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Scattered trees are keystone structures – Implications for conservation

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ABSTRACT

Scattered trees are prominent features in many landscapes worldwide, including natural landscapes, cultural landscapes, and recently modified landscapes. The ecological importance of scattered trees is widely acknowledged in natural landscapes, but has not been sufficiently appreciated in human-modified landscapes. This paper shows that scattered trees are keystone structures in a wide range of landscapes. At the local scale, ecological functions of scattered trees include: provision of a distinct microclimate; increased soil nutrients; increased plant species richness; increased structural complexity; and habitat for animals. At the landscape scale, ecological roles include: increased landscape-scale tree cover; increased connectivity for animals; increased genetic connectivity for tree populations; and provision of genetic material and focal points for future large-scale ecosystem restoration. Furthermore, in disturbed landscapes, scattered trees often are biological legacies that provide ecological continuity through time. In combination, these ecological functions support the argument that scattered trees are keystone structures. That is, their contribution to ecosystem functioning is disproportionately large given the small area occupied and low biomass of any given tree, and the low density of scattered trees collectively. Because scattered trees fulfill unique functional roles in a wide range of scattered tree ecosystems, their loss may result in undesirable ecological regime shifts. A key management challenge in all landscapes with scattered trees is to maintain a balance between recruitment and mortality of trees in an appropriate spatial pattern. Meeting this challenge may represent an important step towards the genuine integration of conservation and production in human-modified landscapes.

"The way things look is not always the way things are. This fact should be cause for consternation among those who are interested in the management of ecological systems. A highly functional landscape structure may go unnoticed - even by people who depend upon its function" (Nassauer, 1992, p. 239).

1. Introduction

Ecosystems with scattered trees occur throughout the world. The origins and ecological roles of scattered trees in natural ecosystems have been intensively studied in many parts of the world, including in the Brazilian Cerrados (Furley, 1999),

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Venezuelan Trachypogon savanna (San José et al., 1991), African savannas (Belsky, 1994), arid rangelands in South Australia (Facelli and Brock, 2000), oak savannas in North America (Nuzzo, 1986) and the forest-tundra transition zone of the boreal forest (Sirois, 1992). Scattered trees are also prominent features of many human-dominated landscapes, including recently cleared landscapes in Central America (Guevara et al., 1992), Africa (Duncan and Chapman, 1999) and temperate Australia (Ozolins et al., 2001), well-established cultural landscapes such as the dehesas in Spain and Portugal (Díaz et al., 1997) or British wood-pastures (Peterken, 1996), and severely disturbed forest landscapes (Gibbons and Lindenmayer, 2002). In this paper, these systems are collectively referred to as "scattered tree ecosystems". This definition is intended to be broader than that of "savanna" (sensu Bray, 1960), and includes natural, cultural and recently modified, as well as disturbed and undisturbed ecosystems (Fig. 1). The key defining feature of scattered tree ecosystems is the dispersed pattern of the trees. Scattered trees are referred to by various synonyms in different areas, including isolated trees (Dunn, 2000), pasture trees (Otero-Arnaiz et al., 1999), paddock trees (Law et al., 2000), and remnant trees (Guevara et al., 1986).

In this paper, scattered tree ecosystems are categorized into three groups for the purposes of discussion: (1) natural (such as savannas), (2) cultural (such as wood-pastures), and (3) recently modified (such as remnant paddock trees in south-eastern Australia) (Fig. 1). The distinction between cultural and recently modified scattered tree ecosystems is that the former have a long-term history of manipulation by humans and have been sustained by cultural systems over a long period of time. In contrast, the latter are recently modified, and often highly modified, and levels of tree cover are often declining. In reality, the distinction between the three categories will be blurred, and both natural and cultural scattered tree ecosystems can be highly modified. Similarly, levels of human modification and natural disturbance often interact, and scattered tree ecosystems therefore occur on a continuum from natural through to recently modified.

Despite large differences in climate and origin, scattered trees in natural, cultural and recently modified landscapes share many key ecological roles as well as several threats to their continued existence. However, especially in modified landscapes, the ecological value of scattered trees has rarely been recognized. The aims of this paper are to:

(1) demonstrate the keystone role of scattered trees;
(2) synthesize key ecological functions of scattered trees and highlight parallels between natural, cultural and recently modified ecosystems;
(3) establish common threats to scattered trees, especially in human-dominated landscapes; and
(4) outline ways in which scattered trees might serve as a landscape management tool to integrate conservation and production in human-modified landscapes.

By outlining the similarities between scattered trees in natural, cultural and recently modified ecosystems, this paper aims to facilitate increased recognition of the importance of scattered trees in modified landscapes. It is argued that native scattered trees exert a disproportionate effect on ecosystem function in a wide range of ecosystems, and that their loss therefore may lead to the deterioration of important ecosystem functions.

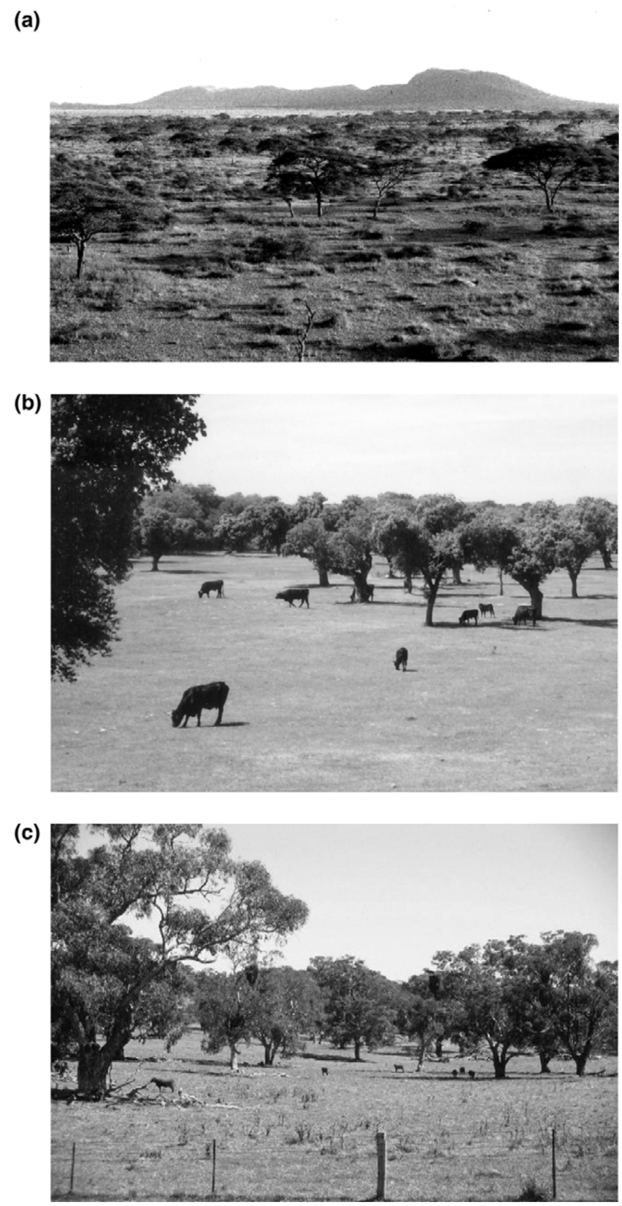

Fig. 1 – Three landscapes with scattered trees, representing a continuum of alteration states: (a) a natural landscape in southern Africa (top; photo by R. Heinsohn), (b) a cultural landscape in southern Spain (middle; photo by D. Gilmour, copyright IUCN), and (c) a recently modified landscape in south-eastern Australia (bottom; photo by A. Manning).

2. Scattered trees are keystone structures

A large amount of evidence demonstrates a wide range of important ecological functions of scattered trees in many natural, cultural, and recently modified landscapes (reviewed in detail below). In various different ecosystems, several authors have independently noted the "keystone" role of scattered trees, for example, in the Negev desert in Israel (Munzbergova and Ward, 2002), and in dehesas in Spain (Plieninger et al., 2003). Tews et al. (2004a,b) considered scattered trees in African savannas as "keystone structures" because:

> "[A] wide array of species groups (e.g. arthropods, birds or mammals) depend on [scattered] trees as a food resource, shelter or nesting site. Consequently, overall species diversity is strongly linked to the quality of this structure" (Tews et al., 2004a, p. 87).

Given many parallel functions of scattered trees across a broad spectrum of vastly different ecosystems, native scattered trees should be recognized as keystone structures in a wide range of landscapes, including natural, cultural and recently modified landscapes. Furthermore, some traditional agroforestry systems using non-native and domesticated tree species can also have important ecological and socio-cultural values (see Herzog, 1998, regarding the European "Streuobst" agroforestry system where fruit trees are undersown with crops or managed grassland). Analogous to the keystone species concept (reviewed by Power et al., 1996), scattered trees are keystone structures because they have a disproportionate effect on the ecosystem relative to the small area occupied and low biomass of any given tree and the low density of scattered trees collectively. It is precisely because scattered trees are not part of a large consolidated patch, that their local and landscape effects are pronounced. In an ecosystem otherwise dominated by ground cover vegetation, a single scattered tree will add a raft of additional or enhanced functions (Fig. 2). In contrast, when part of an existing large patch of trees, the addition of a single tree is less likely to add new functions not already fulfilled by other existing trees.

To maintain functioning ecosystems, it is widely recognized that priority should be given to species that fulfill unique functional roles rather than functionally redundant species (Walker, 1992; Elmqvist et al., 2003). The raft of roles fulfilled by scattered trees suggests that the notion of functional uniqueness should be extended beyond species to include structural features, such as scattered trees. Given the lack of alternative features that could fulfill similar ecological functions to scattered trees, the ability of scattered tree ecosystems to maintain their essential characteristics directly depends on the ongoing existence of scattered trees. Scattered trees are threatened in many modified landscapes (see below). These threats, in combination with the functional uniqueness of scattered trees, suggest that many scattered tree ecosystems are in a precarious state (for example, British wood-pasture, Kirby et al., 1995). That is, their resilience to further disturbance is low, and they are at risk of undesirable regime shifts (for discussions of precariousness, resilience and regime shifts see Folke et al., 2004; Walker et al., 2004). In the following section, various ecological functions of scattered trees are outlined which support the argument that scattered trees are keystone structures.

3. Functions of scattered trees

In natural, cultural and recently-modified landscapes, scattered trees fulfill many functions. The following sections

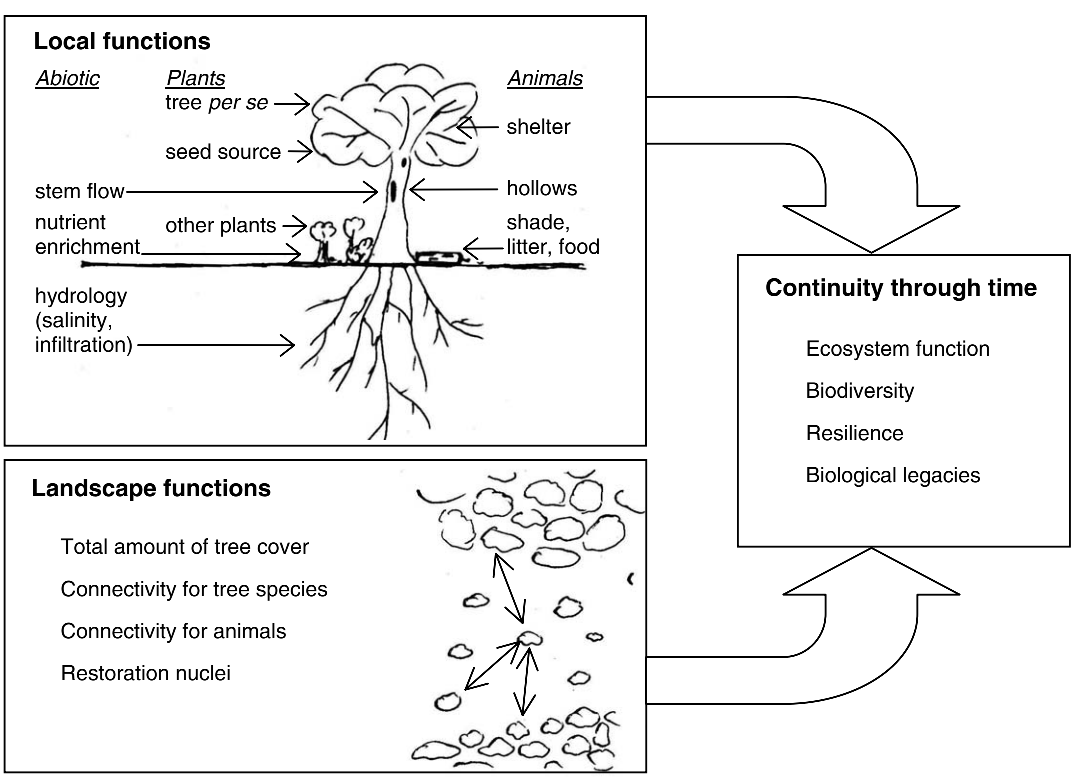

Fig. 2 – Schematic summary of some key ecological functions of scattered trees.

Table 1 – Examples of direct benefits from scattered trees to humans in modified landscapes

Benefit	References
Provision of ecosystem services (sensu Daily, 1997) which are essential for farming	This paper
Provision of fruit in many tropical landscapes	Aguilar and Condit (2001)
Wood products like firewood, fence posts and charcoal	Joffre et al. (1999), Pulido et al. (2001)
Shade and sheltered grazing for livestock	Kirby et al. (1995), Harvey and Haber (1999), Reid and Landsberg (1999), Quelch (2002)
Fodder for livestock in Britain	Peterken (1996)
Preservation of family traditions and real estate values in dehesas	Plieninger et al. (2004)
Recreational value for walkers and hunters in Scotland	Kirby et al. (1995), Quelch (2002)

consider: (1) the local-scale ecological functions of individual trees, (2) their role as biological legacies in modified landscapes, and (3) landscape-scale ecological functions of multiple scattered trees. In addition, examples of direct benefits from scattered trees to humans are given in Table 1.

3.1. *Local-scale ecological functions of scattered trees*

At the local scale, a given scattered tree influences its abiotic environment as well as plant and animal life (Fig. 2). Local changes to the abiotic environment are widely documented in natural, cultural and recently modified landscapes throughout the world, including the dehesas (Joffre et al., 1999), African savannas (Dean et al., 1999), and Australian rangelands (Facelli and Brock, 2000). Typical changes involve a cooler and often wetter microclimate under a given tree due to the interception of radiation and precipitation (Mistry, 2000). Stem flow, water uptake through the root system from below and around the tree, and increased infiltration of water into the soil further enhance the concentration of water near a given tree, especially in otherwise dry environments (Vetaas, 1992; Eldridge and Freudenberger, 2005).

Scattered trees also contribute to a local increase of nutrients, as demonstrated in dehesas (Joffre and Rambal, 1993), in south-eastern Australia (Wilson, 2002), the Brazilian Caatinga (Tiessen et al., 2003), and African savannas (Belsky, 1994). Nutrient levels under scattered trees are typically enhanced by litter accumulation, animal dung, the interception of nutrients by trees, and the accumulation of nutrients by tree roots (Wilson, 2002; Dean et al., 1999; Prober et al., 2002). Many scattered trees in dry savannas form symbiotic relationships with *Rhizobium* bacteria, thereby fixing atmospheric nitrogen and making it accessible to plants (Vetaas, 1992). By increasing the local water balance and nutrient concentration, scattered trees can enhance primary productivity (Ludwig et al., 1999).

Numerous benefits to plant life originate from scattered trees. The most basic benefit to plant diversity is the presence of scattered trees themselves. In recently modified ecosystems, scattered trees often represent samples of the original, pre-modification vegetation, and therefore provide important conservation opportunities in their own right (see Section 3.2). In central American modified landscapes, scattered trees are often represented by more than 50 species (Guevara et al., 1992; Harvey and Haber, 1999; Otero-Arnaiz et al., 1999; Aguilar and Condit, 2001), and in temperate Australia many scattered trees are the remnants of threatened vegetation communities like white box-yellow box-Blakely's red gum woodlands (*Eucalyptus albens/E. melliodora/E. blakelyi*; Gibbons and Boak, 2002). The conservation values of scattered trees per se also has been noted in the Brazilian Cerrados (Furley, 1999), the dehesas (Díaz et al., 1997), and British wood-pastures (Peterken, 1981, 1996; Kirby et al., 1995). Some scattered tree systems, such as dehesas, can have relatively few tree species (*Quercus ilex* and *Q. suber*), but still have high conservation value (Díaz et al., 1997).

Many other plant species typically benefit from the presence of scattered trees. For example, dehesas provide habitat for 30% of vascular plants in the Iberian peninsula (Pineda and Montalvo, 1995). Both in natural savanna landscapes (San José et al., 1991) and human-modified landscapes like in Central America (Guevara et al., 1992) or eastern Australia (Toh et al., 1999), scattered trees often function as "nurse plants" or "fertility islands", in that they provide favorable conditions for the recruitment of other plants (San José et al., 1991; Facelli and Brock, 2000). Plant species richness is typically higher under scattered trees than in the surrounding landscape, as demonstrated in Central America (Guevara et al., 1992), the Negev desert in Israel (Munzbergova and Ward, 2002), arid Australia (Facelli and Brock, 2000), and temperate Australia (Prober et al., 1998).

Scattered trees also are used by a wide range of animals throughout the world, in natural, cultural and recently modified scattered tree ecosystems. The micro-ecosystem surrounding an individual tree greatly enhances structural complexity relative to its surrounds. A wide variety of birds has been documented as using the canopies of scattered trees, for example, in Australia (Law et al., 2000; Fischer and Lindenmayer, 2002a), Central America (Guevara and Laborde, 1993; Harvey and Haber, 1999; Luck and Daily, 2003), southern Africa (Dean et al., 1999), and central Africa (Duncan and Chapman, 1999). Insectivorous bats in Australia forage around the canopy of scattered trees (Law et al., 1999, 2000; Lumsden et al., 2002; Lumsden and Bennett, 2005), and frugivorous bats make extensive use of scattered trees in many tropical landscapes (Duncan and Chapman, 1999; Galindo-González et al., 2000; Galindo-González and Sosa, 2003). A wide variety of canopy invertebrates has been recorded in Australia (Majer and Recher, 2000), and a range of ground-dwelling invertebrates have been documented below scattered trees within the dry, semi-deciduous forest zone in Ghana (Dunn, 2000) and under paddock trees in south-eastern Australia (Oliver et al., 2006). Cavities in scattered trees are used by a variety of birds, mammals, reptiles and amphibians, as documented in Australia (Saunders et al., 1982; Gibbons and Lindenmayer, 2002; Manning et al., 2004a) and southern Africa (Dean et al., 1999).

3.2. Scattered trees as biological legacies

In landscapes that have been disturbed by natural processes or human activities, scattered trees play an important role as "biological legacies" (Elmqvist et al., 2002). Biological legacies are organisms or organically derived structures that persist after a disturbance (Franklin et al., 2000). Biological legacies have several functions including: representation of tree species per se (see above); assisting other species to persist (the so-called "life-boating" function, sensu Franklin et al., 1997); providing habitat for recolonization of a site (structural enrichment); influencing patterns of ecosystem recovery (nucleation); providing a source of energy and nutrients for other organisms; and stabilization of environmental conditions (reviewed by Lindenmayer and Franklin, 2002).

The concept of "nucleation" is used to describe the spreading of recovery from many different foci following a disturbance (Franklin and MacMahon, 2000), and is a particularly important function of scattered trees. In recently disturbed ecosystems, scattered trees can act as "regeneration nuclei" (Guevara et al., 1986). This can be in the form of seed directly from the trees (Cascante et al., 2002; Elmqvist et al., 2002), or indirectly from seeds deposited in droppings by organisms attracted to the trees, such as birds and bats (Guevara et al., 1986; Elmqvist et al., 2002). Scattered trees can therefore function as focal points for future restoration activities (Otero-Arnaiz et al., 1999; see below). Despite reduced genetic variability, the reproductive potential of scattered trees remains high in some landscapes (Cascante et al., 2002), and scattered trees represent potential sources for large-scale natural regeneration of Australian woodlands (Dorrough and Moxham, 2005) and Central American rainforests (Galindo-González et al., 2000). Natural regeneration is a substantially cheaper and ecologically preferable form of restoration than tree planting (McIntyre, 2002; Spooner et al., 2002). The "fertility island" effect of scattered trees (see above) further enhances their ability to act as central points of ecosystem recovery from which plant succession may radiate outwards into other parts of a given landscape (Toh et al., 1999).

Scattered trees are often the oldest living structures in disturbed landscapes and provide important ecological continuity through time. Ironically, although scattered tree ecosystems, such as wood-pastures, are often not regarded as "proper forest" (Rackham, 1998), they can provide refuges for organisms associated with original "natural" forest. For example, wood-pastures in Britain contain structures, species, and communities which are relicts of past management systems as well as original natural forest (Peterken, 1981, 1996; Kirby et al., 1995). Trees in British wood-pastures can live between 300 and 500 years and provide habitat for fungi and invertebrates associated with decaying wood and epiphytes largely absent in other forest types (Peterken, 1981, 1996; Alexander, 1999). Similarly, retained trees in recently logged boreal forests provide habitat continuity for lichen species that are directly dependent on these trees (Hazell and Gustafsson, 1999). Furthermore, in many human-modified ecosystems, scattered trees pre-date the era of tree planting and preserve local tree genotypes (Kirby et al., 1995).

3.3. Landscape-scale ecological functions of scattered trees

In addition to the local-scale ecological functions of a given individual scattered tree, in combination, multiple trees scattered throughout a landscape provide additional ecological functions (Fig. 2). The most obvious landscape-scale function of scattered trees is that they contribute to the overall amount of tree cover in a landscape. The density of trees is of considerable scientific and conservation interest in natural landscapes (Jeltsch et al., 1996; Mistry, 2000). Perhaps more importantly, scattered trees make an important contribution to overall tree cover in many cultural and recently modified landscapes. Recently modified ecosystems such as grazing landscapes in temperate Australia (Gibbons and Boak, 2002) and tropical Central America (Galindo-González et al., 2000) often contain a large proportion of their total remnant tree cover as scattered trees or small clumps of trees.

Tree cover is important for many animal species, and low amounts of tree cover in previously forested landscapes may lead to cascades of extinctions as a result of the simultaneous loss of the amount of unmodified vegetation and landscape connectivity (Andrén, 1994). Despite its modified status, a landscape mosaic characterized by scattered trees often provides habitat for a range of animal species, including birds and bats in both Central America (Guevara and Laborde, 1993; Galindo-González and Sosa, 2003) and south-eastern Australia (Law et al., 2000; Fischer and Lindenmayer, 2002a,b). A key feature of landscapes with scattered trees is that their connectivity remains relatively high for some animals (Guevara and Laborde, 1993; Graham, 2001; Fischer and Lindenmayer, 2002b).

Landscapes dominated by scattered trees can provide valuable foraging habitat for some animal species. For example, lichen forest in the forest-tundra transition zone of the boreal forest in Quebec may represent a large reservoir of forage for large caribou (*Rangifer tarandus*) herds (L. Sirois, pers comm.). Some species of bats and birds that use scattered trees for foraging are important seed dispersers. In tropical modified landscapes, frugivorous bats play a particularly important role in dispersing primary and secondary rainforest plants (Duncan and Chapman, 1999), thus increasing plant genetic connectivity and population viability (Cascante et al., 2002). The survival of bats in these landscapes therefore is considered key to future forest recovery (Galindo-González et al., 2000). Other mutualists of trees, such as pollinators, have been studied less extensively in modified landscapes (but see Ricketts et al., 2004). However, the general notion that a loss of landscape connectivity may result in the disruption of mutualist relationships in fragmented landscapes is well established (Cordeiro and Howe, 2003), and it is reasonable to expect that scattered trees will at least somewhat improve connectivity for a wide range of mutualist species.

More generally, scattered trees enhance landscape heterogeneity (the horizontal patchiness) of landscapes. For modified landscapes, it is widely accepted that other things being equal, increased landscape heterogeneity tends to increase landscape scale species richness (Benton et al., 2003; Luck and Daily, 2003).

In previously densely vegetated landscapes, scattered trees contribute to the "softening" of the matrix surrounding more discrete vegetation remnants (Lindenmayer and Franklin, 2002). Structural contrast at edges is widely acknowledged to result in a cascade of abiotic and biotic changes, ultimately leading to synergistic changes in both plant and animal life (Ries et al., 2004; Harper et al., 2005). Scattered trees reduce the structural contrast between patch edges and the matrix, and therefore reduce the likelihood and intensity of negative edge effects.

4. Threats to scattered trees

Scattered trees in natural, cultural and recently modified landscapes face some similar threats, as well as some threats that are unique to particular ecosystems. The most direct threat to all scattered trees is clearing by humans. For example, the legal and illegal removal of scattered trees is widespread in Australian grazing landscapes (Gibbons and Boak, 2002). Similarly, widespread land clearing continues in some Central American landscapes (Aguilar and Condit, 2001).

A slower, but equally problematic, threat to scattered trees is the lack of natural regeneration. Recruitment failure is often related to high grazing pressure, and may be a problem in natural, cultural and recently modified landscapes with scattered trees. Reduced recruitment of scattered trees has been reported in African savannas (N. Van Rooyen, unpublished data, cited in Jeltsch et al., 1996), Central American farming landscapes (Harvey and Haber, 1999; Graham, 2001), dehesas (Pulido et al., 2001), British wood-pastures (Kirby et al., 1995), and temperate Australian grazing areas (Spooner et al., 2002; Saunders et al., 2003). In the latter, the lack of recruitment threatens the persistence of scattered trees across vast areas of the wheat-sheep zones in eastern and Western Australia. In these landscapes, scattered trees without any younger generations of trees are "the living dead" (sensu Janzen, 1988). Because many scattered trees are dying of old age, a recent study in eastern Australia estimated a narrow window of opportunity spanning only a few decades in which large-scale tree regeneration will be possible (Dorrough and Moxham, 2005).

Some scattered tree ecosystems can be threatened by vegetation encroachment. For example, in many natural dry savannas, overgrazing can lead to shrub encroachment with often detrimental consequences for native species (Meik et al., 2002). In dry savannas, the negative impacts of livestock grazing are often exacerbated by changed fire regimes and strong rainfall events, leading to the invasion of thickets of unpalatable shrubs (Milton et al., 1994; Tews et al., 2004b). Maintaining appropriate grazing pressure is also important in British wood-pastures to sustain trees and open grassy areas in the same location (Kirby et al., 1995). In wood-pastures, both too much and too little grazing can be a threat. If there is too much grazing, trees do not regenerate; if there is too little grazing, open wood-pastures turn into denser forest ecosystems (Peterken, 1981, 1996).

These examples highlight that although the effect of grazing can vary, appropriate grazing regimes are pivotal to the continued existence of many ecosystems characterised by scattered trees. Determining what constitutes an appropriate grazing regime is not straightforward, and depends on the particular ecosystem under investigation. In many cases, choices need to be made about which species are in most urgent need of conservation attention. For example, Martín and Lopez (2002) found that lizard abundance in dehesas increased with dense understory vegetation. However, dense understory vegetation decreased the quality of hunting habitat for the endangered Spanish imperial eagle (*Aquila adalberti*).

Salinity can be an additional threat to scattered trees in both natural and human-dominated dry ecosystems. Scattered trees contribute to maintaining the ground water table at naturally low levels (Stirzaker et al., 2002). The removal of scattered trees, in turn, can lead to a rising ground water table, which can bring naturally occurring salts to the surface. The widespread removal of trees in temperate Australia has led to large-scale salinity problems, which now threaten both biodiversity and agricultural productivity (Saunders and Hobbs, 1995). Similar mechanisms also have led to increased salinity in some natural ecosystems such as the Negev desert in Israel (Munzbergova and Ward, 2002).

More generally, scattered trees may be threatened by poor tree health. In the Mediterranean, the tree root pathogen *Phytophthora cinnamomi* is causing a severe decline of oak species (*Quercus* spp.) (Plieninger et al., 2003). In Australia, rural dieback of eucalypts, where trees are severely defoliated, is leading to large-scale and premature tree death (Landsberg and Wylie, 1983). It is caused by complex interactions between numerous biotic and abiotic factors, including land management practices (Landsberg, 1990). In the United Kingdom, debarking by the introduced grey squirrel (*Sciurus carolinensis*) threatens the long-term persistence of wood-pastures (Mountford and Peterken, 2003).

Finally, land use intensification poses a threat to scattered tree ecosystems. In the Iberian dehesas, regeneration failure of oak has been exacerbated by recent agricultural intensification (Díaz et al., 1997; Pulido et al., 2001) and urban development (Plieninger et al., 2004). In Australia, scattered trees are more likely to be lost in cropping landscapes than in grazing landscapes (Ozolins et al., 2001). In addition, removal of fallen deadwood and standing dead trees for firewood (Driscoll et al., 2000) and the "tidying" of pastures by farmers (Reid, in litt.) can threaten the continued existence of key structural elements. Similar threats have been reported in British wood-pastures. Here, the removal of fallen deadwood and standing dead timber has eliminated mature habitat in many places, and recreation pressures such as car parks, heavy trampling and removal of dangerous branches at iconic locations, and vandalism are important threats to the long-term persistence of wood-pastures (Kirby et al., 1995; Peterken, 1996).

5. Scattered trees and landscape management

5.1. *Landscape management approaches*

One of the great challenges in landscape management is the trade-off between meeting short-term human needs and maintaining the capacity to provide ecosystem services in the long term (Foley et al., 2005). There is a growing debate about the best way to manage landscapes in the face of growing human populations and associated demand for food. This debate has recently been framed as a trade-off between two approaches: "land sparing" versus integrated landscape management (Green et al., 2005; Mattison and Norris, 2005). Land sparing occurs where higher yielding parts of the landscape are intensively farmed to reduce pressure for more farmland. Integrated landscape management (also known as wildlife-friendly farming, sensu Green et al., 2005) is where native species are maintained across entire production landscapes (Green et al., 2005).

While land sparing may be attractive in theory (Green et al., 2005), it may be unsustainable in practice. First, there is no guarantee that land sparing will reduce forest loss because greater farm productivity can induce additional clearance to further increase profitability (Simon and Garagorry, 2005). Second, there is no guaranteed link between intensification in one place and reservation in another. Third, high productivity areas are most likely to be targeted for intensification, but are usually already the least reserved and most modified (Braithwaite et al., 1993; Lindenmayer and Franklin, 2002). Furthermore, the density of many organisms is skewed towards the most productive parts of landscapes (Braithwaite, 1983). Fourth, land sparing can result in the separation of commodity production and non-production areas, which ignores the interdependence of the two and the interaction of pattern and process in landscapes. Fifth, the consequences for long-term sustainability from land sparing are unknown because of potential lag effects on organisms and ecosystem processes arising from landscape consolidation. Sixth, land use intensification often eliminates key landscape elements, such as scattered trees, that obstruct machinery and intensive farming practices (Maron, 2005).

As a consequence of these issues, it may be difficult to differentiate the practical on-ground outcomes of land sparing from the traditional transition of land use, seen throughout human history, towards greater intensification and ecosystem fragmentation (sensu Saunders et al., 1991; McIntyre and Hobbs, 1999; Foley et al., 2005). As discussed above, land use intensification is a major threat to scattered tree ecosystems around the world. Evaluation of land sparing and consolidation of native ecosystems as land management options should first consider their possible shortcomings, and their potential effects on keystone structures such as scattered trees.

5.2. *Scattered trees and integrated landscape management*

Integrated landscape management attempts to reconcile conservation and production in the same landscape (sensu Hobbs and Saunders, 1991), and is practiced in many cultural scattered tree ecosystems, such as the dehesas or British wood-pastures. In integrated landscapes formerly covered by forest or woodland, scattered trees can be used as a useful landscape management tool which can complement conservation reserves and consolidated blocks of remnant vegetation.

Agroforestry, which is defined as "an intimate mixture of trees with farm crops and/or animals on the same piece of land" (Savill et al., 1997, p. 234), is a good example of how scattered trees can be used as a landscape management tool. Agroforestry has significant potential to achieve conservation goals in agricultural landscapes (Harvey et al., 2004; Salt et al., 2004) and lies at the intersection between agriculture and forestry. Both dehesas and wood-pastures are examples of agroforestry.

Some techniques from forestry also offer useful insights on the benefits of integrating scattered trees in landscapes over the long term. The notion of biological legacies (see above) underpins the technique of "green tree retention" which is increasingly being used in boreal forest management (Vanha-Majamaa and Jalonen, 2001). With green tree retention, a certain number of trees are retained permanently after harvesting to mimic conditions after a moderate-intensity natural disturbance (Vanha-Majamaa and Jalonen, 2001; Lindenmayer and McCarthy, 2002). The main purposes of green tree retention are:

- the "life-boating" of species and processes after logging as tree cover is re-established;
- the enrichment of re-established stands with structural elements; and
- the enhancement of landscape connectivity (Franklin et al., 1997).

Green tree retention can maintain canopy continuity, preserve old and large trees and maintain habitat and structural diversity. There are two spatial patterns of green tree retention. First, in "dispersed retention" retained structures are distributed evenly throughout the harvest unit. This form of retention is also useful for dispersing mitigating effects (such as modification of microclimate, hydrology or soil stabilization through roots) over the whole stand (Franklin et al., 1997; Lindenmayer and Franklin, 2002). Second, in "aggregated retention" small patches are retained to be representative of the original stand conditions and to provide intact understory and soil organic layers. Unlike dispersed retention, effects of this approach are confined to the immediate area around the retained patch (Franklin et al., 1997; Lindenmayer and Franklin, 2002). Green tree retention thus contributes to a continuum of possible forest management options, and represents one end which explicitly recognizes the value of scattered trees.

The principles underpinning agroforestry and green tree retention have implications for the management of existing scattered tree ecosystems and formerly wooded and forested landscapes. Variable retention harvest systems (which include green tree retention as a component) provide "a continuum of structural retention options" (Franklin et al., 1997, p. 115). The idea of a continuum of landscape management options, from consolidated patches through to areas of scattered trees offers a promising approach to landscape management. As a practical approach to managing landscapes, this would be highly compatible with recent developments in the area of landscape concepts. Scattered trees do not fit well into schematic "patch-matrix-corridor" landscape models which categorize landscapes either "habitat" or "non-habitat" (McIntyre and Hobbs, 1999; Manning et al., 2004b). This is because they occur in what is generally considered the "matrix". It is now recognized that many landscapes have habitat that is modified, but not destroyed ("landscape variegation" sensu McIntyre and Hobbs, 1999). It is also recognized that vegetation often occurs in spatial continua and habitat boundaries are often indistinct or gradual (McIntyre and Hobbs, 1999; Manning et al., 2004b). Further, different organisms perceive and respond to the same landscape differently (the Continua- *Umwelt* concept, Manning et al., 2004b). This paper demonstrates that many organisms consider scattered trees as important habitat. The maintenance and expansion of scattered trees across landscapes, and the use of techniques such as agroforestry and green tree retention, are highly compatible with these continua-based landscape concepts. It is thus possible to envisage future landscapes where consolidated conservation areas will be embedded within integrated, multi-use scattered tree ecosystems.

In grazing landscapes, such as those in temperate Australia, regeneration of scattered trees could be encouraged through techniques such as micro-restoration. The aim of micro-restoration is to facilitate the regeneration of saplings in the immediate vicinity (<30 m radius) of existing large scattered trees thereby maintaining the spatial pattern of scattered trees (Lindenmayer et al., 2005; Fig. 3). Methods for micro-restoration will be locally specific, and dependent on the specific mechanisms involved in the regeneration of particular tree species. However, methods might include encouragement of regeneration by placing small temporary fences around individual mature trees or groups of trees to exclude grazing, direct planting and seeding, soil scarifying or burning beneath existing trees. Notably, micro-restoration could be useful in complementing existing restoration programs which aim to establish large and consolidated patches of native vegetation (Bennett et al., 2000). Other management strategies might include reduced stocking rates or alternative grazing regimes (Jansen and Robertson, 2001; Spooner et al., 2002).

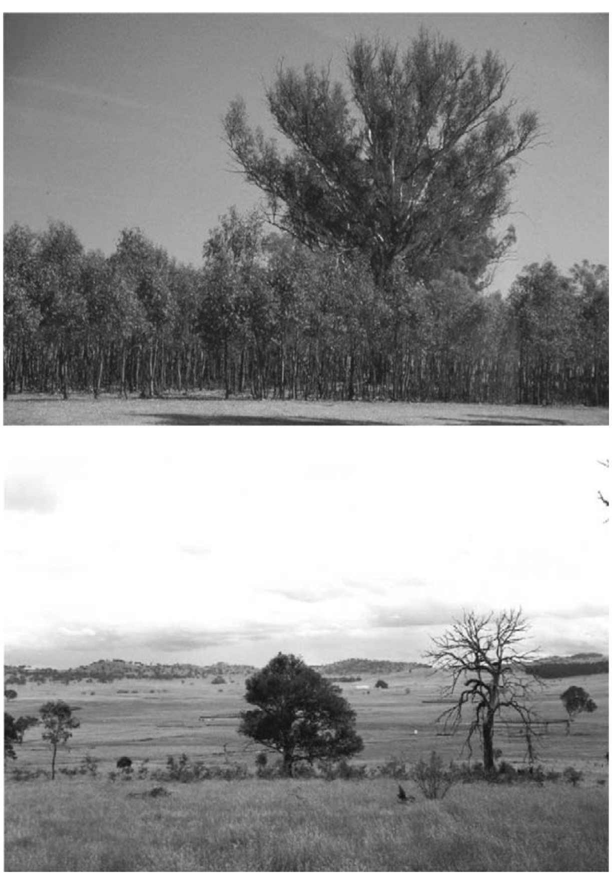

Fig. 3 – Micro-restoration is where tree regeneration is facilitated in the immediate vicinity (<30 m radius) of an existing scattered tree. These examples, from south-eastern Australia, show what micro-restoration might look like (top photo by D. Lindenmayer, bottom photo by A. Manning).

Future landscape management approaches, using a range of tree retention and regeneration techniques, would ideally recognize the complementary contributions of large patches of native vegetation and extensive areas of scattered trees, and provide a promising vision for genuine and sustainable integration of conservation and production.

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