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The clock is ticking—Revegetation and habitat for birds and arboreal mammals in rural landscapes of southern Australia

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Abstract

European land-use has profoundly affected the extent, distribution and structure of Australian native vegetation and these changes have much affected biodiversity and ecosystem processes in agricultural landscapes. We consider the prospects for vegetation and biodiversity under a 'business-as-usual' scenario in which management practices continue as they have been conducted for more than a century. This scenario provides a bleak outlook for ecological health of rural landscapes in southern Australia. The nation is poised at the threshold of a phase of rebuilding rural landscapes, a complex process of managing land-use change for multiple benefits. Assessment of the ecological or biodiversity benefits of revegetation activities is needed for the multi-objective planning processes. Therefore, this paper discusses how landscape reconstruction, and principally revegetation, affect larger, mobile biota such as birds and arboreal mammals. Time-lags in vegetation maturation and senescence are identified as a major influence on the likely success of landscape reconstruction in dealing with probable widespread collapse of terrestrial biodiversity in the wheat-sheep belts of southern Australia.

Keywords: Biodiversity; Habitat restoration; Landscape reconstruction; Optimal landscape design; Time-lags; Revegetation

1. Introduction

The recent Australian National Land and Water Resources Audit (NLWRA, 2002a) painted a bleak picture for the fate of natural resources in Australia, especially for the intensively managed 'wheat-sheep' regions of the southeast and the southwest. The problems of plummeting biodiversity in these regions, the focus of this paper, will not be solved by systems of reserves. Extensive revegetation is needed (Saunders and Hobbs, 1995; Recher, 1999). Extensive land-use change can also be found in other regions of the world, e.g. rural land-use extensification in Europe (Pain and Pienkowski, 1997) and rewilding in North America (http://www.rewilding.org).

Landscape planning models that integrate functions utilizing ecological, biogeochemical, hydrological, agricultural and socio-economic information will be invaluable to landscape reconstruction (Ive et al., 1989). This paper considers the problem of landscape reconstruction almost entirely from the perspective of ecological outcomes, but not because altered hydrology, economics and social outcomes are unimportant. In planning, different disciplines and advocacy groups provide input based almost entirely on their interests. For instance, data and models for analyzing hydrological functioning of landscapes under different vegetation cover exist and are used to design optimal placement of revegetation for salinity amelioration (George et al., 1999; White et al., 2002). Manuals guiding practitioners through the general principles and findings of these models also are available (Stirzaker et al., 2002).

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Therefore, we aim to move our state of knowledge toward an analogous quantitative estimate of the ecological/biodiversity benefits of landscape reconstruction as one major component to consider along with hydrological, production and social concerns, in a multi-objective optimization for any given landscape. Ecologists often have not provided numerical estimates of ecological costs and benefits of various planning scenarios. Insufficient data, high variability and species' idiosyncrasies always are problematic. However, decisions will be made with or without ecologists' input, so saying it is 'too hard' effectively removes ecological considerations from the process. As a counterexample, ecologists have developed methods to quantify the economic benefits of ecological processes, 'ecosystem services', which provide immense benefits for humans (Costanza et al., 1997). Thus, it is possible to provide estimates (incorporating uncertainty) of ecological variables within a complex management framework. While understanding future changes in ecosystem services (e.g. nutrient retention and hydrological functioning) clearly is critical, this is beyond the scope of the current review.

It is important to distinguish here between 'restoration' of remnant vegetation patches and 'reconstructing functioning landscapes'. The former focuses on improving site condition (at fine scales, ca. 10^{-1} to 10^{2} ha), controlling on-site threats by actions such as fencing, weed and pest control, buffering, and also may include facilitating natural regeneration of populations of flora and fauna. Landscape reconstruction is the much more 'big-picture' planning and implementation of land-use change, remnant restoration, and extensive native revegetation needed to prevent on-going declines in ecological function and declining biodiversity over extensive spatial scales (ca. 10^{2} to 10^{7} ha); this incorporates the flows of materials and biota across space (Saunders and Hobbs, 1995; Huxel and Hastings, 1999; Westphal and Possingham, 2003).

We focus on the agricultural landscapes of southern Australia. These are mostly the natural domain of drier eucalypt woodlands and grasslands (Hobbs and Yates, 1999). The focus is on vegetation structure and distribution at both site and landscape scales, namely the size and spacing of trees, shrubs, understorey and fallen timber. Woody vegetation provides most of the habitat structure and resources for animals. Birds and arboreal mammals are highlighted because much is known about them, and they are likely to respond to landscape configuration, especially the arrangement of vegetation at scales above 10 ha (Trzcinski et al., 1999; Radford et al., 2005). First, we outline changes to vegetation structure and dynamics under European land-use in agricultural landscapes of Australia. Second, the vegetation changes expected under 'business-as-usual' management are examined, along with how those changes affect resource provision and biotic responses. Last, we discuss spatial and temporal aspects of habitat and biota and ways to plan site revegetation and landscape reconstruction.

2. European land-use and its consequences

Across Australia, eucalypt woodlands account for the largest proportion of vegetation cleared, 33% and 32 Mha and, with mallee woodlands and shrublands (14%) and eucalypt open woodland (13%), comprise most of the land cleared over the 200 years of European agriculture (>58 Mha, NLWRA, 2001). In the Murray-Darling Basin (ca. 100 Mha), which includes the bulk of the agricultural land in southeastern Australia, ca. 10^{10} trees were cleared (Walker et al., 1993).

Historical tree densities varied across landscapes, both on geographical scales and within vegetation types. Three lines of evidence support this: accounts of early explorers, naturalists and settlers (Rolls, 1981; Parkinson and Mac Nally, 2000); stump measurements (Lunt et al., 2001; Paull, 2001); and surveyor's plans (Lunt, 1997; Fensham and Holman, 1998; Martin, 2005). Estimates of 1800s tree densities from surveyors plans for eastern Australian woodlands range from about 5 to 50 ha^{-1}, with most estimates being between 10 and 20 ha^{-1}. Thus, variation in densities and 'openness' of vegetation were characteristic of vegetation structure in the past. Targets for revegetation clearly should include spatial variation in tree densities. Past densities in many places were much lower than most current replantings.

Land tenure and management practices much influence rates of recruitment and loss of trees in size classes and so, affect vegetation structure (Bennett et al., 1994). Woody vegetation managed as production forest differs from that in conservation reserves and these differ from roadside remnants and from patches on private land. Projecting forward, future vegetation also will differ between these tenures with a range of consequences for the biota and ecosystem processes.

Many large blocks of vegetation on public lands have been managed mainly for timber extraction and, due to systematic removal of large trees, have size distributions skewed towards high densities of small trees. Newly gazetted conservation reserves, many previously managed for wood production, often are dominated by dense, even-aged stands of trees with a shrubby understorey and sparse grasses. Dense, single age-class regeneration often characterizes conservation reserves on old grazing land. Small blocks of vegetation and paddocks on private land may have had middle-sized trees removed for posts and firewood, with removal of dead trees but large trees generally not targeted. Paddocks are dominated by isolated large, spreading trees, nearing senescence, with recruitment of seedlings, sapling and small tree classes suppressed by chronic grazing (Pettit et al., 1998; Clarke, 2002; Gibbons and Boak, 2002). This results in no trees recruiting into middle and large size classes. Shrubs generally are absent from paddocks (McIntyre and Lavorel, 1994; Clarke, 2003). Grasses range from tall tussocks in ungrazed sites to short creeping- and bunch-grasses in areas subject to continual grazing and fertilization (McIntyre and Lavorel, 1994). Roadside verges are an important landscape element in southern Australia. Many verges, although narrow (typically <20 m) nevertheless host some of the best examples of remnant trees, which are extensively used by native fauna (van der Ree and Bennett, 2001; van der Ree, 2002). Verges are exposed to a different disturbance regime to that prior to European settlement, but the current regime may still permit persistence of some disturbance-tolerant shrubs (Spooner, 2005).

Relationships between vegetation structural change and biotic declines are clearest for birds and mammals that rely on hollows formed in large, old trees (Sedgwick and Knopf, 1986; Gibbons and Lindenmayer, 2002). Fallen timber, characteristic of many unperturbed forests and woodlands but often lost during agricultural development (Harmon et al., 1986), is demonstrably advantageous for many small mammals and birds (Mac Nally and Horrocks, 2002; Mac Nally et al., 2002a).

3. Future scenarios

There are many opportunities for rebuilding landscapes including revegetation of agriculturally productive lands. Currently, 80% of agricultural profit to the nation at full equity is derived from <1% of the 454 Mha currently used for agriculture and pastoralism (NLWRA, 2002a). In principle, one can rebuild landscapes without necessarily incurring great losses from foregone production by reorganizing at very broad scales (ca. 10^5 to 10^8 ha). Large areas might be devoted to landscape rebuilding, including land-use intensification in some areas (Dunlop et al., 2002). A triage approach may be appropriate in which some landscapes are considered irredeemable ecologically (use these for acceptable commercial outcomes such as saline-tolerant crops) and concentrate limited resources for ecological restoration in more promising areas (Hobbs and Kristjanson, 2003). Achieving such structural adjustment in social and economic terms is complex, but needs to be addressed.

Altered attitudes to the environment often result in little change to management practice because of constraints on finance, capacity and management skill (NLWRA, 2002b). Ecological restoration is constrained by biophysical conditions and agro-political policies, which are themselves derived from biophysical conditions, social geography and agricultural history (Abensperg-Traun et al., 2004). The Australian environment, especially in the production regions, is characterized by soils that are thin, very old, leached of nutrients and containing large salt stores; rainfall is low and erratic. Profound land degradation in Australia within a very short agricultural history has galvanized community sentiment and involvement over the past 20 years in agro-environmental programs such as Landcare, an Australian landholder-driven, voluntary organization aimed at tackling environmental degradation and achieving sustainable agricultural landscapes. But direct government subsidy of environmental management is small by comparison with European Union countries (Abensperg-Traun et al., 2004). The human population is largely urbanized and rural landscapes have dispersed, low-density populations with little tourism, compared with European countries. These features, poor, fragile biophysical conditions, short and intense agricultural history and a rural population with little economic diversification and low governmental environmental subsidy, together constrain achievable ecological restoration. However, despite the increased effort there has been concern for on-ground actions proceeding without a strong scientific basis (Majer, 2002; Bernhardt et al., 2005). Revegetation programs currently lead to many scattered, small patches and unconnected linear strips and have little impact on the proportion of land covered by vegetation (Freudenberger et al., 2004). These replantings often are ideal for problem species, such as the noisy miner *Manorina melanocephala* in southeastern Australia (Piper and Catterall, 2003), and do little to improve conditions for the majority of declining taxa.

Changing land-use within properties will not achieve landscape reconstruction. The spatial scale (ca. 10^0 to 10^3 ha) is too fine for the necessary changes. This does not mean that individual landholders can do nothing to improve prospects for biodiversity (McIntyre et al., 2002). However, coordinated planning across many properties is necessary and may require many entire properties to be dedicated to the task of landscape reconstruction. One option is to purchase and incorporate properties into the public conservation reserve system. Another option is through land stewardship schemes in which landholders are contracted to carry out revegetation and management aimed at restoring ecological processes, rather than devoted to agricultural production (Morton et al., 1995). A newly developed tool is to auction conservation ‘stewardship’ contracts to landholders (Stoneham et al., 2003), although this would need to be massively scaled up to achieve desirable ecological outcomes and much thought is needed on how to achieve strategic goals at regional scales.

3.1. Business-as-usual

Where temperate woodlands remain, threats continue from further clearing, salinity, grazing, nutrient enrichment, changed fire regimes and exotic species invasion (Hobbs and Yates, 1999; NLWRA, 2001). The mere occurrence of species within landscapes is not sufficient—populations need to be viable. This means a low probability of extinction over a specified period (e.g. 100–200 years) because there is sufficient suitable habitat and ecological resources to: (1) sustain existing individuals; (2) allow adults to successfully breed; and (3) have populations that are large enough to cope with demographic fluctuations and exogenous impacts, such as droughts or very extensive wildfires (Burgman, 2005).

Some ecological consequences of past change have yet to occur. In populations of long-lived species, mature but non-reproducing individuals may give the impression of healthy population sizes using assessments based on occurrence or abundance, but are bound to decline because there is little recruitment. This applies to trees, long-lived understorey and animals that use the vegetation (Hanski and Ovaskainen, 2002). Parrots that have very low reproductive success because of a lack of nesting hollows are examples (Saunders et al., 2003).

Ecological resources afforded by mature vegetation do not 'materialize' immediately. There are long time lags in accumulation and decline phases for many ecologically critical resources. Isolated paddock trees are a characteristic feature of agricultural landscapes in southern Australia. These, more than any other 'resource', are under threat from lack of replacement (Gibbons and Boak, 2002). Paddock trees appear to provide disproportionately high resources for many taxa (Fischer and Lindenmayer, 2002). Estimates of decline of paddock trees range widely, from 0.54 to 2.5% yr^{-1}, suggesting total loss of mature trees in 50–200 years (Ozolins et al., 2001; Gibbons and Boak, 2002).

Fallen timber has been much depleted (up to 85% lost) in River Red Gum *Eucalyptus camaldulensis* forests (Mac Nally et al., 2002b). Fallen timber provides critical foraging and breeding habitat for many invertebrate, reptile, mammal and bird species (Harmon et al., 1986), but it takes hundreds of years to produce large logs on forest floors because the trees have to grow to a large size first. Tree hollows suitable for many of the larger, hollow-dependent fauna cannot occur until trees to reach a large size and suffer an injury and infection by fungi (Gibbons and Lindenmayer, 2002).

Therefore, under a business-as-usual scenario over the next century, there will be few large trees, isolated scattered trees will be lost, and understorey vegetation and ground-layer complexity will continue to diminish and declines in species heavily dependent on these resources almost are guaranteed. Many species also are much rarer in landscapes because of the lack of available habitat. These rarefied populations also are likely to become lost to landscapes as currently managed (Ford et al., 2001; Hanski and Ovaskainen, 2002).

3.2. Landscape reconstruction

Landscape reconstruction can be divided into: (1) restoring existing remnants; (2) revegetation of paddocks in to native vegetation with similar characteristics to previously; and (3) designing functioning landscapes utilizing a mix of (1) and (2). The first two tasks represent endpoints of a continuum of site quality and intervention required. The third task requires knowing, given less that half the areas of most landscapes will be revegetated, what are the optimal strategies for allocating effort among sites to design those landscapes from an ecological perspective. The landscape perspective is critical because there always will be compromises in the kinds of investment made, which may depend on the state of the existing system (Bennett and Mac Nally, 2004). For example, one may choose to augment an existing 10 ha patch with 10 more ha if that is necessary to provide sufficient space for an area-limited species (Lambeck, 1997). There may be several 10 ha patches from which to choose. Existing approaches pay no heed to the existing state of the patches (Westphal and Possingham, 2003; Wilson and Lowe, 2003). With a planning horizon of 100–200 years, one might seek out patches that were not dominated by old trees likely to senesce in the next 20–50 years because they would be dead long before replacements are capable of providing the biodiversity services. Therefore, optimal allocation of effort depends upon existing conditions.

Efficient design for landscape reconstruction has many similarities with spatial conservation planning, especially work on habitat networks (Opdam et al., 2003). Systematic approaches requiring computer models or algorithms using methods from the field of operations research (Margules and Pressey, 2000). Spatial arrangement of vegetation (both existing and planned) is critical to systematic landscape reconstruction; where to put new habitat? This is the nub of the landscape reconstruction question.

There are several existing methods. One, the focal species approach, identifies threats to biodiversity for a particular landscape, and identifies each species thought to be most sensitive to a particular threat (e.g. the species needing the biggest patch, or the species most dependent on vegetated links between patches); this becomes the focal species for that threat (Lambeck, 1997; Brooker, 2002). Potential landscape designs are based on the simultaneous satisfaction of the needs of the focal species. Spatial arrangement also has been addressed by using rules-of-thumb for size and isolation of replantings developed from island biogeography and metapopulation theory without regard to particular species (Wilson and Lowe, 2003; Bennett and Mac Nally, 2004). More sophisticated algorithms for selecting revegetation sites based on particular species' requirements can be derived by adapting conservation-reserve selection techniques (Westphal and Possingham, 2003).

Which types of vegetation, and in what proportions, should be restored? Some workers have used algorithms that select different vegetation types (Pressey et al., 2003). Timetabling of reconstruction actions can be derived, in principle, by using methods for optimal scheduling (Westphal et al., 2003). In many existing models of landscape reconstruction, vegetation is represented as a binary variable (present/absent), effective revegetation is assumed to be feasible and practicable and new vegetation 'appears' immediately in a mature state (Huxel and Hastings, 1999; Westphal and Possingham, 2003; Wilson and Lowe, 2003). As outlined below, we need to advance beyond the simple assumption that mature vegetation can be placed 'magically' in landscapes and new approaches that explicitly take into account vegetation dynamics are required. Analogous approaches may be found in forestry management (Hansen et al., 1993).

3.2.1. Revegetation and vegetation development

Reversing degrading processes to restore diversity, structure and function in temperate eucalypt woodland sites often is difficult (Yates and Hobbs, 1997). Removing the degrading agent alone usually is not enough and substantial intervention is needed. Following active revegetation, growth rates, structural development and species composition can differ widely among sites depending on soils, climate and landform. An explicit consideration of time in restoration planning becomes imperative when regrowth of native vegetation is likely to be very slow (poor nutrients, little water) and where senescing trees dominate existing vegetation. These conditions are widespread in southern Australia and elsewhere (NRE, 1998; Chapman and Chapman, 1999; Lafon et al., 2000). Anticipating the outcomes of management actions is critical when regrowth and maturation are slow relative to planning time-frames. Evidence of planning mistakes or unanticipated outcomes may take years to become apparent and much longer to correct, in which time natural populations may decline to dangerously low levels.

Given that habitat restoration involves decade- and century-long processes, one also must consider accelerated climate change (Hughes, 2003). For many species of *Eucalyptus*, the dominant trees in temperate Australian woodlands, in 50 years the places where climate is suitable for the species will have moved geographically, so that current ranges no longer will be suitable (Hughes et al., 1996). Therefore, future climates must be considered when selecting long-lived species for revegetation.

How fast do trees grow in the nutrient-poor, fairly xeric landscapes of southern Australia? Growth-rate estimates are available from a number of studies (Victorian Department of Natural Resources and Environment unpublished data; Banks, 1997; Stoneman et al., 1997; NRE, 1998; Whitford, 2002; Wormington et al., 2003). These estimates include both single- and mixed-species stands for several species of *Eucalyptus* and from sites in open forest and woodlands with minimal silvicultural management. The median diametric growth rate of the fastest growing trees was 0.6 cm yr^{-1} (10th and 90th percentiles: 0.34–1.06); intermediate growth rates, median 0.35 cm yr^{-1} (0.2–0.6); slowest growing trees had median growth rates of 0.2 cm yr^{-1} (0.08–0.34). Woodland eucalypts can attain diameters of 1–2 m (Banks, 1997) and, with median diametric growth rates of 0.35 cm yr^{-1}, would take nearly 300 years to reach diameters of 1 m.

There are two critical determinants of growth rates—site productivity and suppression by competitors. The wheat-sheep regions are likely to be poor relative to production forestry regions, primarily because of lower rainfall. Within a given rainfall band, forestry is restricted to the poorer soils because agriculture has priority on richer soils. Competition between trees reduces growth rates (Harper, 1977).

Thus, there are two major ways to increase the growth rate of trees, neither of which is widely used. First, space trees more widely. Spacing trees more widely means potentially faster development of reproductive maturity, large boughs, hollows and fallen timber—resources that are important for animals (Harper, 1977). Lindenmayer et al. (2000) showed that the size and number of hollows were proportional to tree diameter divided by the square root of its height, so that shorter, more massive trees had more and larger hollows. Distances between mature tree stems in woodlands in the Murray-Darling Basin have been estimated at between 6 and 15 m (50–300 stems ha^{-1}) (Walker et al., 1993). Tree planting in this region typically has spacings of 2–4 m (500–2000 stems ha^{-1}) (Schirmer and Field, 2000; Anon., 2003), equivalent to closed forest. Therefore, planted patches are denser than desirable or natural for reflecting the structure of native woodlands and forests, for producing critical ecological resources and are likely to limit diametric growth rates.

Second, a more radical solution is to revegetate on agriculturally productive sites. There are at least three reasons for this. First, sites generally available for revegetation are those least likely to significantly reduce agricultural production in farm landscapes—sites with shallow, rocky and nutrient deficient soils or that are waterlogged—and thus yield low growth rates. Second, low-productivity sites are relatively over-represented (and richer sites correspondingly under-represented) in the conservation reserve system for the same reason—value for agricultural production. Third, much current revegetation planning, which is based on reducing groundwater recharge to restore hydrological balance and reduce salinity risk leads to planting on hill- and ridge-tops and upper slopes, the very same low productivity sites mentioned above.

Productive sites (deeper, richer, better-watered soils) support faster growth than poor sites, providing ecological resources sooner and in higher abundance. However, sites that are more productive may support greater weed growth than poorer sites, obstructing recovery of native plant species richness and abundance, and thus requiring more management effort. Hence, there may be a trade-off between the ease of restoration and rate of provision of habitat resources. We anticipate that eventually, decisions need to be made to acquire more fertile areas to accelerate the provision of ecological resources more quickly than the rates given above.

3.2.2. Implications of site restoration for biota

We have little empirical basis for assessing ecological effects of revegetation because it is a recent phenomenon, with some plantings dating to the 1970s but most to the last 10 years. There have been several empirical studies of animal use of revegetated areas in agricultural lands in Australia (e.g. Ryan, 1999; Arnold, 2003; Hobbs et al., 2003; Martin et al., 2004). Woodland-dependent birds are uncommon and edge-dwelling species common in regenerating areas (Green and Catterall, 1998). Wider spacing within revegetated areas produces deeper canopies and supported more canopy-feeding and leaf-gleaning birds (Arnold, 2003). A lack of structural complexity or density of vegetation in different vertical layers probably limits bird diversity (Ryan, 1999; Hobbs et al., 2003).

Given that most empirical studies are restricted to the first 5–30 years after planting, thinking about longer-term effects on biota must be done without direct data. Hence, future projections need to use conceptual models driven by expert opinion or informed inference (e.g. Martin et al., 2005). Here follows a simple heuristic example to demonstrate the importance of vegetation growth and senescence to restoration in a landscape context. Birds are the subject mainly because they are the animals most likely to be responsive to changes in landscape configurations at scales >10 ha (Trzcinski et al., 1999; Radford et al., 2005) and much is known of their resource requirements. Assume that the probability of occurrence of a bird species depends on habitat resources provided by vegetation, such as nesting sites or nectar-rich flowers. As plants grow and vegetation develops, more ecological resources are provided. Senescing plants provide fewer habitat resources, apart from hollows and fallen timber. Changes in resource provision through growth and senescence of vegetation in the landscape affect populations of birds reliant on those resources.

Replanting vegetation in a landscape with scattered patches of old, senescing vegetation leads to two peaks in the population age-structure of trees in the landscape. Initially, existing vegetation provides suitable habitat resources but as plants senesce the suitability and probability of occurrence declines through time to low values in 100 years. Replanted vegetation initially provides few resources, but the probability of occurrence increases through time to high values by 2100, say, because mature plants provide those resources and will continue to do so for hundreds of years. A ‘bottleneck’ arises in the intervening period, perhaps around 2050, because neither senescing vegetation nor replanted vegetation provide many resources, so that the probability of occurrence is low throughout the landscape (Fig. 1a).

Revegetating high productivity sites would yield higher growth rates for replanted vegetation, so providing habitat resources earlier and in greater abundance than on low-productivity sites (Fig. 1b). Consequently, replantings may achieve vegetation structures with high occurrence probabilities earlier and may enable population ‘bottlenecks’ to be overcome. Some high-productivity areas must be revegetated to quickly establish replanted habitat.

One of the main recommendations for landscape restoration is to maximize contiguous areas of habitat (Possingham et al., 2001; Bennett and Mac Nally, 2004). There are at least two reasons for revegetating adjacent to existing remnants that relate to the time course of regrowth. First, as new and old patches have different structure and provide different habitat resources, their adjacency satisfies the needs of species that require different sorts of habitats, or that require multiple resources not provided by any one vegetation patch (Law and Dickman, 1998). Second, adjacency of different stages may assist the colonization of replantings from existing, senescing areas.

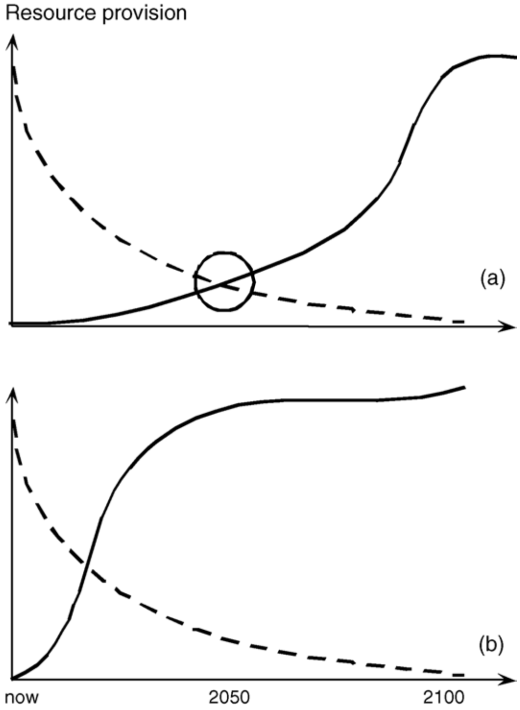

Fig. 1. Timelines of site-based resource provision by senescing trees (dashed lines) and replantings (solid lines) when replantings are (a) on impoverished soils and (b) on high-quality soils. The bottleneck (circled) occurs in (a) when senescing trees and replantings simultaneously provide few ecological resources.

The temporal process of revegetation and associated species’ responses can potentially affect all aspects of landscape reconstruction. Time lags in reconstruction can translate into substantial declines of biota in fragments (Martínez-Garza and Howe, 2003). Given that the spatial configuration of vegetation in reconstructed landscapes affects local rates of extinction and colonization, it can have a major influence on time lags in population recovery (Huxel and Hastings, 1999). It may be necessary to maintain not only a mixture of vegetation types but also patches of different ages to accommodate species with diverse resource requirements (Law and Dickman, 1998; Richards et al., 1999). The optimal sequence of revegetation (Westphal et al., 2003) depends upon vegetation maturation processes, but ways to account for this have not yet been explored.

3.2.3. *Species viability*

As an optimization problem, we need to specify a system model, what is to be optimized in landscape reconstruction and then to define appropriate ‘objective functions’ (Possingham et al., 2001). Objective functions – what are we aiming to achieve? – should explicitly refer to species’ persistence, which includes the provision of sufficient resources for adults to survive and breed, to produce young, and for populations to be large enough to cope with demographic ‘shocks’ (e.g. disease) and external disturbances. To estimate the probability of persistence of a species in alternative landscapes over a specific period (e.g. 200 years) requires three components. First, a population-dynamic model with estimates of birth, death and migration rates. Second, a vegetation-dynamic model to describe senescence and maturation. And third, a landscape-change model to compare alternative designs. Population viability analysis (PVA) has been used widely for analyzing conservation problems and is based on computer simulations of decisions and effects that cannot be done in the real world. PVAs identify factors that are most likely to limit populations and management actions that promote population persistence (Burgman and Possingham, 2000).

There are two main difficulties with PVA for most applications for future landscape planning. First, population-viability models need copious data that we do not and cannot reasonably expect to have. Birth, death and migration rates are known for only 20 populations of woodland bird species across Australia (Ford et al., 2001), and much of this information is likely to vary substantially, both geographically and through time. When a species list for a region might include well over 100 bird species, as well as mammal, reptile, amphibian, invertebrate and plant species, this paucity of data is a severe limitation. Second, there is the problem of computation. Even with rough estimates of the demographic parameters for most species, the number of possible solutions to compare becomes too large to search when extensive landscapes with many species are considered.

3.2.4. *Habitat models and occurrence probability*

An alternative approach is one in which habitat suitability indices are used to infer the probability of occurrence and the potential to support persistent populations (Larson et al., 2004). This approach generally assumes that: (1) species are not limited by dispersal ability or home-range requirements, and (2) there are no density dependencies and interspecific interactions are unimportant. Habitat suitability logically is equated with persistence, and breeding can be successfully undertaken. While these assumptions clearly are not the case in most real world situations, the use of habitat suitability indices can be a useful heuristic way to assess effects of alternative reconstruction plans (e.g. Hansen et al., 1993; Westphal et al., 2003).

How are occurrence and habitat structure related? Different ecological resources will become available at vastly different rates. Tussock grasses, forbs, twiners and many shrubs can reach full reproductive potential and maximum biomass within 10 years (Williams and Roe, 1975; Morgan and Lunt, 1999). Logs, which are key elements not only to foraging birds but also to reptiles, invertebrates and fungi, will not appear until large boughs fall from planted trees (decades to centuries) or may need to be imported, which is probably infeasible (Mac Nally et al., 2002b). We know little about invertebrate responses to revegetation and their role in ecosystem recovery.

Vegetation may not simultaneously provide foraging and breeding resources for a given species. If foraging resources are limited at some times and breeding resources at others, over long time periods, then the population may be chronically limited but for different reasons over those decades to centuries. Models based on species occurrences may lead to planning of revegetation that satisfies foraging needs, but not breeding requirements, and thus may allow survival of individuals but not long-term population persistence. It is important that planning based on survey data or occurrence probabilities takes into account the provision of suitable shelter/foraging and breeding habitat and their proximity if species have seasonal movements (e.g. golden whistler *Pachycephala pectoralis*, Mac Nally, 1995).

As revegetation matures, the suitability of revegetation for any particular species changes. To evaluate the value of revegetated areas for animals we must integrate habitat suitability over time because high quality of habitat in the distant future is only part of the picture; capacity to support populations until that distant future is critical too. Long time lags and bottlenecks for crucial habitat resources require acceleration of the development of certain resources, such as hollows, or artificial supplementation. The latter option may be very expensive or in many cases, infeasible if large areas need to be managed, but may be useful in some cases (e.g. nest boxes, Spring et al., 2001).

Species have different responses to habitat change so particular revegetation actions will favour some but not all species. This leads to management conflicts between species. The adopted solution has to be an integrated one over all species, but it is likely that species will be weighted differently. For example, species favoured by broad-scale clearance (e.g. noisy miner *M. melanocephala*) should be down-weighted, but species of conservation concern (e.g. speckled warbler *Chthonicola sagittata*) need to be given much higher weights. Highest weights probably should be given to species classified as ‘near threatened’ presently, but that will become critically endangered as crucial resources, such as tree hollows, disappear and subsequently severely limit populations (Possingham, 2001).

There probably are several broad patterns of bird-species responses to growth of replanted vegetation. Some species benefit from revegetation because both foraging and breeding resources are provided quickly by the growth and maturation of shrubs and trees. Insectivores gleaning from leaves or by hawking and nesting in foliage of small trees are good examples. These include the yellow thornbill *Acanthiza nana* and rufous whistler *Pachycephala rufiventris* (Fig. 2a). For other species (e.g. striated pardalote *Pardalotus striatus* and southern boobook, *Ninox novaeseelandiae* Fig. 2b), foraging requirements probably are met soon after revegetation begins but breeding resources, such as tree hollows, develop slowly (ca. 150 years).

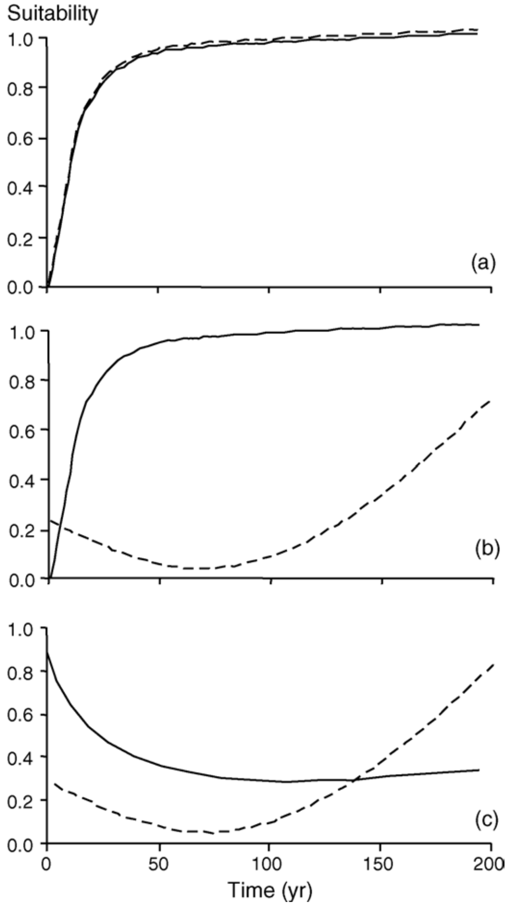

Fig. 2. Schematics of habitat suitabilities for six bird species following revegetation. Suitability of resources are for foraging (solid line) and for breeding (dashed line). Examples are for a lightly grazed site with 1–2 trees ha^{-1} planted with tubestock. (a) Species for which suitability for both foraging and breeding initially is low and increases rapidly. (b) Species for which foraging resources initially are poor but increase rapidly, whereas breeding resources initially decline before a slow increase. (c) Species characteristic of open country for which foraging suitability initially is high but declines as vegetation matures and cover increases, whereas breeding resources gradually increase after an initial delay.

Foraging resources for open-country birds, such as the Australian magpie *Gymnorhina tibicen* and wedge-tailed eagle *Aquila audax*, are satisfied prior to revegetation because of the availability of their ground-dwelling prey, but suitability of those resources declines as vegetation matures and cover increases (Fig. 2c). As mature trees senesce, availability of large boughs for nesting decreases, and then, gradually increases with growth of the new cohort of trees. There are many other patterns, but the ones we have outlined provide a flavour of the possibilities that need to be considered in a joint optimization over all species.

Incorporating time into models of landscape reconstruction substantially complicates planning, making true optimization methods suitable only for very simple problems (Westphal et al., 2003). Complexities are increased by species-specific resource needs. Many species of birds and mammals require different habitats for breeding and for foraging, and those needs differ among species (Law and Dickman, 1998). Through time, the suitability of restored vegetation on a given plot for breeding and for foraging by a given animal species will change.

4. Conclusions

There seems little doubt that sustainable biodiversity management in agricultural landscapes almost certainly will require replanting of large amounts of natural vegetation. Given that only fractions of landscapes ($\leq$30%) are likely to be replanted, setting priorities for planting needs to be optimized given limited areas and funding. How much vegetation will be planted per planting (local amounts)? Where in the landscape and of what kind of vegetation (vegetation community) will be replanted? The time lag in vegetation maturation is a critical knowledge gap in optimal planning of vegetation placement in future landscapes. Time frames of centuries into the future are the appropriate planning (and modelling) horizons.

The ultimate goal is to build an integrated spatial and temporal framework for making optimal decisions for replanting natural vegetation that takes into account time-lags in vegetation development, tree senescence and the time course of providing ecological resources. To do so, the following tasks will need to be undertaken:

- Assembly of data and building of models representing maturation of habitats of a range of types though time.
- Development of quantitative models for locations in landscapes where animals are likely to occur if *mature vegetation* were available to them, and how species may respond to intermediate stages of vegetation maturation.
- Construction of quantitative models describing species' dependence upon locations of suitable habitats in landscapes.
- Building models for finding optimal solutions to vegetation placement and management under specified sets of constraints: how much land will be available; how many resources (seed, money, personnel) will be available for planting and management.

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