Department of Sustainability and Environment

Relationships between disturbance regimes and biodiversity: background, issues and approaches for monitoring

Fire and adaptive management

report no. 91



Relationships between disturbance regimes and biodiversity: background, issues and approaches for monitoring Fire and adaptive management

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Front cover images

Main photo – Regeneration after fire, Bunyip State Park 2010. M. CAMPBELL

Small images (front cover clockwise from top left) – Kookaburra, R. LOYN; Boobook, R. LOYN; Ptilotus macrocephalus and Themeda spp, AR; Bunyip State Park, M. CAMPBELL; Little wattle bird, R. LOYN; Scarlet robin, R. LOYN; (back cover clockwise from top left) – Bunyip State Park, A. MUSGROVE; Pigface Jeparit, N. MACDONALD; Superb fairy-wren, R. LOYN; Yalmy Region, A. POULIOT; Blue Pincushins, M. GELDARD.

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Summary

- 1. The purpose of this document is to provide background information leading towards the development of a program to monitor the relationships between disturbance regimes and biodiversity at large spatial scales. Although many of the principles and much of the discussion is relevant to disturbance regimes in general, we often refer to fire regimes as a specific case.
- 2. Initially, we outline linkages between disturbance, environmental heterogeneity and biodiversity. Ecosystems are naturally heterogeneous, and it is well accepted that environmental heterogeneity is fundamental to species co-existence, and to the maintenance of biodiversity. Disturbance regimes affect environmental heterogeneity by resetting successional processes. Over time, they result in a 'shifting mosaic' or 'mosaic cycle', provide perpetual resource complexity at a variety of spatial scales, and facilitate species co-existence. However, disturbance regimes can also simplify ecosystems and result in species loss, raising questions regarding the characteristics of disturbance regimes may often be challenging.
- 3. Biodiversity is a complex concept incorporating multiple levels of ecological organisation. Even if biodiversity is defined simply as species richness or diversity, it is often difficult to quantify, particularly at large spatial scales. We argue that, at large spatial scales, biodiversity cannot be measured directly and that surrogates or indicators must be used.
- 4. Aspects of biodiversity are often related to environmental variables, which we define as properties, patterns, elements, attributes or structures that can be precisely identified and measured. We suggest that monitoring the relationships between disturbance regimes and biodiversity will require the use of environmental variables as biodiversity surrogates. Consistent with the idea that heterogeneous environments support more species than homogeneous ones, we suggest that combining multiple variables into a composite measure representing landscape-scale environmental heterogeneity will result in a theoretically defensible biodiversity surrogate. We view this as a hypothesis that requires validation.
- 5. Irrespective of what is monitored, a monitoring program will fail if data quality and quantity are not adequate, or if the objectives are not clearly specified. To address this issue, we include a set of monitoring principles designed to promote the efficient and effective collection and use of monitoring data. Monitoring principles specify that monitoring programs should be planned with reference to an underlying ecological model. Further, they suggest that setting precise, quantifiable management objectives, and considering the interrelated issues of experimental design and analytical techniques, are all aspects of good monitoring practices.
- 6. Many components (developing objectives, planning and implementation, data analysis, etc.) need to be integrated for a monitoring program to succeed. The framework proposed for this integration is the adaptive management cycle. The cycle begins with a general ecological model from which specific questions, predictions and management objectives are derived. We provide some recent examples of adaptive management in practice.

1: Introduction

Fire is an important component of south-eastern Australian ecosystems, and planned burning has been used as a broad-scale ecosystem management tool for many years. In Victoria, socio-political and ecological concern stimulated by a few very large bushfires, coupled with recent recommendations by the 2009 Victorian Bushfires Royal Commission (Teague et al. 2010), have resulted in a program of planned burning that ultimately aims to treat 5% of public land per year. The purpose of this program is to reduce fuel loads, protect human life and property, and to maintain ecosystem function (Department of Sustainability and Environment 2008).

Due to substantial uncertainty associated with the response of natural systems to fire (e.g. Clarke 2008, Parr and Andersen 2006), the Victorian State Government is committed to monitoring the impact of its planned burning program (Department of Sustainability and Environment 2006). Part of this effort involves the development of a program to monitor the effects of planned burning on biodiversity at large spatial scales. The purpose of this document is to provide background information facilitating the development of this monitoring program.

One of the key ecological principles underlying the use of fire (or other disturbance) regimes for ecosystem management and biodiversity conservation is that biodiversity is positively associated with environmental heterogeneity. Our primary aim is to review this concept, and show how the strong theoretical links between environmental heterogeneity and biodiversity can be extended to provide an ecological model upon which a program to monitor biodiversity can be based. Our secondary aim is to highlight a number of principles conducive to good monitoring. Finally, we suggest that a successful monitoring program involves the integration of many components (developing objectives, planning and implementation, data analysis, etc.) and that this can be achieved through the process of adaptive management.

There are a number of caveats and limitations to this review that we wish to acknowledge:

- This review is selective and biased by our own area of expertise (animal ecology).
- The relationship between disturbance regimes and biodiversity will clearly be influenced by climate change (e.g. Jackson and Sax 2010; Mouillot *et al.* 2002). For example, climate change may result in increases or reductions in biodiversity that may be temporally transient, resulting in short-term inaccuracies in biodiversity assessment (Jackson and Sax 2010). However, an analysis of the interactions between climate change, disturbance regimes and biodiversity is beyond the scope of this work.
- There is a general consensus that good ecological monitoring is an important aspect of evidence-based land management (Field *et al.* 2007; Lindenmayer and Likens 2010; Nichols and Williams 2006). Nevertheless, ecological monitoring is expensive, including both the direct cost of set up, data collection and analysis, as well as the opportunity cost associated with the diversion of funds from other management activities (Caughlan and Oakley 2001). Questions about whether ecological monitoring programs represent value for money are important and deserve a heightened focus (Possingham et al. 2012). Several frameworks exist for assessing the cost effectiveness of monitoring programs (e.g. Field *et al.* 2004; McDonald-Madden et al. 2010) but we do not deal with them further in this report.
- Our discussion assumes that management of biodiversity will be based on ecological considerations only. In reality, management decisions are likely to be influenced by ecological, social, economic and pragmatic considerations and are likely to involve a trade-off between at least two of these factors. We note that tools are available to derive optimal management decisions given a set of competing objectives (e.g. Kennedy *et al.* 2008).
- Some of our discussion is relevant to the concept of ecosystem resilience, defined as the ability of a system to absorb disturbance and still retain its basic function and structure (Walker and Salt 2006). However, we do not discuss this concept further as it is the subject of a related document (McCarthy 2012).

2: Disturbance, heterogeneity and biodiversity

2.1 Definitions

Disturbance events play an important role in ecosystem regulation, and are known to influence species diversity, plant succession and regeneration, the distribution and abundance of animal populations and nutrient concentration in a range of ecosystem types (Bormann and Likens 1979, Connell 1978, Pickett and White 1985, Sousa 1984). In forest ecosystems, natural disturbances such as wildfire and storms act as major regulating forces (Attiwill 1994a, 1994b; Lugo 2000, Ryan 2002) and, in more recent times, human disturbances such as urbanisation, land clearing and timber harvesting have had a marked impact on forest extent and structure, and on the distribution and abundance of forest-dwelling organisms (Abrams 2003, Dale et al. 2000, Gaston et al. 2003, Thompson et al. 2003, Wilson and Friend 1999). Whether natural or anthropogenic, disturbance has the capacity to affect biodiversity via a number of mechanisms, including its influence on environmental heterogeneity. The interactions between disturbance, environmental heterogeneity and biodiversity within landscapes form an integral part of this document, and we begin with definitions of these terms.

2.1.1 Disturbance

White and Pickett (1985) define disturbance as:

"...any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment."

There are a number of alternative definitions (van der Maarel 1993), but a common theme is the destruction of biomass and the subsequent release or redistribution of resources (space, light, nutrients) that can be used by individuals surviving the disturbance or by those colonising from elsewhere (Sheil and Burslem 2003).

Although White and Pickett's definition incorporates intensity, spatial scale and patchiness (a discrete event can be forceful or weak, large or small, homogeneous or heterogeneous), it does not incorporate time. The concept of 'disturbance regime' meets this need, and is used to characterise disturbance in terms of event intensity, patchiness, pattern, and both spatial and temporal scale. This idea is well developed in the field of fire science, where the effect of fire on ecosystems may be described by the combined and potentially interacting effects of intensity, size, patchiness, frequency and season (Gill 1981, Whelan 1995). Definitions of and discussion regarding these (and other) descriptors of disturbance regimes can be found in a number of publications (e.g. Petraitis et al. 1989, Shea et al. 2004, Sousa 1984, White and Pickett 1985).

Disturbances are often classified as natural or unnatural and internal (endogenous) or external (exogenous) to the system. In reality, classifications of this type are often difficult to apply (Sousa 1984). Although some disturbances (e.g. large-scale land clearing) are clearly unnatural, naturalness may simply be a matter of degree. For instance, fires are a natural phenomenon in many systems, but fires influenced by anthropogenic factors may result in relatively extreme, 'unnatural' impacts. In addition, disturbances such as fires or cyclones may traditionally be thought of as exogenous (White and Pickett 1985), but their impact is clearly influenced by endogenous factors. For example, the relationship between fire regimes and organisms is clearly influenced by endogenous factors such as fuel loads (Walker and Willig 1999). Extending this argument, Sugihara et al. (2006) do not view fire as exogenous at all, but as a process internal and integral to many ecosystems.

Finally, Shea et al. (2004) make a useful distinction between cause, effect and response. For example, a fire event (the cause) may result in the death of individual plants (the effect). The space opened up by these deaths may result in a flush of germination (the response).

Both the effect (e.g. percent mortality) and the response (e.g. recolonisation strategy) may differ between species and may also be influenced by the particular characteristics of a disturbance regime. Regardless of the cause of disturbance, it is the way species are affected and respond that ultimately influences the relationships between disturbance regimes and biodiversity.

2.1.2 Environmental heterogeneity

Environmental heterogeneity has been defined in many ways (Kolasa and Rollo 1991), but it is usually conceived as a multi-facetted concept. Kotliar and Wiens (1990) define heterogeneity as the spatial variance in system attributes influenced by both attribute aggregation (spatial distribution) and contrast (the degree to which attributes differ). In this context, the term 'attribute' refers to whatever environmental variables are selected to quantify heterogeneity. We provide a summary of some common variables in section 3. Along similar lines, Dufour et al. (2006) suggest that environmental heterogeneity contains three main elements: 1. a range (number) of attributes, 2. the spatial configuration of these attributes, and 3. the variation of the first two components over time. The relative abundance or extent of each attribute is also important as this factor influences compositional heterogeneity (Bennett et al. 2006). As with the concept of disturbance, the inclusion of a temporal component to the definition is important, as environmental heterogeneity is temporally dynamic. Thus, given a particular suite of attributes, spatial environmental heterogeneity can be defined in terms of their 1. number, 2. relative abundance, 3. degree of contrast and 4. spatial arrangement. These four elements define a pattern that changes over time, and can be quantified at different spatial scales. Consequently, environmental heterogeneity cannot be represented using a single variable, and multiple variables will be necessary for its comprehensive quantification.

2.1.3 Biodiversity

There are many alternative definitions of biodiversity (e.g. DeLong 1996, Gaston 1996). Gaston (1996) suggests that the term is a synonym for 'the variety of life', and that the breadth and generality of the concept makes it difficult to comprehend. Many definitions include references to different aspects of biodiversity, including genes, organisms and ecosystems. For example, Lindenmayer et al. (2006) define biodiversity as:

"...genes, individuals, demes¹, populations, metapopulations, species, communities, ecosystems, and the interactions between these entities."

As such, biodiversity is all-encompassing and difficult to define and quantify. In this document we focus on aspects of biodiversity that are more easily defined and, in some cases, quantified: species richness and species diversity. Species richness refers simply to the number of species within a sample unit. Species diversity combines richness and relative abundance, and is commonly expressed using one of a number of diversity indices, such as the Shannon index (Magurran 2004). The relative merits of some diversity indices have been the subject of recent research (Buckland et al. 2005, Lamb et al. 2009). Further, the concepts of alpha, beta and gamma diversity act as scaling terms and refer to diversity within an ecosystem, between ecosystems, and of a whole region, respectively. Nevertheless, Whittaker et al. (2001) argue that substantial confusion surrounds these terms, and that more meaning is reflected by the terms local, landscape and macro-scale diversity. We acknowledge there are other aspects to biodiversity (e.g. genetic diversity, community diversity, functional diversity, molecular diversity) that we do not discuss in this document.

2.1.4 Landscape scale

Although concepts such as disturbance, heterogeneity and biodiversity are relevant at any scale, much of the focus on biodiversity conservation, management and monitoring occurs at the 'landscape scale'. Urban et al. (1987) suggest that a landscape is "...a mosaic of heterogeneous land forms, vegetation types and land uses..." and refer to areas tens of thousands of hectares in size. We consider the term 'mosaic' potentially problematic, as it invokes images of patches of land arranged in space, whereas many organisms are more likely to perceive their environment as a continuous surface (Fischer and Lindenmayer 2006, Fischer et al. 2004, Mitchell and Powell 2003, section 3.4.2). For the purposes of this document, we define landscapes, irrespective of their composition, as areas greater than about 100 square km (10 000 ha). We also use the term 'large-scale' to refer to areas of this size. This corresponds to the scale at which humans transform natural landscapes into cultural ones (Delcourt and Delcourt 1988), and also to the scale at which public land management in Victoria often occurs. With respect to biodiversity, we recognise this definition is arbitrary and reflects a human-centred view of scale – for a micro-organism, a landscape may well be defined as a few cubic centimetres.

2.2 Alternative explanations for the maintenance of biodiversity

There are several models proposed to explain the maintenance of biodiversity, which can be broadly defined by those assuming the existence of equilibrium or non-equilibrium states. Equilibrium models assume that abiotic factors (climate, topography, etc.) limit biodiversity, and that processes such as competition, predation, dispersal and extinction interact to perpetuate a level of diversity approaching this limit. In contrast, non-equilibrium models predict that biodiversity is regulated by processes that control competitive interactions. As such, non-equilibrium models assume the existence of a competitive hierarchy where, in the absence of a disturbing force, some species will drive others to extinction. A major point of difference is that non-equilibrium models do not assume diversity is fixed by the capacity of the environment, but that it depends on spatial and temporal environmental fluctuations that influence the ability of strong competitors to exclude others.

It is not our intention to discuss further alternative models for the maintenance of biodiversity – this issue is well covered in the literature (e.g. Chesson 2000, Huston 1994, Petraitis et al. 1989, Rosenzweig 1995, Sarr et al. 2005, Wilson 1990). Rather, we summarise ideas promoting disturbance as a major force in the maintenance of biodiversity from a non-equilibrium perspective, drawing heavily on the concepts of temporal succession and patch dynamics.

2.3 The influence of disturbance on biodiversity

In this section, we touch on two main paradigms relating disturbance to biodiversity. The first focusses on relationships between disturbance regimes, environmental heterogeneity and biodiversity, while the second considers the direct effect of disturbance frequency on the ability of organisms to reproduce. The commonality between the two is that life-history attributes are critical to the way organisms respond to disturbance. Heterogeneity–biodiversity relationships are often discussed in the context of animals (e.g. Fraser 1998, Kerr and Packer 1997, Lack 1969, Tews et al. 2004), although the associated concepts are also relevant to plants (Bazzaz 1975, Lundholm 2009, Ricklefs 1977). Conversely, the effect of disturbance frequency on reproductive ability is usually discussed in the context of plants (e.g. Gill 1981, Noble and Slatyer 1980), although it has recently been extended to animals (MacHunter et al. 2009).

2

2.3.1 Disturbance and environmental heterogeneity

Ecosystems are naturally heterogeneous, and it is well accepted that environmental heterogeneity is fundamental to species co-existence (Sousa 1984) and to the maintenance of biodiversity (Shea et al. 2004). These ideas have been espoused in the ecological literature for some time (e.g. Bazzaz 1975, Lack 1969, Ricklefs 1977) and reviewed from several perspectives (Benton et al. 2003, Hobbs and Huenneke 1992, Huston 1994, Lundholm 2009, Rosenzweig 1995, Sarr et al. 2005, Tews et al. 2004). Recent studies provide evidence for a positive relationship between environmental heterogeneity and species diversity for a variety of taxa and spatial scales (e.g. Bennett et al. 2006 and references therein, Dufour et al. 2005, Williams et al. 2002, Wohlgemuth et al. 2008).

Heterogeneous environments enable organisms to subdivide resources (Reice 1994) and facilitate niche differentiation. A niche, which Hutchinson (1957) defines as a n-dimensional hypervolume, refers to the range of resources and conditions required for a species to persist. In theory, each species occupies a different niche and limits itself (via intraspecific competition) more than it limits its competitors (Chesson 2000). Consequently, less abundant species are expected to have higher population growth rates than more abundant species, preventing competitive exclusion and facilitating co-existence (Levine and HilleRisLambers 2009).

The ability of species to establish niches is influenced by life-history attributes including growth rate, physical structure, and timing of life-cycle events such as reproduction and dispersal (Pickett and White 1985). For example, some species are good dispersers and colonisers, and thus succeed in relatively young, open habitats. In contrast, others are good competitors and dominate older habitats where space and other resources are limited (Petraitis et al. 1989). In general, heterogeneous landscapes contain a variety of habitats (environmental conditions, resource states) and will facilitate the co-existence of species with different life-history strategies. In a simulation study, Shmida and Ellner (1984) found that species with similar basic resource requirements can co-exist in a heterogeneous environment as long as elements of their life-history are different.

Disturbance events can affect the degree of environmental heterogeneity by resetting or partially resetting the successional process (Kleyer et al. 2007). Ecological succession refers to the process of temporal change in community composition and is dependent on the existence of different life-history strategies. The traditional view of succession (e.g. Clements 1916) is that early successional stages are characterised by resources such as space and light, and tend to be dominated by colonising species that invest heavily in dispersal and rapid growth. As the succession progresses, biomass increases, resources become limited and species with better competitive abilities replace the early colonisers. Finally, in late-successional stages, only the strongest competitors remain to form a stable, climax community. More recent work suggests that the sequence of species replacement is influenced by many factors (e.g. climate, the location of colonists or seeds, the level of herbivory or predation) and a directional trajectory ending in a stable climax is rarely observed. Regardless of specific influences at a particular location, the successional process reflects the general existence of a competitive dominance hierarchy, where good competitors replace good colonisers over time. Disturbances can interrupt this process by re-establishing an earlier successional stage, thus favouring species with good dispersal and colonisation potential.

Although the concept of succession is most often applied to sessile organisms, sessile and mobile organisms are usually strongly inter-linked (Tews et al. 2004). Sessile species often provide the starting point for food webs and contribute to the structural complexity of a

site (Begon et al. 2006). Mobile species use sessile species as food or shelter and changes in these resources resulting from the successional process will have flow-on effects to mobile organisms. For example, the process of plant succession causes the availability of both structural and nutritional resources to change with time. Changes to these primary factors may influence dispersal ability, competition and predation in mobile species, thus facilitating a concomitant change in faunal community composition. Such changes, however, may be most pronounced after some time lag (Ernoult et al. 2006), a fact that has important implications for quantifying biodiversity dynamics following a disturbance (Jackson and Sax 2010). For example, a single survey of vertebrate biodiversity shortly after a disturbance event provides information about immediate effects, but does not help quantify any long-term changes that might occur. Finally, feedbacks may also occur from mobile to sessile organisms. For example, increasing deer populations resulting from forestry activities and the subsequent creation of early-successional landscapes have resulted in substantial damage to native vegetation in some parts of the world (Côté et al. 2004).

Disturbance events are likely to have heterogeneous spatial effects, and different disturbance events may interact with each other at a variety of spatial and temporal scales (Arnold 1995, Sousa 1984). For example, a fire may represent a discrete disturbance event and create a single burnt area, but due to topographic variations, the area is unlikely to be burnt uniformly. At some time in the future, a tree may fall as a result of the fire, creating a secondary, smaller disturbance. The fallen tree may provide a variety of resources (a regeneration site for seedlings in the crown; a nesting site for birds in the upturned root mass) that differ from other locations within the fire, and from adjacent unburnt sites. Each disturbance event (the fire, the tree fall, etc.) interrupts the successional process at some scale, alters the pattern of resource availability and influences competitive interactions between species with different life-history attributes. Disturbance events influencing environmental heterogeneity at small scales (e.g. tens of centimetres) provide a variety of microhabitats that may be critical for altering competitive dominance hierarchies and facilitating the recruitment of new species into a disturbed area (Sousa 1984).

At large spatial scales, disturbance events of different sizes and intensities interact, and together result in a multitude of spatially nested successional states, forming an identifiable pattern of environmental heterogeneity. This pattern is not static, but at a given location, changes over time as succession progresses and new disturbances occur, resulting in a 'shifting mosaic' (Bormann and Likens 1979) or 'mosaic cycle' (Kleyer et al. 2007). Depending on the disturbance regime, shifting mosaics can provide perpetual resource heterogeneity at a variety of spatial scales. As outlined earlier, this enables species with alternative life-history strategies and resource requirements to persist within a landscape, even though some species will be absent from particular locations at any given time.

Although there is substantial evidence for linkages between disturbance regimes, environmental heterogeneity and biodiversity, the effect of disturbances on local species diversity is difficult to predict. Local responses are influenced by disturbance size, severity and patchiness, the nature of subsequent disturbances occurring at the same location and characteristics of the species present. These factors are, in turn, affected by abiotic variables such as soil type, topography and climate. For example, Keeley et. al. (2005) propose four alternative hypotheses to explain post-fire recovery of plant populations, which identify a range of potentially important mechanisms that may be operating. Consequently, disturbance–environment–biodiversity relationships are often complex and location-specific. In the context of fire science, recent critiques of the 'pyrodiversity begets biodiversity' paradigm (Clarke 2008, Parr and Andersen 2006) suggest that the proposed positive relationship between heterogeneous fire regimes and biodiversity either does not exist or remains vague and unsubstantiated. In another example, fire severity has influenced community structure or species abundance on some occasions (Chappell and Agee 1996, Kotliar et al. 2007, Lindenmayer et al. 2009a, Ooi et al. 2006, Schimmel and Granström 1996, Smucker et al. 2005), but not in others (Keeley et al. 2008, Lindenmayer et al. 2008b, Lindenmayer et al. 2008c). The reasons for the absence of severity effects in some studies remain unclear, but environmental context, such as the presence and size of refuges from which species can recolonise severely burnt sites, may play a role (Whelan et al. 2002).

In addition, interactions between a series of disturbance events with different characteristics (the regime) and the subsequent heterogeneity that results, means that the classic successional process of species replacement over time rarely occurs uniformly at large scales. Even in fire-sensitive ecosystems such as Victorian ash forests, stands containing both overstorey and understorey species of different ages are relatively common, indicating that some fires only kill a portion of the plant community (Lindenmayer et al. 2000a). As a consequence, the assumption that environmental heterogeneity, resource availability and thus the relative abundance of various species can be predicted by the date of the last fire may be faulty. Although time-since-fire (or related concepts such as seral or growth stage) may be a good predictor of the abundance of some species in some ecosystems (e.g. Brown et al. 2009), there is substantial evidence that many animals respond to specific characteristics of the habitat which are often unrelated to time-since-disturbance (Di Stefano et al. 2011, Driscoll and Henderson 2008, Keith et al. 2002, Letnic et al. 2004, Lindenmayer et al. 2008c, Monamy and Fox 2000, Southgate et al. 2007). For example, Monamy and Fox (2000) show that post-fire recolonisation rates of swamp rats (Rattus *lutreolus*) and eastern chestnut mice (*Pseudomys gracilicaudatus*) are related to vegetation density rather than time per se. In addition, both Letnic et al. (2004) and Driscoll and Henderson (2008) demonstrate the potential importance of site effects, where differences between study locations may explain patterns of abundance irrespective of time-since-fire. There is a growing literature suggesting that habitat classifications such as time-sincedisturbance are poor surrogates for species distribution and abundance. Consequently, generalisations and simplifications about relationships between disturbance regimes and biodiversity are subject to uncertainty and should be treated as hypotheses to be tested.

Although we have focussed on the importance of environmental heterogeneity for biodiversity, and the potential for heterogeneity to be increased by certain disturbance regimes, it is important to recognise that the relationship between disturbance, heterogeneity and biodiversity may be bi-directional (Reice 1994). For example, a fire regime clearly influences vegetation structure across a landscape, but the spatial pattern of vegetative biomass also influences the extent and impact of the next fire (Sousa 1984). In addition, Hughes et al. (2007) suggest that biodiversity per se may have important effects on disturbance regimes, and that reciprocal diversity–disturbance relationships could influence patterns of diversity in nature. While such feedbacks may well influence the disturbance–biodiversity relationship, detecting them empirically remains a challenge (Hughes et al. 2007).

This account has covered some of the main ways in which disturbance, environmental heterogeneity and biodiversity are linked. It has not been our intention to describe the mechanisms by which disturbance can alter biodiversity, as this is an area requiring a separate treatment (e.g. Roxburgh et al. 2004, Shea et al. 2004). In addition, we have not attempted to cover the relationship between biodiversity and aspects of ecosystem function (e.g. the diversity–stability and diversity–productivity hypotheses: Tilman and Downing 1994, Tilman et al. 2006, Tilman et al. 1996), a field containing an extensive literature. We have suggested that disturbance regimes can promote environmental heterogeneity, which, in turn, is important for the maintenance of biodiversity. However, we also note that disturbance regimes can simplify ecosystems and result in species loss (Bradstock 2008, Denslow 1985), or facilitate other undesirable outcomes such as biological invasions (Hobbs and Huenneke 1992). For example, Bradstock (2008) argues that while large wildfires may

not adversely affect biodiversity in south-eastern Australian ecosystems, an increase in their frequency may have negative effects.

2.3.2 Vital attributes theory: disturbance frequency and reproductive capacity

Disturbance regimes may also affect biodiversity via their influence on a suite of characteristics collectively known as vital attributes. Although the theory of vital attributes was originally articulated in the context of vascular plants (Noble and Slatyer 1980), it is also relevant to other taxa (e.g. MacHunter et al. 2009). The concepts associated with the theory have been recently reviewed in another DSE report (Gill 2008), so we will only summarise them here.

Contrary to the classic model of plant succession (Clements 1916), the particular pattern of species replacement through time may be influenced by a number of factors (e.g. Keeley et al. 2005). According to one hypothesis, succession in plant communities is critically influenced by a small number of life-history characteristics known as vital attributes (Connell and Slatyer 1977, Gill 1981, Noble and Slatyer 1980). There are three main categories of vital attributes: 1. methods of post-disturbance colonisation, 2. methods of resource allocation to growth and development, and 3. the timing of critical events, such as reproductive maturity and death (Noble and Slatyer 1980). Each species has a particular set of vital attributes, which influences the timing of its entry and the length of its persistence in a succession. As part of this scheme, disturbance frequency interacts with plant vital attributes to influence community composition (Noble and Slatyer 1980). For example, if two disturbances occur before any plant species has a chance to reach reproductive maturity, only species with soil-stored seed will persist into the future. Similarly, long periods without disturbance may result in the disappearance of species with relatively short lives and a short-lived seed pool. Noble and Slatyer (1980) provide detailed examples of these effects in an Australian and American context.

In Australia, a number of studies have used the vital-attributes system to predict the response of different plant species to the frequency of fire events (e.g. Bradstock and Kenny 2003, Bradstock et al. 1997, Watson et al. 2009), while others have investigated fire frequency within alternative frameworks (Morrison et al. 1996, Morrison et al. 1995, Pekin et al. 2009, Watson and Wardell-Johnson 2004). In general, findings are consistent with Noble and Slatyer's original model, indicating, for example, that increased fire frequency may result in the loss of obligate seeders from a community (Bradstock et al. 1997), or that obligate seeders are more sensitive to changes in fire frequency than species that reproduce vegetatively (Watson et al. 2009).

In general, the model described above suggests that plant species will be lost from a community if fires are either too frequent or too infrequent. This has led to the calculation of 'acceptable' or 'tolerable' fire intervals for various plant communities (e.g. Bradstock and Kenny 2003) and the adoption of this principle by fire management agencies in many parts of Australia (e.g. Kenny et al. 2004, Tolhurst and Friend 2001). In Victoria, tolerable fire intervals are calculated using the vital attributes of a few fire-sensitive species (Key Fire Response Species) within 32 broad vegetation communities known as Ecological Vegetation Divisions or EVDs (Cheal 2010). However, this system involves a number of simplifications and assumptions (Clarke 2008), which adds substantial uncertainty to the ecological impacts of associated fire-based management practices. For example, it is assumed that deriving vegetation age-class distributions using data from several vascular plants will provide for the needs of other species, including fauna. This remains a hypothesis that requires testing.

2.4 Management action, uncertainty and monitoring

As stated above, the vital attributes model of Noble and Slatyer (1980) forms the basis for fire management in Victoria, despite containing a number of untested assumptions (Clarke 2008). Other models that could be used include replicating historical fire regimes (e.g. Hunter 1993) or drawing on theoretical constructs such as intermediate disturbance (Connell 1978) or environmental heterogeneity (Bazzaz 1975; Kerr and Packer 1997; Lack 1969) hypotheses. In addition, an alternative technique is being developed that uses data from multiple species to derive an age-class distribution that, in theory, minimises the chance that any species will be lost from the wider community (McCarthy 2012). Due to our imperfect knowledge, and the naturally variable nature of ecological systems, none of these systems, or any other, will provide certain, predictable ecological outcomes. In addition, recommendation 56 of the 2009 Victorian Bushfires Royal Commission (Teague *et al.* 2010) has led to a substantial increase in planned burning across Victoria. The response of biota to this action is largely unknown, adding another layer of uncertainty to fire management planning.

Despite this uncertainty, land management agencies must develop and implement strategies to conserve biodiversity. In Victoria, planned fire is regarded as a broad-scale management tool that can help meet this objective, along with other land management goals such as the protection of human life, assets and property (DSE 2008). In order to determine the effectiveness of planned fire as a biodiversity conservation strategy, the relationship between multiple fires (the fire regime) and a range of biotic responses and processes must be monitored. The development of a long-term monitoring strategy is seen as particularly important to generate baseline data against which future changes in the composition of biological communities can be judged (Magurran *et al.* 2010). In addition, monitoring data can be used to parameterise mathematical models enabling the influence of alternative fire regimes on biodiversity to be predicted.

In the remainder of this document we outline a framework for monitoring the relationship between disturbance regimes and biodiversity. Although the principles we outline are relevant more generally, our focus is on monitoring the influence of fire regimes in forested ecosystems.

3

3: Monitoring biodiversity

3.1 Land management and the scale of monitoring

It has been argued, successfully we believe, that the landscape is an appropriate spatial scale for the management and conservation of biodiversity, since monitoring and managing separate, disconnected patches within a dynamic, interconnected landscape is unlikely to be effective (Fahrig 2001, Franklin 1993, Lindenmayer et al. 2008a, Margules and Pressey 2000, Noss 1983,1996). Consequently, monitoring programs with objectives relating to biodiversity conservation and management should at least be established at a large spatial scale (the spatial extent of each program will depend on specific objectives and resources, but we suggest at least 100 square kilometres). Nevertheless, processes influencing individual species and biodiversity in general are not limited to a single scale (Addicott et al. 1987, Holling 1992, Kotliar and Wiens 1990, Noss 1990, Williams et al. 2002), and there is no best scale for studying ecological phenomena (Fischer and Lindenmayer 2002, Levin 1992). Consequently, monitoring at multiple scales is recommended.

It has also been argued that biodiversity conservation would benefit from environmental heterogeneity at multiple scales (Bennett et al. 2006, Lindenmayer et al. 2008a, Lindenmayer et al. 2006) and, if this advice is recast as a management objective, monitoring programs should aim to detect environmental heterogeneity at a number of scales concurrently. Such a strategy is consistent with hierarchy theory (Allen and Starr 1982, O'Neill et al. 1986, Urban et al. 1987), which proposes that ecosystems can be described as a spatially and temporally nested series of units, each restricted or controlled by the next-largest scale, but incorporating the patterns and process occurring at smaller scales. An example from Urban et al. (1987) considers forest gaps and stands as two levels of a hierarchy. The colonisation of gaps by plants is regulated by the life-history parameters and competitive interactions between species, and these factors interact to determine species composition. However, the species present in one gap may influence competitive interactions in another (e.g. by acting as a source of propagules for a particular species) and such gap-scale processes may influence the composition of forest stands. Consequently, deciphering patterns at larger scales requires understanding processes and interactions at the underlying levels of the hierarchy.

We suggest that data at multiple scales will be important for monitoring the relationships between fire regimes and biodiversity, and propose a tri-scaled approach, with monitoring occurring at the landscape, patch/macrohabitat and plot/microhabitat level. We include some examples of methods and indicator variables that may be relevant at the different scales (Figure 1).

3.2 Approaches to monitoring

Given the diversity and context-specific nature of the concept, it is not surprising that many indicators of biodiversity exist. Quantifying species richness and diversity is common in small-scale studies (Gaston 1996), but measuring these variables at large scales is impossible for more than a few easily detectable species (Franklin 1993). Further, even at small scales it is impossible to assess biodiversity in its entirety, so biodiversity monitoring, which aims to predict the 'true' but unknown patterns of species distributions and related ecological processes from a small set of measurable variables, will always require some degree of surrogacy (Faith 2003). The use of single species or groups of species as indicators or surrogates has been proposed (reviewed by Caro 2010), but these concepts have been criticised from a number of fronts (e.g. Andelman and Fagan 2000, Lindenmayer et al. 2006, Lindenmayer et al. 2000b, Lindenmayer and Likens 2011). This is not to say monitoring individual species has no value; there are several reasons why species-specific data should be collected as part of an integrated program to conserve biodiversity (Eisner et al. 1995). Nevertheless, there seems little justification for using single species or particular taxa as general biodiversity surrogates (but see Brooks et al. 2004 for an opposing view).



Figure 1 Three spatial scales suggested for monitoring the effects of planned burning on biodiversity, along with examples of surrogate environmental variables and data-collection methodology.

1 McGarigal et al. (2002) provide a list and description of many indices developed to quantify landscape and class level spatial pattern.

An alternative is to use environmental variables as surrogates for biodiversity (Belbin 1993, Faith and Walker 1996a, Lindenmayer et al. 2000b, Noss 1990). We argued in section 2 of this report that heterogeneous environments will generally support more species than homogeneous ones, but we did not elaborate on how environmental heterogeneity might be quantified. Here, we suggest that spatial environmental heterogeneity, which we defined in section 2.1.2, is simply a reflection of a physical environmental state or pattern, and thus can be well represented using environmental variables. We define environmental variables as properties, patterns, elements, attributes or structures that can be precisely identified and measured. Although individual variables measured at the site scale may or may not correlate with the occupancy or abundance of individual species, or with species richness or diversity measures (e.g. Lindenmayer et al. 2002), we expect that environmental variables measured across a landscape will reflect the patterns within it, be related to underlying processes, and ultimately influence the distribution and abundance of species (Forman and Godron 1986, Pickett and Cadenasso 1995, Turner 1989, Turner et al. 2001, Wiens 1995). The hypothesised linkages between disturbance regimes, environmental heterogeneity and ecosystem processes, and the predicted relationship of all these elements with biodiversity, represents an ecological model upon which biodiversity monitoring may be based (Figure 2).



Figure 2 General ecological model representing relationships between disturbance regimes, environmental variables, ecosystem processes and biodiversity. The terms on the left-hand side of the diagram indicate multiple levels of surrogacy, where environmental variables may be used as surrogates for quantifiable aspects of biodiversity, which, in turn, act as a surrogate for biodiversity, the unknown 'target parameter'.

As outlined by Sarkar et al. (2005), environmental variables can be considered 'indicator surrogates' that are linked to 'measurable' aspects of biodiversity, the 'true surrogates'. In turn, the 'true surrogates' are considered to represent biodiversity as a whole, which in this case is the 'target parameter', the system attribute we really want to know about (Figure 2). A major assumption associated with this approach is that there will be a high degree of congruence between environmental variables and actual biological distributions. Establishing an appropriate ecological model and carefully choosing environmental variables that have strong theoretical or empirical links to aspects of biodiversity will increase the likelihood of meeting this assumption, but in many cases the data needed to establish these links are missing. Lindenmayer and Likens (2011) suggest that validating a surrogacy relationship requires information regarding (a) the conditions under which the relationship does and does not exist and (b) the mechanisms underlying the relationship. Only when the mechanisms are understood can relationships between environmental variables and aspects of biodiversity be predicted with some certainty. Assuming that links between environmental variables and aspects of biodiversity exist when they do not will lead to ineffective monitoring. Consequently, validation of environmental variables as biodiversity surrogates should be an ongoing concern.

Because environmental variables are numerous and of many different types, grouping them into a smaller number of categories results in a more manageable scheme for considering their use as biodiversity surrogates. Further, we differentiate between variables that may be guantified at a specific location (site-scale variables) and those that need to be measured over larger areas (landscape-scale variables). The list below is not meant to be definitive, but simply to highlight some of the main groups of environmental variables that appear in the literature.

3.3 Site-scale environmental variables

3.3.1 Biophysical variables

Biophysical variables include factors such as climate, terrain and soil type. It is well known that biophysical variables can be used to predict the distributions of some species (e.g. Busby 1986) and that the composition of biological communities changes along biophysical gradients (Marini et al. 2011, Rahbek 1995, Whittaker 1960). There are numerous studies that have established relationships between biophysical variables and aspects of biodiversity. For example, Hawkins (2010) demonstrated strong relationships between climatic variables and regional butterfly species richness. Garnier-Gere and Ades (2001) have found that solar radiation and temperature range both predict more than 50% of the genetic variation between 68 populations of Alpine Ash (Eucalyptus delegatensis). A recent analysis by Sarkar et al. (2005) indicated that biophysical variables including mean annual temperature, mean annual precipitation, slope, elevation, aspect and soil type are effective surrogates for large species datasets in Canada and Australia.

3.3.2 Biochemical variables

Biochemicals are biologically important elements and molecules. They interact to form biogeochemical cycles, such as the water, carbon and nitrogen cycles that are integral to ecosystem functioning. These cycles influence factors such as plant germination and growth, and the flow of nutrients and energy between plants and animals, and thus affect the distribution and abundance of species. There are numerous ways biochemical variables can influence biodiversity. As an example, we consider the effect of nutrients and toxins in leaves on the distribution and abundance of herbivorous mammals.

Both foliar nutrient and toxins (plant secondary metabolites) are important determinants of forage quality for herbivorous animals (DeGabriel et al. 2008, Marsh et al. 2003). Moreover, the concentration of foliar nutrients and toxins varies spatially, resulting in a heterogeneous

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landscape with respect to food resources (Moore et al. 2010). Consequently, it is unsurprising that the distribution and abundance of herbivorous mammals in south-eastern Australia is influenced by both foliar nutrient and toxin concentrations (Braithwaite et al. 1984, Braithwaite et al. 1983, Cork and Catling 1996 and references therin, Moore et al. 2010, Youngentob et al. 2011). The influence that plant toxins have on forage quality, and the effects this has on habitat choices and behaviour of marsupial folivores, has recently been reviewed (DeGabriel et al. 2010).

Biochemical variables may often be laborious to collect, involving both field sampling and laboratory processing. However, some suites of variables, such as the chemical constituents of canopy leaves, can be quantified using remote sensing technologies (e.g. Ebbers et al. 2002, Huang et al. 2007, Majeke et al. 2008), making them viable options for large-scale monitoring programs.

3.3.3 Structural variables

As their name suggests, structural variables (also known as structural elements or attributes) quantify the physical structure of forests, woodlands and other ecosystems. Structural variables are many and varied, and are used to quantify factors such as the biomass of litter and logs, vertical and lateral vegetation structure, and characteristics of overstorey trees. The importance of structural variables to terrestrial fauna has been the subject of recent review (Bunnell et al. 1999, McElhinny et al. 2006) and ecosystem structure has been promoted as a biodiversity surrogate on a number of occasions (e.g. Lindenmayer et al. 2000b; Noss 1999, 1990).

Structural variables are often used as independent predictors in statistical models of species occupancy, abundance or habitat selection (e.g. Di Stefano et al. 2011, Godbout and Ouellet 2010, Lindenmayer et al. 2008c, 1994; Swan et al. 2008). As a specific example, the amount and spatial arrangement of coarse woody debris has been found to be important for a wide range of species (Dickman 1991, Harmon et al. 1986, MacNally et al. 2001, MacNally and Horrocks 2008). Structural variables are sometimes combined to generate indices of structural complexity (reviewed by McElhinny et al. 2005), which have also been correlated with the abundance of individual species (e.g. Catling and Burt 1995, Catling et al. 2001, Watson et al. 2001) and with measures of faunal assemblages such as species richness and diversity (Tews et al. 2004 and references therein). We discuss composite variables further in section 3.5.

3.3.4 Land systems and other land-based ecological classifications

Land systems are defined as an area or group of areas where there is a consistent pattern of topography, soil and vegetation (Walker 1991), and are often mapped from aerial photographs or satellite images at scales between 1:50 000 and 1:1 000 000. Other similar ecological classifications have also been derived (e.g. environmental units: Pressey et al. 1996). Although these kinds of landscape classifications were not developed as biodiversity surrogates, they are based on variables likely to influence the distribution and abundance of species (Oliver et al. 2004). Thus, in theory, a diversity of land systems should reflect a diversity of species, a hypothesis central to the use of land systems for selecting priority areas for conservation (Pressey and Taffs 2001, Purdie et al. 1986).

A number of studies have tested the hypothesised links between land systems (and other similar classifications) and aspects of biodiversity (e.g. Carmel and Stoller-Cavari 2006, Grantham et al. 2010, MacNally et al. 2002, Oliver et al. 2004, Wessels et al. 1999). For example, Oliver et al. (2004) have found that different land systems represent different biological assemblages of vascular plants, invertebrates and soil microbes, and thus act as surrogates for these taxa. Nevertheless, Grantham et al. (2010) caution that the effectiveness of land system-type classifications as biodiversity surrogates is difficult to assess and depends on a variety of factors.

3.3.5 Disturbance regime characteristics

Earlier in this report, we discussed the links between disturbance regimes, environmental heterogeneity and biodiversity. In section 2.3.1 we argued that disturbance regimes result in temporal cycles of environmental change at a variety of spatial scales, generating a complex and perpetually changing environment that facilitates species co-existence. Further, in section 2.3.2 we summarised vital-attributes theory, which predicts that assemblage composition will be determined by both species-specific life-history attributes and disturbance frequency. Following from these considerations, characteristics of the disturbance regime, such as intensity, size, patchiness, frequency and season, may be viable surrogates for biodiversity.

In the context of fire science, these characteristics are often described as 'fire-history' variables and, as we outlined in section 2.3.1, they appear to be correlated with individual species or assemblages in some situations but not in others. As we mentioned previously, the influence of disturbance regimes on biodiversity is complex and involves interactions with other factors. Consequently, the utility of disturbance regime characteristics as surrogates for biodiversity remains unclear and further work is needed to address this question.

We suggest that the utility of disturbance characteristics as biodiversity surrogates will improve with the increasing sophistication and accuracy of mapping techniques and as high-quality mapping data accumulate over time. For example, two important characteristics of fire regimes include (a) intra-fire heterogeneity and (b) the spatial and temporal pattern generated by overlapping patches resulting from multiple fires that have occurred in the past (Parr and Andersen 2006). However, traditional fire-mapping techniques generate rather low-resolution data with respect to these characteristics, thus reducing the capacity to detect any potential links with biodiversity. We are hopeful that emerging remote sensing technologies (e.g. Boschetti et al. 2010, Miura and Jones 2010, Norton et al. 2009, Turner et al. 2003) will help solve these problems in the near future.

3.4 Landscape-scale environmental variables

3.4.1 Landscape patterns

A fundamental theory underpinning the field of landscape ecology is that environmental heterogeneity, reflected as guantifiable spatial and temporal patterns, is related to ecological processes and, ultimately, to the distribution and abundance of species (Forman and Godron 1986, Pickett and Cadenasso 1995, Turner 1989, Turner et al. 2001, Wiens 1995). For example, many of the papers reviewed by Bennett et al. (2006) have noted that spatial properties of landscapes (e.g. the diversity of land classes) are correlated with faunal assemblages. Consequently, metrics of spatial (or temporal) pattern may be considered as surrogates for biodiversity in some situations.

Spatial pattern metrics are commonly derived from the familiar patch-based representations of landscapes shown in categorical maps (but see McGarigal et al. 2009 for the derivation of metrics from continuous surfaces). Data are usually available as layers in a geographical information system (GIS) and the computation of metrics is conducted using specialised software (McGarigal et al. 2002). There are many available metrics designed to quantify different aspects of spatial pattern; the review by McGarigal and Marks (1995) and documentation available via the internet² provide good initial summaries. Two major classes of metrics are those that represent landscape composition (the richness or diversity of elements) and landscape configuration (the spatial arrangement of elements). In studies that have separated the effect of the two, landscape composition appears to be more strongly related to the make-up of faunal assemblages (Bennett et al. 2006).

2 http://www.umass.edu/landeco/research/fragstats/documents/fragstats_documents.html With so many metrics available (the software FRAGSTATS – McGarigal et al. 2002 – calculates > 100), it is difficult to know which metrics to choose. We suggest that the analysis by Cushman et al. (2008) provides a good starting point. These authors identify seven components, each comprising a number of correlated metrics, that are likely to be universal and consistent properties of landscape pattern. These components may be thought of as a minimum set for the characterisation of spatial pattern in any landscape and could be investigated as potential surrogates for biodiversity monitoring. However, the final choice of metrics should always be guided by expected relationships between the measured aspect of spatial pattern and the process of interest (Tischendorf 2001). Following from our arguments in section 2.3.1, metrics that quantify aspects of spatial heterogeneity (e.g. Li and Reynolds 1994) may be suitable.

Finally, we note that recent work highlights some potential problems associated with the use of spatial pattern metrics. For example, the value of many metrics is scale-dependant (Smith et al. 2011, Wu et al. 2002) and data linking metrics to ecological processes are often lacking (Li and Wu 2004). A number of additional limitations and challenges are outlined by Li and Wu (2004, 2007).

3.4.2 Habitat extent

The existence of sufficient habitat is fundamental for the conservation of biodiversity (Fahrig 2003, Foley et al. 2005, Pimm and Raven 2000) and, in general, larger habitat patches contain more species. This trend is often linked to the theory of island biogeography (MacArthur and Wilson 1967), which predicts that species diversity is regulated by immigration, emigration and extinction. Accordingly, both the location of a habitat patch in relation to its neighbours, as well as the size of the patch, critically influences the ability of species to colonise and persist. However, larger patches of habitat are likely to be more environmentally variable (Lack 1969, Pacini et al. 2009), leading to the existence of a positive patch size–heterogeneity relationship. Consequently, any increase in species diversity with habitat area is expected to result from more environmental heterogeneity within larger habitat patches (Rosenzweig 1995).

An important general issue relating to the use of 'habitat extent' as a biodiversity surrogate is the way habitat is defined (Hall et al. 1997). Habitat is often defined simply as 'forested land' (e.g. Smith et al. 2011), but this is clearly an over-simplification. Further, there has been substantial discussion in the literature about the relevance of patch-based definitions of habitat (e.g. Fischer et al. 2004, Fischer and Lindenmayer 2006, Lindenmayer et al. 2008a, McGarigal et al. 2009, Mitchell and Powell 2003). Such definitions assume that a patch of habitat has sharp edges and is internally homogenous, but it is clear that most animals do not perceive habitat in this way. Kotliar and Wiens (1990) suggest a model where landscapes are viewed as a hierarchical mosaic of patches within patches at a range of spatial scales. An alternative is to view habitat as a continuous surface with peaks and troughs representing high- and low-habitat suitability respectively (Fischer et al. 2004, Fischer and Lindenmayer 2006, Mitchell and Powell 2003). The definition and measurement of habitat is complex, often species-specific and requires careful consideration. In many cases, the model used to classify landscapes (e.g. patch-based, continuous) and the definition of habitat will be interconnected.

3.4.3 Significant habitats or landscape components

In addition to habitat area, certain habitat types or landscape components have been shown to be particularly important for biodiversity conservation. For example, the importance of aquatic systems to terrestrial biodiversity is widely recognised (reviewed by Naiman and Decamps 1997). Aquatic systems in terrestrial landscapes include a body of permanent or ephemeral water (river, stream, lake, gully, etc.) and the adjacent terrestrial vegetation that may be influenced by elevated water tables or flooding (Naiman et al. 1993). Aquatic systems may support more species directly than other parts of the landscape (Naiman et al. 1993), or may support different species, thus contributing to regional biodiversity (Sabo et al. 2005). In dry forest ecosystems of south-eastern Australia, wet gullies have been identified as important for the conservation of a range of species, including birds (MacNally et al. 2000) and arboreal marsupials and small terrestrial mammals (Soderguist and MacNally 2000). Naiman et al. (1993) suggest that riparian corridors may be the part of the landscape most sensitive to environmental change. Nevertheless, Lindenmayer et al. (2009b) have found that wet gullies are not an important predictor of bird species richness or assemblage composition. This finding acts as a reminder that the links between environmental variables and aspects of biodiversity are probably never universal and may often be influenced by location-specific factors.

3.5 Composite measures of environmental heterogeneity

As outlined in section 2, the diversity of organisms and associated processes in a landscape should be influenced by the underlying level of environmental heterogeneity. Based on the theory and empirical evidence reviewed above, we would expect more species to persist in environmentally heterogeneous landscapes than in simple ones. Consequently, a measure of landscape-scale environmental heterogeneity has strong theoretical and empirical backing as a biodiversity surrogate (Faith and Walker 1996a, 1996b; Ferrier 2002). However, environmental heterogeneity is a reflection of complex, multi-scale patterns and cannot be adequately represented using a single variable. A potential solution to this problem is to generate a composite measure of environmental heterogeneity by combining a suite of variables, each measuring a different aspect of environmental pattern.

In general, a number of environmental variables collected at a single location may be combined to reflect a multi-dimensional environmental state. Repeating this exercise at multiple locations across a landscape will generate data reflecting how heterogeneous the landscape is with respect to the measured variables. These data can be analysed in a univariate context using an index to represent environmental heterogeneity at each site (see, for example, indices of structural complexity outlined in section 3.3.3), and then calculating a measure of variability (e.g. coefficient of variation) to represent landscapelevel heterogeneity. Alternatively, the data can be analysed in a multivariate context using ordination techniques (e.g. Faith and Walker 1996a). The ordination of environmental variables, and the similarity matrix underlying this process, represent the heterogeneity of ecological space within a landscape and thus, in theory, predict the capacity of the landscape to support a wide range of species or functional groups. This idea was originally part of a proposed method for selecting priority sites for biodiversity conservation (Faith 2003, Faith et al. 2004, Faith and Walker 1996a, 1996b), but, as far as we are aware, has not been suggested as a biodiversity monitoring technique. We think that these ideas may be useful in a monitoring context, but that they require further refinement and testing.

4: Monitoring program design and implementation: the importance of monitoring principles

We have argued above that biodiversity data are difficult and expensive to collect, and thus environmental variables may be used as surrogates. This provides a general approach to monitoring and indicates the types of variables that should be measured, but, on its own, will not necessarily result in successful monitoring.

Independent of the general approach, monitoring programs are often unsuccessful due to process failures, such as poor planning and inadequate experimental design (Elzinga et al. 2001, Field et al. 2007, Legg and Nagy 2006, Lindenmayer and Likens 2009). Below, we outline several 'monitoring principles' that should be considered as part of the monitoring process.

4.1 Planning the program: ecological monitoring should be based on ecological models and specific questions or objectives

In order to maximise learning, ecological monitoring programs should be designed around ecological models and associated predictions (Legg and Nagy 2006, Lindenmayer and Likens 2009, Nichols and Williams 2006, Yoccoz et al. 2001). Nichols and Williams (2006) argue that monitoring programs should be designed to elucidate underlying processes by discriminating between competing models and predictions (the 'alternative hypotheses' of Platt 1964), and from this perspective there is little distinction between monitoring and research. For example, four hypotheses have been proposed to explain the post-fire recovery of vegetation communities (Keeley et al. 2005) and data from an appropriately designed monitoring program may be used to distinguish between them. Nevertheless, we recognise that monitoring at this level may not always be possible, particularly at large scales, and that compromises may need to be made between information quality and achievability. However, the identification or development of an ecological model should be the first step in the monitoring process, as models provide the basis for asking appropriate questions and setting specific, quantifiable objectives (Lindenmayer and Likens 2009).

4.2 Clearly stated management objectives are necessary to measure progress

Management objectives are "...clearly articulated descriptions of a measurable standard, desired state, threshold value, amount of change, or trend...for a particular population or indicator" (Elzinga et al. 2001). We assume that one of the reasons for implementing a monitoring program is to determine if management objectives are being met. As stated in section 4.1, management objectives should be related to questions based on an underlying ecological model. Numerous sources emphasise the importance of well thought-out management objectives and their precise definition. For example, Noss (1999) suggests that "...goals and objectives create the entire context and sense of purpose for assessment and monitoring. We assess and we monitor to measure our progress towards meeting established goals and objectives...". Additionally, Wintle and Lindenmayer (2008) argue that a failure to clearly specify management objectives in terms of quantifiable attributes makes demonstrating ecologically sustainable forest management impossible.

Management objectives often relate to benchmarks or standards describing a minimum acceptable state, or a baseline describing the state of the system prior to management. Ideally, standards and baselines are derived from data, but they may also be influenced by socio-political imperatives (Nichols and Williams 2006). Management objectives should be quantifiable and stated precisely, including spatial and temporal limits and the degree of uncertainty deemed acceptable. Some examples of precisely stated management objectives based on an ecological model (Figure 2) are shown in Table 1.

 Table 1. Setting specific, measurable management objectives based on predictions derived from the ecological model in Figure 2.

Prediction from ecological model	General objective	Spatial scale	Potential indicators	Example of a specific management objective
Heterogeneous environments will contain more species than homogeneous ones	Detect change in landscape heterogeneity through time	Large	Spatial pattern metrics	Relative to a reference state, be 90% sure that management does not cause a reduction in the value of Shannon's diversity index (calculated on pre-defined land classes) by > 20%. Assess with reference to a defined study area and monitor over time.
		Medium	Indices of habitat complexity	Relative to a reference state, be 90% sure that management does not cause a reduction in Newsome and Catling's (1979) habitat complexity score by >20%. Monitor over time.
Environmental heterogeneity (as represented by environmental variables) will influence traits, behaviours and processes	Detect change in traits, behaviours or processes in response to changes in heterogeneity	Medium	Population size	 Be 90% sure that the population size of Species X is greater in Area A than in Area B. A specific scenario might be: Species X is known to require both young and old vegetation to breed successfully (e.g. Law and Dickman 1998). 50% of the vegetation in Area A has been recently burnt while 50% remains unburnt. 90% of the vegetation in Area B has been burnt while 10% remains unburnt.
			Reproductive success	
			Home range size	
			Habitat selection	
Environmental heterogeneity (as represented by environmental variables) is linked to measurable aspects of biodiversity	Detect relationship between environmental heterogeneity and measurable aspects of biodiversity	Large	Composite environmental variable	Be at least 90% sure that a composite environmental variable explains ≥ 50% of the variance in species richness. Assess through time with reference to a defined study area. Conduct sample size calculations to estimate the number of temporal data-points required.

4.3 Testing model-based predictions or management objectives with confidence requires good experimental design

Design features include what, where and how often an indicator variable is measured (Elzinga et al. 2001). The design of a monitoring program is closely linked to the underlying ecological model, and the predictions and management objectives that flow from it. An important design issue worth highlighting is the need for a Before–After Control–Impact (BACI)³ design before the causal effects can be inferred (Downes et al. 2002). For example, detecting causal relationships between disturbance, environmental heterogeneity and biodiversity, requires a BACI design.

In some cases, however, inferring causation from monitoring data may be impossible due to constraints on experimental design. In the context of fire regimes, the location of control or reference sites is problematic as, particularly in fire-prone ecosystems, it would be difficult and possibly undesirable to maintain sites that were exempt from fire. In this case, the best design may be to measure a set of indicator variables across the landscape and through time. A spatially extensive sampling program will permit the collection of information relevant to the scale at which landscapes are managed, and a temporal stream of data will enable change to be related to the fire regime, which plays out over time. If desired, data collected early in the time-series can be used as a reference-state to which data collected later in the time-series can be compared. The design leading to such a comparison is well established, and known as Intervention Analysis in the ecological literature (Stewart-Oaten and Bence 2001).

Determining an appropriate sample size is an aspect of experimental design that has received considerable attention (e.g. Cohen 1988). It is an issue that should be considered in the planning phase of monitoring programs, as inadequate sample size is one of the main reasons why monitoring programs fail (Elzinga et al. 2001, Field et al. 2007, Legg and Nagy 2006). If the sample size is small, there will be insufficient data to test predictions, or to determine if management objectives have been met. The required sample size will depend on a combination of factors including specific objectives, indicator variables and the degree of uncertainty considered acceptable. In ecology, sample size calculations have traditionally been considered in the context of statistical power analysis (Peterman 1990, Toft and Shea 1983), but they can also be considered from the perspective of interval estimation and precision (Di Stefano et al. 2005, Steidl and Thomas 2001). These concepts are linked to different analytical approaches, which are briefly discussed in section 4.4.

4.4 Data analysis is part of monitoring

Elzinga et al. (2001) define monitoring as "...the collection and analysis of repeated observations or measurements to evaluate changes in condition...". An important part of this definition is that both the **collection** and **analysis** of data are considered part of the monitoring process.

Although the need to analyse monitoring data seems obvious, the absence of appropriate analysis has been identified as another common failure of monitoring programs (Elzinga et al. 2001). Field et al. (2007) argue that data should be analysed early in a monitoring program, and the results used to assess the adequacy of data quantity and quality. Data analysis is closely linked to objectives and experimental design, and should be considered in detail before a monitoring program is implemented. In many cases, data analysis is complex and should be conducted in conjunction with a professional statistician, who, ideally, would be part of a multidisciplinary team including scientists, land managers and policy makers (Lindenmayer and Likens 2009).

Rigorous data analysis will often involve using formal statistical tests, but there are several theoretical and philosophical frameworks within which these can be conducted and the output interpreted. Traditionally, ecological data have been analysed using null hypothesis significance tests, but the strict application of this approach is subject to substantial criticism (Anderson et al. 2000, Johnson 1999), particularly with respect to its usefulness as a decision-making tool in the context of ecosystem management (Nichols and Williams 2006, Walshe et al. 2007). Amongst other analytical and interpretive approaches (reviewed by Stephens et al. 2007), information-theoretic methods can be used to compare competing models (Burnham and Anderson 2002), while confidence intervals provide a flexible means for assessing change in an indicator variable, or comparing the estimated state of the system to a pre-specified target or threshold (Di Stefano 2004, Walshe et al. 2007). Bayesian methods (e.g. McCarthy 2007) enable the formal incorporation of prior data into the analytical process. The benefits and limitations of different techniques should be considered carefully before proceeding.

5: A framework for monitoring the relationships between disturbance regimes and biodiversity

In earlier sections of this document, we suggested a general approach for biodiversity monitoring that involved using environmental variables as biodiversity surrogates. Further, we suggested that a number of common problems with monitoring programs can be avoided by considering a set of monitoring principles which outline a defensible process for planning, design and data analysis. In this section, we outline a framework that enables different elements of a monitoring program to be integrated so that findings are used to improve management practice.

5.1 Adaptive management

Adaptive management⁴ (Walters 1986) is a framework for monitoring management actions and has frequently been endorsed in the ecological literature (e.g. Lindenmayer et al. 2008a, 2000b; Noss 1999). Often referred to as 'learning by doing', adaptive management involves a cyclical series of events that include developing objectives, implementing management actions, establishing a monitoring program and using the resulting data to inform future management decisions (Elzinga et al. 2001, Schreiber et al. 2004). The adaptive management cycle (Figure 3) provides a way to integrate the elements of monitoring described in this document.



Figure 3 Example of (a) passive and (b) active adaptive management cycles. Differences between the two are shown in bold. Active adaptive management increases the capacity to improve management strategies and learn from monitoring data. In both diagrams, developing and assessing management objectives, and testing predictions based on the ecological model, are considered as two different streams of the process. Diagrams adapted from Elzinga et al. (2001).

Fundamental to the concept of adaptive management is an acknowledgement that management will usually proceed in the light of substantial uncertainty, and that current management actions can be used to learn about the system being managed. Walters and Holling (1990) differentiate between passive and active adaptive management, referring to passive monitoring of established management practices, and the active use of management actions as experiments to test alternative models and hypotheses (see Figure 3, a and b). In passive adaptive management, management practices are developed on the basis of the best current knowledge and thus maximise the chances of meeting management objectives in the short term. In contrast, active adaptive management involves modifying management practices to test competing models, and thus it tradesoff an increased probability of meeting objectives in the short term against the potential longer term benefits of increased learning. One of the difficulties with active adaptive management is that managers must allocate limited resources between (a) managing the system on the basis of the best available knowledge and (b) experimenting with alternative management actions to increase knowledge and reduce uncertainty. This decision will often be difficult, although statistical tools are available to help optimise the outcome (e.g. McCarthy and Possingham 2007).

The process of adaptive management has been reviewed thoroughly (e.g. Allan and Stankey 2009, Elzinga et al. 2001, Schreiber et al. 2004) and it is not our intention to repeat this exercise here. We simply suggest that following the adaptive management process and understanding the underlying philosophy is an important part of a monitoring program designed to improve land management practices. Box 1 contains four examples that illustrate alternative applications of both the passive and active forms of adaptive management. Additional information and examples may be found in two recent books on the topic (Allan and Stankey 2009, Lindenmayer and Likens 2010).

Box 1. Adaptive management: case studies utilising passive and active approaches

- 1. Whelan (2003) presents a study utilising both a passive and active strategy in the conservation of an endangered species, the Illawarra Greenhood Orchid (*Pterostylis gibbosa*). Initially, a perceived threatening process (grazing by feral animals) was controlled through grazing exclusion, with monitoring of orchid flowering used to assess the outcome of this management action. Subsequently, in response to a developing fire hazard (increased grass growth following the removal of grazers), prescribed fire was proposed as a means of dealing with this new risk. To evaluate effectiveness of the competing management strategies, a research design was employed (burned/unburned), with replication of treatments, to experimentally assess the impact on the orchid population. Recruitment of orchids was shown to be independent of the fire treatment, allowing managers a means of reducing bushfire risk without compromising ecological outcomes.
- 2. Land management practices in British Columbia were evaluated to see whether associated management objectives (in regard to values such as biodiversity, cultural heritage, soils, water, etc.) were being met. In the 'Coast Forest Strategy' (Smith 2009), both passive and active approaches were examined with regard to their utility to test and monitor the effectiveness of a number of variable-retention harvesting strategies. Five experimental comparisons (each with three replicates) were established with a number of biodiversity and silviculture 'indicators' monitored. Stakeholders were engaged with the project through involvement in a science panel, and working and advisory groups, evaluating new information and providing advice to management concerning potential improvements in forest practices.
- 3. In north-west Italy, heathlands are currently under threat from changes in traditional land management practices; primarily involving inappropriate use of fire and grazing. Despite the lack of formal knowledge concerning the impact of alternate approaches, clear management objectives were developed for *Calluna* heathlands within a nature reserve. These included the creation of a mosaic of seral stages conforming to a reference structure and composition state, and reduction of tree encroachment. An active strategy was employed, where eight alternative fire prescriptions were evaluated using an experimental research design (Ascoli et al. 2009). Pre- and post-fire conditions were monitored using an established protocol, with data used to compute landscape metrics and compare landscape structure changes against management policy and objectives. Ongoing treatment and monitoring will inform future management actions.
- 4. The timing of water drawdown in impoundments on a wildlife refuge could impact shorebirds through changes to food resources and associated effects on reproductive success. Williams (2011) compared three potential management-imposed solutions to this problem, using passive and active approaches, and evaluated their impact in terms of objectives, costs and potential learning rates. Single- and multiple-response models were developed and then assessed using information collected over time (monitoring). This allowed insight into both temporal habitat change and also the linkage between habitat conditions and wildlife responses. The latter outcome is important but often overlooked in resource management problem-solving (i.e. links between pattern and process).

6: Conclusions

A substantial body of ecological theory and much empirical research points to a positive relationship between environmental heterogeneity and at least some aspects of biodiversity. In this report we have attempted to show how the proposed heterogeneity-biodiversity relationship can be used as a basis for biodiversity monitoring.

Drawing from the field of landscape ecology (Forman and Godron 1986, Pickett and Cadenasso 1995, Turner 1989, Turner et al. 2001, Wiens 1995), environmental heterogeneity can be viewed as spatial and temporal patterns that occur at multiple scales. These patterns can be guantified using a range of environmental variables, from biophysical aspects of the system such as climate and terrain, to metrics representing the patterns formed by different land classes. As such, environmental variables represent the state of the system, which is expected to be related to underlying ecological processes and to the distribution and abundance of species.

Based on these expected relationships, we propose that environmental variables can be used as biodiversity surrogates in a large-scale monitoring program. However, point estimates of individual environmental variables in isolation are not sufficient. We have argued that representing landscape-scale heterogeneity requires the quantification of multiple variables at different spatial scales across the focal landscape. Combining these variables will result in a composite measure of heterogeneity that may be used to track the influence of disturbance regimes through time and indicate the likely effect of landscape change on biodiversity. This general methodology is summarised in Figure 4.



Figure 4 The development of a composite environmental variable (EV) from a series of individual environmental variables measured at multiple scales (e.g. large, medium, small). The composite environmental variable is a multiscaled representation of environmental heterogeneity and is theoretically linked to biodiversity (BD). The relationship is marked with a "?" as it requires empirical validation. If a relationship exists, the composite environmental variable can be used to track the temporal effect of landscape change on biodiversity.

However, a number of questions remain. Which variables should be chosen for inclusion in the final set? Which methodology should be used to generate the composite variable? Does the composite variable have any value as a biodiversity surrogate? This last question represents a critical assumption and is depicted in Figure 4 as the broken link between the composite variable and biodiversity. The validation of this assumption is necessary to justify the credibility of the environmental surrogacy approach, and will require focussed and ongoing research and monitoring.

Irrespective of what is measured, monitoring programs often fail because they lack focussed questions relating to specific, quantifiable objectives, or because aspects of their statistical design and analysis are inadequate. In order to prevent these types of problems, we recommend following a set of well-established monitoring principles that outline a defensible process for monitoring program development, implementation and analysis. Finally, adaptive management is identified as a framework for incorporating monitoring results into management practice, and learning by doing.

7: References

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