrestrial and freshwater ecosystems was dependent on the size of the dominant producers and consumers in the ecosystems. Land clearing and agricultural development has done precisely this in Australian catchments distorting the balance of elements and leading to increased exports.

## Land use change and aquatic ecosystem impacts: complexity, hysteresis effects and non-linear responses

Before the clearing of the land for agriculture, deep-rooted perennials that had evolved a diverse range of functional types largely dominated Australian catchments (Pate and Bell 2000). They were highly efficient users of the available water and a long-term quasi-equilibrium had developed (Hatton et al. 1997, Specht and Specht 1999). In addition there was close coupling of nutrient cycling and uptake. We have replaced this dominant land use type with a mosaic of much less efficient, largely agricultural, ecosystems that leak water and nutrients because of reduced biodiversity and reduced water use efficiency and nutrient recycling. The hydrological balance has been disturbed and the balance between evaporation, recharge and runoff has been changed (Wu et al. 2000). Water quality in lakes and rivers reflects the dominant land use in their catchments (Carpenter et al. 1998, Crosbie and Chow-Fraser 1999, Arbuckle and Downing 2001). If we are to preserve water quality and our lakes and estuaries, the challenge is to replace what function we can.

How much of the original landscape function must we replace? The data clearly show that once 50% of the original native Australian bush is removed then the hydrological and nutrient fluxes from catchments are disturbed enough to greatly increase exports (Walker et al. 1998). Even removing 20-30% of the forest cover in American watersheds gives a 10% chance of increasing nutrient exports to the median level of predominantly agricultural or urban catchments (Wickham et al. 2000). Given the range of possible agricultural crops (without developing totally new perennial crops), the only practical way to replace landscape function is to replace it in the form of mosaics of annual and perennial plants, patches of remnant native ecosystems surrounded by farmland. The question is then to what extent is this possible, and to what extent can a mosaic of different land uses contain hydrological and nutrient fluxes at landscape scales?

Connectivity between the catchment and the river is a key factor. We do know that riparian strips even a few metres wide reduce N exports from cleared land quite effectively (Davies and Nelson 1994, Vought et al. 1994). Riparian zones 10-20 metres wide reduce N exports by 60-80% (Vought et al. 1994). Reduction of riparian strips in agriculture contributes greatly to catchment exports, particularly in areas where row crops are grown. Given that inputs of nutrients to rivers are largely sourced from riparian vegetation there are very good arguments for ensuring that wide riparian strips, dominated by native vegetation are replaced along Australian riverbanks. Of course, water extraction leading to drastic changes in river flow patterns is also a factor that will make it difficult to restore large amounts of the original riparian native vegetation. Control of extractions and the restoration of the original environmental flow patterns – including the longer-term interannual variability – is a key requirement for effective river management (Puckridge et al. 1998, 2000).

For a number of reasons it appears that mosaics of larger blocks of native vegetation interspersed with pastoral and cropping land would be better than the same proportion of catchments divided into smaller fragments. As long as grazing is controlled, biodiversity and ecosystem function are both improved in larger fragments (Saunders et al. 1991) and, if strategically placed so as to control and intercept runoff from farmlands, these larger fragments would also control connectivity to the river channels. Larger fragments have more species and more complete biophysical function (Specht and Specht 1999). There are therefore some complex non-linear interactions between the landscape pattern, the precise manner of the fragmentation and the landscape function. These complex interactions do however appear to have some simple underlying causes.

We need to pay greater attention to the links between plant growth forms and soil microstructure. Macropores are clearly important for the role they play in controlling infiltration and runoff. Constant tillage and trampling by cattle changes the soil flora and fauna, eliminates macropores and favours erosive surface flows (Greene 1992, Holt et al. 1996). Larger forested fragments with higher infiltration under the trees would make more effective use of runon water and nutrients.

If we are to protect water quality and landscape function then we need to not only build biodiversity in habitat fragments but also restore the biophysical functioning and biogeochemistry of the mosaics of land uses in catchments (Hobbs and Morton 1999). We need to pay more attention to soil biodiversity and function and the effects of particular functional groups of organisms (Bengtsson 1998). This will require an appreciation of landscape function at all scales – from macropores to entire catchments. There is therefore an emergent property of the spatial arrangement and connectivity between ecosystems fragments at landscape scales. Clearing changes patchiness and subtly alters landscape function (Ludwig et al. 1997, Wu et al. 2000). This is the essence of landscape ecology (Barbault 1995, Ludwig et al. 1997). Structure is important in the longer-term dynamics of landscapes (Shugart 2000).

The strength of interactions between species will have a big impact on the restoration of ecosystems. If ecosystems act as complex adaptive systems with pervasive and strong interactions between species then restoration will be difficult (O'Neill 1999) and there will be surprises (Loucks 1985). On the other hand if inter-specific interactions are weaker and environmental drivers are dominant (eg Austin 1999, Anderson et al. 2000) then ecosystem reconstruction is still possible as long as regional biodiversity is not compromised, immigration is still possible and mortality rates are not too high. These are important questions that must be answered. I argue here that inter-specific interactions in patchy landscapes are weak and that some simple underlying physiological and interaction models can explain much.

There are some important hysteresis effects in ecosystems that must be considered. These are "points of no return" in landscape restorations that are to be avoided if at all possible. Muradian (2000) and Scheffer et al. (2001) have reviewed some of the causes for these hysteresis effects in ecosystems. One very good example is the switch between alternative states in shallow lakes and estuaries (Scheffer 1998, Scheffer et al. 1993, Harris 1999b). These shallow water bodies switch between macrophyte and phytoplankton dominated states. Once switched from clear and macrophyte dominated to turbid and phytoplankton dominated they are very difficult to switch back again (Scheffer 1998, Harris 1999b).

In catchments both fire and erosion can cause long term state shifts that can be difficult to reverse. In arid savannahs, fire regimes and overgrazing can cause switches between states dominated either by grasses or woody shrubs (Ludwig et al. 1997). Australian plant successions may suffer irreversible damage if clearing is accompanied by erosion and loss of soil nutrients (Walker et al. 2001). Lyons and Schwartz (2001) have shown that invasion of communities by exotic species was more likely when the overall biodiversity was reduced. However, other work has shown that loss of biodiversity from habitat fragmentation may be difficult to reverse because species loss may lead to community closure (Lundberg et al. 2000), although the lack of widespread evidence for strong competitive interactions (Gordon 2000) must make this a weak effect.

Surface runoff rises as an exponential function of rainfall (Specht and Specht 1999) and runoff and erosion events are spatially limited and confined to high rainfall events (McIvor et al. 1995, Heathwaite and Dils 2000). In the Australian context storm flows carry a very large fraction of the total N and P loads in only a small portion of the year (Olive and Walker 1982, Cullen and O'Loughlin 1982) so that there are significant methodological problems in measuring the exports from catchments (Cullen et al. 1978). Much of the water and nutrient runoff from catchments comes from relatively small areas and in relatively short time periods in most cases (Cullen et al. 1978, Olive and Walker 1982, Cullen and O'Loughlin 1982, Caitcheon et al. 1995, Dillon and Molot 1997, Wallbrink et al. 1998, Pionke et al. 2000, Prosser et al. 2001).

The pervasive non-linearity in the reposes of catchments to clearing (Bott 1993, Walker et al. 1998, Eyre et al. 1999) is strong evidence of some degree of non-linear interactions between species and their distributional mosaics. However, this may simply be an emergent pattern that arises from small-scale interactions between species diversity, complementarity and functional redundancy (Chapin et al. 1998, 2000, Tilman 1999). It is heartening to know that large-scale landscape properties can be built up from simple small-scale interactions (Kaitala et al. 2001, Wootton 2001) and that the emergent properties can be modelled as the result of local processes (Ritchie and Olff 1999). In any case, simpler models of ecosystems that show emergent properties, whilst not perfect, may be

usable in an adaptive management framework and may be useful guides to action and catchment restoration (Bigelow et al. 2001).

## Modelling and prediction

There is a recent move towards the construction of large-scale GIS-based models of catchment structure and function for use as decision support systems for catchment management (eg Ormerod and Watkinson 2000, Viney et al. 2000, Sklar et al. 2001, Cassell et al. 2001, Gentile et al. 2001). There are well known problems with hydrological models involving interactions between model complexity, parameterisation and data adequacy (Loague and Freeze 1985, Beven 1989, 1993, Jakeman and Hornberger 1993, Hatton et al. 1994) as well as adequate knowledge of the underlying processes (Haus 1990). It really is important to know if "more is different" (Anderson 1972) and whether there are important cross-scale non-linearities in the responses of ecosystems.

If this is so then it will only ever be possible to model the emergent properties as entities at larger scales (Harris 1998) and fully parameterised biophysical models of processes in catchments will never be able to be validated properly. The modelling and understanding of the relationships between land use change, hydrology and nutrient exports is important because of the non-linearities and hysteresis effects present in these systems – not just in the catchments but also in the receiving waters. What the models must reproduce is not just the annual average flows but also the frequency and magnitude of flood events and the effects of land use change on these events.

Models of the emergent properties of ecosystems are widely used in catchment and ecosystem impact models (Harris 1998). I now argue that some simple algorithmic models of physiology and disturbance that can realistically reproduce landscape function underlie these models of emergent properties. There is hope therefore that despite the pessimism of Harris (1998) there are some simple underlying rules which can be understood and explained and that in terrestrial, as in aquatic ecosystems, the world may indeed be "simpler than we think" (Harris (1999a).

The algorithmic process models logically underlie the dynamical simulation models. These algorithmic models of individual survival and growth must account for the outcomes of numerous processes – disturbance, dispersal, birth, growth and death for different species and functional groups in the ecosystem – and the process base for both model types must be basically the same. Much can be predicted from a basic understanding of some basic physics, physiology and the design of the organisms (Harris and Griffiths 1987, Harris 1999a, b, 2001) but the fundamental difference between the two types of models is the lack of spatial pattern and emergence in the dynamical models. Spatially explicit models of individual dispersal, growth and death show the emergence of large-scale patterns (Wootton 2001). Patch dynamics are critical in terrestrial habitats (Wu and Loucks 1995) whereas temporal dynamics, (rainfall, flood, drought, ENSO) are dominant in fluid environments. Catchments are combinations of both but the spatial

patterning and emergence is critical in terrestrial systems (Wootton 2001). Dynamical simulation models do not adequately represent the spatial emergence that is so critical for the function of catchments. The function of the entire entity is an emergent property and therefore prediction is limited except in terms of statistical properties at a fairly high level (Harris 1998).

Harris (1997, 1999c) showed that estuarine and coastal systems are strongly non-linear in their response to nutrient loads and that hysteresis is common. Once pushed from a seagrass dominated state to a phytoplankton dominated state recovery is difficult (Harris et al. 1996). Shallow lakes show very similar state shifts (Scheffer 1998, Scheffer et al 1993, 2001) and there is at least anecdotal evidence for a similar response in Australian rivers (Harris 2002). The systems responses are produced by the non-linear physiological interactions between the dominant functional groups (Harris 1997, 1998, 1999c).

There are important and subtle differences in the model responses when nutrient loads are either modelled as smooth functions of time or are strongly pulsed (as in nature). Estuarine and coastal ecosystems appear to be highly sensitive to changes in the frequency and magnitude of pulsed inputs of sediment and nutrients (Webster and Harris, in prep.) – and this is precisely what has been changed by anthropogenic changes in the catchments. Changing the frequency distribution of nutrient loads whilst keeping the annual average load constant produces major changes in the biomass of dominant functional groups in estuarine models (Webster and Harris, in prep.). Infrequent loading events lead to dominance by phytoplankton. Just as model estuarine systems respond strongly and non-linearly to changes in the statistical properties of their nutrient loads and flushing regimes (Harris 1999b,c, Webster and Harris, in prep.), rivers are also highly sensitive to changes in their flow regimes. Degradation in water quality (and dominance by phytoplankton) seems to be more probable and severe in situations where nutrient loads are increased and where there are prolonged periods of low flushing or stagnation (Harris 2002) – this is precisely analogous to the estuarine response. This has a direct bearing on the environmental flows debate in rivers – the ecosystem response is a function not just of the changes in the annual flows in rivers but also of the frequency and magnitude of floods, often over periods of years (Puckridge et al. 1998, 2000).

If changing the statistical distribution of nutrient loads changes the dominant functional groups in aquatic systems, then we might expect changes in the statistical distributions of water and nutrient availability to produce analogous effects on land. Changes to the frequency and magnitude of rainfall events and floods (for example) must interact strongly and non-linearly with the physiology and spatial pattern of species distributions in catchments. These responses would be exacerbated by clearing and fragmentation. The effects of climate change might therefore be subtler and more severe than is predicted by annually averaged model responses.

Land use change produces some highly complex events in both catchments and receiving waters: catchment and ecosystem physiologies are strongly and non-linearly linked. I have tried to show here that there is much that we know and there may be some hope that simple models of ecosystems have some realism. The biodiversity, growth forms and physiologies of the dominant species influence the transfer functions of water and nutrients from the land to the sea. Some simple models of biology and physiology provide the underlying rules that determine the emergent properties of landscapes. Despite spatial complexity and all the apparent variability that ecosystems display (non-linear responses and hysteresis effects) there is good evidence that the world may indeed be simpler than we think (Harris 1999a) and that both on land and in the water models based on some simple physics, physiology and the evolved design of the dominant organisms may be used to explain much (Harris and Griffiths 1987).

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