The role of connectivity in Australian conservation

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The existing system of nature reserves in Australia is inadequate for the long-term conservation and restoration of native biological diversity because it fails to accommodate, among other elements, large scale and long-term ecological processes and change, including physical and biotic transport in the landscape. This paper is an overview of the connectivity elements that inform a scientific framework for significantly improving the prospects for the long-term conservation of Australia's biodiversity. The framework forms the basis for the WildCountry programme. This programme has identified connectivity at landscape, regional and continental scales as a critical component of an effective conservation system. Seven categories of ecological phenomena are reviewed that require landscape permeability and that must be considered when planning for the maintenance of biological diversity and ecological resilience in Australia: (1) trophic relations at regional scales; (2) animal migration, dispersal, and other large scale movements of individuals and propagules; (3) fire and other forms of disturbance at regional scales; (4) climate variability in space and time and human forced rapid climate change; (5) hydroecological relations and flows at all scales; (6) coastal zone fluxes of organisms, matter, and energy; and, (7) spatially-dependent evolutionary processes at all scales. Finally, we mention eight cross-cutting themes that further illuminate the interactions and implications of the seven connectivity-related phenomena for conservation assessment, planning, research, and management, and we suggest how the results might be applied by analysts, planners, scientists, and community conservationists.

Key words: Connectivity; Landscape permeability; Biodiversity; Conservation; WildCountry; Australia.

INTRODUCTION

IN Australia and globally, nature and society face a historically unprecedented wave of extinction and ecological degradation (Wilson 2002). Although large ecological reserves are an essential core component of any biodiversity conservation programme, protected areas comprise only about 6–12% of the land globally (IUCN 2003) and nationally (Mackey *et al.*, in press) and are typically widely dispersed and isolated. This percentage of strictly protected land is too small — by a factor of five or ten, even if the reserves were optimally distributed (Soulé and Sanjayan 1998).

In response, critics of conventional conservation (e.g., Soulé and Terborgh 1999) often suggest that long-term prospects for biodiversity will be enhanced the more the entire landscape, irrespective of tenure, is managed as a conservation (rather than a production) matrix. Such a transformation, however, will demand a bolder and more systematic approach to nature protection. This will require increases in the area protected, enhanced biotic and abiotic connections between core protected habitat areas, and reconsideration of the economic and recreational activities on lands where native ecosystems still dominate.

In North America and elsewhere, it has been recognized that existing conservation initiatives fail to provide sufficient area and ecological connectivity to accommodate the key, large-scale, long-term ecological processes necessary to sustain natural systems (Soulé and Terborgh 1999). Neither do they allow for evolutionary adaptation to environmental change. The current situation for biodiversity in Australia is similar (Australian Government 2001). During the last two centuries 19 vertebrate species have become extinct and a further 10 have disappeared from the mainland (AMO 2004). If current trends in land use and degradation continue unabated, the future will be as grim or worse (compare Recher 1999; Garnett and Crowley 2000). Not only is vertebrate biodiversity at risk from the intensification of land use (especially logging, grazing and cropping) and invasive species, but most conservation responses to threatening processes do not consider the necessity of large-scale connectivity processes.

In response, in 2000 the Wilderness Society Australia launched the WildCountry Project (WildCountry) in partnership with other non-government organizations, government at state and local levels, industry and private

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landowners, and the Wildlands Project USA (Wildlands). Mackey *et al.* (in press) present the scientific and technological framework for this project, including the need for a more extensive system of protected (core) areas. The continent-wide, WildCountry conservation plan will be developed and implemented through co-operative regional projects and partnerships. The goal is to comprehensively address and halt the continuing degradation of Australia's biotic diversity by providing a positive, detailed, science-based vision for the integration of existing conservation programs into an expanded, interconnected system of core reserves, and the compatible management of off-reserve lands and waters. The purpose of this paper is to encourage discussion of just one of the essential elements of such a project — the maintenance and restoration of large-scale ecological connectivity at landscape, regional and continental scales.

CONNECTIVITY FOR BIODIVERSITY PROTECTON

Change and heterogeneity at all geographic scales are as much a cause of natural diversity as they are products. In other words, dynamic ecological processes or flows are essential for both the evolution and the persistence of species and ecosystems. Ecosystems are open systems and will decay if cut off from continuous or episodic inputs of many kinds or if barriers prevent biotic and abiotic flows. Thus, ecosystem integrity and resilience require ongoing exchanges of energy, water and nutrients. Some interchanges or flows require locations to be contiguous or adjacent. Alternatively, such flows may involve tele-connections — aerial exchanges and flows between distant locations. The terms landscape connectivity and landscape permeability are frequently employed in conservation biology to remind us of this ecological imperative for interchange.

Interchanges of plants and animals (or their propagules) that maintain species diversity occur at many temporal and spatial scales, from local to intercontinental and from daily to decadal or much longer. Organisms must be able to move in order to forage, migrate, and disperse to locate new territory or other habitat resources. In Australia, the ubiquity of relatively infertile soils and extreme temporal and spatial variability in rainfall and productivity periodically requires many species to move long distances (Nix 1974; Morton *et al.* 1995). At a local scale the persistence of populations may be compromized in the absence of export and import of both individuals (for demographic rescue) and genetic material to maintain heterozygosity and minimize inbreeding and genetic drift (Soulé 1980). Finally, species diversity can depend on the presence of effective numbers of highly interactive species (see below) that often require landscape permeability at regional scales (Terborgh *et al.* 1999; Soulé *et al.* 2003). Long-term ecological resilience, therefore, requires all of these kinds and scales of movement (Dobson *et al.* 1999).

We assume, therefore, that the maintenance of movements and flows at all scales is a critical component of any conservation strategy. The term "connectivity" is generally used to convey this idea, though it lacks specificity. Some of the terms in use for the planned or designated conservation elements that allow for connectivity or the persistence of essential movements and flows are landscape linkages, wildlife or ecological corridors, and stepping stones. Because the term "corridor" is used in many other contexts, including for utility rights-of-way, recreational routes, networks of protected areas, and roads, and because the term is colloquially associated with narrow passageways in the built environment, it is falling out of favor in the conservation biology literature. The phrase "landscape permeability" is often substituted for connectivity, in part because (1) it suggests the importance of dynamic processes, (2) it reminds us of the species-specific nature of obstacles to movements, (3) it requires conservationists to consider the landscape (including the "matrix" of unprotected country) as a whole, rather than focusing on narrow, defined corridors.

CONNECTIVITY FOR EXTENSIVE ECOLOGICAL PROCESSES IN AUSTRALIA

The major objective of this paper is to briefly describe the ecologically extensive processes in Australia most relevant to the conservation of biodiversity. We identify seven such connectivity-related phenomena. Our premise is that conservation in Australia cannot succeed unless conservation planning addresses these phenomena at all relevant spatial and temporal scales. The following sub-sections briefly describe this "set of seven."

1. Critical species interactions

Species with relatively high per capita interaction strengths have been referred to as keystone species (Paine 1969; Ledec and Goodland 1988; Power and Mills 1995) or strongly interacting species (Soulé *et al.* 2003). Among the ecologically important activities of such species are the creation of structures such as cavities, burrows, and dams, and interactions such as predation, pollination, and competition. While climate and climatically driven primary productivity are ultimate determinants of productivity and the structural qualities of vegetation, species themselves often play a major role in regulating species diversity and how energy, water and nutrients are distributed in an ecosystem (Soulé *et al.* 2003). The interactions of animal species, for example, can have profound effects on the number of trophic levels and on the distribution, abundance, and population dynamics of species in the same and in other levels (Hairston *et al.* 1960).

The disappearance of relatively interactive species, therefore, often causes profound simplification and restructuring of ecosystems, and can initiate ecological chain reactions, or trophic cascades that may lead to the disappearance of entire ecosystems, causing a rapid decrease in species diversity (Paine 1969; Arnold and Wassersug 1978; McNaughton *et al.* 1989; Hall *et al.* 1992; Gillespie and Hero 1999; Oksanen and Oksanen 2000; Terborgh *et al.* 2001; Soulé *et al.* 2003). This is why so much emphasis is placed on the wolf and other large carnivores by conservation planners in North America (Soulé and Noss 1998). Australian ecosystems are unique in that the native marsupial carnivore fauna has been largely replaced by introduced placental predators (dingoes *Canis lupus dingo*, foxes *Vulpes vulpes* and cats *Felis catus*), yet the interactions among these exotic species can be critical for the survival of many of the persisting marsupials (Lundie-Jenkins *et al.* 1993; Corbett 1995; Risbey *et al.* 2000; O'Neill 2002). Thus, it is essential that conservation networks be designed so that major ecological players persist in core areas. In other words, the landscapes that surround core areas must be permeable to dispersing and migrating individuals of relatively interactive species. In the absence of such permeability, the risk of local extirpation of such species in core areas is high.

Among highly interactive species (1) are mycophagus mammals (Johnson 1996); honeyeaters (Paton *et al.* 2000); water birds (Roshier *et al.* 2001); frugivores, granivores and other insectivores (NLWRA 2002); pollinators and animal dispersers of seeds and fungal spores. Conservation biologists and planners should identify as many of these species as possible, and determine the threats to their dispersal or migration routes. In other words, the landscapes that surround core areas must be permeable to dispersing and migrating individuals of relatively interactive species. In the absence of such permeability, the risk of local extirpation of such species in core areas is high. The potential impacts on such species of deleterious interactions, such as those identified between exotic grasses and altered fire regimes in northern Australia (Dwyer *et al.* 2001), also need to be considered.

2. Long distance biological movement

Conservation planning must explicitly consider long distance biological movement. Both vertebrates and invertebrates can have stages in their life cycles that are associated with large-scale movement (Isard and Gage 2001). Anywhere between 30 and 60% of Australian woodland and open-forest bird are non-residents and their persistence in a region may depend on large-scale movements that occur either seasonally (migratory) or from year to year (episodic or dispersive) (Griffioen and Clark 2002; Recher and Davis 2002). The propagules of all plants disperse, with the scale of movement depending on life history attributes and the extent to which dispersal is aided by wind, animal vectors or water flow.

Long distance animal movement is strongly associated with temporal variability in primary productivity and associated food resources (Nix 1976). While parts of the continent experience relatively high levels of seasonally reliable primary productivity, the entire continent is subject to extreme year to year variability in precipitation (Hobbs *et al.* 1998). This year-to-year variability, coupled to the semi-arid and arid climatic regimes that dominate around 70% of the continent, has been a core factor in the evolution of Australia's wildlife and on the commonness of dispersive life history characteristics.

It follows that, among other things, habitat loss, fragmentation and modification reduces the likelihood of wildlife finding suitable resources, and thereby decreases the probability of reproductive success and survival. Large areas incorporating an interconnected network of patches are essential for many species in such dynamic systems. In addition, the removal of any particular patch — including those that serve as "stepping stones" for long-distance movements — may affect the whole system, with consequences far beyond the proportional loss of habitat in the system as a whole. Over time, the cumulative effects of patch removal can lead to widespread extirpation of species, in part because some patches are more critical than others owing to their precise locations and the resources they provide (Woinarski 1992, 2000; Price *et al.* 1999).

The present and future obstacles to long-distance movements need to be evaluated when considering the long-term viability and ecological effectiveness of interactive species and the potential for speciation as discussed below. Such obstacles may be caused by processes outlined below, including deleterious fire regimes (Mackey *et al.* 2002), the construction of barriers like roads, dams and fences, the failure of hydroecological processes, global climate change and drought, and the degradation of appropriately spaced habitat resources such as water, food, and resting sites. Finally, the protection of refugia that provide resources to dispersive species during times of stress is of paramount importance (Mackey *et al.* 2002). Conservation plans must ensure that the landscape is permeable to movements in and out of remote refugia, even if the intervals between the episodic events that provoke such movements may be on the order of centuries.

3. Disturbance at local and regional scales

Many categories of disturbance, both natural and anthropogenic, affect landscape permeability. Among these are fire, vegetation clearance, livestock grazing, foraging by feral carnivores and herbivores, weed invasion, and built structures such as roads and dams (Hobbs 2003). Disturbance is natural and inevitable, but anthropogenic disturbance often exceeds the historic range of variability and intensity of natural disturbance regimes. In systems fragmented by vegetation clearance and modification, such as many of the woodlands and grasslands in eastern and southern Australia, broad landscape processes have been disrupted for many decades leading to altered fire regimes (Gill and Williams 1996; Hobbs 2002). Moreover, species and life stages respond idiosyncratically to disturbance. Conservation plans, therefore, must create scenarios for every possible kind and degree of disturbance to ensure that the projected network of protected areas remains permeable at appropriate spatial and temporal scales to all native species. All categories of disturbance need to be considered independently and in combination.

Fire, because it can be an important tool in management, and because it interacts with many other categories of disturbance, is heuristically useful for grasping the complexity of landscape permeability. Fire affects the permeability of landscapes for individual species (Williams *et al.* 1994; Whelan *et al.* 2002), and different kinds and schedules of burning in space and time can affect migration, dispersal, and other kinds of animal movements. For example, the continued depletion of old-growth vegetation by frequent burning has been identified by Woinarski (1999) as a process threatening a number of fire sensitive bird species in Australia due to the loss of habitat. These birds have relatively limited dispersal ability and low reproductive rates, exacerbating their vulnerability to frequent fire (Woinarski 1999). Whether fire enhances or inhibits landscape connectivity for native flora and fauna depends on the geographic scale of analysis, the ecological context, and the characteristics of species.

4. Global climate change

In coming decades, it is likely that human-forced global climate change will contribute massively to the extirpation of species and ecosystems (Howden *et al.* 2003; Thomas *et al.* 2004). The general basis of this statement is that the climatic envelope within which species currently persist will either (a) cease to be found anywhere or (b) shift geographically such that species are unable to disperse and relocate to a landscape that supports an essential resource.

On the other hand, climate change may enable many species to disperse into landscapes where current competitors and diseases cannot follow (Dobson *et al.* 2003; Johnson and Cochrane 2003). Many species will be able to expand their geographic ranges, with implications for spatially extensive evolutionary processes and for the spread of invasive species (McKenney *et al.* 2003), including infectious diseases (Williams *et al.* 2002). The ecological effects of climate change in the oceans is likely to be as great as those elicited in terrestrial systems (Seibal and Fabry 2003).

Maintaining connectivity in the face of major climate changes will prove a formidable challenge, and decision makers are already being called upon to mitigate negative effects wherever possible (National Task Group on the Management of Climate Change Impacts on Biodiversity 2003). Conservation planners, too, must consider climate change scenarios in developing plans for the persistence of biodiversity. First, major, climatically-driven biome changes cannot be accommodated by small or isolated protected areas. Large, contiguous areas are needed to accommodate essential movements and flows. Moreover, even small relictual assemblages, such as patches of rainforest in northern Australia (Russel-Smith *et al.* 1992), may be the sources of species that will constitute future plant communities when climate change leads to novel conditions (Nix 1982; Hopkins *et al.* 1993). Second, proposed natural resource management strategies should, where necessary, include the translocation of threatened species and the maintenance of habitat linkages to promote species migration and dispersal (Hannah and Salm 2003).

Nevertheless, the resilience of Australia's biota should not be underestimated. The ability of species to evolve and persist on a continent subject to extraordinary climatic variability over millions of years may have pre-adapted them to overcome some kinds of distributional obstacles.

5. Hydroecology

Hydroecology (Mackey *et al.* 2001) describes the role that vegetation plays in regulating surface and subsurface hydrological flows at local and regional scales, and the importance of water availability to ecosystems and animal habitat. The significance of hydroecology in Australia is amplified by high year-to-year variability in rainfall. Because water is so scarce in most of Australia, attention at all scales to catchment processes, particularly the influence of vegetation cover on infiltration and evaporation, is critical for maintaining perennial springs and water holes, river base flows, and perennial and seasonal stream flows.

Interruptions of hydroecological processes, whether natural or artificial, can impede regional- and continental-scale phenomena. For example, estuarine food abundance for migrating birds may depend on water catchment processes occurring hundreds of kilometers from the ocean (Tracy *et al.* 2004). Hydroecological processes are critical for biodiversity conservation at local, regional, and continental scales because they underpin landscape primary productivity and habitat values. Though such processes have been more often discussed in the context of land degradation and salinity problems (e.g., Littleboy *et al.* 2003), conservation planners and managers must attend to whole-of-catchment dynamics that influence water flow and quality, especially the extent and condition of the vegetation cover and other factors affecting groundwater recharge and discharge.

6. Coastal zone fluxes

Inland and coastal human settlements, agriculture, aquaculture, and industry have increased the inputs of nutrients and biologically active chemicals in coastal ecosystems. The consequences — including pesticide-related extirpation of bird populations, heavy metal pollution of fishes, and off-shore, anoxic "dead zones" — are well documented (Crowder and Norse, in press). Phytoplankton blooms in rivers, bays and littoral habitats are increasing in severity and frequency, often to the detriment of benthic communities. Coral reefs are particularly sensitive to nutrient enrichment (Koop *et al.* 2001).

Natural flows and movements in coastal areas are often interrupted or curtailed by fresh water impoundments and diversions, dredging, chemical pollution, commercial boat traffic, the use of estuaries for aquaculture and recreational boating, and the construction of jetties and breakwalls. These activities and structures can interfere with many ecological and behavioural processes, including reproduction in terrestrial, fresh water, and marine species and the movements of inorganic and organic materials that support estuarine biota and that provide sand and sediments for beaches, estuaries, and bays. The fitness of animals such as migrating shorebirds is affected by coastal zone fluxes of pollutants and by the construction of barriers to water flow such as dams. Many of the activities mentioned above create barriers — sensory, physical, and chemical — to the movements of organisms and their propagules in the water column and in benthic and reef communities.

In the absence of explicit planning and protection, the continuing creation of anthropogenic barriers to natural flows and movements in coastal regions may prove catastrophic for human and natural communities. Given the inevitability of commercial development in the coastal zone, a coastal zone conservation planning framework that explicitly incorporates fluxes of energy and matter and animal movements is a conservation and economic priority for Australia.

7. Spatially-dependent evolutionary processes

Biodiversity protection must attend to the conditions necessary for continuing evolution, particularly the potential for adaptation to changing environmental conditions and for speciation (Frankel and Soulé 1981). Ultimately, evolutionary processes require the movement of organisms over relatively long distances. Not only is gene flow (a major source of genetic variability) dependent on connectivity, but landscape permeability is a requisite for range expansion, often a key stage in evolutionary differentiation and speciation (Avise 2000).

Range expansion serves to spread new genetic variants across the landscape (Moritz 1991; Kearney *et al.* 2003) and to deliver genetically continuous populations into areas that may later become isolated and differentiated. The latter process is exemplified by closely related (sister) taxa in southeastern and southwestern Australia (e.g., Roberts and Maxson 1985), and by the occurrence of mesic-adapted plant and animal communities in isolated pockets within the arid zone (Bowman 1996). Habitat fragmentation in the future could preclude these processes. For species with limited mobility, including many amphibians, even local habitat destruction and the resulting deterioration in landscape permeability can militate against natural evolutionary processes (Driscoll 1998). Genetic differentiation and evolutionary diversification of populations depend on the maintenance of habitat integrity on a regional basis.

For these reasons conservation strategies need to accommodate shifts and expansion of geographic ranges so that evolutionary processes can operate over millennia at local to continental scales (Soulé 1980; Moritz *et al.* 2000). Widespread habitat loss and modification may preclude gene flow and range expansion (Woinarski and Ash 2002; Driscoll 2004) and probably will effectively eliminate speciation and adaptive evolutionary processes. Habitat reconstruction, strategic habitat management, and the restoration of landscape linkages are needed to reinstate natural evolutionary processes.

CROSS-CUTTING CONNECTIVITY ISSUES IN AUSTRALIAN CONSERVATION

The current distribution of protected areas is too sparse and poorly connected to adequately protect Australia's biodiversity in perpetuity. Unless these deficits are corrected soon, the hemorrhaging of biodiversity can only accelerate. The "set of seven" connectivity-related phenomena described in the previous section is just the first step in developing a useful connectivity analysis to inform planning. In part, this is because the interactions among these phenomena are at least as important as the phenomena themselves. When the concern is the long-term persistence and accessibility of refugia, for example, planners must model how an increase in fire size and intensity affects habitat and the long-distance movements of terrestrial animals. For example, refugia for Leadbeater's Possum *Gymnobelideus leadbeateri* and other arboreal mammals were found to depend on vegetation structure, which in turn is influenced by the pattern of fire in space and time (Mackey *et al.* 2002).

The twin purposes of this section are to provide a foundation for the integration of the seven categories into a comprehensive biodiversity protection strategy and a preliminary tabular synthesis (Table 1) of interactions among the seven categories so that conservation workers can better grasp the complex spatial, temporal, biological, and social dimensions of the conservation challenge. Table 1 illustrates the complexity and interactions of the seven phenomena in the context of seven cross-cutting themes that affect the planning, efficacy, and long-term persistence of conservation networks.

We use the term "cross-cutting themes" as a rubric for this synthesis, because from the perspectives of planning and management, it is essential to avoid over-simplified, single-factor analyses. The seven connectivity-related phenomena are referred to below by their numbers in parentheses in order to facilitate cross-referencing. We recognize that this brief synthesis is not comprehensive. In particular, the symbols (words, letters) used in the cells of Table 1 are meant only to alert conservationists to potential interactions and problems. We hope, however, that the table will be useful as a guide and checklist for analysis, planning, and management of conservation systems, including protected area networks.

Scale and context

The first row in Table 1 reminds us that scale and context issues are relevant to all of the seven connectivity issues. For example, the conservation value of any particular habitat patch or site depends on its size and its ecological and geographic contexts (5, 6). In addition, propinquity of sites generally increases their utility for maintaining ecological flows and dispersal of plants and animals (2), including relatively interactive species (1). Nevertheless, even relatively isolated patches, such as pockets of forest, wetlands, or estuaries, may serve a critical "stepping stone" function at regional and continental scales for migrating or dispersing biota (2), for the persistence of metapopulations, and for tracking ecosystem characteristics during climate change (4). Thus, a small and isolated reserve in the highly cleared wheatbelt in

Table 1. Probable relationships between the seven connectivity phenomena and the cross-cutting issues.

	Connectivity-related phenomena						
Cross-cutting issues	(1) Species interactions	(2) Long-distance movement	(3) Distubance	(4) Climate change	(5) Hydro-ecology	(6) Coastal Zone fluxes	(7) Evolutionary processes
Scale and context	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Conservation phase	P, M	P, m	P, M	P, m	P, m	P, M	P, m
Core area impacts	S, l	L	S, l	s, L	L	S, L	S, L
Matrix impacts	D	D	B	D	D	D, B	B
Spatial and temporal analyses	?	Yes	Yes	Yes	Yes	Yes, ?	?
Change	C, A	C, A	T, C, A	T, A	T, C, A	T, C, A	T, C, A

Symbol interpretation

Yes – clear utility or relevance; P – highly relevant to planning and design; M – highly relevant to management and stewardship; m – often relevant to management and stewardship; S – highly relevant to scale issues; s – sometimes relevant to scale issues; L – highly relevant to location issues; l – sometimes relevant to location issues; D – potential for "sink" problems; B – potential for "barrier" problems; ? – utility unknown or doubtful; T – sensitive to technological innovation; C – sensitive to climate; A – sensitive to intensification or other changes in agriculture.

south-west Western Australia will have a higher conservation priority than otherwise realized if it coincides with a dispersal route for birds between the arid and mesic zones (2). Moreover, the value of particular sites can increase over time due to the cumulative effects of habitat degradation (3) and patch extirpation. Finally, whether a type of disturbance, such as fire, is beneficial or harmful to connectivity depends on the habitat and species under consideration. It would be hard to exaggerate the significance of context in conservation, particularly when analysed from the perspective of appropriately long temporal scales, including those relevant to evolutionary change and diversification (7).

Conservationists must think about connectivity at multiple geographic scales as well. For example, connectivity for less vagile organisms, such as amphibians, is usually a local issue, whereas connectivity for migratory birds can be regional, continental, and inter-continental (2). Both temporal and spatial scales must be considered when the concern is the potential for recolonization following local extirpation or for speciation. Planners should avoid the trap of the "generic" or all-purpose, "one size fits all" corridor, and must depend on specialists to alert them to species-specific connectivity issues (7).

Disturbance of any kind alters the ecological context, affecting ecological flows and movement. For example, fire regimes are altered when systems are fragmented by vegetation clearance and modification (3), such as in woodlands and grasslands in eastern and southern Australia (Gill and Williams 1996; Hobbs 2002). A landscape that is fragmented by roads may be prone to frequent, anthropogenic burning and thus to local extinction of fire-sensitive species. In addition, frequent fires for fuel reduction can adversely affect the persistence of plant species that require long intervals between fires (Mackey *et al.* 2002). It is even possible that revegetation could be hazardous to native species because it might increase the probability of fires spreading into undisturbed habitat (Wasson 2003). At the opposite extreme, local vegetation clearing may result in the absence of fire over long periods. This can occur where the fire management goals for agriculture differ from those for native flora (Keith *et al.* 2002a). Thus, context determines whether fire increases or decreases connectivity, or whether it benefits or reduces biodiversity locally or regionally.

Conservation phases

As indicated in the second row the Table 1, conservation is carried out in phases, including an assessment/analytical phase, a design and planning phase (both of which are indicated by "P" in Table 1), and a management/stewardship phases (indicated by "M" or "m" in Table 1). For example, the significance of episodic, long-distance dispersal (2) and future shifts in geographic range due to climate variability and change (4) may be more germane to the identification of potential core areas and "stepping stone" habitat patches during the design phase than for day-to-day management. Similarly, the locations and qualities of barriers to movement (2), such as dams or highways, and the role of evolutionary phenomena (7) should be addressed during the analysis, planning, and design phases. Proposals for future dams or highways are likely to be both design and management concerns. On the other hand, the design and implementation of appropriate fire regimes (3), both in core areas and on matrix (or compatible use) lands are likely to be a perennial issue for management.

The planning phase is critical because mistakes of omission and lack of vision may not be correctable in the future. In coastal areas, for example, planners must consider potential conflicts between the necessity of habitat permeability for many species and the likelihood of intensive development (6). The virtual certainty of future growth and disturbance (3) in heretofore undeveloped coastal areas such as in northern Australia could severely curtail fresh water flows (5) and animal migrations that are critical for the integrity of coastal ecosystems (2).

Core area enhancement

All seven of the connectivity phenomena affect the conservation value, long-term viability, species diversity, and resilience of core areas. The phenomena inform decisions about issues of size and scale ("S" or "s") in the third row of Table 1) of core areas and their location ("L" or "l"). Depending on the kinds and likelihoods of threats, each potential linkage zone connecting core areas should be evaluated for its contribution to the viability of highly interactive species (1), and the probable conservation utility under various scenarios of disturbance (3), development, climate change (4) and other perturbations. In particular, the interaction of connectivity and disturbance regimes (3) needs be deeply embedded into planning processes (Williams 2003) and integrated across all land tenures (Esplin *et al.* 2003). Such systematic analyses will also be of value for developing management plans for core areas and compatible use lands (see below) and waters (Hale and Lamb 1997; Lindenmayer and Recher 1998; Lindenmayer and Franklin 2002).

Potential core areas should be carefully examined with regard to the impact of land-use changes that compromise connectivity. Wetlands, for example, are likely to be selected as core areas, but they are highly susceptible to water diversion or draining, agricultural development, land clearing (3) and other land-use changes. Economic development of estuaries and their catchments endangers subsistence economies and reduces the quality of life for people living in coastal areas (5, 6). Only those estuaries in remote regions of tropical Australia or western Tasmania are in a nearly pristine state (Tracy *et al.* 2004). In addition, many coastal fisheries have disappeared because of overfishing (which perturbs species interactions) and habitat disturbance (3) locally and in distant catchments (Crowder and Norse, in press).

Fresh-water habitats and the core areas that contain them are particularly sensitive to changes in hydroecological processes that can often operate over long distances (5). Among the many examples that illustrate this is the increasing level of water extraction from the Great Artesian Basin. The Basin covers 1 117 000 km² — 22% of the Australian continent — and it has persisted for tens of thousands of years. The Basin stores around 8 700 million megalitres and feeds over 1 000 remote springs and soaks that support wetland ecosystems, including many endemic species and communities (GABCC 2003), and that are refugia (2) during droughts. Widespread extraction of water from the great artesian basin threatens to decrease the number and size of natural springs, thereby reducing population sizes and increasing the risk of extinction of endemic species (Ponder *et al.* 1995; Tyre *et al.* 2001). In tropical Australia, maintenance of the integrated subsurface/surface hydrological processes is essential to the biology and ecology of the plants and animals of the region (Horn 1995; Horn *et al.* 1995).

The matrix

The long-term prospects for biodiversity will be enhanced the more the entire landscape, irrespective of tenure, is managed as a conservation (rather than a production) land. Advancing this objective, however, will require (a) the mitigation of threats posed by matrix lands and waters to biodiversity, (b) better linking and buffering of core areas, and (c) changed land use and management to promote landscape permeability for ecological flows. Row 4 of Table 1 suggests how connectivity to non-core, matrix areas can affect the integrity of species and ecosystems in cores; "D" indicates the potential for deleterious effects related to "sink-like" qualities in matrix areas or to harmful disturbances emanating from such areas; "B" indicates processes in matrix areas can create barriers to movements and flows.

Some "matrix" or non-core areas in the vicinity of high value core sites may provide connectivity that helps to sustain populations of vulnerable species, even if such areas lack the qualities necessary for permanent residency. On the other hand, lands and waters under intensive economic uses such as irrigated agriculture and aquaculture may entrain "sink-like" conditions such as high mortality rates (*sensu* Pulliam and Danielson 1991), and create barriers that threaten natural ecological flows and movements. In any case, all non-core areas should be examined systematically for their current and potential connectivity conservation opportunities and threats to biodiversity. For instance, it should not be assumed that presumptive compatible use areas, including pastoral or forestry lands, would benefit particular taxa. Plantations, though they may provide shelter, foraging, and nest sites, can have elevated mortality rates for some or all life history stages such as nestling birds. Other "sink-like" qualities of matrix areas can include low insect productivity and toxicity caused by herbicide (for understory) and insecticide use (Richard Hobbs, pers. comm.). Planners must also assume that the kinds of economic uses on matrix lands will change and possibly intensify over time.

Wide-ranging species (2) may be particularly vulnerable to the sink-like qualities of unreserved, matrix lands where survival rates of foraging or dispersing individuals are low. This is particularly problematic for highly interactive species such as predators (1). The tolerance of matrix land managers for dingoes, for example, may affect their densities in core areas and indirectly affect the persistence of small marsupials (O'Neill 2002). Dingoes control Feral Pigs *Sus scrofa*, kangaroos (*Macropus* spp.) and Emus *Dromaius novaehollandiae* (Pople *et al.* 2000; Newsome *et al.* 2001); they also may determine the local distribution, numbers and predatory impacts of cats and foxes (Corbett 1995; Edwards *et al.* 2002; O'Neill 2002), which can cause local decline and extinction of the smaller marsupials, including native carnivores (Lundie-Jenkins *et al.* 1993; Risbey *et al.* 2000; Morris *et al.* 2003). Conservation planners need to know more about these potential benefits for native vegetation and marsupials. If such benefits occur, it would behoove planners to consider whether dog fences, poisoning, and access to water sources help or hinder the protection of native ecosystems.

Spatial and temporal analyses

The large-scale connectivity processes discussed here are essential for biodiversity assessments and planning. Data are often lacking, however, to conduct the necessary space/time studies at the required scales. For example, climate change (4) in the past has altered the composition of ecological "communities" and species that are associated now may no longer be sympatric in the future (Graham and Lundelius 1984). Thus interspecies interactions (1) that we take for granted today, such as pollination, seed dispersal, predator-prey relations, herbivory, and plant-microbial symbioses (Hughes 2003) will be less predictable and are beyond the capacity of current models to predict.

Nevertheless, certain phenomena may be amenable to analysis by GIS and remote sensing tools. It is possible to analyse threatening processes such as land clearing and over-grazing (3), the likely locations of refugia (2) and aspects of hydroecology (5). Analysis of other phenomena, including the habitats of threatened species and the roles of predators as top-down regulators of ecosystems (1), will typically rely on new field surveys (perhaps complemented by remotely sensed information) or may require deliberate field experimentation at local or regional scales.

Each issue that arises during any of the conservation phases mentioned above should be scanned with a checklist of available methodologies in order to prevent gaps in analytical rigour. For example, advances in geographic information systems, environmental modelling, and remote sensing enable the classification, mapping, and tracking of the temporal variability in the distribution and availability of primary production and hence food resources (Landsberg and Warning 1997; Austin *et al.* 2003; NASA 2003). These analytical capabilities add to existing technologies and aid in identifying core habitat, together with dispersal and migration linkages (2) at local, landscape, regional and continental scales (Mackey *et al.* 1988, 1989, 2001; Lesslie 2001; Mackey and Lindenmayer 2001; Nix *et al.* 2001).

Anticipating change

The ecological, economic and social systems in which conservation operates are dynamic and difficult to predict, although we can be quite certain of some changes in Australia. One of these is that human populations will continue to grow in coastal areas. Row six of Table 1 suggests certain obvious categories of change that are likely to exacerbate landscape permeability and flows during the next few decades; these categories are changes in technology ("T"), changes in climate ("C"), and agricultural intensification ("A").

Technology will continue to be a major driver of changes on the land. The increasing rate of technological innovation will exacerbate development pressures in heretofore-intact country. One of the most threatening technologies to Australia's biodiversity is the desalinization of sea water. Fresh water produced by desalinization, even if relatively expensive, may open up vast areas for marina and resort development (6), and even expensive fresh water may open the flood gates to intensive forms of farming and aquaculture. Another threatening technology that will emerge in the next decade or so is all-season, all-terrain vehicles capable, for instance, of carrying people and goods throughout seasonally flooded regions such as northern Australia. Such transport will accelerate economic development, tourism, and habitat fragmentation.

Dramatic changes in climate are also likely (4). The average global surface temperature is projected to increase by about 2.5°C to 3°C by this century's end (Kerr 2004) with the projected rate of warming very likely to be without precedent during the last 10 000 years (Taylor 1999). Sea levels are predicted to rise between 0.5 and 2 m. The future climate suggested by regionally-scaled global change models for Australia is detailed in CSIRO (2001). Annual average temperatures are projected to be 1.0–6.0°C warmer over most of Australia by 2070. By 2070, the range of predicted change in precipitation is -20 to +20%, with locally unpredictable consequences for the biota.

The future of non-protected areas is uncertain given current rates of land conversion, population growth, agricultural intensification, and species introductions, not to mention rapid, unpredictable technological innovations that facilitate access to intact country, human aspirations in the poorer nations, and the desires of investors to maximize profits using ecologically unsustainable practices. Therefore, some of the current discussion about the conservation value of unreserved or small areas (e.g., Daily *et al.* 2001; Rosenzweig 2003), if interpreted too broadly, can lead non-ecologists to a false sense of security about the utility and compatibility of matrix or off-reserve lands for biodiversity protection. Improved long-term conservation outcomes will not occur on non-protected areas by accident. Rather, careful long-term planning is an imperative. Planning for the long-term conservation of biodiversity must assume worst-case scenarios and take an unashamedly cautionary approach. The current limited knowledge about most of the ecological connectivity issues discussed here is further impetus for a precautionary stance.

CONCLUSIONS

This paper identifies a set of seven ecological processes and phenomena that require connectivity at continental, regional and landscape scales. This "set of seven" is part of the preliminary scientific framework for the WildCountry Programme — a new approach to conservation assessment and planning in Australia initiated by The Wilderness Society. The overarching goal of WildCountry is to protect Australia's biodiversity by creating an expanded system of core reserves, sustained by ecologically permeable landscape linkage zones and compatible management of off-reserve lands and waters.

The next step is to examine these seven processes and their interactions in the context of particular regions to determine how they will be regulated and optimized — singly and in combination — to maintain native biodiversity in perpetuity at all spatial and temporal scales. This effort will require both systematic research and broad consultation through informal contacts, literature reviews, workshops, conferences, and partnerships across all sectors. It will also require a more realistic, rigorous approach to conservation in general.

Culturally, one of the major impediments to effective conservation, worldwide and in Australia, is the ignorance of connectivity's role in sustaining ecological dynamics and diversity. Though society has been relatively successful in protecting scenic landscapes and isolated intact country and wild rivers, most of these successes will be pyrrhic victories in a few decades if greater attention is not paid to connectivity. Knowledge about the phenomena related to natural flows and movements has been increasing, and there is a growing effort to attend to the regional and continental scales in conservation (Soulé and Terborgh 1999), but nowhere have these phenomena been systematically integrated into conservation assessment and planning on regional and continental scales.

Effective ecological connectivity for biodiversity conservation will be an ongoing research and development challenge if for no other reason than all ecosystems will be subject to climate change, exotic species introduction, and new kinds of landscape-altering technologies that must elicit a "futuristic attitude" in conservationists. Conservation planners must assume attempts will be made to exploit for private benefit virtually every landscapes or natural resource on or near the continent using technologies that cannot even be imagined today. The key actions we can take now to enable biodiversity to survive are to (a) conserve in perpetuity large, contiguous areas to promote the integrity of natural processes across regionally-scaled climatic gradients (ensure that the landscape remains permeable to all beneficial ecological processes), (b) design such systems to ensure effective movements and fluxes under all imaginable scenarios, (c) protect regionally anomalous ecosystems or refugia as the possible sources of species for ecosystems under future climate, and (d) implement natural resources management practices that do no harm to native biodiversity and allow its continuing evolution.

We must assume, however, that conservation networks will always be a work in progress, needing to adapt to changing environmental and cultural circumstances. The creation of networks of protected areas designed with appropriate kinds and levels of connectivity is just the beginning of a millennial project to protect the unique flora and fauna of Australia.

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