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SPECIAL PAPER

# Using historical ecology to understand patterns of biodiversity in fragmented agricultural landscapes

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**ABSTRACT**

**Aim** To enhance current attempts to understand biodiversity patterns by using an historical ecology approach to highlight the over-riding influence of land-use history in creating past, current and future patterns of biodiversity in fragmented agricultural landscapes.

**Methods** We develop an integrative conceptual framework for understanding spatial and temporal variations in landscape patterns in fragmented agricultural landscapes by presenting five postulates (hypotheses) which highlight the important role of historical, anthropogenic disturbance regimes. We then illustrate each of these postulates with examples drawn from fragmented woodlands in agricultural areas of south-eastern Australia, and discuss these findings in an international context. Location examples are drawn from agricultural areas in south-eastern Australia.

**Results** We conclude that there is limited potential to refine our understanding of patterns of biodiversity in human-modified landscapes based on traditional concepts of island biogeography, or simple assumptions of ongoing destruction and degradation. Instead, we propose that in agricultural landscapes that were largely cleared over a century ago: (1) present-day remnant vegetation patterns are not accidental, but are logically arrayed due to historic land-use decisions, (2) historic anthropogenic disturbances have a major influence on current ecosystem conditions and diversity patterns, and (3) the condition of remnant ecosystems is not necessarily deteriorating rapidly.

**Main conclusions** An historical ecology approach can enhance our understanding of why different species and ecosystem states occur where they do, and can explain internal variations in ecological conditions within remnant ecosystems, too often casually attributed to the 'mess of history'. This framework emphasizes temporal changes (both past and future) in biotic patterns and processes in fragmented agricultural landscapes. Integration of spatially and temporally explicit historical land-use information into ecological studies can prove extremely useful to test hypotheses of the effects of changes in landscape processes, and to enhance future research, restoration and conservation management activities.

**Keywords**

**Anthropogenic disturbance, Australia, benchmarks, cultural landscape, fragmentation, land-use history, remnant vegetation, restoration, state and transition model.**

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## INTRODUCTION

Throughout the world, the development of agriculture has resulted in the rapid transformation of continuous ecosystems to landscapes dominated by crops and pastures, within which small remnants of the original vegetation are retained (e.g. Hobbs & Saunders, 1994; Yates & Hobbs, 1997a; de Blois *et al.*, 2001, 2002). The analogy between remnant patches in agricultural

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landscapes and islands in seascapes has enabled island biogeography theory (MacArthur & Wilson, 1967) to be extended to agricultural landscapes world-wide (Burgess & Sharpe, 1981; Gilpin & Soulé, 1986; Hanski & Simberloff, 1997). However, a recent review of fragmentation experiments (Debinski & Holt, 2000) revealed that most fragmentation studies exhibited species richness patterns contrary to predictions based upon island biogeography theory. Levenson (1981), for example, showed that species–area relationships were incapable of predicting plant species abundances. The contradictory nature of many studies has led to ongoing questions about the utility of the fragmentation paradigm (Simberloff & Abele, 1982; Gilpin & Soulé, 1986; Usher, 1987; Robinson *et al.*, 1992; Hanski & Simberloff, 1997; Davies *et al.*, 2001; Watson, 2002; Hobbs & Yates, 2003; Lindborg & Eriksson, 2004).

Landscape ecology considers spatial and temporal interactions across the landscape and the influences of spatial patterns on biotic and abiotic processes (Levin, 1992; Wiens, 1997; Baker, 1999; Turner *et al.*, 2001). The discipline emerged from attempts to develop an all-encompassing fragmentation paradigm (Turner, 1989; Naveh & Lieberman, 1990; Wiens, 1997; Naveh, 1998). Despite general acceptance by plant and animal ecologists, landscape ecology has often been criticized for: (1) concentrating mainly on spatial patterns and ignoring temporal changes (Hobbs, 1999; Turner *et al.*, 2001), and (2) tending to exclude people from the landscape (Hammett, 1992; Kirkpatrick, 1999). Recent studies have placed greater emphasis on changes in functional aspects of remnant ecosystems in fragmented landscapes (e.g. Saunders *et al.*, 1991; Hobbs *et al.*, 1993; Kearns *et al.*, 1998), and have highlighted that some landscapes are better described as variegated rather than fragmented, since the landscape matrix is not necessarily hostile to all species (McIntyre & Barrett, 1992; McIntyre & Hobbs, 1999). However many studies are still conceptually based on traditional patch area–isolation concepts (Wilcove *et al.*, 1986; Laurance & Bierregaard, 1997).

The apparent contradictory nature of many fragmentation studies may simply reflect the short time frame of observations, which often cannot encompass the many indirect feedbacks that occur in anthropogenic disturbed landscapes (Debinski & Holt, 2000). Agricultural landscapes are characterized by dramatic changes on varying time-scales. Some short-term changes are predictable in periodicity (such as annual cultivation of crops) and even type (i.e. change in crops), but due to hysteresis (lag effects), longer term changes in fragments are poorly understood (MacDonald & Smith, 1990). For example, many tree species may live for centuries, and since adult plants are often less sensitive to changes in environmental conditions than juvenile stages, current patterns may simply represent a slow process of gradual extinction (Adamson & Fox, 1982; Hobbs, 1987; Bennett, 1993; Foster, 2000; Saunders *et al.*, 2003). An alternate hypothesis for interpreting the contradictory nature of many fragmentation studies is the over-riding imprint of spatially variable, historical anthropogenic disturbances, which selectively advantage some taxa and disadvantage others (Wilcove *et al.*, 1986). Unfortunately our ability to detect the effects of short- and long-term processes may be clouded by what Dovers (2000) describes as our 'amnesia', or ignorance of past human events and their residual effect on landscapes.

'Historical ecology' has been cited as a new paradigm in which ecologists view ecosystems as *historically* and spatially influenced non-equilibrium systems that are complex and open to human inputs (Hammett, 1992; Balée, 1998; Swetnam *et al.*, 1999; Egan & Howell, 2001). This framework recognizes that: (1) historical events play a major role in ecology, as changes in abiotic conditions or species composition that happened in the past can have large and often irreversible effects on the structure and dynamics of present-day ecosystems (de Blois *et al.*, 2001, 2002), and (2) remnant ecosystems may exist in various non-equilibrium states due to a complex history of anthropogenic disturbance regimes (Naveh, 1998; Pyne, 1998; Motzkin *et al.*, 1999; Lugo & Gucinski, 2000; de Blois *et al.*, 2002). Historical ecology shares a similar approach to the 'environmental history' discipline, since both are interdisciplinary; however, the latter tends to focus on the development of a narrative driven 'story' (Bowman, 2001; Griffiths, 2002), whilst historical ecology is more akin to traditional biogeography in its attempts to quantify human relationships with the landscape.

Building on disturbance ecology, the historical ecology framework recognizes that landscape elements may have evolved with human inputs to such an extent that abandonment of human interference may lead to impoverishment of structural and biological diversity (Solon, 1995; Naveh, 1998; Kirkpatrick, 1999; Ross *et al.*, 2002; Spooner *et al.*, 2004a,b). This approach highlights that not all human activity leads to degradation, and that humans are an integral component of landscape dynamics (Gragson, 1998; Naveh, 2000; Peterson, 2000). Agricultural landscapes contain remnant ecosystems that have evolved from different historical management regimes, economies and political policies (Ihse, 1995). By detailing the history of human activity and resulting changes in vegetation structure, composition and pattern, we can examine biotic responses to novel anthropogenic disturbance processes and devise appropriate conservation strategies (Reed, 1990; Foster *et al.*, 1998, 2003; Naveh, 1998; Swetnam *et al.*, 1999; Bowman, 2001; Miller & Hobbs, 2002; Ross *et al.*, 2002).

The aim of this paper is to enhance current attempts to understand patterns of biodiversity in fragmented agricultural landscapes, by using an historical ecology perspective to highlight *the over-riding influence of land-use history in creating past, current and future patterns of biodiversity across a range of spatial scales*. We present a series of conceptual postulates to enhance our understanding of biodiversity patterns in ways that cannot be met by existing frameworks. We then illustrate each of these postulates with examples, largely drawn from fragmented woodlands in south-eastern Australia. We summarize the key implications of these postulates, and conclude by discussing the potential advantages of using this approach in future studies of biodiversity patterns in agricultural landscapes elsewhere.

## FIVE HISTORICAL ECOLOGY POSTULATES

People are the key drivers of disturbance regimes and the consequent ecosystem attributes in agricultural landscapes. Consequently, anthropogenic disturbance history is a primary determinant of past, present and future landscape patterns and elements. The following five postulates (hypotheses) describe the role of humans in landscape modification, and highlight the contribution which historical ecology can make to our understanding of the factors affecting remnant composition, structure and function in fragmented agricultural landscapes.

**1.** Spatial patterns of remnants are the result of previous human land-use decisions, and interactions with the biophysical environment. Consequently, spatial patterns of landscape elements are often predictable and arrayed in logical ways.

**2.** Historical land tenure is a strong predictor of disturbance history and, consequently, of current ecosystem conditions.

**3.** Anthropogenic disturbances and resultant ecosystem attributes have changed over time and continue to change. Some deleterious disturbance regimes have declined in intensity over time, leading to potential improvements in vegetation condition. Consequently, *a priori* assumptions of ongoing degradation are not always valid.

**4.** Some functionally important species or remnant ecosystems may now depend on current or future anthropogenic disturbances for their maintenance and persistence.

**5.** A history of anthropogenic disturbances has created a range of distinct and sometimes novel ecosystem states, which differ in structure, composition and function.

Human impacts on vegetation and biodiversity are widely recognized in Europe (e.g. recent studies by Gulinck & Wagendorp, 2002; Lindborg & Eriksson, 2004), increasingly in the Americas (e.g. Foster *et al.*, 1998, 2003; Swetnam *et al.*, 1999; Bolliger *et al.*, 2004) and elsewhere (e.g. Perry & Enright, 2002). A common conclusion of many studies is that historical land-use legacies have a strong and sometimes over-riding influence on the dynamics of present-day ecosystems. In Australia, a number of studies have demonstrated the enormous potential of using an historical ecology approach (see summaries by Lunt, 2002 and Stubbs & Specht, 2002). However, to the best of our knowledge, none of these studies has articulated the contribution that historical ecology can make to our understanding of the ecology of fragmented agricultural landscapes in as succinct a fashion as the five postulates presented above.

## EXAMPLES OF EACH POSTULATE

**Postulate 1.** *Spatial patterns of remnants are the result of previous human land-use decisions, and interactions with the biophysical environment. Consequently, spatial patterns of landscape elements are often predictable and arrayed in logical ways.*

This postulate is well illustrated by historical patterns of European settlement and agricultural development in Australia. In the 1840s, European pastoralists took up large leasehold arrangements in south-eastern Australia of up to 100,000 acres (40,000 ha) (Roberts, 1935). In the 1860s, legislation was enacted to break the pastoralists' monopoly of the land to allow new settlers to purchase crown leasehold land (e.g. Powell, 1970). Land 'battles' erupted, and in an attempt to maintain land control, early pastoralists rapidly cleared their holdings to show 'improvements' which gained them pre-emptive rights to purchase. Pastoralists also exploited loopholes in the legislation to request that certain strategic land portions be reserved as stock, water or timber reserves, to prevent land claims by settlers. Many of these reserves were later revoked and surreptitiously purchased by pastoralists when funding permitted (Gammage, 1986; Ferry, 1995; Spooner, 2005). Despite these tactics, due to the enormity of land area under lease, new settlers were successful in taking out many land claims in the 1870–1890s, and economics dictated that most freehold land titles were promptly cleared for cropping or grazing (Powell, 1970; Griffiths, 2002).

During the land battles of the 1860–90s, surveys were carried out to subdivide the country into counties and parishes, and to erect reserves for town commons, cemeteries, schools and other activities (Winston-Gregson, 1985). In many cases, parishes were not subdivided in a grid-based system as in the United States of America, but proceeded in an *ad hoc* fashion as land was purchased (Powell, 1970; Hallman, 1973). The effect on the landscape was profound; a mosaic of paddocks developed, interlaced by narrow 1-chain wide (20.12 m) road reserves, which ensured that all titles had access to water (Marshall, 1999). A network of Travelling Stock Routes (TSRs), many up to 1-mile wide, was also surveyed to enable large herds of domestic stock to be moved to markets (Hibberd, 1978). By the 1890s, apart from road, forest and other crown land reserves, most landscapes had been cleared for agriculture (Buxton, 1967). The scale and rapidity of these changes have been described as 'an apocalyptic event for Australian ecosystems' (Adamson & Fox, 1982, p. 110).

Since the late 1800s, spatial patterns in agricultural landscapes have remained relatively stable. This stability is well illustrated in Fig. 1, which shows the localities of proclaimed reserves in an area of southern New South Wales (NSW) in the 1870s (Fig. 1a) and patches of remnant vegetation in 2000 (Fig. 1b). The reason that all patches of remnant vegetation now exist is because these areas were proclaimed as reserves for other land-use purposes (e.g. road reserves, water reserves and TSRs) in the late 1800s. As a result, spatial patterns of remnants usually do not follow environmental gradients (except in the case of water reserves), but were dictated by prior administrative decisions during early agricultural development (Main, 1993; Hobbs & Saunders, 1994; de Blois *et al.*, 2002).

The stability of broad landscape patterns over the past 110–140 years means that archived cadastral plans and other historical information provide an invaluable data source for identifying how past human land-use decisions have created present vegetation patterns, and for analysing temporal changes in spatial patterns of remnants at different landscape

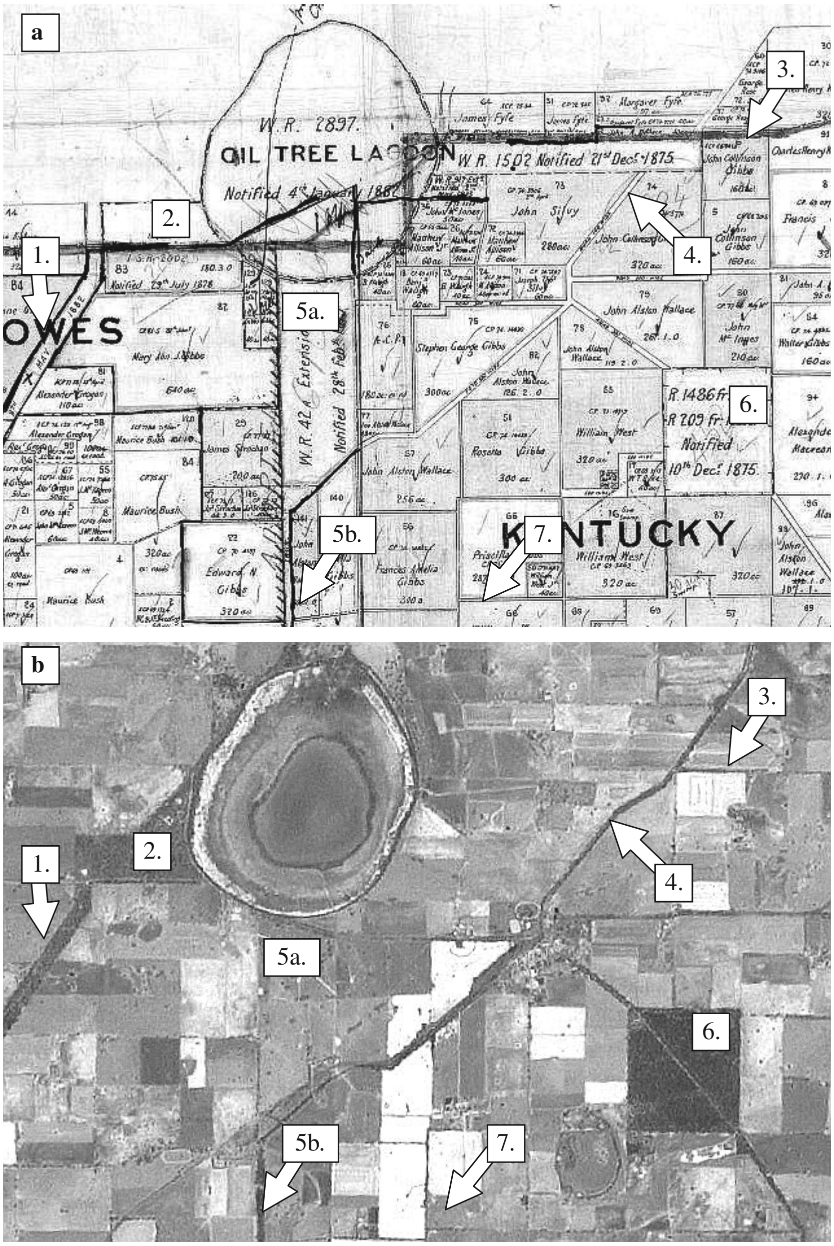


**Figure 1** An example of the influence of land-use history on present-day landscape elements in south-eastern Australia. (a) A section of an 1870s pastoral map of 'Quat Quatta Run' and (b) the equivalent 2000 Landsat panchromatic image, showing: (1) a wide Travelling Stock Route, (2) a stock reserve – note that only the area north of the old pastoral boundary remains, (3) remnant vegetation in a road reserve situated along a pastoral/parish boundary, (4) a wide 3-chain (60.3 m) road reserve, originally surveyed for stock purposes, (5a) a 'water reserve', partly resumed in the 1870s, the remainder (5b) exists as a narrow corridor of native vegetation, (6) an area reserved as a forest reserve in 1875, latter declared as 'Kentucky State Forest' in 1917, and (7) numerous 1-chain (20.12 m) road reserves which are unused, but serve as important refuges and corridors for native vegetation (pastoral map courtesy of NSW LPI 2001).

scales. Jeans (1978) was one of the first Australian authors to recognize the potential of using archived survey records and maps to reconstruct previous vegetation patterns. Winston-Gregson (1985) used archived cadastral maps to predict rural settlement patterns, and demonstrated that 'nodes' of previous settlement could be pinpointed by (1) portion numbers, which are numerically indexed, (2) concentrations of small land portions, and (3) junctions of historic stock routes in conjunction with other topographical features. Similarly, Ferry (1995) found that temporal patterns of freehold land development in the New England district of NSW could be explained by successive legislative phases in the 1860–70s. In a more extensive study, Gammage (1986) used archived cadastral maps to explain the spatial arrangement of major landscape elements in the Narrandera region of NSW. In this study, contrasts between current aerial photographs and previous cadastral maps clearly showed the legacy of nineteenth century land battles, in terms of the location, shape and arrangement of land portions and reserves on the present-day landscape.

These studies have demonstrated that current patterns of landuse and remnant native vegetation in agricultural landscapes are predictable rather than erratic or chaotic. They were created intentionally (albeit for other purposes) by nineteenth-century surveyors and administrators as part of European settlement of Australia. In contrast, the conservation of remnant vegetation has traditionally been explained by the 'worthless land hypothesis' which contends that most native vegetation was preserved in areas of minimal economic utility, such as on steep mountains or infertile soils (Runte, 1977; Hall, 1988). In productive agricultural regions this hypothesis has little explanatory power because most areas can readily be converted to agriculture (isolated rocky hills are the obvious exception). As demonstrated, current patterns of remnant vegetation are the legacy of prior land-use decisions which prevented vegetation clearance, usually for reasons not allied to current conservation philosophies. Therefore the more we know about historic land development policies and socio-economic conditions, the more we can understand and predict the current spatial arrangements of remnant vegetation and associated biota.

**Postulate 2.** *Historical land tenure is a strong predictor of disturbance history, and consequently, of current ecosystem conditions.*

The term 'land tenure' does not denote a simple binary division between public and private land, but instead encompasses a diversity of land uses and public land reserves – including roadside reserves, town commons, cemetery reserves, and many more – which vary in spatial arrangement, administrative history and permitted land uses. In many agricultural regions, different land management practices have been conducted in different land tenures for over 100 years, creating distinctive ecosystem states. For example, small cemetery reserves have escaped grazing for over a century, and have consistently been shown to possess a distinct suite of plants that has been eliminated or grossly depleted across the broader landscape (Stuwe & Parsons, 1977; Lunt, 1995, 1997a; Prober & Thiele, 1995). Consequently, simple but extremely accurate predictive models of the current distributions of once-widespread species (such as grazing sensitive *Microseris* and *Diuris* species) can easily be made on the basis of land tenure (e.g. 'visit old country cemeteries') (Prober & Thiele, 1995). We know of no other predictive models of the distributions of widespread, fragmented species that approach this level of accuracy. Furthermore, information on the location of cemeteries in relation to rural towns could be used to model the spatial distribution, and potential degree of genetic isolation, of grazing-sensitive species across landscapes.

It could be argued that the restriction of disturbance-sensitive species to small refugia like cemeteries is consistent with a traditional view of biotic decline in agricultural landscapes, where isolated populations follow a simple uni-directional trajectory of degradation and decline under increasing disturbance intensity (e.g. Moore, 1973; Yates & Hobbs, 1997a). However, this uni-directional model does not adequately account for the wide divergence in structure and composition that is witnessed when multiple land tenures are examined. Lunt (1995, 1997a) presented a more complex 'habitat segregation' model of plant distributions in remnant woodlands in eastern Victoria, based on land tenure and disturbance history. Over the past 150 years, the original flora has been segregated into two distinct communities; some species are now primarily restricted to rail reserves and cemeteries, whilst others are found in the most 'intact' woodland patches in conservation reserves. The habitat segregation model highlighted that different historical land uses have promoted different subsets of the original biota, and current composition and structure can be accurately predicted on the basis of historical land tenure. More importantly, since few propagules can disperse between small, isolated remnants, future conservation options are totally constrained by historical land management (Lunt, 1997b).

The strong influence of historical land tenure on current ecosystem conditions is well illustrated by ecological studies of road reserves. Road reserves in agricultural regions contain important repositories of remnant vegetation and create important linkages amongst remnants. Their importance for fauna has been well described (e.g. Cale, 1990; Bennett, 1991, 1993; Hobbs & Saunders, 1994; van der Ree & Bennett, 2001). Bennett *et al.* (1994) compared the size structures of dominant woodland trees in northern Victoria across a range of land tenures, and demonstrated consistent differences in tree size structures between linear roadside remnants and larger forested areas. Roadside remnants contained higher densities of large, old hollow-bearing trees than larger forest reserves, where timber harvesting has been more intensive. These differences in vegetation structure between land tenures affect arboreal fauna, and many hollow-dependent species now have higher population densities in small, linear roadside remnants than in larger forested areas (van der Ree *et al.*, 2001; van der Ree & Bennett, 2003).

Whilst Australian ecologists have often compared habitat attributes between road reserves and other land tenures, few have explored the factors that account for variations in habitat quality within road reserves; such variation is commonly attributed to unexplained 'historical noise'. However, Spooner & Lunt (2004) explained considerable variation in roadside habitat quality by comparing roadside conservation values against the date that road reserves were first surveyed. Road reserves surveyed in the 1870s, when clearing commenced, were of significantly higher conservation value than those surveyed in later decades, in areas increasingly degraded by prior agricultural development. For example, 40% of road segments declared in the 1870s were of high conservation value compared to 22% of road segments declared in the 1900–70s (Spooner & Lunt, 2004). These differences in the current conservation value of individual road reserves represent important 'landuse legacies' (Foster *et al.*, 2003), and illustrate the long-lasting impact of a short but intensive period of agricultural development which occurred in the late 1800s (Spooner & Lunt, 2004; Spooner, 2005). This historical context enables us to recognize subtle differences in vegetation structure within roadside vegetation, and enables us to understand why these differences exist. Once again, spatial patterns are not erratic, but are a direct result of historical land-uses.

**Postulate 3.** *Anthropogenic disturbances and resultant ecosystem attributes have changed over time and continue to change. Some deleterious disturbance regimes have declined in intensity over time, leading to potential improvements in vegetation condition. Consequently a priori assumptions of ongoing degradation are not always valid.*

Agricultural landscapes such as those in Australia have experienced catastrophic changes owing to vegetation clearance, changes to pre-settlement fire regimes, grazing by domestic stock, invasions by exotic weeds, rabbit introductions and associated land degradation problems such as soil erosion and dryland salinity (e.g. McBarron, 1955; Adamson & Fox, 1982; Wilson, 1990; Benson, 1991; Yates & Hobbs, 1997a). Heavy grazing by stock and feral animals has had the most widespread adverse impacts in Australia (Wilson, 1990). Historical photos (e.g. Reed, 1990; Noble, 1997) reveal that at the end of the nineteenth century, degradation was so complete that not a blade of grass was left standing in many regions (Browne, 1972; Bayley, 1979).

The debilitating impact of rabbits on the Australian environment and agriculture is part of Australian folklore. Rabbits reached plague proportions in south-eastern Australia in the mid-1880s (McBarron, 1955; Rolls, 1969; Stodart & Parer, 1988). Rabbits denuded understoreys by grazing palatable herbage, ring-barking trees and shrubs, and eating plant roots (Hamilton, 1892; Crisp & Lange, 1976; Tiver & Andrew, 1997). Added to this destruction, landholders often destroyed native shrubs that harboured rabbits (McBarron, 1955; Prichard, 1990).

In 1951, the myxoma virus was released in an attempt to control rabbit numbers and, in conjunction with the use of 1080 poison, caused rabbit populations to collapse (Ratcliffe, 1956; Stodart & Parer, 1988). The resultant decline in grazing pressure led to immediate improvements in landscape conditions, including widespread recruitment of woody species in many regions (Ratcliffe, 1956; Rolls, 1969; Noble, 1997). Recruitment of white cypress-pine (*Callitris glaucophylla* J. Thompson & L.A.S. Johnson) was well-documented owing to its importance for forestry (Lindsay, 1948; Lacey, 1972, 1973). *Callitris* seedlings are palatable to rabbits and stock, and few *Callitris* regenerated throughout agricultural areas of south-eastern Australia until myxomatosis was introduced in the 1950s. The resultant dense 'wheat-field' regeneration of *Callitris* necessitated major changes to silvicultural practices, including intensive thinning of dense regeneration (Lacey, 1972, 1973).

The ecological legacy of the historical decline in rabbit grazing pressure is apparent today, and post-1950s *Callitris* regeneration is abundant in many remnants. This phenomenon has resulted in significant improvements in vegetation structure since the 1950s in many remnants and, in turn, has provided habitat benefits to other biota. For example, Seddon *et al.* (2003) assessed factors controlling bird diversity in remnant woodlands of central NSW, and found that bird diversity was significantly greater in remnants containing complex and shrubby understoreys. One of the major contributors to understorey complexity was post-1950s *Callitris* regeneration. Before this regeneration pulse, the vegetation structure in most remnants would have been extremely simple (mature trees above a heavily denuded understorey), as rabbits precluded recruitment of most species (Moore, 1953; McBarron, 1955; Allen, 1998). Thus, from an historical perspective, understorey complexity in many remnants has undoubtedly improved over the past 50 years. Indeed, for birds requiring complex understoreys, current patch conditions are likely to be more suitable than those that existed throughout the early and mid-1900s.

In addition to damage by rabbits, grazing by domestic stock is a major cause of woodland decline in southern Australia (e.g. Adamson & Fox, 1982; Wilson, 1990; Benson, 1991; Sivertsen, 1993; Yates & Hobbs, 1997a,b). However, stock numbers have varied considerably over the past 120 years (Fig. 2). In 1892, sheep numbers in NSW peaked at 61.8 million, before plunging to 26.6 million in 1903 due to drought and economic forces. Numbers subsequently rose to over 72 million in the 1960s and 1970s, before declining to less than 40 million in the late 1990s; the lowest level since the late 1800s (Australian Bureau of Statistics, 2004). Consequently, in many regions, comparisons of current grazing impacts across different land tenures (e.g. roadside versus paddock comparisons) are likely to greatly underestimate the historical legacy

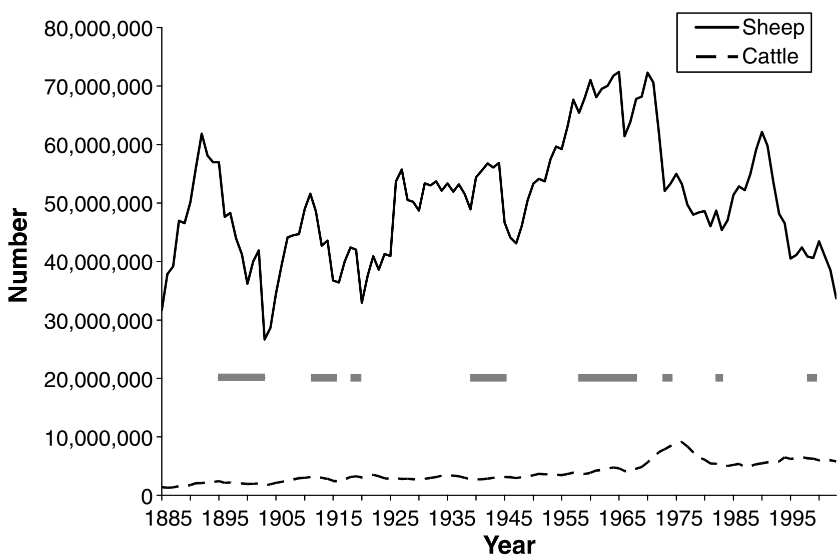


**Figure 2** Sheep and cattle numbers in New South Wales, Australia (1885–2000) showing fluctuations over the last century. Grey bars denote major periods of drought (Australian Bureau of Statistics, 2004).

of heavier grazing in the past. Furthermore, in some regions the potential for landscape recovery as a result of reduced grazing pressure may now be greater than at any time in the past century.

Even in regions with high sheep densities, grazing intensities in many remnant woodlands situated on public land have declined since the 1970s, as a result of increasing community pressure for biodiversity conservation (e.g. Land Conservation Council, 1986, 1987). Not surprisingly, recent increases in the cover of native shrubs in many nature reserves in coastal south-eastern Australia have been attributed to declines in grazing and burning during the last 30 years (Bennett, 1994; Lunt, 1998; Costello *et al.*, 2000). Similarly, stock grazing pressure has declined greatly in many roadside reserves since the 1950s, as most stock are now transported by trucks rather than being herded along roads or stock routes by drovers (McKnight, 1977; Prichard, 1991). While declines in grazing pressure do not necessarily lead to improvements in native plant diversity (see Postulate 5, below), opportunities for tree and shrub regeneration are enhanced, which in turn benefits species requiring more complex understoreys. These historical changes in grazing intensity epitomize the more general principle that anthropogenic disturbances and resultant ecosystem attributes continue to change over time, and not always in negative ways.

We emphasize that this postulate is applicable to agricultural landscapes that were largely cleared over a century ago. Elsewhere in the world, extensive land clearance is still occurring, resulting in catastrophic biodiversity losses (Ford *et al.*, 2001; McAlpine *et al.*, 2002). In these places, ecological conditions are undoubtedly declining rapidly. However in regions that were cleared and fragmented long ago, current biodiversity patterns and trends reflect a range of processes operating at different spatial and temporal scales. Conservation biologists, by training, focus on negative trends and processes (Young, 2000). However, to conserve biota in human-modified landscapes, we need to recognize that not all human processes are negative (Kirkpatrick, 1999), otherwise we constrain our potential to achieve positive outcomes. An historical ecology perspective enhances our ability to accurately interpret multi-directional long-term ecosystem trends.

**Postulate 4.** *Some functionally important species or remnant ecosystems may now depend on current or future anthropogenic disturbances for their maintenance and persistence.*

A complementary perspective to that of ongoing degradation and species impoverishment is that most of the damage has already been done. In south-eastern Australia, most agricultural landscapes were cleared by the end of the nineteenth century. Therefore many species that survived the initial impacts of European settlement may possess attributes that enable them to withstand present-day human impacts on the landscape (Wilcove *et al.*, 1986; Low, 2002).

The importance of anthropogenic disturbance regimes in maintaining roadside populations of *Acacia* shrubs was recently highlighted by Spooner *et al.* (2004a,b). In many woodland landscapes in southern Australia, native shrubs have been greatly depleted and are now mostly restricted to roadside reserves or small areas of low agricultural value. Remaining patches are of high importance for many fauna (e.g. Mac Nally & Horrocks, 2000; Seddon *et al.*, 2003). Studies of *Acacia* age structures and roadside disturbance data revealed that roadside *Acacia* dynamics were driven by one predominant disturbance regime: soil disturbance from roadwork graders (Spooner *et al.*, 2004a,b) (Fig. 3). At different spatial scales, shrub spatial patterns were significantly affected by a range of factors associated with roadwork disturbance regimes, including distances to neighbouring towns, road management category and the width of linear roadside corridors (Spooner *et al.*, 2004a). Although previous natural disturbances (e.g. fire) have long been excluded from roadsides, disturbance by grading promotes resprouting species and germination from soil seed banks, allowing *Acacia* species to expand along many roadsides (Spooner *et al.*, 2004b). While this form of disturbance has obvious deleterious effects on many other biota, these studies highlight the importance of novel anthropogenic disturbances in maintaining some functionally important native plant species (Fig. 3).

The importance of anthropogenic disturbance regimes for biodiversity conservation is most obvious in ecosystems requiring burning or grazing regimes to maintain plant and animal biodiversity (Keith *et al.*, 2002). Native grasslands and grassy woodlands in southern Australia have been highly fragmented since settlement, and are restricted to small, isolated remnants. In fertile, productive sites, frequent disturbance by burning, mowing or grazing is required to maintain plant diversity (e.g. Gilfedder & Kirkpatrick, 1994). In the absence of disturbance, large dominant native grasses (e.g. Kangaroo Grass, *Themeda triandra* Forssk.) may rapidly out-compete associated native forbs, and potentially lead to permanent reductions in plant diversity (Lunt & Morgan, 2002). Since natural fire regimes have been eliminated from most agricultural areas, anthropogenic disturbances such as prescribed fire are now required to maintain plant diversity. So little is known of pre-European fire regimes, that prescribed ecological fire regimes do not attempt to mimic 'original' or 'natural' disturbance regimes (Lunt & Morgan, 2002).

For a variety of reasons, it is often not appropriate or possible to burn small grassland and woodland remnants. In such cases, conservation managers are now attempting to maintain plant diversity and rare fauna habitat using strategic grazing by domestic stock. For example, in the recently proclaimed Terrick Terrick National Park in northern Victoria, grazing by sheep (which are normally excluded from national parks in Australia) is being trialled to maintain plant diversity in high quality native grasslands. Since the reserve was managed as a grazing property for over a century, current biodiversity patterns have been strongly influenced by a long history of grazing by stock (Foreman, 1999; Bruce & Lunt, 2003). Given the historical adverse impacts of stock grazing – and continued adverse impacts in many ecosystems including alpine grasslands (Williams & Ashton, 1987; Wahren *et al.*, 1994) – using stock

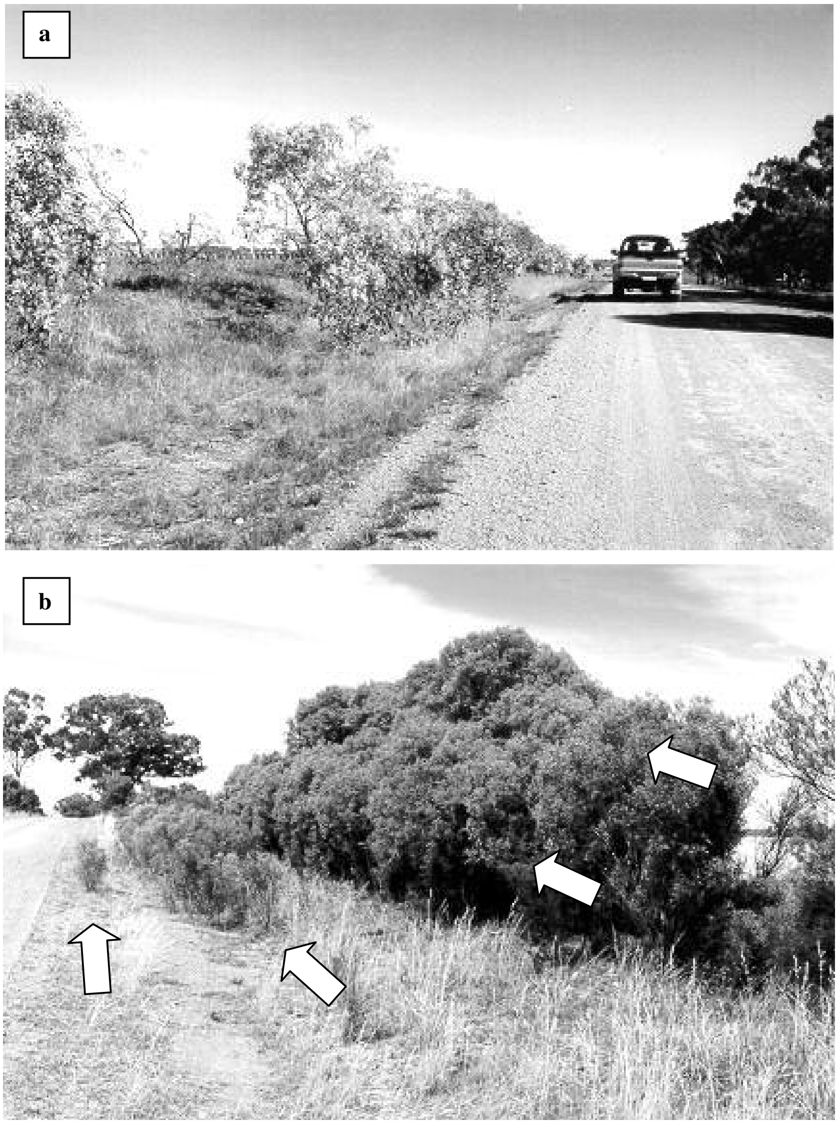


**Figure 3** Narrow road reserves in a typical agricultural landscape in south-eastern Australia. (a) A long linear stand of *Acacia pycnantha* Benth. (golden wattle), showing even-aged pulsed recruitment along a drainage line as a result of a previous grading event, and (b) a stand of *Acacia difformis* R.T. Baker (drooping wattle, a vigorous resprouting species), showing 'stair-step' pulsed recruitment from successive grading events by heavy machinery, indicated with arrows (photos P. Spooner).

to achieve conservation goals is ecologically and politically challenging. Nevertheless, this example highlights the fact that some threatened ecosystems rely upon anthropogenic disturbances for their maintenance and persistence.

The importance of maintaining anthropogenic disturbance regimes to achieve conservation objectives is well established in parts of Europe (e.g. Bakker, 1989; Gómez Sal *et al.*, 1999). However, this approach is not widely acknowledged or adopted in Australia. Since Australian ecosystems did not evolve with intensive ungulate grazing (Mack, 1989), the use of grazing stock to achieve conservation objectives is particularly challenging. These examples highlight the importance of maintaining human relationships in human-modified landscapes throughout the world (Kirkpatrick, 1999; Swetnam *et al.*, 1999; Dovers, 2000); this need is not restricted to areas such as Europe that have a lengthy history of human land management. Changes in anthropogenic disturbance regimes can dramatically alter ecosystem composition, structure and function, and many species and ecosystems now require ongoing human manipulation for their continued persistence.

**Postulate 5.** *A history of anthropogenic disturbances has created a range of distinct and sometimes novel ecosystem states, which differ in structure, composition and function.*

The above examples highlight that different historical disturbance regimes have promoted and demoted different taxa and processes in different sites – thus they have created a wide variety of novel ecosystem states, of differing species composition and structural complexity. For example, adverse changes to woodland understoreys as a result of stock grazing have been well documented, and many Australian studies have found a decline in the diversity and abundance of native perennial forbs and grasses and an increase in exotic annuals and ephemerals with increasing stocking levels (e.g. Moore, 1973; Adamson & Fox, 1982; Wilson, 1990; Sivertsen, 1993; Pettit *et al.*, 1995; Pettit & Froend, 2001). Grazing trials have demonstrated that recovery after grazing exclusion is not assured: some sites remain in a degraded steady state, some have improved in composition and structure, whilst some have become further degraded. In many remnant ecosystems, certain ecological thresholds have been passed which may be irreversible without further human intervention (Yates *et al.*, 2000; Pettit & Froend, 2001; Allcock, 2002; Spooner *et al.*, 2002).

State and transition models (STMs) have been widely used to describe non-linear ecological changes, especially in semi-arid regions where ecosystem changes are often triggered by episodic weather events (e.g. floods, droughts and fires) (Westoby *et al.*, 1989a,b; Hobbs & Norton, 1996; Yates & Hobbs, 1997b). STMs are equally applicable to agricultural landscapes where historical human disturbances have forced remnant ecosystems into different ecosystem states. Yates & Hobbs (1997b) highlighted the importance of STMs from a restoration perspective, with examples from West Australian woodlands. However, their model is essentially uni-directional, with each degrading transition progressively eliminating more species or processes.

An historical ecology framework suggests that uni-directional degradation sequences are unlikely to be found whenever a wide range of historical disturbance regimes and land tenures is investigated. Instead, remnant vegetation is likely to have been pushed into multiple states, each conserving (or promoting) different subsets of the original biota and ecosystem processes (Lodge & Whalley, 1989; Lunt, 1997a; Prober *et al.*, 2002). For example, recent studies have identified multiple vegetative states that can co-occur in White-box (*Eucalyptus albens* Benth.) woodlands depending on the nature and extent of anthropogenic disturbances, and have highlighted how adverse soil changes have created barriers to subsequent restoration (Allcock, 2002; Prober *et al.*, 2002; Allcock & Hik, 2004).

The development of STMs has many implications for research, management and restoration activities. (1) It is often not possible to assess systems as intact or degraded along uni-directional pathways. Instead, more complex appraisals are needed. (2) Management objectives and advice have to be state-specific. For example, remnants in cemeteries, which have been subject to little or no grazing, cannot be managed in the same way as more heavily grazed remnants in forest or conservation reserves (e.g. Lunt, 1995). (3) Criteria other than 'naturalness' are required in the selection of conservation reserves or development of conservation programs (Reed, 1990; Oliver *et al.*, 2002). (4) Conservation programs should aim to achieve regional goals by incorporating a wide variety of ecosystem states, and by managing different states in complementary ways, rather than by attempting to realize all goals within all states. And (5) restoration objectives also have to be state-specific. There is little point in attempting to 'restore' all states to the same end point, as different states contain different biota and barriers to restoration.

This differs from current approaches of either conserving the most 'intact' examples of remnant ecosystems and local populations of rare or threatened species, or selecting and linking large sites largely on the basis of spatial patterning rather than variations in internal composition. To complement these valuable approaches, it may be profitable to conserve (and potentially link) a network of multiple states each conserving different components of the original species pool. Historical information may provide an efficient mechanism for predicting where different states are likely to exist across the landscape.

## Common themes from case studies

A key point to emerge from this paper is that the distributions of many species and the vegetation structures of many remnants may be predicted to various extents by enhancing our understanding of regional land-use histories. In human-modified landscapes, there is a limit to the potential to refine our understanding of these issues based on traditional conceptual frameworks of island biogeography, or simple assumptions of ongoing destruction and degradation. Instead, existing frameworks can be greatly enhanced by incorporating an historical ecology perspective. The five historical ecology postulates we present are strongly supported by numerous examples from the international literature (Ihse, 1995; Motzkin *et al.*, 1999; Swetnam *et al.*, 1999; de Blois *et al.*, 2001; Foster *et al.*, 2003; Lindborg & Eriksson, 2004; Lundgren *et al.*, 2004), although they have not before been articulated in such an explicit fashion. The following three 'themes' emerge from this synthesis:

- *Present-day landscape patterns are not accidental, but are often arrayed in logical ways.* The current arrangement, composition and structure of remnant vegetation in agricultural landscapes is not accidental, rather it has been created by administrative and other historical land-use decisions (many of which are now largely forgotten), overlaid on natural spatial heterogeneity. The more we know about the history of landscapes, the better we will be able to understand, describe, predict and manage patterns of remnant woodland vegetation and associated biota.
- *Remnant ecosystems may not be as 'intact' as we would like to think.* There are consistent differences in ecosystem composition, structure and processes amongst remnants subject to different administrative and management decisions. Thus, historical land tenure provides a useful predictor of current biodiversity patterns. Much of the variability in current ecosystem states can be understood in light of past human activities.
- *The condition of remnant ecosystems is not necessarily deteriorating.* Current levels of anthropogenic disturbance may have fundamentally changed in frequency and intensity over decadal and century time-scales. For example, in many remnants in agricultural landscapes of south-eastern Australia, present-day disturbances are less intense than those imposed from the late-1800s to mid-1950s, owing to lower populations of humans, domestic stock and feral animals (especially rabbits). Consequently, implicit assumptions of ongoing degradation may not always be warranted.

## CONCLUSIONS

This historical ecology framework fills three major gaps in research on fragmented agricultural landscapes. First, it enhances our ability to understand *why* different ecosystem states and attendant species occur where they do in highly modified human landscapes. Where biotic patterns are tightly associated with historical land tenures and management, then spatial distributions may be predicted readily and modelled across landscapes. Second, this approach overcomes the current paucity of conceptual frameworks available to explain internal variations in ecological conditions within remnant ecosystems (or types of remnants, e.g. hedgerows or roadside reserves); too often this variation is dismissed as 'noise' or the 'mess of history' (Tiver & Andrew, 1997). Rather than viewing human modified systems as inherently complex and messy (Forman, 1998), the incorporation of past human management as an explanatory variable may allow some ecological patterns to be more easily interpreted. Third, the recognition of anthropogenic disturbance regimes as a major driver of biotic patterns more firmly places *temporal change* (both past and future) on the research agenda in fragmented woodlands (Ross *et al.*, 2002), to complement the current pre-occupation with spatial patterns. Similarly, explicit examination of the ecological effects of historical disturbance regimes provides a more applied role for historical ecology studies, compared to retrospective regional descriptions.

Attempts to document historical changes in vegetation conditions do not imply (as has often been suggested) that we should aim to restore past conditions. Past conditions are often inappropriate and usually practically unattainable, and such restoration attempts are likely to fail (Swetnam *et al.*, 1999; Bolliger *et al.*, 2004). Instead, by clearly documenting the wide range of ecological transformations that have occurred due to human modification of landscapes (instead of uni-directional degradation sequences), notions of attaining 'pre-settlement conditions' become far more tenuous; instead more realistic goals can be set for future research and restoration activities.

In conclusion, we do not suggest that an historical ecology framework should replace existing paradigms or approaches; instead we believe that there is a strong need to expand intellectual activity beyond the spatial fragmentation paradigm that currently reigns. History *per se* can provide fascinating insights into the development of agricultural landscapes and their human inter-relations, but can be descriptive, subjective, and riddled with ambiguities, exaggerations and misinterpretations (Swetnam *et al.*, 1999). By contrast, the incorporation of spatially and temporally explicit historical attributes into landscape ecology studies can greatly expand our understanding of the factors driving biotic patterns in fragmented agricultural landscapes. Further integration of historical information into ecological studies can prove extremely useful to test hypotheses of the effects of changes in landscape processes (Noble, 1997; Bowman, 2001), and can provide an integrated conceptual framework to guide future research, restoration and conservation management activities.

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